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Wetland, Forest, and Open Paddy Land Are the Key Foraging Habitats for Germain's Swiftlet (*Aerodramus inexpectatus germani*) in Southern Thailand

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Abstract

Germain's swiftlets (*Aerodramus inexpectatus germani*) are farmed regularly in Southeast Asia and produce highly valuable nests for which there is an increasing demand. Some populations of this species are thought to be decreasing, but little is known about the habitat used by swiftlets for foraging. Here, we focused on this swiftlet's foraging habitat selection and describe their daily and seasonal variations in habitat use. We predict that the prey capture attempts would be highest during twilight periods of each day, but that overall capture rates would vary with season and habitat type. Prey capture attempts at different times of the day and seasons in five different habitats were investigated and compared to flying insect availability (estimate as biomass). For each habitat, insects were trapped immediately 5–10 m above vegetation levels (i.e., tree canopy and open paddies) and 0–5 m above water surfaces in water body habitat. The highest foraging intensity occurred over water bodies, forest, and open paddy land; all of which contained high numbers of major prey insects (Hymenoptera, Diptera, and Hemiptera). Foraging during the wet season was at a greater intensity than during the dry season which was associated with increased insect availability. This suggested that food supply in each habitat type, time of day, and season influenced the bird's foraging habitat use. To conserve populations of this swiftlet, it is therefore important to protect wetlands, forest areas, and open paddy land to support natural insect prey within the foraging range of local swiftlets.

Keywords

Edible-nest swiftlet, *Aerodramus fuciphagus*, feeding habitat, insect availability, Southern Thailand

The Germain's swiftlet (*Aerodramus inexpectatus germani*; Cranbrook, Goh, Lim, and Mustafa, 2013) is commercially farmed for its edible white nests. Some populations of this species appear to be declining as a result of overexploitation, for example, populations on the islands of Sabah and Sarawak in Malaysia and Andaman and Nicobar in India (Chantler & Driessens, 2000; Lau & Melville, 1994; Sankaran, 2001). However, although the overall trend is suspected to be a decline, there are few quantitative data available (BirdLife International, 2014). In southern Thailand, swiftlet houses appear to have low occupancy rates; 46.2% ($N=13$) of new buildings constructed in the last 7 years at Pak Phanang, a major site for swiftlet farming, were occupied (Petkliang, unpublished data). Similarly, only 20–30% of swiftlet enterprises in Penang, Malaysia,

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were estimated to be occupied (Thorburn, 2014). These relatively low occupancy rates are probably due to a combination of factors: the failure of the microclimate of buildings to simulate a cave-like environment (Ibrahim, Teo, & Baharun, 2009) and limited suitable foraging habitat due to the deforestation associated with agricultural expansion and urbanization in southern Thailand (Chuangchang & Tongkumchum, 2014; Prabnarong & Thongkao, 2006) and Malaysia (Lim, 2011). Populations of aerial feeders such as swiftlets are likely to be limited by the availability of insects as reported in barn swallow (Møller, 2013) and that land use changes can have significant impacts on insect availability and therefore impact aerial insectivorous birds (Græbler, Korner-Nievergelt, & Hirschheydt, 2010).

Swiftlets feed on the wing and forage over a range of open and forest habitats (Lim & Cranbrook, 2002). Major prey items identified in swiftlet diets include Hymenoptera (17–44% of the diet), Diptera (8–39%), Hemiptera (7–35%), Coleoptera (1–5%), and Isoptera (0–10%; Langham, 1980; Lourie & Tompkins, 2000; Nguyễn Quang, Quang, & Voisin, 2002; Viruhpintu, 2002). Foraging distances from Germain's swiftlet breeding sites are reported to be <25 km (Viruhpintu, 2002), similarly reported for a radio telemetry study at Pak Phanang in southern Thailand (Gale and Pierce, unpublished data). However, there is limited knowledge regarding the preferred habitats used for foraging and the patterns of food availability across different habitats. For example, in the Andaman Islands, India, Manchi and Sankaran (2010) examined the foraging habits and habitat use of the edible-nest swiftlet, *A. fuciphagus inexpectatus*, at 1–2 km around their breeding sites and found that the birds were more active over forested areas than over open land, but insect prey availability was unknown. The foraging site usage of glossy and pygmy swiftlets in Philippine are varies by time and microhabitat (Collin, 2000). Nevertheless, foraging patterns of aerial insectivorous birds such as swifts (Chantler & Driessens, 2000), swallows (Brown & Brown, 2001; Græbler et al., 2010; Møller, 2013), and sand martins (Bryant & Westerterp, 1980) are known in Europe and North America. These could be applied to understanding the foraging of Germain's swiftlet. For example, in cliff swallows, the foraging habitat heterogeneity and land use diversity appear to influence prey insect distribution which varies across sites and plays a role in colony choice (Brown, Sas, & Brown, 2002).

Understanding foraging habitat selection in Germain's swiftlets is also important because of the swiftlets economic value and the functional role they provided in insect pest control in areas they inhabit (Viruhpintu, 2002); this also has implications for swiftlet conservation and management. Furthermore, foraging intensity, habitat characteristics, and food availability are required to

understand habitat use in the broader context of fitness and natural selection (Beyer et al., 2010).

Our study investigated habitat selection in time and space by Germain's swiftlet inferred from the number of prey capture attempts and food availability. We hypothesized that if availability of prey is the primary factor in foraging habitat selection based on energy profitability (Stephens, Brown, & Ydenberg, 2007), Germain's swiftlet should be attracted to specific habitats and at times when larger numbers of prey are present (Chantler & Driessens, 2000). Our predictions were that (a) the number of prey capture attempts will be higher during twilight periods, a time period when higher numbers of insects are observed in tropical zones (Basset, Novotny, Miller, & Kitching, 2003), and that the number of prey capture attempts will be higher during the wet season because of the rainfall related emergence of both terrestrial and aquatic insects (Fukui, Murakami, Nakano, & Aoi, 2006), particularly in tropical ecosystems (Kishimoto-Yamada & Itioka, 2015). We also predicted that (b) the number of prey capture attempts in the Germain's swiftlet will vary between habitat types because of specific habitat characteristics such as vegetation density, canopy cover, and number of tree layers that all affect insect diversity and abundance (Khalig, Javed, Sohail, & Sagheer, 2014; Scherber, Vockenhuber, Stark, Meyer, & Tscharrntke, 2014; Wolfe, Johnson, & Ralph, 2014).

Methods

Study Species

Germain's swiftlet is one of eight subspecies of edible-nest swiftlets (Chantler & Driessens, 2000) and are regularly commercially farmed in Southeast Asia (Cranbrook et al., 2013). The swiftlet-nest industry has expanded rapidly to meet consumer demand and currently generates 1.6 billion U.S. dollars per year for the Southeast Asian regional economy (Thorburn, 2015). Many of these swiftlet populations appear to be restricted to coastal habitats or other habitats where large caves are available for nesting and roosting. They also now use abandoned houses or buildings specifically constructed for swiftlets to roost and nest (Lim, 2011). Germain's swiftlets leave roost sites to feed at dawn and return at dusk, using echolocation to fly within dark caves or buildings (Lim & Cranbrook, 2002). Populations of swiftlets breed all year, but greater breeding activity occurs from January to May as well as between July and October in the eastern coast of peninsular Thailand (Phongchoo, 1985; Petkliang, unpublished data). During the first peak, nests are built and eggs are laid in late January and nestlings fledge in early May. During the second peak, nests with eggs are found in late July and nestlings fledge in October.

Study Sites

This study was conducted in Hat Yai, Songkhla, (7° 0' 12" N and 100°28' 4" E, 1,600 km²; Figure 1) on the eastern coast of peninsular Thailand. In this study area, the total annual rainfall averages approximately 1,863 mm per year but significantly different between seasons. The dry season (rainfall < 100 mm per month) occurs from February to May (Meteorological Department, 2009), and the primary wet season (rainfall 120–600 mm per month) occurs from August to December and is due to the north-east monsoon (Wangwongchai, Sixoing, & Qingcun, 2005). Colonies of Germain's swiftlet are concentrated in the city of Hat Yai (with more than 30

buildings specifically built for swiftlets). Based on an estimated foraging range of < 25 km, a 40 × 40 km² grid, centered on Hat Yai city, was used to sample the potential foraging area for swiftlets. Habitat within the grid was classified into five types based on land-use data from the Land Development Department, Thailand. The proportions of each habitat within the grid were 68.8% tree-dominated agricultural land (rubber, oil palm, orchard, and other tree plantations), 17.1% open paddy land (rice field, grassland, annual crops such as cucumber, pumpkin, and bean), 8.8% urban, 3.8% forest (mangrove, peat swamp, and lowland evergreen forest), and 1.5% water bodies (ponds, rivers, lakes included the shoreline; Mitsch

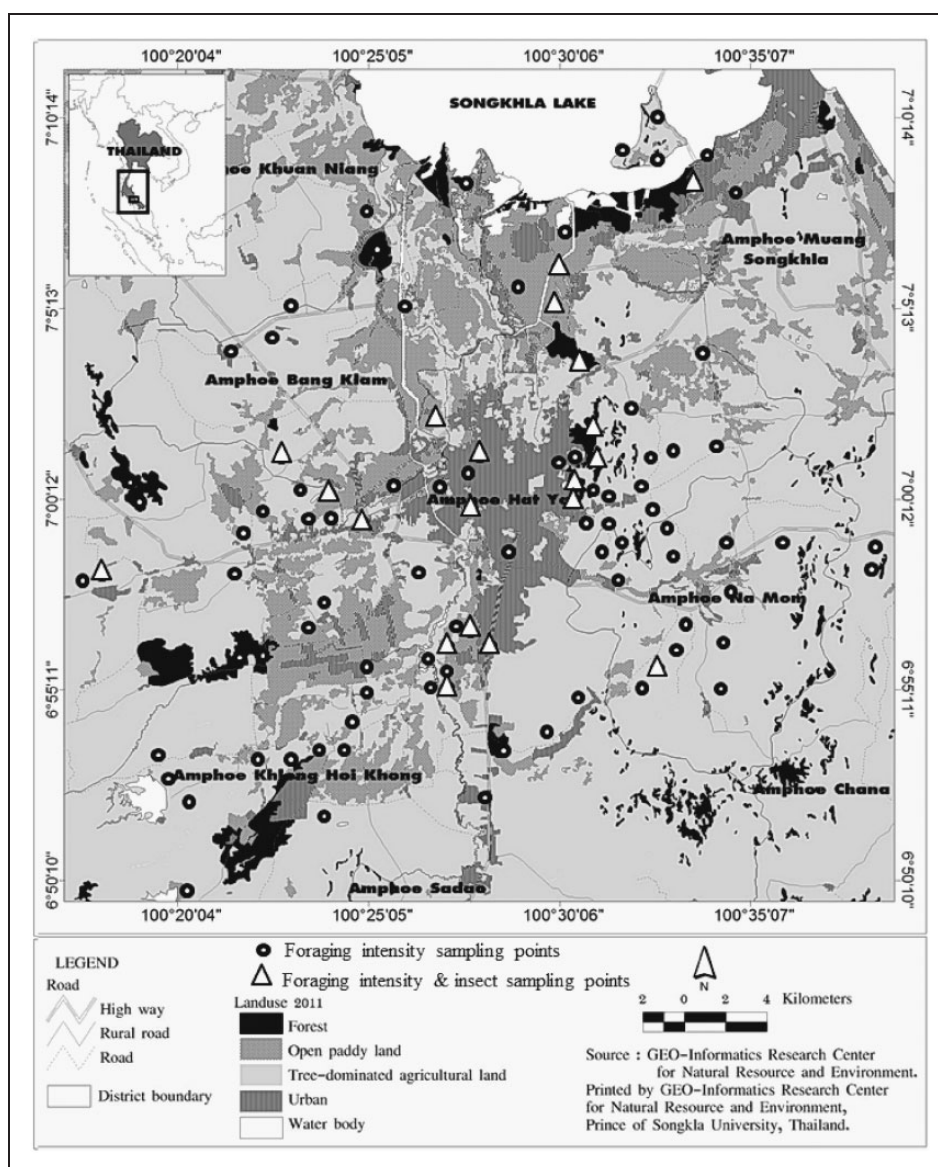


Figure 1. Map of 100 sampling points, which included 80 swiftlet foraging intensity sampling points and 20 sampling points which in addition to swiftlet foraging intensity samples, also included insect sampling, covering all five habitat types noted in the legend within a 40 × 40 km block covering the estimated foraging range of Germain's swiftlets nesting in Hat Yai, Songkhla, Southern Thailand.

Table 1. Available Habitat Types in the Study Area (%) Within a 25-km Radius of Focal Swiftlet Colonies of Hat Yai, Southern Thailand.

Main characteristics	Forest (3.8%)	Open paddy land (17.1%)	Tree-dominated agricultural land (68.8%)	Urban (8.8%)	Water bodies (1.5%)
Canopy height (m)	10–25 (tree)	<10 (emergent trees)	10–20 (trees)	<15 (trees)	<15 (trees at shoreline)
Percentage canopy cover	70–90	0–20	40–70	0–20	0–20
Tree density/ha (gbh > 10 cm)	>400	<50	100–400	<50	<100
Sampling objective: temporal variation in prey capture attempts	<i>n</i> = 12	<i>n</i> = 12	<i>n</i> = 12	<i>n</i> = 12	<i>n</i> = 12
Prey capture attempts per habitat	<i>n</i> = 12	<i>n</i> = 12	<i>n</i> = 52	<i>n</i> = 12	<i>n</i> = 12
Insect biomass	<i>n</i> = 4	<i>n</i> = 4	<i>n</i> = 4	<i>n</i> = 4	<i>n</i> = 4

Note. Includes habitat characteristics and number of sampling points for each study's primary objectives. Gbh = girth at breast height.

& Gosselink, 2007; i.e., vegetation within 50 m from their edges; Table 1). To minimize the effect of distance from the colony on habitat selection, each habitat type was recorded at four distance categories from the colony sites: (a) 0–5 km, (b) 5–10 km, (c) 10–15 km, and (d) 15–20 km. In addition, sampling points were equally assigned to each quadrant: north, east, south, and west. To minimize edge effects and provide a buffer zone (Bibby, Burgess, & Hill, 1992), sampling points were located after randomly walking at least 100 m into a particular habitat type (found using a GIS database). Once a sampling point was identified, a 100 m radius circular area was determined, and the habitat type assigned was based on the habitat type that contributed >70% of the area. The distance between each sampling point was >500 m. At each sampling point, habitat characteristics were recorded, including canopy height, (e.g., trees at the shoreline of water bodies and emergent trees of open paddy land), canopy cover, and tree density using the point-centered quarter method (Mitchell, 2007). Average canopy height was calculated using a range finder (Leupold GX-1 with a maximum range of 365 ± 1 m), and canopy cover percentage was assessed using a densiometer (Table 1).

Data Collection

Foraging intensity. A total of 100 fixed sampling points (Table 1) were used to measure foraging intensity across habitats. Of these, 60 points were used to assess diurnal and seasonal variation in foraging intensity. The foraging intensity was defined as the number of prey capture attempts of focal birds (Fauchald & Tveraa, 2003). Prey capture attempt rate was defined as the number of attempts by birds to catch insects on the wing per minute. To standardize for swiftlet detectability in different habitat types, open areas were selected as observation points where birds could be observed above the vegetation canopy. At each sampling point, scan sampling was used to count the number of

swiftlets. Flocking birds were either counted individually if in small groups or counted in estimated blocks of 5 or 10, depending on the size of the flock (Bibby et al., 1992). Foraging intensity was sampled by randomly selecting at least four individuals and recording individual prey capture attempts per minute.

Temperature and humidity were recorded at each of the 100 sampling points. Wind speed and rainfall data were collected from the nearest weather station of the Thai Meteorological Department at the time of the observations.

Habitat variation in foraging intensity. The number of sampling points assigned to each habitat was in proportion to the area of each habitat type within the grid (Table 1). Only the peaks of foraging activity, early morning (06:00–08:30) and late afternoon (14:30–18:30), were used to compare prey capture attempts across different habitats. Data were collected at each sampling point during seven sessions (i.e., two samples per session) from February 2014 to March 2015 (1,400 total observations). The seven sessions covered both the breeding and nonbreeding periods.

Diurnal and seasonal variation in foraging intensity. To determine diurnal and seasonal variation in foraging intensity, 60 sampling points covering the five habitat types (12 points per habitat) were sampled. Diurnal differences in the number of prey capture attempts were examined by sampling within three periods of each day: morning (early morning after sunrise, 06:30–10:30), midday (late morning to early afternoon, 10:30–14:30), and late afternoon (late afternoon to evening before sunset, 14:30–18:30). These samples were collected at each of 60 sampling points during three sessions from February to July 2014, providing a total of 540 observation periods.

The annual foraging pattern of prey capture attempts (February 2014 to March 2015) was examined using only high activity periods: early morning (06:30–10:30) and late afternoon (14:30–18:30). For seasonal comparisons,

two sessions during the dry season (February to May 2014) and two sessions during the primary wet season (August to November 2014) were compared.

Aerial insect availability. Aerial insects were sampled at 20 of the sampling points (four per habitat type). Insects were sampled at 0–5 m above the water surface by using floating cylindrical sticky traps, and at canopy height, and 5–10 m above the canopy, using a pole (a series of aluminum tubes attached with a rope and a single fixed pulley on the top) with four, 20 × 30 cm cylindrical sticky traps attached (Appendix). Total trap area was 2,400 cm² at each sampling point. Based on Taylor (1962), insect sampling was limited to daylight periods, with daily rainfall < 20 mm and an average wind speed < 16 km/h. For estimating diurnal patterns of insect biomass, insects were collected at 20 sites during three sessions (February 2014 to July 2015). In each session, 20 traps were opened for 4 hr during three diurnal periods (morning, midday, and late afternoon). These corresponded to the bird foraging observation periods at each site and provided a total of 720 trap hr. To estimate annual patterns in insect biomass, the traps were left open for 12 hr at the 20 trap sites for a total of seven sessions (February 2014 to March 2015), resulting in 140 trap sessions and 1,680 trap hr. For wet and dry season comparisons, we selected the insect traps sampled from February to May to represent the dry season and insect traps sampled from August to November to represent wet season (in total 80 traps and 960 trap hr).

Arthropod samples were stored in a refrigerator (4°C) and identified to order or family with the aid of a compound and stereo microscope following Triplehorn and Johnson (2005). The proportion of each captured insect taxa and number of individuals were recorded. The body length of arthropods was measured and results converted to insect biomass by using regression equations following Lumsden and Bennett (2005).

Data Analysis

The R statistical package (V3.2.4, R Development Core Team 2016) was used for all analyses. Generalized linear mixed models (GLMMs) using restricted maximum likelihood (libraries nlme and lme, respectively) were applied to determine foraging habitat use, with the number of prey capture attempts per minute as the response variable. For temporal diurnal variation, fixed effects included time of day, habitat type, and insect biomass sampled per 4 hr. Sampling session was included as a random effect. For the seasonal analysis, fixed effects included season, habitat type, and daily insect biomass. Session in each season was considered a random effect.

A one-way analysis of variance (ANOVA) was used to compare average mean number of prey capture attempts

per minute and insect biomass at different time periods and habitat types, and pairwise comparisons were applied when the ANOVA results were significant. Independent sample *t* tests were used to compare average mean foraging intensity and biomass of prey insects between wet and dry seasons.

Bartlett tests of homogeneity of variance and Anderson–Darling normality tests were applied to test statistical assumptions.

Results

For all habitats combined, the prey capture attempts occurred in 80.9% of 1,400 observations (>5,000 birds). The proportion of observations including prey capture attempts by habitat were 85.1% (143/168) at water bodies, 84.5% (142/168) above both forests and open paddy land, 79.2% (133/168) above urban areas, and 71.2% (518/728) above tree-dominated agricultural land.

Diurnal and Seasonal Variation in Foraging Intensity

Swiftlets emerge from roost sites during early morning (05:30–07:00) and return in the early evening (18:00–19:30) often after sunset. The rate of prey capture attempts by swiftlets varied with both time of the day and time of year. The birds showed the highest rate of prey capture attempts in the morning and late afternoon and the lowest intensity at midday, with peak rates 1 hr after sunrise and an hour before sunset. The number of birds detected was also lower at midday when birds appeared to glide at high altitudes with little evidence of foraging. The best-fit GLMM model showed no interaction between time of day and habitat, $F(8, 125) = 1.76$, $p = .089$. The main factors that affected the number of prey capture attempts were time of day, $F(2, 125) = 38.63$, $p < .001$, and insect biomass in each time period, $F(1, 125) = 13.64$, $p < .001$ (Table 2). There was a significant difference in the rates of prey capture attempts among different times of day in all habitat types, $F(2, 140) = 41.19$, $p < .001$ (Figure 2a). Similarly insect biomass was significantly higher in the late afternoon compared to morning and midday, $F(2, 163) = 4.68$, $p = .010$ (Figure 2b).

The annual pattern of prey capture attempts within the study area from February 2014 to March 2015 showed lower rates during the dry season that increased during the transition between dry to wet seasons and was highest during the wet season. Likewise, the rates were lower in the second transition from wet to dry season (Figure 2c). Overall, the rate of prey capture attempts was significantly higher in the wet than in the dry season, $t(634) = -9.01$, $p < .001$. The annual patterns of insect biomass showed a similar trend to rates of prey capture attempts (Figure 2d) with the average insect biomass

Table 2. Results of Generalized Linear Mixed Models to Detect the Effects of Time of Day, Habitat Type, and Insect Biomass on the Number of Swiftlet Prey Capture Attempts.

Explanatory fixed factors	F value	p value
(A) Daily		
Intercept	286.18	<.001**
Insect biomass	13.64	<.001**
Time of day	38.63	<.001**
Habitat type	2.14	.078
Time of day: Habitat type ^a	1.76	.089
(B) Season		
Intercept	94.02	<.001**
Insect biomass	10.10	.001*
Season	4.25	.040*
Habitat type	11.15	<.001**
Season: Habitat type ^a	2.92	.022*

Note. (A) daily = morning, midday, and late afternoon; (B) season = wet (August to November 2014) and dry (February to May 2014).

* $p < 0.05$; ** $p < 0.001$.

^aIndicates an interaction.

being significantly higher during the wet season compared to the dry season, $t(158) = -2.21$, $p = .028$.

Habitat Variation in Foraging Intensity

The best fit GLMM for assessing the effect of habitat type, season, and insect biomass on the rate of prey capture attempts found that all of these factors affected foraging intensity of swiftlets: habitat type, $F(4, 167) = 11.15$, $p < .001$; insect biomass, $F(1, 167) = 10.10$, $p = .001$; and season, $F(1, 167) = 4.25$, $p = .040$ (Table 2).

Using forest habitat as the intercept in multiple regressions, we found no significant difference in foraging rates between forest, water bodies and open paddy, and lower rates for tree-dominated agricultural land and urban habitats (Figure 3a, Table 3).

There was a significant interaction between season and habitat type, $F(1, 167) = 2.92$, $p = .022$ (Table 2), and we found there were significantly more prey capture attempts during the wet season than dry season in open paddy land and tree-dominated agricultural land. In contrast, foraging rates over water bodies, forests, and urban lands, the

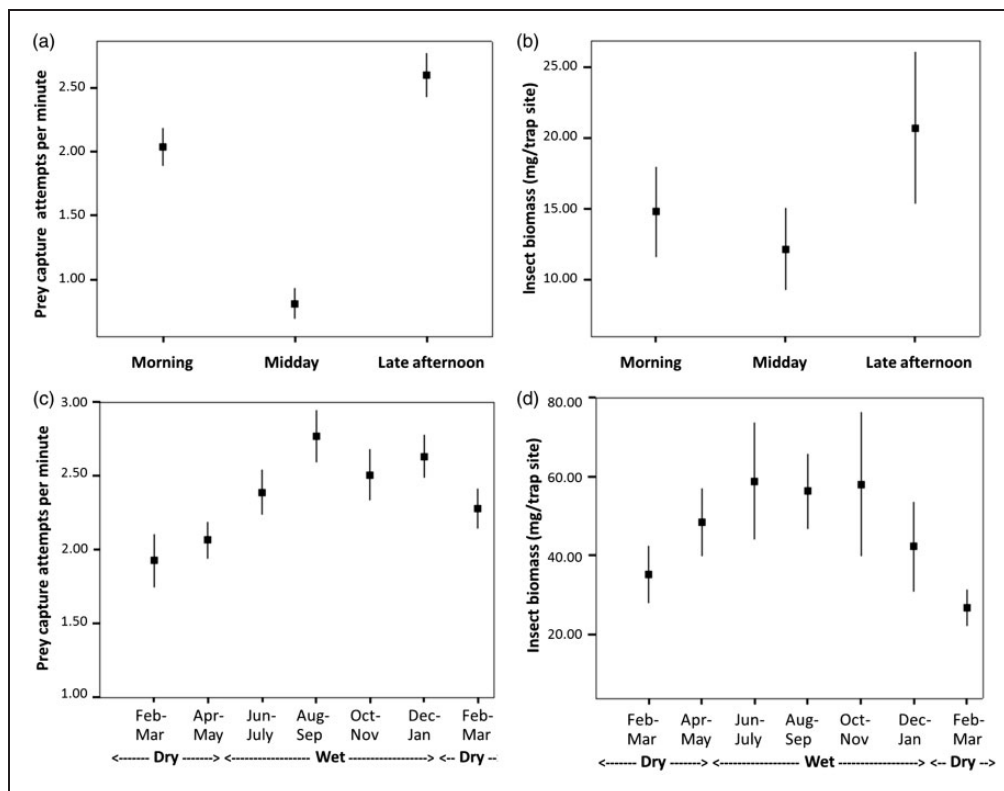


Figure 2. Temporal variation (February 2014 to March 2015) in prey capture attempts: diurnal differences in (a) average number of swiftlet prey capture attempts per minute (mean \pm 2 SE) of 540 observations and (b) the average insect biomass in mg per trap site (180 traps opened for 4 hr of sampling, total 720 hr); yearly pattern in the (c) average number of swiftlet prey capture attempts per minute based on 1,400 observations and (d) the average insect biomass in mg per trap site (140 traps opened for 12 hr, total 1,680 hr).

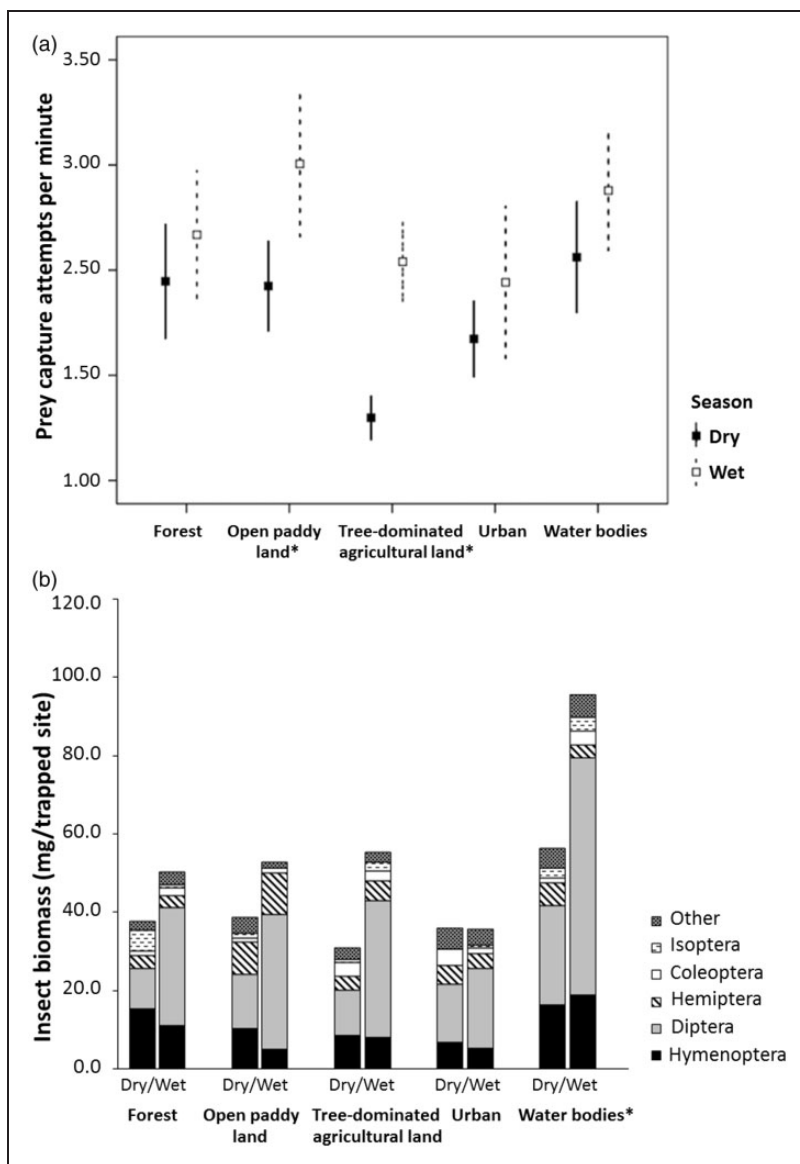


Figure 3. (a) The average number of swiftlet prey capture attempts per minute (mean \pm 2 SE) showing significantly more attempts during the wet than dry in open paddy land and tree-dominated agricultural land ($p < .001$) and (b) the average insect biomass in mg per trap site (2,400 cm² trapping area) in different habitats using 80 traps, 960-trap hr during the wet and dry season from 20 sample points. There were significantly higher insect biomass over water bodies than others ($p < .001$). The bars also show the proportion of flying insect taxa trapped in each habitat type by season.

Table 3. Summary of Multiple Regression Coefficients to Detect the Effects of Habitat Type on the Number of Prey Capture Attempts per Minute Using Forest Habitat as the Intercept.

Explanatory variables	Estimate	SE	t value	p value
Intercept	2.780	.340	8.010	<.001**
Open paddy land	-0.457	.300	-1.524	.129
Tree-dominated agricultural land	-1.059	.307	-3.442	.007*
Urban	-0.780	.315	-2.474	.014*
Water body	0.346	.312	1.108	.269

* $p < 0.05$; ** $p < 0.001$.

number of prey capture attempts were not significantly different between seasons (Figure 3a).

The insect biomass was significantly higher, $F(4, 175) = 8.63, p < .001$, over water bodies than other habitats but did not vary among the other habitats. However, the average total insect biomass in open paddy land was higher than above tree-dominated agricultural land, forest, and urban, respectively (Figure 3b). The biomass of Hymenoptera, which probably forms a major portion of the swiftlet’s diet, was significantly different between habitat types, $F(4, 175) = 5.63, p < .001$. The highest Hymenoptera biomass was recorded above water

bodies, followed by forest then tree-dominated agricultural land, open paddy land, and urban, respectively. Diptera, the second major diet component and the most common prey were significantly different between habitat types, $F(4, 175) = 4.60$, $p = .001$, with the highest biomass over water bodies, followed by open paddy land, tree-dominated agricultural land, forest, and urban land, respectively (Figure 3b). In addition, the dipteran biomass in open paddy land with livestock was significantly more than open paddy land without livestock (34.69 ± 24.79 mg per trap site [mean \pm SD], $n = 11$, and 14.37 ± 11.59 mg per trap site, $n = 16$, respectively; Mann-Whitney U test, $U = 30$, $p = .003$).

Discussion

We found significant temporal and spatial variation in the foraging intensity of Germain's swiftlet in relation to available insect biomass.

Diurnal and Seasonal Variation in Foraging Intensity

The Germain's swiftlet showed significant differences in foraging rates at different periods of the day, with the highest intensity of foraging during the early morning and the late afternoon and the lowest intensity at midday. Higher foraging rates during these periods can be explained by the emergence of more flying insects during twilight, a pattern observed in insects occurring in lowland tropical forest in Southeast Asia (Basset et al., 2003; Kishimoto-Yamada & Itioka, 2015). The frequency of nestling feeding activities by parent swiftlets is likewise concentrated in the hour after dawn and an hour before dusk (Viruhpintu, 2002; Petkliang unpublished data), supporting evidence of greater foraging intensities during the twilight period. Late afternoon feeding before sunset is also important as birds generally acquire more energy reserves before the end of the day (Bednekoff & Houston, 1994) as they require food for feeding nestlings and energy for nest building (saliva production) at night (Lim & Cranbrook, 2002; Medway, 1962). Although nest building is regularly carried out all night, it is most frequently observed between 18:00–22:00 and 04:00–06:00 (Ramji, Lim, & Rahman, 2013; Petkliang, unpublished data). Some birds return to the nest after first emergence in the morning to continue nesting building and feed their nestlings (Ramji et al., 2013) before initiating long foraging trips during midday (Viruhpintu, 2002). Greater foraging intensities in the late afternoon and early morning have also been reported in the edible-nest swiftlet in India (Manchi & Sankaran, 2010).

The lower foraging intensity at midday may be a consequence of swiftlets being aerial feeders and nonstop flyers; swiftlets can climb to higher altitudes around midday using thermal lifts to conserve energy but

showed little evidence of foraging. Alternatively, swiftlets might follow insects carried by rising air currents, as do migratory swifts (Dokter et al., 2013), but we need more observations at heights of over 100 m to confirm this. However, purple martin (*Progne subis*), an aerial insectivore which can fly up to 1,889 m above the ground, nevertheless mostly forage below 200 m, where their prey occur (Helms, Godfrey, Ames, & Bridge, 2016). This is in agreement with other observations of swifts which rarely forage above 100 m because insect numbers generally decline above this altitude (Chantler & Driessens, 2000). Potential windbreaks for insects can lead, for example, to greater food availability for Cliff swallows over edge areas, that is, tree lines, hillsides, and buildings (Brown et al., 2002) and close to the tree canopy (Basset et al., 2003).

Prey capture attempts were significantly greater during the wet season than during the dry season. The primary explanation for this is that the average total insect biomass per site was significantly higher during the wet season than the dry season, probably due to the increased emergence of aquatic as well as terrestrial insects during this time, as has been observed elsewhere (Fukui et al., 2006). Most tropical arthropods exhibit their abundance peaks during the wet season or the transition period from dry to wet and may change in response to seasonal changes in rainfall (Kishimoto-Yamada & Itioka, 2015). Increases in insect biomass during the wet season were mainly influenced by changes in dipteran biomass which was approximately double that of the dry season. The increase in dipteran biomass in this study was similar to wet season increases observed in forest and savanna in Brazil (Tidon, 2006).

Seasonal variation in insect biomass could also be related to vegetation structure (Cody, 1981). During the wet season, all vegetated study sites had higher cover of green vegetation due to rainfall or newly planted annual crops which likely provided more resources for insects. Rainfall affects plant growth which in turn could stimulate insect behavior and reproduction (Kishimoto-Yamada & Itioka, 2015). In contrast, during the dry season, the open paddy land and tree-dominated agricultural land were usually dry with yellow-brown mostly dead annual plants and reduced leaf area (such as for perennial crops) and therefore probably had lower insect biomass. Even in forest habitat, fig wasps and canopy flies also vary because of leaf flushing and flowering of canopy trees in Southeast Asia (Sakai, 2002). Consequently, climatic variation due to seasonal changes can cause changes in the food supply, which in turn influences foraging habitat selection for this species as also found in other insectivorous birds (Kishimoto-Yamada & Itioka, 2015; Wolfe et al., 2014).

In addition to food availability, higher wet season foraging intensity may be associated with peaks of

breeding, which occurred during the wet season (Lim, 2011). For example, the peak of swiftlet hatching and fledging occurred in the wet season from April to July in the upper, eastern coast of peninsular Thailand (Viruhpintu, 2002) and during August to November in Sarawak, Malaysia (Lim, 2011).

Habitat Variation in Foraging Intensity

Foraging intensity was highest above the swiftlets preferred habitats, water bodies, forest areas, and open paddy land. Our results provide evidence that variation in insect availability was associated with different intensities of foraging, consistent with other studies that find birds select foraging habitat based on patch quality, that is, the patches which provide the highest profitability (Sanchez-Clavijo, Hearn, & Quintana-Ascencio, 2016; Stephens et al., 2007).

The most intensive foraging occurred over water bodies, which showed greater availability of all insect taxa, both aquatic species over the water and terrestrial insects above the banks adjacent to water bodies. Fukui, et al. (2006) found that riparian habitats contained larger numbers of insects. Such habitats can provide greater abundances of insects year round, thus water bodies with green vegetation may be considered long-term, high-quality patches (Watanabe, Ito, & Takahashi, 2014).

The forest habitat was an important source of Hymenoptera, which is a major diet component for swiftlets (Nguyễn Quang et al. 2002). For example, Lourie and Tompkins (2000) reported that forests were an important source of Hymenoptera for swiftlets in Malaysia and that Hymenoptera comprised the largest proportion in food boluses collected from nestlings fed by swiftlets foraging over forest canopy in eastern Thailand (Ponak, 2004). The forest also had higher temporal species turnover than the other habitats, and this probably leads to the greater overall diversity of Hymenoptera in forest habitats (Tylianakis, Klein, & Tscharrntke, 2005).

Open paddy land had quite similar total insect biomass compared to forested areas, but the dominant insects were Diptera and Hemiptera, which are also major swiftlet diet components (Lourie and Tompkins, 2000; Viruhpintu, 2002). Insect abundance is usually higher when annual plants are green during the early wet season (Kishimoto-Yamada & Itioka, 2015), which may explain the higher prey capture attempts in this habitat. Field observations during our study also showed that dipterans were more abundant in the presence of livestock similar to a previous study on the barn swallow (Grüebler et al. 2010). Overall, open paddy land will likely be higher quality habitat when it is covered with green plants and partly flooded during the wet season.

The lower complexity of the vegetation structure of monoculture tree crop plantations was associated with

lower insect biomass during the dry season. Previous studies have found that insect biomass in rubber plantations was less than half that of forest habitat (Phommexay, Satasuk, Bates, Pearch, & Bumrungsri, 2011). Although tree-dominated agricultural areas were not intensively used in general by the swiftlets, they are known to use this habitat during the termite-swarmling periods in the early wet season (Davies, Eggleton, van Rensburg, & Perr, 2015; Petkliang, unpublished data). Termites are a high-energy and protein-rich prey item and were found to be the main component of the swiftlet diet during swarming periods (Viruhpintu, 2002).

Swiftlets foraging over urban habitat had fewer prey capture attempts and this habitat regularly showed lower insect biomass, although this habitat attracted flying insects when artificial light sources were turned on (Perkin, Holker, & Tockner, 2013). This habitat therefore probably provides a supplementary food source during twilight.

In conclusion, the highest foraging intensity occurred during the late afternoon to sunset and early morning after sunrise, and foraging intensity was higher during the wet season than during the dry season. The preferred foraging habitats were found to be over water bodies, forest, and green open paddy land. These temporal and spatial differences in foraging intensity can be explained by temporal and spatial changes/variation in insect biomass. Germain's swiftlet seemed to select foraging habitat based on the quality of the food supply (Chantler & Driessens, 2000) and perhaps use habitat characteristics to identify richer food resources (Khalig et al., 2014; Wolfe et al., 2014).

Implications for Conservation

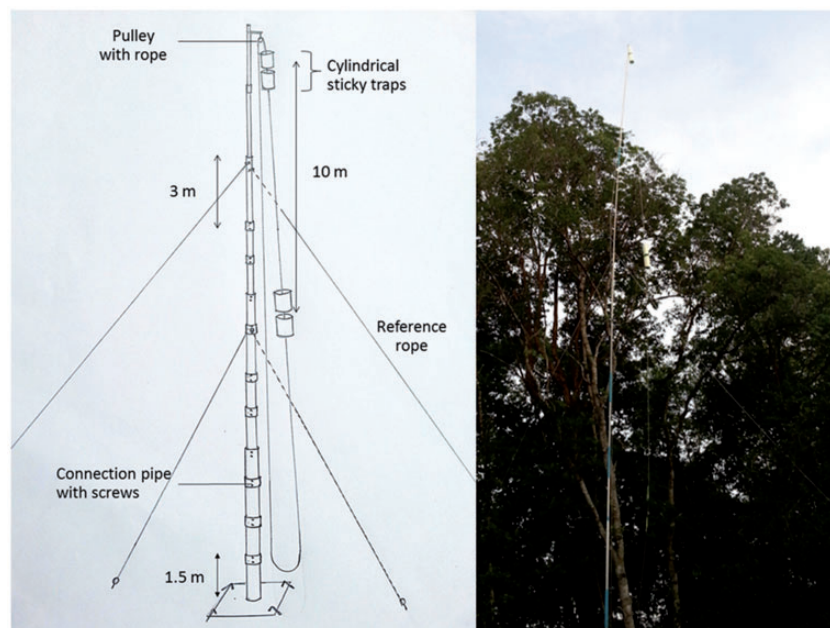
This study highlights the need for greater protection of water bodies, forest, and open paddy lands that provide natural prey insects for swiftlet populations. Conservation practices should be designed, that is, planting or maintaining the vegetation growth at the banks adjacent to water bodies as riparian buffers, for restoring water bodies and insect resources (Gilbert et al., 2015). For privately owned areas, the use of vegetation fences at property boundaries could be encouraged by land management agencies and swiftlet farmers. In addition, public water sources need better protection through local government and nongovernmental actions because we found lower intensity of use over water bodies which had lower water quality (Petkliang, unpublished data), however the relationship between swiftlet use and water quality needs further investigation.

The information provided here on habitat use may also guide local swiftlet farmers regarding the establishment of suitable nesting sites for Germain's swiftlet in closer proximity to their preferred foraging habitats.

Swiftlets act as pest control agents in agricultural areas (Viruhpintu, 2002) and thus swiftlet farming provides additional benefits to adjacent farm crops. Disseminating information about the ecological and economic significance of foraging habitat use of Germain's swiftlet to farmers could help raise awareness about the benefits of maintaining and improving natural habitats, hence promote local protection of water bodies, forest, and the management of open paddy lands. Currently, many water bodies and forests are heavily impacted by human activities in Southeast Asia (Primack & Corlett, 2005). Such habitat losses will impact the sustainability of the swiftlet industry and thus swiftlet farmers and local governments need to be more informed such that they can make more sustainable land-management decisions. Because this species is protected by law, conflicts between swiftlet farmers and governments over land use and land management could be improved by increased availability of higher quality data, starting with more detailed data on population trends, including population vital rates, and quantification of how swiftlets might benefit agriculture through insect control and how land use change and farming practices impact on swiftlet prey.

Appendix

Pole for flying insect trapping: a series of aluminum tubes attached with a rope on a single fixed pulley on the top. The cylindrical sticky traps (total 2,400 cm² trapping area) were attached on that rope at canopy height and 5–10 m over the canopy. The height of the pole was adjusted by adding aluminum tubes from the bottom.



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