

Differences in foraging times between two feeding guilds within Old World fruit bats (Pteropodidae) in southern Thailand

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Abstract: Bats are important but understudied pollinators in the Palaeotropics, and much about their interactions with night-blooming, bat-pollinated plant species is still unknown. We compared visitation times to flowering and fruiting plant resources by nectarivorous bat species (obligate pollinators) and frugi-nectarivorous bat species (facultative pollinators) throughout the night to examine the temporal variability that occurs within Pteropodidae foraging. Timing of pollination is an important determinant of plant reproductive success and more temporally restrictive than fruit dispersal. We netted 179 nectarivorous bats and 209 frugi-nectarivorous bats across 367 total mist-net h at five plant species providing floral resources and six plant species providing fruit resources. We found that all three nectarivorous bat species in southern Thailand forage significantly earlier in the evening (20h30 versus 22h00), and over a significantly shorter time interval (1.73 h versus 3.33 h), than do the five most commonly netted frugi-nectarivorous species. These results indicate that the two feeding guilds may be imposing different selective pressures on bat-pollinated plant species and may comprise different functional groups. We propose that the observed differences in bat foraging times are due to temporal constraints imposed by the rewards of the plant species that they visit.

Key Words: chiropterophily, feeding guild, functional group, pollination, pteropodid, temporal variation

INTRODUCTION

Understanding species interactions is a key objective of ecology. Plant-pollinator relationships have long fascinated naturalists (Darwin 1862, Sprengel 1793), yet in spite of over two centuries of research, much of this field remains unexplored given the enormous diversity of pollination interactions found in nature (Faegri & van der Pijl 1966, Willmer 2011). Consequently, ecologists have devised means of classifying and organizing these diverse interactions to better understand them. Pollinators, for example, can be classified into functional groups based on the similar selective pressures they exert on plant species, and independent of their relatedness to one another, as a way of describing their interactions with flowers (Fenster *et al.* 2004). Insect taxa are commonly classified into different functional groups at the family or genus level (e.g. pollen-collecting bees and oil-collecting bees), but vertebrate pollinators have received less attention and

are more often grouped at the level of order, or even class, as is common with nectarivorous birds and bats (Faegri & van der Pijl 1966, Muchhala & Thomson 2010).

While flower-visiting bats have typically been categorized into a single functional group (Faegri & van der Pijl 1966, Muchhala & Thomson 2010), recent studies by Tschapka (2003) and Frick *et al.* (2013) have investigated the possibility that pollinating bat species differentially affect plant reproductive success, and thus comprise more than one functional group. These studies showed that a plant's reproductive success can vary greatly depending on whether it is pollinated by a nectar-specialist or an opportunistic visitor from another feeding guild. Furthermore, both studies proposed that the mechanism responsible for these differences was nectaring posture, with perching species delivering more pollen (Frick *et al.* 2013) or setting more fruit (Tschapka 2003) than hovering species. While there are no similar studies comparing the feeding guilds of pollinating bats in the Palaeotropics, we expected different findings from these Neotropical studies since Old World pollinating

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bats (family Pteropodidae) nearly always land on flowers rather than hover, even nectar-specialist pteropodids (Bumrungsri *et al.* 2008, Fleming *et al.* 2009, Marshall 1983).

Instead, we wanted to compare the foraging times of pteropodid feeding guilds, since floral visitation time is another mechanism through which pollinators can influence plant reproductive success. Floral visitation time is important since flowers often have a peak receptivity for gamete transfer, so animal species visiting at different times of the night may result in seed set that differ quantitatively and/or qualitatively (Groman & Pellmyr 1999, Howell & Roth 1981). Several studies have documented temporal partitioning in nectarivorous bats (Fischer 1992, Singaravelan & Marimuthu 2004, Thomas & Fenton 1978), and even slight differences in visitation time can have large impacts, particularly since most bat-pollinated flowers in the Palaeotropics are only open for one night (Bumrungsri *et al.* 2008, 2009; Faegri & van der Pijl 1966, Sritongchuay *et al.* 2008, Willmer 2011). Yet previous studies of foraging times have only compared the visits of two or three bat species at just one plant species, providing a limited view of this complex system (Bumrungsri *et al.* 2013, Marshall 1985).

To better understand real-world processes, we sampled the Old World bat community at bat-visited plant species in southern Thailand. Our objective was to examine the nightly foraging times of nectar-specialist bats and frugi-nectarivorous bats to compare temporal variation in their interactions with common bat-visited plant species. We hypothesized that these two groups would forage at different times during the night, given that they rely primarily on different food resources. Consistent differences between the foraging times of nectarivorous and frugi-nectarivorous bat species could indicate that these two feeding guilds are acting as distinct functional groups.

STUDY SITE

This work was conducted in southern Thailand across four provinces (Phatthalung, Satun, Songkhla and Trang) during July–August 2011. The region consists predominantly of lowland tropical rain forest interspersed with urban and agricultural areas. Bat-visited plant species are found in all habitat types. Bats were caught from a representative sample of lowland tropical rain forest, mangrove forest, rubber plantations and mixed fruit orchards. Average temperature, humidity and annual rainfall across southern Thailand are in the range 26.3–28.3°C, 76–84% and 1716–2725 mm, respectively (Thai Meteorological Department, www.tmd.go.th/en).

STUDY SPECIES

Many pteropodid bat species are abundant and important pollinators in southern Thailand (Bumrungsri *et al.* 2008, 2009; Sritongchuay *et al.* 2008). Common bat species include *Cynopterus brachyotis* (Muller), *C. horsfieldi* (Gray), *C. sphinx* (Vahl), *Eonycteris spelaea* (Dobson), *Macroglossus minimus* (Geoffroy), *M. sobrinus* (Andersen) and *Megaerops ecaudatus* (Temminck). Species can be categorized into two feeding guilds, nectarivorous and frugi-nectarivorous. Nectar-specialist *Eonycteris* and *Macroglossus* species have the elongated rostrums and tongues characteristic of nectarivores, and feed almost exclusively on floral resources. In contrast, the remaining species have relatively robust rostrums, short tongues, and consume both floral and fruit resources (Bumrungsri *et al.* 2007, 2013; Francis 2008, Hodgkison *et al.* 2004a, Marshall 1983, 1985). Most of the pteropodid species in this study predominantly roost in foliage, either solitarily or in small groups (Balasingh *et al.* 1995, Campbell *et al.* 2006, Kunz & Fenton 2003), but *E. spelaea* roosts colonially in limestone karst caves (Bumrungsri *et al.* 2009, Suyanto & Struebig 2007).

A number of common local plant species are known to be pollinated by pteropodid bats and exhibit an array of reproductive flowering strategies throughout the year. With respect to the food resources they provide, they all exhibit the following important floral traits: copious nectar production that peaks early in the evening as well as pollen dehiscence early in the evening (Bumrungsri *et al.* 2009, Sripaoraya 2005). Self-incompatible, bat-pollinated plant species in this study include *Durio zibethinus*, a big-bang species that can produce over 1000 flowers per tree per night (Bumrungsri *et al.* 2009, Gould 1978); *Oroxylum indicum* (Bignoniaceae), which flowers year-round in southern Thailand (Sritongchuay *et al.* 2010); *Parkia speciosa* (Fabaceae), which exhibits a cornucopia phenology, flowering from April to October; and four *Sonneratia* species (Lythraceae; Bureau of Mangrove Resources Conservation 2009): *S. alba* and *S. ovata* have a multiple bang phenology, *S. caseolaris* flowers year-round and *S. griffithii* is currently under study by the authors (Start 1974; A. Stewart, pers. obs.). Finally, *Musa acuminata* (Musaceae), the only self-compatible species (Andersson 1998) investigated here, also flowers continuously throughout the year (Gould 1978, Pillay & Tenkouano 2011, Sripaoraya 2005).

Bat-dispersed plant taxa bearing ripe fruit during the period of data collection included *Ficus* species (Moraceae), *Lansium domesticum* (Meliaceae), *Manilkara zapota* (Sapotaceae), *Nephelium lappaceum* (Sapindaceae), *Sandoricum koetjape* (Meliaceae) and *Syzygium cumini* (Myrtaceae) (Marshall 1985). *Ficus* fruits are a steady-state resource; while individual plants mass fruit, fruiting is not synchronous within or among species, such that

Table 1. Cumulative capture frequency (total number individuals netted/total number nights sampled) at bat-visited plant species in southern Thailand for each pteropodid species included in the analyses. Plant species listed along top (with number of nights in parentheses), from left to right: *Durio zibethinus*, *Musa acuminata*, *Oroxylum indicum*, *Parkia speciosa*, *Ficus* species, *Lansium domesticum*, *Manilkara zapota*, *Nephelium lappaceum*, *Sandoricum koetjape* and *Syzygium cumini*. Bat species listed along left side, from top to bottom: *Eonycteris spelaea*, *Macroglossus minimus*, *M. sobrinus*, *Cynopterus brachyotis*, *C. horsfieldi*, *C. sphinx*, *Megaerops ecaudatus*, *Penthetor lucasi*, *Rousettus amplexicaudatus*, *R. leschenaulti*. Asterisks denote nectarivorous species, all others are frugi-nectarivorous.

	Flowering					Fruiting					
	<i>Durio</i> (1)	<i>Musa</i> (12)	<i>Orox.</i> (6)	<i>Park.</i> (12)	<i>Sonn.</i> (4)	<i>Ficus</i> (11)	<i>Lans.</i> (3)	<i>Man.</i> (1)	<i>Nep.</i> (3)	<i>Sand.</i> (4)	<i>Syzy.</i> (1)
* <i>E. spe</i>	0	3.33	2.33	3.92	0	0	0	0	0.33	0.25	0
* <i>M. min</i>	0	1.58	0	0.17	2.75	0.27	0	0	0	0	0
* <i>M. sob</i>	2	2.33	0.17	0.17	0	0.55	0	0	0	0	0
<i>C. bra</i>	3	0.17	0.17	0.17	0	0.55	0	0	0.33	0.25	0
<i>C. hor</i>	2	1.25	0.67	0.75	0	2.27	0	0	1.67	2	1
<i>C. sph</i>	6	2.83	1.17	0.67	0	3.82	0.33	0	1.33	2.25	0
<i>Me. eca</i>	6	0.17	0	0	0	0.09	0	1	0	0	0
<i>P. luc</i>	0	0	0	0	0	0	0	0	0	0.25	0
<i>R. amp</i>	0	0	0	0	0	0	0.33	0	0	0	0
<i>R. les</i>	0	0	0	0	0	0	0	1	0	0	0

fruits are available year-round. All other focal fruiting species are big bang resources. In southern Thailand, *Ficus* and *S. cumini* are not cultivated, *S. koetjape* is both wild and cultivated, while *L. domesticum*, *M. zapota* and *N. lappaceum* fruits are cultivated.

METHODS

Assessing foraging times

We captured bats from 24 locations in southern Thailand (6°32'–7°46'N, 99°47'–100°16'E), which were all at least 1 km apart. Mist nets (polyester, 38-mm mesh; Avinet Inc., Dryden, NY) were placed near flowering and fruiting individuals of the aforementioned plant species to catch foraging bats. Sampling effort varied between 1–12 nights per plant species (Table 1), depending on availability; because sample sizes were small for several species, we grouped them into two categories (flowering versus fruiting resources) for analysis. Nets were open from 18h00 (sunset occurred around 18h40) until approximately 03h00 for a total of 33 nights between 1 July and 10 August 2011. Since previous work has demonstrated vertical stratification among fruit bats (Hodgkison *et al.* 2004b), we placed nets at a range of heights to obtain a representative sampling of foraging bats ($N \geq 6$ nights per height interval of 3 m, up to 12 m). Nets were positioned as close as possible to the flowers of bat-pollinated plants or to the fruits of bat-dispersed plants. Thus, any individuals caught were assumed to have been foraging at the plant species where they were netted. Additionally, placing mist nets close to vegetation made the nets less visible, allowing for relatively high capture success rates.

Nets were checked for bats at least every 30 min. For each netted individual, we recorded species, sex, reproductive status, time of capture, geographic coordinates, habitat type and the plant species at which the bat was netted. Individual bats were identified to species following Francis (2008). We then determined the bat's feeding guild (nectarivore or frugi-nectarivore) based on literature (Bumrungsri *et al.* 2007, 2013; Francis 2008, Hodgkison *et al.* 2004a, Marshall 1983, 1985) corroborated with personal observation of foraging choices made in the field (A. Stewart). Male reproductive classes consisted of juvenile and adult (determined from examination of phalangeal epiphyses); female reproductive classes consisted of juvenile, lactating, pregnant and non-reproductive (all following Kunz & Parsons 2009).

Statistical analysis

To assess whether bat feeding guild (nectarivore versus frugi-nectarivore), food resource type (floral versus fruit), or time influenced pollinator foraging behaviour, we used the GLIMMIX procedure in SAS 9.2 (SAS Institute Inc.) to perform a general linear model with mixed effects. In the mixed model, the dependent variable was capture rate (bats per mist-net h), with 1 mist-net h (mnh) defined as one net open for 1 h. The independent variables in the model were bat feeding guild, food resource type, time of night (specified as a class variable) as a random effect within feeding guild estimated using an autoregressive covariance matrix (AR1), and all two-way interactions. Degrees of freedom for all tests were estimated using the Kenward-Roger option. Additional covariates (species within feeding guild, sex, reproductive class) were initially incorporated but subsequently removed due to a lack

Table 2. A general linear model with mixed effects (GLIMMIX, SAS 9.2) demonstrates the effects of bat feeding guild (nectarivore or frugi-nectarivore), food resource type (floral or fruit) and time on pteropodid bat capture rates in southern Thailand. ndf, numerator degrees of freedom; ddf, denominator degrees of freedom.

	ndf	ddf	F	P
Bat feeding guild	1	77	6.37	0.01
Food resource type	1	49	1.73	0.19
Time	7	350	6.68	<0.0001
Feeding guild × resource	1	49	14.0	0.0005
Feeding guild × time	7	350	2.68	0.01

of model convergence. As two-sample Kolmogorov–Smirnov tests revealed no significant differences in foraging time distributions for these variables, data across species within feeding guild, sex and reproductive class were pooled for all subsequent analyses. The distribution was assumed Poisson with a log link and statistical significance was assumed if $P < 0.05$. Model fit was assessed by examining the raw and Pearson's residuals as well as DFBETA plots. The variability in the foraging periods of nectarivorous and frugi-nectarivorous bats were compared with F-tests using R 2.15.2 (R Development Core Team).

RESULTS

We netted a total of 388 pteropodid bats of ten species (Table 1; Appendix 1) over 367 total mnh; 229 mnh at flowering plants ($N = 35$ sites), 138 mnh at fruiting plants ($N = 23$ sites). The mixed model found that bat feeding guild, time, the feeding guild by resource interaction and the feeding guild by time interaction all significantly influenced bat capture rate (Table 2). While food resource type was not significant ($P = 0.19$), it was kept in the model since it was part of a significant two-way interaction. We found no evidence for a resource by time interaction ($P = 0.84$), so this term was removed from the model.

Frugi-nectarivorous bats had significantly higher overall visitation rates to all pooled food resources than nectarivorous bats ($P = 0.01$), but the significant feeding guild by resource interaction ($P = 0.0005$) revealed that visitation rate is dependent on food resource type (Figure 1a; Table 2). Specifically, nectarivorous bats strongly preferred flowering plants, visiting flowering plants (mean \pm SD, 0.68 ± 0.48 bats per mnh) over six times more frequently on average than fruiting plants (0.10 ± 0.15 bats per mnh), and frugi-nectarivorous bats preferred fruiting plants (0.78 ± 1.21 bats per mnh) over flowering plants (0.43 ± 0.57 bats per mnh), as expected.

As a whole, pteropodid bats did not have a constant foraging rate between 18h00 and 03h00 ($P < 0.0001$);

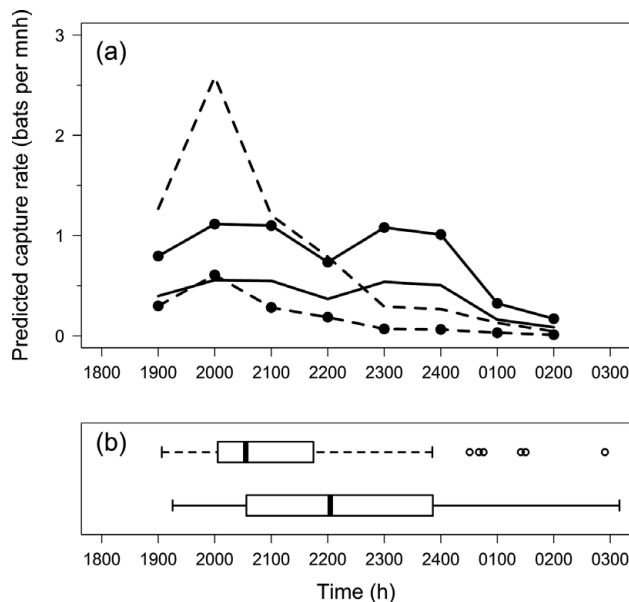


Figure 1. Foraging times of pteropodid bat feeding guilds at bat-visited plant species in southern Thailand throughout the night. Bat capture rates of nectarivores (dashed lines) and frugi-nectarivores (solid lines) at flowering (unmarked) and fruiting (circles embedded within lines) resources predicted from the generalized linear mixed model (a). Boxplots of observed nectarivorous (dashed line, $N = 179$) and frugi-nectarivorous (solid line, $N = 211$) bat nettings in southern Thailand, depicting the quartiles and outliers as defined based on 1.5 times the interquartile range (b).

instead, their foraging activity rose until 20h00 and then decreased until 03h00 (Figure 1a). This preference for early foraging was significantly stronger in nectarivorous bats than in frugi-nectarivorous bats ($P = 0.01$; Figure 1b); the median foraging time was 20h30 for nectarivorous bats ($N = 178$) and 22h00 for frugi-nectarivorous bats ($N = 211$). Foraging by nectarivorous bats also occurred over a significantly narrower period of time than foraging by frugi-nectarivorous bats (interquartile range, IQR = 1.73 h and 3.33 h, respectively; F-test, $P < 0.0001$; Figure 1b). Comparing the distribution of foraging time by bat species revealed that these results were not driven by any one species alone; all nectarivorous species had earlier and less variable foraging times than the frugi-nectarivorous species (Figure 2).

DISCUSSION

This study compared differences in the foraging times of Old World nectarivorous versus frugi-nectarivorous bats to examine their interactions with plants that depend on them for pollination and/or seed dispersal. We found that nectarivorous bats foraged significantly earlier in the evening, and over a significantly shorter time

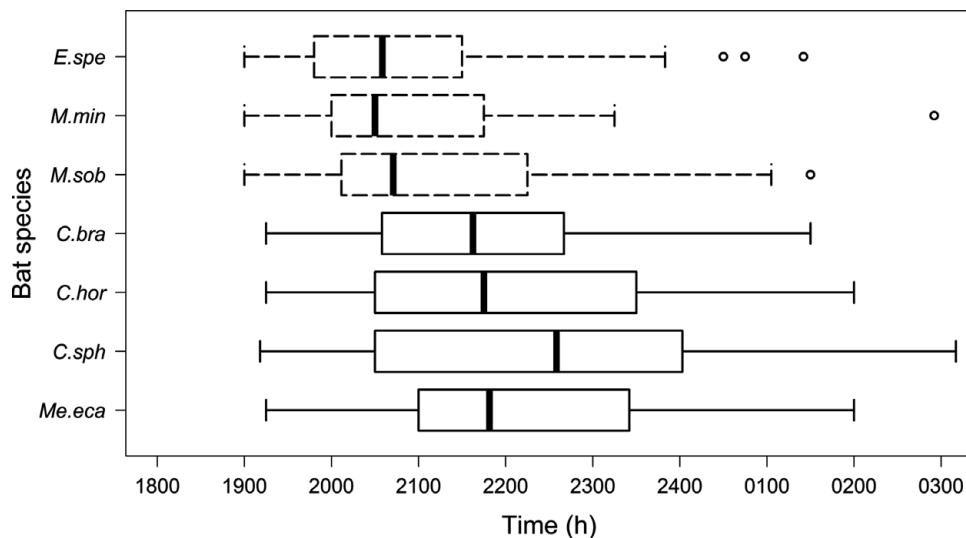


Figure 2. Boxplots displaying foraging time distributions of the most commonly netted nectarivorous (dashed lines) and frugivorous (solid lines) bat species encountered in this study (southern Thailand). Species (with number of bats netted in parentheses), top to bottom: *Eonycteris spelaea*, *E.spe* (105); *Macroglossus minimus*, *M.min* (35); *M. sobrinus*, *M.sob* (39); *Cynopterus brachyotis*, *C.bra* (16); *C. horsfieldi*, *C.hor* (69); *C. sphinx*, *C.sph* (111); *Megaerops ecaudatus*, *Me.eca* (10).

period, than frugivorous bats. Similar findings have been reported in the Neotropics; a number of studies have shown that frugivorous bat activity occurs throughout most of the night (Aguiar & Marinho-Filho 2004, Castro-Arellano *et al.* 2009, Pedro & Taddei 2002, Presley *et al.* 2009; but see Mancina & Castro-Arellano 2013), and La Val (1970) showed that early foraging activity is especially pronounced among nectarivorous bats. These differences between nectarivorous and frugivorous bats may result from a number of causes that are not mutually exclusive, including commuting distance between roost and foraging ground, meeting daily energetic requirements, interspecific competition, and/or the temporal resource constraints imposed by the plant species they prefer to visit.

If commuting distance were an important predictor of capture time, we would expect later capture times for bats commuting from rare, patchily distributed roosts (such as caves) than from abundant, uniformly distributed roosts (such as in foliage); cave roosts, on average, are farther from a randomly selected netting site than foliage roosts, and therefore require longer commute times, as was observed by Thomas & Fenton (1978). We would also expect greater variation in the capture times of bats commuting from cave roosts since the closest cave roost may be very near (short commute time) or very far (long commute time) from a randomly selected netting site, whereas the distance to the closest foliage roost is much less variable. Since nearly 60% of the nectarivorous bats in this study were cave-roosting *E. spelaea* and 94% of frugivorous bats in this study belonged to foliage-roosting *Cynopterus* spp., we would thus expect

nectarivorous bats to exhibit later and more variable capture times than frugivorous bats. We would particularly expect to see early capture times for frugivorous bats since previous work has shown that *Cynopterus* individuals typically forage within 500 m of their night roost (Funakoshi & Akbar 1997, Marimuthu *et al.* 1998) and several *Cynopterus* roosts were observed within the study area. Contrary to these expectations, capture times of nectarivorous bats were earlier and less variable than those of frugivorous bats, indicating that commuting distance is not a main predictor of arrival time at fruiting and flowering resources.

Several previous studies have suggested that phytophagous bats must begin foraging early in order to meet high daily energetic requirements, particularly since fruit and nectar are relatively poor food resources and flight is energetically costly (Mancina & Castro-Arellano 2013, Presley *et al.* 2009). Yet these requirements apply to both nectarivorous and frugivorous bat species, which does not directly explain why nectarivorous bat species forage earlier than frugivorous bat species. It is possible that differences in the nutrient composition of fruit versus floral resources (which include both pollen and nectar), and/or different nutrient requirements of the two feeding guilds, contribute to the observed foraging differences between nectarivorous and frugivorous bat species. Thus, the relationship between pteropodid diet composition, their dietary requirements, and the nutrient content of their food resources should be examined before making any conclusive statements.

Another possible explanation for the observed difference in frugivorous and nectarivorous bat

capture times is that species forage during different times in order to reduce interspecific competition at shared resources. Previous studies showing temporal partitioning between pairs of pteropodid species have, in fact, suggested that interspecific competition is a driving factor (Fischer 1992, Singaravelan & Marimuthu 2004), and it likely contributes to the differences in foraging times seen in this study. However, interspecific competition alone does not explain why nectarivorous bats foraged earlier than frugi-nectarivorous bats, rather than the reverse trend. Indeed, if interspecific competition were the main cause, we would expect to see temporal partitioning among nectarivorous species throughout the night, rather than observing concentrated nectarivorous-bat activity early in the evening. Thus, we propose that differences in the foraging times of frugi-nectarivorous and nectarivorous bat species are explained in large part by the resource constraints imposed by the plant species they visit.

Many plant species have overcome the challenges of immobility by relying on the services of animals to disperse their gametes (pollen) and offspring (seeds) (Barrett & Harder 1996), however, pollination and seed dispersal are precise processes that must occur within specific periods of time. A fruit that is removed from the plant too early will not be fully developed, while an uneaten fruit that drops to the ground beneath its parent plant faces limited dispersal and greater competition with its parent and siblings (Howe & Smallwood 1982). Likewise, there is an optimal timeframe for pollination; fertilization can only occur when pollen is mature and stigmas are receptive (Faegri & van der Pijl 1966). Thus, most animal-assisted plant species have adaptations that encourage pollinators and seed dispersers to perform their services within the optimal time period. For example, unripe fruits often contain secondary compounds that make them unpalatable (Cipollini & Levey 1997), and flowers typically produce the most nectar when they are receptive to pollination (Cruden *et al.* 1983, Martín-Rodríguez *et al.* 2009, Reynolds *et al.* 2009). This temporal variability in resource quality imposes selective pressures on the foraging times of pollinators and seed-dispersers; animals that forage when nectar and fruit are most palatable and abundant receive the greatest energetic benefits.

However, the temporal constraints that plants impose on pollinators are often more restrictive than those imposed on seed dispersers. This is particularly true among plant species visited by bats. While mature, bat-dispersed fruits are accessible for days, most bat-pollinated flowers are only open for a few hours (Bumrungsri *et al.* 2009, Faegri & van der Pijl 1966), providing a much narrower window of opportunity for their visitors. For example, *Oroxylum indicum* flowers begin opening around 19h00 and the corollas drop by

02h00 (Sritongchuay *et al.* 2008). Additionally, nectar production and sugar concentration typically decline over the course of a night (Elangovan *et al.* 2000, Elmqvist *et al.* 1992, Sriporaya 2005, Vikas *et al.* 2009; A. Stewart, unpubl. data), placing even stronger selection on early foraging. Aguiar & Marinho-Filho (2004) observed that Neotropical phytophagous bat species foraged early in the evening and also suggested declining nectar production throughout the night as a possible explanation. Since the nectar of a given flower is only available for a few hours, in contrast to a fruit which can be available for days, we might expect the foraging times of nectarivorous bats to be less variable than those of frugi-nectarivorous bats.

Indeed, our data reveal that nightly foraging by nectarivorous bats does occur within a narrower time range than that of frugi-nectarivorous bats. Furthermore, the interquartile range of nectarivorous-bat foraging activity occurs between 20h00 and 21h44, which coincides with peak nectar production times of bat-pollinated plant species reported in other studies (20h00–22h00; Bumrungsri *et al.* 2008, Elmqvist *et al.* 1992, Sritongchuay *et al.* 2008, Vikas *et al.* 2009; A. Stewart, unpubl. data). The interquartile range of all frugi-nectarivorous bat foraging activity (20h30–23h50) is not only broader, it is also later in the evening when nectar production has declined for many flowering plant species, which reflects their non-obligate reliance on floral resources.

Our results demonstrate that nectarivorous and frugi-nectarivorous bats appear to be acting as two distinct functional groups that are likely to impose different selective pressures on the plant species they visit. We propose that pteropodid bats utilize different foraging strategies that are shaped by the plant species they visit. However, confirming this hypothesis requires observation of bat-visited plant species throughout the year to verify that the results we observed are consistent across all months of the year, since flowering and fruiting seasons vary by plant species. Furthermore, future work should compare the relative contributions of different pteropodid species to the pollination success of the plant species they visit, as differences in floral foraging times by pollinating bats may translate into important differences in a plant's reproductive success. Given that the timing and duration of anthesis varies among different plant species, the outcomes will likely span a continuum from plant species that are greatly affected by foraging time differences, to species that are barely influenced. By studying the interactions of nectarivorous and frugi-nectarivorous bat species with the plants they visit, we can better understand plant-animal interactions and how these important visitors promote the reproductive success and genetic diversity of many agricultural and native plant species.

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Appendix 1. Number of bats (per species, sex, and reproductive class) caught foraging at bat-associated plant species in southern Thailand. Bat species, left to right: *Eonycteris spelaea*, *Macroglossus minimus*, *M. sobrinus*, *Cynopterus brachyotis*, *C. horsfieldi*, *C. sphinx*, *Megaerops ecaudatus*, *Penthetor lucasi*, *Rousettus amplexicaudatus*, *R. leschenaulti*. Asterisks denote nectarivorous species, all others are frugi-nectarivorous. Non-repro. = non-reproductive.

	* <i>E. spe</i>	* <i>M. min</i>	* <i>M. sob</i>	<i>C. bra</i>	<i>C. hor</i>	<i>C. sph</i>	<i>Me. eca</i>	<i>P. luc</i>	<i>R. amp</i>	<i>R. les</i>	Total
Male											
Juvenile	31	7	8	0	27	23	2	1	1	0	100
Adult	19	13	11	11	25	39	4	0	0	0	122
Female											
Juvenile	15	4	5	2	7	18	2	0	0	0	53
Lactating	20	3	8	3	7	17	2	0	0	1	61
Pregnant	8	0	0	0	1	7	0	0	0	0	16
Non-repro.	12	8	7	0	2	7	0	0	0	0	36
Total	105	35	39	16	69	111	10	1	1	1	388