

FEEDING BEHAVIOUR OF THE DAWN BAT (*EONYCTERIS SPELAEA*) PROMOTES CROSS POLLINATION OF ECONOMICALLY IMPORTANT PLANTS IN SOUTHEAST ASIA

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Abstract—*Eonycteris spelaea* is recognized as the principal pollinator of most chiropterophilous plants in SE Asia. The present study describes its feeding behaviour and clarifies its role in cross pollinating these highly self-incompatible plants. Ten individuals of *E. spelaea* were radio-tracked during the flowering period of durian (*Durio zibethinus*) and petai (*Parkia speciosa*) in an agricultural mosaic in southern Thailand. *Eonycteris spelaea* makes a mean of seven visits per hour to these trees and 80-86% of each feeding bout involves visits to multiple conspecific trees. During each visit, 93% of *D. zibethinus* stigmas and 50% of *P. speciosa* stigmas were loaded with conspecific pollen. *Eonycteris spelaea* was the most common bat visitor to the trees. High visitation frequency and conspecific pollen deposition by *E. spelaea* to *D. zibethinus* and *P. speciosa* indicates that this nectarivorous bat is an effective pollinator. Mixed planting of chiropterophilous trees in fruit orchards is recommended to ensure regular visits of *E. spelaea*. Protecting natural roost caves of *E. spelaea* is also essential in order to maintain the vital ecosystem service provided by these bats.

Keywords: *Eonycteris*, effective pollination, *Parkia* spp., *Durio zibethinus*

INTRODUCTION

Although bat pollination is relatively uncommon among existing pollination systems, which rely heavily on insects, over 528 species of 250 genera of plants from tropical and subtropical regions show various degrees of dependency on bats for pollination (Dobat & Peikert Holle 1985; Fleming & Muchhala 2008; Fleming et al. 2009). Some of these plants are either economically valuable for human use as food and timber or ecologically important members of arid and semi-arid ecosystems of America and Africa and mangrove forests of Southeast Asia (Fujita & Tuttle 1991; Mickleburgh et al. 1992; Yetman 2007; Fleming et al. 2009, Kunz et al. 2011). In Southeast Asia, commercial crops such as durian (*Durio zibethinus*) and the canopy leguminous trees (*Parkia speciosa* and *P. timoriana*) generate millions of dollar each year through local and global markets (Fujita & Tuttle 1991; Lim & Luder 1997; Kingston 2010; Bumrungsri et al. 2013). A study of the pollination of *D. zibethinus* and *P. speciosa* by fruit bats in southern Thailand estimated crop values of 137 million USD in 2008 (Petchmunee 2008). Production of durian fruit is important for the livelihoods of farmers in several countries in South and Southeast Asia while durian production in some areas is low and erratic (Subhadrabandhu et al. 1991; Honsho et al. 2004) especially where nectarivorous bats have been exterminated.

Eonycteris spelaea is the largest nectarivorous bat in South and Southeast Asia. It was inferred from a diet study in west Malaysia that *E. spelaea* is a long distance forager (~38 km, Start 1974). More recently, radio-tracked bats were located up to 18 km from the roost cave in an agricultural mosaic (Acharya et al. in press). High mobility in bats is described as a potential factor in promoting gene flow between plants in fragmented habitats (Law & Lean 1996; Corlett 2004; Molina-Freaner et al. 2003; Fleming et al. 2009). The annual diet of *E. spelaea* consisted of over 31 plant species in the west Malaysian mainland (Start 1974) and eleven taxa in southern Thailand (Bumrungsri et al. 2013). *Durio zibethinus*, *Parkia* spp. and *Musa* spp. are major components of the diet of *E. spelaea* during their flowering season (Start 1974; Bumrungsri et al. 2013).

The pollination biology of *D. zibethinus* and two species of *Parkia* showed that they are highly or exclusively self-incompatible and require cross pollination for fruit set (Valmayor et al. 1965; Soepadmo & Eow 1971; Bumrungsri et al. 2008, 2009). Although insects were major visitors to inflorescences of *D. zibethinus* and a common visitor to *Parkia*, fruit bats, especially *E. spelaea*, have been identified as their principal or sole pollinators (Bumrungsri et al. 2008, 2009). The larger body surface of *E. spelaea* may facilitate more pollen transfer during each visit than insects. However, it is still unknown how the foraging behaviour of this bat promotes out-crossing between conspecific trees.

In pollination biology, the effectiveness of flower visitors as pollinators (Stebbins 1970), is measured by the number of compatible pollen grains transferred by a visit of the

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pollinator (Primack & Silander 1975; Fenster 1991; Mayfield et al. 2001) or the resultant fruit set after such a visit (Spears 1983; Schemske & Horvitz 1984). In addition, a legitimate pollinator is defined as a pollen vector that deposits conspecific pollen onto the stigma during a visit (Fleming & Sosa 1994). The objective of the present study was to describe the foraging behaviour of *E. spelaea* on *D. zibethinus* and *Parkia* spp. We hypothesized that this behaviour would promote out-crossing of these plants, and that *E. spelaea* is thus an effective and legitimate pollinator.

MATERIALS AND METHODS

Study species

Eonycteris spelaea

The dawn bat (*Eonycteris spelaea*) is a 40-80 g nectarivorous bat which normally forms large colonies inside large caves in the Oriental region, from the Indian subcontinent to Southeast Asia and Asia-Pacific as far as East Timor (Bates & Harrison 1997). The home-range size of *E. spelaea* in agricultural areas extends to almost 500 ha and the foraging area up to 60 ha (Acharya et al. in press). *Eonycteris spelaea* has a strong fidelity to its foraging areas, consistently using them for at least several months (Acharya et al. in press). It emerges from its roosts 43 ± 13 min (mean \pm SD, $N = 64$ nights) after sunset and spends 6 h 17 min \pm 1 h 56 min away from the cave. Mature females spent significantly longer foraging than mature males and immature individuals (Acharya et al. 2015).

The conservation value of *E. spelaea* across Southeast Asia is linked to its role as the pollinator of economically and ecologically important plants such as *Durio*, *Parkia* and coastal mangrove trees (Kingston 2010; Kunz et al. 2011; Bumrungsri et al. 2013). Although the IUCN Redlist categorises the species as "lower risk" (IUCN 2014), population declines have been recorded in *E. spelaea* colonies in Thailand (Bumrungsri et al. 2008). Cave tourism and harvesting for bushmeat are common threats to the bats in Southeast Asia (Mickleburgh et al. 2009).

Durio zibethinus and *Parkia* spp.

Durio zibethinus is a commercial species of the subfamily Bombacoideae (family Malvaceae), commonly planted in the countries of Southeast Asia (Brown 1997). Durian trees are characterized by ephemeral mass flowering as well as the classical syndrome of chiropterophilous flowers such as nocturnal anthesis, a musty smell and cauliflory (Faegri & van der Pijl 1979). The major durian flowering in our study areas occurred during April and May. The flowering period extended for only 2-3 weeks. Each night, durian flowers start to open in the late afternoon and anthesis occurs after dusk when the flowers have fully opened. The flowers are hermaphroditic and protogynous so that the stigma protrudes spatially beyond the anthers. Durian flowers begin nectar secretion in the late afternoon and cease when the floral parts including the corolla and androecia drop. Floral abscission occurs around 01h00 and all the flowers have dropped by 06h00. The nectar which accumulates up to 19h00 (the time when the bat activity

begins) was measured as c. 0.37 ml and the secretion rate thereafter was 0.05 ml h⁻¹ until floral abscission (Bumrungsri et al. 2009). The sucrose concentration of durian nectar was highest (21.9%) during the evening and then decreased gradually later in the night (Sripaoraya 2005; Bumrungsri et al. 2009).

Two species of *Parkia* (*P. speciosa* and *P. timoriana*) are common in both wild and cultivated areas of Southeast Asia. *Parkia speciosa* produces flowers from mid-May to mid-September while *P. timoriana* does so from October to December in our study sites. The inflorescences of *Parkia* spp. consists of compact biglobose bell heads called capitula each of which possess thousands of small tubular flowers. The capitula open during the evening for only one night. *Parkia speciosa* produces a few (up to 20) capitula while *P. timoriana* produces a greater number of capitula per tree per night. The flowering period of a tree lasts for 4-5 weeks in both species. We radiotracked the bats to flowering patches of *P. speciosa*, which is the preferred species by the villagers for cultivation.

Each capitulum of *P. speciosa* consists of three types of flowers: fertile (hermaphrodite), nectar-secreting and staminoidal (Hopkins 1984). Each capitulum comprises 2-3 thousand flowers, of which 70 to 75% are fertile (Bumrungsri et al. 2008). The capitula of *P. speciosa* begin to flower around 18h00 and anthesis and nectar secretion starts at 19h30. Each capitulum produces a nectar volume of 12.4 ml night⁻¹, with the highest volume and sucrose concentration from 20h00 to 21h00, which decreases gradually until 02h00 when nectar secretion ceases (Sripaoraya 2005; Bumrungsri et al. 2008).

Study Areas

This study was carried out in agricultural areas in Rattaphum district, Songkhla Province, Southern Thailand. We identified two colonies of *E. spelaea* in caves 10 km apart (Srikesorn Cave: 07° 04' 29.3" N, 100° 10' 07.4" E and Khaosoidao Cave: 06° 58' 53.91" N, 100° 08' 25.21" E). The land-use pattern within a 20 km radius around Srikesorn Cave consists of 26% tropical lowland forest (inside Ton Nga Chang wildlife sanctuary) and 74% agricultural mosaic and human settlements (data source: Southern GIS centre, Prince of Songkla University). The agricultural mosaic is dominated by rubber plantations (67%) with the remaining land used for fruit orchards and human settlements (33%). The fruit orchards comprise mixed fruit crops with various tropical fruits including durian (*D. zibethinus*), rambutan (*Nephelium lappaceum*), longsat (*Lansium domesticum*), mangosteen (*Garcinia mangostana*), santol (*Sanorium koetjape*), banana (*Musa* spp.), longan (*Dimocarpus longan*), mango (*Mangifera indica*), coconuts (*Cocos nucifera*), champoo (*Syzygium samarangense*) and palm (*Arenga* spp.). These orchards are patchily distributed in a flat lowland area along natural streams adjacent to tropical forest. *Parkia* trees were grown semi-wild or cultivated in house yards, fruit orchards, roadside and forest edges. Wild banana patches were found along the forest ravine and in early stage rubber plantations. Indian trumpet flower (*Oroxylum indicum*), cotton trees (*Bombax ceiba*) and kapok trees (*Ceiba pentandra*) were

sporadic food resources for nectarivorous bats in the study area.

Radio-tracking

Ten individuals of *E. spelaea* were radio-tracked, five of which foraged at *Parkia* patches and the other five at *Durio* patches. Bats were caught in mist nets as they emerged from the cave or at flowering patches of the trees at foraging areas. The tagged individuals comprised mature and immature males and females, none of which were pregnant or lactating. We used radio tags (PD-2C, Holohil Ltd., Canada, wt. 4.0 g with cable-tie collars; Biotrack, UK, wt. 2.26 g). The weight of the radio-tags comprises 4.3 to 6.9 % of bat's body weight. Bats were fed with sugar syrup and released after collar attachment. Portable receivers (TRX-1000S, and 3-element Yagi antenna; Wildlife Materials, Carbondale, Illinois, USA) were used to receive radio-signals. The bats were tracked mostly by walking through fruit orchards. We used the homing-in technique, i.e. the bats were followed to their feeding trees and night roosts (White & Garrott 1990; Amelon et al. 2009). The bats' positions were confirmed using the 'close approach' method i.e. the bats were directly observed either flying around the tree or landing on inflorescences to drink nectar (Law & Lean 1999).

Assessment of foraging movements and tree visitation

Eonycteris spelaea used one to three foraging areas, up to 8 km apart, in a night (Acharya et al. in press). The identified foraging areas were surveyed during the afternoon before each tracking night, potential food trees located and their flowering status noted. When the bats arrived in the area at night, the trees they visited were confirmed with the aid of radio-signals or through direct observation of bats visiting the trees. The foraging behaviour of a tagged bat was noted from its arrival to its departure from the foraging area. While foraging, *E. spelaea* established a night roost in each foraging area and foraged intermittently. The duration of each foraging movement is referred to as a foraging bout. The bats visited several flowers on one or more trees during each foraging bout.

We waited at flowering trees of *D. zibethinus* and *P. speciosa* and examined the bats visitation behaviour and their movement pattern along the patches. The foraging bout began when the bat flew away from the night roost to forage and ended when it returned to the night roost for resting. Whether the bat confined its feeding to a single tree or multiple trees was recorded for each foraging bout. While visiting a particular tree, whether the bat was alone or in a group was also recorded. The numbers of individuals involved in group visitations and the time of these visitations were also noted. Visits were defined as the landing of a bat on the flower, whereas hovering of a bat as it approached an inflorescence (which often shook the long pedicel of *P. speciosa*), was not recorded as a visit if the bat did not land on the capitulum. Light from head lamps and cameras was reduced to minimize disturbance of foraging bats.

Pollen load examination

The number of stigmas with pollen and the number of pollen grains deposited on the stigmatic surface by the bat during a single visit were examined for *D. zibethinus* and *P. speciosa* flowers. A durian inflorescence comprises up to a 100 tightly packed flowers, only some of which open in a night so that only some of them touch the bat's body surface during a single visit and this may result in an underestimate of pollen load. Hence opened flowers were thinned to adjust the cluster size to 5-10 flowers. All the flowers were carefully emasculated during the afternoon (before anthesis). The stigmas were first covered by drinking straws to prevent pollen mixing while removing anthers. The anthers were then excised using scissors. The emasculated inflorescences were enclosed in a plastic cage to exclude flower visitors. The plastic cage was removed at night until a single visit by a bat had occurred and it was then replaced. Capitula of *P. speciosa* were difficult to emasculate due to their complex structure and hence we caged the capitula in the late afternoon before anthesis, and again removed these at night. An infrared closed-circuit television (CCTV) camera was placed at least a metre away from the flower and the live video was monitored on a screen positioned at the base of the tree. Immediately after a bat had landed on a target flower and departed, we enclosed the flower again with the plastic cage and the stigmas were collected the next morning. We collected all stigmas of bat-visited inflorescences of durian, and randomly sampled fifty stigma tips of *P. speciosa*. Transverse sections of the stigma surface were mounted on slides using gelatinous fuchsin dye and the numbers of conspecific and heterospecific pollen grains were counted.

Bat survey at flowering patches

Mist nets of various lengths (6, 9, 12 or 18 m) were stretched between c. 4 m poles under or adjacent to the flowering patches of *D. zibethinus* and *P. speciosa* trees. Bats were captured for 3-4 hours during the night for a total of 36 mist net hours at six durian orchards and 40 mist net hours at five *P. speciosa* patches. The captured bats were identified to species using Francis (2008). Canopy foraging bats (*Pteropus spp.*) were counted directly against the sky background.

Data Analysis

The duration of foraging bouts was compared between durian and *Parkia* food patches using Wilcoxon Mann Whitney U tests. Individuals were identified first by capital letter for gender (M = male, F = Female), followed by a three digits to indicate the frequency of the transmitter (KHz) used to tag the bat. Mean \pm SD are used throughout.

RESULTS

Foraging bouts and movement pattern

Soon after sunset *E. spelaea* arrived at a foraging area and flew around for 5 to 10 min. They then flew to a night roost and rested for 2-3 min before commencing regular bouts of foraging. In each foraging bout, the bats visited a number of

TABLE I. Summary of feeding behaviour of radio-tagged *E. spelaea* on *D. zibethinus* and *P. speciosa*. Bat ID denotes first letter of the bat's gender (M = male, F = Female), followed by three digits to indicate the frequency of the transmitter (KHz) used to tag the bat. The values are given as mean \pm SD throughout with number of samples in brackets.

Bat ID	Major food patch	Foraging bout duration [min]	Multiple tree visits per bout [%]	Number of conspecific trees visited per bout	Percentage of lone visits to a tree by the bat	Visitation rate: trees per hr (range, N)	night roost distance in m from the feeding trees (range, N feeding trees)
M240	<i>D. zibethinus</i>	8 \pm 3 (46)	85 (45)	not available	59 (22)	3 \pm 4 (0-13, 12)	107 \pm 56 (50-232, 21)
F280a	<i>D. zibethinus</i>	12 \pm 12 (46)	100 (45)	not available	52 (25)	6 \pm 4 (0-14, 8)	336 \pm 106 (536-184, 20)
F280b	<i>D. zibethinus</i>	11 \pm 9 (20)	91 (20)	not available	31 (16)	9 \pm 8 (0-28, 12)	464 \pm 541 (92-1666, 14)
F288	<i>D. zibethinus</i>	10 \pm 4 (36)	92 (25)	not available	44 (16)	3 \pm 3 (0-6, 10)	797 \pm 679 (91-1681, 14)
M480	<i>D. zibethinus</i>	10 \pm 8 (44)	74 (42)	not available	77 (22)	12 \pm 13 (0-59, 29)	146 \pm 59 (48-282, 20)
F419	<i>P. speciosa</i>	13 \pm 9 (35)	79 (29)	4 \pm 2 (4)	81 (21)	7 \pm 6 (0-16, 19)	247 \pm 103 (50-382, 14)
F599	<i>P. speciosa</i>	10 \pm 10 (40)	90 (20)	3 \pm 1 (6)	70 (23)	8 \pm 3 (4-11, 10)	157 \pm 45 (97-235, 14)
M518	<i>P. speciosa</i>	7 \pm 7 (51)	93 (28)	3 \pm 1 (6)	71 (17)	16 \pm 13 (0-42, 10)	876 \pm 736 (87-1985, 17)
M619a	<i>P. speciosa</i>	10 \pm 10 (25)	81 (21)	3 \pm 1 (8)	74 (19)	7 \pm 3 (3-14, 16)	109 \pm 77 (31-245, 16)
M619b	<i>P. speciosa</i>	12 \pm 10 (25)	88 (25)	3 \pm 1 (5)	72 (25)	9 \pm 4 (4-19, 17)	160 \pm 140 (45-452, 16)

feeding trees and returned to the night roost. These roosts were established in each foraging area on a non-food tree with a dense canopy. The average distance between the feeding trees and primary night roosts was 372 \pm 439 m (range 31-1896 m, N = 166 from ten night roosts of ten bats). Additional night roosts were established when the feeding trees were more isolated and where the bat spent a few minutes before moving off to forage in another patch, finally returning to the primary night roost.

The duration of 367 foraging bouts was recorded for ten individuals, 192 bouts from five bats at *D. zibethinus* patches and 176 bouts from five bats at *P. speciosa* patches. The average foraging bout duration in durian patches was 10 \pm 8 min (range 1-48 min) and 10 \pm 9 min (range 1-59 min) in *P. speciosa* patches. The time allocated for foraging bouts by individual bats was not significantly different between *D. zibethinus* and *P. speciosa* patches (Wilcoxon Mann Whitney U test, W = 18029, P = 0.22). Foraging bouts tended to be longer as the night progressed.

Eonycteris spelaea visited multiple conspecific flowering trees for 86% of 123 recorded foraging bouts in *P. speciosa* patches and 88% of 179 recorded foraging bouts in *D. zibethinus* patches (Tab. I). The percentage of single tree visitation during foraging bouts was low (14% for *P. speciosa* and 12% for *D. zibethinus*). On average, *E. spelaea* visited 3 \pm 1 *P. speciosa* trees (range 1-7) during each

foraging bout. Durian trees were planted a few metres apart in orchards and hence it was difficult to assess the number of trees actually visited by the bat in each bout. However, we noticed that the tagged individuals confined themselves to a few durian trees during a particular foraging bout. The trees selected for such visits changed from night to night apparently based on flower availability. When foraging on *P. speciosa*, the bats did not concentrate on particular trees during foraging bouts and most of the trees were visited sequentially. Heterospecific tree visitations were not seen when the bats were feeding on *Parkia* or *D. zibethinus* during their major flowering periods, but were observed when a few flowers remained, after peak flowering. In addition to *D. zibethinus* and *P. speciosa*, several tagged bats were observed feeding on *O. indicum* and *Musa* spp.

Tree visitation

When a bat approached a flowering tree, it circled or flew beneath the canopy, passing close to the inflorescence, often hovering at exposed inflorescences of *P. speciosa*. However, *E. spelaea* was never seen extracting nectar from a flower while hovering. When feeding, it landed on an inflorescence transiently, for 1 to 2 seconds, and flew away. The visits were often repeated at the same tree and at the same or at a different inflorescence or, alternatively, the bats switched to another food tree with no rest. The inter-tree movement while foraging was not predictable but the bats

repeatedly used identical flight paths when approaching feeding trees.

While visiting trees, tagged individuals arrived alone at *D. zibethinus* for 64% of 101 observations and for 82% of 105 observations at *P. speciosa* trees (Tab. 1). Groups of up to seven individuals visited *D. zibethinus* trees and up to three individuals visited *P. speciosa* trees. Audible vocalizations of *E. spelaea* were common in durian patches but rare in *P. speciosa*. However, we did not see any agonistic behaviour, like chasing between the bats when they visited flowers.

Bats visited *D. zibethinus* tree 7 ± 10 times per hour (ranging from no visits to 59 visits, 5 bats observed for 71 hrs) and *P. speciosa* trees for 7 ± 6 times per hour (ranging between no visits to 42 repeated visits per hour, 5 bats observed for 72 hrs, Tab. 1).

Pollen load experiment

A total of 118 durian flowers in 30 inflorescences from 18 different trees were collected after single visits by a bat. The *Durio* inflorescences comprised of 4 ± 1 flowers. Ninety three percent of bat-visited stigmas were loaded with pollen grains. One hundred and ten of 118 (93%) stigmas received conspecific pollen while only eight of 118 (7%) received heterospecific pollen. Individual stigmas received 11 ± 18 conspecific pollen grains (range 1-27). Heterospecific pollen grains were observed in five of 30 inflorescences, mostly *Musa* spp. and a single case of *P. speciosa*. Each stigma with heterospecific pollen had 4 ± 4 (range between 1 and 12) grains of *Musa* pollen.

Twelve capitula of *P. speciosa* were collected after a visit by a bat. Fifty stigmas were randomly examined from each capitulum. In total, 600 stigmas were observed under a microscope to determine the number with a pollen load. Three hundred and thirteen stigma tips had received pollen grains, of which 301 (~96% of pollen load) were conspecific and 12 (~4%) were heterospecific (identified as *Musa* spp.). Of the 50 stigma tips examined from each capitulum, 25 ± 10 (range 12-40) were loaded with conspecific pollen comprising $50 \pm 20\%$ (range 24-80) of observed stigmas. Only two percent of capitula were found with heterospecific pollen grains.

Bat survey

A total of 149 bats were captured at durian orchards, and the majority were *E. spelaea* with 123 bats (83%), followed by *Rousettus* spp. (15 bats, 10%), *Macroglossus sobrinus* (9 bats, 6%) and the remaining 2% included one each of *Cynopterus* spp. and *Megaerops* spp. Two individual *Pteropus* were observed at one of the capture sites, foraging at the top of tall durian trees. In *P. speciosa* patches, 66 bats were captured, *E. spelaea* comprised 63 (95%), *M. sobrinus* 2 (3%) and *Cynopterus* spp. 1 (2%).

DISCUSSION

It is clear that *E. spelaea* typically visits multiple conspecific trees during most feeding bouts and feeds actively throughout the night. Additionally, each single visit

of nectarivorous bats, most of which are presumed to be *E. spelaea* based on the capture records, resulted in the deposition of conspecific pollen onto most of the stigmas of their food plants. Repeated visits to the feeding trees for several hours during the night can thus result in extensive pollen transfer between the trees. As a result, this foraging behaviour promotes cross pollination of these chiropterophilous plants. Since *E. spelaea* deposits quantities of conspecific pollen onto the stigma during every visit, we can thus claim that it is a legitimate and effective pollinator of these plants. This confirms and extends previous studies which reported that *E. spelaea* is the principal pollinator of the investigated chiropterophilous plants in mainland Southeast Asia (Bumrungsri et al. 2008, 2009; Srithongchuay et al. 2008). Durian fruit set in open pollination was as low as 0-1.4% in an orchard where bats were not seen foraging (Honscho et al. 2004). Acharya et al. (in press) found that a tagged bat moved between three isolated durian patches, eight kilometres apart when the durian was in flower, and when flowering ceased, confined itself to a single foraging area with *Parkia* and banana. The evidence of patch to patch movement by *E. spelaea* is thus crucial to the pollination of spatially separated chiropterophilous plants that are usually patchy in space and time in the human-modified landscape.

Eonycteris spelaea shows generally similar foraging behaviour in *Durio* and *Parkia* patches. The average number of foraging bouts, the inter-tree movement patterns and the tree visitation rates for *Durio* and *Parkia* feeders were almost identical. The size of foraging areas for *E. spelaea* at *Durio* and *Parkia* orchards was not significantly different (Acharya et al. in press). This identical foraging behaviour may be a compromise between energy expenditure of the bats and the nectar parcelling strategy of different plants. *Durio* trees produce abundant flowers but less nectar per flower than *Parkia* which produces fewer flowers but a higher nectar volume (Bumrungsri et al. 2008, 2009). *Parkia* inflorescences received more visits as the tree density and floral abundance is generally lower as compared to mass flowering and gregarious planting of durian trees in orchards.

The heterospecific pollen deposition on stigmas suggests that *E. spelaea* is a generalist nectarivore that visit different tree species in a night. Bats require a mixed diet to acquire the variety of nutrients they require, since these vary between different plants and plant parts (Courts 1998). Nectar is rich in sugar and water but poor in calcium, protein and lipids (Barclay 2002; Nelson 2003). In this study, *Musa* spp. and *O. indicum* were recorded as alternative food resources for *E. spelaea* in *Durio* orchards and *Parkia* patches. *Parkia* spp. and *Musa* spp are the major food resources for *E. spelaea* in the study area (Bumrungsri et al. 2013). Flowering times and positioning of anthers and stigma of these chiropterophilous plants limit outcrossing between heterospecific plants. For *O. indicum*, pollen is deposited on the dorsal surface of visiting bats (Srithongchuay et al. 2008), thus avoiding contamination with heterospecific plants. With such a strategy, those uncommon chiropterophilous plants can still benefit from cross pollination by *E. spelaea*.

Eonycteris spelaea shows strong fidelity to its foraging area and tagged bats regularly visit the same foraging areas for at least four months (Acharya et al. in press). The availability of other chiropterophilous plants such as *Musa* and *O. indicum* with aseasonal and steady-state flowering benefits nectarivorous bats by providing continuity of food supply throughout the year. The provision of alternative food resources for nectarivorous bats in fruit orchards is thus recommended, as it may encourage regular visits by bats, increasing the reliability of the pollination service for chiropterophilous fruit crops. Since the effective pollination period (i.e. the duration that flowers are still able to set fruit) of these plants is typically short, lasting only one night (Honsho et al. 2007), the reliability of pollinators is thus crucial for fruit set.

In conclusion, *Eonycteris spelaea* is a legitimate and effective pollinator of both *Durio* and *Parkia* in an agricultural landscape. Its high mobility means that it is capable of pollinating crops in a patchy agricultural landscape as well as those native plants in fragmented forests distant from the roost cave. Hence local populations of *E. spelaea* are crucial for natural pollination of chiropterophilous plants across the landscape. Protection of local colonies of *E. spelaea* and maintaining local chiropterophilous plant populations in the ecosystem is vital for pollination reliability and contributes to sustained production of fruit crops. Cave tourism, quarrying and bushmeat consumption are common threats to the cave bats in Southeast Asia and elsewhere (Mickleburgh et al. 2009) and should be controlled. Public education about the ecosystem service provided by bats should be undertaken especially in areas adjacent to bat colonies.

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