Association of bat flies (Diptera: Streblidae) and bats: Richness and host specificity in Western Mexico

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ABSTRACT

As part of a widespread ecological study on the ectoparasites of bats in Western Mexico, we report new information on the specificity, and distribution of bat flies in a geographical transition zone between the nearctic and neotropical zones. Fifteen (15) species of bats representing three families (Mormoopidae, Phyllostomidae, and Vespertilionidae) were collected in 10 locations throughout western Mexico. A total of 276 bat flies, representing 6 genera and 25 species, were identified four species of the bat flies are new records for the region indicating an expansion of the distribution for *Trichobius corynorhini* (Cockerll, 1910), *T. hoffmannae* (Guerrero & Morales-Malacara, 1996), *T. intermedius* (Peterson & Hürka, 1974) and *Nycterophilia natali* (Wenzel, 1966). These records update the species richness of streblids to 40 species in the state of Jalisco, representing 65.6% of the total number of 61 species of streblids recorded in Mexico. The interaction network showed a high degree of specialization of the bat flies towards their hosts (H2' = 0.92). Similarly, the specificity indices showed that there is a high ecological specificity (SI) with an average of 92%. of all the bat flies was associated with their primary hosts, while the average value of specificity of the phylogenetic trees (S_{TD}) of the six streblid species that presented more than one host was 1.7%, indicating a high specificity. The results of this study provide relevant information on bat-parasite associations and highlight the need for further research to obtain information on the geographic distribution of streblids and their hosts.

1. Introduction

Parasites are key components of biodiversity in the ecosystem due to the relevance of the interactions they establish with their hosts. As specialized consumers, they take resources from their host and stimulate their host's immune response, but in some cases, they can cause a chronic secondary infection (Hudson, 2005). While parasites themselves may not directly cause their hosts' death, they can increase the risk of predation and even alter host morphology and decrease their reproductive success (Hudson, 2005; Frainer et al., 2018). The latter is why the role of parasitism at the ecosystem level has gained momentum directing efforts to understand the patterns that govern this interaction.

The Order Chiroptera, with about 1400 species, exhibits a high diet diversity (frugivores, nectarivores, piscivores, carnivores, insectivores, and hematophagous) and plays diverse roles in ecosystems (Simmons and Cirranello, 2020), making it an important group by providing

environmental services that benefit humans, as pollinators, seed dispersers and natural regulators of insect pests (Patterson et al., 2003; Cleveland et al., 2006; Kunz et al., 2011). Despite being the second most numerous taxonomic Order of mammals after rodents, we still know very little about the interactions with their ectoparasites.

The ectoparasitic flies of bats (Diptera: Streblidae), known as streblids, are hematophagous organisms that specialize in this group of mammals; this is a result of a long evolutionary history (Wenzel et al., 1966; Dick and Patterson, 2006; Poinar and Brown, 2012) that has derived from several morphological adaptations of streblids, such as reduction of the eyes and wings, a strongly sclerotized body provided with backward directed setae and/or ctenidium, with claws on the tarsi that facilitate locomotion through the dense fur of their host (Wenzel and Peterson, 1987; Dick and Patterson, 2007; Dick and Dittmar, 2014).

Ecological studies on streblids and their relationship with their hosts have increased in the last decade. Some factors that may influence

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variation in streblid parasite loads are host migration, seasonal changes, effects of fragmentation and urbanization, host roosts type, and vegetation type (Pilosof et al., 2012; Zarazúa-Carbajal et al., 2016; Bolívar-Cimé et al., 2018; Salinas-Ramos et al., 2018; Palheta et al., 2020; Zamora-Mejías et al., 2020; Hiller et al., 2021; Tlapaya-Romero et al., 2021; Urbieta et al., 2021). The results of these studies provide relevant information for understanding parasite-host dynamics. However, it is important to emphasize that we still do not have complete knowledge of the streblid species richness because there are still regions where information is scarce.

In Mexico in the last decade, in addition to ecological studies, inventories of the species of streblids and their hosts have also been conducted, providing new records for the country and the description of new species, thus increasing the number of taxa to 16 genera and 61 species (Cuxim-Koyoc et al., 2015, 2016; Colín-Martínez et al., 2018; Cuxim-Koyoc et al., 2018; Tlapaya-Romero et al., 2023). The state of Jalisco is in an important geographic transition zone between the Nearctic and Neotropical regions resulting in great biological diversity and endemism of fauna and flora (Santana et al., 2004). However, only three studies of streblids report 34 species in 21 bats (Ramírez-Martínez et al., 2016; Zarazúa-Carbajal et al., 2016; Salinas-Ramos et al., 2018). Recent studies in this region have described two new species of bat flies, and two new records for the country (Graciolli et al., 2021; Tlapaya-Romero et al., 2023). increasing the number of species of streblids in the country from 59 (Cuxim-Koyoc et al., 2018) to 61 (Tlapaya-Romero et al., 2023); these last findings an indicator that the knowledge of streblids is still ongoing and highlights the importance of continuing with faunistic and taxonomic studies.

Studies on taxonomy, richness, and abundance of streblids are the first step for the development of future research in coevolution and biogeography (Dick and Gettinger, 2005) since, in addition to providing information on the geographic distribution of species, they also provide information on the hosts. Thus, studies of this nature will also allow us to determine the specificity of the different species of streblids among their hosts; this information is relevant to understanding these ectoparasites' role as possible vectors of pathogens among host species. Although most species of streblids are specific to one host species (monoxenous), others may be associated with more than one in the same genus (stenoxenous) or the same subfamily or family (oligoxenous), on the other hand, there are the polixenous species, which are those that parasitize more than one family (Herrin and Tipton, 1975; Morales-Malacara, 1998; Dick and Gettinger, 2005; ter Hofstede and Fenton, 2005; Voigt and Kelm, 2006; Dick and Patterson, 2007; Colín-Martínez et al., 2018). These are particularly relevant because while a species exhibiting high host specificity has limited potential to act as a disease vector, a generalist species can be an important vector for spreading disease and epidemics (Woolhouse et al., 2005). However, despite the fact that authors have reported that the species of the Family Streblidae are specialists in one species or different closely related species, for example, the same genus (Wenzel et al., 1966; Dick and Patterson, 2007). Cases of polixenous species have been documented, that is, species that are parasitizing different families, however, the latter has been refuted arguing that such associations may be due to cross-contaminations (Cuxim-Koyoc et al., 2018; Estrada-Villegas et al., 2018), so it is important to continue documenting these associations.

The term host specificity is the measure to which a parasite taxon is restricted to a number of host species used at a given stage of the life cycle. Highly specific parasites are restricted to one host species and the specificity decreases as the number of host species used increases (Poulin, 2007). The specificity of parasites can be measured from two perspectives, one ecological and the other phylogenetic. Dick and Gettinger (2005) measured the specificity using an index that considers the total percentage of individuals of a streblid species in each host species (SI), providing information on how many species use a parasite and to what extent it exploits each host species host. In such a way that a high abundance and prevalence of hosts in a single host would indicate a high specificity.

Poulin and Mouillot (2003) propose another way of measuring the specificity of a parasite which measures the average taxonomic distinctness of all host species used by a parasite species. That is, if the parasite exploits species of the same genus or different genera but of the same family or different families or orders. In this way, if a parasite is exploiting more than one species, but all the species are closely related because they belong to the same genus, we will be talking about a high specificity regardless of the abundance and/or prevalence of the parasite. The specificity index (S_{TD}) provides a simple way to measure parasite specificity from an evolutionary perspective (Poulin 2007).

The present study aims to describe the infra-community of streblids in bat populations of Western Mexico through a network of interactions between streblids and bats, as well as to determine the specificity of streblids towards their hosts (SI and S_{TD}) from the samples deposited in the Zoonosis Ecology Laboratory (LEZ, by its initials in Spanish) of the University of Guadalajara, where specimens collected from the South Coast, Sierra Occidental, and Sierra Amula of the state of Jalisco and some localities of Colima are stored.

2. Materials and methods

We processed samples deposited in the LEZ and extracted from bats captured in different localities of the state of Jalisco and Colima, obtained from systematized collections carried out in the field between November 2012 and May 2022 (Fig. 1). We identified the material using a Zeiss Stermi 200-C stereo microscope, following the keys Wenzel et al. (1966), Wenzel (1976), Guerrero (1993, 1994, 1995a,b), and the descriptions of Peterson and Ross (1972), Peterson and Hůrka (1974) and Guerrero and Morales-Malacara (1996) Subsequently, we integrated the faunistic list and the infracommunity composition (richness and abundance) of streblids in each host species. With the data obtained, we elaborated an interaction network of bat hosts with their corresponding ectoparasitic flies using the plotweb function implemented in the bipartite package (Dormann et al., 2009) for R v3.3.1 (R Core Team, 2016), omitting contaminated samples. To determine the contaminations, we take into account systematic studies that report the abundance and prevalence of streblids in their host species. In this way, when we find host species that have been widely studied and an unreported species of streblid was found with a low prevalence (<1%), we consider it an association due to contamination.

Based on the total abundance of collected streblids, we calculated a specificity index (SI) by taking the percentage of total bat fly individuals of a single species found on each bat host (Dick and Gettinger, 2005; Estrada-Villegas et al., 2018). We calculated the mean infestation and prevalence of each species of streblid in each host species (the samples only represent the infested bat population). To be more precise about the specificity, we also calculate the specificity index (S_{TD}) proposed by Poulin and Mouillot (2003), which measures the average hierarchical taxonomic distinctness (classes, orders, families, genera, and species) of all host species used by a parasite species. In such a way that the average taxonomic distinctness is the number of steps in the hierarchy that must be taken to reach a taxon common to two host species. Therefore, if two host species are congeners, one step (from species to genus) is necessary to reach a common node in the taxonomic tree; if the species belong to different genera, but the same family, two steps will be necessary; and so on, with these number of steps averaged across all host species pairs. The index value S_{TD} is inversely proportional to specificity: where a high index value means that, on average, the hosts of a parasite species are not closely related, and a value of one or close to one means that the hosts used are closely related (see Poulin and Mouillot 2003; Poulin 2007).

We use only three taxonomic levels above species (genus, family, order) since streblids only parasitize the Chiroptera order, thus the maximum value that the STD index can take (when the host species belong to different families) is 3, and its lowest value (when all hosts are
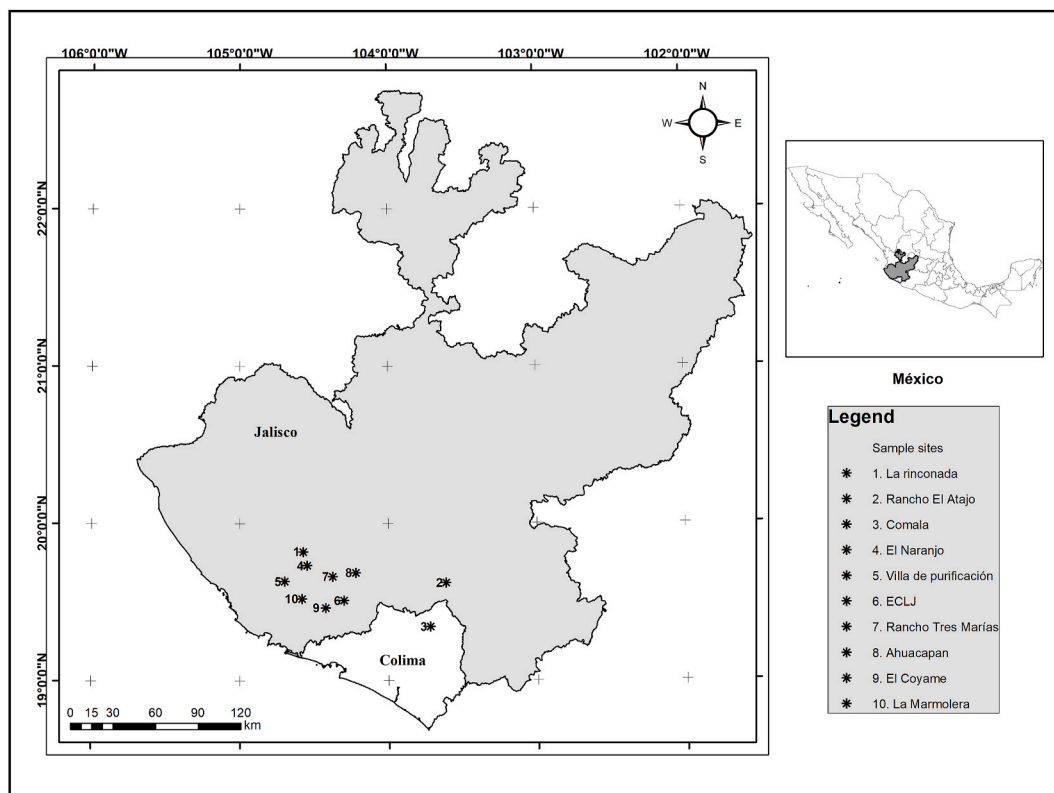
Fig. 1. Location of the streblid collection sites between 2012 and 2022.

congeners) is 1. The S_{TD} cannot be applied to species of parasites that infect a single species, since these parasites are highly host-specific, in the same way when there are only a couple of host species, the taxonomic distance can be calculated by counting the steps necessary to get there from one species to another, since otherwise there are not enough species to be able to average the summation.

To study the associations between bats and streblids, the term primary hosts has been used (Dick and Gettinger 2005; Estrada-Villegas et al., 2018) referring to the hosts that are used by a parasite. Whereas, the term "non-primary host" refers to records of streblids in hosts that are a consequence of contamination during the collection of streblids in the field (Estrada-Villegas et al., 2018). We observed that among the host species used by a species of parasite, there is a wide variation between the abundance and prevalence of ectoparasites, so we use the term "primary host" only for that species that presents the highest values of prevalence and abundance of streblids, thus there is only one primary host. While a secondary host will be the one that presents a lower prevalence and abundance of the streblid species in relation to the primary host. In this way, we will be able to evaluate which hosts are the most widely used among the spectrum of species parasitized by each species of streblid. The term non-primary host was used to indicate cross-contamination associations possibly from handling hosts in the field.

3. Results

We identified 124 samples from 15 species of bats in three families: Mormoopidae, Phyllostomidae, and Vespertilionidae. Also, 275 specimens belonging to eight genera and 25 species of streblids, of which four species are new records for the state, and the presence of *T. brennani* in the state of Jalisco was confirmed (Table 1). We determined contamination in six samples. The host species with the highest richness of streblids was *Glossophaga mutica* (Merriam, 1898), harboring four species, while *Corynorhinus Mexicana* (Allen, 1916), *Chiroderma salvini*,

(Dobson, 1878) and *Anoura geoffroyi* (Gray, 1838) a single species. In the case of *Dermanura azteca* (Andersen, 1906) and some individuals of *Sturnira parvidens* (Goldman, 1917), we found 20 individuals of the genus *Megistopoda* (Macquart, 1852) that could not be determined, despite having the characteristics of *Megistopoda proxima* (Séguy, 1926) such as broad wings, posterior femur only slightly longer than the abdomen and prescutum with short but strong setae along the median suture and transverse median suture, they presented variations in the shape and size of the thorax, the arrangement of the setae of the prescutum and scutum as well as the number of facets on the eyes, and the body size was smaller.

The interaction network consisted of 15 species of bats and 25 species of streblids, characterized as highly specialized, with $H2' = 0.92$, and modularity ($Q = 0.77$) forming 16 unique associations between streblids and their hosts, as seen in Fig. 2. The degree of nesting was remarkably low ($NODF = 6.7$), as was the connectivity ($C = 009$) Seven modules were formed, of which three were made up of a single host species associated with a single species of streblids, while one module was made up of a one host species associated with four species of streblids, the remaining three modules were made up of the as follows: the first was made up of four species belonging to two genera of phylogenetically close hosts (*Artibeus* and *Dermanura*) associated with five species of the *Trichobiinae* subfamily, The second module consisted of five host species, four of which belong to the Mormoopidae family and one species to the Phyllostomidae family, which were associated with eight species of streblids belonging to two subfamilies (*Nycterophiliinae* and *Trichobiinae*), The third module was made up of two species of the genus *Stunira* and three species of streblids belonging to the *Trichobiinae* subfamily (Fig. 2).

The values of the specificity indices showed that most of the species of the streblid infra-community are specific. The SI gave a result that 23 of the 25 species of streblids were associated with one primary host species, with more than 60% occurring on a single host species, indicating high host specificity, thus we were able to categorize 12 species of

Table 1

Host bat species and identified streblid species. N = number of samples. *Contamination. ECLJ: Estación Cientifica Las Joyas.

Host bat species	N	Streblid species	N	Locality
Artibeus jamaicensis	18	Trichobius intermedius	3	La Rinconada
		Megistopoda proxima	*1	Rancho El Atajo
		Trichobius caecus	*1	Rancho El Atajo
		Aspidoptera phyllostomatis	33	Rancho El Atajo
		Megistopoda aranea	10	Comala Rancho El Atajo
		Paratrichobius longicrus	3	El Naranjo Rancho El Atajo
Artibeus lituratus	2	Trichobius intermedius	2	El Naranjo
		Paratrichobius longicrus	2	El Naranjo
		Megistopoda proxima	*1	Rancho El Atajo
Dermanura azteca	3	Megistopoda próximans	2	Rancho Tres Marías
		Paratrichobius longicrus	2	Rancho El Atajo
Dermanura tolteca	7	Trichobius intermedius	7	Villa de Purificación
		Paratrichobius longicrus	4	Villa de Purificación Rancho El Atajo ECLJ
		Paratrichobius lowei	3	Rancho El Atajo
Chiroderma salvini	1	Megistopoda proxima	*2	Rancho El Atajo
Sturnira parvidens	24	Megistopoda próxima	15	Rancho El Atajo ECLJ
		Megistopada sp	14	Rancho Tres Marías
		Aspidoptera delatorreli	11	Rancho Tres Marías
		Trichobius brennani	1	El Coyame
Sturnira hondurensis	24	Megistopoda proxima	45	Rancho El Atajo ECLJ Rancho Tres Marías Ahuacapán
		Aspidoptera delatorrei	2	Ahuacapán
Sturnira sp	1	Megistopoda proxima	2	Rancho El Atajo
Desmodus rotundus	2	Trichobius parasiticus	2	Villa de Purificación Rancho El Atajo
Glossophaga mutica	14	Trichobius intermedius	*1	Villa de Purificación
		Trichobius dugesii	14	La Marmolera
		Paraeuctenodes longipes	1	Sin datos
		Trichobius diphyllae	3	La Marmolera
		Trichobius uniformis	2	La Marmolera
Anoura geoffroyii	3	Exastinion clovisi	7	Villa de Purificación Rancho tres Marías
Leptonycteris yerbabuenae	2	Metelasmus pseudopterus	*3	El Coyame
		Nycterophilia coxata	24	El Coyame
		Trichobius sphaeronotus	3	El Coyame
Mormoops megalophylla	11	Trichobius leionotus	4	El Coyame
		Nycterophilia natali	2	La Marmolera
		Trichobius hoffmannae	10	La Marmolera
		Trichobius sphaeronotus	1	La Marmolera
Pteronotus fulvus	1	Nycterophilia parnelli,	1	La Marmolera
		Trichobius leionotus	1	La Marmolera
Pteronotus mesoamericanus	8	Nycterophilia natali	1	La Marmolera
		Trichobius caecus	5	Villa de Purificación
		Trichobius johnsonae	7	La Marmolera Villa de Purificación

Table 1 (*continued*)

Host bat species	N	Streblid species	N	Locality
		Trichobius sparsus	13	Villa de Purificación
Pteronotus personatus	2	Trichobius johnsonae	1	La Marmolera
		Nycterophilia fairchildi	1	La Marmolera
Corynorhinus mexicana	1	Trichobius corynorhini	2	ECLJ
TOTAL	124		275	

streblids as monoxenus, two stenoxenous species, one oligoxenous species, and one polixenous species (Table 2). The SI showed that all streblid species had a primary host, even in those ectoparasites that presented an index of less than 60% and that were associated with more than two hosts, as was the case with *Paratrichobius longicrus* (Miranda Ribeiro, 1907) and *T. intermedius* parasitizing four and three host species, respectively, however, abundance and mean infestation were concentrated in *Dermanura tolteca* for both species.

The S_{TD} shows that *P. longicrus* has a high specificity (1.66), while *T. intermedius* was less specific (2.0), however, this value could be influenced by the number of hosts (since the formula is less sensitive when the number of hosts is low. Of the eight phylogenetic trees formed *T. johnsonae*, *M. proxima*, and *A. delatorrei* were the most specific species when parasitizing species of the same genus. While *T. sphaeronotus* was the least specific species since it was found parasitizing two species from different families (Fig. 3).

4. Discussion

Faunal studies of ectoparasites allow us to broaden our understanding of parasite-host relationships. With the results of our study, the distribution of four species of streblids in an important area, such as the transition zone between the Nearctic and Neotropical regions, is expanded. We also report *T. sphaeronotus* parasitizing *Mormoops megalophylla* (Peters, 1986). This association is reported in other studies (Cuxim-Koyoc et al., 2018; Ramírez-Martínez et al., 2016); however, it is questioned whether it was accidental or an association that was not well documented because *T. sphaeronotus* is a characteristic parasite of bats of the genus *Leptonycteris* (Cuxim-Koyoc et al., 2018; Guerrero and Morales-Malacara, 1996; Tlapaya-Romero et al., 2019). Our results suggest that there are few records of *T. sphaeronotus* on *M. megalophylla* because it is a secondary host, being found in a few individuals in the population since *Leptonycteris* species are its primary hosts.

The occasional presence of individual bat flies on non-primary hosts that are not from the same family as the primary host is most likely due to contamination in the mist net or when handling the bat, as has already been pointed out by other authors (Dick and Patterson, 2007; Cuxim-Koyoc et al., 2018). Some authors have emphasized the remarkable host-specificity of the streblids that becomes evident when avoiding cross-contamination by following sampling protocols; however, even when such protocols are followed, there will always be the possibility that some samples will become contaminated. In our experience handling bats in the field, we have observed how some bat flies have a great ability to move outside the host, to the point of leaving the host and climbing onto the safety gloves we use to handle them. If care is not taken in these cases, we can collect bat flies from hosts in other individuals. But, such contaminations can be detected when we find very specific and sometimes very abundant species in host species belonging to families other than the primary host and in a few individuals of the new host and low abundances. According to Wenzel et al. (1966) and Graciolli and Dick (2004), *M. pseudopterus* appears to be a specialist of Stenodermatinae bats, particularly the genus *Artibeus*. We found a sample that corresponded to *Leptonycteris yerbabuenae* (Martinez and Villa, 1940) with three specimens of *M. pseudopterus*, so it was considered contamination; under the same criteria, we reported five more
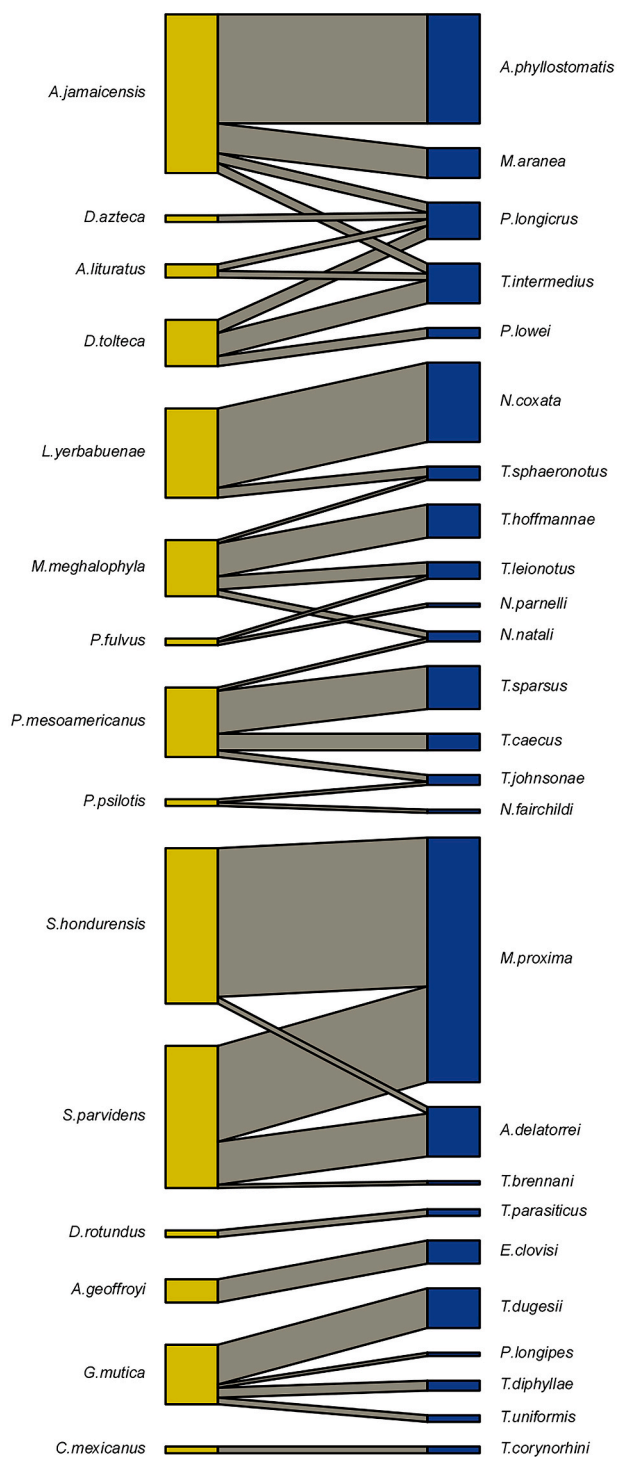
Fig. 2. Taxonomic trees with the S_{TD} value for the hosts that presented more than two species of parasites.

samples as contamination.

The results show a high specificity (SI and S_{TD}) and specialization ($H2'$) which reinforces what was reported by other authors (Dick and Gettinger, 2005; Dick and Patterson, 2007; Hernández-Arciga et al., 2016; Estrada-Villegas et al., 2018; Urbieta et al., 2021) on the high specificity of the family Streblidae. The network of interactions shows in a very interesting way how the species associate in a very specific way, where the first and third blocks are made up of hosts of the Stenodermatinae subfamily, the species of the first block belong to the Stenodermatini tribe and are grouped in the Artibeina subtribe (Hoofer

Table 2

List of identified species of streblids. Host (n = number of host samples/NI = number of host infested; SI = specificity index, percentage of total flies of a single species found on each host; MI = average mean parasite infestation in the parasitized population. *Primary host. [M] = Monoxenous, [S]=Stenoxenous, [O]=Oligoxenous, [P]=Polixenous.

Species	Host (n/NI)	SI (%)	P (%)	IM (%)
Aspidoptera delatorrei[S]	*Sturnira parvidens* (24/11)	86.7	45.8	1.18
	Sturnira hondurensis (24/2)	13.3	8.3	1
Aspidoptera phyllostomatis[M]	*Artibeus jamaicensis* (18/13)	100	72	2.54
Exastinion clovisi[M]	*Anoura geoffroyi* (3/3)	100	100	2.33
Megistopoda aranea[M]	*Artibeus jamaicensis* (18/8)	100	44.4	1.25
Megistopoda proxima[S]	*Sturnira hondurensis* (24/22)	60.8	91.7	2.04
	Sturnira parvidens (24/18)	39.2	75	1.6
Nycterophilia coxatas[M]	*Leptonycteris yerbabuenae* (2/1)	100	50	24
Nycterophilia fairchildi[M]	*Pteronotus psilotis* (2/1)	100	50	1
Nycterophilia natali[O]	*Mormoops megalophylla* (11/2)	66. 7	18.2	1
	Pteronotus mesoamericanus (8/1)	33.3	12.5	1
Nycterophilia parnelli,[M]	*Pteronotus fulvus* (1/1)	100	100	1
Paraeuctenodes longipes[M]	*Glossophaga mutica* (14/1)	100	7.14	1
Paratrichobius longicrus[O]	*Artibeus jamaicensis* (18/3)	27.3	16.7	1
	Artibeus lituratus (2/2)	18.2	100	1
	Dermanura azteca (3/2)	18.2	66.7	1
	Dermanura tolteca (7/3)	36.4	42.8	1.3
Paratrichobius lowei[M]	*Dermanura tolteca* (7/2)	100	28.6	1.5
Trichobius brennani[M]	*Sturnira parvidens* (24/1)	100	4.2	1
Trichobius caecus[M]	*Pteronotus mesoamericanus* (8/3)	100	37.5	1.7
Trichobius corynorhini[M]	*Corynorhinus mexicana* (1/1)	100	100	2
Trichobius diphyllae[M]	*Glossophaga mutica* (14/3)	100	21.4	1
Trichobius dugesii[M]	*Glossophaga mutica* (14/10)	100	71.4	1.2
Trichobius hoffmannae[M]	*Mormoops megalophylla* (11/5)	100	45.4	2
Trichobius intermedius[O]	*Dermanura tolteca* (7/2)	58.3	28.6	3.5
	Artibeus lituratus (2/1)	16.6	50	2
	Artibeus jamaicensis (18/2)	25	11.1	1.5
Trichobius johnsonae[S]	*Pteronotus mesoamericanus* (8/2)	66.7	25	1
	Pteronotus psilotis (2/1)	33.3	50	1
Trichobius leionotus[O]	*Mormoops megalophylla* (11/4)	80	36.4	1
	Pteronotus fulvus (1/1)	20	100	1
Trichobius parasiticus[M]	*Desmodus rotundus* (2/2)	100	100	1
Trichobius sparsus[M]	*Pteronotus mesoamericanus* (8/5)	100	62.5	2.6
Trichobius sphaeronotus[P]	*Leptonycteris yerbabuenae* (2/1)	75	50	3
	Mormoops megalophylla (11/1)	25	9.0	1
Trichobius uniformis[M]	*Glossophaga mutica* (14/1)	100	7.1	1

et al., 2008; Baker et al., 2016) due to their phylogenetic closeness, while the third block made up of two Sturnira species belong to the Sturnirini tribe because these two species are phylogenetically distant. of the Artibeina subtribe. These results reinforce what has been reported by other authors (Wenzel et al., 1966; Dick and Patterson, 2007) who point out that flies are specific to one host species, and that when they parasitize more than one host, they are closely related. This is clearly seen with *P. Longicrus* which parasitized four species of bats from the same subtribe. On the other hand, the second block was the most heterogeneous as it was made up of five host species of different genera and different families. This group is striking because these bat species have been found sharing shelter (Ayala Téllez et al., 2018; Tlapaya-Romero, 2020), so we could infer that although *T. sphaeronotus* were initially exclusive to *Leptonycterys yerbabuenae* at some point in the life history of the species, some species of streblids began to exploit a new resource
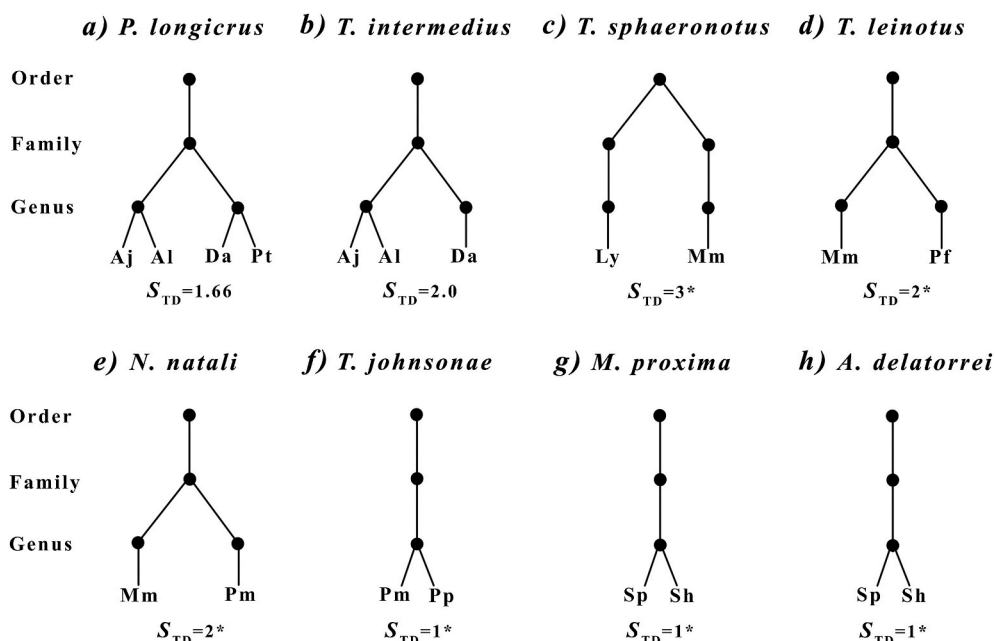
Fig. 3. Interaction network between bats and ectoparasites captured in Western Mexico. The lines represent interactions between species, and the width of the line indicates the strength of the interactions.

(*Mormoops megalophylla*) possibly because the resource was available (spatially). So we infer that in addition to evolutionary forces, there are also ecological factors that are determining these associations. This idea is supported by the associations formed between the Family Moormopidae and the *Nycterophilia* genus which is restricted to hot caves (Morse et al., 2012) which are also the sites used by the five host species that we report. In this way, the specificity indices as well as the ecological networks, in addition to indicating the specificity and specialization of the parasites towards their hosts, can also clarify the evolutionary or ecological factors that determine the associations between parasites and hosts. In this way, we could explain that possibly the associations with primary hosts occurred at first by evolutionary processes, while the secondary hosts were subsequently determined by ecological processes.

In this study, 13 species of streblids were classified as monoxenous. In the case of some species of the genus *Nycterophillia*, which in this study occurs in a single host species, is important to note that in these cases the host sample size is small. Other studies have found that this genus parasitizes more than one species of the Mormoopidae family (Guerrero and Morales-Malacara, 1996; Salinas-Ramos et al., 2018; Tlapaya-Romero et al., 2019). It is important to highlight the above since as Poulin (2008) mentions, there is an evident danger in the use of these estimates of specificity when making this estimate from a single sample in a single sampling site and comparing it with a second, from which there are records of a very wide geographical area and on a regular basis, and of several populations of the same host species over a long period of time. Thus a high host specificity will be the product of inadequate sampling. Therefore, we enhance the importance of continuing with the efforts to know the geographic distribution of the different species of streblids in the country, as well as their host species, since with more robust data we will be able to avoid wrongly measuring the specificity.

Ethics approval

The samples were collected under the auspices of the collection permit SEMARNAT: 09/K4-0423/04/21.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Author contributions

M.M. Ramírez Martínez: Planned, designed, and coordinated the study and conducted the fieldwork, collected the specimens (bat flies and bats), identified the bat species, and reviewed the manuscript. L. Tlapaya Romero: performed the taxonomic identification of streblids, developed the formal analysis, and wrote the paper. All authors read and approved the final manuscript.

Availability of data and materials

Not applicable.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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