Structure and composition of Nycteribiidae and Streblidae flies on bats along an environmental gradient in Northeastern Brazil

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Abstract: Bats can be parasitized by several arthropod groups, including ectoparasitic flies. The high host specificity is a common phenomenon between flies and bats. In recent years, more efforts have been employed to understand how environmental variables can influence richness and parasitic load (PL). However, many gaps still need to be filled in order to better understand this issue. We analyzed the PL of flies on bats sampled in three environments with different rain volume and vegetation types to verify if are correlated with the rainfall and if there are differences in the PL on bats within and between environments. In overall, there was no correlation between rainfall and PL in the same environment, nor difference between the three environments. When tested separately, *Carollia perspicillata* (Linnaeus, 1758) had a difference in prevalence of flies between environments and *Artibeus planirostris* (Spix, 1823) had a greater abundance of flies in the rainy season in a semiarid area. There was no difference in PL between male and female bats. Our results suggest that bat-fly interactions are driven by several factors, not only by the amount of rainfall or vegetation, and that different host species may respond differently, with no obvious general pattern.

Key words: Atlantic Forest, bat ectoparasitic flies, Caatinga, Chiroptera, host-parasite relationships, Nycteribiidae, Streblidae

Introduction

Bats are the second largest group of mammals and can be parasitized by several groups of ectoparasites such as mites, ticks, bugs, fleas, and flies (Marshall 1981, 1982; Fenton and Simmons 2014). Among the ectoparasites of bats, especially in the tropics, the hematophagous flies of the families Nycteribiidae and Streblidae (Diptera: Hippoboscoidea) are the most frequently found on these hosts (see Frank et al. 2014). Nycteribiids and streblids have an association with bats at least since the Miocene (15–20 million years ago), currently covering more than 500 described species worldwide (Marshall 1981; Dick and Patterson 2006; Poinar and Brown 2012).

Contrary to what would be expected, due to the host's diverse ecological and behavioral characteristics, bat ectoparasites are highly specialized occurring on a single bat species or on congeners, in most cases, and for streblids and nycteribiids, for example, there is a phylogenetic history with their hosts (e.g., Dittmar et al. 2006; Dick 2007; Dick and Patterson 2007; Santos et al. 2013; Barbier and Graciolli 2016). Although the high specificity of flies by bat hosts seems to be a unanimous and widespread issue among the vast majority of researchers (e.g., Wenzel et al. 1966; Wenzel 1976; Dick and Patterson 2007; Dittmar et al. 2015; Lourenço et al. 2016; Barbier et al. 2016), the structure and composition along the geographic distribution of species has been little explored (e.g., Barbier and Bernard 2017).

Nevertheless, especially in recent years, studies have indicated some influence, even if indirect, of environmental variables on species richness and parasitic load (hereafter PL) of ectoparasitic flies occurring on bats (e.g., Stanko et al. 2006; Pilosof et al. 2012; Zarazúa-Carbajal et al. 2016). On the other hand, patterns for parasite communities are more complex to predict, since, in addition to environmental characteristics, host factors (e.g., morphology, evolutionary traits) also play an important role in such associations (e.g., Krasnov et al. 1998) and may vary between different biogeographical regions (e.g., Korallo et al. 2007; Poulin 2007; Krasnov et al. 2003, 2011, 2012). Thus, in order to increase the knowledge on these issues, it is essential investigate such associations in the most diverse scales and regions.

Here, we analyzed the PL of ectoparasitic flies (Streblidae and Nycteribiidae) on bats (Chiroptera) sampled in three environments with different rain volumes and vegetation types in Northeastern Brazil to verify, mainly, (i) whether the PL (prevalence, mean intensity, and mean abundance) are correlated with the seasonal rainfall; (ii) whether there are differences in the PL on the bats within and between environments and between host sexes; and (iii) whether the total abundance of bat ectoparasitic flies is different between the rainy and dry period in each researched environment. Our hypothesis was that the PL would be influenced by rainfall within the same environments and, considering vegetation is directly influenced by rainfall, we also predicted that the PL would be affected by the type of habitat sampled. We also predicted that the PL would be different between male and female bats and total abundance would be distinct seasonally.

Materials and methods

Study area

In the state of Pernambuco, Northeastern Brazil, there is a remarkable climatic gradient in the east-west direction, from a more humid environment on the eastern coast, passing through a transition area (locally known as *agreste*), until the western semiarid (Andrade 1980, 1989; Lins 1989; Barbosa et al. 2002; Ferraz 2002; Andrade-Lima 2007; Lima 2007). Fieldwork was conducted in three environments along that gradient (Fig. 1), hereafter wet area (*WA*), transitional area (*TA*), and semiarid area (*SA*). The coordinates of each sampled site can be found in Appendix A.

WA – The Saltinho Biological Station is a 562 ha Federal Reserve of Atlantic Forest, near Tamandaré city (ICMBio 2015). The climate is constantly hot (annual temperature averaging 25°C) and humid with a dry season in the summer and a rainy season (1,500–2,000 mm) along autumn-winter (Barbosa et al. 2002; Ferraz 2002). Composed mainly of secondary forest in advanced natural regeneration, Saltinho was created in 1983 and is currently one of the largest Atlantic Forest fragments of Pernambuco (Brasil 1983; ICMBio 2015).

TA – The *agreste* is a microregion of Northeastern Brazil extending from the state of Rio Grande do Norte to the southeast of the state of Bahia (Rizzini 1979). Characterized as a transitional area between the Atlantic Forest and Caatinga, the *agreste* has intermediate characteristics with humid sites such as the coast, and others dry as in semiarid area (Andrade 1980, 1989; Lins 1989). The region's climate is classified as BSh's, following Köpen, and the mean annual temperature is 25°C with an annual rainfall of 599 mm, marked by irregularity throughout the year. The captures were carried out in the municipality of Chã Grande.

SA – The Catimbau National Park has 62,292 ha and located in the central region of the state of Pernambuco. Its area covers the municipalities of Buíque, Tupanatinga, and Ibimirim and it is identified as a priority area for conservation of Caatinga, mainly because it harbors rare and endemic species (MMA 2002). Rainfall to the region is concentrated from April to June, with an annual average ranging from 300 mm to 500 mm (SUDENE 1990; Rodal et al. 1998). Like other regions of Caatinga, rainfall is historically very irregular, and there may be long periods of drought.

Data collection

From July 2014 to June 2015, bats were monthly sampled using 10 mist nets (12 m × 2.5 m), set at the ground level during six hours at the sunset; except in July 2014 and June 2015, there were no captures in the *TA* and *SA* respectively. Therefore, WA obtained 144 h of captures, TA 114 h, and SA 138 h. At the end of the captures period, we obtained an effort of 3,960 mist-net-hours (mnh) (one 12 m × 2.5 m net open for 1 h equals 1 mnh) (Table 1) or 117,000 m^2.h according to Straube and Bianconi (2002). The monthly precipitation in each area was obtained from INPE/SUDENE/CPTEC (2016) based on information from weather stations in the municipalities of Tamandaré (for *WA*), Chã Grande (for *TA*), and Buíque (for *SA*).

Each captured bat was individually placed in clean cotton bags, used only once in each night. The entire body surface and wing membranes of the hosts were checked to find possible ectoparasites. The ectoparasitic flies were collected with soft forceps and placed in properly labeled vials containing 70% ethanol for later identification in the laboratory. All specimens' manipulation, *in situ* or *ex situ*, was conducted in order to prevent contamination of the parasites through the hosts, following Barbier and Bernard's (2017) recommendations.

After screening, the bats were measured, sexed, and marked on the back with non-toxic ink (permanent marker type) to recapture control in the same sampling period and released. Recaptures were not considered for data analysis. Bats were handled according to Sikes et al. (2011) and fieldwork was authorized by MMA/ICMBio/SISBIO (permits #43816-1 and #43816-2) and Ethics Committee on Animal Care–UFPE (permit #23076.027916/2015-13).

Species identification

For bat species identification, we followed Gregorin and Taddei (2002), Gregorin and Ditchfield (2005), Gardner (2008), Díaz et al. (2011), Moratelli et al. (2011), Feijó et al. (2015), and Moratelli and Dias (2015). We followed Nogueira et al. (2014) for bat nomenclature. For flies, we followed the diagnoses and/or taxonomic keys available in Guimarães (1938), Guimarães and D'Andretta (1956), Wenzel et al. (1966), Wenzel (1976), and Guerrero (1998). We followed Graciolli and Dick (2008) and Dick and Graciolli (2008) for flies' nomenclature. Voucher specimens are deposited in the Mammal Collection (UFPE) and in the Entomological Collection (CE–UFPE) of Federal University of Pernambuco.

Data analysis

In order to quantitatively describe the parasite's populations, we used prevalence (number of infested hosts with a particular parasite species/number of examined hosts), mean intensity (number of parasites of a particular species/number of hosts infested with that parasite), and mean abundance (number of individuals of a particular parasite species on a particular host species/number of hosts of that species examined; including both infected and uninfected hosts) (*sensu* Bush et al. 1997). Non-primary associations were not considered in the analyzes (*sensu* Dick 2007). The PL were calculated with the program Quantitative Parasitology–QPweb 1.0.13 (Reiczigel et al. 2013), with a 95% confidence interval.

We used Spearman's (r_s) correlation to test for all bat species at once the relationship between rainfall and PL (prevalence, mean intensity, and mean abundance), separately for each sampled area. For this, we used the monthly rainfall values in each environment studied and the PL calculated for the bat hosts sampled there. To verify whether different bat species may present different results, we tested the same correlation separately for the two most abundant species in the three environments – *Artibeus planirostris* (Spix, 1823) and *Carollia perspicillata*

(Linnaeus, 1758). To test in general whether PL on bat hosts differs between environments, we used the Kruskal-Wallis (*H*) test. In order to verify in detail whether PL on the same host species responds differently in the three environments studied, we also analyzed separately for the two most abundant bat species in the three environments. We also used Kruskal-Wallis (*H*) to determine if there was a difference in PL between male and female bats captured in the same environment. Additionally, for each environment, we verified whether the total fly abundance parasitizing *A*. *planirostris* and *C*. *perspicillata* was influenced by seasonality (rainy and dry period), using Mann-Whitney (*U*) test. We chose to analyze such influence only for the host species that were more representative of each study area (≥ 30 captures; see Rózsa et al. 2000). Moreover, bat species with no parasites, even if abundant, were excluded from all comparative statistical analyses. Data normality was verified with the Shapiro-Wilk test. We used the program PAST 3.16 for the analyses (Hammer et al. 2001), with the significant level at $P < 0.05$.

Results

In total, we captured 1,572 bats of 36 species and 28 genera of the families Phyllostomidae (26 species), Vespertilionidae (5 species), Molossidae (2 species), Emballonuridae (1 species), Mormoopidae (1 species), and Noctilionidae (1 species) (Table S1). Among the captured bats, 967 (61.5%) were parasitized by flies (Table S1). *Artibeus lituratus* (Olfers, 1818), *A*. *planirostris*, *C*. *perspicillata*, *Glossophaga soricina* (Pallas, 1766), *Lonchophylla mordax* Thomas, 1903, and *Myotis lavali* Moratelli, Peracchi, Dias & Oliveira, 2011 were the most infested species, accounting for 1,224 bats (~ 78%) and 2,565 flies (~ 70%).

The *WA* was the site with the highest number of bat captured (n = 921) and species (23 spp.), followed by the *SA* (n = 436; 21 spp.), and the *TA* (n = 215; 12 spp.) (Tables 2, 3, 4). The top-three most abundant bat species were: *C*. *perspicillata* (n = 440; 48%), *M*. *lavali* (n = 168;

18%), and *A. planirostris* (*n* = 70; 8%), in the *WA* (Table 2); *A. planirostris* (*n* = 81; 38%), *C. perspicillata* (*n* = 44; 20%), and *Sturnira lilium* (É. Geoffroy, 1810) (*n* = 25; 12%), in the *TA* (Table 3); *A. planirostris* (*n* = 145; 33%), *L. mordax* (*n* = 72; 16.5%), and *G. soricina* (*n* = 62; 14%), in the *SA* (Table 4). *Dermanura cinerea* Gervais, 1856 (*n* = 73) and *Molossus molossus* (Pallas, 1766) (*n* = 44) were also abundant in the *WA*, but were not infested by flies and were excluded from all analyses.

We collected 3,688 flies of 39 species and 13 genera of the families Streblidae (37 species) and Nycteribiidae (2 species) (Table S2). The *WA* was the environment with the highest number of collected flies (*n* = 2,397 flies, on 583 bats), followed by *SA* (*n* = 927 flies, on 268 bats), and *TA* (*n* = 364, on 116 bats) (Tables S2). The top-three most abundant fly species were: *Trichobius joblingi* Wenzel, 1966 (*n* = 1,092), *Basilia travassosi* Guimarães, 1938 (*n* = 400), and *T. dugesioides dugesioides* Wenzel, 1966 (*n* = 227), in the *WA*; *T. joblingi* (*n* = 93), *Megistopoda aranea* (Coquillett, 1899) (*n* = 66), and *B. travassosi* (*n* = 39), in the *TA*; *T. lonchophyllae* Wenzel, 1966 (*n* = 171), *T. diphyllae* Wenzel, 1966 (*n* = 169), and *Trichobius* sp. 3 (*n* = 107), in the *SA*.

Among the most captured bats (≥ 30), the prevalence of flies ranged from 3.2% (*Trichobius* sp. 1 on *A. lituratus*) to 79.3% (*T. joblingi* on *C. perspicillata*) in *WA* (Table 2); from 11.1% (*A. phyllostomatis* on *A. planirostris*) to 75.0% (*T. joblingi* on *C. perspicillata*) in *TA* (Table 3); and from 5.6% (*Strebla* sp.) to 66.7% (*T. lonchophyllae*) both on *L. mordax* in *SA* (Table 4).

There was no correlation between rainfall and PL in the same environment, evaluating species neither together nor individually for *A. planirostris* and *C. perspicillata* throughout the study period (Table 5). There was no significant difference between the PL in the three studied environments (prevalence: $H = 1.617$, $P = 0.4454$; mean intensity: $H = 3.027$, $P = 0.2201$; mean abundance: $H = -0.0147$, $P = 1$). Evaluating separately, there was a difference only in the prevalence of flies on *C. perspicillata* ($H = 6.265$, $P = 0.0435$). Mean intensity ($H = 0.2141$, $P = 0.8976$) and mean abundance ($H = 2.388$, $P = 0.3028$) for this same species were not significantly. We also found no difference in PL on *A. planirostris* (prevalence: $H = 3.468$, $P = 0.1753$; mean intensity: $H = 0.0114$, $P = 0.9942$; mean abundance: $H = -1.774$, $P = 1$). There are also no differences in PL between the host sex (prevalence: $H = 0.0641$, $P = 0.9684$; mean intensity: $H = 0.5547$, $P = 0.4559$; mean abundance: $H = 0.1146$, $P = 0.7349$). When we evaluated the total abundance of flies on *A. planirostris* and *C. perspicillata*, by rainy and dry period in each environment, there was a difference for *A. planirostris* in the *SA* ($U = 2243.5$, $P = 0.0001$), being higher in the rainy period (Fig. 2). Interestingly, on *C. perspicillata*, also in the *SA*, there was a marginally significant difference ($U = 122$, $P = 0.0635$), but with higher abundance in the dry period (Fig. 2).

Discussion

When sampling along an ecological gradient from Atlantic Forest to the dry forest in Northeastern Brazil we observed that, contrary to our predictions, the prevalence, mean intensity, and mean abundance of bat ectoparasitic flies were not influenced by rainfall, and there was no significant difference of such indices between environments, analyzing in general. On the other hand, the prevalence of flies on *C. perspicillata* was different between environments and abundance on *A. planirostris* captured in semiarid environment was higher in the rainy season. Although environmental variables are often highlighted as one of the main influences on the host-parasite association (e.g., Morand and Poulin 1998; ter Hofstede and Fenton 2005; Bordes et al. 2008), our results suggest that the interactions between bats and ectoparasitic flies were driven by other factors rather than the amount of rainfall or vegetation alone, and that different host species may respond distinctly.

Environmental variables have recently been identified in some studies as a driver for PL and host interactions. Pilosof et al. (2012), for instance, recently found an effect of temperature and precipitation on the abundance of bat ectoparasitic flies in Venezuela using a meta-analysis. However, as indicated by Pilosof et al. (2012), there is a need for an approach with local data at the time of capture. In a meta-analysis, many details are suppressed in favor of a more general examination, such as the existence and/or analysis of microenvironments, which could otherwise result in more detailed knowledge about host-parasite relationship (e.g., Lourenço et al. 2016). Our data, both from hosts and ectoparasitic flies, were obtained *in situ* and collected with rigorous methodology (see Materials and methods) and the information about rainfall was provided on a small scale (local data). This set of features can favor the obtaining of information that better represent the interactions between bats and their ectoparasitic flies along a climatic gradient.

Besides that, for host specificity, for example, small- and large-scale analysis is important because different responses in host-parasite relationships can be observed at the local or regional level (e.g., Krasnov et al. 2011). For fleas, links between their own communities, host communities, and habitat types appears to manifest differently across geographic regions. Among-habitat, differences in flea assemblages within a host species in temperate zones appear to be less pronounced than those in desert habitats (see Laudisoit et al. 2009). The greater the number of environments and regions sampled for streblids and nycteribiids, the greater our capacity to understand the interactions with their bat hosts, especially because widely distributed species can respond in distinct ways along their geographic distribution.

Another factor that should be considered when studying the relationship between ectoparasites and their hosts is data robustness. Some studies analyzing the effect of seasonal and/or vegetation variation on bat ectoparasitic flies have used relatively low numbers of both individuals and species [e.g., Zarazúa-Carbajal et al. (2016) (145 bats, 246 flies); Rivera-García et al. (2017) (318 bats, 836 flies)]. We analyzed data from 1,153 infested bats of six species, parasitized with 2,265 flies of 12 species, considering only those most representative hosts in the sample (≥ 30). On the one hand, it is likely that the refinement of our data is showing in more detail the host-parasite relationship between environments with different vegetation and rainfall. On the other hand, it is important that similar studies investigate this association in distinct regions in Brazil to confirm whether there is a regional influence or if this pattern is the same regardless of location. In fact, the two host species we analyzed separately – *A. planirostris* and *C. perspicillata* – presented difference in total abundance (seasonally) and prevalence (between environments) of flies, respectively.

Salinas-Ramos et al. (2018) also found heterogeneous results according to the species when studying the seasonal variation of the load of bat ectoparasitic flies in a dry tropical forest in Mexico. Of the four bat species studied by these authors, some experienced a significant increase in the PL in the wet season (higher mean intensity and mean abundance), while other species had the highest PL in the dry season. Apparently, there is no general pattern and each species is likely to respond in a particular way: the same species of host and parasite may present different traits in different locations and, when analyzed in a macroscale, no general patterns are found among parasite richness and some ecological variables (see Poulin 2007). Our results seem to corroborate this statement, since the abundance on *A. planirostris*, for instance, was only statistically different in the *SA* and on *C. perspicillata* was the same in all environments (despite a tendency to be more intense in the dry period of the *SA*).

We did not find any influence of host sex on the relationship between ectoparasitic flies and bats. Recently, Frank et al. (2016) observed that tree cover was not a significant predictor of bat ectoparasitic flies abundance in Costa Rica. On the other hand, they found that PL on a particular bat host can be changed in a sex-specific way, through habitat change. Patterson et al. (2008) observed that, in most cases, female bats were more frequently and heavily parasitized. Nonetheless, Moura et al. (2003) and Presley (2007), for example, also found no correlation between the host sex and parasite community structure on the greater bulldog bat *Noctilio leporinus* (Linnaeus, 1758), a species with sex-based social system. This question remains open, but there will probably be a species-specific response.

A highly specific relationship

Our study reinforces the close relationship between bats and their ectoparasitic flies, indicating that host characteristics may be more important than environmental variables. In fact, in Northeastern Brazil, bat ectoparasitic fly species richness are also correlated with the bat host species richness and distinct groups can be recognized among biomes, both for bat and fly species, showing that the occurrence of flies is dependent on their specific host (Barbier and Bernard 2017).

Due to the high host specificity, the abundance of bat ectoparasitic flies is likely to be affected mainly by host species density as recently suggested by Pilosof et al. (2012). Complementary, Arneberg et al. (1998) found a stronger positive association between host population density and average of parasite abundance within mammalian taxa. It is also the case of fleas on small mammals, where the host composition appears to better explain the variance in flea species composition than environmental variables, for example (Laudisoit et al. 2009). The more complex a system, the less likely we are to achieve quantitatively accurate predictions and to find general laws (Kauffman 1993). Parasite communities are complex systems and they exist in non-equilibrium conditions, a situation where contingencies should be predominant (see Rohde 2006). Thus, as presented here, it is reasonable to say that richness and abundance of bat ectoparasitic flies are more strongly correlated with the number of species and concentration of bats in a given area rather than on external factor surrounding them. However, there is still no consensus as to how innumerable variables can affect the relationships between bats and their ectoparasitic flies. In contrast, many gaps need to be fulfilled in order to expand our understanding of this issue.

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Table 1. Sampled sites, annual rainfall, sampling effort, and bat captures in three different environments in the state of Pernambuco, Northeastern Brazil, between July 2014 and June 2015.

Environment	No. of sites	Annual rainfall (mm) *	No. of bat captures	No. of bat species	Effort (mnh) [a]	Capture ratio [b]	Species ratio [c]
Wet area	4	1,498.58	921	23	1,440	0.639	0.025
Transitional area	3	934.88	215	12	1,140	0.188	0.056
Semiarid area	9	608.93	436	21	1,380	0.315	0.048
Total	16	-	1,572	-	3,960	-	-

[a] Mist-net-hours, [b] Number of bat captures divided by effort, [c] Number of bat species divided by number of bat captures, * Available from http://proclima.cptec.inpe.br/balanco_hidrico/balancohidrico.shtml.

Table 2. Parasite load of ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) on bats (Mammalia: Chiroptera) in the *WA* environment in the state of Pernambuco, Northeastern Brazil, between July 2014 and June 2015.

Bat (23 species)	EH	IH	Fly (25 species)	N	P% (CI)	MI (CI)	MA (CI)
Carollia perspicillata	440	383	*Speiseria ambigua*	204	30.5 (26.2–35.0)	1.52 (1.38–1.71)	0.464 (0.384–0.553)
			Strebla guajiro	88	14.8 (11.6–18.4)	1.35 (1.20–1.55)	0.200 (0.155–0.257)
			Trichobius anducei	76	13.6 (10.6–17.2)	1.27 (1.15–1.40)	0.173 (0.132–0.218)
			Trichobius costalimai *	6	0.2 (0–1.3)	6.00 (NA)	0.014 (0–0.041)
			Trichobius joblingi	1,092	79.3 (75.2–83.0)	3.12 (2.90–3.37)	2.480 (2.270–2.700)
Myotis lavali	168	108	*Basilia travassosi*	400	65.5 (57.8–72.6)	3.64 (3.16–4.30)	2.380 (1.990–2.900)
Artibeus planirostris	70	24	*Aspidoptera phyllostomatis*	21	18.6 (10.3–29.7)	1.62 (1.15–2.31)	0.300 (0.143–0.529)
			Megistopoda aranea	35	28.6 (18.4–40.6)	1.75 (1.35–2.45)	0.500 (0.300–0.771)
			Paratrichobius longicrus *	1	1.4 (0–0.8)	1.00 (NA)	0.014 (0–0.043)
Artibeus lituratus	31	11	*Aspidoptera phyllostomatis* *	1	3.2 (0.1–16.7)	1.00 (NA)	0.032 (0–0.097)
			Megistopoda aranea *	3	3.2 (0.1–16.7)	3.00 (NA)	0.097 (0–0.290)
			Paratrichobius longicrus	15	29.0 (14.2–48.0)	1.67 (1.22–2.00)	0.484 (0.226–0.806)
			Trichobius sp. 1	1	3.2 (0.1–16.7)	1.00 (NA)	0.032 (0–0.097)

Phyllostomus discolor	28	26	*Strebla hertigi*	4	14.3 (4.0–32.7)	1.00 (NA)	0.143 (0–0.250)
			Trichobioides perspicillatus	79	75.0 (55.1–89.3)	3.76 (2.43–6.00)	2.820 (1.680–4.640)
			Trichobius costalimai	84	82.1 (63.1–93.9)	3.65 (2.71–4.78)	3.000 (2.040–4.140)
Glossophaga soricina	27	12	*Speiseria ambigua* *	1	3.7 (0.1–19.0)	1.00 (NA)	0.037 (0–0.111)
			Strebla cf. *carvalhoi*	2	3.7 (0.1–19.0)	2.00 (NA)	0.074 (0–0.222)
			Trichobius dugesii	16	44.4 (25.5–64.7)	1.33 (1.00–1.75)	0.593 (0.333–0.889)
			Trichobius uniformis	4	11.1 (2.4–29.2)	1.33 (1.00–1.67)	0.148 (0–0.370)
Trachops cirrhosus	11	11	*Strebla mirabilis*	5	27.3 (6.0–61.0)	1.67 (1.00–2.00)	0.455 (0–0.909)
			Trichobius dugesioides dugesioides	227	100 (71.5–100)	20.64 (12.10–33.50)	20.600 (11.400–34.200)
Artibeus obscurus	5	1	*Trichobius* sp. 1	1	200 (0.5–71.6)	1.00 (NA)	0.200 (0–0.400)
Sturnira lilium	3	1	*Megistopoda proxima*	1	33.3 (0.8–90.6)	1.00 (NA)	0.333 (0–0.667)
			Speiseria ambigua *	3	33.3 (0.8–90.6)	3.00 (NA)	1.000 (0–2.000)
Lophostoma brasiliense	2	1	*Mastoptera minuta*	1	50.0 (1.3–98.7)	1.00 (NA)	0.500 (0–0.500)
			Pseudostrebla greenwelli	1	50.0 (1.3–98.7)	1.00 (NA)	0.500 (0–0.500)
Platyrrhinus lineatus	2	1	*Paratrichobius longicrus*	1	50.0 (1.3–98.7)	1.00 (NA)	NA
			Trichobius angulatus	2	50.0 (1.3–98.7)	2.00 (NA)	1.000 (0–1.000)

Tonatia saurophila	2	2	*Strebla galindoi*	10	100 (15.8–100)	5.00 (3.00–5.00)	5.000 (3.000–5.000)
Lonchorhina aurita	1	1	*Strebla altmani*	2	100 (2.5–100)	2.00 (NA)	NA
			Trichobioides perspicillatus *	1	100 (2.5–100)	1.00 (NA)	NA
			Trichobius flagellatus	7	100 (2.5–100)	7.00 (NA)	NA
Phyllostomus elongatus	1	1	*Trichobius* cf. *persimilis*	2	100 (2.5–100)	2.00 (NA)	NA
Dermanura cinerea	73	0	–	–	–	–	–
Molossus molossus	44	0	–	–	–	–	–
Platyrrhinus sp.	4	0	–	–	–	–	–
Desmodus rotundus	3	0	–	–	–	–	–
Chiroderma doriae	2	0	–		–	–	–
Artibeus cf. *fimbriatus*	1	0	–	–	–	–	–
Chiroderma villosum	1	0	–	–	–	–	–
Molossus rufus	1	0	–	–	–	–	–
Rhinophylla pumilio	1	0	–	–	–	–	–
Total:	921	583		2,397			

EH, number of examined host; IH, number of infested host; P%, prevalence; MI, mean intensity; MA, mean abundance; *WA*, wet area; CI, 95% confidence interval; NA, not available; * Non-primary association.

Table 3. Parasite load of ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) on bats (Mammalia: Chiroptera) in the *TA* environment in the state of Pernambuco, Northeastern Brazil, between July 2014 and June 2015.

Bat (12 species)	EH	IH	Fly (15 species)	N	P% (CI)	MI (CI)	MA (CI)
Artibeus planirostris	81	37	*Aspidoptera phyllostomatis*	16	11.1 (5.2–20.0)	1.78 (1.22–2.44)	0.198 (0.086–0.395)
			Megistopoda aranea	66	42.0 (31.1–53.5)	1.94 (1.59–2.35)	0.815 (0.580–1.110)
			Paratrichobius longicrus *	3	1.2 (0–6.7)	3.00 (NA)	0.037 (0–0.111)
Carollia perspicillata	44	35	*Speiseria ambigua*	15	22.7 (11.5–37.8)	1.50 (1.10–1.90)	0.341 (0.159–0.591)
			Strebla guajiro	12	25.0 (13.2–40.3)	1.09 (1.00–1.27)	0.273 (0.136–0.413)
			Trichobius joblingi	93	75.0 (59.7–86.8)	2.82 (2.21–4.09)	2.110 (1.550–3.070)
			Trichobius uniformis *	1	2.3 (0.1–12.0)	1.00 (NA)	0.023 (0–0.068)
Sturnira lilium	25	16	*Aspidoptera falcata*	23	36.0 (18.0–57.5)	2.56 (1.56–3.89)	0.920 (0.400–1.680)
			Megistopoda aranea *	6	8.0 (1.0–26.0)	3.00 (1.00–3.00)	0.240 (0–1.040)
			Megistopoda proxima	26	44.0 (24.4–65.1)	2.36 (1.64–3.09)	1.040 (0.560–1.680)
Artibeus lituratus	22	12	*Megistopoda aranea* *	1	4.5 (0.1–22.8)	1.00 (NA)	0.045 (0–0.136)
			Paratrichobius longicrus	22	50.0 (28.2–71.8)	2.00 (1.35–2.91)	1.000 (0.500–1.680)
Platyrrhinus lineatus	10	5	*Paratrichobius longicrus*	6	40.0 (12.2–73.8)	1.50 (1.00–2.00)	0.600 (0.100–1.300)

			Trichobius angulatus	4	20.0 (2.5–55.6)	2.00 (1.00–2.00)	0.400 (0–1.200)
Myotis lavali	6	6	*Basilia travassosi*	38	100 (54.1–100)	6.33 (3.67–8.83)	6.330 (3.500–9.170)
Glossophaga soricina	5	1	*Trichobius dugesii*	1	20.0 (0.5–71.6)	1.00 (NA)	0.200 (0–0.400)
			Trichobius uniformis	3	20.0 (0.5–71.6)	3.00 (NA)	0.600 (0–1.200)
Phyllostomus discolor	3	3	*Strebla hertigi*	1	33.3 (0.8–90.6)	1.00 (NA)	0.333 (0–0.667)
			Trichobioides perspicillatus	2	33.3 (0.8–90.6)	2.00 (NA)	0.667 (0–1.330)
			Trichobius costalimai	24	100 (29.2–100)	8.00 (6.00–9.67)	8.000 (6.000–9.670)
Eptesicus brasiliensis	2	1	*Basilia travassosi*	1	50.0 (1.3–98.7)	1.00 (NA)	0.500 (0–0.500)
Dermanura cinerea	14	0	–	–	–	–	–
Molossus molossus	2	0	–	–	–	–	–
Noctilio leporinus	1	0	–	–	–	–	–
Total:	215	116		364			

EH, number of examined host; IH, number of infested host; P%, prevalence; MI, mean intensity; MA, mean abundance; *TA*, transitional area; CI, 95% confidence interval; NA, not available; * Non-primary association.

Table 4. Parasite load of ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) on bats (Mammalia: Chiroptera) in the *SA* environment in the state of Pernambuco, Northeastern Brazil, between July 2014 and June 2015.

Bat (21 species)	EH	IH	Fly (24 species)	N	P% (CI)	MI (CI)	MA (CI)
Artibeus planirostris	145	79	*Aspidoptera phyllostomatis*	84	32.4 (24.9–40.7)	1.79 (1.47–2.13)	0.579 (0.414–0.766)
			Megistopoda aranea	88	35.2 (27.4–43.5)	1.73 (1.43–2.10)	0.607 (0.448–0.807)
Lonchophylla mordax	72	51	*Speiseria ambigua* *	1	1.4 (0–7.5)	1.00 (NA)	0.014 (0–0.042)
			Strebla sp.	4	5.6 (1.5–13.6)	1.00 (NA)	0.056 (0.014–0.111)
			Trichobius lonchophyllae	171	66.7 (54.6–77.3)	2.98 (2.38–3.83)	1.990 (1.490–2.650)
Glossophaga soricina	62	36	*Speiseria ambigua* *	2	3.2 (0.4–11.2)	1.00 (NA)	0.032 (0–0.081)
			Strebla guajiro *	2	3.2 (0.4–11.2)	1.00 (NA)	0.032 (0–0.081)
			Trichobius dugesii	30	29.0 (18.2–41.9)	1.67 (1.22–2.29)	0.484 (0.290–0.806)
			Trichobius uniformis	29	46.8 (34.0–59.9)	1.97 (1.59–2.38)	0.919 (0.613–1.240)
Carollia perspicillata	40	17	*Speiseria ambigua*	4	7.5 (1.5–20.4)	1.33 (1.00–1.67)	0.100 (0–0.263)
			Trichobius joblingi	27	37.5 (22.7–54.2)	1.80 (1.33–2.47)	0.675 (0.375–1.080)
Xeronycteris vieirai	27	24	*Trichobius* sp. 3	107	88.9 (70.8–97.6)	4.46 (3.38–7.15)	3.960 (2.890–6.250)
Micronycteris sanborni	21	18	Streblid **	3	9.5 (1.2–30.4)	1.50 (1.00–1.50)	0.143 (0–0.429)

			Trichobius sp. 2	64	85.7 (63.7–97.0)	3.56 (2.39–5.28)	3.050 (2.000–4.670)
Platyrrhinus lineatus	11	9	*Paratrichobius longicrus*	4	36.4 (10.9–69.2)	1.00 (NA)	0.364 (0.091–0.545)
			Trichobius angulatus	29	81.8 (48.2–97.7)	3.22 (2.00–4.11)	2.640 (1.550–3.730)
Anoura geoffroyi	8	6	*Exastinion clovisi*	18	75.0 (34.9–96.8)	3.00 (1.83–4.50)	2.250 (1.000–3.750)
			Trichobius propinquus	4	25.0 (32.0–65.1)	2.00 (1.00–2.00)	0.500 (0–1.500)
Histiotus diaphanopterus	8	1	*Basilia* sp.	2	12.5 (0.3–52.7)	2.00 (NA)	0.250 (0–0.750)
Diphylla ecaudata	7	7	*Trichobius diphyllae*	169	100 (59.0–100)	24.14 (16.30–30.70)	24.100 (16.500–30.400)
Artibeus lituratus	6	3	*Paratrichobius longicrus*	15	50.0 (11.8–88.2)	5.00 (1.00–9.00)	2.500 (0.167–7.000)
Desmodus rotundus	5	4	*Strebla wiedemanni*	5	60.0 (14.7–97.4)	1.67 (1.00–2.00)	1.000 (0–1.600)
			Trichobius parasiticus	27	80.0 (28.4–99.5)	6.75 (5.25–8.00)	5.400 (2.000–7.200)
Myotis lavali	5	3	*Basilia travassosi*	15	60.0 (14.7–94.7)	5.00 (4.00–5.67)	3.000 (0–4.800)
Lonchorhina aurita	3	3	*Trichobius flagellatus*	9	100 (29.2–100)	3.00 (2.00–4.00)	3.000 (2.000–4.000)
Pteronotus gymnonotus	2	2	*Nycterophilia parnelli*	1	50.0 (1.3–98.7)	1.00 (NA)	0.500 (0–0.500)
			Trichobius sp. 4	16	100 (15.8–100)	8.00 (NA)	8.000 (1.000–8.000)
Sturnira lilium	2	2	*Megistopoda proxima*	3	100 (15.8–100)	1.50 (1.00–1.50)	1.500 (1.000–1.500)
Micronycteris sp.	6	0	–	–	–	–	–

Rhogeessa sp.	3	0	–	–	–	–	–
Lasiurus blossevillii	1	0	–	–	–	–	–
Molossus molossus	1	0	–	–	–	–	–
Peropteryx sp.	1	0	–	–	–	–	–
Total:	436	265		936			

EH, number of examined host; IH, number of infested host; P%, prevalence; MI, mean intensity; MA, mean abundance; *SA*, semiarid area; CI, 95% confidence interval; NA, not available; * Non-primary association; ** Undescribed genus.

Table 5. Spearman (r_s) correlation test between rainfall and parasitic load for all species at once and separately for *Artibeus planirostris* and *Carollia perspicillata*, between July 2014 and June 2015 in three environments in the state of Pernambuco, Northeastern, Brazil.

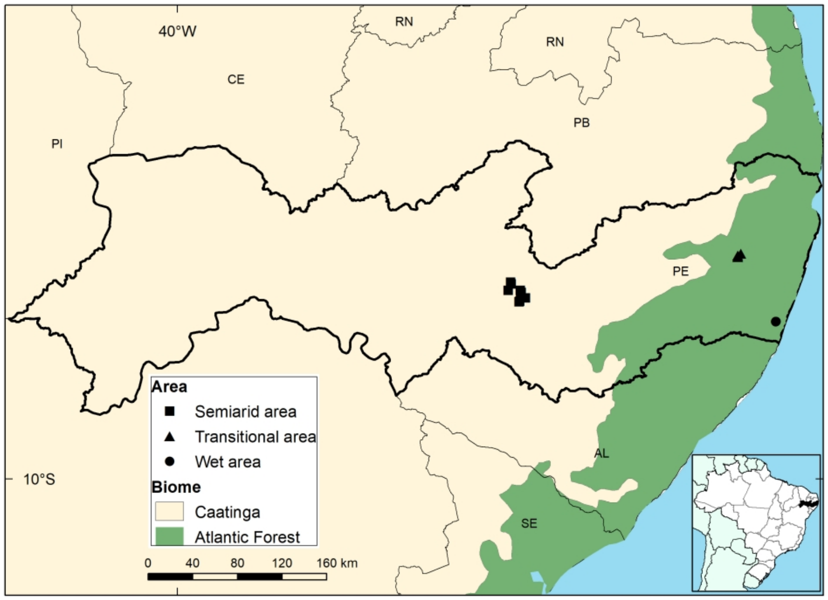
Environment	Rainfall (mm) *	Prevalence		Mean intensity		Mean abundance	
		General					
		r_s	p	r_s	p	r_s	p
WA	1,498	0.1409	0.2341	-0.0542	0.6486	0.0713	0.5516
TA	934	0.2579	0.1472	0.0543	0.7638	0.2048	0.2527
SA	608	0.2061	0.1426	0.2061	0.1426	-0.2014	0.1745
		Artibeus planirostris					
		r_s	p	r_s	p	r_s	p
WA	1,498	0.0899	0.7702	-0.0785	0.7987	0.0988	0.7860
TA	934	0.2658	0.3383	0.0772	0.7844	0.2270	0.4160
SA	608	0.3378	0.2375	0.2500	0.3887	0.1204	0.7095
		Carollia perspicillata					
		r_s	p	r_s	p	r_s	p
WA	1,498	0.2365	0.1018	0.0512	0.7270	0.2453	0.0894
TA	934	0.3251	0.1881	0.0812	0.7486	0.2512	0.3147
SA	608	-0.4485	0.2652	-0.0061	0.9956	0.0588	0.9222

WA, wet area; TA, transitional area; SA, semiarid area; * Available from http://proclima.cptec.inpe.br/balanco_hidrico/balancohidrico.shtml.

Figure legend

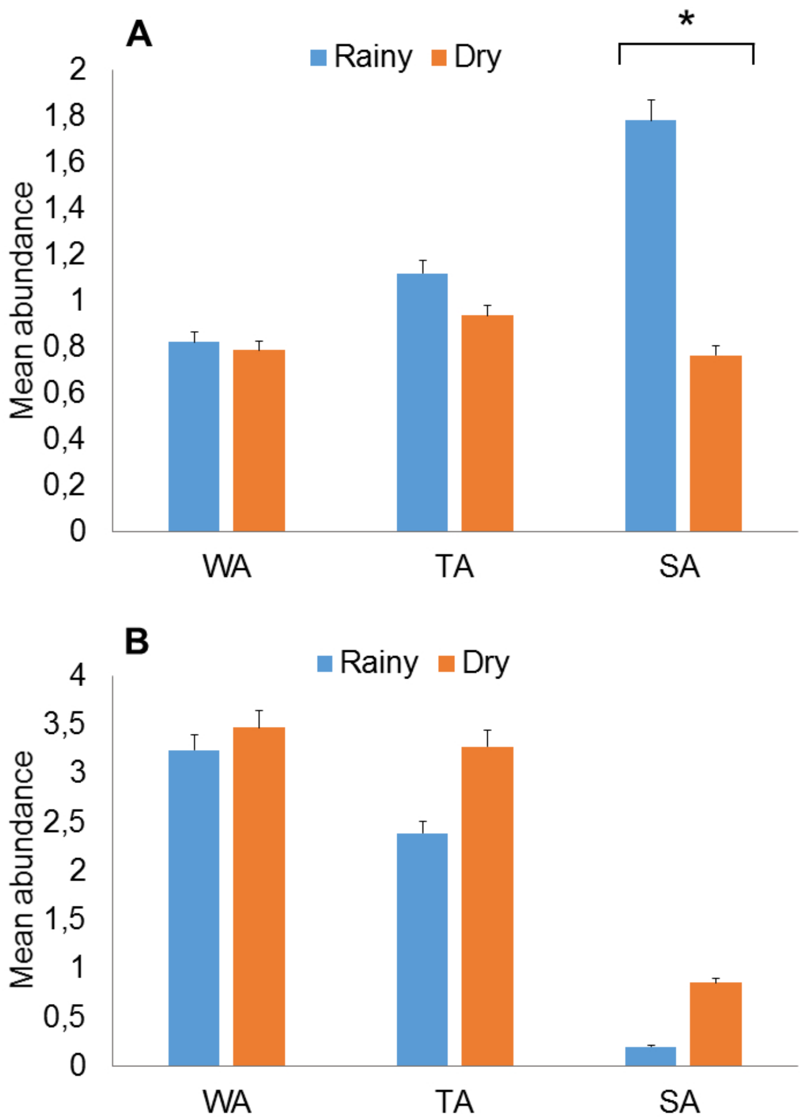
Fig. 1. Study sites for bats (Mammalia: Chiroptera) and their ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) in the state of Pernambuco (PE), Northeastern Brazil. States – AL: Alagoas, CE: Ceará, PB: Paraíba, PI: Piauí, RN: Rio Grande do Norte, SE: Sergipe. Map data: ArcGIS 10 (ESRI 2015).

Fig. 2. Mean abundance of ectoparasitic flies on (A) *Artibeus planirostris* (WA: $U = 472.5$, $P = 0.5978$; TA: $U = 865$, $P = 0.7753$; SA: $U = 2243.5$, $^{*}P = 0.0001$) and (B) *Carollia perspicillata* (WA: $U = 54093$, $P = 0.6535$; TA: $U = 473$, $P = 0.7692$; SA: $U = 122$, $P = 0.0635$) in rainy and dry periods between July 2014 and June 2015 in three environments in the state of Pernambuco, Northeastern Brazil. WA, wet area; TA, transitional area; SA, semiarid area.



Study sites for bats (Mammalia: Chiroptera) and their ectoparasitic flies (Diptera: Nycteribiidae and Streblidae) in the state of Pernambuco (PE), Northeastern Brazil. States – AL: Alagoas, CE: Ceará, PB: Paraíba, PI: Piauí, RN: Rio Grande do Norte, SE: Sergipe. Map data: ArcGIS 10 (ESRI 2015).

279x215mm (300 x 300 DPI)



Mean abundance of ectoparasitic flies on (A) *Artibeus planirostris* (WA: *U* = 472.5, *P* = 0.5978; TA: *U* = 865, *P* = 0.7753; SA: *U* = 2243.5, **P* = 0.0001) and (B) *Carollia perspicillata* (WA: *U* = 54093, *P* = 0.6535; TA: *U* = 473, *P* = 0.7692; SA: *U* = 122, *P* = 0.0635) in rainy and dry periods between July 2014 and June 2015 in three environments in the state of Pernambuco, Northeastern Brazil. WA, wet area; TA, transitional area; SA, semiarid area.

60x88mm (300 x 300 DPI)

Appendix A. Geographic coordinates of the sampled sites in the three environments in the state of Pernambuco, Northeastern Brazil. *WA*, wet area; *TA*, transitional area; *SA*, semiarid area.

WA – 08°43'49.32" S, 35°10'34.95" W; 08°43'52.8" S, 35°10'41.4" W; 08°43'44.4" S, 35°10'36.8" W; and 08°43'49.5" S, 35°10'39.2" W.

TA – 08°11'55.8" S, 35°28'59.3" W; 08°12'34.5" S, 35°29'00.0" W; and 08°11'00.9" S, 35°27'30.7" W.

SA – 08°34'16.2" S, 37°14'50.2" W; 08°32'04.1" S, 37°14'05.4" S; 08°34'02.4" S, 37°14'30.8" W; 08°28'42.8" S, 37°20'07.1" W; 08°32'17.8" S, 37°11'40.6" W; 08°25'41.4" S, 37°18'34.4" W; 08°28'44.8" S, 37°14'12.9" W; 08°24'41.8" S, 37°18'54.6" W; and 08°29'44.1" S, 37°13'50.2" W.