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

Zong Xian Lim, Alan T. Hitch, Benjamin P. Y.-H. Lee, Dolyce H.W. Low, Erica Sena Neves, Sophie A. Borthwick, Gavin J.D. Smith, Ian H. Mendenhall, *, Ian H. Mendenhall

Department of Biological Sciences, National University of Singapore, Singapore

Department of Wildlife, Fish and Conservation Biology, University of California at Davis, CA, 95616, USA

Wildlife Management Division, National Parks Board, 1 Cluny Rd, Singapore, 259569

Programme in Emerging Infectious Diseases, Duke-NUS Medical School, 8 College Rd, Singapore, 169857

National University of Singapore Graduate School for Integrative Sciences and Engineering, Singapore

Duke Global Health Institute, Duke University, Durham, NC, 27710, USA

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 peltage, 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 (BCCI) (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 (Miller, 1838), while

| Bat species                      | Female bats caught & ectoparasite | Male bats caught & ectoparasite | Total & Prevalence |
|---------------------------------|-----------------------------------|---------------------------------|--------------------|
| Cynopterus brachyotis           | 34/56 (60.7%)                     | 13/20 (65%)                    | 47/76 (61.8%)     |
| Eonycteris spelaea              | 81/99 (81.8%)                     | 84/100 (84%)                   | 165/199 (83.2%)  |
| Leptocyclopodia ferrarii        | 26/1 (26%)                        | 121/169 (72.8%)                | 147/195 (75.1%)  |
| Eucampsipoda sundaica          | 19/21 (90.5%)                     | 19/21 (90.5%)                  | 38/42 (90.4%)    |
| Penthetor lucasi                | 30/41 (92.2%)                     | 84/100 (84%)                   | 114/141 (80.5%) |

Table 1: Nycteribiids and their associated bat host. Prevalence is the proportion of a sampled species infested with nycteribiids.
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 nycteribiid species, Eucampsipoda penthetoris (Theodor, 1955) and Archinycteribia octophalma (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 nycteribids, infestation per bat was highest for L. ferrarii, ranging from 0 to 11, whereas A. octophalma was observed to have the lowest range of 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.

Nycteribiid 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 nycteribid 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.

![Fig. 1. Pteropodid fruit bats in Singapore with their ectoparasitic Nycteribidae bat flies. Cynopterus brachyotis (a) and Leptocyclopodia ferrarii (b); Eonycteris spelaea (c) and Eucampsipoda sundaica (d); Penthetor lucasi (e), Eucampsipoda penthetoris (f), and Archinycteribia octophalma (g).](image)

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

### 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 | 0.005831** | −4.86125 | −0.89921 | 0.06098402 |
|               | Sex        | 1.52026     | 3.576 | 0.004394** | 0.715875 | 2.3993535 | 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.
infested compared to 60% of female bats. This incongruity with pre-
rate in male
creasing the likelihood of lateral and vertical transmission (Patterson
is generally higher in female bats due to their higher survivorship, in-
infestation (4.573) compared to adult female bats (Tables 1 and 2). This
C. brachyotis
diroost
Comparatively,
both
success. Roosting behavior and
nycteribiid infestation on the hosts.

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.

e specia and C. brachyotis 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).

Host roosting behavior may also influence nycteribiid infestation
success. Roosting behavior and fidelity differ between C. brachyotis and
both E. spelea 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. spelea 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, in-
creasing 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. spelea, the latter having nearly 82%
infested compared to 60% of female bats. This incongruity with
previous studies may result from E. spelea 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 ne-
gative effect on infestation rate (Table 2). Hosts in better condition
(higher BBCI) can allocate more effort into grooming, which has previ-
ously 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 sur-
face 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 sea-
sonality.

Nycteribiids infesting pteropodid bats in Singapore have a mono
xenous 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 (para-
sitizes more than one host species of the same genus), while E. sundaica
was recorded as a pleioxenous (parasitizes hosts from a single family)
(Azhari et al., 2015). In Thailand, both L. ferrarii and E. sundaica were
recorded as polioxenous species (parasitizes hosts from multiple un-
related taxa), with L. ferrarii found on both C. brachyotis and E. spelea
(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. Differ-
ences 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 op-
portunities and interaction, and subsequent minimizes opportunities
for nycteribiid 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 spe-
cies 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 3
Model selection results using WAIC (Watanabe–Akaike information criterion) for intensity. Intensity was tested with a Bayesian Poisson regression model.

| Model   | WAIC  | pWAIC | dWAIC | SE   | dSE  |
|---------|-------|-------|-------|------|------|
| Species | 832.5 | 4.3   | 0.0   | 0.9  | 36.21|
| BBCI*Species | 837.0 | 4.7   | 0.5   | 0.1  | 37.45|
| Age     | 848.2 | 2.3   | 15.7  | 0.0  | 35.82|
| BBCI*Age | 848.8 | 3.6   | 16.3  | 0.0  | 35.74|
| BBCI    | 856.2 | 2.6   | 23.7  | 0.0  | 37.41|
| BBCI*Sex | 856.3 | 4.3   | 23.8  | 0.0  | 36.09|
| Intercept| 859.1 | 1.6   | 26.6  | 0.0  | 37.92|
| Sex     | 860.5 | 3.1   | 28.0  | 0.0  | 37.72|

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.

Table 4
Nycteribiidae species and their host association in other countries.

| Nycteribiidae Species | Singapore (this study) | Malaysia | Thailand |
|----------------------|------------------------|----------|----------|
| Leptocyclopodia ferrarii | Cynopterus brachyotis | Cynopterus brachyotis | Cynopterus brachyotis |
|                      |                        | Cynopterus horsfeldii | Cynopterus sphinx |
|                      |                        | Eonycteris spelaea | Eonycteris spelaea |
|                      |                        | Rousettus leschenaultii | Rousettus leschenaultii |
|                      |                        | Rousettus amplirostris | Megaderma sp. |
|                      |                        | Megaderma sp. | Megaurospis ecuadatus |
|                      |                        |                       |                       |
| Eucampsipoda sundaica | Eonycteris spelaea | Eonycteris spelaea | Cynopterus sphinx |
|                      |                        | Rousettus leschenaultii | Eonycteris spelaea |
|                      |                        | Rousettus amplirostris | Rousettus leschenaultii |
|                      |                        | Megaderma sp. | Megaderma sp. |
|                      |                        |                       | Hipposideros lekaguli |
|                      |                        |                       | Rhinolophus euryops |
| Archonycteris octophthalmica | Penthetor lucasi | Penthetor lucasi | - |
| Eucampsipoda penneri | 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

This study was supported by the Duke-NUS Signature Research Program funded by the Ministry of Health, Singapore, the National Medical Research Council (NMRC/BNIG/2005/2013) and the NUS-Global Asia Institute grant NIHA-2011-1-005. BPYH Lee was supported by a National Parks Board Postgraduate Scholarship and the Wildlife Reserves Singapore Conservation Fund.

References

Acharya, P.R., Racey, P.A., McNeil, D., Sothibhandhu, S., Bumrungsri, S., 2015. Timing of cave emergence and return in the dawn bat (Eonycteris spelaea, Chiroptera: Pteropodidae) in Southern Thailand. Mamm. Stud. 40, 47–52.

Alvarez, J.D., Lit Jr., I.L., Alviola, P.A., 2015. Bat flies (Diptera: Nycteribiidae) from Mount Makiling, Luzon Island: new host and distribution records, with a checklist of species found in the Philippines. Check List. 11, 1509.

Azhar, I., Khan, F.A.A., Ismail, N., Abdullah, M., 2015. Checklist of bat flies (Diptera: Nycteribiidae and Streblidae) and their associated bat hosts in Malaysia. Check List. 11, 1777.

Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 577–583.

Carlson, C.J., Burgio, K.R., Dougherty, E.R., Phillips, A.J., Bueno, V.M., Clements, C.F., Castaldo, G., Dallas, T.A., Cizauskas, C.A., Cumming, G.S., Dona, J., Harris, N.C., Jovani, R., Mironov, S., Muellerklein, O.C., Proctor, H.C., Getz, W.M., 2017. Parasite biodiversity faces extinction and redistribution in a changing climate. Sci. Adv. 3, e1602422.

Dick, C.W., Dittmar, K., 2014. Parasitic Bat Flies (Diptera: Streblidae and Nycteribiidae): Host Specificity and Potential as Vectors, Bats (Chiroptera) as Vectors of Diseases and Parasites. Springer, pp. 131–155.

Dick, C.W., Patterson, B.D., 2006. Bat Flies: Obligate Ectoparasites of Bats, Micromammals and Macroparasites. Springer, pp. 179–194.

Dick, C.W., Patterson, B.D., 2007. Against all odds: explaining high host specificity in dispersal-prone parasites. Int. J. Parasitol. 37, 871–876.

Francis, C.M., Barrett, P., 2008. A Field Guide to the Mammals of South-East Asia. New Holland Publishers.

Hill, J.E., McNeely, J.A., 1975. The Bats and Bat’s Parasites of Thailand. Applied Scientific Research Corp of Thailand Bangkok.

Kunz, T.H., 1982. Roosting Ecology of Bats, Ecology of Bats. Springer, pp. 1–55.

Lane, D.J., Kingston, T., Lee, B.P.-H., 2006. Dramatic decline in bat species richness in Singapore, with implications for Southeast Asia. Biol. Conserv. 131, 584–593.

Lee, V.N., Mendenhall, I.H., Lee, B.P.-H., Posa, M.R.C., 2018. Parasitism by bat flies on an urban population of Cynopterus brachyotis in Singapore. Acta Chiropterol. 20, 177–185.

Lewis, S.E., 1996. Low roost-site fidelity in pallid bats: associated factors and effect on group stability. Behav. Ecol. Sociobiol. 39, 335–344.

Maa, T., 1971. Revision of the Australian bat flies. Pac. Insects Monogr. 28, 1–118.

Marshall, A.G., 1982. Ecology of insects ectoparasitic on bats. In: Ecology of Bats. Springer, pp. 369–401.

McElreath, R., 2016. rethinking: statistical Rethinking book package. R package version 1.

Olival, K.J., Dick, C.W., Simmons, N.B., Morales, J.C., Melnick, D.J., Dittmar, K., Perkins, S.L., Dazzak, P., DeSalle, R., 2013. Lack of population genetic structure and host specificity in the bat fly, Cyplocopia horsfieldi, across species of Pteropus bats in Southeast Asia. Parasites Vectors 6, 231.

Patterson, B.D., Dick, C.W., Dittmar, K., 2008a. Parasitism by bat flies (Diptera: Streblidae) on neotropical bats: effects of host body size, distribution, and abundance. Parasitol. Res. 103, 1091–1100.

Patterson, B.D., Dick, C.W., Dittmar, K., 2008b. Sex biases in parasitism of neotropical bats by bat flies (Diptera: Streblidae). J. Trop. Ecol. 24, 387–396.

Putze, S.A., Lane, D.J., Kingston, T., Lee, B.P.-H., 2005. The microchiropteran bat fauna of Singapore. Acta Chiropterol. 7, 237–247.

Presley, S.J., 2012. Sex-based population structure of ectoparasites from Neotropical bats. Biol. J. Linn. Soc. 107, 56–66.

Team, R.C., 2019. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria 2013 version 3.0. 2.

Ter Hofstede, H.M., Fenton, M.B., Whitaker, J., John, O., 2004. Host and host-site specificity of bat flies (Diptera: Streblidae and Nycteribiidae) on Neotropical bats (Chiroptera). Can. J. Zool. 82, 616–626.

Theodor, O., 1967. Illustrated Catalogue of the Rothschild Collection of Nycteribiidae (Diptera) in the British Museum (Natural History); with Keys and Short Descriptions for the Identification of Subfamilies, Genera, Species and Subspecies.

Venables, W.N., Ripley, B.D., 2013. Modern Applied Statistics with S-PLUS. Springer Science & Business Media.

Watanabe, S., 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. J. Mach. Learn. Res. 11, 3571–3594.