

High-Resolution GPS Tracking of Lyle's Flying Fox Between Temples and Orchards in Central Thailand

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ABSTRACT Hunting and loss of natural habitats increasingly threaten tropical biodiversity and ecosystems, particularly in Southeast Asia. Flying foxes often persist in anthropogenic areas where other wildlife has vanished, and where they play a significant ecological role in vegetation regeneration in disturbed habitats. Detailed knowledge on the foraging behavior of flying foxes is crucial for understanding how they survive in degraded habitats and for the management of human-wildlife conflicts. Thailand still harbors large colonies (several thousand individuals) of Lyle's flying fox (*Pteropus lylei*), a species ranked as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List, at temples situated in agricultural landscapes. We used high-resolution global positioning system (GPS) loggers to study the movement and foraging behavior of this species at 2 temples in central Thailand during 2 seasons. We analyzed GPS and acceleration data of 19 tagged individuals, and assessed habitat use and diet. Foraging individuals commuted between day roosts and foraging areas each night, followed by small-scale movements in foraging areas, and showed high site fidelity during the study period. Maximum linear distances between day roosts and foraging areas varied greatly between individuals (2.2–23.6 km) but were similar between seasons. Tracked bats mostly foraged in farmland, plantations, and gardens, yet our data indicate that small mangrove remnants constitute important habitat components for Lyle's flying fox. We recorded a highly diverse diet of 34 food plant species, comprised of exotic crops and native plants as available. Our results suggest that conservation and landscape managers should preserve remaining native trees and natural vegetation in the study area as resources for Lyle's flying fox, at the same time reducing potential for conflicts between bats and humans on crops. They can further be used for public information campaigns integrating the potential of Lyle's flying fox as dispersers of useful plants and the human health risks through zoonotic diseases associated with hunting and consumption of this species. © 2015 The Wildlife Society.

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Anthropogenic influences are causing massive changes in many ecosystems worldwide, especially forested ones. We are only starting to investigate the consequences that these changes will have on individual species as well as the long-term health and stability of these ecosystems. Old World fruit bats (Chiroptera: Pteropodidae) constitute a particularly affected group of organisms. More than 289 plant species are known to depend on pollination and seed dispersal by Old World fruit bats, providing essential ecosystem services in different habitats of the Old World tropics (Start and Marshall 1976, Fujita and Tuttle 1991, Mickleburgh et al. 1992, Muscarella and Fleming 2007, Kunz et al. 2011). More than half of these plants are used by humans, accounting for 23% of products from human-used plants in the Old World tropics and thus being of great economic importance (Fujita and Tuttle 1991, Hodgkison et al. 2003). The genus *Pteropus* is the largest genus of Old World fruit bats and contains more than 50 species, with the majority of species occurring on oceanic islands and in (sub-) tropical Asia. The high mobility of these flying foxes, especially of the larger species, makes them particularly relevant pollinators and seed dispersers in degraded or fragmented landscapes (Corlett 2009). In general, their movement patterns are influenced by the spatio-temporal distribution of food and roosting resources (Nelson 1965, Eby 1991).

Despite their ecological importance and increased conservation attention, flying foxes are globally threatened by habitat loss and hunting (Fujita and Tuttle 1991, Mickleburgh et al. 1992, Corlett 1998). Species- and site-specific studies on foraging ecology in particular are rare (Banack 1998, Stier and Mildenstein 2005) but essential to understand the ecological role of flying foxes in their ecosystems. Most species of flying foxes are gregarious and roost in large colonies, yet roosting requirements and preferences, important for the understanding of population dynamics and the estimation of threats to the bats, are not well understood (Hahn et al. 2014).

In Southeast Asia, conditions for flying foxes are especially critical. The relative deforestation rate and associated wildlife habitat loss in Southeast Asia is the highest for all tropical regions (Sodhi et al. 2004). In Thailand, loss of natural forests exceeded 50% within 3 decades (1961–1998; Waggener 2001). In this context, expansion of agricultural lands must dramatically influence resource quantity and quality for flying foxes in the formerly forested habitats, raising the question if they are able to cope with these changes. In addition, hunting pressure is exceptionally high (Corlett 2007, Epstein et al. 2009, Harrison et al. 2011, Scheffers et al. 2012). Like many flying foxes, Lyle's flying fox (*Pteropus lylei*) is valued as bushmeat, used in traditional medicine, and persecuted as an orchard pest. As with most congeners, it is easy to hunt because of its large body size and formation of conspicuous colonies in trees (Fujita and Tuttle 1991; Mickleburgh et al. 1992, 2009). Loss of natural habitats also increases contact zones of humans and flying foxes, boosting the potential for human-wildlife conflicts as well as spillover events of zoonotic diseases with implications on human health (Epstein et al. 2006, Wolfe et al. 2007,

Daszak et al. 2012, Wood et al. 2012). In particular, Lyle's flying fox has been identified as host of Nipah virus, a human and livestock pathogen (Olson et al. 2002; Reynes et al. 2005; Wacharapluesadee et al. 2005, 2010). Adverse effects of this finding on the perception of flying foxes by humans could exacerbate anthropogenic threats to Lyle's flying fox and other flying foxes, creating a demand for studies that address the ecological benefits they provide to avoid potentially severe consequences on local ecosystems.

To fill some of these knowledge gaps, we targeted Lyle's flying fox in Thailand where this species occurs in a region that is densely inhabited by humans. Lyle's flying fox is 1 of only 2 *Pteropus* species restricted to the mainland, and the only *Pteropus* species in mainland Asia (Mickleburgh et al. 1992). This might imply particular ecological traits, but foraging ecology of Lyle's flying fox and its diet remain undocumented. The known distribution of Lyle's flying fox is limited to few colonies of several 100–1,000 individuals in Thailand, Vietnam, Cambodia, and a small disjunct area in southern China (Bumrungsri et al. 2008). The species is ranked as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List because of substantial population declines, and it is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; <http://www.cites.org/eng/app/appendices.php>, accessed 16 Apr 2014).

We employed high resolution global positioning system (GPS) telemetry to assess the ecological implications of Lyle's flying fox in an anthropogenic landscape, elucidating relations between nightly movements, activity patterns, resource use, and roosting behavior during 2 different seasons in Thailand. Understanding of these parameters is essential to develop conservation strategies as well as advance interdisciplinary research by assessing disease spillover risks based on flying fox ecology (de Jong et al. 2013). We anticipated that Lyle's flying fox is a central-place forager that returns to its respective day roost after foraging. Because natural vegetation was scarce in the study area, we predicted that the bats would have large foraging ranges of several kilometers to fulfill their requirements. We further expected to detect seasonal differences in the foraging behavior, based on spatio-temporal changes in resource availability. In addition to our assumption that Lyle's flying fox—like most of its congeners—feeds on a broad variety of plants, we aimed to investigate whether, and to what extent, it forages on exotic agricultural crops or native forest plants in a human-shaped environment, thereby evaluating the potential for seed dispersal or pollination. Based on our results, we assessed the ecological role of Lyle's flying fox for vegetation regeneration in an agricultural landscape and estimated impact on the local human population, ultimately providing information to mitigate conflicts between Lyle's flying fox and humans.

STUDY AREA

We captured most of the tracked bats from a colony roosting in the Wat Luang (WL) Buddhist temple ("Wat" in Thai; 13°30'18.90"N, 101°09'54.90"E), Chonburi Province in the

eastern part of Thailand Inner Gulf. The size of this colony fluctuated between approximately 8,300 and 12,700 individuals during a period from October 2005 to September 2006 (Wacharapluesadee et al. 2010). We caught additional bats from Wat Pho Bang Khla (WP; 13°43'20.30"N, 101°12'6.70"E), which is roughly 24 km north of WL in Chachoengsao Province. The WP colony comprised between approximately 7,000 and 18,800 individuals according to a recent count in 2010 (Hengjan 2011). The landscapes within a 20-km radius of the colonies had a well-developed infrastructure and were characterized by an agricultural matrix, lacking noteworthy patches of natural vegetation. Land use included farming of rice and other crops, orchards and gardens, plantations, fallows, and various animal farms, including fish and shrimp. The climate in the area is tropical-monsoonal, with a dry season from November to March, followed by a hot inter-monsoonal period until May, and a wet season from May to October.

METHODS

We collected data during 2 seasons in 2012: during the hot inter-monsoonal period in April and early May, and during the early dry season in November and early December. We caught flying foxes at WL during 7 afternoons between 1600 and 1800 hours in both seasons (24–26 Apr, 9–11 Nov, 21 Nov). At WP, we captured bats for tracking from 0500 to 0630 and from 1700 to 1830 hours on 17 and 18 November. We employed locally produced fishing nets, which were erected between the upper ends of 2 5–7-m-long bamboo or metal poles to capture bats when leaving the colony. We kept captured individuals in soft cloth bags until processed. We briefly anesthetized all individuals selected for tracking with an isoflurane inhalation to reduce stress to the animal and facilitate handling. We recorded body mass (in g) and forearm length (in mm) of all individuals, and determined sex and reproductive state. All techniques for capturing and handling of bats followed standard methods (Sikes et al. 2011). In parallel, national disease researchers collected anal swabs and blood samples to test for Nipah virus. Permits to capture bats were issued by the Department of National Parks, Wildlife and Plant Conservation in Thailand (DNP 0909.204/2686).

We deployed 32 GPS loggers (e-obs GmbH, Grünwald, Germany) on 30 adult males (WL Apr: 10, WL Nov: 10, WP: 10) and 2 adult females (WL Nov: 1, WP: 1). In April, most females were carrying young and thus we did not consider them for tracking to prevent extra load, stress, or abandonment of the young. The 2 females tracked in November were post-lactating. Mass of the GPS loggers used at WL (LiPo III) was 20.5 g and constituted 3.1–4.4% of the body mass (mean body mass \pm SD: 539.7 \pm 55.8 g, $n=21$), well below the 5% recommended for tracking devices of flying vertebrates (Aldridge and Brigham 1988). At WP, we used GPS loggers fitted with different batteries (Primary III) with a mass of 25.5 g, accounting for 4.3–6.1% of the body mass (mean body mass \pm SD: 533.6 \pm 60.5 g, $n=11$). This slightly exceeded 5% of the body mass in 2 tracked bats but remained below 10%, which is considered as

maximum threshold in bats weighing more than 70 g in several studies (O'Mara et al. 2014). We glued most loggers ($n=23$) between the scapulae with skin adhesive (Manfred Sauer GmbH, Lobbach, Germany) after trimming the dorsal fur, followed by a second layer of instant glue. Previous studies with other bat species have shown that this attachment method causes no injuries to the animals, and that loggers fall off within a period of 2 weeks. The last batch of loggers ($n=9$) was first superglued and then sewed on to T-shaped pieces of leather. We then tied these leather collars around the bats' neck with surgical thread (Safil C, B. Braun Petzold GmbH, Melsungen, Germany) that decomposes after about 1 month (O'Mara et al. 2014). All bats were hand fed with mangoes or bananas at the end of the handling procedure and subsequently released. We assigned bat identifications (IDs) that corresponded to the serial number of the logger attached.

GPS Loggers

The loggers were flexibly programmable to record GPS locations, 3-axial acceleration data, as well as flight speed and height. We obtained this information through remote download with a base station (Basestation b5, e-obs GmbH, Grünwald, Germany), which connected to the loggers with an ultra high frequency (UHF) radio link as soon as the base station was within reading distance of the logger (i.e., within a radius of 100–200 m). In addition, the loggers produced radio signals (i.e., pinger) 2 hours each day to allow localization of the bats with a radio receiver (AOR AR8200, AOR LTD., Tokyo, Japan) if they were outside the range of the base station. Both base station and radio receiver were connected with a 10-element Yagi-antenna (e-obs, Munich, Germany). Specifically, we applied the following settings: GPS on from 1759 to 0601 hours local time, pinger on from 1000 to 1200 hours, acceleration data collection 15 s/min at a byte count of 1,188 (56.23 Hz) on 3 axes during the entire runtime of the loggers, base station radio interval for data download of 20 seconds, and data collection stopped when battery voltage below 2.785 V (LiPo III) or 2.458 V (Primary III) to retain sufficient battery capacity for data download. We collected GPS fixes every 1,800 seconds when bats were stationary. As soon as bats started flying, the interval switched to 150 seconds. For more detailed information on the logger programming, please contact the authors or e-obs.

Corresponding to the pinger settings, we walked through the bat colonies every day between 1000 and 1200 hours for data download, scanning through the frequencies and approaching located loggers. The base station was operating simultaneously. When it established connection to a logger, data download started automatically. We transferred successfully downloaded data with a secure digital (SD) memory card from the base station to a notebook computer. We restricted all subsequent analyses to loggers from which at least 2 24-hour cycles of data were downloaded. In addition, we did not analyze data from the first night following logger attachment if not otherwise mentioned, to minimize potential effects of handling on the behavior of the

bats. We performed all *t*-tests and Mann–Whitney *U*-tests for statistical comparison of data samples with SIGMA-STAT Version 3.5 (Systat Software, San Jose, CA).

Spatial Data

We extracted GPS points with the decoder software provided by the logger manufacturers, and plotted them in Google Earth (Version 7.1). We also transferred all data to Movebank (www.movebank.org; Wikelski and Kays 2010), a global repository of animal movement data, where they are publicly visible. We used ArcView GIS 3.2a (ESRI, Redlands, CA) in Universal Transverse Mercator (UTM) coordinates (UTM zone 47N) to calculate cumulative distances flown per night and individual by connecting all GPS points from complete nights starting at 1800 until 0600 hours with straight lines. In addition, we measured maximum foraging distances for each individual from its colony to the most distant GPS point.

Based on the spatial context, we assigned GPS points to 3 categories: roost (all points in immediate vicinity of the colonies), commute (all points connecting a colony and a foraging area, or discrete foraging areas), and foraging (all points other than the day roosts where bats spent time at night but were not commuting). This classification was later visually checked for consistency and refined with acceleration data, whereby roost and forage included all behavioral categories described below, and commute was restricted to flight activity.

Acceleration Data

The acceleration sensor output reflects changes in the orientation of the logger as well as accelerated translational movements. We plotted acceleration data with the Movebank acceleration viewer tool (<https://www.3dyne.com/movebank-acceleration-viewer>, accessed 17 Nov 2013; Holland et al. 2009) that visualizes deflections of the device on 3 perpendicular axes. We assigned fruit bat behavior to 7 categories based on certain patterns in the acceleration data (see Fig. S1, available online at www.onlinelibrary.wiley.com): resting (sleeping or otherwise non-moving), moving (active but not flying), flying (15-second burst completely composed of flying activity, i.e., commuting between roosts and food trees or between food trees), fanning (continuous wing flapping in otherwise resting position), starting (flight activity set in during the 15-second burst), landing (flight activity stopped during the 15-second burst), and short flight (flight activity started and ended during the 15-second burst). We cross-checked classification of acceleration data with GPS points in Google Earth. We exported categorized acceleration data to Excel for further analyses.

To check for seasonal differences in activity patterns, we used only acceleration data of bats from WL, which were exposed to the same environment, for consistent data sets. Further, we restricted analyses to data of the second night and day after logger attachment, resulting in 24 hours of acceleration information for each individual ($n = 16$). Acceleration data of subsequent nights did not show significant differences in 3 randomly chosen individuals. We defined beginning of night at 1800 hours local time,

beginning of day at 0600 hours local time. We calculated the percentage of each behavioral category in the overall activity budget per night and day, as well as percentages of acceleration categories within certain GPS point categories at night.

Habitats and Diet

We visited most sites used by the bats at night for ground-truthing based on GPS points (27 Apr–8 May, 12 Nov–4 Dec 2012). We used a hand-held GPS receiver (Garmin GPSmap 62s, Garmin, Olathe, KS) to home in on the foraging individuals. The high data accuracy of the loggers allowed identification of feeding and roosting (groups of) trees of each bat. We noted the habitat type at each locality. We recorded information on feeding remains below trees, such as chewed pieces of fruits and/or bat droppings, if available and used this information to verify the actual use as a food tree and/or feeding roost. We identified all relevant trees, most of them to species level. To test for seasonal differences in food plant species composition of bats from WL, we computed a matrix of pairwise Sørensen distances based on presence-absence of food plants in the diet of each individual using PC-ORD 5 (MjM Software Design, Gleneden Beach, OR). We subsequently grouped distance values into inter- and intraseasonal pairings, for statistical comparison of dietary dissimilarity within and between seasons.

RESULTS

We downloaded data from 24 of the 32 GPS loggers. We excluded 5 of the 24 loggers from further analyses because the retrieved data did not cover a minimum of 2 24-hour cycles. The 8 loggers without downloaded data were most likely on bats that did not return to WL or WP within the battery lifetime of the logger for unknown reasons, or on bats that removed the logger while away from the colony. Data of the remaining 19 loggers resulted in 97 tracking nights and 6,076 GPS bearings (Table 1). On average, we collected data for 5.1 ± 1.6 nights per bat (range: LiPo III 3–8 nights, Primary III 5–10 nights). Mean number of GPS points per individual was 320 ± 124 (range: 182–705; Table 1). We obtained 11,347 acceleration bursts on the second night and 11,492 acceleration bursts on the second day after logger attachment from tracked bats from WL for both seasons.

Movement Patterns and Flight Distances

Movements of the tracked bats in the study area were characterized by commuting flights between day roosts and foraging areas, or between different foraging areas, and small-scale movements within the foraging areas (Fig. 1). Site fidelity to foraging areas was high for most individuals during the tracking period; the majority of tracked bats ($n = 13$) almost exclusively exploited the same foraging areas every night, up to a maximum of 10 nights (bat 2277; Table 1). The other individuals ($n = 6$) also repeatedly frequented the same localities but either included additional areas or shifted some localities during the tracking period.

The maximum linear distances from day roosts to foraging areas varied considerably between individuals (2.2–23.6 km;

Table 1. Number of tracking nights and global positioning system (GPS) points, maximum linear distances (all distances in km) between colonies in Wat Luang (WL) and Wat Pho Bang Khla (WP) and foraging areas (max. dist.), cumulative distances during the second tracking night (cum dist n2), and mean cumulative distances (cum dist \bar{x}), with mean and standard deviation (SD) values, of 16 tracked males of Lyle's flying foxes at WL and 3 tracked males of Lyle's flying foxes at WP, Thailand, in 2012.

Locality	Season	Bat ID	No. nights	No. GPS points	Max.dist	Cum dist n2	Cum dist \bar{x}	
WL	Apr May	2268	4	259	3.8	11.6	13.6	
		2272	4	228	5.2	14.8	14.6	
		2274	8	392	7.1	13.3	16.7	
		2286	5	268	8.7	30.8	25.1	
		2289	5	319	5.5	17.4	16.0	
		2292	5	249	12.7	28.6	21.7	
		2296	5	312	17.1	14.1	24.6	
		2298	5	251	16.1	4.8	17.5	
		2299	5	312	18.5	38.0	39.1	
			\bar{x}	5.1	287.8	10.5	19.3	
WL	Nov	SD	1.2	50.8	5.7	10.8		
		2269	3	185	9.2	20.2	20.7	
		2270	5	253	9.7	25.2	22.9	
		2273	4	311	22.3	43.8	44.5	
		2287	3	182	17.1	31.8	31.8	
		2290	6	521	19.0	42.7	41.4	
		2293	4	264	15.0	25.9	27.2	
		2295	6	424	2.2	8.9	8.3	
			\bar{x}	4.7	305.7	13.5	28.4	
			SD	1.3	125.7	6.9	12.3	
WP	Nov	2276	5	343	7.2	29.4	16.7	
		2277	10	705	4.0	11.2	10.0	
		2284	5	298	23.6	49.2	49.5	
			\bar{x}	6.3	448.7	11.6	29.9	
			SD	2.5	223.1	10.5	19.0	
Total			97	6,076				
	\bar{x}		5.1	319.8	11.8	24.3		
	SD		1.6	123.7	6.6	12.9		

Table 1). Mean maximum distances recorded at WL during November (13.5 km) were longer than during April (10.5 km), but this was not statistically significant ($t=0.96$, $P=0.356$). Both mean cumulative nightly distances per individual, and cumulative distances of second tracking nights, also varied considerably among individuals (mean: 8.3–49.5 km; second night: 4.8–49.2 km; Table 1). As with maximum linear distances, mean values for cumulative distances recorded in November exceeded values in April (Table 1) but did not differ statistically (mean: $t=1.39$, $P=0.185$; second night: $t=1.57$, $P=0.137$).

Activity Patterns

There were no seasonal differences between nightly activity budgets of the tracked bats based on behavioral categories from acceleration data. The time used for commuting as determined with GPS and acceleration data was not significantly higher in November ($8.0 \pm 3.9\%$; Table 2) than April ($4.9 \pm 3.4\%$). However, bats spent significantly more time at foraging areas and less at the day roost in November compared to April (Table 2). Activity budgets during the time spent in foraging areas were similar in both seasons. During the day, only the categories fanning (higher in Apr) and moving (higher in Nov) showed significant seasonal differences (Table 2).

Habitat Use and Diet

Habitat use of tracked Lyle's flying foxes of both colonies reflected the agricultural landscape of the study area, and the lack of natural habitats. All 19 individuals foraged

almost exclusively in orchards, plantations, mixed tree rows planted as living fences between fish or shrimp ponds, farm yards, fallows, and tree stands alongside roads. More than half (52.6%; $n=10$) of the tracked individuals visited temples other than WL and WP for feeding and roosting at night. Almost a quarter (21.1%; $n=4$) of the bats occasionally foraged in small patches of mangrove remnants along rivers. Given the anthropogenic character of the study area, the number of potential contact zones and encounters between bats and humans as well as domestic animals was high.

Based on the tracking data of 1 individual from WL in November (bat 2287), which did not return to the temple colony for some days, we discovered an additional day roost of Lyle's flying fox ($13^{\circ}35'21.26''N$, $101^{\circ}02'01.63''E$). This colony was located in a narrow strip of mangrove trees in a swamp area along the Bang Pakong River, 17 km northwest of WL and 23 km southwest of WP. It comprised approximately 1,000–2,000 individuals at the time of visit, and bats used *Avicennia alba* as roosting trees.

Assessment of diet included data of all tracking nights of the 19 bats, including the first night after logger attachment. The bats used 34 plant species as food, predominantly fruits (Table 3). Consumption of leaves and flowers is generally difficult to detect with ground-truthing because feeding signs are barely traceable, but we included 3 non-fruiting plant species (*Acacia auriculiformis*, *Eucalyptus* sp., *Markhamia stipulata*) on the list because GPS data provided high evidence for their use.

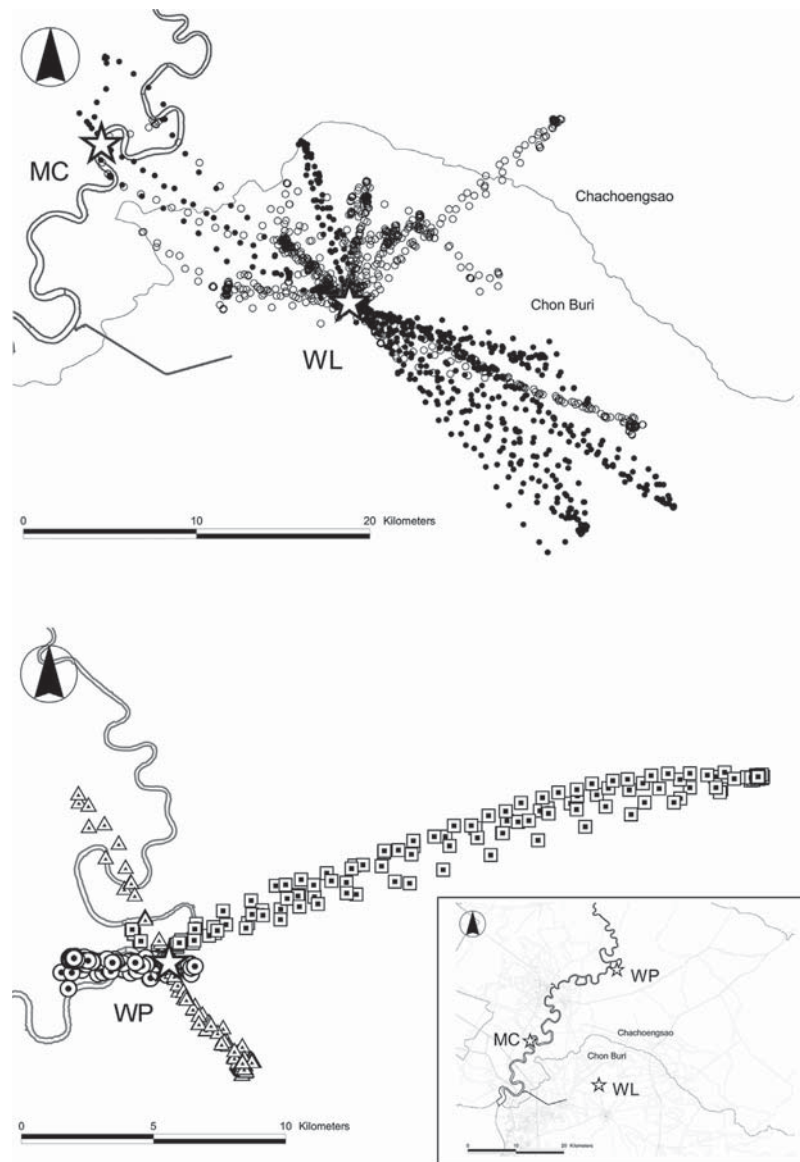


Figure 1. Global positioning system (GPS) tracks of 19 Lyle's flying foxes in Wat Luang (WL) and Wat Pho Bang Khla (WP), Thailand, 2012 (stars: colonies, MC: mangrove colony). Above: WL and MC (empty circles: Apr–May, solid circles: Nov). Below: WP (triangles: bat 2276, squares: bat 2284, circles: bat 2277). Bang Pakong River plotted as dark grey doublet in all maps.

Overall, mango (*Mangifera indica*) was the most frequently eaten fruit, which was consumed by 10 bats. Bananas (*Musa* sp.) ranked second ($n=7$ bats), and tamarind (*Tamarindus indica*) third ($n=6$ bats). Figs (*Ficus* spp.) represented the most common genus with the highest percentage in the total number of food plant species (20.6%, $n=7$). Almost half of the 34 food plant species (47.1%, $n=16$) were each consumed by only 1 individual. For both study periods, the list of food plants comprised various native species such as Chinese fig (*Ficus microcarpa*), monkey jack (*Artocarpus lakoocha*), ivy gourd (*Coccinia grandis*), and gaub tree (*Diospyros malabarica*) as well as introduced trees, for example strawberry tree (*Muntingia calabura*), papaya (*Carica papaya*), and cashew (*Anacardium occidentale*). All of the fruits consumed by the bats are considered useful for humans to some degree, and many of

them are likely dispersed by the bats. Some fruits are of high economic value such as mango and cashew. Others, such as the native fig trees, are appreciated for their shade. The mangrove apple (*Sonneratia caseolaris*) constitutes the only species that does not grow on agricultural land, and it was restricted to the only mangroves in the study area along the Bang Pakong River.

Diet of the bats varied between seasons. The overall number of food plant species recorded during November ($n=27$) was considerably higher than during April ($n=17$). In addition, we recorded more food plant species exclusively in November ($n=17$) than in April ($n=7$). Composition of food plant species was less similar between individuals during different seasons than within seasons (Mann–Whitney U -test: $T=2,903$, $P=0.002$; Fig. 2). Tracked bats tended to use a higher number of food plant species per individual in

Table 2. Percentage of night-time spent in each global positioning system (GPS) category (commuting, foraging, roosting) and activity budgets (%) based on 24 tracking hours of 16 Lyle's flying foxes (Apr–May $n = 9$, Nov $n = 7$) from Wat Luang, Thailand, 2012. We used Mann–Whitney U -tests or t -tests to compare between seasons (Apr–May vs Nov). The 2 behavioral categories rest and flight highlight that tracked bats showed similar activities in foraging areas during different seasons.

	Apr–May			Nov			Mann–Whitney U -test			t -test	
	\bar{x}	SD	median	\bar{x}	SD	median	T	P	t	P	
GPS categories											
% commuting	49	3.4	3.7	8.0	3.9	7.5	73	0.169			
% foraging	57.9	13.6	57.5	79.2	7.1	81.5	86	0.006			
% roosting	37.2	12.9	32.0	12.8	4.7	13.3	29	0.001			
Foraging area activity											
% rest during foraging	44.7	12.1	48.9	42.8	9.1	40.3			0.333	0.744	
% flight during foraging	4.0	2.6	3.8	4.0	1.6	3.8			0.043	0.966	
Day activity											
% fanning	20.9	7.5	21.1	5.3	6.0	2.5			4.271	<0.001	
% moving	16.9	4.1	16.8	29.0	9.8	26.5			3.367	0.005	
% resting	62.7	10.5	66.6	65.2	13.8	71.0			0.399	0.696	

November (mean: 5.7 ± 2.8) than in April (mean: 3.6 ± 1.3 ; $t = 2.071$, $P = 0.054$).

DISCUSSION

The results of this first study on the foraging ecology of Lyle's flying fox showed that individuals used the agricultural landscapes within a roughly 20-km radius around their day roosts. Neither movement patterns nor activity budgets exhibited significant seasonal differences except for the length of nightly foraging activity. Tracked bats foraged on a diverse diet of agricultural crops and native forest plants with seasonal changes in composition. Our results revealed that Lyle's flying fox is able to persist in a landscape profoundly shaped by human land use, which is possibly because of the availability of safe day roost sites and sufficient food resources.

Deployment of advanced GPS loggers allowed us to collect spatial and temporal data at a high resolution, which is not possible with the more commonly used satellite transmitters. The latter are highly valuable for observations of long distance movements of flying foxes (Epstein et al. 2009, Breed et al. 2010), but high inaccuracy and low frequency of location fixes limit their use for studies of fine-grained movements. Our GPS loggers were battery-powered and had rather limited life spans because the mass of the batteries was constrained by the total weight the animals could carry. However, to obtain insights into seasonal variability, we spaced data collection as to cover 2 climatically distinct seasons, while we recognize that the foraging behavior of Lyle's flying fox might be different at other times of the year.

During consecutive tracking nights, most of the bats from both temples showed high site fidelity to foraging areas. This behavior was not surprising because bats save time and energy by returning to predictable food resources that are available for a certain period (von Helversen and Winter 2003). Some individuals shifted foraging areas during the tracking time, and in some cases we observed that the previously visited trees had stopped or reduced fruiting. This reflected that bats turned to other food sources when a source got depleted over time and/or through food competitors. Tracked bats sporadically also visited additional localities, probably either to scout for upcoming food resources, or to get supplementary food items required to complement their diet (e.g., plants exclusively found in mangrove habitats).

Both overall nightly activity budgets and relative activity budgets in foraging areas were similar during different tracking seasons, although tracked Lyle's flying foxes spent a higher proportion of time in foraging areas in November compared to April. Given that the proportion of resting time was nearly equal between seasons for both night and day, our data suggest that the bats required stable amounts of resting time to maintain their energy balance. This feature was particularly marked during the day, when fanning activity increased significantly during the hot season, facilitating thermoregulation (Ochoa–Acun and Kunz 1999, Markus and Blackshaw 2002). A higher proportion of time spent fanning was accompanied by a reduction of moving activity

Table 3. Food plant species of 19 individuals of Lyle's flying fox at Wat Luang (WL) and Wat Pho Bang Khla (WP), Thailand, 2012 (X: direct evidence from feces or feeding remains; O: information based on evidence from location data but with no direct evidence from feces or feeding remains). If not otherwise mentioned, the plants were visited by Lyle's flying fox for their fruits (Fl: flower, L: leaves).

Species	WL		WP
	Apr	May	Nov
<i>Acacia auriculiformis</i> (earleaf acacia)			X (Fl/L)
<i>Anacardium occidentale</i> (cashew)	X		
<i>Artocarpus lakoocha</i> (monkey jack)			X
<i>Carica papaya</i> (papaya)			X
<i>Coccinia grandis</i> (ivy gourd)			X
<i>Diospyros malabarica</i> (gaub tree)	X		
<i>Diospyros rhodocalyx</i>			X
<i>Eucalyptus</i> sp. (eucalyptus)	O (Fl/L)		O (Fl/L)
<i>Ficus benjamina</i> (weeping fig)			X
<i>Ficus concinna</i>			X
<i>Ficus glaberrima</i>			X
<i>Ficus microcarpa</i> (Chinese fig)	X		X
<i>Ficus religiosa</i> (sacred fig)			X
<i>Ficus rubiginosa</i> (rusty leaf fig)	X		X
<i>Ficus rumphii</i> (Rumpf's fig)			O
<i>Malpighia emarginata</i> (acerola)			X
<i>Mangifera indica</i> (mango)	X		X
<i>Mamilkara zapota</i> (sapodilla)			X
<i>Markhamia stipulata</i>			O (Fl/L)
<i>Microcos tomentosa</i>			O
<i>Mimusops elengi</i> (Spanish cherry)			X
<i>Morinda citrifolia</i> (Indian mulberry)	X		X
<i>Muntingia calabura</i> (strawberry tree)	X		X
<i>Musa</i> sp. (banana)	O		X
<i>Passiflora foetida</i> (wild maracuja)	O		
<i>Pithecellobium dulce</i> (Manila tamarind)	O		
<i>Psidium guajava</i> (common guava)	O		X
<i>Sandoricum koetjape</i> (santol)	O		
<i>Sonneratia caseolaris</i> (mangrove apple)	X		
<i>Syzygium cumini</i> (black plum)	X		
<i>Syzygium jambos</i> (Malabar plum)			X
<i>Syzygium samarangense</i> (Java Apple)	X		X
<i>Tamarindus indica</i> (tamarind)	X		X
<i>Terminalia catappa</i> (tropical almond)			X

and vice versa, obviously offsetting each other, without effects on the proportion of time spent resting.

Identification of 34 food plant species revealed that Lyle's flying fox fed on a broad variety of plants, most of which are also used by humans. The majority of food plants was visited for fruits. Most of the fruits consumed by Lyle's flying fox in this study are also known to be used by other flying foxes in the Asia-Pacific region, notably mangos and other commercial fruits such as cashew and tamarind (Stier and Mildenstein 2005, Luskin 2009, Vendan and Kaleeswaran 2011), as well as different fig species (Stier and Mildenstein 2005, Luskin 2009, Sudhakaran and Doss 2012, Prasad et al. 2014). Fruits in the genus *Artocarpus* and *Syzygium* are also repeatedly documented in the diet of flying foxes (Banack 1998, Nelson et al. 2000a, Stier and Mildenstein 2005, Luskin 2009). Our study may represent a reasonable approximation of the diet of Lyle's flying fox during 2 seasonal extremes within the study landscapes. Assessment of the diet of Lyle's flying fox in different habitats throughout its range, however, would likely yield a different list of food plant species. Further studies in different habitats are thus required to comprehend the influences of habitat condition on the diet and foraging ecology of Lyle's flying fox, and its potential as a seed disperser and pollinator.

Composition of food plant species of individual flying foxes varied between seasons, with a high number of food resources exclusively used during 1 study period. Seasonal differences in diet as a consequence of changes in food availability are known from other flying foxes in the Asia-Pacific region (Banack 1998, Stier and Mildenstein 2005, Mahmood-ul-Hassan et al. 2010). While seasonal patterns in fruiting and flowering are likely in native trees such as the gaub tree, monkey jack, and mangrove apple, the 3 most frequently used food plant species, the cultivated crops mango, banana, and tamarind, were consumed by bats during both study periods. The stable supply of agricultural crops likely reduced seasonal shifts and potential bottlenecks of food resources in the diet of Lyle's flying fox, and seasonal differences might be more pronounced if bats used only natural food plants with a limited temporal availability. The number of food plant species, both combined and on an individual level, also varied between seasons, with a greater number of plants used in November than in April. It is tempting to relate this observation to the peak production of mango during the latter season, when plenty of mango plantations constituted a major and predictable resource for Lyle's flying fox. Although commercial production of mangos is frequently extended with chemical agents in Thailand throughout the

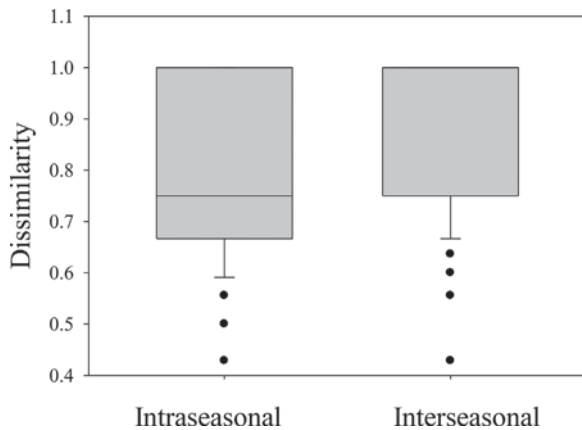


Figure 2. Box plots of intra and inter seasonal differences in diet (Sørensen distances) between 16 individuals of Lyle's flying fox from Wat Luang, Thailand, 2012. Dots represent outliers. For the interseasonal box plot, both the median (line) and the third quartile (upper box extent) have the value 1.

year (Nartvaranant et al. 2000, Benjawan et al. 2006), fruiting of mango trees was clearly reduced in November. The number of available fruit species might have increased shortly after the wet season in November.

Out of the 31 plant species used as fruit resources by the bats, at least 42% were cash crops, and at least 39% were native forest plants. Regarding the fruits intensively used by humans, competition for these resources between bats and humans has substantial potential for a conflict of interest. However, bats are probably contributing to seed dispersal and natural regeneration of some of the cash crops (see also Bumrungsri et al. 2013). In addition, flying foxes preferentially consume ripe fruits that would no longer be useful for commercial purposes (Banack 1998, Nelson et al. 2000b). Our data also indicate that Lyle's flying fox used native food plants when they were available, in line with previous studies demonstrating that flying foxes use orchard plants after natural forest food plants have become rare (*P. samoensis*, Nelson et al. 2000a, *P. vampyrus*, Mohd-Azlan et al. 2001). Foraging areas of Lyle's flying fox were almost exclusively situated in agricultural lands because cultivation and inherent loss of natural forest habitats have shaped the study area. Agricultural crops were seemingly beneficial for Lyle's flying fox, and might have increased food availability for flying foxes compared to forest habitats where food resources would be expected to have a lower density in an equal-sized area.

Lyle's flying foxes, however, also visited small remaining patches of mangroves and scattered individuals of native trees, and these foraging bouts could have important implications for the regeneration of these vegetation patches (Shanahan et al. 2001, Hodgkison et al. 2003). Flying foxes are particularly effective when dispersing small seeds that are swallowed, such as those of figs, over long distances in fragmented and degraded landscapes such as our study area (Shilton et al. 1999, Corlett 2009, Sritongchuay et al. 2014). Larger seeds are also frequently carried away from the fruiting tree to a feeding roost, and we observed dispersal distances of 300 m for seeds of the gaub tree, surpassing

reported regular distances of 200 m (Corlett 2009). The importance of flying foxes for seed dispersal of native tree species as well as their potential for wasteland regeneration and nutrient cycling (Luskin 2010) might outweigh any economic damage caused by Lyle's flying fox in the study area. Lyle's flying fox is also likely to play essential roles in mangrove regeneration in the study area. Pteropodids are generally recognized to be indispensable for pollination and seed dispersal of the mangrove apple (van der Pijl 1982, Watzke 2006). Mangrove habitats are increasingly rare in Thailand and threatened by agricultural expansion, mostly through shrimp farming (Hazarika et al. 2000, Barbier 2003). In the study area, only small pockets along the Bang Pakong river remain.

The high number of native fig species ($n = 6$) in the diet of tracked bats underlines the relevance of native vegetation in the study area for Lyle's flying fox. Figs probably constituted food resources with a high nutritional value for the bats because they are rich in nutrients such as calcium and protein compared to cultivated fruits (Nelson et al. 2000a). Previous studies have already highlighted the importance of figs as keystone species for flying foxes (Fujita and Tuttle 1991, Nelson et al. 2000a, Shanahan et al. 2001), potentially even limiting their occurrence (Stier and Mildenstein 2005). Consequently, preservation of fig trees is likely vital to fulfill nutritional requirements of the local colonies of Lyle's flying fox.

Alongside foraging habitats, suitable roost sites are a major factor determining the occurrence and movements of flying foxes. The 2 main day roosts in the study area, WL and WP, harbored the majority of Lyle's flying foxes throughout our study, contrasting the behavior of other *Pteropus* species that commonly show nomadism and only seasonal roost fidelity in relation to spatio-temporal changes in food availability (Nelson 1965, Tidemann et al. 1999, Banack and Grant 2002, Gumal 2004, Roberts et al. 2012). In an urbanized area of Australia, however, year-round food availability probably led to increasing residency and loss of migratory behavior in grey-headed flying foxes (*P. poliocephalus*; McDonald-Madden et al. 2005). The stable supply with mixed food resources observed in our study may have also fostered residency of bats, although this assumption is limited given that no data about migration in Lyle's flying fox is available. In addition, both temples are traditional roosting sites providing suitable roost trees (Hahn et al. 2014) where bats are safe from hunting (Hillman 2005). Persistence of the roost site in the mangrove patch, which is accessible to people because of its small size and thus exposes the bats to hunters (Mohd-Azlan et al. 2001), testifies to the significance of mangroves as roosting habitat for Lyle's flying fox (Pierson and Rainey 1992).

According to local farmers, Lyle's flying fox is hunted as an orchard pest in the study area. Awareness among people of the likely contribution to the dispersal of both ecologically and economically valuable plants by flying foxes appeared to be scarce. To sustain the services provided by the bats, it is crucial to maintain local colony sizes of Lyle's flying fox above a certain threshold value below which their ecological

functionality and effectiveness as seed disperser is expected to be compromised (McConkey and Drake 2006). Finally, our interviews revealed that Lyle's flying fox is hunted in the study area for bushmeat and traditional medicine. Bats are highly valued as an ingredient of curries, and fresh blood is considered a powerful energy drink. The latter practice might not only result in depletion of local colonies of Lyle's flying fox but also have serious implications for human health as consumption of fresh blood is very likely to facilitate transmission of the Nipah virus (Wacharapluesadee et al. 2006) and other human pathogens (see also Epstein et al. 2006). Elimination of hunting would thus reduce the risk of disease transmission and at the same time aid to safeguard the ecological benefits provided by the bats.

MANAGEMENT IMPLICATIONS

The continuous existence of large colonies of Lyle's flying fox in the agricultural landscape of the study area points to a highly flexible foraging behavior in this species. We expect the foraging behavior of Lyle's flying fox to be different in another habitat setting, emphasizing that site-specific information constitutes the base of sound conservation management. The conservation status of Lyle's flying fox as Vulnerable (Bumrungsri et al. 2008), threats from hunting, and the loss of natural habitats in the study area highlight the need for continuous monitoring of the colonies at WL and WP to observe population trends, and emphasize the necessity of implementing an effective hunting ban. To alleviate conflicts with humans, we recommend future research on food preferences of Lyle's flying fox, and on the dependence of food plants on seed dispersal or pollination by bats. At the same time, managers should strive to retain native food plants and natural vegetation in the agricultural landscape of the study area to reduce consumption of and dependence on orchard fruits. If compatible with human land use, we anticipate that the bats would plant their own resources through seed dispersal, facilitating rejuvenation of natural vegetation in the longer term. Remaining patches of mangroves should be strictly protected from agricultural encroachment, preserving important foraging and roosting habitats of Lyle's flying fox. Enhancement of mangrove habitats in the study area would additionally benefit other wildlife and shoreline protection to prevent flooding. The bats at the temple colonies are used to and tolerate humans, and safety at these roosting sites as well as roosting trees should be continually maintained. We further recommend the installation of information plates at the temples that highlight the ecological role of Lyle's flying foxes as nocturnal gardeners while at the same time raising awareness of the risks associated with hunting and consumption of flying foxes for disease transmission, particularly for Nipah virus. Finally, information campaigns targeting local people should convey the message of crucial ecosystem services provided by the bats, their contribution to human well-being, and thus improve the public perception of flying foxes while minimizing human-wildlife conflicts.

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