

Small Pteropodid Bats are Important Pollinators of Durian in Terengganu, Malaysia

Suey Yee Low¹, Muhammad Nur Hamzah Zulfemi¹, Siti Nor Shaffinaf Mohamad Shukri¹, Aida Hidayah Abu Samah¹, Hasrul Zaman Hassan Basri², Muhammad Haffidzie Mohd Shuhaimi², Harizah Nadiyah Hamzah¹, Muhammad Aidil Zahidin², Muhammad Syamsul Aznan Ariffin² and Nor Zalipah Mohamed^{1*}

¹Faculty of Science and Marine Environment, Universiti Malaysia Terengganu, 21030 Kuala Nerus, Terengganu, Malaysia

²Institute of Tropical Biodiversity and Sustainable Development, Universiti Malaysia Terengganu, 21030 Kuala Nerus, Terengganu, Malaysia

ABSTRACT

Bats are often misunderstood as agricultural pests and have received little attention for conservation efforts. However, bats are critical pollinators to commercially important agricultural products, such as durians. This study intends to confirm the role of small pteropodid bats as pollinating agents to flowering durian trees. Samplings were conducted in April 2018 to record bats visiting the flowers of two durian species, *Durio zibethinus* and *Durio lowianus* at Malaysian Agricultural Research and Development Institute (MARDI) Jerangau, Terengganu. Captured bats were swabbed for conspecific pollen load on their

bodies to determine their potential role as pollinators. One hundred thirty-one (131) pollen swabs were collected from three pteropodid bat species: *Eonycteris spelaea* Dobson, *Cynopterus brachyotis* Dobson, and *Cynopterus horsfieldii* Gray. Only *E. spelaea* and *C. brachyotis*, however, were found with conspecific pollen loads on their bodies. Between the two, *E. spelaea* showed a higher potential to be the pollinating agent for the durian trees. Hence, they recorded more individuals carrying many conspecific pollen grains while visiting the trees. Thus,

ARTICLE INFO

Article history:

Received: 29 March 2021

Accepted: 31 May 2021

Published: 20 August 2021

DOI: <https://doi.org/10.47836/pjtas.44.3.05>

E-mail addresses:

eulynnlow96@gmail.com (Suey Yee Low)

hamzah.hu29@gmail.com (Muhammad Nur Hamzah Zulfemi)

shaffinafshukri@gmail.com (Siti Nor Shaffinaf Mohamad Shukri)

aidahidayah.as@gmail.com (Aida Hidayah Abu Samah)

hasrulzaman93@gmail.com (Hasrul Zaman Hassan Basri)

m.haffidzie@gmail.com (Muhammad Haffidzie Mohd Shuhaimi)

nadiyahz2088@gmail.com (Harizah Nadiyah Hamzah)

aiditarsier@gmail.com (Muhammad Aidil Zahidin)

syamsulaznan@gmail.com (Muhammad Syamsul Aznan Ariffin)

zalipah@umt.edu.my (Nor Zalipah Mohamed)

* Corresponding author

this finding will hopefully reduce the misconceptions held on bats and conserve them in Malaysia.

Keywords: Conspecific pollen, *Cynopterus brachyotis*, *Durio lowianus*, *Durio zibethinus*, *Eonycteris spelaea*, pollen load, pollinating agent

INTRODUCTION

From 18 bat families worldwide, only two families: the Pteropodidae, which occurs in Paleotropical regions and the Phyllostomidae, which occurs in the Neotropical regions, are specialised floral visitors (Fleming et al., 2009). These bats have been identified as very active and regular flower visitors of many plant species, transporting large pollen loads on different parts of their bodies (Heithaus et al., 1974; Sazima & Sazima, 1978). Consequently, they are critical pollinating agents for approximately 250 plant genera (Fleming et al., 2009).

Many of the plants pollinated by bats (known as chiropterophilous plants) are endemics (Fleming & Muchhala, 2008), and many are of considerable economic value (Bumrungsri et al., 2013; Fujita & Tuttle, 1991; Kunz et al., 2011). In Malaysia and Thailand, for example, the pteropodid bats were reported as pollinating agents for ecologically and economically important plants such as durian (*Durio zibethinus*), bananas (*Musa* spp.), Indian trumpet (*Oroxylum indicum*), kapok tree (*Ceiba pentandra*), bitter bean (*Parkia speciosa*), and mangrove apples (*Sonneratia* spp.) (Acharya et al., 2015; Bumrungsri et al., 2013; Lim et al., 2018; Nor Zalipah et

al., 2016; Nuevo-Diego et al., 2019; Stewart & Dudash, 2017). Of these, durian was a vital cash crop for both countries. In 2015, for example, Malaysia and Thailand were reported to have exported a total of USD 405 million worth of durian (Mokhzani, 2017).

Despite being economically important pollinating agents, fruit growers deter the pteropodid bats from visiting their fruit crop trees (Aziz et al., 2016). Thus, resulting in failed fruit sets particularly, for the self-incompatible tree species such as durian (Bumrungsri et al., 2009; Lim & Luders, 1998). Therefore, this study highlighted the critical role of the pteropodid bats as pollinating agents in the agricultural area, not only to the durian (Genus *Durio*) trees they visited, but also to the other fruit crops they might visit during their foraging activities. The information gained from this study will help to reduce the misconception of bats as agricultural pests and consequently contribute to the conservation of the bat population in Malaysia.

MATERIALS AND METHODS

Study Site

The study was conducted at the Malaysian Agricultural Research and Development Institute (MARDI) Jerangau (4° 48' 370" N 103° 8' 680" E), located at Hulu Terengganu District in Terengganu, Peninsular Malaysia (Figure 1). The establishment of this station was to conduct research and development related to agriculture, food, and agro-based industries. Apart from office buildings, laboratories, and staff quarters, this station also consists of approximately

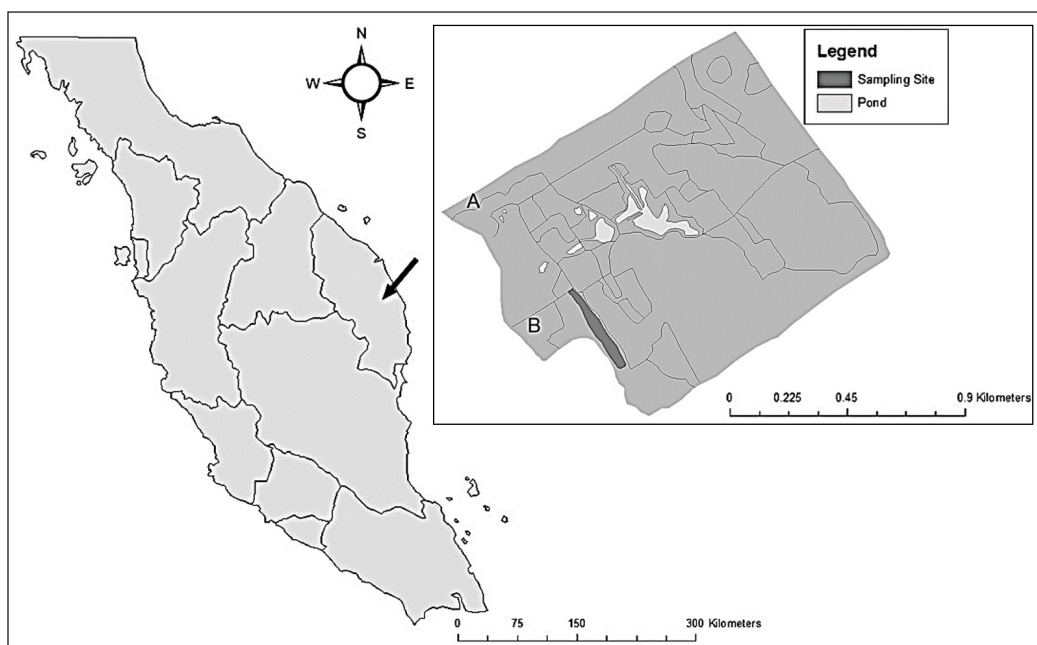


Figure 1. Arrow indicates the location of the sampling site at Hulu Terengganu, Peninsular Malaysia. Inset map shows the durian plantation area near the office (A) and staff quarter's compound; (B) where the mist nettings were conducted

145 ha of an orchard planted with various fruit crops such as durian (*Durio* spp.), banana (*Musa* spp.), mangosteen (*Garcina mangostana*), papaya (*Carica papaya*), and rambutan (*Nephelium lappaceum*) for various research and development activities. Of this area, approximately 145 ha is planted with eight durian species (*Durio dulcis*, *Durio graveolens*, *Durio kutejensis*, *Durio lowianus*, *Durio oxyleyanus*, *Durio oblongus*, *Durio singaporensis*, and *Durio zibethinus*), with the majority being *D. zibethinus* trees, the most cultivated species in the genus of *Durio* (Idris, 2011). At the study area, durian trees of all species were observed to flower simultaneously between March and April every year (N. H. Mohd Zainal Abidin, personal communication, July 22, 2019). This station is surrounded by

oil palm plantations manage by Terengganu Development and Management (TDM) Sdn. Bhd. and Federal Land Development Authority (FELDA).

Bat Trapping and Pollen Swab

Bat trappings were conducted on nine nights throughout April 2018, during the flowering time of the durian trees at the study area. We observed the peak flowering of *D. zibethinus* trees for the first three weeks of the month, followed by the peak flowering of *D. lowianus* trees on the fourth week when most of the *D. zibethinus* trees ceased flowering. Thus, trappings were conducted for six nights between April 5th and 21st for bats visiting the flowering *D. zibethinus* trees, and four nights between April 20th and 28th for bats visiting the flowering *D.*

lowianus trees. For each trapping night, a total of 5-14 nylon mist nets (height: 4 m, width: 9 m) were set up at 1800 h with the aid of two aluminium poles and placed close to the flowering trees. The nets were left open throughout the netting nights and were tended to usually in two-hour intervals, starting from 1900 h to 0100 h, and between 0600 h and 0700 h the following day. In Indonesia, the peak visitation of pteropodid bats to durian (*D. zibethinus*) flowers was observed between 2000 h and 2400 h (Sheherazade et al., 2019). Thus, the nets were checked as regularly as possible during this period to avoid distress and potential harm to the netted bats. In total, bat trappings were conducted for 696 and 348 net-hour for *D. zibethinus* and *D. lowianus*, respectively.

When bats were netted, nets were lowered, and the bats were screened for pollen loads. Sheherazade et al. (2019) reported that the head of pteropodid bats was usually in contact with the stigma and anthers while foraging at the durian (*D. zibethinus*) flowers. Therefore, the pollen grains adhering to the bat's head were collected by carefully rubbing cotton wool buds to their heads individually. The cotton wool buds were then kept in a 1 ml centrifuge tube containing 75% ethanol to preserve the pollen grains for pollen identification. Bats were then removed from the net, measured using a plastic vernier calliper (forearm length, ear length, tail length, and tibia length) and weighed using a digital balance (FEJ 600A, Colonial Weighing Australia Pty. Ltd, Australia). Species identification was made following

the keys provided by Kingston et al. (2006) and Francis (2008). Before being released at their point of capture, the bats were marked with non-toxic nail polish at the nail of their hind leg to give unique numbering for individual recognition upon recapture (Zulfemi et al., in press). Pollen swabs from recaptured individuals were considered distinct samples.

Pollen Observation and Identification

Pollen grains collected were observed under an optical light microscope (CH20, Metric Optics Sdn. Bhd., Malaysia) in the laboratory. For each sample, 1 µl of ethanol with pollen grains was transferred onto a glass slide using a micropipette for the microscopic observation. The microscope was attached with an eyepiece camera (84 mm length x 23 mm diameter, Dino-eye AM 423X, AnMo Electronics Corporation, Taiwan) to identify pollen. The pollen counts were conducted for ten slides for each sample, and the total number of pollen grains carried by the bats was extrapolated for 1 ml of ethanol. Pollen was identified by comparisons with known pollen types collected at the study area for references and by referring to Mohamed (2014).

Data Analysis

IBM SPSS Statistics (version 20) was used to analyse the data. A comparison of the number of pollen types carried by each bat species was conducted using the Kruskal-Wallis test. In contrast, Friedman's analysis of variance (ANOVA) for repeated measures was used to test the significant difference

(Field, 2013) in the number of pollen grains according to pollen types for *E. spelaea* and *C. brachyotis*. Wilcoxon sign-ranked test was used to determine the significant difference in conspecific and heterospecific pollen loads of *E. spelaea* and *C. brachyotis*. As the durian pollen grains could not be differentiated into their species level from observation under the light microscope, all of them were classified as conspecific. In contrast, the non-viable *Durio* pollen grains were grouped with the other non-durian pollen grains as heterospecific. On the basis that non-viable pollen also does not result in fertilisation (their relatively smaller size distinguished the non-viable *Durio* pollen grains by in comparison to the viable grains, and their translucent appearance when observed under the light microscope). Multiple comparisons (step-down method) were conducted following significant results of Kruskal-Wallis and Friedman's ANOVA tests for the data that violated the normality assumption.

RESULTS AND DISCUSSION

Bat Species Visiting Durian Trees

A total of 118 individuals of pteropodid bats were captured visiting durian trees, consisting of only three species: *Eonycteris spelaea* (lesser dawn bat), *Cynopterus brachyotis* (lesser short-nosed fruit bat), and *C. horsfieldii* (Horsfield's fruit bat). From the total individuals recorded, seven *E. spelaea* individuals and four *C. brachyotis* individuals were recaptured once, with one of *E. spelaea* recaptured twice. Thus, this study recorded 131 captures. The most frequently captured was *E. spelaea* ($\chi^2 = 67.99$, $df = 2$, $p < 0.05$), 81 captures, followed by *C. brachyotis* with 48 captures. At the same time, the least caught was *C. horsfieldii*, with only two individuals netted (Figure 2). The capture rates calculated was higher for *D. lowianus* (0.24 individuals per net-hour) than for *D. zibethinus* (0.07 individuals per net-hour), with *E. spelaea* as the most commonly caught bat species for both durian species (Table 1).

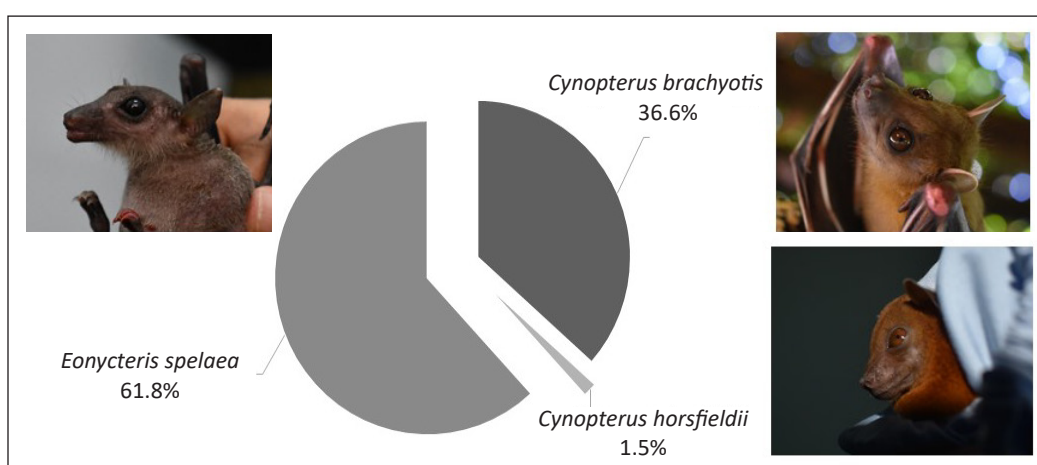


Figure 2. Number of captures (in %) for each bat species recorded at the Malaysian Agricultural Research and Development Institute (MARDI) Jerangau

Table 1

Capture rates (individuals per net-hour) of the pteropodid bats caught visiting durian trees at the Malaysian Agricultural Research and Development Institute (MARDI) Jerangau

Bat species	<i>Durio zibethinus</i>	<i>Durio lowianus</i>
<i>Eonycteris spelaea</i> (N = 81)	0.0330 (n = 23)	0.1667 (n = 58)
<i>Cynopterus brachyotis</i> (N = 48)	0.0316 (n = 22)	0.0747 (n = 26)
<i>Cynopterus horsfieldii</i> (N = 2)	0.0014 (n = 1)	0.0029 (n = 1)
Total	0.0661 (n = 46)	0.2443 (n = 85)

Note. N represents the number of captures for each bat species, and n represents the number of captures according to bat species for each durian species

Diet could explain the sequence of bat capture frequencies recorded in this study. As the nets were set up near the flowering durian trees, *E. spelaea* individuals were the most captured because it is one of the three specialised nectar-feeding bat species reported in Peninsular Malaysia (Gould, 1978). This bat species are known to feed mainly on floral resources such as nectar, pollen grains and flower petals of the chiropterophilous plants such as durian (Bumrungsri et al., 2013; Lim et al., 2018; Start & Marshall, 1976; Thavry et al., 2017). The other two specialised nectar-feeding bats in Peninsular Malaysia are *Macroglossus minimus* (long-tongued nectar bat) and *Macroglossus sobrinus* (long-tongued fruit bat). Both of which, however, were not recorded visiting the durian flowers in this study.

In contrast to *M. sobrinus*, which is reported as a more inland species, *M. minimus* lives in the coastal areas and has never been recorded away from mangrove areas. *Macroglossus* species are known to roost close to their food resources (within a 2 km radius) and do not commute long distances to feed (Start & Marshall, 1976).

Stewart et al. (2014) reported *M. sobrinus* as a flower visitor of durian trees in southern Thailand. Nevertheless, based on our nettings and their small travelling distance from their roosting site, both *Macroglossus* species are suggested, probably absent at our study site. *Eonycteris spelaea*, on the other hand, is a cave dweller known to travel long distances during the night in search of food (Ahmad Yazid et al., 2019; Start & Marshall, 1976), while *C. brachyotis* roosts under large leaves of trees, especially palms (Francis, 2008; Kingston et al., 2006; Tan et al., 1997). Both *C. brachyotis* and *C. horsfieldii* are common and abundant in all habitats, including orchards and plantations (Kingston et al., 2006). The presence of various fruiting and flowering trees at the study site, surrounded by oil palm plantations, provides abundant food resources and offers suitable habitat for these pteropodid bats.

Other than *C. brachyotis* and *C. horsfieldii*, *Cynopterus sphinx* (greater short-nosed fruit bats) and *Rousettus amplexicaudatus* (Geoffroy's rousette) were among the most common pteropodid bats caught visiting flowering durian trees and other chiropterophilous plants such as

banana (*Musa* spp.), Indian trumpet (*O. indicum*), and bitter bean (*P. speciosa*) in agricultural areas in southern Thailand (Sritongchuay et al., 2019; Stewart et al., 2014). These bats, particularly from the genus *Cynopterus*, are frugivorous, in which the most common component of their diet is fruit (Bumrungsri et al., 2007; Tan et al., 1998). Fruits are generally rich in energy but deficient in protein. Therefore, frugivorous bats are also known to visit flowering trees to consume floral parts and even leaves to fulfil their dietary requirements for protein (Rajamani et al., 1999).

Bats as Pollen Vectors in Agricultural Areas

Of the total 131 samples observed, 11 samples from *E. spelaea* and 14 from *C. brachyotis* were negative for pollen load. These 25 samples (19%) were thus excluded from further analysis.

A total of 12 pollen types were found on bat individuals with pollen load. These include *Durio* spp., *Sonneratia* spp., *C. pentandra*, *O. indicum*, *Elaeis guineensis* (oil palm), and six unidentified pollen types. In total, *E. spelaea* (n = 70) were found to carry the most significant number of pollen types which was 10 (1-5 pollen types per individual), followed by *C. brachyotis* (n = 34) with nine types (1-5 pollen types per individual). On the other hand, *Cynopterus horsfieldii* (n = 2) carried only *Musa* spp. and *Sonneratia* spp. pollen grains, which were also recorded for the other two bat species (Figure 3). Other than pollen grains of these two plant species, both *E. spelaea* and *C. brachyotis* were also found to carry five similar pollen types: *Durio* spp., *O. indicum*, *E. guineensis*, unknown pollen type A, and unknown pollen type B. The number (mean ± SE) of pollen types carried by *E. spelaea* (2.20 ± 0.13), *C. brachyotis*

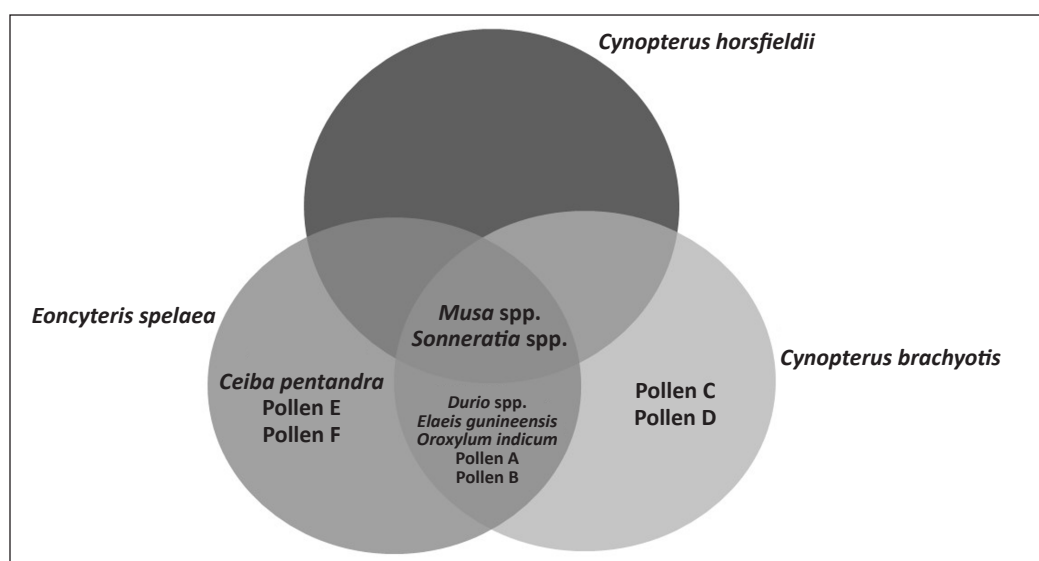


Figure 3. The Venn diagram of pollen types carried by the pteropodid bats caught at the Malaysian Agricultural Research and Development Institute (MARDI) Jerangau

(1.16 ± 0.17), and *C. horsfieldii* (1.50 ± 0.50) were found to be significantly different by the Kruskal-Wallis Test ($H = 8.876$, $df = 2$, $p = 0.012$), detected only between *E. spelaea* and *C. brachyotis*.

Results show that all bat species carried more than one pollen type on their bodies, indicating their visits to multiple tree species to fulfil their energy and nutrient requirements (Courts, 1998). Other than the chiropterophilous plants (*Musa* spp., *Durio* spp., *Sonneratia* spp., *C. pentandra*, *O. indicum*), pollen grains of oil palm (*E. guineensis*) were also recorded for *E. spelaea* and *C. brachyotis*. To our knowledge, oil palm has never been reported as a food source for pteropodid bats, even by Lim et al. (2018). Their study detected the plant materials occurring in the faeces of the pteropodid bats using DNA metabarcoding. These two bat species were reported to be the most common pteropodid bat species caught in the oil palm plantations in Malaysia (Mohd-Azlan et al., 2019; Syafiq et al., 2016), although no report indicated that they use oil palm plantations as a roosting site. Tan et al. (1997) reported that *C. brachyotis* could alter broad-leafed palms to form tents, while *E. spelaea* is a cave roosting species (Francis, 2008; Kingston et al., 2006). With oil palm pollen grains on the bats' bodies, it is unlikely that they roost in the oil palm plantation. Instead, they might collect the airborne pollen grains while manoeuvring through the plantations to get to the study site to forage for food.

Many chiropterophilous plants are of economic importance, highlighting a

significant contribution of the pteropodid bats to human society. For example, *Durio* spp., *Parkia* spp., and *O. indicum* are commercial cash plants in Southeast Asia (Bumrungsri et al., 2013; Fujita & Turtle, 1991). On the other hand, *Sonneratia* spp. are exclusive mangrove trees (Tomlinson, 1986), playing an important role to protect coastal areas with their ability to reduce wave magnitude (Mazda et al., 2006). Thus, suggesting a high ecological importance of these bats to Terengganu, a state with a long coastline and large mangrove areas (Mohd Lokman & Sulong, 2001). Furthermore, in Terengganu, this genus was demonstrated to be mainly pollinated by pteropodid bats foraging at their flowers (Mohamed & Adzemi, 2017; Nor Zalipah et al., 2016), further emphasising the importance of these bats to the coastal communities.

From the ten pollen types observed for *E. spelaea*, pollen grains (mean \pm SE) of *Durio* spp. were the most commonly found (344.29 ± 61.98), followed by *Musa* spp. (170.00 ± 49.11). These two pollen types were found to be significantly higher (Friedman's ANOVA, $\chi^2 = 248.62$, $df = 9$, $p < 0.001$) in the numbers of pollen load recorded for this bat species as compared to other pollen types (Table 2). On *C. brachyotis*, the most commonly found pollen grains were *Musa* spp. (311.76 ± 87.01), which was significantly the highest in the number of grains among the nine pollen types (Friedman's ANOVA, $\chi^2 = 153.49$, $df = 8$, $p < 0.001$). For *C. horsfieldii*, pollen grains of *Musa* spp. (350.00 ± 150.00) also recorded the highest in number, although the

Table 2

Number (mean \pm SE) of each pollen type carried by the pteropodid bats caught at the Malaysian Agricultural Research and Development Institute (MARDI) Jerangau

	<i>Eonycteris spelaea</i> (n = 70)	<i>Cynopterus brachyotis</i> (n = 34)	<i>Cynopterus horsfieldii</i> (n = 2)
<i>Durio</i> spp.	344.29 \pm 61.98 ^a	41.18 \pm 13.43 ^a	-
<i>Sonneratia</i> spp.	14.29 \pm 6.84 ^b	2.94 \pm 2.94 ^a	50.00 \pm 50.00
<i>Ceiba pentandra</i>	2.86 \pm 2.86 ^b	-	-
<i>Musa</i> spp.	170.00 \pm 49.11 ^a	311.76 \pm 87.01 ^b	350.00 \pm 150.00
<i>Oroxylum indicum</i>	1.43 \pm 1.43 ^b	79.41 \pm 79.41 ^a	-
<i>Elaeis guineensis</i>	132.86 \pm 124.22 ^b	5.88 \pm 4.10 ^a	-
Pollen A	11.42 \pm 3.83 ^b	17.65 \pm 7.87 ^a	-
Pollen B	34.29 \pm 14.80 ^b	2.94 \pm 2.94 ^a	-
Pollen C	-	100.00 \pm 94.03 ^a	-
Pollen D	-	2.94 \pm 2.94 ^a	-
Pollen E	2.86 \pm 2.01 ^b	-	-
Pollen F	24.29 \pm 11.41 ^b	-	-

Note. Different superscript letters indicate significant difference ($p < 0.05$) between the pollen types from Kruskal-Wallis Test conducted for *E. spelaea* and *C. brachyotis*

difference in comparison to the other pollen types (*Sonneratia* spp.) was not statistically significant due to the small sample size (only two individuals).

Sonneratia spp. and *Musa* spp. were not only found on all the bat species captured in this study but pollen grains of *Musa* spp. were found in high numbers in all bat species. *Musa* spp. are steady-state plants (Stewart & Dudash, 2018), which bear a few flowers every day for several months (Heithaus et al., 1975), hence providing enough food resources for bats over extended periods. *Sonneratia* spp. in Setiu, Terengganu were found to flower year-round but with different peak flowering times between species (Nor Zalipah et al., 2020). Indeed, both *Sonneratia* spp. and *Musa* spp. are highly reliable food sources for bat species to forage at as compared to *Durio* spp. which showed the big-bang

flowering strategy (Stewart & Dudash, 2018), in which plants flower massively only for a few days in a year (Gentry, 1974). The same finding was also reported by Thavry et al. (2017), in which pollen grains of *Sonneratia* spp. and *Musa* spp. were the main component in the diet of *E. spelaea* all year-round in Cambodia.

Other than *Musa* spp., Bumrungsri et al. (2013) concluded that *Parkia* spp. was the primary plant food source that provided pollen grains to *E. spelaea* continuously throughout the year in Thailand. However, pollen grains of *Parkia* spp. were not reported in our study for all bat species. During the peak flowering events of big-bang plants, pteropodid bats were found to switch their diets and utilise both the big-bang and steady-state plants (Bumrungsri et al., 2013; Stewart & Dudash, 2018; Thavry et al., 2017). The six unidentified pollen

types were not reported on bats' pollen load by Mohamed (2014) in the mangroves of Setiu, Terengganu. Nevertheless, the small number of grains recorded (except for Pollen C), contamination from airborne pollen was possible.

The pollen could also be from the 55 plant taxa listed by Lim et al. (2018) as an essential food source for the pteropodid bats in Peninsular Malaysia. However, no source of the plant parts (whether the plant materials in the faeces were pollen grain, seed, flower parts, and leaves) identified in the study was provided. Thus, we could not confirm the identification of the six unidentified pollen types recorded in our study. As digested pollen grains were generally corresponding to the pollen loads on the bats' bodies (Bumrungsri et al., 2013), foraging at the flower thus may result in the pollination of the flowers (Nor Zalipah et al., 2016; Stewart & Dudash, 2017). Nevertheless, the bats' function as pollen vectors in the agricultural areas should not be overlooked. With their high mobility (Horner et al., 1998; Marshall, 1983), pollen dispersal by bats will affect the genetic structure of the plant community, and hence has significant evolutionary consequences (Fleming & Kress, 2013).

Bats as Pollinating Agents of Durian Trees

Durian pollen grains were recorded on only two bat species and were not found on *C. horsfieldii*. However, from the total captured, 54% (38 individuals from the total 70) of *E. spelaea* and 23% (eight individuals from the

total 34) of *C. brachyotis* individuals were found with the conspecific pollen grains. Of these, five (7%) and two (6%) individuals of the former and latter species respectively were carrying only the conspecific pollen grains on their bodies at the time of their capture.

For these two bat species, however, the number of heterospecific pollen grains on the bats' bodies was higher than the conspecific pollen grains at the time of their capture (Figure 4). For *E. spelaea* the number (mean \pm SE) of conspecific pollen grains was only 211.43 ± 47.09 as compared to 527.14 ± 136.00 grains of heterospecific pollen (Wilcoxon signed-rank test, $T = 573.50$, $p = 0.001$). *Cynopterus brachyotis* recorded 532.35 ± 152.01 heterospecific pollen grains, notably higher than the 32.35 ± 11.73 conspecific pollen grains (Wilcoxon signed-rank test, $T = 533.00$, $p < 0.001$). *Eonycteris spelaea*, however, was found to carry a significantly higher number of conspecific pollen grains (211.43 ± 47.09) as compared to *C. brachyotis* (32.35 ± 11.75) as detected by the Mann-Whitney test conducted ($U = 762.50$, $p = 0.001$).

Conspecific pollen load on the bodies of flower visitors was recently proven to be a strong indication of the pollen transfer to the stigma of the flowers to initiate pollination (Stewart & Dudash, 2017). We reported more individuals of *E. spelaea* carrying conspecific pollen grains than *C. brachyotis*. The number of the conspecific pollen grains was also significantly higher than the latter bat species. Hence *E. spelaea* was a more important pollinating agent

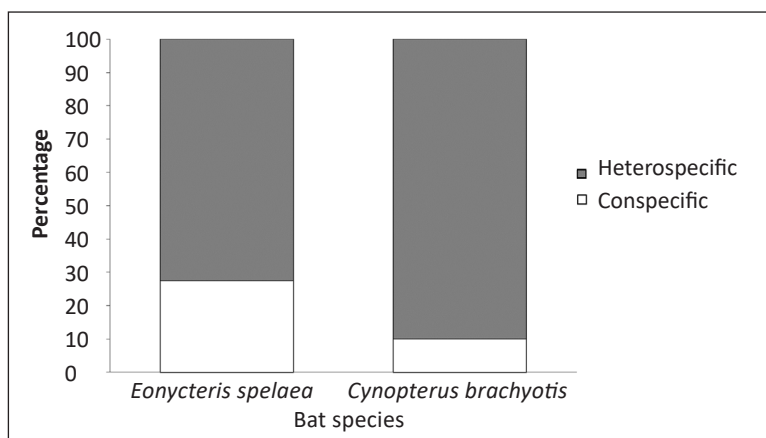


Figure 4. Composition of conspecific and heterospecific pollen grains observed for *Eonycteris spelaea* (n = 70) and *Cynopterus brachyotis* (n = 34) caught at the Malaysian Agricultural Research and Development Institute (MARDI) Jerangau

for durian than *C. brachyotis*. *Eonycteris spelaea*, as nectarivorous bats, was also touted to be the more important pollinating agent as compared to other frugivorous pteropodid bats (such as *C. brachyotis* and *C. horsfieldii*) foraging at *D. zibethinus* in agricultural areas in southern Thailand (Stewart & Dudash 2017; Stewart et al. 2014). Thus, not only *E. spelaea* visited the flowering durian trees significantly more often than the frugivorous bats, but the former also carried significantly more conspecific pollen grains on their bodies than the latter. For the frugivorous bats visiting flowering trees to forage for floral resources such as *Rousettus leschenaultii* (Leschenault's rousette) high visitation compensates for their low conspecific pollen load, thus also providing reliable pollination service to the trees they visited (Stewart & Dudash, 2017).

Another study has also reported *E. spelaea* as the principal pollinating agent of *D. zibethinus* in agricultural areas

of southern Cambodia (Thavry et al., 2017). A similar finding was also reported on semi-wild durian, which is sparsely distributed in secondary forests in managed agroforest areas in Sulawesi, Indonesia (Sheherazade et al., 2019). In that study, two larger pteropodid bats, *Pteropus alecto* (black flying fox) and *Acerodon cebelensis* (Sulawesi flying fox), were also pollinating agents of the durian trees. However, their visitation frequencies to the flowers were lower than those recorded by *E. spelaea*. Other studies in Peninsular Malaysia by Aziz et al. (2017) reported that a giant pteropodid bat on Tioman Island, the island flying fox (*Pteropus hypomelanus*), was a more effective pollinating agent for *D. zibethinus* as compared to *E. spelaea*. However, this giant pteropodid bat is confined only to islands in the Indo-Australian region (Francis, 2008). Thus, it is not present in the study area of the present study. Furthermore, compared to the small pteropodid bats, the two flying foxes recorded in Malaysia,

Pteropus hypomelanus and *Pteropus vampyrus* (large flying fox), are protected under the Wildlife Conservation Act (2010). Hence, less attention is given to the small pteropodid bats in Malaysia, probably due to underestimated economic and ecological functions. The information gain from this study nevertheless has contributed to a greater understanding of the importance of these small pteropodid bats.

CONCLUSION

Three small pteropodid bats, namely, *Cynopterus brachyotis*, *Cynopterus horsfieldii*, and *Eonycteris spelaea*, were captured when visiting flowering durian trees (*Durio zibethinus* and *Durio lowianus*) at agricultural areas in Hulu Terengganu. All three species were found to carry pollen grains on their bodies. *Cynopterus brachyotis* and *E. spelaea* carried multiple pollen types on their bodies, thus indicating their essential role as pollen vector and pollinating agents in the study area. *Cynopterus horsfieldii*, on the other hand, with only two individuals caught, recorded two pollen types, not including durian pollen grains. For the other two bat species, *E. spelaea* was likely to be a more important pollinating agent of durian than *C. brachyotis*. Not only was *E. spelaea* frequently captured near the flowering trees, but the majority of the captures were also found to carry a significantly high number of conspecific pollen grains on their bodies. High conspecific pollen load may contribute to the high potential of pollen transfer

from the bats' bodies to the stigma of the durian flowers they forage at, resulting in the pollination of the flowers. Hence, the small pteropodid bats in agriculture areas have high conservation value due to their essential role in pollinating the cash crop durian trees.

ACKNOWLEDGEMENTS

We want to thank Prof. Dr. Mohd Tajuddin Abdullah and Assoc. Prof. Dr. Nobuyuki Yamaguchi of the Institute of Tropical Biodiversity and Sustainable Development (Universiti Malaysia Terengganu) for their constructive comments and help with this article, and also the Faculty of Science and Marine Environment, for logistical support and equipment to conduct this research. The fieldwork was conducted with the permission of the Malaysian Agricultural Research and Development Institute (MARDI) Jerangau, Terengganu. We would also like to express our gratitude to Mr. Muhamad Zaki Bin Mohamed Nor, the Head of MARDI Jerangau, and his staff for their kind help and assistance throughout our sampling in 2018. Thanks are also due to Mr. Noor Hisham Bin Mohd Zainal Abidin, the current plantation manager of MARDI Jerangau, and ChM. Dr. Samsiah Jusoh, the current Head of Centre of Excellence, MARDI Jerangau, for providing information and constructive comments on preparing this article. This research was funded by Nagao Natural Environment Foundation (UMT Vot Number NAGAO53240/2018) awarded to M. Nor Zalipah.

REFERENCES

- Acharya, P. R., Racey, P. A., Sotthibandhu, S., & Bumrungsri, S. (2015). Feeding behaviour of the dawn bat (*Eonycteris spelaea*) promotes cross pollination of economically important plants in Southeast Asia. *Journal of Pollination Ecology*, 15(7), 44-50. <http://doi.org/10.26786/1920-7603%282015%295>
- Ahmad Yazid, N. N., Gunawan, S. H., Roslan, A., Nor Zalipah, M., & Abdullah, M. T. (2019). Note on pollen and seeds dispersed by pteropodid bats in Kenyir Forest Area, Terengganu. In M. T. Abdullah, A. Mohammad, M. Nor Zalipah, & M. S. Lola (Eds.), *Greater Kenyir landscape-social development and environmental sustainability: From ridge to reef* (pp. 171-179). Springer. https://doi.org/10.1007/978-3-319-92264-5_16
- Aziz, S. A., Clements, G. R., McConkey, K. R., Srithongchuay, T., Pathil, S., Abu Yazid, M. N. H., Campos-Arciez, A., Forget, P., & Bumrungsri, D. (2017). Pollination by the locally endangered island flying fox (*Pteropus hypomelanus*) enhances fruit production of the economically important durian (*Durio zibenthinus*). *Ecology and Evolution*, 7(21), 8670-8684. <https://doi.org/10.1002/ece3.3213>
- Aziz, S. A., Olival, K. J., Bumrungsri, S., Richards, G. C., & Racey, P. A. (2016). The conflict between pteropodid bats and fruit growers: Species, legislation and mitigation. In C. C. Voigt & T. Kingston (Eds.), *Bats in the anthropocene: Conservation of bats in a changing world* (pp. 377-426). Springer. https://doi.org/10.1007/978-3-319-25220-9_13
- Bumrungsri, S., Lang, D., Harrower, C., Sripaoraya, E., Kitpipit, K., & Racey, P. A. (2013). The dawn bat, *Eonycteris spelaea* Dobson (Chiroptera: Pteropodidae) feeds mainly on pollen of economically important food plants in Thailand. *Acta Chiropterologica*, 15(1), 95-104. <https://doi.org/10.3161/150811013X667894>
- Bumrungsri, S., Leelapaibul, W., & Racey, P. A. (2007). Resource partitioning in sympatric *Cynopterus* bats in lowland tropical rain forest, Thailand. *Biotropica*, 39(2), 241-248. <https://doi.org/10.1111/j.1744-7429.2006.00245.x>
- Bumrungsri, S., Sripaoraya, E., Chongsiri, T., Sridith, K., & Racey, P. A. (2009). The pollination ecology of durian (*Durio zibenthinus*, Bombacaceae) in southern Thailand. *Journal of Tropical Ecology*, 25(1), 85-92. <http://doi.org/10.1017/S0266467408005531>
- Courts, S. E. (1998). Dietary strategies of the Old World fruit bats (Megachiroptera, Pteropodidae): How do they obtain sufficient protein. *Mammal Review*, 28(4), 185-194. <https://doi.org/10.1046/j.1365-2907.1998.00033.x>
- Field, A. (2013). *Discovering statistical using IBM SPSS statistics* (4th ed.). Sage Publications.
- Fleming, T. H., & Kress, W. J. (2013). *The ornaments of life, coevolution and conservation in the tropics*. The University of Chicago Press.
- Fleming, T. H., & Muchhala, N. (2008). Nectar-feeding bird and bat niches in two worlds: Pantropical comparisons of vertebrate pollination systems. *Journal of Biogeography*, 35(5), 764-780. <https://doi.org/10.1111/j.1365-2699.2007.01833.x>
- Fleming, T. H., Geiselman, C., & Kress, W. J. (2009). The evolution of bat pollination: A phylogenetic perspective. *Annals of Botany*, 104(6), 1017-1043. <https://doi.org/10.1093/aob/mcp197>
- Francis, C. M. (2008). *A field guide to the mammals of South-East Asia*. New Holland Publishers.
- Fujita, M. S., & Tuttle, M. D. (1991). Flying foxes (Chiroptera: Pteropodidae): Threatened animals of key ecological and economic importance. *Conservation Biology*, 5(4), 455-463. <https://doi.org/10.1111/j.1523-1739.1991.tb00352.x>
- Gentry, A. H. (1974). Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica*, 6(1), 64-68. <https://doi.org/10.2307/2989698>

- Gould, E. (1978). Foraging behavior of Malaysian nectar-feeding bats. *Biotropica*, 10(3), 184-193. <https://doi.org/10.2307/2387904>
- Heithaus, E. R., Fleming, T. H., & Opler, P. A. (1975). Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology*, 56(4), 841-854. <https://doi.org/10.2307/1936295>
- Heithaus, E. R., Opler, P. A., & Baker, H. G. (1974). Bat activity and pollination of *Bauhinia pauletia*: Plant-pollinator coevolution. *Ecology*, 55(2), 412-419. <https://doi.org/10.2307/1935229>
- Horner, M. A., Fleming, T. H., & Sahley, C. T. (1998). Foraging behaviour and energetics of a nectar-feeding bat, *Leptonycteris curasoae* (Chiroptera: Phyllostomidae). *Journal of Zoology*, 244(4), 575-586. <https://doi.org/10.1111/j.1469-7998.1998.tb00062.x>
- Idris, S. (2011). *Durio of Malaysia*. Malaysia Agricultural Research and Development Institute.
- Kingston, T., Lim, B. L., & Zubaid, A. (2006). *Bats of Krau Wildlife Reserve*. Penerbit Universiti Kebangsaan Malaysia.
- Kunz, T. H., de Torrez, E. B., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, 1223(1), 1-38. <https://doi.org/10.1111/j.1749-6632.2011.06004.x>
- Lim, T. K., & Luders, L. (1998). Durian flowering, pollination and incompatibility studies. *Annals of Applied Biology*, 132(1), 151-165. <https://doi.org/10.1111/j.1744-7348.1998.tb05192.x>
- Lim, V. C., Ramli, R., Bhassu, S., & Wilson, J. J. (2018). Pollination implications of the diverse diet of tropical nectar-feeding bats roosting in an urban cave. *PeerJ*, 6, e4572. <https://doi.org/10.7717/peerj.4572>
- Marshall, A. G. (1983). Bats, flowers and fruit: Evolutionary relationships in the Old World. *Biological Journal of the Linnean Society*, 20(1), 115-135. <https://doi.org/10.1111/j.1095-8312.1983.tb01593.x>
- Mazda, Y., Magi, M., Ikeda, Y., Kurokawa, T., & Asano, T. (2006). Wave reduction in mangrove forest dominated by *Sonneratia* sp.. *Wetlands Ecology and Management*, 14(4), 365-378. <https://doi.org/10.1007/s11273-005-5388-0>
- Mohamed, N. Z. (2014). *The role of nectar-feeding bats (Pteropodidae) in pollination ecology of the genus Sonneratia at Setiu mangrove areas, Terengganu, Malaysia* [Unpublished Doctoral dissertation]. University of Bristol.
- Mohamed, N. Z., & Adzemi, A. F. (2017). Experimental pollinator exclusion of *Sonneratia alba* suggest bats are more important pollinator agents than moths. *Journal of Sustainability Science and Management*, (Special Issue 3), 17-23.
- Mohd Lokman, H., & Sulong, I. (2001). *Mangroves of Terengganu*. Penerbit Universiti Malaysia Terengganu.
- Mohd-Azlan, J., Kaicheen, S. S., Lok, L., & Lawes, M. J. (2019). The role of forest fragments in small mammal conservation in an oil palm plantation in Northern Sarawak, Borneo. *Journal of Oil Palm Research*, 31(3), 422-436. <https://doi.org/10.21894/jopr.2019.0034>
- Mokhzani, C. W. (2017, May 13). King of fruit. *The Star*. <https://www.thestar.com.my/business/business-news/2017/05/13/the-china-factor-in-durian-prices/>
- Nor Zalipah, M., Mohd Sah, S. A., & Jones, G. (2016). The potential significance of nectar-feeding bats as pollinators in mangrove habitats of Peninsular Malaysia. *Biotropica*, 48(4), 425-428. <https://doi.org/10.1111/BTP.12335>
- Nor Zalipah, M., Mohd Sah, S. A., & Jones, G. (2020). Flowering biology of mangroves (Genus *Sonneratia*) and the role of bats in their pollination in Peninsular Malaysia. In M. N. Grigore (Ed.), *Handbook of halophytes: From*

- molecules to ecosystems towards biosaline agriculture* (pp. 1-16). Springer.
- Nuevo-Diego, C. E., Stewart, A. B., & Bumrungsri, S. (2019). Pollinators increase reproductive success of a self-compatible mangrove, *Sonneratia ovata*, in Southern Thailand. *Tropical Natural History*, 19(2), 88-102.
- Rajamani, L., Aminah, A., Zubaid, A., Tan, K. H., & Kunz, T. H. (1999). Chemical composition of leaves consumed by the lesser dog-faced fruit bat, *Cynopterus brachyotis*, in Peninsular Malaysia. *Acta Chiropterologica*, 1(2), 209-214.
- Sazima, M., & Sazima, I. (1978). Bat pollination of the passion flower, *Passiflora mucronata*, in southeastern Brazil. *Biotropica*, 10(2), 100-109. <https://doi.org/10.2307/2388012>
- Sheherazade, Ober, H. K., & Tsang, S. M. (2019). Contributions of bats to the local economy through durian pollination in Sulawesi, Indonesia. *Biotropica*, 51(6), 913-922. <https://doi.org/10.1111/btp.12712>
- Sritongchuay, T., Hughes, A. C., & Bumrungsri, S. (2019). The role of bats in pollination networks is influenced by the landscape structure. *Global Ecology and Conservation*, 20, e00702. <https://doi.org/10.1016/j.gecco.2019.e00702>
- Start, A. N., & Marshall, A. G. (1976). Nectarivorous bats as pollinators of trees in west Malaysia. In J. Burley & B. T. Styles (Eds.), *Variation, breeding and conservation of tropical forest trees* (pp. 141-149). Academic Press.
- Stewart, A. B., & Dudash, M. R. (2017). Flower visiting bat species contribute unequally toward agricultural pollination ecosystem services in southern Thailand. *Biotropica*, 49(2), 239-248. <https://doi.org/10.1111/btp.12401>
- Stewart, A. B., & Dudash, M. R. (2018). Foraging strategies of generalist and specialist Old World nectar bats in response to temporally variable floral resources. *Biotropica*, 50(1), 98-105. <https://doi.org/10.1111/btp.12492>
- Stewart, A. B., Makowsky, R., & Dudash, M. R. (2014). Differences in foraging times between two feeding guilds within Old World fruit bats (Pteropodidae) in southern Thailand. *Journal of Tropical Ecology*, 30(3), 249-257. <https://doi.org/10.1017/S0266467414000042>
- Syafiq, M., Nur Atiqah, A. R., Ghazali, A., Asmah, S., Yahya, M. S., Aziz, N., Puan, C. L., & Azhar, B. (2016). Responses of tropical fruit bats to monoculture and polyculture farming in oil palm smallholdings. *Acta Oecologica*, 74, 11-18. <https://doi.org/10.1016/j.actao.2016.06.005>
- Tan, K. H., Zubaid, A., & Kunz, T. H. (1997). Tent construction and social organization in *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. *Journal of Natural History*, 31(11), 1605-1621. <https://doi.org/10.1080/00222939700770861>
- Tan, K. H., Zubaid, A., & Kunz, T. H. (1998). Food habits of *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. *Journal of Tropical Ecology*, 14(3), 299-307. <https://doi.org/10.1017/S0266467498000236>
- Thavry, H., Cappelle, J., Bumrungsri, S., Thona, L., & Furey, N. M. (2017). The diet of the cave nectar bat (*Eonycteris spelaea* Dobson) suggests it pollinates economically and ecologically significant plants in Southern Cambodia. *Zoological Studies*, 56(17), 1-7. <https://doi.org/10.6620/ZFS.2017.56-17>
- Tomlinson, P. B. (1986). *The botany of mangroves*. Cambridge University Press.
- Zulfemi, M. N. H., Low, S. Y., Mohamad Shukri, S. N. S., Abu Samah, A. H., Hassan Basri, H. Z., Mohd Shuhaimi, M. H., Hamzah, H. N., Zahidin, M. A., Ariffin, M. S. A., Nor Zalipah, M. (in press). Flower visiting bats to durian trees: Species richness and population size. *Journal of Sustainability Science and Management*.

