RESEARCH ARTICLE

Host-parasite associations in a population of the nectarivorous bat *Anoura geoffroyi* (Phyllostomidae) in a cave in a Brazilian ferruginous geosystem

Luísa Lauren Lima Vidal[1], Leopoldo Ferreira Oliveira Bernardi[2], Sonia Aparecida Talamoni[1]

1 *Programa de Pós-graduação em Biologia de Vertebrados, Departamento de Ciências Biológicas, Pontifícia Universidade Católica de Minas Gerais, Avenida Dom José Gaspar, 500, 30535-610, Belo Horizonte/MG, Brazil* **2** *Departamento de Entomologia, Universidade Federal de Lavras, Lavras/MG, Brazil*

Corresponding author: Sonia Aparecida Talamoni (talamoni@pucminas.br)

Abstract

Parasitic relationships between Neotropical bats and their ectoparasites are not well known, even though parasitism is one of the factors that can affect the fitness of a host population. This study characterized parasite-host relationships in relation to sex, age, body size and reproductive status in a population of *Anoura geoffroyi* using the indices of Prevalence, Mean Intensity and Mean Abundance. Total prevalence for 93 sampled bats was 94.6%. Two species of streblid flies that are considered primary parasites of *A. geoffroyi*, *Exastinion clovisi* (n = 203) and *Anastrebla modestini* (n = 152), were the most abundant ectoparasites, followed by *Trichobius* sp. (n = 7). Two mite species, *Periglischrus vargasi* (Spinturnicidae) (n = 98) and *Spelaeorhynchus praecursor* (Spelaeorhynchidae) (n = 11), were also found. We recorded higher mean abundance and intensity of parasitism in pregnant females compared to reproductive males and reproductively inactive females, for different specific associations of ectoparasites. Host age and body condition had no effect on the parasitological indices. Even with high rates of parasitism, parasitic load did not influence host body condition, but infestation rates by mites were higher in reproductive males and higher by flies in reproductive females, showing that ectoparasites can have variable influences between the different stages of the life history of these host bats. Thus, the reproductive activity of the hosts could be an adverse factor for resistance to parasite infestations.

Introduction

Ectoparasitism can have a strong influence on host populations (Brown and Brown 2004; Møller and Saino 2004). Its diversity is directly influenced by several factors such as geographic distribution, roost environment and by host biology, morphology and behavior (Rui and Graciolli 2005; Postawa and Nagy 2016). Pressures resulting from parasitism can increase the rate of predation on hosts, weaken host physical condition, and increase disease incidence, which can result in decreases in survival and reproduction (Neuhaus 2003; Brown and Brown 2004; Ter Hofstede and Fenton 2005). Ectoparasites may have more significant influence on bat populations, as most bats are gregarious, that can form colonies of thousands of individuals and often roost in places with limited space, such as caves (Bredt et al. 1999; Lourenço and Palmeirim 2007, 2008; Guimarães and Ferreira 2014), which is the case for *Anoura geoffroyi* Gray, 1838 (Guimarães and Ferreira 2014; Farias et al. 2018; Reis 2018).

Anoura geoffroyi (Chiroptera: Phyllostomidae) is a nectarivorous bat (13–18 g) (Koopman 1994; Reid 1997) with a wide geographic distribution in the Neotropical region, from Mexico to Peru, Bolivia, and Brazil (Simmons 2005). The species has a strong association with natural cavities and preferably uses caves as diurnal roosts (Arita 1993; Guimarães and Ferreira 2014), where colonies of hundreds of individuals can form (Bredt et al. 1999; Farias et al. 2018; Reis 2018). The species presents seasonal population dynamics with a monoestrous reproductive pattern and reproductive activity occurring during the rainy season (Zortéa 2003; Farias et al. 2018).

Among the species of ectoparasites found on bats dipterans and mites are the most common. Dipterans of the family Streblidae are obligatory blood-sucking ectoparasites of bats, they are viviparous and have three larval stages that develop in the female's uterus, the pupa that develops in the host's roost and the adult, which is the hematophagous ectoparasite (Dick and Patterson 2006). Likewise, mites of the family Spinturnicidae are exclusive parasites of bats and complete their entire life cycle on the host's body. The dispersion of these mites requires direct contact between hosts, which is facilitated by the social behaviors of bats, such as copulation, birthing of young, parental care and the habit of living in groups. They are commonly found on the patagium of the host (Rudnick 1960; Lourenço and Palmeirin 2007; Almeida et al. 2015). In temperate region, it was observed that sex, age, and reproductive status of the host strongly influences the reproductive activity of parasites, and, according to the authors, reproduction of ectoparasites of many temperate cave-dwelling bats is mostly regulated by the reproductive cycle of their bat hosts (Lourenço and Palmeirim 2008).

Studies related to different aspects of the association between ectoparasites and bats in the Neotropical region are still scarce. Thus, there is a knowledge gap about parasitological relationships resulting from the numerous factors that influence ectoparasitism in bats such as sex, age and reproductive status of the host, among others (Rui and

Graciolli 2005; Patterson et al. 2007; Patterson et al. 2008; Postawa and Nagy 2016). The present study aimed to understand the ecological aspects involved in the interaction between ectoparasites and the phyllostomid bat *A. geoffroyi* in a colony that uses a ferruginous cave as a diurnal roost and has been present at the site for many years. The effects of bat sex, age, reproductive status, and body condition on the rate of ectoparasite infestation were investigated. Considering that the species exhibits seasonal monoestric reproductive activity during the rainy season, we hypothesize here that ectoparasites may have variable influences between the different stages of the hosts' life history, as well as in relation to their body condition.

Methods

Study area

The studied colony of *A. geoffroyi* lives in the ferruginous cave named Piedade (19°49'20"S, 43°40'33"W, 1,414 m altitude). The colony is formed by groups of varying sizes (5 to 20 individuals). Maximum abundance is observed in the reproductive period with a few hundred of individuals (Farias et al. 2018). The cave is situated in Serra da Piedade, located in Monumento Natural Estadual Serra da Piedade (state park), state of Minas Gerais, Brazil, and has a horizontal projection of about 360 m (Pereira et al. 2012). Serra da Piedade is situated in the Quadrilátero Ferrífero ferruginous geosystem (Bueno 1992), which harbors the largest iron ore reserve in Brazil (Souza and Carmo 2015). At present, there are 46 open pit mines reported from the region, which may pose a threat to local fauna and flora (Souza and Carmo 2015). The vegetation in the region varies with altitude, with semi-deciduous forest in the lower parts and altitudinal fields or rupestrian field at higher altitudes (Bueno 1992). The climate of the region is subtropical of altitude (Cwa), according to the Köppen classification. There are two well defined seasons with a rainy season from October to March (corresponding to spring-summer months) and a dry season from April to September (corresponding to the autumn-winter months) (Bueno 1992).

Data collection

Diurnal campaigns to the roost of *A. geoffroyi* (cave environment) were carried out on September 9, 2017; January 24, 2018; and September 18, 2018 to capture bats and collect ectoparasites. Bats were captured with a mist-net (12 × 3 m) installed inside the cave about 50 m from the colony, from 8:00 h to 14:00 h, which was checked every 20 minutes. To minimize the disturbance of the colony, the researchers remained outside waiting for the capture of bats in flight. With at least three openings inaccessible, the placement of mist nets outside the cave was not possible. The use of a pole net was also not possible due to the great height of the cave. Due to the difficulties imposed by local conditions, diurnal collections were used, which proved to be viable following the protocol of Farias et al. (2018). Information related to sex, age, body mass (grams), forearm

length (millimeters) and reproductive status was obtained for each captured animal. Bats were released without marking, shortly after the collection of ectoparasites and biometric data. The degree of ossification of the metacarpal epiphyses was evaluated to determine age (Anthony 1988). Reproductive status was analyzed by observing secondary reproductive characteristics (Farias et al. 2018). Inactive males had poorly developed testes, while active males presented fully developed scrotal testes. Pregnant or lactating females were considered reproductively active, while others were considered inactive.

Ectoparasites were collected by inspecting the pelage of the bats with the naked eye and using fine-tipped forceps to transfer them to individual containers (containing 70% ethanol) for each bat (Graciolli and Carvalho 2001). The ectoparasites were prepared as described in DeBlase and Martin (1980). Samples of each ectoparasite species were chosen under a stereomicroscope, and then these samples were placed on a microscope slide and cleared in Hertwig's solution (chloral hydrate). This solution is a clearing agent for microscopic examination and is commonly used in the diet analysis of small mammals (DeBlase and Martin 1980; Talamoni et al. 2008). After this process, the ectoparasites were mounted on a slide in a drop of glycerin and covered by a coverslip. Dipterans and mites were then identified under an optical microscope (10×), using dichotomous keys (Graciolli and Carvalho 2001; Herrin and Tipton 1975; Wenzel et al. 1976; Peracchi 1990).

Parasitological indices were calculated to analyze the infestation in the population and the association with each parasite, except for the species *Spelaeorhynchus praecursor* Neuman, 1902 (Spelaeorhynchidae), which was poorly sampled in the present study. Prevalence (P; number of infested hosts/number of hosts examined × 100) expressed as a percentage, Mean Intensity (MI; number of parasites/number of infested hosts) and Mean Abundance (MA; number of parasites/total number of hosts examined) were calculated (Bush et al. 1997). The influence that host sex, age (adult, non-adult) and reproductive status have on the parasitological indexes was investigated. All young and sub-adult animals of both sexes were included in the non-adult class, being differentiated by the presence of cartilaginous epiphyses and all being sexually immature (Farias et al. 2018). Mean intensities and mean abundances were compared by Student's *t*-test with randomization and 2000 replicates. The influence of host biological parameters on prevalence was evaluated by Fisher's exact test. Analyses were performed using Quantitative Parasitology 3.0 software (Rózsa et al. 2000). The Body Condition Index (BCI) (body mass/forearm length; Reichard and Kunz 2009) was used to investigate the relationship between host body condition and parasitic load through Spearman correlation tests. All tests were run using Bioestat 5.3 software (Ayres et al. 2007) with a significance level of 5%.

Results

A total of 93 bats were captured, 88 of which were infested, resulting in a prevalence rate of 94.6% (0.8–1.0, CI 95%). The total of 471 ectoparasites collected included flies of three species of the family Streblidae – *Anastrebla modestini* Wenzel, 1966
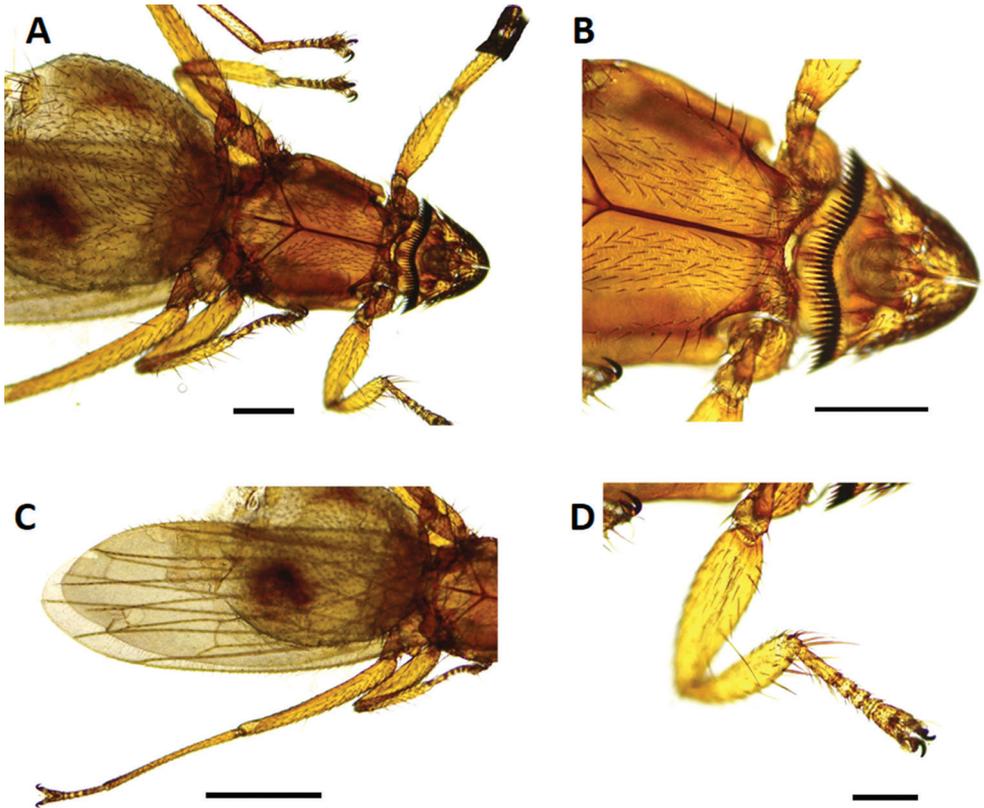
Figure 1. A ventral view of *Anastrebla modestini*, 40× magnification **B** detail of head, 100× **C** detail of wing and leg, 100× **D** detail of femur and setae, 100×. Leica DM500 optical microscope. Scale bars: 0.5 mm (**A–D**).

(n = 152, Fig. 1), *Exastinion clovisi* (Pessoa & Guimarães, 1936) (n = 203, Fig. 2) and *Trichobius* sp. (n = 7, Fig. 3). Specimens of two species of mites were also collected – *Periglischrus vargasi* Hoffmann, 1944 (Spinturnicidae, n = 98, Fig. 4) and *S. praecursor* (n = 11, Fig. 5). Mean Intensity (MI) was 5.35 (± 3.47) ectoparasites per host while Mean Abundance (MA) was 5.06 (± 3.58) ectoparasites per host.

Infestation analysis for all ectoparasites (Table 1) revealed that host sex did not affect P (p = 1.00), MA (t = 1.14; p = 0.24) or MI (t = 1.31; p = 0.18). Reproductively active and inactive males showed no differences in the indexes (P: p = 1.0; MI: t = -1.31, p = 0.21; MA: t = -1.52, p = 0.16), as was also the case for pregnant and inactive females (P: p = 0.55; MI: t = 0.30, p = 0.75; MA: t = 0.83, p = 0.39). On the other hand, pregnant females had higher MA than reproductively active males (t = 2.12, p = 0.03) (Table 1).

For the specific association between *A. geoffroyi* and *E. clovisi* (Table 2), female hosts had higher MA (t = 2.31, p = 0.02) than did male hosts, while for the association between *A. geoffroyi* and *A. modestini* (Table 2), pregnant females had higher P (p = 0.02) and higher MA (t = 2.87, p = 0.006) than did inactive females. Pregnant
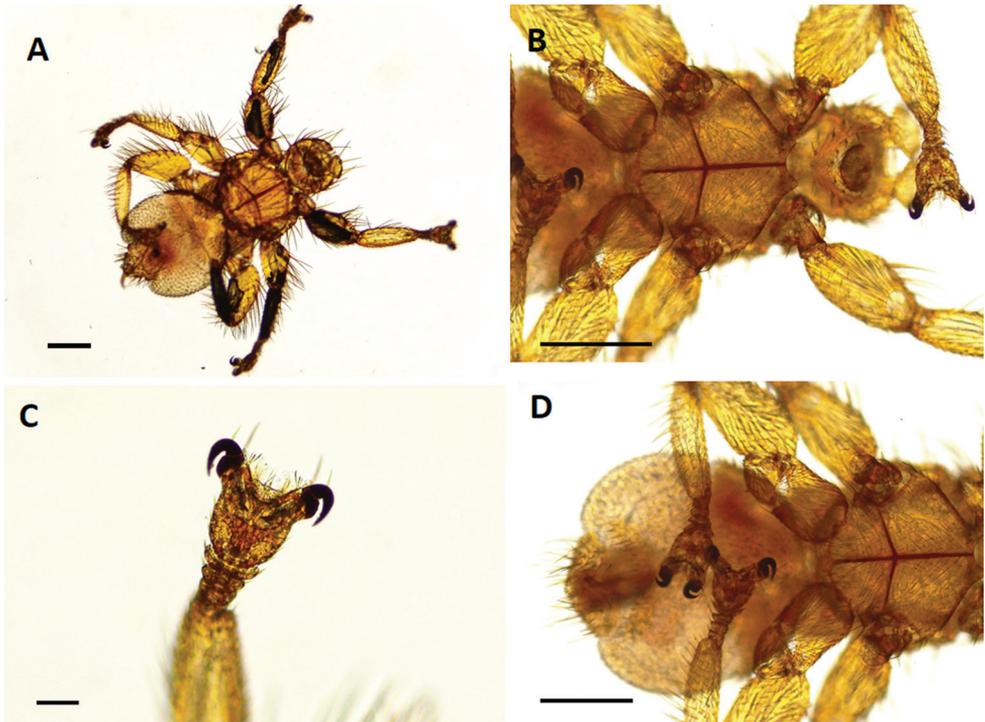
Figure 2. A dorsal view of *Exastinion clovisi*, 40× magnification **B** detail of thorax, 100× **C** distal detail of the leg, 100× **D** detail of abdomen, 100×. Leica DM500 optical microscope. Scale bars: 0.5 mm (**A, B, D**); 0.1 mm (**C**).
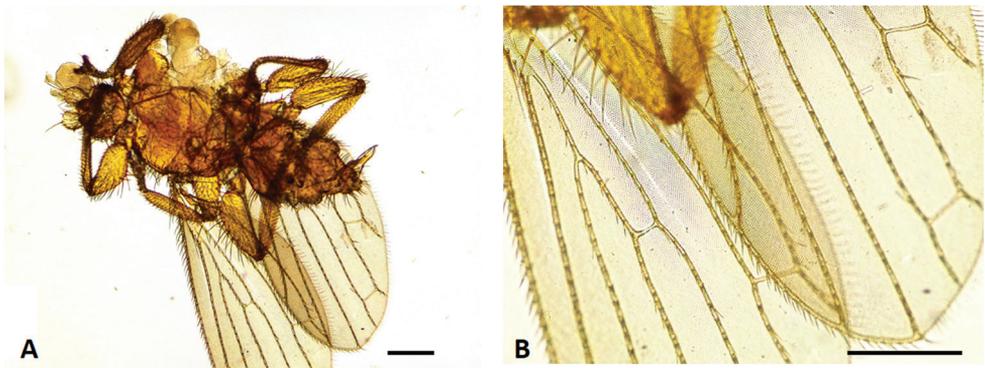

Figure 3. A dorsal view of *Trichobius* sp., 40× magnification **B** detail of wing, 100×. Leica DM500 optical microscope. Scale bars: 0.5 mm (**A, B**).

females were also more parasitized than reproductive active males, with significant differences in P (p = 0.005), MA (t = 3.32, p = 0.006) and MI (t = 1.99, p = 0.04). For the association between *A. geoffroyi* and the mite *P. vargasi* (Table 2), MA and MI were
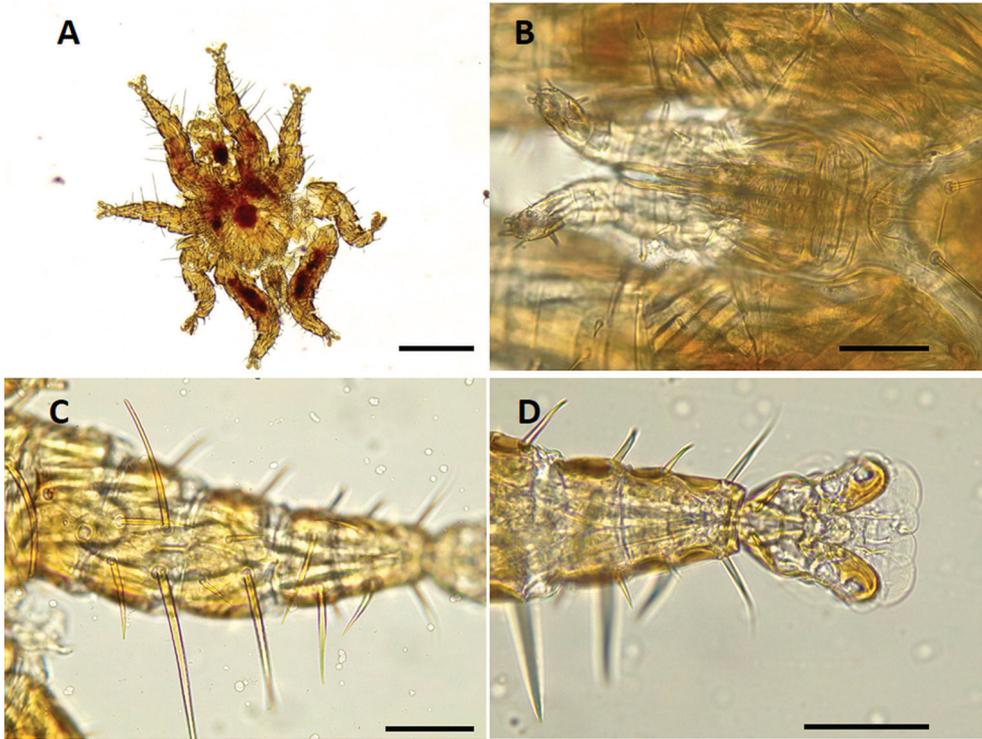
Figure 4. A specimen of *Periglischrus vargasi*, 40× magnification **B** detail of gnatossome, 400× **C** detail of setae insertion in the leg, 400× **D** distal detail of the leg, 400×. Leica DM500 optical microscope. Scale bars: 0.5 mm (**A**); 0.1 mm (**B–D**).

Table 1. Number of hosts examined (N), infected (in parentheses), Prevalence (P), Mean Intensity (MI) and Mean Abundance (MA), with Confidence Intervals (CI 95%), for ectoparasites of *Anoura geoffroyi* in Piedade cave, located in Serra da Piedade, state of Minas Gerais. Inactive males had poorly developed testes and inactive females were those who did not show evidence of pregnancy and lactation. * = Significant differences.

Host		N	P (%) (CI 95%)	MI (CI 95%)	MA (CI 95%)
Sex	Female	50 (47)	94.0 (0.8–0.9)	5.8 (4.8–6.8)	5.4 (4.4–6.4)
	Male	43 (41)	95.3 (0.8–0.9)	4.8 (3.8–6.0)	4.6 (3.6–5.7)
Reproductive status	Reproductive male	32 (30)	93.8 (0.7–0.9)	4.2 (3.3–5.4)	4.0 (3.0–5.0)*
	Inactive male	11 (11)	100 (0.7–1.0)	6.3 (3.9–9.3)	6.3 (3.9–9.3)
	Pregnant female	18 (18)	100 (0.8–1.0)	6.0 (4.5–7.5)	6.0 (4.5–7.5)*
	Inactive female	32 (29)	90.6 (0.7–0.9)	5.6 (4.5–6.9)	5.1 (3.9–6.4)
Age	Adult	52 (51)	98.1 (0.8–0.9)	5.1 (4.3–6.0)	5.0 (4.2–5.9)
	Non-adult	41 (37)	90.2 (0.7–0.9)	5.6 (4.5–6.9)	5.0 (3.9–6.4)

higher for pregnant females compared to inactive females (MA: t = -2.79, p = 0.009; MI t = – 2.93, p = 0.01), while reproductively active males were more parasitized than pregnant females with respect to MA and MI (MA: t = -2.34, p = 0.02; MI: t = -3.17, p = 0.01) (Table 2).
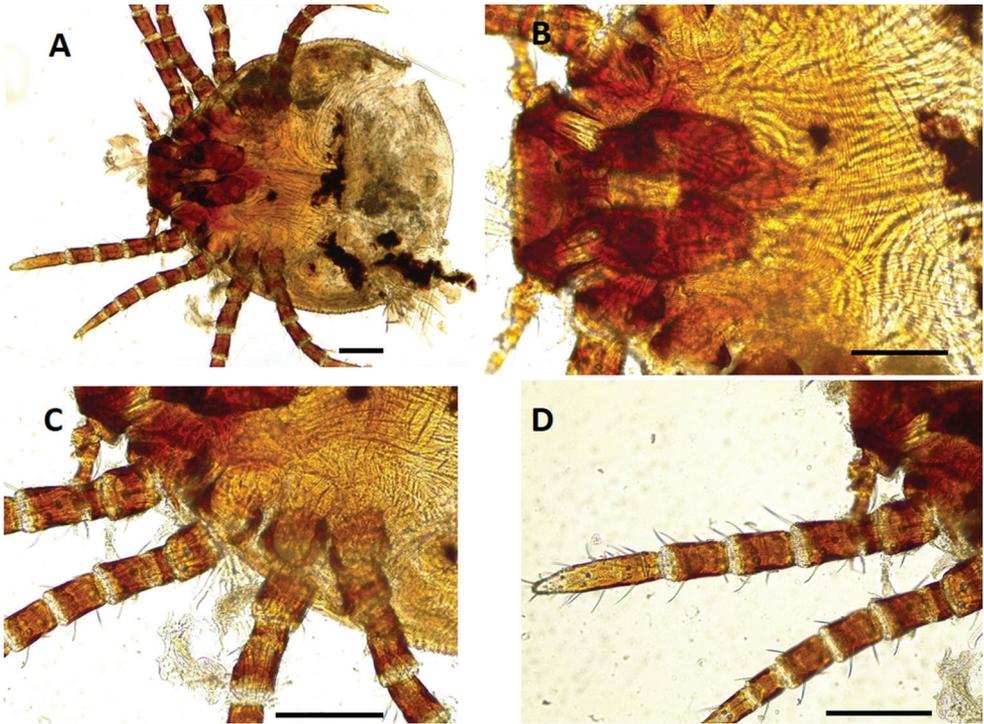
Figure 5. A specimen of *Spelaeorhynchus praecursor*, 40× magnification **B** detail of gnatossome, 100× **C** detail of legs, 100× **D** detail of leg and setae, 100×. Leica DM500 optical microscope. Scale bars: 0.5 mm (**A–D**).

Analyses found no correlation between host BCI and parasitic load for males in general (r_s = -0.05; n = 43; p = 0.70); for reproductively active males (r_s = -0.05; n = 32; p = 0.75); for inactive males (r_s = 0.19; n = 11; p = 0.75); for females in general (r_s = 0.002; n = 50; p = 0.98); for pregnant females (r_s = 0.17; n = 18; p = 0.740); for inactive females (r_s = -0.26; n = 32; p = 0.14); for adults (r_s = 0.13; n = 52; p = 0.33) and for non-adults (r_s = -0.21; n = 41; p = 0.17).

Discussion

The present study registered two common species of parasitic flies belonging to the family Streblidae, *A. modestini* and *E. clovisi*, both having already been registered as primary parasites of *A. geoffroyi* (Wenzel et al. 1976). Both species are widely distributed in the Neotropical region, as are their hosts (Komeno and Linhares 1999; Graciolli and Rui 2001; Bertola et al. 2005; Simmons 2005; Moras et al. 2013; Dornelles and Graciolli 2017; Trujillo-Pahua and Ibáñez-Bernal 2018). *Trichobius* spp. was not abundant in the present study, although some species of the genus have been previously registered on *A. geoffroyi*, such as *Trichobius tiptoni* (Graciolli and Rui 2001) and *T. propinquus* (De Vasconcelos et al. 2015), or *Trichobius* sp. (*dugesii* complex) (Reis 2018).

Table 2. Number of hosts examined (N), infected (in parentheses), Prevalence (P), Mean Intensity (MI) and Mean Abundance (MA), with Confidence Intervals (95% CI), for specific interactions of *Exastinion clovisi*, *Anastrebla modestini* and *Periglischrus vargasi* with *Anoura geoffroyi* in Piedade cave, located in Serra da Piedade, state of Minas Gerais. Inactive males had poorly developed testes and inactive females were those who did not show evidence of pregnancy and lactation. * = Significant differences.

Host-parasite relationship		N	P (%) (CI 95%)	MI (CI 95%)	MA (CI 95%)
Exastinion clovisi					
Sex	Female	50 (40)	80.0 (0.6–0.8)	3.3 (2.7–4.1)	2.6 (2.0–3.4)*
	Male	43 (27)	62.0 (0.4–0.7)	2.5 (2.0–3.2)	1.6 (1.1–2.1)*
Reproductive status	Reproductive male	32 (18)	56.3 (0.3–0.7)	2.5 (1.9–3.1)	1.4 (0.9–2.0)
	Inactive male	11 (9)	81.8 (0.4–0.7)	2.6 (1.6–4.1)	2.1 (1.0–3.5)
	Pregnant female	18 (15)	83.3 (0.5–0.9)	2.9 (2.0–3.9)	2.4 (1.6–3.3)
	Inactive female	32 (25)	78.1 (0.6–0.9)	3.5 (2.6–4.6)	2.7 (1.9–3.7)
Age	Adult	52 (39)	75.0 (0.6–0.8)	2.9 (2.3–3.5)	2.1 (1.6–2.7)
	Non-adult	41 (28)	68.3 (0.5–0.8)	3.2 (2.4–4.1)	2.2 (1.5–3.0)
Anastrebla modestini					
Sex	Female	50 (33)	66.0 (0.5–0.7)	2.73 (2.1–3.4)	1.80 (1.2–2.4)
	Male	43 (26)	60.5 (0.4–0.7)	2.38 (1.6–3.8)	1.44 (0.9–2.4)
Reproductive status	Reproductive male	32 (18)	56.3 (0.3–0.7)*	1.89 (1.3–2.5)*	1.06 (0.6–1.5)*
	Inactive male	11 (8)	72.7 (0.3–0.9)	3.50 (1.5–7.5)	2.55 (1.0–6.0)
	Pregnant female	18 (17)	94.4 (0.7–0.9)*	3.06 (2.1–4.0)*	2.89 (2.0–3.7)*
	Inactive female	32 (16)	50.0 (0.3–0.6)*	2.38 (1.6–3.6)	1.19 (0.6–1.9)*
Age	Adult	32 (16)	67.3 (0.5–0.7)	2.60 (2.0–3.1)	1.75 (1.2–2.3)
	Non-adult	11 (8)	58.5 (0.4–0.7)	2.54 (1.7–4.0)	1.49 (0.9–2.5)
Periglischrus vargasi					
Sex	Female	50 (24)	48.0 (0.3–0.6)	1.7 (1.3–2.0)	0.84 (0.5–1.1)
	Male	43 (22)	51.2 (0.3–0.6)	2.5 (1.8–3.3)	1.30 (0.8–1.9)
Reproductive status	Reproductive male	32 (14)	43.8 (0.2–0.6)	2.7 (2.0–3.7)*	1.22 (0.6–1.9)*
	Inactive male	11 (8)	72.7 (0.3–0.9)	2.1 (1.2–3.6)	1.5 (0.7–2.8)
	Pregnant female	18 (6)	33.3 (0.1–0.5)	1.1 (1.0–1.3)*	0.3 (0.1–0.6)*
	Inactive female	32 (18)	56.3 (0.3–0.7)	1.9 (1.5–2.2)*	1.0 (0.7–1.5)*
Age	Adult	52 (24)	46.2 (0.3–0.6)	1.9 (1.5–2.5)	0.9 (0.6–1.2)
	Non-adult	41 (22)	53.7 (0.3–0.6)	2.3 (1.7–3.0)	1.2 (0.7–1.7)

The mites *P. vargasi* and *S. praecursor* have reduced host specificity, commonly occurring on several Neotropical bat species (Herrin and Tipton 1975; Moras et al. 2013; Almeida et al. 2015). The present study found *S. praecursor* specimens to strongly attach to the tragus of the host, a behavior that has been regularly recorded for this species (Fain et al. 1967; Peracchi 1990).

Our data showed a high prevalence rate of most parasites. A study with *Artibeus lituratus* and *Sturnira lilium*, frugivorous phyllostomid bats that commonly roost in treetops and/or human buildings, found much lower prevalence rates, with 3.4% and 9.1% prevalences, respectively (Dornelles and Graciolli 2017). Environmental factors and host behavior can influence prevalence rates, while type of diurnal roost occupied by the host is one of the factors that indirectly influences prevalence rates (Kunz 1982; Ter Hofstede and Fenton 2005). A host habit of changing roosts can disrupt the life cycle of ectoparasitic flies, which spend part of their life cycle inside the roosts, while such movements would not affect mites, because they spend their entire life cycle on the host's body (Kunz 1982; Lewis 1995).

The studied bat population has used Piedade cave as a diurnal roost for at least a decade and the species is known to prefer caves (Guimarães and Ferreira 2014). Caves

represent favorable diurnal roosts for many bats, as they provide a stable microclimate and protection against predators and adverse weather (Kunz 1982; Lewis 1995). Because such roosts are confined spaces, the very habit of living in a group facilitates body contact and the host-switching activity of ectoparasites. Therefore, it is plausible to hypothesize the existence of an association between the high prevalence rate recorded in the present study (94.6%) and the type of shelter (cave) used, although further investigation is needed.

The present study registered an influence of host sex on the Mean Abundance in the association between *E. clovisi* and female hosts. Higher infestation levels for females have been frequently reported in the literature (Christie et al. 2007; Patterson et al. 2008; Presley and Willig 2008). By adding the reproductive status of females to the analysis, the results were able to reveal that pregnant females were more parasitized by flies than were non-pregnant females and males. Similar results were found by Reis (2018) in a study conducted in another cave inhabited by *A. geoffroyi*. The greater fly parasitism of pregnant females is consistent with observations for other bat species such as *A. lituratus* (Bertola et al. 2005), *Megaderma lyra* (Sundari et al. 2005), *Miniopterus schreibersii* (Lourenço and Palmeirim 2008), and *Cynopterus brachyotis* (Lee et al. 2018).

The Lourenço and Palmeirim (2008) study in temperate zone showed that four parasite species had a similar reproductive pattern, reproducing more intensively during the pregnancy and nursing seasons of *M. schreibersii*, mainly on pregnant and juvenile bats. The authors concluded that this may be an adaptive trait in which the reproductive cycles of the parasite species are adjusted to the cycles of their hosts in a seasonal environment. This hypothesis could explain our results and those of other studies with similar results. Further studies focusing on the synchrony of the reproductive cycles of ectoparasites and their hosts, in other regions with marked seasonality, may bring new clarifications about this relationship.

Thus, especially for pregnant female, a lower immunological defense during the reproductive phase, due to endocrine changes inherent to reproduction (Grossman 1985; Christie et al. 2000) can facilitate their greater infestation during a period of greater reproductive activity of their ectoparasites (Lourenço and Palmeirim 2008). Reproductively active males, on the other hand, were more parasitized by *P. vargasi*, than were pregnant females. *Anoura geoffroyi* males exhibit polygyny and the mating season is relatively short (3 months) (Farias et al. 2018). The energy expenditure directed by these animals for mating in a short period may lead to a more debilitated health condition, facilitating the infestation by mites. Thus, the reproductive activity of the hosts could be an adverse factor for resistance to parasite infestations (Christie et al. 2000), even though it does not affect their body condition. However, other factors acting together can contribute to this result (Lourenço and Palmeirim 2008), needing to be tested.

Even with high parasitism rates, the data of the present study demonstrated that parasite load did not influence host BCI. Although BCI is commonly used in studies involving parasites, it has also presented contradictory results in different studies about it being correlated or not with parasite load (Marshall 1982; Christe et al. 2000; Lučan 2006; Lourenco and Palmeirim 2007; Pearce and O´Shea 2007; Lee et al.

2018). According to Postawa and Nagy (2016), even if ectoparasite density varies, the health of the host is unlikely to be affected, as ectoparasites feed mainly on host lymph and blood and do not directly consume other resources such as fatty acids, so there is no direct impact on BCI.

Acknowledgements

References

Almeida J, Serra-Freire NM, Peracchi AL (2015) Anatomical location of *Periglischrus iheringi* (Acari: Spinturnicidae) associated with the great fruit-eating bat (Chiroptera: Phyllostomidae). Revista Brasileira de Parasitologia Veterinaria 24: 361–364. https://doi.org/10.1590/S1984-29612015022

Almeida JC, Martins MA, Guedes PG, Peracchi AL, Serra-Freire NM (2016) New records of mites (Acari: Spinturnicidae) associated with bats (Mammalia, Chiroptera) in two Brazilian biomes: Pantanal and Caatinga. Brazilian Journal of Veterinary Parasitology 25: 18–23. https://doi.org/10.1590/S1984-29612016005

Anthony ELP (1988) Age determination in bats. In: Kunz TH (Ed.) Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, 47–57.

Arita HT (1993) Conservation Biology of the Cave Bats of Mexico. Journal of Mammalogy 74: 693–702. https://doi.org/10.2307/1382291

Ayres M, Júnior Aires M, Ayres DL, Santos ADAS (2007) BioEstat 5.0: aplicações estatísticas nas áreas das ciências biológicas e médicas, 364–364.

Bertola PB, Aires CC, Favorito SE, Graciolli G, Amaku M, Pinto-Da-Rocha R (2005) Bat flies (Diptera: Streblidae, Nycteribiidae) parasitic on bats (Mammalia: Chiroptera) at Parque Estadual da Cantareira, São Paulo, Brazil: Parasitism rates and host-parasite associations. Memórias do Instituto Oswaldo Cruz 100: 25–32. https://doi.org/10.1590/S0074-02762005000100005

Bredt A, Uieda W, Magalhães ED (1999) Morcegos cavernícolas da região do Distrito Federal, centro-oeste do Brasil (Mammalia, Chiroptera). Revista Brasileira de Zoologia 16: 731–770. https://doi.org/10.1590/S0101-81751999000300012

Brown CR, Brown MB (2004) Group size and ectoparasitism affect daily survival probability in a colonial bird. Behavioral Ecology and Sociobiology 56: 498–511. https://doi.org/10.1007/s00265-004-0813-6

Bueno MET (1992) Geografia da Serra da Piedade. In: Duarte RH (Org.) Serra da Piedade. CEMIG, Belo Horizonte, 136 pp.

Bush AO, Lafferty KD, Lotz JF, Shostak AW (1997) Parasitology meets Ecology on it own terms: Margolis et al. revisited. The Journal of Parasitology 83(4): 575–583. https://doi.org/10.2307/3284227

Christe P, Glaizot O, Evanno G, Bruyndonckx N, Devevey G, Yannic G, Patthey P, Maeder A, Vogel P, Arlettaz R (2007) Host sex and ectoparasites choice: preference for, and higher survival on female hosts. Journal of Animal Ecology 76: 703–710. https://doi.org/10.1111/j.1365-2656.2007.01255.x

Christe P, Giorgi MS, Vogel P, Arlettaz R (2003) Differential species-specific ectoparasitic mite intensities in two intimately coexisting sibling bat species: resource-mediated host attractiveness or parasite specialization? Journal of Animal Ecology 72(5): 866–872. https://doi.org/10.1046/j.1365-2656.2003.00759.x

Christie P, Arlettaz R, Vogel P (2000) Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). Ecology Letters 3: 207–212. https://doi.org/10.1046/j.1461-0248.2000.00142.x

DeBlase AF, Martin RE (1980) A Manual of Mammalogy With Keys to Families of the World. Dubuque, IA, Wm. C. Brown Company Publishers.

De Vasconcelos PF, Falcão LAD, Graciolli G, Borges MAZ (2015) Parasite-host interactions of bat flies (Diptera: Hippoboscoidea) in Brazilian tropical dry forests. Parasitology Research 115: 367–377. https://doi.org/10.1007/s00436-015-4757-8

Dick CW, Patterson BD (2006) Bat flies: Obligate ectoparasites of bats. Micromammals and Macroparasites: From Evolutionary Ecology to Management: 179–194. https://doi.org/10.1007/978-4-431-36025-4_11

Dornelles GDP, Graciolli G (2017) Streblid bat flies on Phyllostomid bats from an Island off the coast of São Paulo, Brazil. Papéis Avulsos de Zoologia 57: 31–36. https://doi.org/10.11606/0031-1049.2017.57.04

Fain A, Anastos G, Camin J, Johnston D (1967) Notes on the genus *Spelaeorhynchus* description of *S. praecursor* Neumann and of two new species. Acarologia 9(3): 535–556.

Farias TO, Talamoni SA, Godinho HP (2018) Reproductive Dynamics of the Nectarivorous Geoffroy's Tailless Bat *Anoura geoffroyi* (Glossophaginae) in a Highland Neotropical Area of Brazil, with Evidence of a Mating Period. Acta Chiropterologica 20: 251–261. https://doi.org/10.3161/15081109ACC2018.20.1.019

Graciolli G, Rui AM (2001) Streblidae (Diptera, Hippoboscoidea) on bats (Chiroptera, Phyllostomidae) in the Northeast of Rio Grande do Sul, Brazil. Iheringia – Serie Zoologia s/v: 85–92. https://doi.org/10.1590/S0073-47212001000100009

Grossman CJ (1985) Interactions between gonadal steroids and the immune system. Science 227: 257–261. https://doi.org/10.1126/science.3871252

Guimaraes MM, Ferreira RL (2014) Morcegos cavernícolas do Brasil: novos registros e desafios para conservação. Revista Brasileira de Espeleologia 2: 1–33.

Herrin CS, Tipton VJ (1975) Spinturnicid mites of Venezuela (Acarina: Spinturnicidae). Brigham Young University Science Bulletin, Biological Series 20(1): 1–72. https://doi.org/10.5962/bhl.part.5666

Komeno CA, Linhares AX (1999) Batflies Parasitic on Some Phyllostomid Bats in Southeastern Brazil: Parasitism Rates and Host-parasite Relationships. Memórias do Instituto Oswaldo Cruz 94: 151–156. https://doi.org/10.1590/S0074-02761999000200004

Koopman KF (1994) Chiroptera: Systematics. Handbook of Zoology, VIII (Mammalia). Berlin and New York: Walter de Gruyter, 217 pp.

Kunz TH (1982) Roosting ecology of bats. In: Kunz TH (Ed.) Ecology of Bats. Plenum Publishing Corporation, Boston, New York, 55 pp. https://doi.org/10.1007/978-1-4613-3421-7_1

Lee VN, Mendenhall IH, Lee BPYH, Posa MRC (2018) Parasitism by Bat Flies on an Urban Population of *Cynopterus brachyotis* in Singapore. Acta Chiropterologica 20: 177–185. https://doi.org/10.3161/15081109ACC2018.20.1.013

Lewis SE (1995) Roost Fidelity of Bats: A Review. Journal of Mammalogy 76(2): 481–496. https://doi.org/10.2307/1382357

Lourenço SI, Palmeirim JM (2007) Can mite parasitism affect the condition of bat hosts? Implications for the social structure of colonial bats. Journal of Zoology 273: 161–168. https://doi.org/10.1111/j.1469-7998.2007.00322.x

Lourenço SI, Palmeirim JM (2008) Which factors regulate the reproduction of ectoparasites of temperate-zone cave-dwelling bats?. Parasitology Research 104: 127–134. https://doi.org/10.1007/s00436-008-1170-6

Lučan RK (2006) Relationships between the parasitic mite *Spinturnix andegavinus* (Acari: Spinturnicidae) and its bat host, *Myotis daubentonii* (Chiroptera: Vespertilionidae): Seasonal, sex- and age-related variation in infestation and possible impact of the parasite on the host condition and roosting behaviour. Folia Parasitologica 53: 147–152. https://doi.org/10.14411/fp.2006.019

Marshall AG (1982) Ecology of insects ectoparasitic on bats. In: Kunz TH (Ed.) Ecology of Bats. Plenum Publishing, New York, 369–401. https://doi.org/10.1007/978-1-4613-3421-7_10

Møller AP, Saino N (2004) Immune response and survival. Oikos 104: 299–304. https://doi.org/10.1111/j.0030-1299.2004.12844.x

Moras LM, Bernardi LF de O, Graciolli G, Gregorin R (2013) Bat flies (Diptera: Streblidae, Nycteribiidae) and mites (Acari) associated with bats (Mammalia: Chiroptera) in a high-altitude region in southern Minas Gerais, Brazil. Acta Parasitologica 58: 556–563. https://doi.org/10.2478/s11686-013-0179-x

Neuhaus P (2003) Parasite removal and its impact on litter size and body condition in Columbian ground squirrels (*Spermophilus columbianus*). Proceedings of the Royal Society B: Biological Sciences 270: 1994–1996. https://doi.org/10.1098/rsbl.2003.0073

Patterson BD, Dick CW, Dittmar K (2007) Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). Journal of Tropical Ecology 23(2): 177–189. https://doi.org/10.1017/S0266467406003816

Patterson BD, Dick CW, Dittmar K (2008) Parasitism by bat flies (Diptera: Streblidae) on neotropical bats: Effects of host body size, distribution, and abundance. Parasitology Research 103: 1091–1100. https://doi.org/10.1007/s00436-008-1097-y

Pearce RD, O'Shea TJ (2007) Ectoparasites in an urban population of big brown bats (Eptesicus fuscus) in Colorado. Journal of Parasitology 93: 518–530. https://doi.org/10.1645/GE-973R.1

Peracchi AL (1990) Contribuição ao estudo da família Spelaeorhynchidae Oudemans, 1902 (Acarina, Mesostigmata). Brazilian Journal of Biology 7(1–2): 1–29. https://doi.org/10.1590/S0101-81751990000200001

Pereira MC, Rodet JGMA, Salgado AAR (2013) Aspectos genéticos e morfológicos das cavidades naturais da Serra da Piedade, Quadrilátero Ferrífero, MG. Revista Brasileira de Geomorfologia 13(4): 465–476. https://doi.org/10.20502/rbg.v13i4.315

Postawa T, Nagy Z (2016) Variation of parasitism patterns in bats during hibernation: the effect of host species, resources, health status, and hibernation period. Parasitology Research 115: 3767–3778. https://doi.org/10.1007/s00436-016-5138-7

Presley SJ, Willig MR (2008) Intraspecific patterns of ectoparasite abundances on Paraguayan bats: Effects of host sex and body size. Journal of Tropical Ecology 24: 75–83. https://doi.org/10.1017/S0266467407004683

Reichard JD, Kunz TH (2009) White-Nose Syndrome inflicts lasting injuries to the wings of Little Brown Myotis (*Myotis lucifugus*). Acta Chiropterologica 11: 457–464. https://doi.org/10.3161/150811009X485684

Reid FA (1997) A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, New York, 334 pp.

Reis AS (2018) *Anoura Geoffroyi* Gray, 1838: História natural de duas colônias associadas a cavernas localizadas no Quadrilátero Ferrífero, Minas Gerais, Brasil. Thesis, Belo Horizonte, Brazil: Pontifícia Universidade Católica de Minas Gerais, Minas Gerais.

Rózsa L, Reiczigel J, Majoros G (2000) Quantifying parasites in samples of hosts. Journal of Parasitology 86(2): 228–232. https://doi.org/10.1645/0022-3395(2000)086[0228:QPISOH]2.0.CO;2

Rudnick A (1960) A revision of the mites of the family Spinturnicidae (Acarina). University of California Press 17: 157–284.

Rui AM, Graciolli G (2005) Moscas ectoparasitas (Diptera, Streblidae) de morcegos (Chiroptera, Phyllostomidae) no sul do Brasil: associações hospedeiros-parasitos e taxas de infestação. Revista Brasileira de Zoologia 22: 438–445. https://doi.org/10.1590/S0101-81752005000200021

Silva C, Graciolli G, Rui A (2009) Novos registros de ácaros ectoparasitos (Acari, Spinturnicidae) de morcegos (Chiroptera, Phyllostomidae) no Rio Grande do Sul. Pacific Insects 15: 469–471.

Simmons NB (2005) Order Chiroptera. In: Wilson DE, Reeder DM (Eds) Mammal Species of the World: a Taxonomic and Geographic Reference. Johns Hopkins University Press, Baltimore, 312–529.

Souza FCR, Carmo FF (2015) Geossistemas ferruginosos no Brasil. In: Carmo FF, Kamino LHY (Orgs) Geossistemas Ferruginosos do Brasil: Áreas prioritárias para a conservação da diversidade geológica e biológica, patrimônio cultural e serviços ambientais, 3i Editora, Belo Horizonte, 47–76.

Sundari AA, Bogdanowicz W, Varman DR, Marimuthu G, Rajan KE (2012) Ectoparasite *Raymondia lobulata* infestation in relation to the reproductive cycle of its host – The greater false vampire bat *Megaderma lyra*. Journal of Parasitology 98: 60–62. https://doi.org/10.1645/GE-2833.1

Talamoni SA, Couto D, Cordeiro Junior DA, Diniz FM (2008) Diet of some species of Neotropical small mammals. Mammalian Biology 73: 337–341. https://doi.org/10.1016/j.mambio.2007.09.008

Ter Hofstede HM, Fenton MB (2005) Relationships between roost preferences, ectoparasite density, and grooming behaviour of neotropical bats. Journal of Zoology 266: 333–340. https://doi.org/10.1017/S095283690500693X

Trujillo-Pahua L, Ibáñez-Bernal S (2018) New Geographical Records of Bat flies (Diptera: Streblidae) associated with phyllostomid bats (Chiroptera: Phyllostomidae) in the West Highlands of Mexico. Journal of Medical Entomology: 1–11. https://doi.org/10.1093/jme/tjy166

Wenzel RL (1976) The streblid batflies of Venezuela (Diptera: Streblidae). Brigham Young University Science Bulletin: Biological series 20: 1–177. https://www.biodiversitylibrary.org/page/7798295

Zortéa M (2003) Reproductive patterns and feeding habits of three nectarivorous bats (Phyllostomidae: Glossophaginae) from the Brazilian Cerrado. Brazilian Journal of Biology 63: 159–168. https://doi.org/10.1590/S1519-69842003000100020