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RESEARCH

Ectoparasitic flies of bats (Mammalia: Chiroptera) in urban green areas of northeastern Brazil

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Abstract

In urban and degraded areas, ectoparasite abundance can be affected by increasing human population density and habitat fragmentation. This study aimed to characterize the ectoparasitic fly community associated with bats in the urban green areas of Sergipe, Brazil. Campaigns were conducted monthly, for two consecutive nights, between September 2019 and February 2021. To capture the bats, ten mist nets were set up inside and at the edge of the habitat fragments. All ectoparasites found were removed from the bats and stored in 70% alcohol. The specificity index, parasitological rates, and level of parasite aggregation were calculated, and the influence of host sex and seasonality on parasitological rates were verified for the most parasitized bats. The collected ectoparasites corresponded to the families Nycteribiidae ($S=1$; $n=26$) and Streblidae ($S=13$; $n=849$), with *Trichobius costalimai* and *Medistopoda aranea* being the most abundant species. For some interactions, there was an influence of host sex on the prevalence rates, with the highest number of parasites being found on females, which can be explained by their greater susceptibility to parasitism owing to their long stay in roosts. The seasonality influenced the parasitological rates, and opposing patterns (from what was expected) were observed for some interactions; this influence may be due to the biological differences between parasite species. This study provides relevant data on this interaction, especially for urban areas in northeastern Brazil, expanding the number of studies in the State of Sergipe and promoting future studies.

Keywords Discrepancy index · Parasitological rates · Phyllostomidae · Streblidae · Urbanization

Introduction

Previous studies have suggested that environmental changes, such as urbanization, can significantly influence the interactions between bats and their ectoparasites (Lafferty and Kuris 2005; Pilosof et al. 2012; Frank et al. 2016). However, the complex relationships among the environment, host, and parasite make it difficult to predict how environmental changes will affect their interaction (Lafferty and Kuris 2005). Few studies have used this approach in urban areas; thus, the patterns of parasitism in this type of environment remain unclear (Ramalho et al. 2018, 2021; Urbieta et al. 2014, 2018).

In urban and degraded areas, ectoparasite abundance can be influenced by increased human population density and habitat fragmentation (Bolívar-Cime et al. 2018; Ramalho et al. 2018; Urbieta et al. 2018). According to Urbieta et al. (2018), ectoparasite prevalence rates and average infestation intensities in urban environments may be lower than that in forest environments. This result may be associated with the quality of proximal roosts in the sampled environment, where poor quality shelters lead bats to change shelters more often, reducing the probability of parasite transmission (Barbier and Graciolli 2016). In addition, parasite specificity may also be lower in more urban areas owing to the increased density of bats within a shelter, therefore facilitating parasite transmission (Urbieta et al. 2018).

Bat ectoparasites, as streblids, spend most of their life cycle associated with bats and depend on their roosts to find new hosts; thus, their abundance is highly influenced by the environmental factors that affect bats (Pilosof et al. 2012; Dittmar et al. 2015; Urbieta et al. 2021). The abundance of

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parasites increases in environmental conditions favorable for their development and decreases when these conditions are harmful to them (Tinsley et al. 2011). According to Rui and Graciolli (2005), during dry seasons (high temperatures and low precipitation), parasitism increases because the reproductive rates of the ectoparasites increases, whereas during the rainy seasons (low temperatures and high precipitation), reproductive rates decrease and mortality rate is higher. Furthermore, it is believed that the geographic distribution, body size, behavior, and sex of the host are also conditions that determine the parasite community structure (Prevedello et al. 2005; Ter Hofstede and Fenton 2005; Krasnov and Poulin 2010). Regarding the sex of bats, female bats may be more parasitized because they are less active, stay longer in the shelters, and form colonies during their reproductive period (Marshall 1982; Komeno and Linhares 1999).

Many populations of bat ectoparasites such as, mites, dipterans, and ticks, feed on their hair follicles, body fluids, or blood (Whitaker et al. 2009). Diptera (of the Streblidae and Nycteribiidae families) are hematophagous and exclusive bat parasites (Dick 2007). In Brazil, 98 species of Streblidae (Graciolli 2022) and 27 species of Nycteribiidae are known (Graciolli and Hrycyna 2022).

In this study, we aimed to characterize the community of ectoparasites associated with bats in urban green areas in northeastern Brazil, describe the specificity indices and parasitological rates, verify parasite aggregation in the hosts, identify infracommunities, and evaluate the influence of host sex, and environmental conditions (precipitation and temperature) on parasitological rates. Our hypotheses were the following: (1) female bats are more parasitized than males owing to the longer time spent in their roosts (Komeno and Linhares 1999); and (2) periods with lower rainfall and higher temperatures lead to an increase in parasitism rates due to the increase in the reproductive rate of the parasites in these conditions (Rui and Graciolli 2005).

Material and methods

Study area

This study was conducted in three urban green areas in Grande Aracaju, Sergipe (Fig. 1). The sampled areas belong to the Campus São Cristóvão da Universidade Federal de Sergipe (UFS; 10° 55′ 34.3″ S; 37° 06′ 09.2″ W), Secretaria de Estado da Fazenda de Sergipe (SEFAZ; 10° 54′ 38.8″ S; 37° 05′ 27.9″ W), and Vila Militar dos Oficiais do Exército (Vila; 10° 55′ 31.6″ S; 37° 03′ 36.7″ W). The minimum distances between the areas are 2.15, 4.17, and 3.5 km from UFS to SEFAZ, UFS to Vila, and Vila to SEFAZ, respectively. The UFS area is a remnant of the Atlantic Forest, encompassing approximately 0.99 ha, and is located next to a fragment of the native forest associated with the Poxim River. This area has dense vegetation, a closed canopy, and intense artificial light surrounding the fragment. The SEFAZ

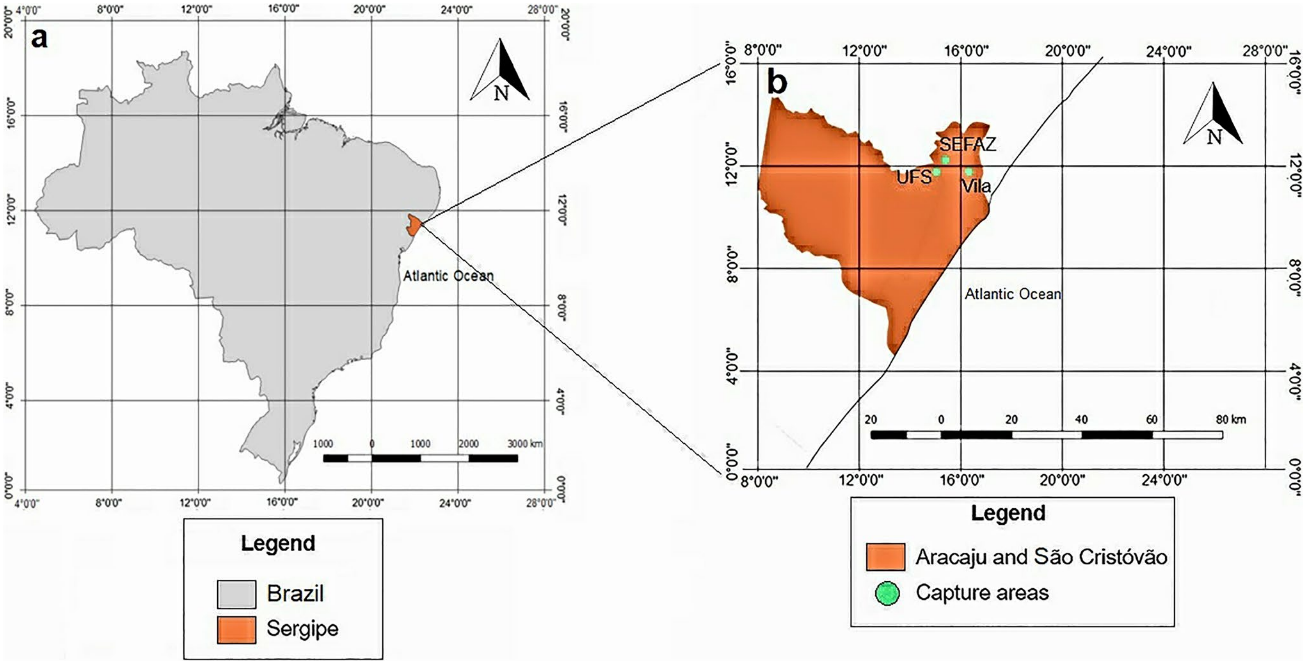

Fig. 1 (**a**) Brazil with State of Sergipe in highlight. (**b**) The municipalities with indication of the urban green areas (UFS, SEFAZ and Vila) used for capturing bats located in Grande Aracaju, Sergipe

area is equivalent to a fragment of approximately 1.58 ha and is characterized by a banana plantation (*Musa* sp.) with low vegetation and a dense understory. However, other areas within SEFAZ contain a higher diversity of plant species, less dense understory, and a closed canopy. In the Vila area, the green area is approximately 1.56 ha, characterized by the predominance of widely spaced almond trees (*Terminalia catappa* L.), which can reach heights of 12 to 15 m; this area lacks an understory and closed canopy (personal observation). During the study period (September 2019 to February 2021), the accumulated precipitation was 1773.4 mm, with an average temperature range of 24.7 to 29.3 °C. December 2019 had the lowest rainfall (8 mm) and April 2020 had the highest (284.6 mm) (INMET 2021).

Data collection and analysis

In the UFS and SEFAZ areas, campaigns were conducted in September and November 2019; January, June, July, August, September, and November 2020; and January 2021. In the Vila area, campaigns were conducted in September and November 2019, January and December 2020, and January and February 2021. These campaigns were conducted monthly, over two consecutive nights, in each area. It should be noted that the irregularity of the field campaigns occurred because of the quarantine related to the COVID-19 pandemic beginning in March 2020. Therefore, campaigns were suspended in March 2020 and continued in June 2020 in the UFS and SEFAZ areas and only resumed in the Vila area in December 2020, as it is a residential area.

To capture bats, ten mist nets (9×3 m, mesh 20 mm) were placed on the inside and edge of the green areas, which remained open between sunset and midnight. These nets were inspected every 30 min, and each captured animal was marked with a numbered ring on the left forearm and released to check for possible recaptures between the areas. The bats were then identified based on the methods described by Díaz et al. (2016) and Reis et al. (2017). Each bat was inspected for ectoparasitic flies, which were collected manually and stored in microtubes containing 70% ethyl alcohol at 92.8° INPM. Ectoparasitic flies species were identified under a stereomicroscope (BEL Engineering; SZT model), according to the morphological characteristics described by Guerrero (1994a, b; 1995).

The specificity index (SI) of the ectoparasites was calculated according to Dick and Gettinger (2005). Prevalence rates (*P*; %) and mean infestation intensity (MI) were obtained according to Bush et al. (1997) with their respective confidence intervals (CI; 95%). The discrepancy index (*D*) was calculated to analyze parasite aggregation on the hosts (Poulin 1993). These rates were calculated using the Quantitative Parasitology software (QPweb) (Reiczigel et al. 2019). Primary associations ($P > 5\%$) between two or more ectoparasitic flies species in the same host were identified and characterized as infracommunities.

For statistical analysis, only the most representative bat species ($n \geq 30$) and the primary associations were considered. The influence of host sex on the prevalence rates was verified using the chi-square test, and the mean intensity was verified using the *t* test. A general linear model (GLM) was used to analyze the influence of precipitation and temperature on the prevalence rates and mean infestation intensity. Data normality was tested using the Shapiro–Wilk test, and statistical analyses were performed using R software 4.1 (R Core Team 2021), with a significance level of 5%.

Results

A total of 568 bats were captured, where only 278 (48.94%) were parasitized. The parasitized bats were among ten species that belong to the Phyllostomidae ($S = 8$) and Vespertilionidae ($S = 2$) families. A total of 875 bat flies were collected, and they comprised 13 species of the Streblidae family ($n = 849$) and one species of the Nycteribiidae family ($n = 26$; Table 1). The most parasitized bats in relation to the total were *Artibeus lituratus* (Olfers, 1818) ($n = 101$; 36.3%), *Artibeus planirostris* (Spix, 1823) ($n = 53$; 19.1%), *Platyrrhinus lineatus* (É. Geoffroy, 1810) ($n = 35$; 12.6%), and *Phyllostomus discolor* (Wagner, 1843) ($n = 32$; 11.5%). The single most parasitized host was a representative of *P. discolor*, on which there were 23 individuals of *Trichobius costalimai* (Guimarães, 1937) and two individuals of *Trichobioides perspicillatus* (Pessôa and Galvao, 1937). The most abundant ectoparasite species were *T. costalimai* (28.8%) and *Megistopoda aranea* Coquillett, 1899 (13.6%).

Four of the registered associations were considered non-primary ($P < 5\%$; Table 1). Considering only the primary associations, the highest prevalence values were obtained for the interactions between *Myotis lavali* Moratelli, Peracchi, Dias and Oliveira, 2011 and *Basilia travassosi* Guimarães, 1938 (85.7%), *Myotis riparius* Handley, 1960 and *B. travassosi*, *P. discolor* and *T. costalimai*, and *Phyllostomus hastatus* (Pallas, 1767) and *Trichobius longipes* (Rudow, 1871) (all 100%). The highest mean intensity values were found for *P. discolor* and *T. costalimai* (8.5), and *P. hastatus* and *T. longipes* (13.0). Regarding the specificity index, 11 associations (36.3%) had values greater than 90%. For the discrepancy index, 62.5% of the parasite-host associations presented a value greater than 0.70 (Table 1). Infracommunities were recorded on 18.3% of the parasitized bats, all of which were composed of individuals from different genera. The most recorded infracommunities were *Paratrichobius longicrus* (Miranda-Ribeiro, 1907) and *Trichobius* sp. (*dugesii* complex) parasitizing *A. lituratus*, and *T. perspicillatus* and *T. costalimai* parasitizing *P. discolor* (Table 2).

The influence of host sex on parasitological rates is shown in Table 3. A difference was observed only in the prevalence

Table 1 List of ectoparasites recorded in bats captured in urban green areas of the Grande Aracaju, Sergipe. Prevalence rates (*P*; %), mean intensity (MI), confidence interval (CI) at a 95% confidence level, specificity index (SI; %), and discrepancy index (*D*)

Hosts (*N* captured)	*N* parasitized (%)[1]	Ectoparasites (*N*)	*P* % (95% CI)	MI (95% CI)	SI (%)	*D* (95% CI)
Artibeus lituratus (221)	101 (45.7)	*Aspidoptera phyllostomatis* (4)	1.3 (0.00–0.03)□	1.3*	12.9	0.98 (0.94–0.99)
		Megistopoda aranea (9)	3.2 (0.01–0.06)□	1.3*	6.9	0.96 (0.93–0.97)
		Paratrichobius longicrus (92)	24.4 (0.18–0.30)	1.7*	98.9	0.75 (0.68–0.80)
		Trichobius costalimai (2)	0.9 (0.00–0.03)•	1.0*	0.7	0.98 (0.96–0.99)
		Trichobius joblingi (2)	0.9 (0.00–0.03)•	1.0*	13.3	0.98 (0.95–0.99)
		Trichobius sp. (complexo *dugesii*) (97)	21.3 (0.16–0.27)	2.0*	98.9	0.78 (0.71–0.82)
Artibeus obscurus (36)	16 (44.4)	*Aspidoptera phyllostomatis* (7)	11.1 (0.03–0.26)	1.7*	22.5	0.86 (0.67–0.91)
		Megistopoda Aranea (21)	36.1 (0.20–0.53)	1.6*	16.1	0.48 (0.29–0.62)
Artibeus planirostris (125)	53 (42.4)	*Aspidoptera phyllostomatis* (20)	12.8 (0.07–0.19)	1.2*	64.5	0.86 (0.7–0.91)
		Megistopoda Aranea (100)	35.2 (0.26–0.44)	2.3*	76.9	0.64 (0.54–0.71)
		Trichobius sp. (complexo *dugesii*) (1)	0.8 (0.00–0.04) •	1.0*	1	0.98 (0.94–0.98)
Carollia perspicillata (18)	8 (44.4)	*Speiseria ambigua* (2)	11.1 (0.01–0.34)	1.0*	100	0.84 (0.52–0.89)
		Trichobius joblingi (12)	38.9 (0.17–0.64)	1.7*	80	0.57 (0.26–0.73)
Myotis lavali (7)	6 (85.7)	*Basilia travassosi* (21)	85.7 (0.42–0.99)	3.5*	80.7	0.12 (0.00–0.25)
Myotis riparius (1)	1 (100.0)	*Basilia travassosi* (5)	100.0 (0.02–1.00)	5.0*	19.2	0.12 (0.00–0.25)
Phyllostomus discolor (32)	32 (100.0)	*Strebla hertigi* (1)	3.1 (0.00–0.16)□	1.0*	100	0.93 (0.81–0.93)
		Trichobioides perspicillatus (29)	56.3 (0.37–0.73)	1.6*	100	0.42 (0.24–0.57)
		Trichobius costalimai (273)	100.0 (0.89–1.00)	8.5*	99.2	0.00*
		Trichobius joblingi (1)	3.1 (0.00–0.16)•	1.0*	6.6	0.93 (0.81–0.93)
Phyllostomus hastatus (1)	1 (100.0)	*Trichobius longipes* (13)	100.0 (0.02–1.00)	13.0*	100	0.00*
Platyrrhinus lineatus (84)	35(41.6)	*Paratrichobius longicrus* (1)	1.2 (0.00–0.06)□	1.0*	1.1	0.97 (0.92–0.97)
		Trichobius angulatus (95)	42.8 (0.22–0.43)	2.6*	100	0.56 (0.43–0.64)
Sturnira lilium (32)	25 (78.1)	*Aspidoptera falcata* (47)	62.5 (0.43–0.78)	2.3*	100	0.36 (0.18–0.51)
		Megistopoda proxima (20)	31.3 (0.16–0.50)	2.0*	100	0.66 (0.45–0.78)
Total	278	875				

[1] The value in parentheses corresponds to the % of individuals parasitized in relation to the total captured for each species

•Associations considered non-primary

□Despite the low prevalence, the associations were considered natural

*The confidence interval at 95% was zero for all associations

Table 2 Infracommunities of ectoparasites observed in bats captured in the urban green areas of the Grande Aracaju, Sergipe

Infracommunity	Hosts	Occurrence in the host (*N*)
Paratrichobius longicrus + *Trichobius* sp. (complexo *dugesii*)	*Artibeus lituratus*	15
Aspidoptera phyllostomatis + *Megistopoda aranea*	*Artibeus obscurus*	2
Aspidoptera phyllostomatis + *Megistopoda aranea*	*Artibeus planirostris*	10
Speiseria ambigua + *Trichobius joblingi*	*Carollia perspicillata*	1
Trichobioides perspicillatus + *Trichobius costalimai*	*Phyllostomus discolor*	18
Aspidoptera falcata + *Megistopoda proxima*	*Sturnira lilium*	5

of the associations between *A. lituratus* and *Trichobius* sp. (complexo *dugesii*) ($\chi^2 = 4.48$; $p = 0.049$), *Artibeus obscurus* (Schinz, 1821) and *M. aranea* ($\chi^2 = 7.72$; $p = 0.007$), and *Artibeus planirostris* (Spix, 1823) and *M. aranea* ($\chi^2 = 4.03$; $p = 0.049$) in which the highest parasite numbers were obtained from females. The influence of temperature on the prevalence ($F = 5.35$; $p = 0.04$) and mean intensity ($F = 5.02$; $p = 0.04$) of the interaction between *A. lituratus* and *P. longicrus*, showed a decrease in parasitological rates during periods with higher temperatures. For the interaction between

Table 3 Prevalence (*P*; %) and mean intensity (MI) of ectoparasites associated with males and females of *Artibeus lituratus*, *Artibeus planirostris*, and *Carollia perspicillata* in urban green areas of the Grande Aracaju, Sergipe

Hosts	Ectoparasites	Males		Females	
		P (%)	MI	*P* (%)	MI
Artibeus lituratus	*Paratrichobius longicrus*	16.67	1.60	26.57	1.76
	Trichobius sp. (complexo *dugesii*)	12.22*	2.09	25.17*	2.06
Artibeus obscurus	*Megistopoda aranea*	22.22*	1.25	45.00*	1.78
	Aspidoptera phyllostomatis	5.56	1.00	15.00	2.00
Artibeus planirostris	*Megistopoda aranea*	23.08*	1.44	38.89*	2.49
	Aspidoptera phyllostomatis	7.69	2.33	16.67	1.13
Phyllostomus discolor	*Trichobioides perspicillatus*	58.82	1.70	44.44	1.50
	Trichobius costalimai	100.00	7.71	100.00	7.89
Platyrrhinus lineatus	*Trichobius angulatus*	26.32	2.60	39.22	2.85
Sturnira lilium	*Aspidoptera falcata*	88.24	2.33	75.00	2.50
	Megistopoda proxima	23.53	5.25	37.50	2.50

*Association where $p < 0.05$

Platyrrhinus lineatus and *Trichobius angulatus* Wenzel, 1976 ($F = 7.70$; $p = 0.02$), temperature only influenced the prevalence rate, with the same interaction pattern observed between *A. lituratus* and *P. longicrus*. The mean intensity obtained for the interaction between *P. discolor* and *T. costalimai* was influenced by both precipitation ($F = 9.04$; $p = 0.02$) and temperature ($F = 24.58$; $p = 0.002$), indicating that the mean intensity decreased with increasing temperature, and prevalence rate increased with increasing precipitation (Fig. 2).

Discussion

All ectoparasites recorded in this study have been previously reported in the State of Sergipe (Bezerra et al. 2016; Soares et al. 2017; Bezerra and Bocchiglieri 2018; Barbier et al. 2019). The most representative family in this study is Streblidae (97%); this family of ectoparasites is commonly found in association with phyllostomid bats (Graciolli and Aguiar 2002; Prevedello et al. 2005); thus, the high representation of Streblidae in this study may be related to the high capture rate of bats belonging to the Phyllostomidae family. Several species of this family often inhabit disturbed and fragmented habitats and are well-adapted to landscapes dominated by plantations, secondary vegetation, and urban environments (Bertola et al. 2005; Reis et al. 2007; Esbérard et al. 2014; Herr et al. 2015; Nunes et al. 2017). In addition, the plant species used in urban afforestation is a potential food source for these bats (Müller and Reis 1992; Zortéa and Chiarello 1994; Reis et al. 2011), contributing to their occurrence in these types of environments.

The richness of bat flies found in this study ($S = 14$) was lower than that recorded by Bezerra et al. (2016), Soares et al. (2017), Bezerra and Bocchiglieri (2018), and Barbier

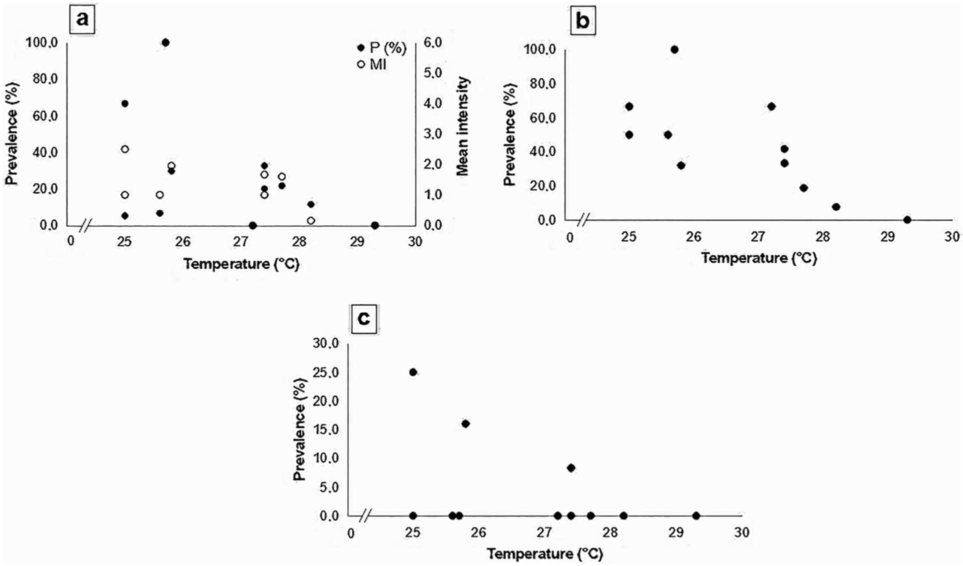

Fig. 2 Relationship between temperature (°C), precipitation (mm), and prevalence rates (%) and mean intensity for interactions between (**a**) *Artibeus lituratus* and *Paratrichobius longicrus*, (**b**) *Platyrrhinus lineatus* and *Trichobius angulatus*, and (**c**) *Phyllostomus discolor* and *Trichobius costalimai* observed in urban green areas of the Grande Aracaju, Sergipe

et al. (2019) whose studies were conducted in the preserved areas of the Atlantic Forest of Sergipe. Compared to urban areas, the richness found in this study was equivalent to that recorded by Urbieta et al. (2018) ($S=14$) in Cerrado and lower than that recorded by Palheta et al. (2020) ($S=21$) in Amazon. These variations in the richness of ectoparasites may be associated with different sampling efforts and the environmental conditions of the areas (Pilosof et al. 2012). Furthermore, Bertola et al. (2005) and Dick and Gettinger (2005) reported that a greater richness of ectoparasites may be directly related to a greater richness of hosts. Thus, the highest richness of ectoparasites recorded by Palheta et al. (2020) might be associated with the greater richness of bats captured at the study site in area of Amazon remnants. Despite the lower sampling effort, the similarity in the richness of ectoparasitic flies in relation to the study conducted by Urbieta et al. (2018) may be associated with the greater abundance of bats recorded in the sampled area, e.g., *Artibeus lituratus*, *Artibeus planirostris*, and *Platyrrhinus lineatus*. This may have allowed for a better sampling of the parasites, since the more bats examined, the greater the chance of associations being recorded.

The most parasitized bats were *A. lituratus*, *A. planirostris*, *P. lineatus*, and *P. discolor*; this may be associated with the high number of captures of these species in the sampled areas. These species have been frequently reported in urban environments, and their occurrence may be related to the availability of food resources (insects attracted by the lighting in urban areas and planting of fruit trees) (Barros et al. 2006; Ferreira et al. 2010; Nunes et al. 2017; Leal et al. 2019). The highest parasite load was found on *P. discolor*, which use more durable and less exposed roosts (caves, tree hollows, and human dwellings), and may present a greater number of ectoparasites, as the increased durability and decreased exposure of their roosts increase the probability of the hosts being present at the time of the parasite outbreak (Ter Hofstede and Fenton 2005; Willig et al. 2007; Reis et al. 2017). Additionally, the most abundant ectoparasites were *T. costalimai* and *M. aranea*; this may be associated with the high abundance of their hosts, *P. discolor* and *Artibeus* spp., respectively. Such associations have also been commonly reported in other studies in different ecoregions (Graciolli and Rui 2001; Bezerra et al. 2016; Hrycyna et al. 2019; Barbier et al. 2021). The species *P. discolor* has a generalist diet, which may favor its occurrence in urban areas (Kwiecinski 2006); whereas species of the genus *Artibeus* are considered opportunistic, with varied feeding habits, and may benefit from fruit plants used in local trees and public roads in Aracaju, accounting for their high occurrence in these environments (Zortéa and Chiarello 1994; Barros et al. 2006; Santos et al. 2015).

Regarding parasitological rates, apart from the interaction between *P. discolor* and *T. costalimai*, other interactions may have overestimated values because of the low number of captured hosts. For the specificity index, only 41.6% of the associations presented a value greater than 90%, indicating low specificity; this was also reported by Santos et al. (2013), Bezerra and Bocchiglieri (2018), and Palheta et al. (2020). The parasitological rates and specificity indices showed variations when compared to other studies (P %$=0.6$ to 100; MI$=1.0$ to 20.0) (Santos et al. 2013; França et al. 2013; Palheta et al. 2020; Biz et al. 2021), including areas of the Atlantic Forest in the State of Sergipe, which may be lower or higher than those previously reported (Bezerra et al. 2016; Soares et al. 2017; Bezerra and Bocchiglieri 2018; Barbier et al. 2019).

Low specificity and may be a result of habitat degradation, where very fragmented areas with low shelter availability can cause multiple species to share a single roost (Cottontail et al. 2009). This could result in an increased contact between different bat species, favoring the transmission of ectoparasites (Cottontail et al. 2009). Overall, the degree of specificity can present great variation (1.0 to 100). This is due to the adaptation processes of the host and the phylogeny of the parasite and host (Balashov 1984), since the presence of the same species of parasite on more than one host species host can occur because of the inheritance of genetic characteristics from the ancestor (Poulin and Rohde 1997). The physical approach of the hosts is necessary for parasitism to occur, and it is believed that most of the parasites are highly specific (Marshall 1982), with high specificity being a frequent feature in the relationship between ectoparasites and bats (Fritz 1983; Giorgi et al. 2004). However, previous studies in urban areas have reported that lower parasite specificity is possible, as the low quality and availability of shelters would favor contact between different bat species and increase the transmission of ectoparasitic flies between them (Barbier and Graciolli 2016; Urbieta et al. 2018). In addition, the non-primary associations can be the result of contamination or occasional infestation, which could have occurred during the capture of the animals or through the sharing of shelters between different host species (Graciolli and Carvalho 2001; Dick 2007; Aguiar and Antonini 2016), thus, may can explain the registered associations considered non-primary 33.3% ($n=8$).

Differences in parasitological rates may also be due to variations in the richness and abundance of the bat community, the biogeographic history of the area, to host size, and roost characteristics (Rui and Graciolli 2005; Hiller et al. 2018). In addition, environmental differences between areas, such as temperature and precipitation, directly affect bat flies (Eriksson et al. 2020), where their rate of development may be favored in places with higher temperatures and lower rainfall (Gray et al. 2009; Pilosof et al. 2012). This can influence the survival of pupae, reducing the abundance of parasites on hosts that use exposed shelters (Dittmar et al. 2009; Pilosof et al. 2012).

Previous studies suggest that a decrease in prevalence rates and average intensities could be due to poor roost quality and availability in urban environments (Urbieta et al. 2018), which would cause bats to have less fidelity to the shelter, making parasite infestation difficult (Barbier and Graciolli 2016; Urbieta et al. 2018). However, some bat species may be favored in places with a higher degree of anthropization (Willig et al. 2007) while other species may be unable to explore the urban matrix, and are therefore restricted to vegetation fragments (Nunes et al. 2017), thus, consequently increasing their local density (Medellín et al. 2000; Willig et al. 2007). Therefore, an increase in density promotes greater aggregation of individuals, facilitating the transmission of flies and resulting in greater infestation (Pilosof et al. 2012).

Regarding the discrepancy index, most interactions (> 60%) presented high aggregation values, corroborating the findings of Barbier and Graciolli (2016) and Barbier et al. (2019). These high values indicate a disproportionate distribution of parasites on the hosts, where most of the parasites occur in groups and are found in a minority of hosts, i.e., most hosts are parasitized by a few parasites, and only a few hosts are parasitized by many parasites. This form of distribution is known as an aggregate (Dajoz 2005; Barbier and Graciolli 2016; Barbier et al. 2019).

All infracommunities identified and the associations found in this study have been previously recorded (Bezerra et al. 2016; Dornelles and Graciolli 2017; Bezerra and Bocchiglieri 2018), and were all composed of parasite species of different genera. Infracommunities can be molded by limiting the similarity or environmental filtering (Ingram and Shurin 2009; Krasnov et al. 2014). Limiting similarity is characterized by the association of unrelated parasites that reduce competition among themselves because there is less niche overlap. This allows a few species to adapt and exploit a single host, which could result in associations between different species of the same genus that share ecological and adaptive characteristics (Ingram and Shurin 2009; Krasnov et al. 2014). Thus, the infracommunities observed in this study may be shaped by the limiting similarity. In addition, some studies have demonstrated that ectoparasites exhibit spatial segregation on the host body, where different parasite species show preferences for certain parts of the host, facilitating the coexistence of different species (Bittencourt and Rocha 2002; Almeida et al. 2015).

Regarding the influence of host sex on parasitism, the higher prevalence rates in females found in this study corroborated the findings of Bertola et al. (2005) and Bezerra and Bocchiglieri (2018), who found higher rates of parasitism in females of *Sturnira lilium* (E. Geoffroy, 1810), *Carollia perspicillata* (Linnaeus, 1758), and *A. lituratus*. The greater parasitism in some females may be related to them staying longer in the shelter, owing to their more gregarious behavior during the reproductive stage and the care of their offspring. Additionally, during reproduction, females may become less active and reduce their grooming intensity, which is one of the main causes of parasite mortality (Marshall 1982; Komeno and Linhares 1999; Schaik and Kerth 2017).

In this study, for some interactions, the opposite of what was expected was observed; specifically, a decrease in prevalence rates and average intensity with increasing temperature, and an increase in average intensity with increasing precipitation. This result may be associated with low-temperature range (24.7 to 29.3 °C) and precipitation (8.2 to 274 mm) in the region during the period of this study. In addition, the influence of seasonality may be related to the behavior of each species; this may harm the survival of some species and favor the development of others (Pilosof et al. 2012; Zarazúa-Carbajal et al. 2016). According to Marshall (1982), the temperature can directly affect the reproductive rate of some parasites, in addition to copulation, oviposition, egg survival, and adult longevity. Considering the importance of parasitism in the control and maintenance of the host community, analyzing the influence of host characteristics on the abundance and distribution of ectoparasites is important to provide information on the aspects that shape this interaction. Thus, this study provides relevant data on this interaction, especially for urban areas in northeastern Brazil, increasing the number of studies in Sergipe and promoting future studies.

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Author contribution R.H.S.B.: methodology, validation, formal analysis, investigation, writing—original draft. A.B.: conceptualization, methodology, formal analysis, resources, writing—review and editing, supervision.

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Declarations

Competing interests The authors declare no competing interests.

Ethics approval The animals were captured, tagged, and when necessary collected, with permission granted by the Biodiversity Information and Authorization System/ICMBio (SISBIO # 71378–1 and 71378–5).

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