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Original Article

Water bodies are a critical foraging habitat for insectivorous bats in tropical agricultural landscapes of central Thailand

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Abstract

Agricultural intensification and homogenization of land use are known to have a negative impact on biodiversity. Bat activity was monitored in five land use types that included paddy fields, field crops, forests, settlements, and water bodies from November 2015 to October 2016 in central Thailand. We recorded 37,610 one-minute intervals with bat calls and 623 feeding buzzes that represented 16 bat species. Bat foraging activity was dominated by open space and edge species. Bat activity was significantly higher over water bodies but was not correlated with insect biomass. There was a significantly higher bat activity index (two-fold) in the hot-dry season than at other times, especially over water bodies. This pattern was obvious in *Myotis siligorensis, Taphozous melanopogon*, and *Chaerephon plicatus*. High feeding activity during the hot-dry season could reflect higher nutrient and water demand of lactating females. Maintaining water bodies and forest patches in farmland is important for bat conservation.

Keywords: acoustic monitoring, bat activity, habitat use, hot dry season, limestone forest, paddy field, water bodies

1. Introduction

Agricultural landscapes cover approximately 40% of our planet's terrestrial ecosystems and will expand with increasing human population growth and resource use (FAOSTAT, 2011; Defries, Rudel, Uriarte, & Hansen, 2010). The expansion of agricultural landscapes results in decreased biodiversity due to the use of agro-chemicals and the homogenization of the landscape (Benton, Vickery, & Wilson, 2003; Bianchi, Booij, & Tscharntke, 2006; Liira, Aavik, Parrest, & Zobel, 2008). One of the documented effects is the decline in the populations of many bat species worldwide (Jones, Purvis, & Gittleman, 2003; Safi & Kerth, 2004). Homogenization of the agricultural matrix reduces the natural structural elements which consequently remove potential habitats for bats and their prey. In addition, agro-chemicals can be directly harmful to bats and also reduce the availability of their prey (William-Guillen, Olimpi, Maas, Taylor, & Arlettaz, 2016).

However, agricultural landscapes tend to be structurally heterogeneous (Kalda, Kalda, & Liira, 2015) consisting mostly of cultivated land and aquatic habitats. Several studies have highlighted the importance of water bodies, especially for bats. They are associated with an abundance of prey (Fukui, Murakami, Nakano, & Aoi, 2006) and several bat species are specialized to forage in aquatic habitats (Fenton & Bogdanowicz, 2002). Many bat species also use bodies of water as landmarks for orientation and navigation (Serra-Cobo, Lopez-Roig, Marques-Bonet, & Lahuerta, 2000). For conservation of insectivorous bats, it is therefore essential to maintain a habitat and manage the area for insect resources. Habitat use is the way an animal uses the physical and biological resources in a habitat, for foraging, shelter, nesting, escape, or other life history traits (Krausman, 1999). Spatially, authors reported greater bat abundance in primary forests compared to disturbed forests and agricultural land; however, species richness seemed to be less different (William-Guillen *et al.*, 2016; Furey, Mackie & Racey, 2010). Activity patterns of bats may respond to a variety of factors, including the abundance of insects, air temperature, relative humidity, and energetic demands imposed by pregnancy. Factors that are correlated with activity levels differ among

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studies and may be area and species specific (Hayes, 1997). Season was reported to affect bat activity patterns in temperate regions (O' Donnell, 2000) but studies in tropical regions are very limited. For Old World tropical bats, births occur primarily in April and May while lactation follows during May to July in northern Vietnam (Furey *et al.,* 2010). Theoretically, bats in this region increase foraging activity during these periods to meet its energetic and nutrient requirements. In addition to foraging grounds, roosts are also of critical resource in agricultural landscapes.

In the present study, the spatial and seasonal variations in the activities of insectivorous bats were examined in central Thailand where agriculture is very intensive. Passive acoustic monitoring and insect sampling were conducted over one year in five major habitat types: paddy field, field crops, forest over limestone hills, settlements, and water bodies. It is hypothesized that the foraging activity of insectivorous bats is highest in forest as it provides highest food availability and a complex canopy structure. In addition, bat foraging intensity is greatest during the early rainy season (May–July) when it is the general breeding season for bats in this area.

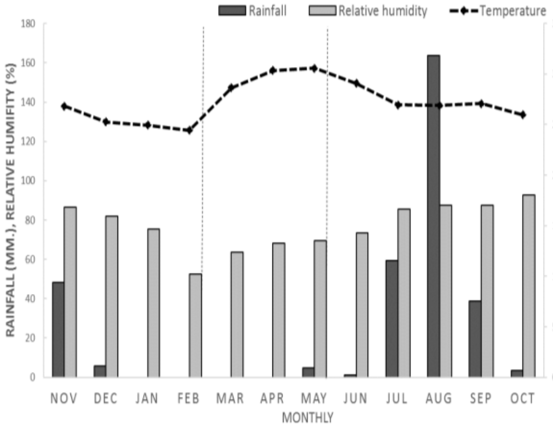

Figure 1. Climate conditions (monthly rainfall (mm., grey bar), relative humidity (%, dark bar), and average air temperature (°C, dot line) in this area from November 2015 to October 2016. Seasons are marked with lines. Note that in this year, the rainy season was two months delayed; therefore, the hot-dry season extended from March to June. Source: Lopburi Meteorological Station and Tak Fa Meteorological Station in 2015 to 2016.

2. Materials and Methods

2.1 Study area

Our study area was located in Chao Phraya river plain in central Thailand mainly in Lopburi Province, latitude 14°42' - 15°18'N, longitude 100°22' - 100°51'E, 400-600 m asl.. There are generally three seasons: a cool dry season (November to February), a hot dry season (March to May), and a rainy season (June to October). In 2016, the climate in Southeast Asia was affected by El Nino and was extremely dry especially in April (Thirumalai, DiNezio, Okumura, & Deser, 2017). The rainy season was delayed and began in July (Figure 1); therefore, June was classified as a dry season in this study. The average ambient temperature is 28.3 ºC with an annual rainfall of about 1,147 mm. Limestone outcrops with caves are patchily present which harbour several bat species such as *Taphozous* spp., *Rhinolophus* spp., *Hipposideros* spp., and *Myotis siligorensis*. There are four cave colonies of wrinkle-lipped free-tailed bats (*Charephon plicatus*) that include the Wat Khao Wongkot cave (15°1'N, 100°32'E), Wat Don Dueng cave (15°8'N, 100°37'E), Wat KhaoWong cave (15°10'N, 100°24'E), and Wat Suwan Khiri Pidok cave (Takra Thong) (14°49'N, 100°46'E) which harbor about 500,000, 100,000, 400,000, and 50,000 bats, respectively (S. Binlasoi, pers. com) (Figure 2). To classify the habitats in the study area, a 25 km radius for three large colonies and a 10 km radius for a smaller colony were drawn on a land use map provided by the Land Development Department of Thailand. The major land uses were classified into five main categories: paddy field (35%), field crops (30%), forests (15%), settlements (15%), and water bodies (10%). Only one planting period in the paddy fields took place during the rainy season of 2016 because of the drought caused by El Nino. Sugarcane, maize, sunflower, millet, and cassava are the main field crops planted year-round. Forest refers to forest patches over a limestone hill which is deciduous with bamboo in which most trees shed leaves during the hot dry season. Trees are generally small and sparsely distributed with a top canopy of around 10 m. The settlements are mostly small rural communities living around a temple. The water bodies are relatively large including artificial reservoirs, natural lakes, major irrigation canals that are 20 m wide, and minor irrigation canals that are 6 m wide. Sugar palm (*Borassus flabellifer*) which harbors *Scotophilus* spp. was rare.

2.2 Bat acoustic sampling

Data were collected every month from November 2015 to October 2016. Passive acoustic monitoring was carried out with an Anabat Bat detector (SD2, Titley Electronics) that was kept in a box attached to a pole at 5 m above the canopy or water surface except in the forest. It was tilted at approximately 45° (Avila-Flores & Fenton, 2005) and recorded from 18:30 h to 06:00 h. In the forested area, the bat detector was set at canopy level by hanging the box on the highest branches of standing trees in gaps. Thus, acoustic sampling represented well the open space bat species and edge space bat species while it under-represented narrow space bats which forage in the understory with faint calls. Sampling effort was in proportion to habitat percentage (Table 1). In each habitat, 5–30 nights of recording were undertaken in each season. Recording was not conducted in the same position in each season. Sampling sites in each habitat were at least 300 m apart. Acoustic sampling within forests took place at least 150 m from the edge. Recording stations in every habitat were as far from artificial lighting as possible. Acoustic sampling was not carried out in heavy rain or during the full moon period (moon light >50%). The guild structure of insectivorous bats was categorised according to Schnitzler & Kalko (2001) and Denzinger & Schnitzler (2013). These include open space bats which forage high above the ground and far from vegetation, edge space bats which forage near the edges of vegetation and in vegetation gaps, and narrow space bats which forage close to surfaces such as leaves or ground.

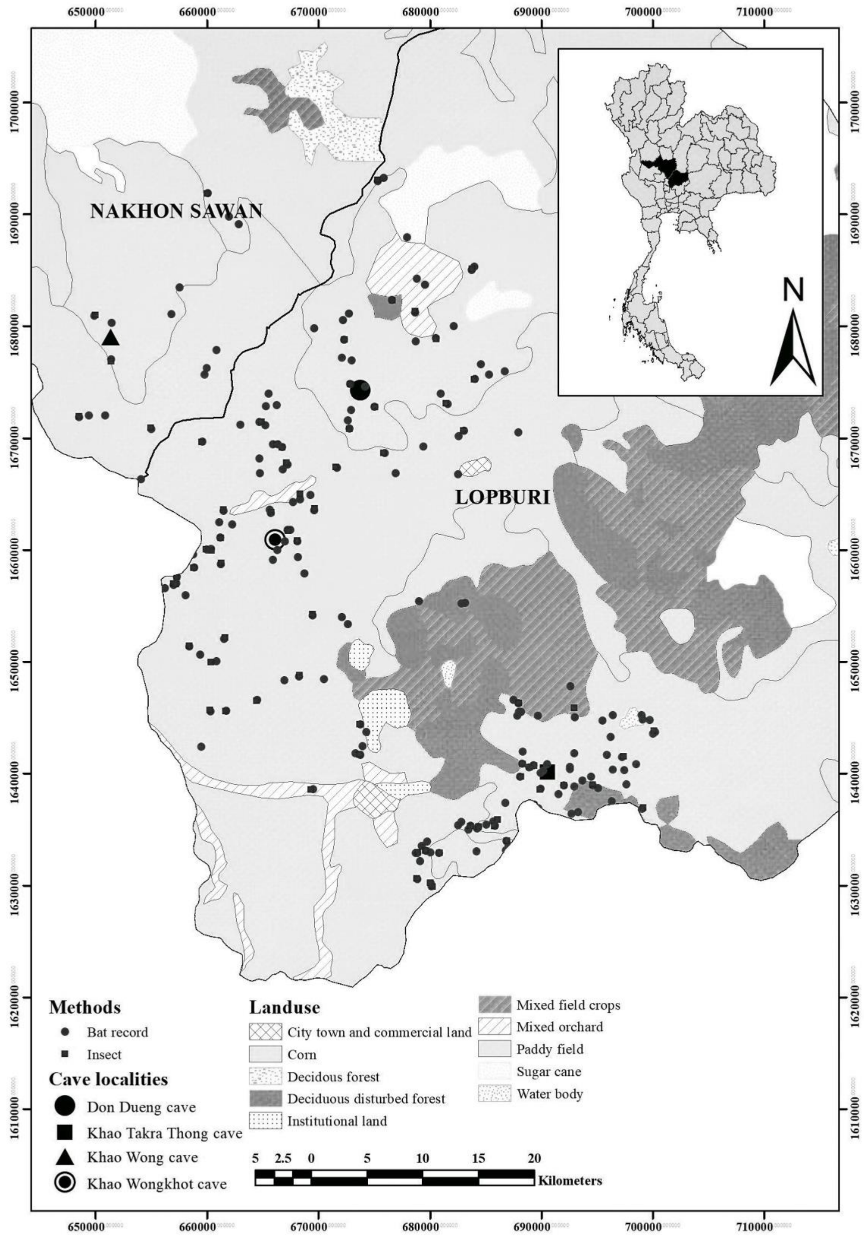

Figure 2. Distribution of bat monitoring points (●) and insect sampling points (■). Locations of four colonies of *Chaerephon plicatus* are shown.

Table 1. Sampling effort in different habitats and seasons for bat/insect. Percent of each habitat was based on the Present Land Use Monitoring: Executive Information System from the Land Development Department of Thailand.

Habitat (%)	Season			Total
	Cool dry	Hot dry	Rainy	
Paddy fields (35%)	30/11	29/11	28/11	87/33
Field crops (30%)	21/6	22/7	20/7	63/20
Forests (15%)	10/5	10/3	9/4	29/12
Settlements (15%)	10/4	11/4	9/4	30/12
Water bodies (10%)	7/3	6/3	5/3	18/9
Total (100%)	78/29	78/28	71/29	227/86

2.3 Insect sampling

Insect sampling was conducted with modified light-suction traps set randomly at 5 m high above the canopy or water surface in each habitat. Trapping was also in proportion to habitat percentage. In each season, 3–12 traps were set in each habitat from 18:30 h to 06:00 h (Table 1). Insect traps were at least 50 meters from the acoustic monitoring stations. Insect specimens were identified to the order level following Tripplehorn & Johnson (2005). The insects were separated into 12 size categories based on body length following Phommexay, Satasook, Bates, Pearch, & Bumrungsri (2011), i.e. 0.1–2.0, 2.01–4.00, 4.01–6.00 and likewise to 22.01–24.00 mm. Insect biomass was estimated with $W=(0.0305)\ L^{2.62}$ where W=dry mass (mg) and L=body length (mm) (Rogers, Hinds, & Bushchbom, 1976).

2.4 Sound analysis

The echolocation calls of bats were analyzed with the AnalookW program. Acoustic activity index which is the presence/absence of species during one-minute intervals was determined. A given night was divided into one-minute intervals, and a species is recorded as present if there were at least two calls in a series (Miller, 2001). Feeding buzzes that are emitted when bats approach prey were also counted. The bats were classified to species based on call characters, i.e. frequency of maximum energy, minimum frequency, and call duration, by comparing the calls to the call library of the Bat Research Unit, Prince of Songkhla University (Bumrungsri & Parson, 2005; Hughes *et al.*, 2010a, 2011b). Although bat call references in this area are not complete and there is no call library for frequency division bat detection, the call characters of each species used in this study were based on call references in Thailand made from time expansion bat detectors together with published references (Soisook *et al.*, 2008; Dejtaradol, 2009; Douangboubpha *et al.*, 2010; Surlykke *et al.*, 1993). In some cases, call characters of two species overlapped to some extent and were represented as a species complex such as *Rhinolophus malayanus* and *R. coelophyllus*. Details of call characters of each species found in this study were based on Analook software presented in Suksai (2018).

2.5 Statistical analysis

Zero-inflated regression tests in generalized linear regression (GLM) were used to examine variation in bat passes among habitats. Negative binomial regression in GLM was introduced to examine the differences in bat activity in each season. Quasi-Poisson regression, which is a type of generalized linear regression, was used to determine the insect biomass in each habitat and season. Spearman's correlation test was used to investigate the relationship between bat passes, insect biomass, and other factors. Tukey-Kramer tests were used to investigate the significant differences between pairs of groups. All statistical analyses were conducted using R software 3.4.3 for Windows. All data are presented as mean±SE.

3. Results

The recorded data found 14 species, 6 genera, and 5 families of bats from 227 acoustic monitoring nights (163,440 min) in all habitats with 37,610 one-minute intervals of bat calls and 623 feeding buzzes (Table 2). The most speciose family was the Hipposideridae (*Hipposideros pomona*, *H. armiger, H. larvatus*, and *H. diadema*), followed by Rhinolophidae (*Rhinolophus coelophyllus/R. malayanus, R.pusillus*, and *R. pearsonii*), Vespertilionidae (*Myotis muricola*, *M. siligorensis*, *Scotophilus kuhlii*, and *S. heathii*), Emballonuridae (*Taphozous melanopogon* and *T. theobaldi*), and only one molossid bat (*Chaerephon plicatus*). The total number of species recorded in each habitat was similar: 12 species in settlements, 13 species in forests, paddy fields, and water bodies and 14 species in field crops. The five most common species were *M. siligorensis* (40.9% of total bat passes), *Chaerephon plicatus* (18.2 %), *Taphozous melano-*

Table 2. List of insectivorous bat species recorded in five habitats in central Thailand (Field crop, Settlement, Forest, Paddy field and Water bodies). Average number of one-minute intervals with bat calls per night±standard error (±SE), and bat functional group are shown (continued).

Species of insectivorous bats	Percent contribute	Average number of one-minute intervals with bat calls per night (± SE)					Functional group
		Field crops (n=63)	Settlement (n=30)	Forests (n=29)	Paddy fields (n=87)	Water bodies (n=18)	
Family Hipposideridae							
Hipposideros pomona	0.07	0.06±0.04	-	-	-	0.06±0.05	Narrow space
Hipposideros armiger	0.25	0.21±0.09	-	1.45±1.17	0.05±0.05	-	Edge space
Hipposideros larvatus	1.67	2.71±0.71	7.13±5.90	1.66±0.73	0.60±0.19	8.00±6.32	Edge space
Hipposideros diadema	1.95	3.00±1.31	0.1±0.1	0.79±0.49	5.40±1.73	2.89±2.18	Edge space
Family Molossidae							
Chaerephon plicatus	18.17	20.98±5.30	29.27±8.62	24.14±11.33	33.39±7.02	57.22±17.0	Open space
Family Vespertilionidae							
Myotis muricola	7.61	9.67±2.39	14.57±4.28	4.55±1.38	13.99±3.32	25.89±15.10	Edge space
Myotis siligorensis	40.94	40.36±7.81	43.07±10.70	33.45±12.84	75.76±10.57	222.33±52.37	Edge space
Scotophilus kuhlii	4.32	5.11±1.47	6.2±3.40	2.28±1.76	6.18±1.38	30.67±26.67	Open space
Scotophilus heathii	2.02	1.67±0.44	1.00±0.6	1.55±0.7	5.77±1.32	5.11±4.37	Open space
Mean per habitat		103.68±12.96	123.00±26.53	160.59±64.05	163.91±21.98	469.94±88.70	
Species of Bats		14	12	13	13	13	

pogon (9.6 %), *Myotis muricola* (7.6 %), and *Taphozous theobaldi* (6.8 %) while another species accounted for less than 4% of bat passes. These species were dominant in every habitat. Each bat species showed a trend in their habitat preferences. While many species preferred the water bodies, including *T. theobaldi*, *C. plicatus*, *M. muricola*, *M. siligorensis*, and *S. kuhlii*, some species showed a preference for forests such as *R. pearsonii*. In addition, *T. melanopogon* showed a preference for both forest and water bodies (Table 3). Bat activity in this agricultural habitat was dominated by open space or edge space species.

3.1 Bat activity variation between habitats

Bats activity was different in all five habitat types. On average, the bat activity index per night over water bodies (469.94±88.70 one-minute intervals with bat call, n=18) was significantly higher than other habitats (Zero-inflated regression, χ^2=9862.27, P<0.001). Activity indices in the forest (160.58±64.05, n=29) and paddy fields (163.91±21.98, n=87) did not differ significantly from each other (P=0.86) but were significantly higher than those in settlements (123.40±26.53, n=30) and field crops (103.68±12.97, n=63) (P=0.06) (Figure 3a). As with one-minute interval bat calls, feeding buzzes per night were significantly higher over water bodies (19.22±7.26) (P<0.05). However, feeding buzzes were similar between forests (1.17±0.7), paddy fields (1.67±0.44), settlements (1.07±0.53), and field crops (1.05±0.33).

From the five insect orders found in the study sites, Lepidoptera accounted for the highest biomass (177.69±25.98 mg, 48% of total insect biomass), followed by Coleoptera (73.05±20.57 mg, 20%), Diptera (61.51±23.10 mg, 17%), Hymenoptera (35.60±48.0 mg, 9%), Hemiptera 19.45±11.30 mg, 5%), and others (1.69±2.50 mg, 1%).The insect biomass per night did not show significant variation between each habitat (Quasi-Poisson regression, χ^2=4.49, P>0.05). Insect biomass over water bodies (532.80±400.25 mg, n=9), field crops (361.86±150.79 mg, n=20), and paddy fields (262.35± 72.47 mg, n=33) was slightly higher than settlements (206.33

Table 3. List of insectivorous bat species recorded in five habitats in central Thailand (Field crop, Settlement, Forest, Paddy field and Water bodies). Average number of one-minute intervals with bat calls per night±standard error (±SE), and bat functional group are shown.

Species of insectivorous bats	Percent	Average number of one-minute intervals with bat calls per night (±SE)					Functional group
		Field crops (n=63)	Settlement (n=30)	Forests (n=29)	Paddy fields (n=87)	Water bodies (n=18)	
Family Emballonuridae							
Taphozous melanopogon	9.59	6.24±1.35	6.9±3.32	36.8±24.98	15.33±4.19	33.50±15.15	Open space
Taphozous theobaldi	6.84	3.40±0.72	8.1±1.61	14.66±12.50	3.87±0.84	75.28±42.03	Open space
Family Rhinolophidae							
Rhinolophus coelophyllus / malayanus	2.89	7.67±1.58	0.4±0.25	10.38±3.41	2.74±0.76	3.00±2.09	Narrow space
Rhinolophus pusillus	0.63	1.17±0.78	1.6±0.67	2.68±1.12	0.24±0.16	1.00±0.58	Narrow space
Rhinolophus pearsonii	3.04	1.43±0.89	5.07±2.14	26.21±25.08	0.59±0.26	5.00±2.13	Narrow space

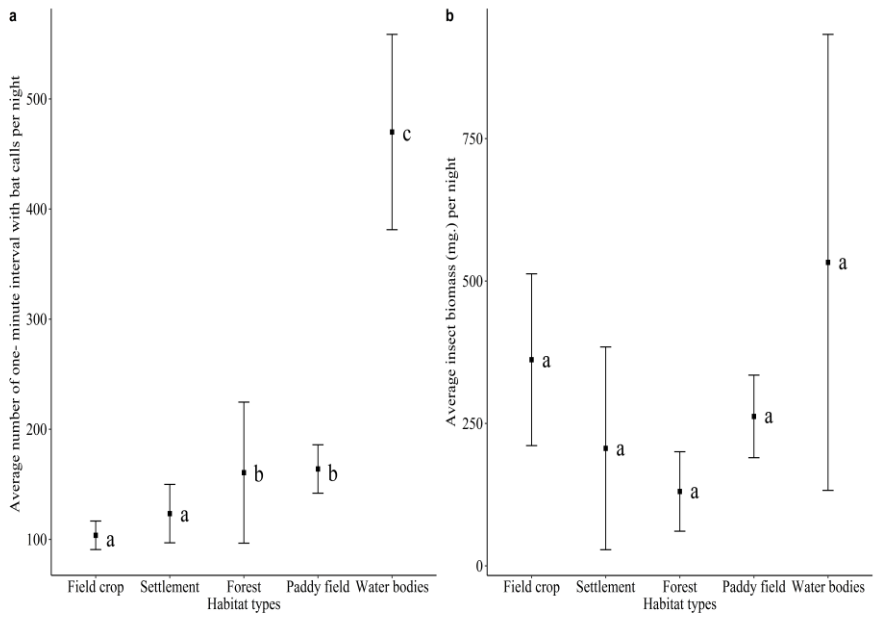

Figure 3. Average number of one-minute intervals with bat calls per night (±SE) (a), average insect biomass (mg.) per night (±SE) (b) in five habitat types in Lopburi. Different letters mean statistically different.

±177.99, n=12) and forests (130.59±69.75, n=12) (Figure 3b). No correlation between bat activity and insect biomass was found (r=−0.03, P>0.05). However, the bat activity index was negatively correlated with relative humidity (r=−0.35, P<0.001), while the number of insects was significantly and positively correlated with relative humidity (r=0.28, P<0.01) and negatively significant with temperature (r=−0.22, P<0.05).

When the bats were divided into functional groups, water bodies had a significantly higher number of bat activity indices than other habitats in every guild (GLM, χ^2=9553.54, P<0.001) (Appendix A). The foraging activity indices of open space bats over water bodies and in forests and paddy fields were significantly higher than in settlement areas and field crops (P<0.001). For edge space bats, their activity over water bodies was very high and significantly different from other habitats. Although narrow space bats showed similar foraging activity across all habitats, their activities also differed between some habitats.

3.2 Seasonal variation in bat activity

Bat activity generally varies between seasons. In the hot dry season, there was a significantly higher bat activity index (241.74±28.17, n=78) than other seasons (negative binomial regression, χ^2=17.50, P<0.001), while it was not much different between the rainy (114.82±24.98, n=71) and cool dry seasons (135.92±25.85, n=78) (P>0.05) (Figure 4a). Specifically, most activity was recorded from March to April (296.63±53.83) while it was lowest from September to October (103.77±45.33). The foraging activity over water bodies was higher in the hot dry season (682.17±161.67) compared to the cool dry season (335.14±103.04) and rainy season (404±194.7) (Appendix B). *M. siligorensis*, *C. plicatus*, and *T. melanopogon* increased their activity in the hot dry season. Feeding activity varied between seasons. Again, feeding buzzes were significantly higher on average in the hot dry season (P<0.05) (7.67±1.34 buzzes) followed by the cool dry season (3.42±1.44 buzzes), and the lowest was in the rainy season (0.75±0.30 buzzes).

3.3 Seasonal variation in insect biomass

The average nocturnal insect biomass per night was highest in the cool dry season (516.73±0.14 mg, n=29) followed by the hot dry season (220.43±89.15, n=28) and the rainy season (123.31±33.91, n=29). There was a statistically significant difference (Quasi-Poisson regression, χ^2=8.61, P<0.01) in biomass between the cool dry and rainy seasons (Figure 4b). The bat activity index in each season was not correlated with insect biomass (P>0.05). Different groups of insects dominated in different habitats and these patterns changed in different seasons except for Diptera which were always dominant over water bodies in every season. Their biomass contributed 60–90% of total insect biomass in this habitat in every season (Appendix C). Diptera contributed 90% of insect biomass in the hot-dry season over water bodies when bat foraging activity was highest.

4. Discussion

Based on these results, this study is the first to highlight the importance of water bodies as foraging grounds in a tropical agricultural landscape. Although our hypothesis that forest was the most important habitat for insectivorous bats in this landscape, it was not supported. Forest and paddy field were the second most important habitats for bats in farmland landscapes. Water bodies were suggested as important foraging habitats for many insectivorous bat species (Fukui *et al.,* 2006). Since bodies of water were shown to provide higher biomass of emergent adult aquatic insects, pond or stream has positive effects on the foraging activity of

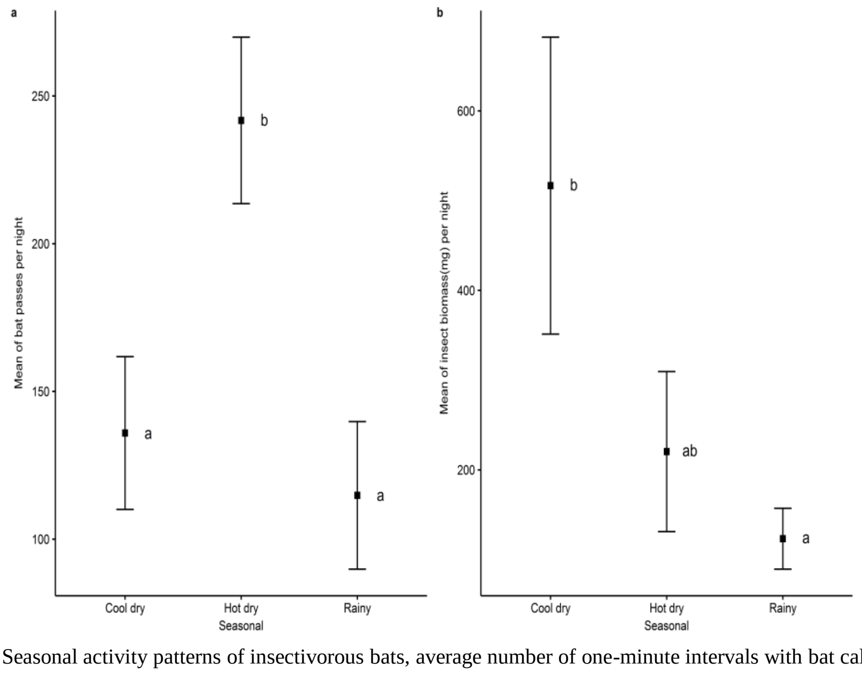

Figure 4. Seasonal activity patterns of insectivorous bats, average number of one-minute intervals with bat calls per night (±SE) (a) and average insect biomass (mg.) per night (±SE) (b) in each season.

bats (Racey, Swift, Rydell, & Brodie, 1998). In addition, aquatic insects have less well-developed flight abilities compared to terrestrial insects (Brodsky, 1994) thus it is easier for bats to capture them. For water bodies, surrounding vegetation and size can be important factors determining insect biomass and consequently bat foraging activity. The presence of trees around water bodies also impacts insect abundance as trees can create a shelter against wind, rain, and predators more than open space (Zahn & Maier, 1997). For bats, trees along water bodies also reduces the intensity of light that lead to lower predation risk (Rydell, Entwistle, & Racey, 1996). In aquatic habitats, wind can be an important factor for foraging bats. In windy conditions, trawling bats like *Myotis* spp. are less active, presumably because wind reduces the insect abundance and makes ripples on the surface of the water, thus reducing the detection ability of targets (Russo & Jones, 2003). In contrast, smooth water surfaces provide a less cluttered acoustic return from the echolocation pulses for detecting and recognizing prey (Greif & Siemers, 2010). The size of aquatic habitats also influences the diversity of feeding bats in arid and semi-arid areas. Razgour, Korine, & Saltz (2010) found that the activity of bats in the Negev Desert increased significantly according to the size of the pond. Wider ponds provide greater densities of insect prey and have the capacity to support more insect species which offers productive and predictable foraging opportunities for bats (Racey *et al.*, 1998).

Different bat species show variations in habitat preference. Most dominant species, which are open space and edge space foragers, prefer water bodies and paddy fields. These open space bats are characterised by long and narrow wings, and are adapted for fast but relatively unmaneuverable flight in open places (Altringham, 1999). Their low echolocation frequencies allow them to detect prey at some distance, so they can hunt insects in uncluttered spaces, high above the ground or above the canopy (Schnitzler & Kalko, 2011). Based on the present study, particular species of bats showed strong habitat preferences, for example *M. siligorensis* and *M. siligorensis* preferentially forage over water bodies. They also foraged in scattered secondary growth deciduous trees and a sugar cane field, usually 2–5 m above the ground and at least some meters away from the nearest vegetation (Surlykke *et al.,* 1993). Rhinolophid bats have been known as forest specialists. Their wings and echolocation calls are suited to such highly cluttered habitats (Schnitzler & Kalko, 2011; Denzinger & Schnitzler, 2013).

4.1 Seasonal variation in bat activity

Bat activity indices and feeding buzzes were significantly higher in the hot dry season. This pattern resulted mostly from the increased activity of three bat species, namely *M. siligorensis*, *C. plicatus*, and *T. melanopogon* over water bodies. The increased activity probably resulted from breeding nutrient requirements and the availability of Diptera, the dominant diet of these bats, in this habitat in such critical periods. Wei *et al.* (2006) showed that Diptera contributes about half of the diet by volume in *M. siligorensis*. The *Taphozous* spp. are opportunistic feeders and the authors showed that they also consumed large amounts of Diptera (Srinivasulu & Srinivasulu, 2005; Wei *et al.,* 2008; Weterings, Wardenaar, Dunn, & Umponstira, 2015). Thonjued, Bumrungsri, Kitpipit, & Chotigeat (2018) used direct PCR-DGGE techniques to reveal that *C. plicatus* fed mostly on dipterans in central Thailand. These bats were known to be pregnant, giving birth from March to May (*C. plicatus*: Leelapaibul, Bumrungsri, & Pattanawiboon, 2005; Hillman, 1999; Furey, Racey, Ith, Touch, & Cappelle, 2018 and *T. melanopogon*: Badwaik, 1988, Lim, Cappelle, Hoem, & Furey, 2018). During the hot dry season, Diptera are mostly present over water bodies and contributed 55.3% of all dipteran biomass in all habitats. During lactation, females adjust their foraging activity to meet their energy demands (Barclay, 1989; Adams & Hayes, 2008). Insect-eating bats increase foraging time (Barclay, 1989) but reduce home range size (Henry, Thomas, Vaudry, & Carrier, 2002) during lactation in response to an increase of 25% of body mass in milk. Lactating females had significantly more feeding bouts compared to pregnant females (Henry *et al.,* 2002). In addition to higher food requirements, lactating female bats also need more drinking water. In seasonal tropical regions, high temperatures and low relative humidity in the hot dry season causes high rates of evaporative water loss in reproductive females. Adams & Hayes (2008) found that lactating bats visited water resources 13 times more often compared to non-breeding adult females. The milk is composed of 72–76% water and the body water flux increased significantly during lactation (Kunz, Stack, & Jenness, 1983; Wilde, Kerr, Knight, & Racey, 1995). So, bats need to fly to drink more often mostly in the evening and at dawn. The success in reproduction in female insectivorous bats is related directly to water availability (Adams & Hayes, 2008). This water requirement was possibly quite high during the lactation period of 2016 because April was the hottest and driest April on record within 80 years of mainland Southeast Asia (Thirumalai *et al.,* 2017).

In this study, some inherent biases should be noted. First, the detectability of each insectivorous species was not equal. The open space bats and edge space bats have higher intensity calls which are more easily detectable by bat detectors. Consequently, the results of this study tended to be represented by these groups. Regarding narrow space bats, a further study using direct capture could complement the acoustic studies especially in forests. In Southeast Asia, limestone outcrops with patches of forest are common within agricultural landscapes. These forested habitats are known to support bat diversity (Furey *et al.,* 2010). The second limitation is the lack of inter-annual variation. In the study year, the longest dry period with extremely hot and dry weather of over 80 years possibly affected the insect population as well as bat behavior. Future studies should also be conducted in a non-El Nino year. Third, monitoring during the whole night in the present study possibly over-represented the bat species that were active throughout the night. The patterns of habitat preference and seasonal variation of monitoring during the early hours (18:30–21:30 h) was mostly similar to whole night monitoring (Suksai, 2018). Thus, it is believed that the patterns found in this study were real.

4.2 Conservation implication

The present study emphasized the importance of water bodies to bats in a tropical agricultural landscape. To conserve bat populations, it is important to maintain water bodies and also woodlands surrounding water bodies. In addition to harboring wildlife, the woodland can buffer aquatic ecosystems from chemical spray and extreme weather. However, most farms in Southeast Asia tend to clear such vegetation. Water bodies are critical habitats during the breeding period of bats, thus maintaining water bodies consequently helps to maintain populations of pest suppresser agents such as *C. plicatus* and other bats (Leelapaibul *et al.*, 2005; Srilopan, Bumrungsri, & Jantarit, 2018). In addition, forest over limestone, even it is degraded, was found to be important for narrow space bats which are very sensitive to forest alteration (Furey *et al.,* 2010).

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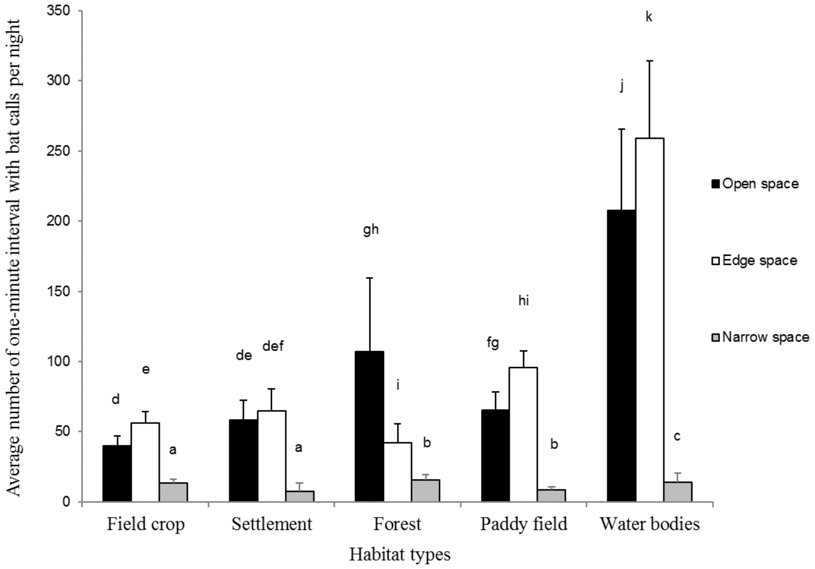
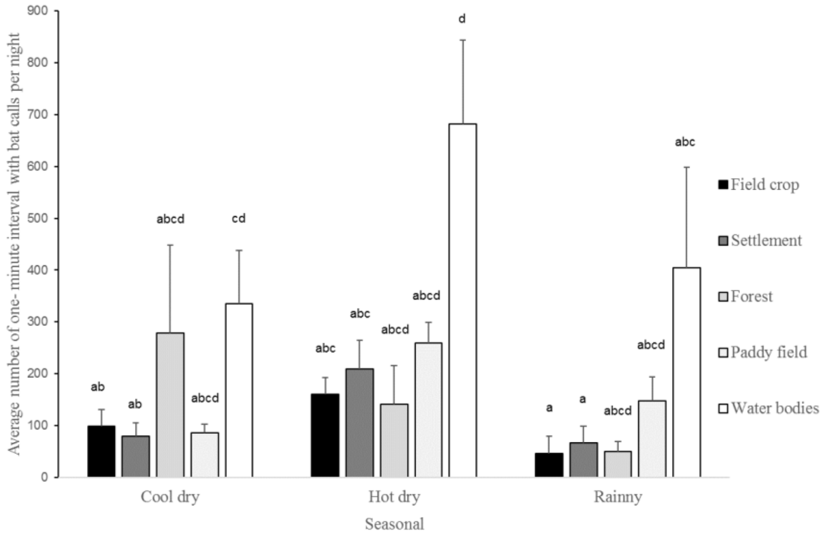
Appendix



Appendix A. Average number of one-minute intervals with bat calls (±SE) of the three functional groups of insectivorous bats in each habitat.



Appendix B. Seasonal activity in each habitat type, the average number of one-minute intervals with bat calls per night (±SE).

Appendix C. Insect orders found in the study sites in each season and habitat type. Average insect biomass±standard error (±SE).

Season	Insect orders	Percent within season	Habitat types (average insect biomass±SE))				
			Field crop	Settlement	Forest	Paddy fields	Water bodies
Cool dry	Coleoptera	15.40	79.89±35.01	6.70±2.61	2.36±1.28	165.37±75.90	139.95±87.73
	Diptera	34.21	127.26±88.20	4.70±4.70	17.05±16.99	71.79±24.53	655.09±601.55
	Hemiptera	6.52	32.18±20.04	0.18±0.18	1.30±1.29	100.10±89.02	33.08±32.48
	Hymenoptera	19.16	484.40±480.44	1.38±1.38	1.13±0.71	3.07±1.91	0.54±0.38
	Isoptera	0.05	-	-	-	-	-
	Lepidoptera	24.30	45.90±32.66	6.45±3.32	225.78±157.85	83.85±30.36	260.05±151.89
	Odonata	-	-	-	-	-	-

	Orthoptera	0.37	-	-	-	0.19±0.18	9.20±9.15

Appendix C. Continued.

Season	Insect orders	Percent within season	Habitat types (average insect biomass±SE))				
			Field crop	Settlement	Forest	Paddy fields	Water bodies
Hot dry	Coleoptera	57.31	9.29±5.26	498.56±496.36	1.98±1.07	61.29±41.22	1.85±0.22
	Diptera	5.29	4.96±4.07	0.83±0.52	1.98±0.99	15.86±8.59	29.27±18.83
	Hemiptera	2.45	8.01±7.48	-	1.97±1.12	13.49±11.34	1.05±1.05
	Hymenoptera	1.65	2.15±1.16	-	0.17±0.15	14.13±12.82	-
	Isoptera	0.26	0.07±0.07	2.49±2.49	-	-	-
	Lepidoptera	31.94	107.75±105.54	40.78±40.78	19.55±19.30	151.20±72.45	-
	Odonata	1.10	7.68±7.68	-	-	3.34±3.34	-
	Orthoptera	-	-	-	-	-	-
Rainy	Coleoptera	7.06	33.08±19.07	1.15±0.62	0.59±0.35	2.38±1.29	3.15±1.06
	Diptera	40.60	35.81±14.42	43.80±21.41	8.06±2.29	46.29±11.55	98.21±54.14
	Hemiptera	2.99	7.33±2.19	0.66±0.26	1.66±0.83	5.46±3.21	1.98±1.00
	Hymenoptera	0.49	0.30±0.19	0.10±0.10	0.83±0.83	0.87±0.54	0.69±0.69
	Isoptera	-	-	-	-	-	-
	Lepidoptera	48.85	157.63±115.52	3.55±2.01	62.03±36.79	47.83±25.28	8.32±8.33
	Odonata	-	-	-	-	-	-
	Orthoptera	-	-	-	-	-	-