Ecology of bat flies in Singapore: A study on the diversity, infestation bias and host specificity (Diptera: Nycteribiidae)

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ABSTRACT

Bat flies are highly-specialized, hematophagous arthropods that are globally ubiquitous. There is little published research on bat flies (Diptera: Nycteribiidae) in Singapore and understanding the diversity of nycteribiids, host association and infestation rates can provide insight into this host-ectoparasite relationship. Nycteribiids were collected from bats trapped in Singapore (2011–2016) and identified using morphological keys. Host-ectoparasite relationships were investigated with logistic regression and Bayesian poisson regression. Nycteribiids were found to be monoxenously associated with their host bat species and host age, sex, species, and BBCI appear to contribute to differences in prevalence and intensity. Differences in host specificity between bat fly species in Singapore and their conspecifics in less disturbed habitats with higher bat biodiversity, such as Malaysia, Philippines and Thailand, suggest that the high host specificity in Singapore derives from the paucity of suitable hosts and abundance of single species roosts and not from their coevolved restrictions to them.

The ecology of bats and bat flies represents a unique host-parasite system. Numerous studies have been conducted on the relationship between bats and their ectoparasites (Dick and Patterson, 2006; Ter Hofstede et al., 2004). The interplay between ectoparasite and host exists from the immunological and molecular level to the population and community scale (Presley, 2012). Certain bat species are parasitized by only one species of bat fly, while other bat species are parasitized by several species (Azhar et al., 2015; Dick and Dittmar, 2014). There are a number of host specific bat flies, which may be in part driven by roosting behavior (Lee et al., 2018). High roost fidelity and long-term utilization of sites ensures a continuous source of hosts for emergent adult flies and the use of shared and bat-dense ingress and egress spaces can lead to host switching by these flies. Large colony sizes in roosts provide opportunities for emerging adult flies to find new hosts, though multi-species roosts can facilitate inter-specific encounters (Dick and Patterson, 2007).

Bat flies are insects (Order: Diptera) that are divided into two families, the Nycteribiidae and Streblidae. These are specialized, obligatory ectoparasites that live in the fur and wing membrane of their hosts, are obligate blood feeders, and are viviparous (Dick and Patterson, 2006). Nycteribiids are secondarily wingless with a dorso-ventrally flattened body, allowing them to move through the bat's pelage, press close to the host's body or hide in small cracks on the roosting medium (Dick and Patterson, 2006). They have well sclerotized integuments with setae or combs to protect against abrasive damage and assist in locomotion, while their claws and backward-pointing setae help them secure a firm foothold on their host (Dick and Patterson, 2006; Marshall, 1982).

The family Nycteribiidae are a large and diverse group, found globally and comprised of 12 genera and 275 species (Dick and Patterson, 2006). Their life strategy and limited biological capacity to disperse often limit their distribution to that of the host species they infest (Alvarez et al., 2015; Patterson et al., 2008a). This geographic range may be large if their volant hosts fly long distances and if they use both home and foraging roosts. This behavior can facilitate the spread of bat flies, leading to panmictic populations (Olival et al., 2013).

However, cross-species infestation can depend on the availability of mixed species roosts and to a lesser extent, shared foraging sites may provide opportunities for cross infestation (Dick and Patterson, 2007).

Understanding the ecology of host-ectoparasite dynamics will provide insight into the drivers of host specificity. This is especially important in Singapore as bat habitat in this country has become increasingly fragmented, having lost a majority of its native biodiversity, including several species of bats that require specific habitat parameters (Lane et al., 2006). There may have also been the subsequent extirpation of their ectoparasites as these arthropods are completely reliant on their hosts (Carlson et al., 2017). Singapore has resident opportunistic bat species that take advantage of the urban landscape, but also other species that are habitat specialists (Pottie et al., 2005). To better understand the ecological dynamics of Nycteribiid bat flies in Singapore, we identified bat flies collected from 2011 to 2016 from bats in Singapore and seek to investigate the following questions: 1) host-ectoparasite association in Singapore; 2) effects of biological characteristic of host bat (sex, age and body condition) on infestation rates and ectoparasite burden.

Bat collections were undertaken with approval from the National Parks Board (NP/RP11-011-3a) and the National University of Singapore Institutional Animal Care and Use Committee (IACUC Permit #B01/12). Bats were trapped from seven locations (Kent Ridge Park, Rifle Range Road, Bukit Timah Nature Reserve, Telok Blangah Hill Park, Dairy Farm Nature Park, Pulau Ubin, and Coney Island Park) throughout Singapore from April 2011 to April 2016. Harp traps were used to collect *Penthetor lucasi* from their roosting site in Bukit Timah Nature Reserve, while mist nets were used to trap foraging bats and *Eonycteris spelaea* departing their roost site. Bat flies were collected with forceps and placed into 70% ethanol. These were held at 4 °C until transport to Duke-NUS Medical School where they were placed into a −80 °C freezer until identification. Bat flies were identified on a BioQuip 1429 Chill Table (Bioquip, Rancho Dominguez, CA) and samples were identified using taxonomic keys (Maa, 1971; Theodor, 1967). Details such as morphological discrepancies from the identification keys, sex and number were recorded on a datasheet. Images were taken with an Olympus Microscope Digital camera DP22 (Olympus, Shinjuku, Japan) attached to an Olympus SZ61Stereo microscope (Olympus, Shinjuku, Japan) and processed with Adobe Lightroom (version 4.2) and Adobe Photoshop 2014 (Adobe, San Jose, CA) (Fig. 1).

Ectoparasite host specificity, prevalence and intensity were investigated. Prevalence is defined as the number of infested bats in the sampled population and intensity is defined as the number of parasites found on an infected host (Bush et al., 1997). Host specificity was tested with a Fischer Exact test. Logistic regression was used for prevalence analysis and Bayesian Poisson regression was used for intensity analysis (McElreath, 2016; Venables and Ripley, 2013). Models of prevalence included sex of host, age of host (juvenile or adult), and bat body condition index (BBCI) (weight of host/forearm length) (Lewis, 1996). Model selection for prevalence was conducted with Akaike information criterion (AIC) values. Model selection for intensity was conducted using the Widely Applicable Information Criterion (WAIC) and are listed in Table 3 (Watanabe, 2010). Program R was used for all analyses (Team, 2019).

A total of 355 individual bats representing five species were caught and sampled during the collection period. Three of the five species (n = 319 bats) were found to be infested with nycteribiids (Table 1). The two species of bats not infested were *Rhinolophus lepidus* (Blyth, 1844) and *Scotophilus kuhlii* (Leach, 1821). A total of 591 nycteribiids were collected from the sampled population and four species of nycteribiids were identified (Table 1). Other species of ectoparasites were also collected, specifically spinturnicid mites, streblid flies, one unidentified flea and a beetle in the genus *Xyleborus*. Nycteribiid species were found to be highly host specific (p-value = 0.0000001, Fisher's exact test). *Leptocyclopodia ferrarii* (Rodani, 1878) were only collected on short-nose fruit bats, *Cynopterus brachyotis* (Müller, 1838), while

Table 1
Nycteribiids and their associated bat host. Prevalence is the proportion of a sampled species infested with nycteribiids.

Bat species	Female bats caught & ectoparasite prevalence	Male bats caught & ectoparasite prevalence	Total & Prevalence	Bat fly species	Total number of bat flies	Infestation range	Mean Infestation range
Cynopterus brachyotis	34/56 (60.7%)	13/20 (65%)	47/76 (61.8%)	Leptocyclopodia ferrarii	95	0 to 11	1.28 ± 1.74
Eonycteris spelaea	42/70 (60%)	81/99 (81.8%)	123/169 (72.8%)	Eucampsipoda sundaica	261	0 to 9	1.54 ± 1.63
Penthetor lucasi	31/33 (93.9%)	37/41 (90.2%)	68/74 (91.9%)	Eucampsipoda penthetoris	151	0 to 9	
				Archinycteribia octophthalma	84	0 to 7	
				Total bat flies on Penthetor lucasi	235	0 to 9	3.18 ± 2.44
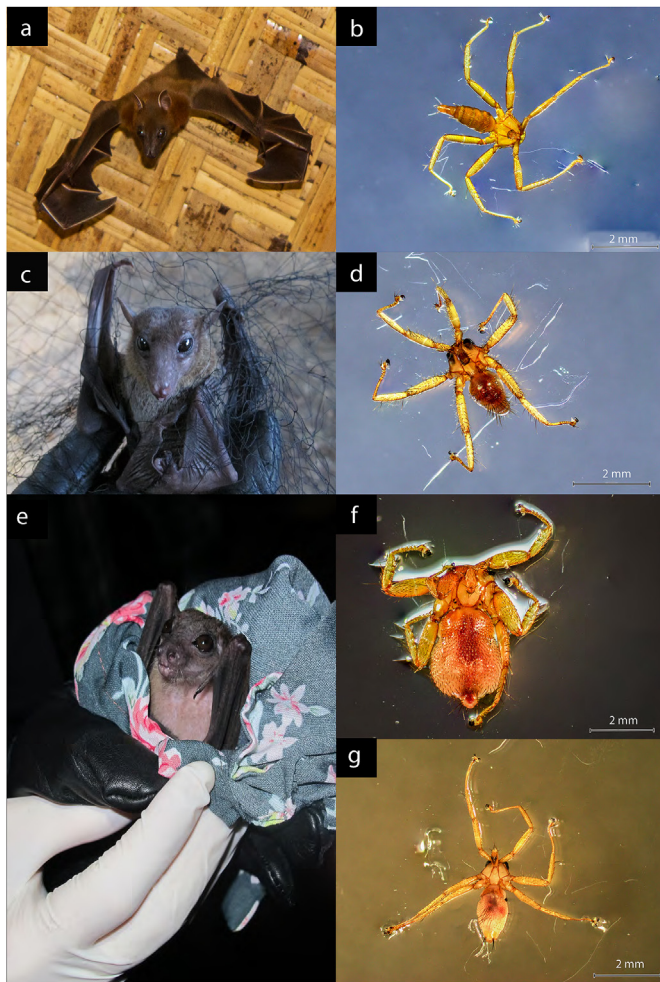
Fig. 1. Pteropodid fruit bats in Singapore with their ectoparasitic *Nycteribiidae* bat flies. *Cynopterus brachyotis* (a) and *Leptocyclopodia ferrarii* (b); *Eonycteris spelaea* (c) and *Eucampsipoda sundaica* (d); *Penthetor lucasi* (e), *Eucampsipoda penthetoris* (f), and *Archinycteribia octophthalma* (g).

Eucampsipoda sundaica (Theodor, 1955) were only collected from cave nectar bats, *Eonycteris spelaea* (Dobson, 1871). *Penthetor lucasi* (Anderson, 1912), the dusky fruit bat, was infested with two nycteriid species, *Eucampsipoda penthetoris* (Theodor, 1955) and *Archinycteribia octophthalma* (Theodor, 1967) (Fig. 1). Differences in prevalence and intensity among host and ectoparasite species were observed.
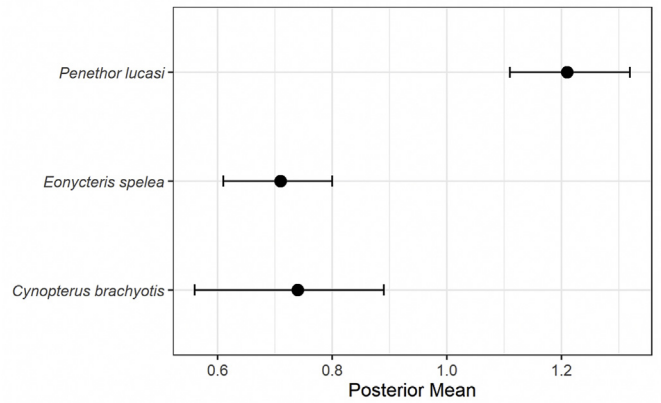
Among the three different host bat species, *P. lucasi* reported the highest prevalence of bat flies (91.9%; Mean: 3.18 ± 2.44) and *C. brachyotis* had the lowest prevalence of bat flies (61.8%; Mean: 1.28 ± 1.74) (Table 1). Among the four species of nycteriibids, infestation per bat was highest for *L. ferrarii*, ranging from 0 to 11, whereas *A. octophthalma* was observed to have the lowest range of

Fig. 2. Posterior mean intensity of the three species of bats and 89% HDPI (High Density Posterior Interval).

infestation per bat, from 0 to 7. Our analysis showed that BBCI and sex significantly affected ectoparasite prevalence (Table 2). Every unit increase in BBCI resulted in the odds of infestation decreasing by 2.80 (CI 95%: 4.9 to −0.9) and the odds of infestation to change by a factor of 0.061 (CI 95%: 0.008–0.4). Among the bat species, infestation rate for *P. lucasi* is significantly different from that of *C. brachyotis*, with the odds ratio of *P. lucasi* being infested over *C. brachyotis* being 8.20 (CI 95%: 2.5–37.2). Sex of host was also found to significantly affect rate of infestation (Table 2). The odds of infestation for an adult male host is 4.57 (CI 95%: 2.0–11.0) times greater than for an adult female host while the odds of infestation for a juvenile female host is 1.076 (CI 95%: 0.4–3.1) times over a juvenile male host.

Nycterbiid intensity is different among host species. Although there is some model uncertainty, the best model finds that bat species is the driving factor between differences in bat fly intensity with a High Density Posterior Interval (HDPI). *Penthetor lucasi* had higher levels of parasite intensity (1.21) than the other host species (HDPI 89%: 1.11–1.32). *Eonycteris spelaea* had an intensity of 0.71 (HDPI 89%: 0.61–0.80) and *C. brachyotis* had an intensity of infection of 0.74 (HDPI 89%: 0.56–0.89) (Fig. 2). There was very little support that the interaction between BBCI and host species plays a role in intensity of infestation, which was the second-best model (Table 3).

In Singapore, each of the three bat species roosted in different locations with different roosting structures. *Eonycteris spelaea* and *P. lucasi* roost in large single-species colonies whereas *C. brachyotis* usually roost in small groups of 4–12 individuals (Francis and Barrett, 2008). *Eonycteris spelaea* was found in two large communal roosts under highways in Singapore, while *P. lucasi* was found in a cave located in Bukit Timah Nature Reserve. Larger roosts facilitate increased contact between bats leading to higher infestation rates. Conversely, species that roost in small groups limit the opportunity for nycteriibid infestation between roosts via bat movement (Dick and Patterson, 2006). *Cynopterus brachyotis* do not have fixed roosts and can be found in palm leaves, foliage, and man-made structures across Singapore. Though *E.*

Table 2
Results for statistical analysis. Prevalence was tested with binary logistic regression. BBCI: Bat Body Condition Index; Sex with respect to male; Age with respect to juveniles, Species with respect to *C. brachyotis*.

Test	Factor	Coefficient	Z	P	CI (25/75)		Odds Ratio
Prevalence	BBCI	−2.78714	3.298	0.005381**	−4.86125	−0.89921	0.06098402
	Sex	1.52026	3.576	**0.00349****	0.715875	2.393535	4.5734343
	Age	0.07345	0.142	0.887184	−0.92659	1.122855	1.07621244
	Sex*Age	−1.68775	−2.365	**0.018053***	−3.11182	−0.29704	0.18493526
	Species: *E. spelaea*	0.41614	0.999	0.317988	−0.40252	1.239303	1.51610395
	Species: *P. lucasi*	2.10467	3.159	**0.001585****	0.920217	3.617089	8.20436365

*p value < 0.05; **p value < 0.01; ***p value < 0.001.

Table 3

Model selection results using WAIC (Watanabe–Akaike information criterion) for intensity. Intensity was tested with a Bayesian Poisson regression model. BBCI: Bat Body Condition Index.

Model	WAIC	pWAIC	dWAIC	weight	SE	dSE
Species	832.5	4.3	0.0	0.9	36.21	NA
BBCI*Species	837.0	4.7	4.5	0.1	37.45	8.85
Age	848.2	2.3	15.7	0.0	35.82	13.45
BBCI*Age	848.8	3.6	16.3	0.0	35.74	13.87
BBCI	856.2	2.6	23.7	0.0	37.41	14.66
BBCI*Sex	856.3	4.3	23.8	0.0	36.09	14.34
Intercept	859.1	1.6	26.6	0.0	37.92	13.95
Sex	860.5	3.1	28.0	0.0	37.72	13.66

pWAIC: estimated effective number of parameters; **dWAIC**: relative difference between the value of WAIC for the top-ranked model and the value of WAIC for each model; **SE**: standard error for the WAIC computations; **dSE**: standard error of the differences between two values of WAIC.

spelaea and *C. bracyhotis* were trapped in the same sampling sites, there was no evidence of co-roosting. *Penthetor lucasi* roosting structure and substrate choice could have significantly contributed to the increased prevalence and intensity of nycteribiid compared to *C. brachyotis* as shown in our sampled population, where *P. lucasi* has an 8.204 times greater chance of infestation and 2.20 times more likely to carry a higher nycteribiid load compared to *C. brachyotis* (Table 2). Conversely, although the roosting behavior of *E. spelaea* and *C. brachyotis* differ, it does not seem to significantly influence the prevalence and intensity of nycteribiid infestation on the hosts.

Host roosting behavior may also influence nycteribiid infestation success. Roosting behavior and fidelity differ between *C. brachyotis* and both *E. spelaea* and *P. lucasi* with *C. brachyotis* being known to regularly switch between roosts. Regular roost switching could be a defense mechanism adapted by the bats to reduce ectoparasite infestation and our *C. brachyotis* results may reflect this lowest prevalence and mean intensity (Table 1) (Azhar et al., 2015; Dick and Patterson, 2006). Comparatively, *E. spelaea* and *P. lucasi* likely have a higher degree of roost fidelity, contributing to the increase chance of nycteribiid infestation than *C. brachyotis*. Overall, males also had a higher odd of infestation (4.573) compared to adult female bats (Tables 1 and 2). This differs from previous work demonstrating that parasitism with bat flies is generally higher in female bats due to their higher survivorship, increasing the likelihood of lateral and vertical transmission (Patterson et al., 2008b). In particular, there was a higher ectoparasite prevalence rate in male *C. brachyotis* and *E. spelaea*, the latter having nearly 82% infested compared to 60% of female bats. This incongruity with previous studies may result from *E. spelaea* mature males spending shorter

than average times away from the roost compared to females because males participate in roost defense (Acharya et al., 2015). This behavior also means male bats are exposed to bat flies for a longer duration in the roosting environment than females, possibly resulting in more frequent rates infestation.

Biological differences between age and sex within a host species also appears to contribute to prevalence. Host BBCI appears to exert a negative effect on infestation rate (Table 2). Hosts in better condition (higher BBCI) can allocate more effort into grooming, which has previously been found to be a major cause of mortality in bat flies, and at the same time, adults with higher BBCI may have relatively more surface area to support increased numbers of ectoparasites (Dick and Patterson, 2006; Marshall, 1982). This observed effect on prevalence of nycteribiids suggests that other factors not investigated within the scope of our study may play a role in our findings, including actual roost size, habitat surrounding the roosts, distance between roosts, the possibility of additional large communal roosts and the impact of seasonality.

Nycteribiids infesting pteropodid bats in Singapore have a monoxenous relationship with their host (parasitizes one host species). This tight association could be due to a variety of factors, including roosting location, roosting habits and host behavior (Kunz, 1982; Ter Hofstede et al., 2004). However, it is interesting to note the difference in host specificity of *L. ferrarii* and *E. sundaica* in Malaysia and Thailand. As summarized in Table 4, *L. ferrarii* was recorded as oligoxenous (parasitizes more than one host species of the same genus), while *E. sundaica* was recorded as a pleioxenous (parasitizes hosts from a single family) (Azhar et al., 2015). In Thailand, both *L. ferrarii* and *E. sundaica* were recorded as polyxenous species (parasitizes hosts from multiple unrelated taxa), with *L. ferarii* found on both *C. brachyotis* and *E. spelaea* (Alvarez et al., 2015; Hill and McNeely, 1975). It is important to note that the two studies reported results collected from a much larger survey area and habitat type compared this work in Singapore. Differences in observed host association may be attributed to two factors. One is a difference in host diversity and availability between Singapore, Malaysia and Thailand. The second is the absence of multi-species roosting sites in Singapore (such as caves) that reduce co-roosting opportunities and interaction, and subsequently minimizes opportunities for nycterbiid host switching (Lane et al., 2006; Patterson et al., 2008a).

There remains much work to be done on the diversity of nycteribiids and their interaction with bats in Southeast Asia. As different bat species have different roosting behaviors, nycteribiids have co-evolved to become host specific and adapt their life cycle to specific hosts (Dick and Patterson, 2006). Studies on host specificity have pointed towards high host specificity by the nycteribiids, with most being monoxenous (Maa, 1971). The four species of nycteribiids identified in this study

Table 4

Nycteribiids species and their host association in other countries.

Nycterbiidae Species	Singapore (this study)	Malaysia [5]	Thailand [22]
Leptocyclopodia ferrarii	*Cynopterus brachyotis*	*Cynopterus brachyotis* *Cynopterus horsefieldii* *Cynopterus sphinx*	*Cynopterus brachyotis* *Cynopterus sphinx* *Eonycteris spelaea* *Rousettus leschenaultii* *Megaderma* sp. *Megaerops ecaudatus*
Eucampsipoda sundaica	*Eonycteris spelaea*	*Eonycteris spelaea* *Rousettus leschenaultii* *Rousettus amplexicaudatus*	*Cynopterus sphinx* *Eonycteris spelaea* *Rousettus leschenaultii* *Megaderma* sp. *Hipposideros lekaguli* *Rhinolophus coelophyllus*
Archinycteribia octophthalma	*Penthetor lucasi*	*Penthetor lucasi*	-
Eucampsipoda penthetoris	*Penthetor lucasi*	*Penthetor lucasi*	-

exhibit monoxenous relationship with their host in Singapore, unlike those in other regions, possibly due to biological factors and the unique landscape topography, including the absence of natural roosting sites for the cave dwelling bats. The restricted range of host occupancy within the sampled species and populations warrant further study to determine why this bias occurs.

Acknowledgements

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