

ORIGINAL ARTICLE

Streblid flies parasitizing cave bats in Carajás, Amazonia, with a new record for Brazil

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* Corresponding author: barbier.eder@gmail.com;  <https://orcid.org/0000-0001-5068-7048>**ABSTRACT**

Streblid flies (Diptera: Streblidae) are hematophagous and highly specialized parasitic insects, found only on bats (Chiroptera). Caves are important roosts for bats but, despite harboring high bat richness, relatively few studies exist on the ecology and biology of streblid flies in cave environments, especially in Amazonia, the largest domain in northern Brazil, with >140 bat species and thousands of caves. To fill some of the gaps in the geographical distribution and interspecific relationships for streblid flies in the region, we sampled bats in six caves in Carajás National Forest, a protected area in Pará state (Brazil). Thirteen of the 14 streblid species found are new records for Carajás, with three new records for Pará state and two for the northern region of Brazil. *Nycterophilia fairchildi* was recorded for the first time in Brazil. Most streblids had host-specific behavior, however, *N. fairchildi*, *Trichobius caecus*, and *T. johnsonae* were less host-specific, parasitizing different *Pteronotus* bat species. The gregarious behavior of *Pteronotus* species and the spatial distribution of their colonies within the caves may be important factors in the flies' exchange among congener hosts and deserve special attention in future studies. Furthermore, studies on ecological interaction networks between bats and their ectoparasitic flies in caves will be useful for a broader understanding of how this relationship is structured over time and space, as well as its impact on both bats and flies.

KEYWORDS: biospeleology, Chiroptera, Diptera, ectoparasites, host-parasite relationship, Streblidae

Moscas estréblidas parasitando morcegos cavernícolas em Carajás, Amazônia, com um novo registro para o Brasil

RESUMO

Moscas estréblidas (Diptera: Streblidae) são insetos hematófagos e parasitas encontrados apenas sobre morcegos (Chiroptera). As cavernas são abrigos importantes para morcegos, mas, apesar de abrigarem alta riqueza desses mamíferos, são relativamente poucos os estudos focados na ecologia e biologia de moscas estréblidas em ambientes cavernícolas, especialmente na Amazônia, o maior domínio no norte do Brasil, com >140 espécies de morcegos e milhares de cavernas. Para preencher algumas das lacunas na distribuição geográfica e nas relações interespecíficas de moscas estréblidas na região, amostramos morcegos cavernícolas em seis cavernas na Floresta Nacional de Carajás, uma área protegida no estado do Pará. Treze das 14 espécies de moscas estréblidas encontradas são novos registros para Carajás, com três novos registros para o Pará e dois para a região norte do Brasil. *Nycterophilia fairchildi* foi registrada pela primeira vez no Brasil. A maioria das espécies de moscas foi hospedeiro-específica; entretanto, *N. fairchildi*, *Trichobius caecus* e *T. johnsonae* foram menos específicas, parasitando diferentes espécies de morcegos do gênero *Pteronotus*. O comportamento gregário das espécies de *Pteronotus* e a distribuição espacial de suas colônias dentro das cavernas podem ser fatores importantes na troca de moscas entre hospedeiros congêneres e merecem atenção especial em estudos futuros. Adicionalmente, estudos sobre redes de interação ecológica entre morcegos e suas moscas ectoparasitas em cavernas serão úteis para uma compreensão mais ampla de como essa relação se estrutura no tempo e no espaço, bem como sobre o seu impacto, tanto sobre os morcegos como sobre as moscas.

PALAVRAS-CHAVE: bioespeleologia, Chiroptera, Diptera, ectoparasitas, relação parasita-hospedeiro, Streblidae

INTRODUCTION

Although most insects are free-living, many have evolved a parasitic lifestyle and have numerous adaptations to live in or on their hosts (Poulin 2007). This is the case of streblids (Diptera: Streblidae), a morphologically diverse, highly specialized group of flies that exclusively parasitize bats (Wenzel *et al.* 1966). These flies spend their entire adult stage on the fur or wing membranes of bats, where both males and females feed on the host's blood (Wenzel *et al.* 1966). Many streblid flies are strikingly host-specific, being restricted to a single bat species (Barbier *et al.* 2019, 2021). On the other hand, some species may show less host specificity, associating with different species of the same genus or even different genera of the same bat family (Dick and Dittmar 2014; Barbier and Bernard 2017). Like its host bats, streblid flies are worldwide in distribution, but much more diverse in the tropics (Dick and Patterson 2006; Dick and Dittmar 2014).

The Brazilian Amazon is, by far, the least studied domain of the distribution range of bat-streblid relationships (Lourenço *et al.* 2016; Barbier and Bernard 2017). Amazonia is one of the regions with the greatest bat species richness in the world (López-Baucells *et al.* 2016) and holds thousands of caves, which are important roosts for more than 70 bat species in Brazil (Oliveira *et al.* 2018). There is little research on bats and their parasites in northern Brazil, and even less in cave environments (Barbier and Benard 2017; Urbietta *et al.* 2022). However, recently there have been significant advances in the study of bat ectoparasitic flies in the region (Hrycyna *et al.* 2019; Palheta *et al.* 2020), revealing a rich diversity of streblid fauna and their potential host bat species. Here we fill a gap in the knowledge about the geographical distribution and

host-parasite relationship of streblid flies on bats in caves in the Carajás National Forest, a protected area in eastern Brazilian Amazonia.

MATERIAL AND METHODS

We collected streblid flies on bats in June and July 2022 during bat monitoring surveys in six caves in the Carajás National Forest (eastern Amazonia), Pará state, Brazil (Table 1; Figure 1). In the region, the caves are located in the upper compartment of rocky ridges that stand out, supported by banded iron formations and *canga* (iron breccia) vegetation (Piló *et al.* 2015). In addition to the *canga* open vegetation, which is restricted to the iron ore rocky outcrops, the predominant vegetation is ombrophilous forest (Piló *et al.* 2015). The sampled caves are located at the foot of scarps in a ridge to the north ($n = 5$) and a ridge to the south ($n = 1$). The minimum and maximum distances between the caves are of approximately 110 m and 45 km, respectively (Figure 1). Fieldwork and sampling collections were authorized by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) through authorization SISBIO

Table 1. Geographic coordinates of the six bat caves sampled in the Carajás National Forest, Pará state, Brazil, in June-July 2022.

Cave code	Geographical coordinates
N4E-0023	06°02'01"S, 50°10'07"W
N5S-0052	06°06'29"S, 50°08'00"W
N5S-0057	06°06'31"S, 50°07'57"W
N5SM1-031	06°06'20"S, 50°08'19"W
N5SM2-0099	06°08'09"S, 50°07'48"W
S11C-0041	06°22'57"S, 50°22'49"W

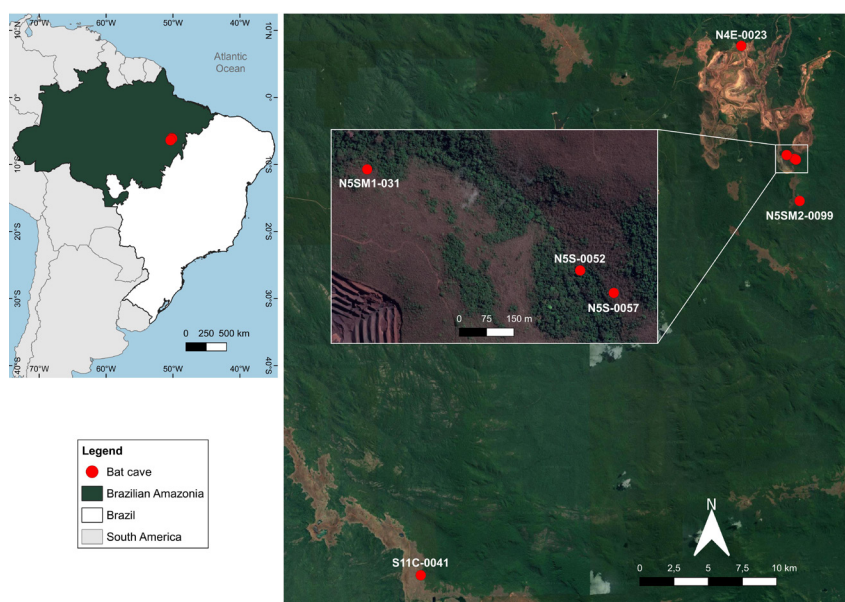


Figure 1. Location of the study area in eastern Brazilian Amazonia and location of the six caves sampled for bats and streblid flies in the Carajás National Forest in June and July 2022. This figure is in color in the electronic version.

79066-1 and the Ethics Committee on Animal Care at Universidade Federal de Pernambuco (protocol # 0092/2021 CEUA/UFPE).

Host bats were captured with hand nets and visually inspected for ectoparasites. Streblid flies were collected with featherweight forceps and preserved in labeled vials with 70% alcohol. Flies were identified at the species level under a stereomicroscope using diagnosis and identification keys proposed by Wenzel *et al.* (1966), Wenzel (1976), and Guerrero (1998). Voucher specimens were deposited in the entomological collection at Universidade Federal de Pernambuco (CE-UFPE) (Table 2). Bats were identified to the lowest possible taxonomic level following López-Baucells *et al.* (2016), Pavan (2019), and Díaz *et al.* (2021). Due to the similarity of external morphological features between *Pteronotus alitonus* and *P. rubiginosus* (Pavan 2019), we were not able to differentiate these two species in the field. In these cases, we kept the identification at the genus level (i.e. *Pteronotus* sp.). One bat of each species was collected, fixed, preserved in ethanol, and deposited as a voucher in the mammal collection at Universidade Federal de Pernambuco.

Based on a weighted matrix (i.e. frequency of observed interactions) containing the streblid fly species as columns and their host bats as rows, we used the ‘visweb’ function from the ‘bipartite’ package in R (Dormann *et al.* 2008; R Core Team 2021) to build a graph illustrating the observed host-parasite interactions. Photographs of fly species were taken

at the Laboratory of Advanced Microscopy and Imagery at Universidade Federal de Pernambuco (LAMI-UFPE) using a stereomicroscope (Zeiss SteREO Discovery.V20).

RESULTS

We collected 107 streblid flies (62 males and 45 females) belonging to 14 species, parasitizing 28 bats belonging to nine species and four families (Table 2). Except for *Strebla proxima*, the other 13 streblid species are the first records for the Carajás National Forest. Furthermore, *Trichobius dugesii* is a new record for Pará state, *T. anducei* and *T. pallidus* are new records for the northern region of Brazil, while *Nycterophilina fairchildi* is a new record for Brazil. Of the 14 streblid species, 11 (79%) occurred on a single bat species (Figure 2). *Trichobius caecus* and *N. fairchildi* were the most generalist streblid species, found parasitizing *Pteronotus gymnonotus*, *P. personatus*, and *Pteronotus* sp. *Nycterophilina fairchildi* was more abundant on *Pteronotus* sp., while *T. caecus* was more abundant on *P. gymnonotus* (Table 2; Figure 2).

Diptera, Streblidae

Nycterophilina fairchildi Wenzel, 1966 (Figure 3a)

Material examined: n = 27 (1 ♂ on a *Pteronotus gymnonotus* bat, 1 ♂ on a *P. personatus*, and 11 ♂ and 14 ♀ on six *Pteronotus* sp.), cave N5SM2-0099, Parauapebas, 30/VI/2022, E. Barbier leg.

Table 2. List of streblid flies (Diptera: Streblidae) collected on cave bats (Chiroptera) in the Carajás National Forest (Pará state, Brazil) in June and July 2022. N flies = number of streblid flies found on each host bat species. Voucher = zoological collection deposit code.

Streblid fly species	♂	♀	Total	Voucher (CE-UFPE)	N flies	Host bat species	Bat family
<i>Nycterophilina fairchildi</i> Wenzel, 1966	13	14	27	100944	1	<i>Pteronotus personatus</i> (Wagner, 1843)	Mormoopidae
					1	<i>Pteronotus gymnonotus</i> (Wagner, 1843)	Mormoopidae
					25	<i>Pteronotus</i> sp.*	Mormoopidae
<i>Nycterophilina parnelli</i> Wenzel, 1966	0	2	2	100945	2	<i>Pteronotus</i> sp.*	Mormoopidae
<i>Strebla guajiro</i> (García & Casal, 1965)	0	3	3	100946	3	<i>Carollia perspicillata</i> (Linnaeus, 1758)	Phyllostomidae
<i>Strebla proxima</i> Wenzel, 1976	1	1	2	100947	2	<i>Peropteryx kappleri</i> Peters, 1867	Emballonuridae
<i>Strebla wiedemanni</i> Kolenati, 1856	0	1	1	100948	1	<i>Desmodus rotundus</i> (É. Geoffroy, 1810)	Phyllostomidae
<i>Trichobius anducei</i> Guerrero, 1998	14	6	20	100949	20	<i>Carollia perspicillata</i>	Phyllostomidae
				100950	13	<i>Pteronotus gymnonotus</i>	Mormoopidae
					4	<i>Pteronotus personatus</i>	Mormoopidae
<i>Trichobius caecus</i> Edwards, 1918					7	<i>Pteronotus</i> sp.*	Mormoopidae
					1	<i>Glossophaga soricina</i> (Pallas, 1766)	Phyllostomidae
					2	<i>Trachops cirrhosus</i> (Spix, 1823)	Phyllostomidae
<i>Trichobius dugesii</i> Townsend, 1891	1	0	1	100951	1	<i>Glossophaga soricina</i> (Pallas, 1766)	Phyllostomidae
<i>Trichobius dugesoides</i> Wenzel, 1966	1	1	2	100952	2	<i>Trachops cirrhosus</i> (Spix, 1823)	Phyllostomidae
<i>Trichobius joblingi</i> Wenzel, 1966	4	2	6	100953	6	<i>Carollia perspicillata</i>	Phyllostomidae
<i>Trichobius johnsonae</i> Wenzel, 1966	4	2	6	100954	1	<i>Pteronotus personatus</i>	Mormoopidae
					5	<i>Pteronotus</i> sp.*	Mormoopidae
<i>Trichobius pallidus</i> (Curran, 1934)	0	1	1	100955	1	<i>Furipterus horrens</i> (Cuvier, 1828)	Furipteridae
<i>Trichobius parasiticus</i> Gervais, 1844	4	6	10	100956	10	<i>Desmodus rotundus</i>	Phyllostomidae
<i>Trichobius uniformis</i> Curran, 1935	2	0	2	100957	2	<i>Glossophaga soricina</i>	Phyllostomidae
Total	62	45	107	–	107	–	–

**Pteronotus alitonus* or *Pteronotus rubiginosus* (see Material and Methods for details).

Remarks: First record in Brazil. The closest known record of *N. fairchildi* to our study area is in Sucre, Venezuela, at least 2,300 km away in a straight line (see Wenzel 1976). Other previously known records are from Colombia, Costa Rica, Mexico, and Panama (Wenzel *et al.* 1966; Jirón and Fallas 1974; Guerrero 1993; Guerrero and Morales-Malacara 1996). Throughout its known geographic distribution, this fly species seems to occur primarily in association with bats of the genus *Pteronotus*. *Nycterophilina fairchildi* resembles *N. parnelli*, but is easily distinguishable by the density of setae present on the thorax (sparser in *N. parnelli*) and by the females having four macrosetae at the distal end of the abdomen (instead of two in *N. parnelli*) (see Wenzel *et al.* 1966) (Figure 3).

Nycterophilina parnelli Wenzel, 1966 (Figure 3b)

Material examined: n = 2 ♀ on a *Pteronotus* sp. bat, cave N5SM2-0099, Parauapebas, 30/VI/2022, E. Barbier leg.

Remarks: Recently, *N. parnelli* was recorded parasitizing an undetermined species of *Pteronotus* in Pará state (Palheta *et al.* 2020) and *P. parnellii* in Amapá state, Brazil (Hrycyna *et al.* 2019). However, the host in Amapá was probably *P. rubiginosus* or *P. alitonus*. *Pteronotus parnellii* (Gray, 1843) is morphologically similar to *P. rubiginosus* and *P. alitonus*, and is currently considered restricted to Cuba and Jamaica (Pavan 2019). In a Caatinga dry forest area in northeastern

Brazil, *N. parnelli* had already been recorded on *P. gymnonotus* (Barbier *et al.* 2019).

Strebla guajiro (García & Casal, 1965) (Figure 4a)

Material examined: n = 3 ♀ on three *Carollia perspicillata* bats, cave N4E-0023, Parauapebas, 18/VII/2022, E. Barbier leg.

Remarks: This fly species is relatively common, having *C. perspicillata* as its primary host. It occurs throughout the entire distribution range of this bat, from southern Mexico to southern Brazil (Wenzel *et al.* 1966; Barquez *et al.* 2015; Barbier and Bernard 2017). *Strebla guajiro* has been recorded for Brazilian Amazonia, including Pará and neighboring states (Santos *et al.* 2009; Hrycyna *et al.* 2019; Palheta *et al.* 2020).

Strebla proxima Wenzel, 1976 (Figure 4b)

Material examined: n = 2 (1 ♂ and 1 ♀ on a *Peropteryx kappleri* bat), cave N5SM1-031, Parauapebas, 19/VII/2022, E. Barbier leg.

Remarks: Second record for Brazil. In 2018, this fly species was recorded for the first time in the country, also in the Carajás National Forest and in association with *P. kappleri* (Barbier *et al.* 2018). The only other known records for this fly species are from Venezuela (Wenzel 1976).

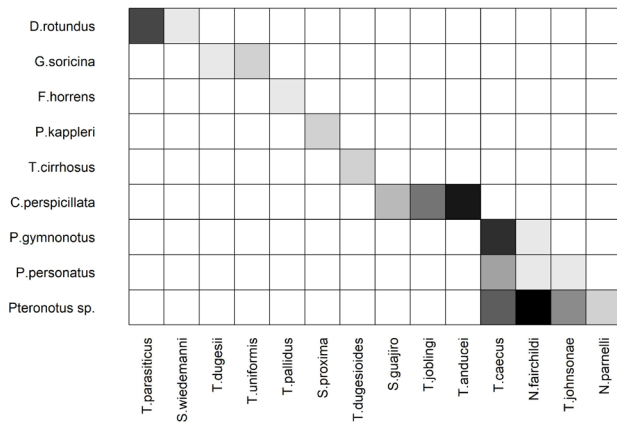


Figure 2. Interactions among cave bats (rows) and streblid flies (columns) in six caves sampled in the Carajás National Forest (eastern Amazonia), Brazil. The darker the cells, the more frequent the observed interaction.

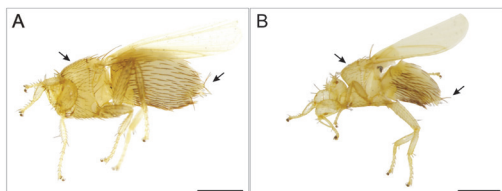


Figure 3. *Nycterophilina* species collected on cave bats in the Carajás National Forest, eastern Brazilian Amazonia. A – female of *Nycterophilina fairchildi*, lateral view; B – female of *Nycterophilina parnelli*, lateral view. Arrows highlight the density of setae present on the thorax and the number of macrosetae at the distal end of the abdomen. Scale bars = 0.5 mm. This figure is in color in the electronic version.

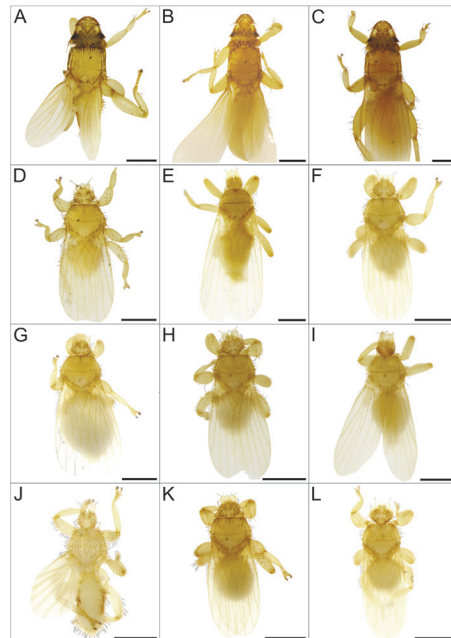


Figure 4. Dorsal view of streblid fly species collected on cave bats in the Carajás National Forest, in eastern Brazilian Amazonia. A – female of *Strebla guajiro*; B – female of *Strebla proxima*; C – female of *Strebla wiedemanni*; D – female of *Trichobius anducei*; E – female of *Trichobius caecus*; F – male of *Trichobius dugesii*; G – female of *Trichobius dugesioides*; H – male of *Trichobius joblingi*; I – female of *Trichobius johnsonae*; J – female of *Trichobius pallidus*; K – male of *Trichobius parasiticus*; L – male of *Trichobius uniformis*. Scale bars = 0.5 mm. This figure is in color in the electronic version.

Strebli wiedemanni Kolenati, 1856 (Figure 4c)

Material examined: n = 1 ♀ on a *Desmodus rotundus* bat, cave N5S-0052, Parauapebas, 16/VII/2022, E. Barbier leg.

Remarks: This fly species is a specific parasite for the common vampire bat, *D. rotundus*, and frequently co-occurs with *Trichobius parasiticus* (Wenzel *et al.* 1966; Wenzel 1976), however, in some areas as the Caatinga dry forest region in Brazil, it seems to be less abundant than the latter (Barbier *et al.* 2019, 2021).

Trichobius anducei Guerrero, 1998 (Figure 4d)

Material examined: n = 20 (14 ♂ and 6 ♀ on four *Carollia perspicillata* bats, cave N4E-0023, Parauapebas, 18/VII/2022, E. Barbier leg.

Remarks: New record for Pará state and the northern region of Brazil. In Brazil, previous records were restricted to the southeastern and northeastern portions of the Atlantic Forest (Lourenço *et al.* 2014; Barbier and Bernard 2017). The distance of approximately 1,700 km between the two most far apart records indicates a wide distribution range for *T. anducei* in the country, which agrees with the fact that its host, *C. perspicillata*, has one of the widest distributions in the Neotropics (Barquez *et al.* 2015).

Trichobius caecus Edwards, 1918 (Figure 4e)

Material examined: n = 24 (11 ♂ and 2 ♀ on six *Pteronotus gymnotus* bats, 3 ♂ and 1 ♀ on three *P. personatus*, and 4 ♂ and 3 ♀ on three *Pteronotus* sp.), cave N5SM2-0099, Parauapebas, 30/VI/2022, E. Barbier leg.

Remarks: Although there is a wide list of bats as transient/non-primary hosts for *T. caecus*, this fly species is considered a primary parasite of Mormoopidae, especially of the genus *Pteronotus* (Guerrero 1994). The species has been collected previously in northern Brazil, also in Pará state, on an unidentified *Pteronotus* species by Palheta *et al.* (2020).

Trichobius dugesii Townsend, 1891 (Figure 4f)

Material examined: n = 1 ♂ on a *Glossophaga soricina* bat, cave N5S-0057, Parauapebas, 16/VII/2022, E. Barbier leg.

Remarks: *Trichobius dugesii* is a typical parasite of the widely distributed *G. soricina* (Guerrero 1995). The species was already known from the border of the Amazon biome in the northeastern Brazilian state of Maranhão (e.g. Santos *et al.* 2009), and further north from the Brazilian Amazonian state of Amapá (Hrycyna *et al.* 2019). Our study provides the first record of the species in the state of Pará.

Trichobius dugesioides Wenzel, 1966 (Figure 4g)

Material examined: n = 2 (1 ♂ and 1 ♀ on a *Trachops cirrhosus* bat), cave S11C-0041, Canaã dos Carajás, 12/VII/2022, E. Barbier leg.

Remarks: In northern Brazil, *T. dugesioides* was previously recorded in Pará, Amapá, and Roraima states, also mainly in association with *T. cirrhosus* (Guerrero 1997; Graciolli and Linardi 2002; Hrycyna *et al.* 2019). This fly species was also found parasitizing *T. cirrhosus* in the drier Caatinga biome (Barbier *et al.* 2016).

Trichobius joblingi Wenzel, 1966 (Figure 4h)

Material examined: n = 6 (1 ♂ and 2 ♀ on two *Carollia perspicillata* bats, cave S11C-0041, Canaã dos Carajás, 12/VII/2022, E. Barbier leg.; and 3 ♂ on three *C. perspicillata* in cave N4E-0023, Parauapebas, 18/VII/2022, E. Barbier leg.).

Remarks: *Trichobius joblingi* is one of the most frequent and abundant strebliid fly species reported in the Neotropics (Guerrero 1995; Barbier and Graciolli 2016). In some regions, this fly species occurs on 80% or more of sampled *C. perspicillata* individuals (Barbier and Graciolli 2016; Barbier *et al.* 2019, 2021).

Trichobius johnsonae Wenzel, 1966 (Figure 4i)

Material examined: n = 6 (1 ♂ on a *Pteronotus personatus* bat, and 3 ♂ and 2 ♀ on a *Pteronotus* sp.), cave N5SM2-0099, Parauapebas, 30/VI/2022, E. Barbier leg.

Remarks: Although *T. johnsonae* has a wide distribution, parasitizing *Pteronotus* species in Mexico, Panama, Colombia, and Venezuela, in Brazil it was recorded for the first time only in 2015 (Guerrero 1994; Guerrero and Morales-Malacara 1996; Figueiredo *et al.* 2015). The scarcity of records in Brazil is likely related to the few records of their hosts in traditional bat surveys, since most *Pteronotus* bats are captured inside or when emerging from caves. Palheta *et al.* (2020) recorded this fly species in Pará state, but, interestingly, on *Carollia perspicillata* and *Lophostoma carrikeri* (Allen, 1910), which are likely non-primary hosts.

Trichobius pallidus (Curran, 1934) (Figure 4j)

Material examined: n = 1 ♀ on a *Furipterus horrens* bat, cave S11C-0041, Canaã dos Carajás, 12/VII/2022, E. Barbier leg.

Remarks: A specific parasite of *F. horrens*, *T. pallidus* can be considered a rare species (Graciolli and Azevedo 2011). Here, it is recorded for the first time in the northern region of Brazil, and, consequently, for Pará state. Previous records in the country included the northeast and southeast regions (Graciolli and Azevedo 2011; Graciolli and Carvalho 2012; Barbier *et al.* 2016). *Furipterus horrens* is a nationally threatened bat species in Brazil (MMA 2022).

Trichobius parasiticus Gervais, 1844 (Figure 4k)

Material examined: n = 10 (4 ♂ and 6 ♀ on a *Desmodus rotundus* bat), cave N5S-0052, Parauapebas, 16/VII/2022, E. Barbier leg.

Remarks: Like *Strebla wiedemanni*, *T. parasiticus* is a specific parasite of the common vampire bat, *D. rotundus* (Wenzel 1976), and, like its host, it has a wide distribution in South America. The occurrence of *T. parasiticus* on host species other than *D. rotundus* is considered a non-primary association (Barbier *et al.* 2021).

Trichobius uniformis Curran, 1935 (Figure 4l)

Material examined: n = 2 ♂ on a *Glossophaga soricina* bat, cave N5S-0057, Parauapebas, 16/VIII/2022, E. Barbier leg.

Remarks: Although *T. uniformis* is known to occur in Brazil since the 1930s (Guimarães 1937), its presence in Pará state was only recently confirmed (Palheta *et al.* 2020). *Trichobius uniformis*, along with *T. dugesii*, are the streblid species most often found parasitizing *G. soricina* (Barbier and Bernard 2017).

DISCUSSION

We recorded 14 streblid fly species, and provided three new species records for the state of Pará and two for the northern region of Brazil, in addition to the first record of *Nycterophilina fairchildi* for Brazil. Also, except for a single previous record of *Strebla proxima* parasitizing *Peropteryx kappleri* (Barbier *et al.* 2018), there was no information on bat ectoparasitic flies in the Carajás National Forest.

The majority of the streblid flies recorded here had a species-specific association, corroborating the findings of previous studies (e.g. Dick and Dittmar 2014; Barbier *et al.* 2019). On the other hand, three species (*Nycterophilina fairchildi*, *Trichobius caecus*, and *T. johnsonae*) showed lower host specificity, being collected on two to three bat species of the genus *Pteronotus*. It is worth noting that, in the surveyed caves, different *Pteronotus* species often used the same chambers as roost, keeping colonies very close to each other and even forming mixed colonies (E. Barbier, personal observation). This roosting behavior has already been recorded in other caves in the Neotropical region (see Pavan 2019). So, the frequent proximity between congener hosts over time may have facilitated the exchange of their streblid fly species. Furthermore, sheltering closely in perennial roosts such as caves has been pointed out as a possible important driver of host specificity in streblid flies (e.g. ter Hofstede and Fenton 2005).

The distribution range in Brazil of at least six streblid species reported in this study (*N. fairchildi*, *N. parnelli*, *S. proxima*, *T. caecus*, *T. johnsonae*, and *T. pallidus*) is little-known and these species can be considered rare. As an example, *T. pallidus* is a specific parasite for the nationally threatened cave bat *F. horrens* (the only known species of Furipteridae in Brazil). Some studies have indicated high host specificity as the factor most likely to directly influence the possibility of coextinction when hosts are threatened (e.g.

Moir *et al.* 2010; Poulin *et al.* 2011; Colwell *et al.* 2012). Due to the unique association of *T. pallidus* with *F. horrens*, the conservation status of this streblid species is also of concern due to the threat level to its host. Therefore, assessing host specificity can be pointed out as a crucial step in assessing the risk of coextinction (Colwell *et al.* 2012).

Considering the importance of caves for dozens of bat species, and that all endangered bat species in Brazil are cave-dwelling (MMA 2022), it is urgent to improve the knowledge on these species, including basic parameters of host-parasite relationships such as parasite prevalence, abundance, and population structure.

CONCLUSIONS

In this study, we presented new records of streblid flies in a biodiversity-rich but undersampled region in northern Brazil, providing information on the geographic distribution and interspecific interaction of these ectoparasites and their host cave bats. Further studies that evaluate the interactions among cave bats and their ectoparasites in the context of ecological interaction networks will also be of great importance to shed light on questions about how such interactions are modulated in these unique environments, and what impact this has on both bats and parasites.

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REFERENCES

Barbier, E.; Bernard, E. 2017. From the Atlantic Forest to the borders of Amazonia: species richness, distribution, and host association of ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) in northeastern Brazil. *Parasitology Research*, 116: 3043-3055.

- Barbier, E.; Falcão, F.; Bernard, E. 2021. Bat-ectoparasitic fly relationships in a seasonally dry tropical forest in Brazil. *Parasitology Research*, 120: 3507-3517.
- Barbier, E.; Graciolli, G. 2016. Community of bat flies (Streblidae and Nycteribiidae) on bats in the Cerrado of Central-West Brazil: hosts, aggregation, prevalence, infestation intensity, and infracommunities. *Studies on Neotropical Fauna and Environment*, 51: 176-187.
- Barbier, E.; Graciolli, G.; Bernard, E. 2019. Structure and composition of Nycteribiidae and Streblidae flies on bats along an environmental gradient in northeastern Brazil. *Canadian Journal of Zoology*, 97: 409-418.
- Barbier, E.; Hintze, F.; Jardelino, A.C.; Bernard, E. 2018. First record of the bat ectoparasitic fly *Strebla proxima* Wenzel, 1976 (Diptera: Streblidae) from Brazil. *Entomological News*, 127: 369-374.
- Barbier, E.; Prado-Neto, J.G.; Bernard, E. 2016. Records of bat flies (Diptera: Nycteribiidae and Streblidae) in the semi-arid Caatinga in the state of Paraíba, Northeastern Brazil. *Neotropical Entomology*, 45: 740-745.
- Barquez, R.; Perez, S.; Miller, B.; Diaz, M. 2015. *Carollia perspicillata*. The IUCN Red List of Threatened Species 2015: e.T3905A22133716. (<https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T3905A22133716.en>). Accessed on 02 Nov 2022.
- Colwell, R.K.; Dunn, R.R.; Harris, N.C. 2012. Coextinction and persistence of dependent species in a changing world. *Annual Review of Ecology, Evolution and Systematics*, 43: 183-203.
- Díaz, M.M.; Solari, S.; Gregorin, R.; Aguirre, L.F.; Barquez, R.M. 2021. *Clave de Identificación de los Murciélagos Neotropicales*. Fundación PCMA, Tucumán, 211p.
- Dick, C.W.; Dittmar, K. 2014. Parasitic bat flies (Diptera: Streblidae and Nycteribiidae): host specificity and potential as vectors. In: Klimpel, S.; Mehlhorn, H. (Ed.). *Bats (Chiroptera) as Vectors of Diseases and Parasites*. Springer, Berlin, p.131-155.
- Dick, C.W.; Patterson, B.D. 2006. Bat flies: obligate ectoparasites of bats. In: Morand, S.; Krasnov, B.R.; Poulin, R. (Ed.). *Micromammals and Macroparasites: From Evolutionary Ecology to Management*. Springer-Verlag, Tokyo, p.179-194.
- Dormann, C.F.; Gruber, B.; Fruend, J. 2008. Introducing the bipartite package: analysing ecological networks. *R News*, 8: 8-11.
- Figueiredo, D.; Graciolli, G.; Aguiar, L.M.S. 2015. New records of bat flies (Diptera, Streblidae and Nycteribiidae) in Cerrado of Central Brazil. *Check List*, 11: 1761.
- Graciolli, G.; Azevedo, A.R. 2011. Ectoparasites of bats (Chiroptera, Furipteridae), with a description of a new species of *Synthesiostrebla Townsend* (Diptera, Streblidae) from Brazil. *Revista Brasileira de Entomologia*, 55: 501-504.
- Graciolli, G.; Carvalho, C.J.B. 2012. Do fly parasites of bats and their hosts coevolve? Speciation in *Trichobius phyllostomae* group (Diptera, Streblidae) and their hosts (Chiroptera, Phyllostomidae) suggests that they do not. *Revista Brasileira de Entomologia*, 56: 436-450.
- Graciolli, G.; Linardi, P.M. 2002. Some Streblidae and Nycteribiidae (Diptera: Hippoboscoidea) from Maracá Island, Roraima, Brazil. *Memórias do Instituto Oswaldo Cruz*, 97: 139-141.
- Guerrero, R. 1993. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. I. Clave para los géneros y Nycterophiliinae. *Acta Biologica Venezuelica*, 14: 61-75.
- Guerrero, R. 1994. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. II. Los grupos: *pallidus*, *caecus*, *major*, *uniformis* y *longipes* del género *Trichobius* Gervais, 1844. *Acta Biologica Venezuelica*, 15: 1-18.
- Guerrero, R. 1995. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. III. Los grupos: *dugei*, *dunni* y *phyllostomae* del género *Trichobius* Gervais, 1844. *Acta Biologica Venezuelica*, 15: 1-27.
- Guerrero, R. 1997. Catálogo de los Streblidae (Diptera: Pupipara) parásitos de murciélagos (Mammalia: Chiroptera) del Nuevo Mundo. VII. Lista de especies, hospedadores y países. *Acta Biologica Venezuelica*, 17: 9-24.
- Guerrero, R. 1998. Notes on Neotropical batflies (Diptera, Streblidae). I. The genus *Trichobius*, with description of two new species and one new subspecies from Venezuela. *Acta Parasitologica*, 43: 86-93.
- Guerrero, R.; Morales-Malacara, J.B. 1996. Streblidae (Diptera: Calyptratae) parásitos de murciélagos (Mammalia: Chiroptera) cavernícolas del Centro y Sur de México, con descripción de una especie nueva del género *Trichobius*. *Anales del Instituto de Biología. Serie Zoológica*, 67: 357-373.
- Guimarães, L.R. 1937. Sobre as espécies sul americanas do gênero *Trichobius* (Diptera-Streblidae). *Revista do Museu Paulista*, 23: 653-666.
- Hrycyna, G.; Martins, A.C.M.; Graciolli, G. 2019. Infracommunities of bat flies (Diptera: Streblidae and Nycteribiidae) of bats (Mammalia: Chiroptera) in three conservation units in the State of Amapá, Brazil. *Biota Neotropica*, 19: e20180715.
- Jirón, F.P.; Fallas F.B. 1974. Presencia de un representante del género *Nycterophilina* Ferris, 1916 (Diptera: Streblidae) en Costa Rica. *Revista de Biología Tropical*, 22: 67-70.
- López-Baucells, A.; Rocha, R.; Bobrowiec, P.; Bernard, E.; Palmeirim, J.; Meyer, C. 2016. *Field Guide to Amazonian Bats*. Editora INPA, Manaus, 174p.
- Lourenço, E.C.; Almeida, J.C.; Famadas, K.M. 2016. Richness of ectoparasitic flies (Diptera: Streblidae) of bats (Chiroptera) – a systematic review and meta-analysis of studies in Brazil. *Parasitology Research*, 115: 4379-4388.
- Lourenço, E.C.; Patrício, P.M.P.; Pinheiro, M.D.C.; Dias, R.M.; Famadas, K.M. 2014. Streblidae (Diptera) on bats (Chiroptera) in an area of Atlantic Forest, state of Rio de Janeiro. *Revista Brasileira de Parasitologia Veterinária*, 23: 164-170.
- MMA. 2022. Ministério do Meio Ambiente. Portaria MMA nº 148, de 7 de junho de 2022. Diário Oficial da União, Edição 108, Seção 1 (<https://in.gov.br/en/web/dou/-/portaria-mma-n-148-de-7-de-junho-de-2022-406272733>). Accessed on 23 Sep 2022.
- Moir, M.L.; Vesk, P.A.; Brennan, K.E.C.; Keith, D.A.; Hughes, L.; McCarthy, M.A. 2010. Current constraints and future directions in estimating coextinction. *Conservation Biology*, 24: 682-90.

- Oliveira, H.F.M.; Oprea, M.; Dias, R.I. 2018. Distributional patterns and ecological determinants of bat occurrence inside caves: a broad scale meta-analysis. *Diversity*, 10: 49. doi:10.3390/d10030049
- Palheta, L.R.; Urbietta, G.L.; Brasil, L.S.; Dias-Silva, K.; Silva, J.B.; Graciolli, G.; Aguiar, L.M.S.; Vieira, T.B. 2020. The effect of urbanization on bats and communities of bat flies (Diptera: Nycteribiidae and Streblidae) in the Amazon, northern Brazil. *Acta Chiropterologica*, 22: 403-416.
- Pavan, A.C. 2019. Family Mormoopidae (ghost-faced, naked-backed and mustached bats). In: Wilson, D.E; Mittermeier, R.A. (Ed.). *Handbook of the Mammals of the World: Bats. v.9*. Lynx Edicions, Barcelona, p.424-443.
- Piló, L.B.; Auler, A.S.; Martins, F. 2015. Carajás National Forest: Iron ore plateaus and caves in southeastern Amazon. In: Vieira, B.C.; Salgado, A.R.; Santos, L.J.C. (Ed.). *Landscapes and Landforms of Brazil*. Springer, Dordrecht, p.273-283.
- Poulin, R. 2007. *Evolutionary Ecology of Parasites*, 2nd ed. Princeton University Press, Princeton, 332p.
- Poulin, R.; Krasnov, B.R.; Mouillot, D. 2011. Host specificity in phylogenetic and geographic space. *Trends in Parasitology*, 27: 355-61.
- R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<https://www.R-project.org/>).
- Santos, C.L.C.; Dias, P.A.; Rodrigues F.S.; Lobato, K.S.; Rosa, L.C.; Oliveira, T.G.; Rebêlo, J.M.M. 2009. Moscas ectoparasitas (Diptera: Streblidae) de morcegos (Mammalia: Chiroptera) do município de São Luís, MA: taxas de infestação e associações parasito-hospedeiro. *Neotropical Entomology*, 38: 595-601.
- ter Hofstede, H.M.; Fenton, M.B. 2005. Relationships between roost preferences, ectoparasite density and grooming behaviour of Neotropical bats. *Journal of Zoology*, 266: 333-340.
- Urbietta, G.L.; Graciolli, G.; Tavares, V.C. 2022. Review of studies about bat-fly interactions inside roosts, with observations on partnership patterns for publications. *Parasitology Research*, 121: 3051-3061.
- Wenzel, R.L. 1976. The streblid batflies of Venezuela (Diptera: Streblidae). *Brigham Young University Science Bulletin, Biological Series*, 20: 1-177.
- Wenzel, R.L.; Tipton, V.J.; Kiewlicz, A. 1966. The streblid bat flies of Panama (Diptera: Calyptera: Streblidae). In: Wenzel, R.L.; Tipton, V.J. (Ed.). *Ectoparasites of Panama*. Field Museum of Natural History, Chicago, p.405-675.

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