Foraging Habitat Selection and Seasonality of Breeding in Germain's Swiftlet (*Aerodramus inexpectatus germani*) in Southern Thailand

Nutjarin   Petkliang

A Thesis Submitted in Fulfillment of the Requirements for the

Doctor of Philosophy in Biology

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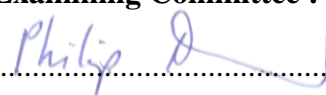**Author**   Mrs. Nutjarin Petkliang

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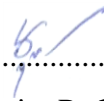
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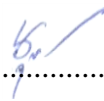
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Major Program   Biology

Academic Year   2016

ABSTRACT

Habitat degradation is major threat that limits animal populations and knowledge of foraging habitat selection is important to support the survival of organisms. Germain's swiftlet (*Aerodramus inexpectatus germani*) produces highly valuable nests and has an important ecological role in ecosystems as an insect predator. However, little is known about the foraging habitat preferences, vertical distribution and factors affecting the timing of breeding, knowledge which may be helpful for managing swiftlet populations. We aimed to determine 1) the preferred foraging habitats, diurnal and seasonal variation on foraging, 2) vertical foraging pattern and 3) the variation in breeding chronology between the west and east of peninsular Thailand, areas with relatively large swiftlet populations. The intensity of foraging within five major habitats was investigated from prey capture attempt and related to insect availability (estimated as biomass). Breeding activities of total 85 breeding pairs were observed using an IP camera at four colonies for three breeding cycles and related to insect biomass in its major foraging habitats. The highest foraging intensity was over water bodies, forest and open paddy land where insect abundance was higher compared to tree-dominated agriculture and urban areas. Foraging intensity was greater in twilight period than midday, the wet season showed higher intensity of foraging compared to the dry season and related to insect biomass. Vertical foraging height influenced by vegetation foliage height where were rich of insect prey. This suggested that food supply affected habitat use and it can affect swiftlet breeding strategies. Breeding time in the western colonies was earlier than the eastern colonies of peninsular Thailand probably due to differences in prey availability which is influenced by the timing of rainfall. Consequently, better protection and management of wetlands, forest and open paddy land within their

foraging range would likely improve the availability of natural insect prey. Nest harvest time should be varies by geographical variation in breeding chronology. This has implications for the sustainability of the swiftlet industry across the species range.

ชื่อวิทยานิพนธ์   การเลือกพื้นที่หากิน และการสืบพันธุ์ตามฤดูกาลของนกแอ่นกินรัง
(Germain's Swiftlwet, *Aerodramus inexpectatus germani*)
ในภาคใต้ของประเทศไทย
ผู้เขียน   นางนุชจรินทร์ เพชรเกลี้ยง
สาขา   ชีววิทยา
ปีการศึกษา   2559

บทคัดย่อ

การสูญเสียแหล่งอาศัยเป็นปัจจัยหลักที่กำหนดลักษณะประชากรของสัตว์ และการเลือก
พื้นที่หากินมีความสำคัญอย่างยิ่งต่อการอยู่รอดของสิ่งมีชีวิต นกแอ่นกินรัง (Germain's swiftlet,
Aerodramus inexpectatus germani) เป็นนกที่สามารถสร้างรังที่มีมูลค่าทางการค้า และมี
บทบาทเป็นผู้บริโภคแมลงในระบบนิเวศ แต่ความรู้ความเข้าใจเกี่ยวกับพื้นที่หากินและปัจจัยที่มีผลต่อ
เวลาสืบพันธุ์ในแต่ละพื้นที่ยังไม่ชัดเจนนัก ความรู้เหล่านี้จะเป็นประโยชน์อย่างยิ่งในการจัดการ
ประชากรนกแอ่นกินรัง การศึกษาครั้งนี้มีวัตถุประสงค์เพื่อ 1) ระบุพื้นที่หากินที่สำคัญของนกแอ่นกิน
รัง ความแปรผันในรอบวัน และฤดูกาล 2) ศึกษารูปแบบการกินอาหารในแนวตั้งของนกแอ่นกินรัง
และ 3) ศึกษาความแปรผันของเวลาสืบพันธุ์ระหว่างกลุ่มประชากรในพื้นที่ภาคใต้ฝั่งตะวันตกและฝั่ง
ตะวันออกซึ่งมีประชากรนกแอ่นกินรังอาศัยอยู่จำนวนมาก โดยการเก็บข้อมูลความเข้มของการกิน
จากจำนวนครั้งที่นกพยายามจับเหยื่อต่อนาที ระดับความสูงที่นกแอ่นกินรังจับเหยื่อ ในแหล่งอาศัย 5
แบบ วิเคราะห์ความสัมพันธ์กับปริมาณแมลงที่เป็นอาหารของนกซึ่งประเมินจากมวลชีวภาพของ
แมลงที่จับได้ในพื้นที่ศึกษา รวมทั้งบันทึกกิจกรรมการสืบพันธุ์ของนกแอ่นกินรังทั้งหมด 85 คู่ โดย
ติดตั้งกล้องวงจรปิดระบบออนไลน์ในฟาร์มเลี้ยง จำนวน 4 ฟาร์ม ติดตาม 3 รอบการสืบพันธุ์ และ
เก็บข้อมูลแมลงในพื้นที่หากินหลักทุก 2 สัปดาห์ พบว่า แหล่งน้ำ ป่า และพื้นที่เปิดโล่ง เป็นพื้นที่หา
กินที่สำคัญที่สุด โดยมีความเข้มของการกินสูงกว่าพื้นที่เกษตรกรรมและชุมชนเมือง สัมพันธ์กับ
ปริมาณแมลง ช่วงเวลาที่มีอัตราการกินสูง ได้แก่ เช้าตรู่ และพลบค่ำ ความเข้มของการกินอาหารใน
ฤดูฝนสูงกว่าในฤดูแล้งซึ่งมีความสัมพันธ์กับปริมาณแมลงในแต่ละช่วงเวลา เรือนยอดของต้นไม้มี
ความสำคัญอย่างยิ่งในการเลือกระดับความสูงในการหากิน เนื่องจากเป็นแหล่งอาศัยของแมลงที่เป็น
อาหารของนก ชี้ให้เห็นว่าปริมาณอาหารที่มีอยู่ในแต่ละแหล่งอาศัย ช่วงเวลา และระดับความสูงมี
อิทธิพลต่อการเลือกใช้เป็นพื้นที่หากิน ซึ่งจะส่งผลกระทบต่อการสืบพันธุ์ของนกด้วย โดยพบว่า นก
แอ่นกินรังในภาคใต้ฝั่งตะวันตกเริ่มกิจกรรมการสร้างรังวางไข่ก่อนภาคใต้ฝั่งตะวันออก และสอดคล้อง
กับปริมาณแมลงซึ่งได้รับอิทธิพลจากปริมาณน้ำฝน ดังนั้น การคุ้มครองและการจัดการพื้นที่ชุ่มน้ำ ป่า
และพื้นที่เปิดโล่งในขอบเขตพื้นที่หากินจะช่วยให้มีแหล่งอาหารธรรมชาติสำหรับนกแอ่นกินรัง และ
ควรกำหนดเวลาการเก็บรังนกต่างกันตามสภาพภูมิศาสตร์ที่มีเวลาสืบพันธุ์ต่างกัน ความรู้ที่ได้จาก
การศึกษาครั้งนี้จะเป็นประโยชน์ต่อการจัดการอุตสาหกรรมรังนกอย่างยั่งยืนต่อไป

ACKNOWLEDGEMENTS

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Background and Rationale

Swiftlet nests are a traditional food in Southeast Asia which have been an important item in Chinese cuisine and medicine. Hence, these have been exploited throughout their range for hundreds of years (Sankaran, 2001). Previously, all white-nest swiftlets have treated as a single species under the former name *Aerodramus fuciphagus* (Lim and Cranbrook, 2002) from at least eight subspecies of edible-nest swiftlet which confined to the Southeast Asian countries (Chantler and Driessens, 2000). Germain's swiftlet (*Aerodramus inexpectatus germani*; Cranbrook et al., 2013) is one of eight subspecies of edible-nest swiftlets and are regularly commercially farmed in Southeast Asia as recorded in Vietnam, Cambodia, Southern Thailand and Northern Peninsular Malaysia (Cranbrook et al., 2013). Many of these populations appear to be restricted to coastal habitats or other habitats where large caves are available for nesting and roosting. Additionally, they now use abandoned houses or even buildings constructed for them to roost and nest (Lim, 2011; Aowphol et al., 2008). In Thailand, the total white-edible nests export value is estimated to be worth 126 million Baht (~ 4.2 million US$) a year (Jory and Saengthong, 2007). In the early 19th century, the volume of trade was enormous: about 9 million nests weighing some 76 tonnes were imported into China each year at US$2000±4000 a kilogram (Lau and Melville, 1994). The demand for edible nests from the international market, such as from Hong Kong and China is ever increasing, despite the recent decrease in imports due to more stringent screening of the processed nests from the Chinese authorities enforcing (Lim, 2011). Populations of some of these species appear to be declining due to overexploitation, such as at Andaman and Nicobar Islands, India; as well as Sabah and Sarawak, Malaysia (Sankaran, 2001; Chantler and Driessens, 2000; Lau and Melville, 1994). Currently, there is a massive increase in available nesting habitat largely due to the construction of buildings (Cranbrook et al., 2013) by regional "farmers". These buildings are specifically designed to accommodate swiftlet roosts and nests (Lim and Cranbrook, 2002). Swiftlet farmers have invested an estimated

3.4 million baht (97,000US$) in the construction of such four-storey house-farms (Murdoch, 2008), 46.26% of these buildings appear to be occupied in Pak Phanang, Nakhon Si Thammarat (pers.obs.). Additionally, only 20-30% of swiftlet enterprises in Penang, Malaysia were occupied (Thorburn, 2014). The reason for the relatively low occupancy is probably due to multiple factors including inadequate microclimate of specific buildings to simulate a cave-like environment (Ibrahim et al., 2009; Manchi and Sankaran, 2011); however, it is also likely that low occupancy is due to population limitations. Populations of aerial feeders like swiftlets are probably limited by the availability of insects (Møller, 2013). *A. fuciphagus* feed on the wing and forage over all kinds of open and forest habitats (Lim and Cranbrook, 2002). The five main prey items are insects from the orders Hymenoptera, Diptera, Homoptera/Hemiptera, Coleoptera and Isoptera (Viruhpintu, 2002; Nguyên Guang et al., 2002; Lourie and Tompkins, 2000; Langham, 1980).

At the population level, habitat selection is the behavioural process by which different individuals in same population actually choose their nesting and foraging habitats (Johnson, 1980). This is shaped by balancing across cost-benefit tradeoffs, i.e. food requirement, predation risk and reproductive success (Bastille-Rousseau et al., 2010). Habitat use patterns results from balancing cost-benefit tradeoffs in both time and space, so we can explain the process of selection through spatiotemporal variation. Habitat types or characteristics within a desired habitat are the proximate reason that animal uses to determine the suitability of a site, while forage availability, shelter, and predator risk, which affects reproductive success and survival, are the ultimate reasons (Cody, 1981).

Unfortunately, there is inadequate information on the foraging habitat selection of the house-farmed white-nest swiftlet. Viruhpintu (2002) reported that the longest distance *A. fuciphagus* forages away from their breeding sites is about 25 km, similarly reported for a radio telemetry study at Pak Phanang in southern Thailand (Gale and Pierce, unpublished data). For other closely related taxa, i.e., *A. maximus* and *A. salanganus* is reported to fly more than 24 km from their breeding caves (Medway, 1962). In the Andaman Islands of India, Manchi and Sankaran (2010) examined the foraging habits and habitat use of edible-nest swiftlet, *A. fuciphagus inexpectatus*. The birds were observed near their breeding sites and not their entire

home range. Manchi and Sankaran also found that these birds were more active in forest areas than in open land. However, the mean percentage of foraging attempts was lower in the forest. This behaviour may depend on food availability which they do not investigate. Additionally, there is variation in the hourly foraging activity but they found it not to be significantly different. While in Thailand, the birds clearly show higher nest feeding activities in the early morning at 0600-0730 hr and late afternoon at 1800-1900 hr (Viruhpintu, 2002). Hence, there is a need for intensive examination of the swiftlet's daily foraging activities as well as prey availability. According to optimum foraging theory, the foraging animal must select a foraging habitat where they can get the highest profitability. If the availability of the prey is a determining factor in foraging habitat selection according to time-energy profitability (Stephens, et al., 2007), birds should be attracted to a habitat containing large numbers of prey insects. Insect abundance influence by climatic conditions (Visser et al., 2006) and varies in different time and space (Basset et al., 2003). For example, Tylianakis et al. (2005) mentioned that habitat type significantly affected the number of individuals and species richness of Hymenoptera. Moreover, to understand foraging habitat selection of swiftlets, it is important to know the vertical foraging activity and relationship to vertical insect abundance in swiftlets major habitat use since swiftlets are aerial insectivores and non-perching birds. This dimension can fulfil the explanation for swiftlet habitat selection in time and space. As Tanabe (2002) mentioned, close canopy forests are relatively homogenous horizontally but are vertically heterogeneous, affecting flying insect dispersal. Didham and Springate, (2003) reported that host-tree phenology, growth rate, and senescence pattern has a strong effect on temporal trends associated to canopy arthropod species. Furthermore, green areas which provide plenty of food for swiftlets are being degraded with the accelerated expansion of swiftlet farming industry, which in turn leads to the issues concerning sustainability (Lim, 2011). Knowledge on foraging habitat selection, prey insect availability and other factors may have an impact on the expansion of swiftlet industry in the future. This information may become useful for regional farmers, so that they may find the best locations for their farms in areas with higher probability of bird occupancy due to rich food resource. With such favourable habitats, swiftlets can construct higher quality nests which will bring higher income for farmers. Moreover,

swiftlets act as pest predator in agriculture (Viruhpintu, 2002) so the swiftlet farming can significantly show benefits to the agricultural community within foraging range of the swiftlets. Understanding swiftlet ecology can help the government in considering the next favourable policy that supports the gradually growth of this industry and gives strategic business advantage.

Furthermore, the bird timing of breeding and moulting seem to be effected by food-supply which influence to breeding success (Sodhi, 2002). Swiftlets feed on flying insects whose dispersal is influenced by climatic conditions, especially the wind (Srygley and Dudley, 2008). Rainfall is linked to swiftlets' breeding seasonality (Manchi, 2009) and wind plays an important role in the ecology of insectivorous birds as shown by relationships with reproductive success and survival (Møller, 2013). As the annual Southwest monsoon (May-October) at Andaman coast occur earlier than Northeast monsoon (November-January) at Gulf of Thailand coast (Meteorological department, 2009), sorainfall at the western coast occur earlier than the eastern coast. The phenology pattern of the reproductive parts of plants show earlier flowering and fruiting for nearly two months in the western part of peninsular Thailand (Tunjai, 2011) that can be associated to arthropods in canopy (Didham and Springate, 2003). Insect abundance may relate to the breeding time of swiftlets so that in different landscape sites where there is variation in climatic conditions, such in the west and east of peninsular Thailand, there possibly are variations in the breeding period of swiftlets. Since in the government law, swiftlet nest harvest time in Thai concession caves are fixed both in the west and east at 3 times per year on the first and second harvest period between March to May and the third harvest on August to September (Thongkleang, 2011), understanding the yearly breeding time can guide lawmakers on the appropriate time and indicating how often the concessionaires can harvest swiftlet nests.

This study can help conserve and manage both ecosystem and economic advantage of swiftlets for sustainable use.

1.2 Review of Literature

1.2.1 Study species

All white edible-nest swiftlet were classified under the name *Aerodramus fuciphagus* (Thunberg 1812) according to Lim and Cranbrook (2002). However, Cranbrook et al. (2013) categorized the white nest swiftlets into two large allopatric species of white-nest swiftlet in Malaysia: identified as Grey-rumped Swiftlet *Aerodramus inexpectatus*, including two subspecies *A. i. germani* and *A.i. perplexus*; and Thunberg's or Brown-rumped Swiftlet *Aerodramus fuciphagus*, with subspecies *A. f. fuciphagus* and *A. f. vestitus.* However, the classification of house-farmed white-nest swiftlet specimens from southern peninsular Malaysia is still unclear and may be excluded from these two species. The specimens from southern Thailand, Vietnam (Nguyên Quang et al., 2002) and Northern Malaysia are classified as the Northern Grey-rumped swiftlets or Germain's swiftlets (*Aerodramus inexpectatus germani*) (Cranbrook et al., 2013; Appendix 1). Aowphol et al., (2008) suggested that the White-nest Swiftlets living in recently established man-made houses in Thailand should be considered members of a single panmictic population. Thus, I will use the term, Germain's swiftlets (*Aerodramus inexpectatus germani*), for house-farmed white-nest swiftlets in this study (Appendix 1).

Germain's swiftlets, previously called White-nest swiftlets (*A. fuciphagus*), is a small bird, with upper parts blackish brown, under parts slightly paler, and rumps that range from whitish to dark grey. They have unfeathered tarsi. Nests are edible and white, consisting wholly of hardened saliva (Lekagul and Round, 1991). Their average body length is 120-130 mm. (Khobkhate, 1999). Viruhpintu (2002) showed that this species has a 118.2 ± 1.94 mm wing length, a 11.62 ± 0.46 mm tarsus length, a 5.19 ± 0.33 mm beak length, a 48.3 ± 2.09 mm tail length, and a 11.4 ± 1.66 g body weight. They nest in caves or sometimes in man-made buildings, and usually re-nest in the same nest site. They use echolocation to fly inside dark caves (Lim and Cranbrook, 2002).

1.2.2 Ecology of swiftlets

Habitats

The world range of the swiftlets extends from western Indian to southern continental Asia, Indonesia, northern Australia, and New Guinea to the islands of the

west and south Pacific (Lim and Cranbrook, 2002). *A. fuciphagus* is a resident in Thailand, living in the caves, offshore islands and mainland along the coastlines, ranging from the East to the Southern part of Gulf of Thailand and Andaman Sea. A study on ecology and distribution of *A. fuciphagus* in Thailand found that they disperse along 156 coastal islands. Birds nest in caves (their natural habitat) and man-made habitats. 1.09 million individuals were found in natural habitats while 0.16 million individuals were found in man-made habitats. They live in both limestone ground caves and caves that have water flowing through it. Good habitats are usually near rivers or coastlines where it is 26-35 °C with 76-90% humidity inside the cave and 30.1–32.4 °C with 70–80% humidity for man-made habitats; low air velocity; and light intensity < 5 lux (Pothieng, 2005; Ibrahim, et al., 2009). From many studies on microclimate, the weekly or monthly average microclimate data in man-made buildings throughout the year were shown but the daily fluctuations of these factors were not demonstrated (Nguyên and Voisin, 1998; Ibrahim et al., 2009; Manchi and Sankaran, 2011). Of which the latter might have an effect on nestling and fledging in swiftlets nests.

Breeding and Nesting

Breeding ecology of the White-nest swiftlets are investigated and showed not significantly different among each experiment as same as in Thailand that Phongchoo (1985), Viruhpintu (2002), Ponak (2004) and Pothieng (2005) determined breeding biology of swiftlets (Table 1.1). Average times of one brood cycle about 92-104 days. The average time of nest building, incubation and nestling feeding were 29.83± 6.3, 23.63± 1.6 and 40.25± 3.0 days, respectively with 15.94±10.5 days for subsequent brood or start building a new nest if it is taken. The two-egg clutch was the normal clutch size with the laying interval of 3.36±2.5 days. The highest percentages of egg laying, hatching success and breeding success at fledging was in January to April. Breeders paired and had nest-site fidelity throughout almost studies. (Viruhpintu, 2002). Male bird is nearly twice as hard working in nest building as the female correlating with the fact that spermatogenesis less energy demanding than oogenesis (Ramji et al., 2013). Parental investments in feeding young were not significantly different between sexes (Viruhpintu, 2002).They can re-nest and breed all year round (Nguyên Guang, 1998). The breeding success at fledging was affected by the quality

of nesting sites. Delay egg and fledging should be missed the rich food resource (Kang et al., 1991).The variation on breeding season is results from the locality of nest sites. In the Andaman Islands, the breeding seasonality in the edible-nest swiftlet is linked with rainfall (Manchi, 2009). In swiftlet farming, the owner usually located their swiftlet house near old colony where was often settle near a river or coastline; the conditions in swiftlet houses were set like the natural cave both microclimate and nest site (Lim and Cranbrook, 2002; Lim, 2011). The coloniality of swiftlets may most often be associated with food resource patch and group foraging (Brown and Brown, 2001).

Table 1.1 Reviews of breeding biology and prey insect determination of white edible-nest swiftlet at difference geographical locations.

Geographical locations	Breeding cycle (days)	Average clutch size	Nest building (days)	Incubation(days)	Nestling to fledging (days)	Breeding success (%)	Breeding peak (month)	Season at breeding peak	Prey type determination	Insect availability
Thailand										
: Southern, Nakhon Si Thammarat (Phongchoo, 1985)	87-102	1-2	30-35	22-25	35-42	-	Jan-Mar	Late wet-early dry	-	-
: Central, Samut Sakhon (Viruhpintu, 2002)	92-104	1.87± 0.3	29.8± 6.3	23.6± 1.6	40.2± 3.0	70.0± 38.1	April	Late dry	Food bolus	-
: Eastern, Trat (Ponak, 2004)	96-120	1-2	30-48	24-27	42-45	-	Feb-May	Dry	Food bolus	-
Malaysia										
: Boneo, Sarawak (Lim and Cranbrook, 2002; Lim, 2011)	120	2	30	19-32	37-54	70.2	Feb-April, Aug-Nov	Late wet, Early wet	Food bolus	-
: Penang (Anun et al., 201)	-	1.8± 0.3	-	22.3± 1.7	44.6± 5.9	62	Jan-Apr	Late wet	-	-
(Langham, 1980)	-	1.92	-	23±3	43±6	48.4	Nov, Feb	Early and late wet	Food balls	-
Vietnam (Nguyen and Voisin, 1998)	-	2	-	-	-	22-86	Dec-Apr	-	Food pellets	-
Indonesia :Java (Mardiastuti et al., 1997)	-	1-2	-	23.6	40	82.8	Nov-Jan	Wet	-	-

Brown and Brown (2001) showed that the colonial birds make the decision on breeding by determining from reproductive success. For example, it may be used in deciding whether to disperse to a new nesting site. This is very interesting that in breeding season, the owner of swiflets farm will broadcast the fledging call to attract the new birds. But in this case, still have limited number of scientific papers that have a good explanation about this attracting method.

For nest site characteristics, Viruhpintu et al. (2002) found that in the cave most white-nest patchesnwere found on the smooth surface of the inward-inclining walls and 1-80 m^2 in patch size. All nest patches were found at smooth and concave wall with supporter. The protruding U-shaped rocks, were found in all nest patches and were used entirely by birds. This suggested that supporters play an important role in the nest survival and the breeding success. Then she set the experiment on the use of artificial nest-sites by swiftlets living in the sacred building, in which the nest-site characteristics at caves were imitated, was successful. This raise the question that how does U-shaped rocks effect to breeding success of *A. fuciphagus*. Moreover, she revealed that swiftlet selected the nest site by the unique characters of the cave wall rather than by random choice. Manchi and Sankaran (2011) supported this result and showed that the species preferred inwardly inclined walls and supporter for nest construction. In contrast, overall 77% of nest sites were rough textured surfaces. These are the studies in natural cave not in house farming. If we prepare same nest sites with same substrates in two building "why birds do not come inside both of building?" it should be have other reasons. According to swiftlets have strong instinct towards nest site fidelity and are perhaps permanently pared. Only some birds which roosting far from any nests, include sexually immature juveniles or non-productive pairs (Lim and Cranbrook, 2002). When the nest sites are plenty, how can we sure that it is suitable nest sites. If it is appropriate sites, the other attracting factors may be patchy food resources and predators as recruitment centre hypothesis or relationship within colony.

Foraging

Swiftlets are aerial feeding insectivores. They feed on the wing and forage over all kinds of open and forest area the main items of prey are small aerial insect (Lim and Cranbrook 2002). The pattern of feeding behaviour (Appendix 2) and type

of insects are not easy to investigate. However, many researchers try to study on their foraging ecology such as type of insects, foraging habit and foraging areas (Nguyên Quang, 1998; Lourie and Tompkins, 2000; Viruhpintu, 2002; Photheing, 2005; Manchi and Sankaran, 2010). Most studies have information on diet and general foraging habits but lack of detailed information such as intake rate and prey availability in natural habitat in certain time of the year. Major studies to food preferences (Lourie and Tompkins, 2000; Nguyên Quang et al., 2002) were based on gut content and bolus collection. However, they can identify only in genera level and this collecting method during feeding would affect nesting success. Now we know that Edible-nest Swiftlets fed mainly Hymenopterans, Dipterans, Homopterans /Hemipterans, Coleopterans and Isopterans (Table 1.2). Dipterans were the main constituents of diet in an urban habitat, whereas Hymenopterans predominated in forest habitat. (Lourie and Tompkins, 2000) Edible-nest spent 17.2 ± 11.4% of their time foraging with significant vary by time period. Swiftlets had spatial variations in twist, flutter, and tail-wing-open foraging behaviors. This species also had diurnal variations in flock size, which were positively related with feeding strategies. They use only 2-3 seconds to catch their prey. *A. fuciphagus* have high speed wing with long and sharp tip. They can fly rapidly both in lower and upper level. The aspect ratio and wing loading should be effect to aerial foraging behaviour. Moreover, the dispersal of flying insect should be control the foraging trail of bird (Manchi and Sankaran, 2010). The optimum prey size of the White nest Swiftlets were 0.5-10.0 mm, while the prey size that found in foodball were 1.0-2.5 mm. (Viruhpintu, 2002).

The dispersal of most insects is influenced by atmospheric conditions. Insect dispersal is affected by the wind as a result, influenced by the presence of windbreaks. Wind reductions, microclimate modifications and vegetation diversity, influence insect distribution in sheltered areas (Srygley and Dudley, 2008; Pasek, 2006). This will be usefulness data to find bird flyway which may indicate to habitat attracting and good choice to select for foraging or nesting area.

Table 1.2 Percentage of prey items per individual.

Prey items	Viruhpintu, 2002 (15 boluses)	Nguyen Quang et al. 2002 (142 preys from gut and boluses)*	Lourie and Tompkins, 2000 (10 boluses)	Langham, 1980 (13 boluses)	Mean proportion of preys	Petkliang, pers.obs. (10 feces from 10 nests)
Hymenoptera	16.3	**43.7**	38.6	**40.8**	**34.8 ± 12.5**	**30.7 ± 14.9**
Diptera	**37.3**	11.5	**39.2**	7.7	23.9 ± 16.6	21.8 ± 13.2
Homoptera/ Hemiptera	35.1	20.3	6.4	15.4	19.3 ± 12.0	18.2 ± 7.4
Coleoptera	1.1	3.9	4.7	3.1	3.2 ± 1.5	3.0 ± 1.3
Isoptera	0	10.2	2.1	0.1	3.1 ± 4.8	1.8 ± 1.6
total percentage of main preys	89.8	89.6	91.0	67.1	84.4± 11.5	75.5 ± 8.7

Note. * average from male, female and chick that showed similar five dominated insect order

Foraging habitat selection

Animal try to maximize the income from the resources available to extend their survival and maximize reproductive success. They must make a decision for foraging on where to eat? When? What prey? And How process? according to optimal foraging model. The fitness of an individual depending on its foraging profit (Stephens et al., 2007).The popular method to assess habitat selection is resource selection function (Bastille-Rousseau et al., 2010) which typically determined by comparing characteristics of used locations to available (Manly et al., 2002). Habitat selection could be inferred from the differently use of habitat (Fauchald and Tvetaa, 2003). Most study on habitat selection usually determined by use the telemetry technique to detect spatio-temporal use locations. Recently, the advances in telemetry technology have proved advantageous but there is still need to collect behavioural and environmental data to quantify survival and reproductive success, which are main keys to understanding animal habitat use in the context of fitness and natural selection (Beyer et al., 2010).

Coloniality

Edible-nest Swiftlets is colonial bird that living in the natural cave or man-made building. Nest in high density, often pack into small, restricted space and feed on areas away from the nests. They exit from the roost sites at dawn and return at dusk. The basic principle selective forces leading to coloniality are the need for individuals to aggregate where there are limited resources, to avoid predators better and find food more easily (Alexander, 1974). Brown and Brown (2001) proposed that a limit of suitable nesting sites commonly leads to avian coloniality needs to be rethought and re-evaluate with data because there still have confliction ideas from many researchers, everything is not already known, in many respect on coloniality just starting. However, the reason that bird will leave the old nest sites may be non-success in breeding. For the young bird that finding for new nest sites may be rely on recruitment center hypothesis that base on the cost and benefits to each individual involved from patchy food resources and nesting sites. Furthermore, the family relations within each nest patch and within colony of the white nest swiftlets still unclear on genetics relationship or social behaviour.

The communication within colony is very interesting, *A. fuciphagus* use echolocation for navigation in the darkness of the caves in which they roost and nest (Medway, 1959). Most studies described the echoclicks as being of double click design. The click consists of two subclicks separated by a short silent interval. The subclicks are heard as only one click, another click is not distinguishable to humans. This is the navigation of *A. fuciphagus*. The only species that have been described as only emitting single clicks are *A. maximus*. (Thomassen et al., 2004). Within the same species, there are several pattern and different in calls frequency. Then the sound of bird had been used to attract new birds to the buildings by broadcasting swiftlets sound both in and outside buildings to present success colony inside building.

1.2.3 Swiftlet farming

From interactive management that is a strategy of species conservation that relies upon coordination of a metapopulation that includes populations living in the wild and in captivity. Then swiftlet houses were established and become popular in Southeast Asia. Swiftlet farming can be defined as a production system of edible bird nests by providing specially designed building for the swiftlets to roost and nest. (Lim

and Cranbrook, 2002) The area where locate near natural habitat were selected to build the swiftlets house. They set the conditions like the natural cave both microclimate and nest site to attract birds. It is believe that the first of such houses in East Java, Indonesia originated from Sedayu in 1880. Recently, the idea of intensive farming techniques has spread to many countries in South East Asia.

In Thailand, swiftlets farming were set up along coastline both Gulf of Thailand and Andaman Sea, include the mainland in peninsular of Thailand. The largest site is Pak Phanang town, Nakhon Si Thammarat province which was the first place where the birds were found nesting in buildings and houses. In 2006 there were at least 158 buildings in town (Boonyanusasn, 2006). The others were built in 34 towns from 18 provinces (Pothieng, 2005). Scientists promote both advantages and disadvantages of swiftlet farming but there is no scientific study to investigate this aspect. Some are concern about the ecological consequences if the swiftlet population is artificially increased. While some people argue that the present swiftlet populations are far below the natural carrying capacity, because their numbers have been severely reduced by overexploitation in the past several decades (Lim and Cranbrook, 2002). Now there are some people have patent in swiftlets farming design (Yik Hei Sia, 2012) or artificial nest sites design (Viruhpintu et al., 2002) which showed high probability to attract birds. However, whether this design can apply throughout its range is still to determine.

1.3 Objective and outline of the thesis

The general objective of my thesis is to investigate foraging habitat selection and breeding time of the Germain's swiftlet. In order to address this issue, I focus on these purposes:

1) To determine foraging habitat selection of the Germain's Swiftlet and its temporal variation.

2) To determine vertical distribution on foraging intensity of the Germain's Swiftlet in its major habitat.

3) To determine the variation in breeding period between the west and east of peninsular Thailand and its relationship between breeding period with prey insect availability.

My work presents finding from depth field experiments on the variation in time, habitat types, vertical distribution and breeding activities in different geographical location, related to flying insect availability and some physical factors. Specifically, my thesis contains the following chapters:

Chapter 1 General introduction

Chapter 2 Wetland, forest and open paddy land are the key foraging habitats
for Germain's swiftlet (*A. i. germani*) in southern Thailand.

Chapter 3 Vertical foraging activity of the Germain's Swiftlet (*A. i. germani*)
affect by vegetation insects within its habitat use.

Chapter 4 Geographical variation in breeding chronology of Germain's
swiftlet (*A. i. germani*) in southern Thailand.

Chapter 5 General discussion and conclusion

Each chapter of major findings is written in manuscript format, which lead to some overlap between them.

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CHAPTER 2

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

2.1 Introduction

The Germain's swiftlet (*Aerodramus inexpectatus germani*; Cranbrook, et al., 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 and Driessens, 2000; Lua and 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 seven 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, 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,et al., 2009), and limited suitable foraging habitat due to the deforestation associated with agricultural expansion and urbanization in southern Thailand (Chuangchang and Tongkumchum, 2014; Prabnarong and 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 (Grüebler, et al., 2010).

Swiftlets feed on the wing and forage over a range of open and forest habitats (Lim and 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 and Tompkins, 2000; Nguyên Quang, et al., 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 and Driessens, 2000), swallows (Brown and Brown, 2001; Grüebler et al., 2010; Møller, 2013) and sand martins (Bryant and 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, et al., 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, et al., 2007), Germain's swiftlet should be attracted to specific habitats and at times when larger numbers of prey are present (Chantler and Driessens, 2000). Our predictions were that (1) 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, et al., 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, et al., 2006), particularly in tropical ecosystems (Kishimoto-Yamada and Itioka, 2015). We also predicted that (2) 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, et al., 2014; Scherber, et al., 2014; Wolfe, et al., 2014).

2.2 Methods

2.2.1 Study species

Germain's swiftlet is one of eight subspecies of edible-nest swiftlets (Chantler and 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). Swiftlet populations appear to be restricted to coastal habitats where caves are available for nesting and roosting. Now they also use other habitats such as abandoned buildings or house farm 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 and 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.

2.2.2 Study sites

This study was conducted in Hat Yai, Songkhla, (7^0 0′ 12″ N and 100^0 28′ 4″ E, 1,600 km^2) (Figure 2.1) 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 primary dry season (rainfall < 100 mm per month) occurs from February to May and the wet season starts from June to January (Meteorological Department, 2009) with primary wet season (rainfall 120-600 mm per month) occurs from August to December and is due to the northeast monsoon (Wangwongchai, et al., 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 <25km, a 40×40 km square 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. These habitats were: tree-dominated agricultural land (rubber, oil palm, orchard, other tree plantations) (68.8%), open paddy land (rice field, grassland, annual crops such as cucumber, pumpkin and bean) (17.1%), urban (8.8%), forest (mangrove, peat swamp, lowland evergreen forest both primary and secondary forest) (3.8%) and water bodies (ponds, rivers, lakes included their shorelines i.e. vegetation within 50 m from their edges (Mitsch and Gosselink, 2007)) (1.5%) (Table 2.1, Appendix 2). 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: 1) 0-5 km, 2) 5-10 km, 3) 10-15 km and 4) 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, et al., 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 2.1).

2.2.4 Data collection

Foraging intensity

A total of 100 fixed sampling points (Table 2.1) 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 and 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 2.1). 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 non-breeding 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 x 30 cm cylindrical sticky traps attached (Appendix 3). Total trap area was 2,400 cm^2 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 four hours 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 hours. To estimate annual patterns in insect biomass, the traps were left open for 12 hrs 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 hours. 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 hours).

Arthropod samples were stored in a refrigerator (4˚C) and identified to order or family with the aid of a compound and/or 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).

2.2.5 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 four-hours. 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 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 pair-wise 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.

2.3 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.

2.3.1 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 one hour 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 ($F_{(8,125)} = 1.76$, $P = 0.089$). The main factors that affected the number of prey capture attempts were time of day ($F_{(2,125)} = 38.63$, $P < 0.001$) and insect biomass in each time period ($F_{(1,125)} = 13.64$, $P < 0.001$) (Table 2.2). There was a significant difference in the rates of prey capture attempts among different times of day in all habitat types ($F_{(2,140)} = 41.19$, $P < 0.001$, Figure 2.2A). Similarly insect biomass was significantly higher in the late afternoon compared to morning and midday ($F_{(2,163)} = 4.68$, $P = 0.010$, Figure 2.2B).

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 2.2C). Overall, the rate of prey capture attempts was significantly higher in the wet than in the dry season ($t_{(634)} = -9.01$, $P < 0.001$). The annual patterns of insect biomass showed a similar trend to rates of prey capture attempts (Figure 2.2D) with the average insect biomass being significantly higher during the wet season compared to the dry season ($t_{(158)} = -2.21$, $P = 0.028$).

2.3.2 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 ($F_{(4,167)} = 11.15$, $P < 0.001$), insect biomass ($F_{(1,167)} = 10.10$, $P = 0.001$) and season ($F_{(1,167)} = 4.25$, $P = 0.040$) (Table 2.2).

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 2.3A, Table 2.3).

There was a significant interaction between season and habitat type ($F_{(1,167)} = 2.92$, $P = 0.022$) (Table 2.2) 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 number of prey capture attempts were not significantly different between seasons (Figure 2.3A).

The insect biomass was significantly higher ($F_{(4,175)}$ = 8.63, P < 0.001) 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 2.3B). 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 < 0.001). 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 = 0.001), with the highest biomass over water bodies, followed by open paddy land, tree-dominated agricultural land, forest and urban land respectively (Figure 2.3B). 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 ± SD), n = 11, and 14.37 ±11.59 mg per trap site, n = 16, respectively; Mann - Whitney U test, U = 30, P = 0.003).

2.4 Discussion

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

2.4.1 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 and 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 and

Houston, 1994) as they require food for feeding nestlings and energy for nest building (saliva production) at night (Lim and 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, et al., 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 and 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, et al., 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 and Driessens, 2000). Potential windbreaks for insects can lead, for example, to greater food availability for Cliff swallows over edge areas, i.e., 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 and 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 and 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/or 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 and Itioka, 2015; Wolfe et al., 2014).

In addition to food availability, higher wet season foraging intensity may also 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).

2.4.2 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, i.e., the patches which provide the highest profitability (Sanchez-Clavijo, et al., 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, et al., 2014).

The forest habitat was an important source of Hymenoptera, which is a major diet component for swiftlets (Nguyên 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, et al., 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 and 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, et al., 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-swarming periods in the early wet season (Davies, et al., 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, et al., 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 and Driessens, 2000) and perhaps use habitat characteristics to identify richer food resources (Khalig et al., 2014; Wolfe et al., 2014).

2.4.3 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, i.e., 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 non-governmental 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 South-East Asia (Primack and 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.

Declaration of Conflicting Interests

The authors declare that there is no potential conflict of interest in the publication of this article.

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Table 2.1 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)
% 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	n=12	n=12	n=12	n=12	n=12
Prey capture attempts per habitat	n=12	n=12	n=52	n=12	n=12
Insect biomass	n=4	n=4	n=4	n=4	n=4

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

Table 2.2 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	<0.001**
Insect biomass	13.64	<0.001**
Time of day	38.63	<0.001**
Habitat type	2.14	0.078
Time of day: Habitat type[a]	1.76	0.089
B) Season		
Intercept	94.02	<0.001**
Insect biomass	10.10	0.001*
Season	4.25	0.040*
Habitat type	11.15	<0.001**
Season: Habitat type[a]	2.92	0.022*

Note. A) daily = morning, midday and late afternoon and B) season = wet (August to November 2014) and dry (February to May 2014). *p<0.05; **p<0.001. [a]Indicates an interaction.

Table 2.3 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.

	Estimate	SE	t-value	P-value
Intercept	2.78	0.340	8.010	<0.001**
Open paddy land	-0.457	0.300	-1.524	0.129
Tree-dominated agricultural land	-1.059	0.307	-3.442	0.007*
Urban	-0.780	0.315	-2.474	0.014*
Water body	0.346	0.312	1.108	0.269

*p<0.05; **p<0.001.
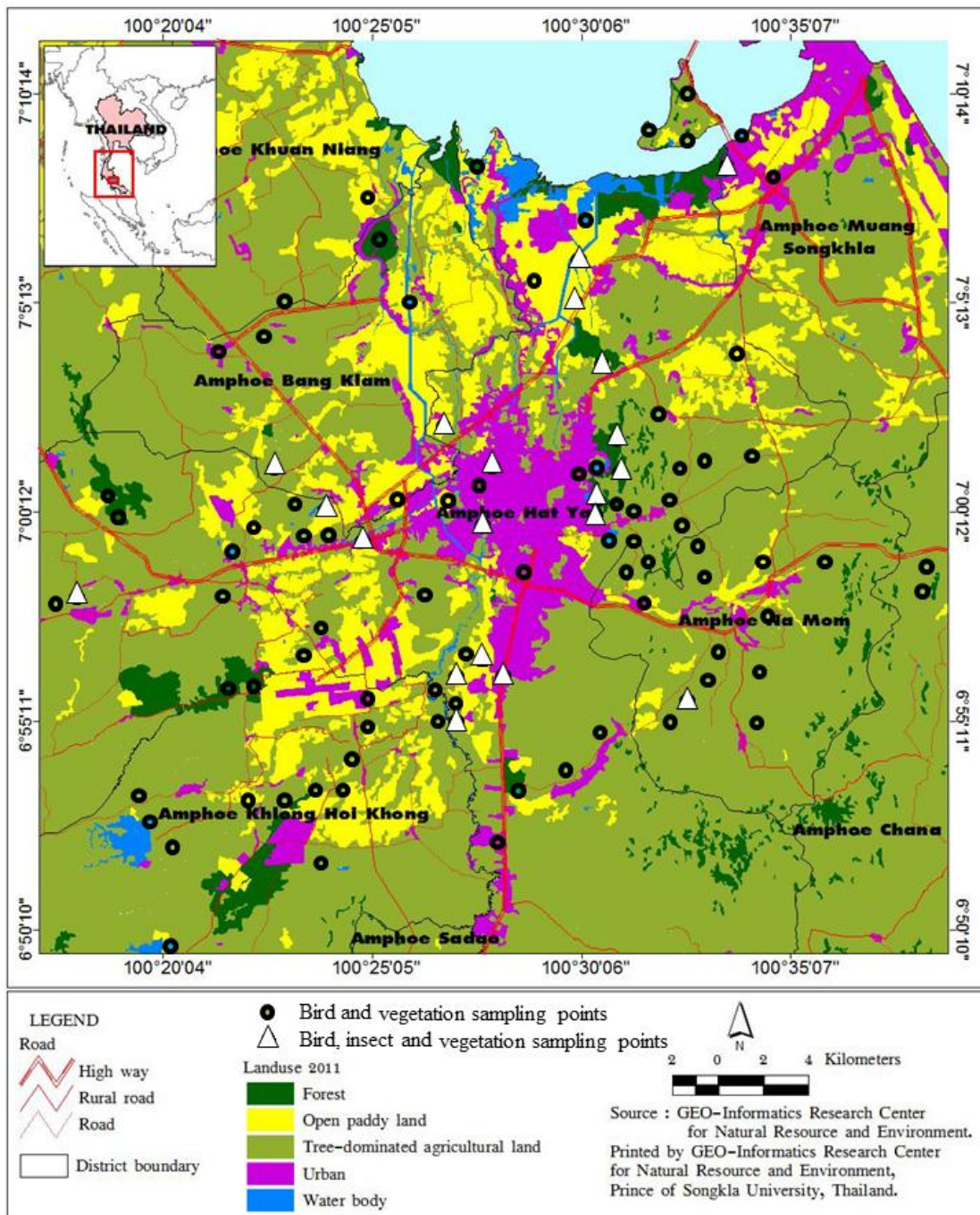
Figure 2.1 Map of 100 sampling points, which included 80 swiftlet foraging intensity sampling points and 20 sampling points which in addition to swiftlet foraging intensity samples, also included insect sampling, covering all five habitat types noted in the legend within a 40 x 40 km block covering the estimated foraging range of Germain's swiftlets nesting in Hat Yai, Songkhla, southern Thailand.

A)

B)

C)

D)
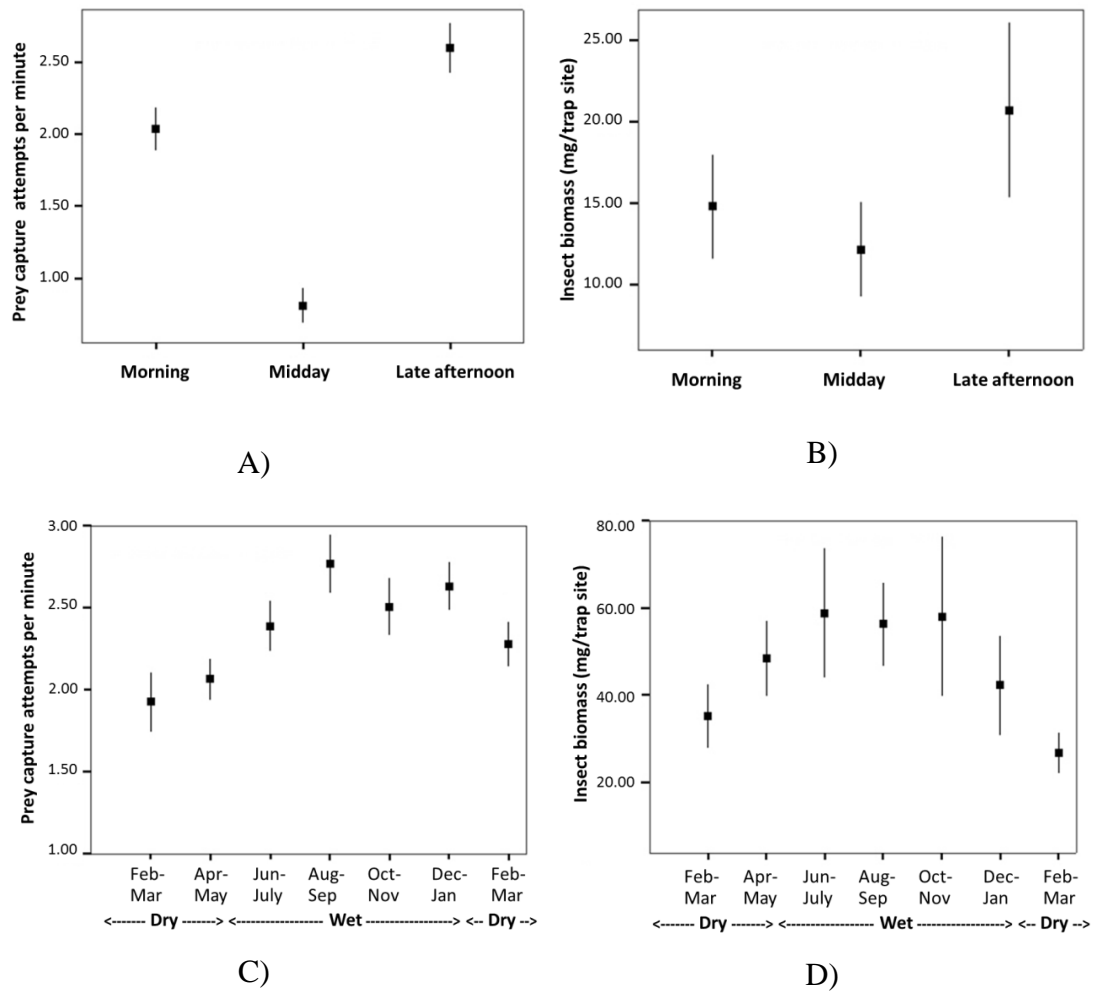
Figure 2.2 Temporal variation (February 2014 to March 2015) in prey capture attempts: diurnal differences in A) average number of swiftlet prey capture attempts per minute (mean± 2SE) of 540 observations and B) the average insect biomass in mg per trap site (180 traps opened for four hours of sampling, total 720 hours); 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 hours, total 1,680 hours).

A)

B)
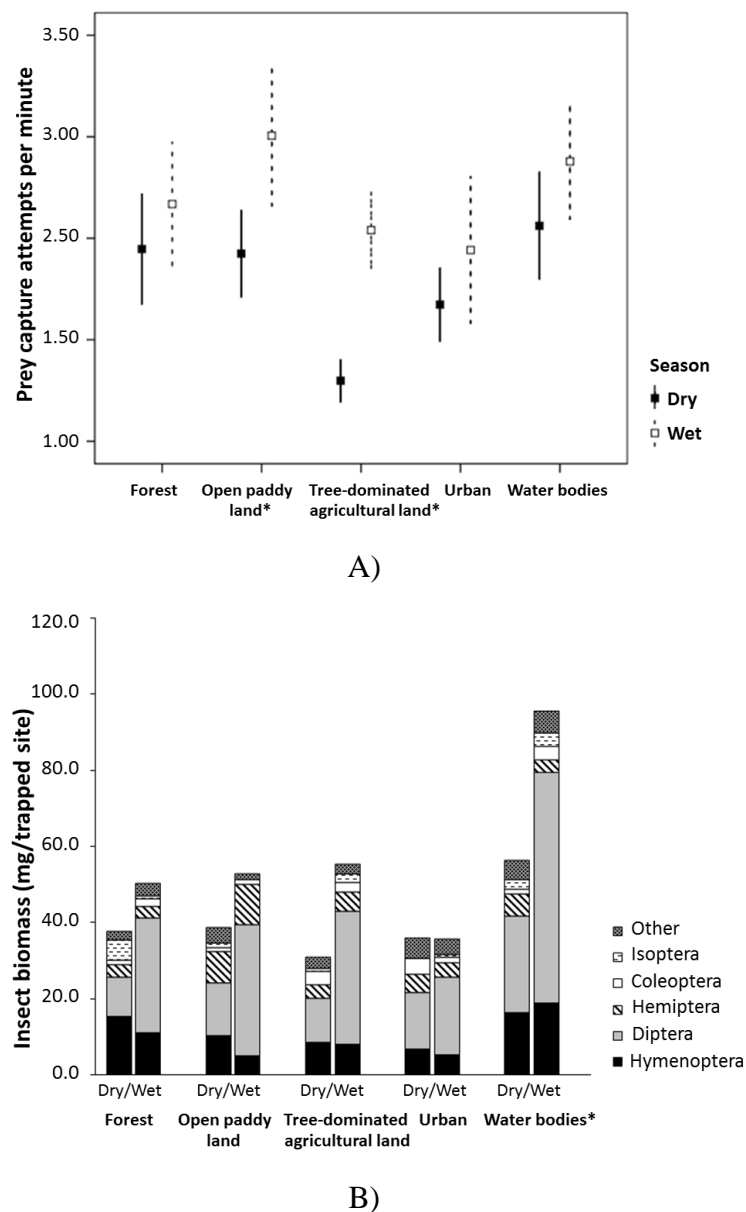
Figure 2.3 A) The average number of swiftlet prey capture attempts per minute (mean ± 2SE) showing significantly more attempts during the wet than dry in open paddy land and tree-dominated agricultural land (P<0.001) and B) the average insect biomass in mg per trap site (2,400 cm^2 trapping area) in different habitats using 80 traps, 960 trap hours during the wet and dry season from 20 sample points. There were significantly higher insect biomass over water bodies than others (P<0.001). The bars also show the proportion of flying insect taxa trapped in each habitat type by season.

CHAPTER 3

Vertical foraging activity of the Germain's Swiftlet (*Aerodramus inexpectatus germani*) affects by vegetation insects within its habitat use.

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Abstract

Vertical distribution of aerial insectivores mainly depended on their vertical prey insect availability. Germain's swiftlets (*Aerodramus inexpectatus germani*) was famous bird farming for their commercial edible-nests. Our goals were to determine 1) the foraging height across habitat types and 2) the foraging intensity at different height and relate to insect availability. The foraging height was recorded and intensity of foraging at different height category were measured and related to insect biomass, trapped at each level. The results showed that foraging height significantly varied in different habitat but was 6.07 ± 6.34 m height on average from canopy. Foraging intensity was highest near vegetation canopy similar to insect availability. This indicated that flying insect availability adjacent to canopy strongly influenced vertical distribution and feeding activity of swiftlets. This finding can raise the significance of vegetation foliage as a main food sources to support swiftlets farming.

Keywords: Edible-nest swiftlet, *Aerodramus fuciphagus*, vertical habitat use, insect biomass, southern Thailand

3.1 Introduction

In natural, availability of food usually heterogeneously distributed because of environmental factors (Begon et al., 2006). Foraging animals try to maximize their profitability base on optimum foraging model (Stephens et al., 2007; Stephens and Krebs, 1986). Aerial insectivores theoretically distribute vertically correspond to vertical prey insect availability and their flying behavior (Waugh and Hails, 1983). Germain's swiftlets (*Aerodramus inexpectatus germani*) or prior named white-nest swiftlets (*A. fuciphagus*) is distribute in Vietnam, Cambodia, southern Thailand and northern peninsular Malaysia (Cranbrook et al., 2013). Birds nesting in natural cave and cave like building, breed year-round with peaks at transition time between dry and wet season (Lim, 2011; Petkliang, unpublished data). Their nests have high commercial valuable and generates 1.6 billion US dollars per year in South-East Asia (Thorburn, 2015). Germain's swiftlets fly with high speed by its long and sharp tip wing (Chantler and Driessens, 2000). They feed on the wing and forage over all kinds of small aerial insect (1-10 mm) (Lim and Cranbrook, 2002), mainly Hymenoptera, Diptera, Hemiptera, Coleoptera and Isoptera respectively (Langham, 1980; Lourie and Tompkins, 2000; Nguyên Guang et al., 2002; Viruhpintu 2002). Some of these insects are known to swarm over canopy such as hymenopterans; fig wasp (Compton et al., 2000) and ant (Helm et al., 2016). Flying insects can move upwards in airborne by thermal lift when temperature increase (Johnson, 1969) and mostly disperse by wind (Pasek, 2006). Tanabe (2002) indicated that close canopy forests are vertically heterogeneous that affect flying insect dispersal. In tropical region, insect distribution was varied by vertical height (Basset et al., 2003). Then foraging intensity of bird may vary in different height depend on altitudinal variation in abundance of airborne insects.

A previous study indicated that Edible-nest swiftlet (*A. fuciphagus*), intensively forage over forest canopy and time spent on foraging attempt (%) in different microhabitats in India indicated the importance of microhabitat at >10 m above forest canopy and >30 m above ground without insect sampling (Manchi and Sankaran, 2010). Although, diet, foraging habits and foraging habitat selection of these swiftlets were documented (Lourie and Tompkins, 2000; Manchi and Sankaran, 2010; Viruhpintu, 2002), none had been documented the height where bird exhibit

highest foraging intensity and its relationship with prey insect abundance. The current study objectives were (1) to examine the Germain's swiftlet foraging height across habitat types and the relationship between foraging height and canopy height. We hypothesized that swiftlets forage at different height in different habitat types since vegetation canopy vary in its height among habitats. In addition, foraging height related to canopy height because canopy level contained more insect than other levels (Basset et al., 2003). As the previous study suggested that Edible-nest swiftlet concentrate its foraging over forest canopy and open land (Manchi and Sankaran, 2010), Pygmy swiftlets (*Collocalia troglodytes*) and Glossy Swiftlets (*C. esculenta*) were observed foraging only over the forest canopy (Collins, 2000). (2) To document the foraging intensity at different height within its major habitat use and relate to prey insect availability at each height level. We predict that number of foraging attempts will be intensive adjacent to vegetation canopy due to insect richness and the availability of prey is a determining factor in foraging habitat selection according to energy profitability (Stephens et al., 2007). Other reasons can be swiftlets wing morphology (Chantler and Driessens, 2000; Collins and Thomas, 2012) and foraging behavior (Manchi and Sankaran, 2010; Waugh and Hails, 1983).

3.2 Methods

3.2.1 Study sites

This study was conducted in swiftlet potential range at Hat Yai, Songkhla (7^0 $0'$ $12''$ N and 100^0 $28'$ $4''$ E, 1600 km^2) (Figure 2.1), the eastern coast of peninsular Thailand where is over 10 years colonization of at least 30 Germain's swiftlet colonies. In the study area, the dry season occurs between February to May with rainfall < 100 mm per month (Meteorological department, 2009) and the primary wet season with rainfall 120-600 mm/month occurs in August to December because of the north-east monsoon (Wangwongchai et al., 2005). Based on the foraging range data (Viruhpintu, 2002; Gale and Pierce, unpublished data), the center of Hat Yai city, which was assumed to be the center of the colonies, a 40×40 km square grid was drawn as being their potential foraging area. Habitat was classified into five types based on land-use data from the Land Development Department, Thailand and vegetation characteristics such as type of trees, tree density and % canopy cover. The

proportions of each habitat within the grid were: tree-dominated agricultural land (rubber, oil palm, orchard, other tree plantations) 68.8%, open paddy land (rice field, grassland, annual crops such as cucumber, pumpkin and bean) 17.1%, urban 8.8%, forest (mangrove, peat swamp, lowland evergreen forest both primary and secondary forest) 3.8% and water bodies (ponds, rivers, lakes included the shoreline (Mitsch and Gosselink, 2007), i.e., vegetation within 50 m from their edges) 1.5% (Table 2.1, Appendix 2). To minimize the effect of distance from the colony on habitat selection, each habitat type was recorded at each of the following distance categories: 1) 0-5 km, 2) 5-10 km, 3) 10-15 km and 4) 15-20 km from the colony. In addition, the sampling points were distributed evenly in four quarters of foraging range: North, East, South, and West. Sampling points were located by randomly walking at least 100 m further on after a relatively homogeneous area of a particular habitat type was found using GIS information to confirm positions and avoid edge effects. 100 m radius circular areas were drawn around each sampling point and were classified based on which habitat contributed >70% of the circular area. In addition, sampling points were surrounded by a buffer zone of similar habitat at least 100 m wide in order to minimize edge effects (Bibby et al., 1992). The distance between each sampling point was at least 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 m and ranging accuracy ±1 m), and canopy cover percentage was assessed with a densiometer (Table 2.1).

3.2.2 Data collection

Swiftlet foraging height

This study was conducted every two months for 14 months from February 2014 to March 2015 (seven sampling sessions). In each session, vertical foraging height from fixed 100 sampling points which were repeatly observed in every session. In each point, at least four individual swiftlets were randomly observed with binocular for their foraging height when birds showed their attempts to catch insects (number of

foraging attempts per minute). Range finder was used to determine vertical height by triangulation technique.

Observations were done only in early morning (06.30-10.30) and late afternoon to evening (14.30-18.30) when feeding activity are highest (Viruhpintu, 2002; Petkliang, unpublished data). The temperature and humidity were recorded in each sampling point. Wind speed and rainfall data were collected from Hat Yai international airport, the nearest weather station of the Thai Meteorological Department at the time of observation.

The swiftlet foraging intensity across different height.

The foraging intensity, defined as number of foraging attempts (Fauchald and Tvetaa, 2003) per minute, was determined in early morning and late afternoon in 20 accessible sampling points for insect trap station, selected from aforementioned 100 sampling points. Foraging height was categorized into four levels from reference height (the uppermost level of a particulr habitat i.e. the ground, water surface or top vegetation canopy which was defined as zero meter, Figure 3.1) because each habitat types showed different canopy height. These four categorized level are 1) 0-5 m (e.g. water surface), 2) 6-15 m, 3) 16-30 m, and 4) >30 m in vertical from reference height. Foraging intensity was recorded from randomly selected three individuals at each height level. Each bird was observed for one minute with binocular. Range finder was used to estimate vertical height by triangulation technique. In addition, opheight was also estimated based on height- marked pole.

The aerial insect were trapped at these bird sampling points by pole attached with 20 x 30 cm cylindrical sticky trap of 1,200 cm^2 at each aforementioned height level, given 3,600 cm^2 per site (Figure 3.1). We failed to trapped the insect at >30 m above ground because the limited of pole height. We tried to raise traps with other equipments such as balloon and kite. These methods are not reliable since they were strongly affected by wind. Insect traps were open on daytime for 12 hrs (0630 - 1830h) at 20 sites in each session for a total of 1,680 hrs. Insect sampling was limited to days with total rainfall lower than 20 mm and average wind speed lower than 16 km/h following previous pilot studies of Taylor (1962).

Arthropod samples were stored in a refrigerator (4°C) and all trapped insects were identified to order or family after Triplehorn and Johnson (2005) with a stereo

microscope. The body length of arthropods was measured and converted to insect biomass by using regression equations following Lumsden and Bennett (2005).

3.2.3 Data analysis

All analyses were conducted in R program version 3.2.4, (R Development Core Team 2016). The Bartlett test of homogeneity of variance and Anderson-Darling normality test were applied to test statistical assumptions. A Kruskal-Wallis test was used to compare average mean foraging height between five habitat types and compare the average foraging intensity and insect availability at different altitude. A post-hoc test, Dunn test (library stats and require PMCMR) was applied for pairwise multiple comparison of mean rank as Zar (2010) states that the Dunn test is appropriate for groups with unequal numbers of observations. Wilcoxon-Mann-Whitney U test was applied to compare average foraging height and prey insects between wet and dry season and also assess between high and low breeding peak. A spearman rank correlation was applied to examine the relationship between foraging height and canopy height. Additionally, one way ANOVA was applied with parametric data that meet with its assumptions such the foraging intensity across all different height levels.

3.3 Results

3.3.1 Swiftlet foraging height

The average foraging height (mean ± SD) of the Germain's Swiftlet was 19.41 ± 6.47 m above ground (Figure 3.1). The foraging height was significantly different between habitat types (n = 1,127, df = 4, Kruskal-Wallis chi-square = 49.32, P < 0.001). Forest showed the highest foraging height (21.56 ± 5.96 m) followed by tree dominated agricultural area (20.29 ± 6.77 m), urban (18.97 ± 5.04 m), water body (17.44 ± 4.87 m) and open paddy land (12.74 ± 5.43 m). Swiftlet foraging height was significant lower in open paddy land than other habitats (post-hoc; Dunn test, P < 0.001, Figure 3.2). The foraging height of Germain's swiftlet significantly related to the reference height of foraging habitat (Spearman rank correlation, n = 1,127, r = 0.548, P < 0.001). In general, birds exhibit forage behavior at 6.07 ± 6.34 m on average above reference height in every particular habitat (Figure 3.1). The foraging height above reference level was significant differences between habitats (n = 1,127,

df = 4, Kruskal-Wallis chi-square = 33.73, P < 0.001). Swiftlets used comparable foraging height above reference level in water body (4.13 ± 5.61 m), forest (4.81 ± 6.92 m), tree-dominated agricultural land (5.92 ± 6.12 m) and urban (6.41 ± 5.73 m). However, it was significantly forage at higher level above reference height in open paddy land (11.11 ± 5.90 m) than others (post-hoc; Dunn test, P < 0.001, Figure 3.3).

For seasonal comparison, foraging height was not significant different between season (Mann-Whitney U test, U = 7457.5, P = 0.092) and between low and high breeding peak (Mann-Whitney U test, U = 7375.5, P = 0.314).

3.3.2 The swiftlet foraging intensity across different height

The major foraging habitats of the Germain's swiftlet infer from high proportion of use from total observation were water bodies, forest and open paddy land (Figure 3.2).The foraging intensity and insect biomass seem to be higher adjacent to reference level than over 30 m above reference height.

In water body habitat, the number of foraging attempt was significantly different across height levels ($F_{(3,133)}$ = 11.26, P < 0.001) which significantly low at > 30 m (1.39 ± 1.47) above reference level (post hoc; Tukey test, P < 0.001), whereas, the intensity of foraging was comparable at 0 - 5 m (3.06 ± 1.38), 6 - 15 m (3.01 ± 1.13) and 16 - 30 m (2.44 ± 1.07) (P > 0.05, Figure 3.4A). Similarly, the insect biomass was not significantly different across vertical level (n = 168, df = 2, Kruskal-Wallis chi-square = 4.98, P =0.061) by comparable at 0-5 m (27.4 ± 34.4), 6-15 m (26.97 ± 33.01) and 16-30 m (28.64 ± 20.07) (P > 0.05, Figure 3.4B).

Forest habitat showed significantly different on number of foraging attempts across vertical level ($F_{(2,102)}$ = 10.57, P < 0.001) by exhibited comparable intensity of foraging at 0-5 m (3.44 ± 1.26) and 6-15 m (3.22 ± 1.45) above canopy but significantly low number of foraging attempts at >15 m (1.93 ± 1.51) above tree canopy (post hoc; Tukey test, P < 0.001) (Figure 3.4C). The insect biomass was not significantly different between 0-5 m and 6-15 m (n = 112, df = 1, Kruskal-Wallis chi-square = 0.45, P =0.518) (Figure 3.4D).

Open paddy land showed significantly different on number of foraging attempts across vertical level ($F_{(3,135)}$ = 11.97, P < 0.001). At > 30 m above reference height was significantly lower number of foraging attempts than other level (post hoc; Tukey test, P < 0.001). There was comparable intensity of foraging at 0 - 5 m (3.48 ±

1.93), 6 - 15 m (3.22 ± 1.19) and 16 - 30 m (2.78 ± 1.33) (Figure 3.4E). The insect biomass at 6-15 m was significantly higher than 0-5 m and 16-30 m above reference height (n = 168, df = 2, P = 0.003) (Figure 3.4F).

There was no significant relationship between the number of foraging attempts and insect biomass across height level over foraging habitat (P > 0.05) at 0 - 5 m, 6 - 15 m and 16 - 30 m above reference height. However, the significantly reducing trend of foraging intensity at upper level was similar to trend of the insect biomass (Figure 3.4).

3.4 Discussion

Our results highlight on two findings, first, the significant differences on Germain's swiftlet foraging height across different habitat types, such vertical height was significantly related to canopy height. Second, the number of foraging attempt adjacent to reference height was seem to be higher than others at over 15 m above reference height.

3.4.1 Swiftlet foraging height

Although swiftlets forage at different height from ground in different habitat types, it was generally similar above canopy height of that particular habitat. The significant positive relationship between foraging height and canopy height indicated that canopy level was the most important foraging level for Germain's swiftlets in accordance with the activity of Edible-nest swiftlet in India (Manchi and Sankaran, 2010) and central Thailand (Viruhpintu, 2002). Additionally, other close species such as Glossy swiftlet and Pygmy swiftlet also prefer to forage close to canopy (Collins, 2000). The major reason can be rich of insect available at canopy level (Basset et al., 2003).

Habitat use of bird is influenced by its wing morphology. The Germain's swiftlet had small body weight, long curve wing with high wing loading and aspect ratio. Thus, they normally fly rapidly (Chantler and Driessens, 2000) and exhibited rapid flight changes during airborne prey captures (Manchi and Sankaran, 2010). The wing morphology and foraging behaviors of Germain's swiftlet suggested that they need open space for flying, searching and catching their prey. This wing is also helps them to forage in edge habitat. So they usually fly above water, above ground and

over canopy of all open paddy land, forest canopy and other open areas where had enough room for maneuver but never fly inside vegetation canopy layer. This is similar to Glossy swiftlet and Pygmy swiftlet foraging habit (Collins, 2000; Collins and Thomas, 2012). This evidence can also found in open space insectivorous bats that seem to concentrate their activity above canopy because of their wing morphology (Marques et al., 2016).

Our results indicated that there were no significant differences on foraging height between wet and dry season. Foraging altitude relied on vegetation canopy height. Thus, low fluctuation on climate in year round in southern Thailand (Meteorological department, 2009) and less changes of tree canopy in study site cause non differences on average foraging level all year round. According to Germain's swiftlet showed all year breeding (low peak and high peak) (Lim, 2011; Viruhpintu, 2002), swiftlet still used similar level in each habitat but exhibited different intensity of use in different habitat type by select rich food source (Cody, 1981, Petkliang, unpublished data) for foraging rather than select foraging level.

Availability of insects at vegetation canopy is the main explanation for foraging height at close to canopy of this swiftlet. This reason was proved by recorded the foraging attempts related to insect biomass at each height level as discussed in next aspect.

3.4.2 The swiftlet foraging intensity and insect availability at different height

The foraging intensity in each vertical level seem to relate with prey insect availability since canopy level contained more insect than over canopy level in accordance with Basset et al. (2003). Then the number of foraging attempts near vegetation canopy was higher than in upper airborne. The main explanation was availability of prey insect which refer to patch quality (Stephens et al., 2007)   .

The reason of high insect availability at 0-5 m and 6-15 m above reference height was the resources for insects. There were plenty of resources for insect on vegetation canopy such as leaf flushing, shoot, flower and fruit (Sakai, 2002). Insects used mostly of life span at vegetation canopy and move in breeding period by breeding insect swarming such as breeding ants and fig wasp, the important swiftlet

prey insects (Lourie and Tompkins, 2000). Reproductive ants can glide and fly over canopy (Helm et al., 2016) and fig wasp can move and dispersal over figs tree canopy by wind (Compton et al., 2000). Flying insects can moves upwards in airborne by thermal lift when temperature was increase (Johnson, 1969). In addition, the wing morphology of swiftlet was limited for flying inside the canopy, so they selected to forage at the edge of habitats and open space of canopy where rich of insect dispersal by wind (Pasek, 2006). Vegetation strip along the road or beside the water bodies also act as wind break that cause rich of insect which mainly disperse by wind, then can attract their predators (Gilbert et al., 2015; Whitaker et al., 2000).

Our results provided evidence that the reference height of open paddy land and water body was not general flying height of the Germain's swiftlet (Fig 2). They usually flied over the emergent tree canopy and decreased foraging level (Viruhpintu, 2002) to 0-5 m above ground/water surface to catch the insects since there were aquatic insect emerged in twilight period and riparian habitats contained large number of insects both aquatic and terrestrial insects (Fukui et al., 2006).

At 16-30 m above reference height was lower used by swiftlet than others lower level. The high variation on foraging intensity caused by the occasionally high insect biomass of breeding insect swarming from their nest in tree canopy (Compton et al., 2000; Lourie and Tompkins, 2000; Phonak, 2007) which influenced by climate (Møller, 2013).

The significant lower number of foraging attempts at >30 m above reference height which farther than the general foraging height can be caused by the limit of vegetation insect dispersal. Physical conditions at more height above the vegetation canopy can be much harsher than below, with high temperature and low humidity (Compton et al., 2000). We need more insect data to support foraging intensity. However, similar trend between vertical foraging attempts and insect availability suggested the significance of reference height as insect sources for Germain's swiftlet.

In conclusion, the Germain's swiftlet used different height across habitat type and was mainly corresponding with vegetation canopy height and their wing morphology. When examined the foraging intensity, the number of foraging attempts per minute was high near reference height, at edge space and open space of habitat. The major explanations were flying insect biomass at each vertical level and the space

supported their foraging behavior. This study can raise the significant of vegetation foliage as a main food sources for swiftlets which is degradated with accelerated expansion of swiftlets farming industry leads to the issues concerning long-term sustainability (Lim, 2011).

Further study should determine the insect available at higher level and the other environmental factors such as wind speed which influence to insect dispersal (Møller, 2013) and temperature which effect to aerial insect movement to upper altitude (Johnson, 1969). Individual swiftlet should be followed to observe their foraging trip. These can support the understanding on swiftlet foraging habitat selection and the resources used that very important to provide the appropriate environments for the swiftlet farming industry such maintaining vegetation patches, vegetation strip and ecological complexity will ultimately protect availability of swiftlets prey insects.

Acknowledgement

3.5 References

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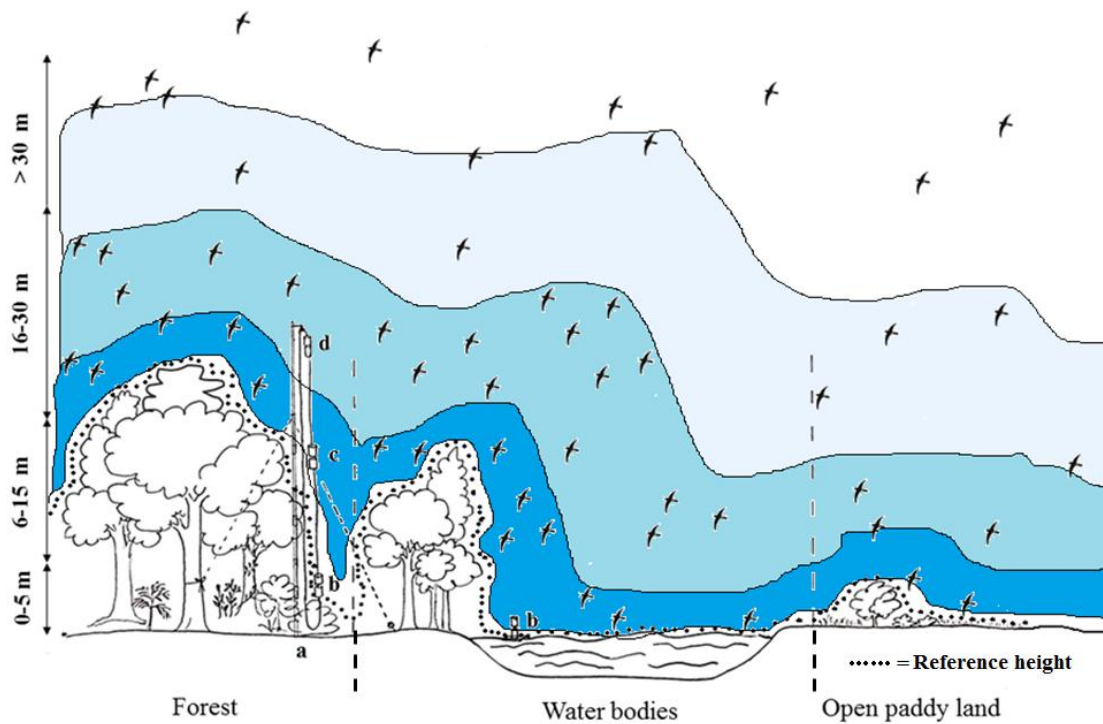
Figure 3.1 Schematic of sampling design and main results of vertical foraging height of the Germain's swiftlet within their major habitat use showing: (a) insect sampling using pole attached with the cylindrical sticky trap at (b) water surface or adjacent to ground, (c) adjacent to canopy and (d) over canopy. Foraging swiftlets were observed at 0-5 m (15.35%), 6-15 m (51.78%), 16-30 m (78.21%) and > 30 m (43.21%) above ground from 280 observations per height level. The foraging height significantly relate to reference height (P < 0.001, dot line represent reference height).
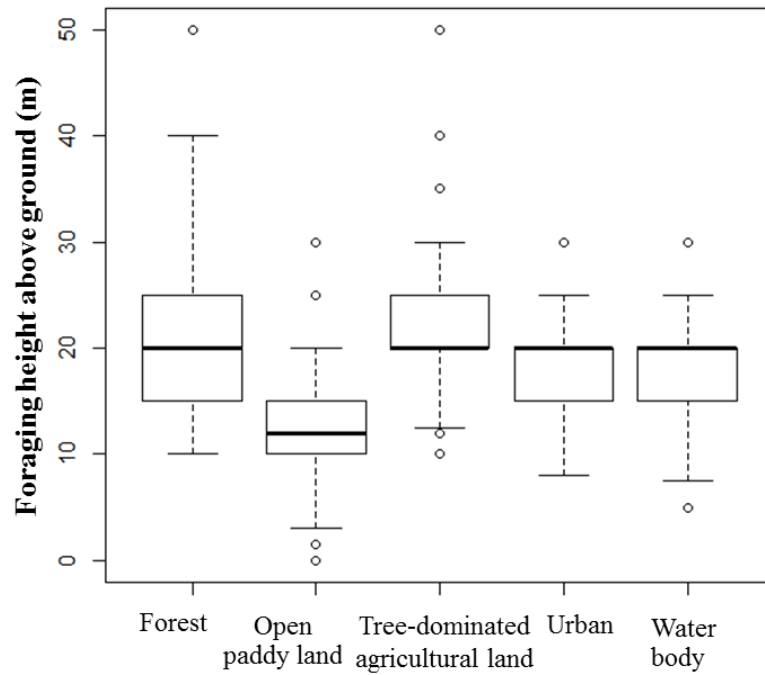
Figure 3.2 The foraging height (mean ± SD) over ground level in each habitat type, showing the significant differences of foraging height between open paddy land and other habitat types (n=1,127, P<0.001).
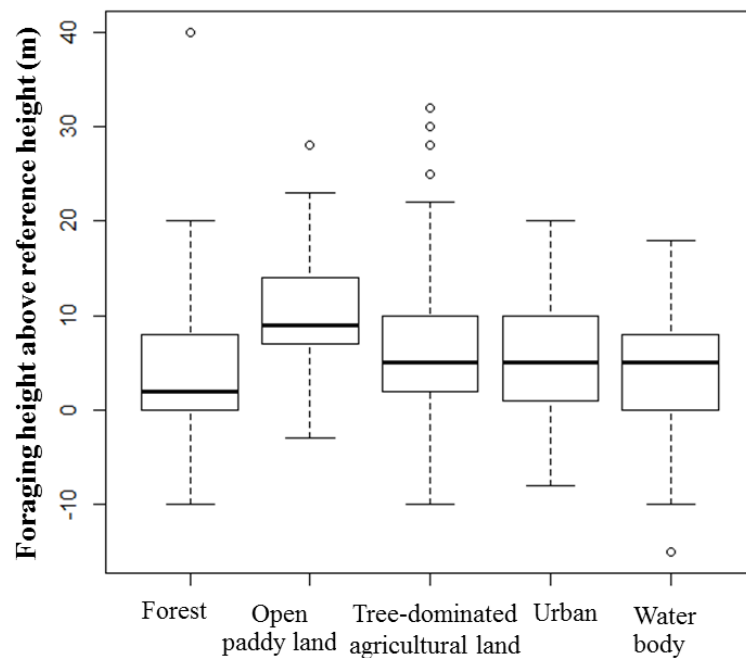
Figure 3.3 The foraging height (mean ± SD) above the reference height (0 m) in each habitat type, showing the significant differences between open paddy land and other habitat types (n=1,127, P<0.001).
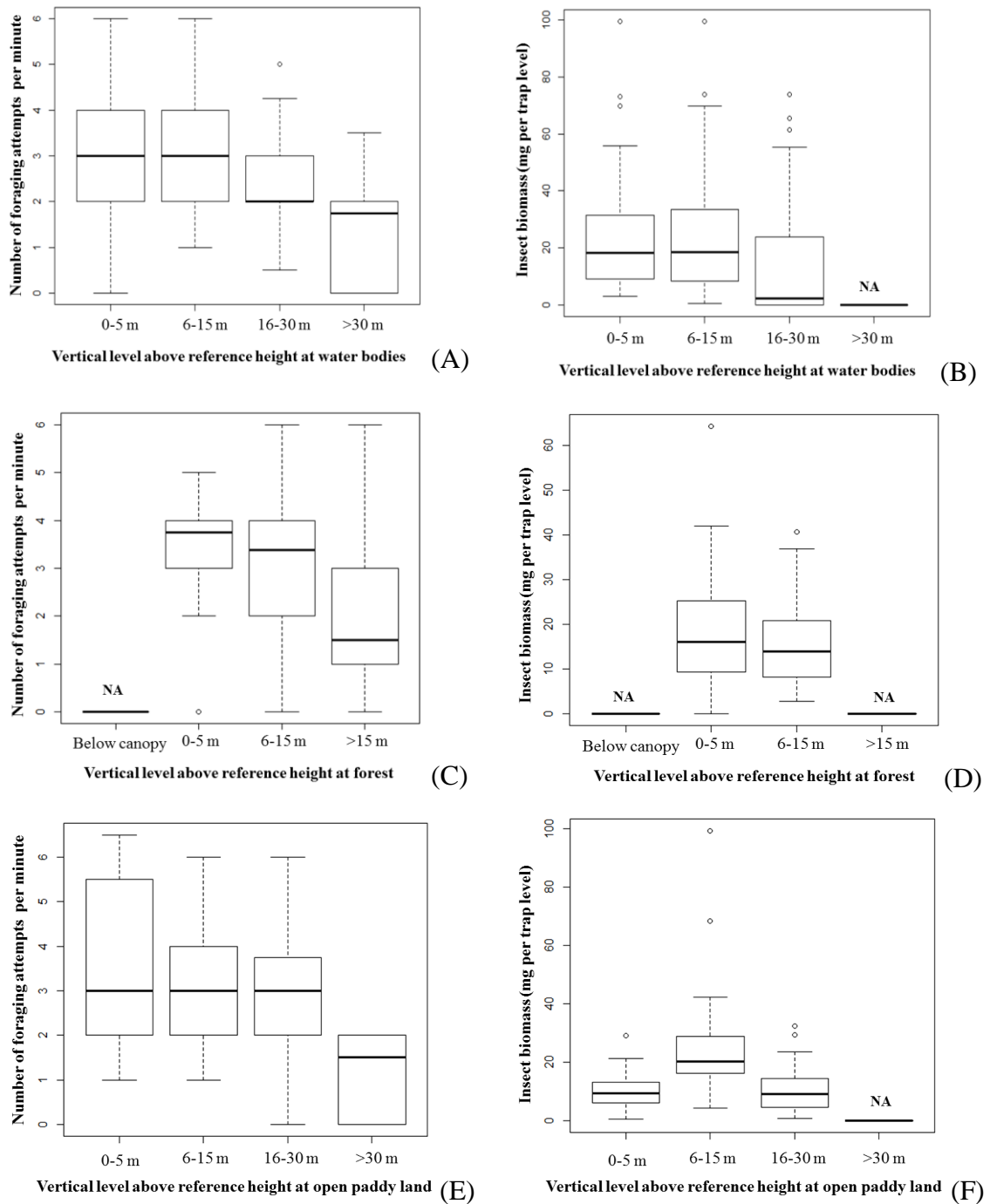
Figure 3.4 The number of foraging attempts per minute (mean ± SD) in each vertical level at water bodies (A), forest (C) and open paddy land (E); insect biomass in mg per trap level at water bodies (B), forest (D) and open paddy land (F) with missing data (NA) at some levels above reference height.

CHAPTER 4

Geographical variation in breeding chronology of Germain's Swiftlet (*Aerodramus inexpectatus germani*) in southern Thailand.

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Abstract

The Germain's swiftlet (*Aerodramus inexpectatus germani*) feeds on flying insects whose dispersal and abundance are influenced by climatic conditions, especially rainfall. In turn, insect availability influences the onset of breeding by swiftlets hence regions with different climatic conditions such as the west and east coast of the Thailand peninsula should differ in swiftlet breeding chronology. Here we aimed to determine the variation in breeding chronology between the west and east coast colonies and relate this to insect availability. For each side of peninsular, at least 40 breeding pairs were continuously observed (July 2014 to October 2015), using an internet protocol infrared camera installed inside each swiftlet house. Flying insects were trapped every two weeks using sticky traps at three permanent stations within major foraging habitats. The onset of breeding in the western colonies was earlier than the eastern colonies. These significant differences were explained by rainfall and food availability that showed synchrony between the nestling feeding period and food

peak. Rainfall of 100-300 mm/month overlapped with peak breeding and peak insect biomass. These findings have significant implications for the sustainability of swiftlet nest harvesting and demonstrate that, to minimize negative reproductive outcomes for the swiftlet, the regimes of harvesting of nests should consider regional climatic conditions.

Key words: Edible-nest swiftlet, *Aerodramus fuciphagus*, swiftlet breeding chronology, flying insect, Southern Thailand

4.1 Introduction

The Germain's swiftlet (*Aerodramus inexpectatus germani*) is farmed regularly for their commercial, edible white-nests. The distribution range of this species includes Vietnam, Cambodia, southern Thailand and northern peninsular Malaysia (Cranbrook et al., 2013). *Aerodramus* spp. are mainly confined to the Southeast Asian countries (Chantler and Driessens, 2000). The swiftlet nest industry generates 1.6 billion US dollars per year for the Southeast Asia regional economy and has expanded rapidly to meet increasing consumer demand (Thorburn, 2015), for example in Hong Kong and mainland China. The demand for swiftlet's nests on the international market is increasing, despite the recent setback with the Chinese authorities enforcing more stringent biosecurity screening of the processed nests (Lim, 2011). However, populations of some of Germain's swiftlet appear to be declining due to overexploitation for example, in Sabah and Sarawak, Malaysia, and on the Andaman and Nicobar Islands in India (Lau and Melville, 1994; Chantler and Driessens, 2000; Sankaran 2001), and the overall trend of the species is suspected to be declining but there is no quantitative data available (Birdlife international, 2014). The government in Thailand dictates the harvest time of nests in 'concession' caves and this is at three fixed time periods across all parts of Thailand and has been done in this way for hundreds of years (Thongkleang, 2011).

We noted high levels of chick mortality during nest harvesting and aimed to determine the timing of breeding and factors influencing breeding activity so as to better inform harvesting and increase the sustainability of this important local industry. Although the swiftlet's breeding biology is known from many studies in

Malaysia, Vietnam and Thailand (Lim and Cranbrook, 2002, Nguyên Quang et al., 2002, Viruhpintu, 2002, Phong et al., 2015), to date, there is no comparison on the timing of breeding in different landscapes or regions. The information on the timing of breeding and its geographical variation will indicate the appropriate (least impact) time and frequency for nest harvesting in each part of its range. Harvesting bird nests during the chick stages can cause population decline as large numbers of chicks fall out of the nest and starve to death during nest collecting.

Bird breeding activities and other energetically costly activities such as moult appear to be effected by food-supply (Sodhi, 2002). Germain's swiftlet feed on flying insects whose dispersal is influenced by climatic conditions (Sygley and Dudley, 2008). Rainfall is also linked to swiftlet breeding seasonality (Manchi, 2009) and wind has been shown to play an important role in the ecology of insectivorous birds (Møller, 2013). In particular, flying insect abundance is higher in the wet season compared to the dry season because of the simultaneous presence of both aquatic and terrestrial insects (Fukui et al., 2006). However, heavy rainfall and strong winds can cause low abundance of airborne insects and reduced foraging activity of birds. Fledging success of insectivorous birds has been shown to be negatively related to rainfall (days >10 mm) during nestling periods (Öberg et al., 2015). For the Thai peninsula, the annual southwest monsoon (May-October) that affects weather on the western coast occurs earlier than the northeast monsoon (November-January) that affects weather on the eastern coast. So, although the rainy season ranges between mid-May to mid-February, the timing of the heavy rainfall events on each side of peninsula differ depending on the arrival time monsoon. (Meterological department, 2009; Wangwongchai, 2005). In addition, the local plant phenology patterns show flowering and fruiting nearly two months earlier on the western side of the peninsular (Tunjai, 2011), a feature likely associated with arthropod abundance in the canopy (Didham and Springate, 2003). Although some studies have examined swiftlet diet simultaneously with breeding chronology (Langham, 1980; Viruhpintu, 2002; Lim, 2011), they have not determined food availability. Our study aimed to measure the breeding period variation between the west and east colonies and relate this to flying insect availability within their major foraging habitats. We hypothesized that the western colonies will breed earlier because of earlier seasonal rainfall that influences

prey insect availability. Swiftlets should synchronize their nest feeding period with peak of insect availability according to energy profitability and breeding success (Stephens et al., 2007; Visser et al., 2006).

4.2 Methods

4.2.1 Study species

The Germain's swiftlet (previously white-nest swiftlets, *Aerodramus fuciphagus*) is a small aerial feeding insectivorous bird. Their five main prey groups are Hymenoptera, Diptera, Hemiptera, Coleoptera and Isoptera (Langham, 1980; Lourie and Tompkins, 2000; Nguyên Quang et al., 2002; Viruhpintu, 2002). Birds nest in natural caves and in man-made structures. In Thailand, approximately 1.09 million individuals are found in natural habitat while 0.16 million individuals are found in man-made habitat (Phothiang, 2005). The breeding cycle and breeding strategies of Germain's swiftlet varied between difference geographical sites (Table 1.1). Viruhpintu (2002) report that in the abandoned buildings of non-harvested nest sites until post fledging in central Thailand, an average brood cycle is approximately 92-104 days. The average durations of nest building, incubation and nestling feeding are 29.83 ± 6.3, 23.63 ± 1.6 and 40.25 ± 3.0 days, respectively with 15.94 ± 10.5 days for subsequent brood or new nest construction (if the nest is removed). The normal clutch size is 1-2 eggs with a laying interval of 3.36 ± 2.5 days (Viruhpintu, 2002). The highest percentages of egg laying, hatching success and breeding success at fledging in central Thailand is from January to April (Viruhpintu, 2002) while in south eastern Thailand the highest breeding percentage is from January to March (Phongchoo, 1985). Most studies find that breeding pairs show strong nest-site fidelity. They can re-nest and breed all year round (Lim and Cranbrook, 2002; Viruhpintu, 2002). Male swiftlets contribute twice as much effort into nest building as the female (Ramji et al., 2013), however parental investment in feeding young is not significantly different between sexes (Viruhpintu, 2002).

4.2.2 Study sites

Four swiftlet farms were used to examine swiftlet breeding chronology. Two colonies located in the eastern coast of the Thai peninsula, one is in Pak Phanang basin (100^0 12′ 6″ E 8^0 20′ 39″ N) Pak Phanang; Nahkon Si Thammarat province

(Appendix 5). This area has the highest number of artificial nest sites in Thailand (Pothieng, 2005). The other colony is in Phattalung province (99^0 58′ 29″ E 7^0 43′ 22″ N), located near the Songkhla lake. These two sites are surrounded by wetlands, agricultural land, field and forest that contain an important wetland site that was declared a RAMSAR site in 2000 (Prabnarong and Thongkao, 2006). The bird colonies on the western of Thailand peninsula were located near the Trang river (Kan Tang; Trang province) (99^0 30′ 36″ E 7^0 24′ 37″ N and 99^0 30′ 47″ E 7^0 26′ 8″ N) and are also surrounded by wetland, agricultural land, fields and forest (Figure 4.1). Previous 10 years rainfall data showed that southern Thailand season were defined as wet when monthly rainfall > 100 mm and dry when monthly rainfall < 100 mm. The western and eastern coasts experience monsoons at different times of year and are separated by a mountainous area that acts as a barrier to the monsoon from the opposite side.

Nest sites were selected that had similar ranges of suitable conditions inside the farms, specifically: temperature 27-35 °C, humidity >70 %, light intensity < 5 lux (Ibrahim et al., 2009) and nest harvested was restricted to the post fledging period.

4.2.3 Data collection

Breeding bird observations

Reproductive activities of birds were video-recorded from the start of nest building until fledging by selecting sample nests from nest patches for which birds had built nests in the previous breeding season; swiftlets have high nest fidelity (Lim and Cranbrook, 2002). Internet protocol infrared cameras (Pan-Tilt IP camera, Fujitel FJ-T6836WITP, 10m IR distance, resolution 720P(1280*720) VGA(640*480)) were installed inside established swiftlet houses to observe the nesting behavior of the colonies during all three breeding bouts from July 2014 to October 2015. Forty-four breeding pairs from two colonies on the western coast and 41 breeding pairs from the two colonies on the eastern coast were continuously monitored online. All recorded video files were automatically stored onto internal hard disks for later viewings.

Average daily and monthly rainfall (mm) and wind speed (km/hr) data were provided by the nearest Metereological station and included in our model.

Insect sampling

Flying insects were sampled at each study site using three permanent stations in major foraging habitats assessed by observing high number of foraging attempts (Petkliang, unpublished data). In each station, flying insect was trapped with 20 x 30 cm attached plates of cylindrical sticky trap, 3,000 cm^2 in total, one place at 5-10 m over canopy level, next one place at canopy level and other one is a floating cylindrical sticky trap used to collect aerial insects at the water surface. Insect sampling was limited to days with total rainfall lower than 10 mm and average wind speed below 16 km/hr which most effective for this method (Taylor, 1962). Insects were trapped for 12 hrs a day every two weeks for 12 months giving 1,044 hrs per site.

Arthropod samples were stored in a refrigerator (4°C) and identified to Order or Family after Tripplehorn and Johnson (2005). We recorded the number of individuals, measured the body length of insects, and converted these to insect biomass using regression equations following Lumsden and Bennett (2005).

4.2.4 Data analysis

Clutch size was recorded as the maximum number of eggs in a nest before incubation commenced, while brood size at hatching and fledgling were recorded as the number of live nestlings after hatching and on the last visit before fledging, respectively. Hatching success (the number of chicks that hatch/clutch size), fledging success (the number of chicks that fledge/ the number of chicks that hatch), and breeding success (the number of chicks that fledged/clutch size) were averaged across individual nests (Møller, 2013). All reproductive parameters of all individual nests were averaged to obtain an estimate for each clutch for the three breeding cycles.

The breeding periods of the western and eastern peninsular were compared using Julian dates. Breeding onset was calculated from the first 25th percentile of laying date, and finishing date from the last 25th percentile of fledging (Dunn et al., 2011).

The synchronization between nest with nestling percentage and peak of insect biomass was defined following Visser et al. (2006) as the difference (days) between the date of peak insect abundance date and the hatching date plus 15 days (i.e. the age of highest food demand for chick growth of the Germain's swiftlet; Ponak, 2004).

A generalized linear mixed model with binomial error distribution and logit-link function was applied to analyze each factor effect on breeding evidence (categorized as breeding -- egg laying to chick fledging or non-breeding -- after chick fled to nest building). Factors included geographic location (west and east), flying insect biomass and rainfall from three breeding cycles. The model parameters were fitted using maximum likelihood (Laplace approximation).

The relationship between food supply (every two weeks insect biomass) and reproductive effort (breeding percentage), also between insect biomass and rainfall were examined by cross-correlation analysis. The sinusoidal patterns from data analysis indicate relationships between biological phenomena separated along the same time series (Wikelski et al., 2000). All analyses were conducted using the program R version 3.2.4, (R Development Core Team 2016).

4.3 Results

Three breeding cycles of Germain's Swiftlet were continuously observed at both the eastern and western study sites. Although these birds can breed up to three times per year, most pairs bred twice a year (74.11%, n=85). On average one brood cycle lasted 101.2 ± 13.1 days in the eastern colonies (71 nests with nestling) and 111.0 ± 16.4 days in the western (121 nests with nestling). Each brood in the western and eastern colonies showed variation in nest building, egg laying with incubation and nest feeding periods (Table 4.1). Nest building and nestling feeding periods were longer in the western colonies than eastern colonies but the incubation period was similar (Figure 4.2).

4.3.1 Breeding time variation

Overall peak breeding times differed between the sites with peak breeding in the western colonies from July to November, and peak breeding at eastern colonies from January to May (Figure 4.3). These periods coincided with the different monsoon periods for the study sites: at western colonies this was the middle to late south-west monsoon (July-October) for the first brood and middle of dry season to early period of the south-west monsoon in (January-May) for second brood. For the eastern colonies, the first brood occurred from onset to middle of the north-east

monsoon (September-December) and the second brood coincides with the closing months of the monsoon to the dry season of the east peninsular (January-May).

We also found variation in the timing of breeding between the west and east colonies. All three broods observed in the western colonies bred 20-50 days earlier than birds in the eastern colonies. Additionally, birds at both sites had a longer subsequence time between 1st and 2nd broods in dry months compared to 2nd and 3rd broods in wet months (Figure 4.2-4.3).

4.3.2 Breeding time, insect biomass and rainfall

It's appears that a high percentage of the fledging period overlapped with high insect biomass both in the western and eastern colonies. For both colonies, the peak food abundance and peak nestling food demands were within ±14 days (Figure 4.4), given nest feeding period (40.25 ± 3.0 days).

Flying insect biomass, geographic location and rainfall were the main predictors of breeding (Z = 4.819, P < 0.001; Z = -6.438, P < 0.001; Z = 2.291, P = 0.021). Furthermore, the interaction between total insect biomass and rainfall, and total insect biomass and geographic location, were strongly significant (Z = -2.72, P = 0.006; Z = 10.07, P < 0.001); the predictive ability of the model was 0.70. Differences in geographic location are associated with different insect biomass which in turn influenced breeding of swiftlets. Insect biomass and rainfall were positive predictors but rainfall influences insect biomass and can showed negative impacts on breeding i.e. when rainfall is too high (Table 4.2).

Cross-correlation analysis of both side of Thai peninsula showed a sinusoidal pattern (Figure 4.5) indicating that breeding, food supply and rainfall were seasonal. The breeding season related to food supply and food supply related to rainfall. In the western colonies, sinusoidal relationship was clear, indicating that breeding and food supply was most strongly positive and significant (P < 0.001) at a lag of -1 (2 weeks), food supply and rainfall also showed significantly positive (P=0.008) at a lag of 1 (2 weeks). Whereas in the eastern colonies, the breeding and food supply was weakly positive related (P=0.093), food supply and rainfall was significantly negative related (P < 0.001) at a lag of -8 (4 months).

When consider the amount of rainfall, more breeding occurred when rainfall was 100-300 mm/month compared to <100 or >300 mm/month. Breeding occurred at high percentages in all three broods in the western colonies as the rainfall rarely got exceeded 300 mm/month, and the dry season was short (January to February). In contrast, in the eastern colonies, the percentage of breeding birds was <50 % with low synchronization between breeding pairs within the same colony when rain >600 mm/month in November to December (Figure 4.6A). Similarly, insect biomass peaked during at beginning and end of the rainy season when rainfall was 100-300 mm/month. In general, lower insect biomass occurred during the dry season and with periods of very heavy rainfall (Figure 4.6B).

4.3.3 Breeding success

Breeding success at western and eastern sites was similar; average 78.97 % and 76.49 %, respectively. However there were some differences between breeding bouts. Lower breeding success occurred during the very heavy rainfall period at September to December in the eastern colonies and heavy rainfall during June to September in the western colonies (Figure 4.3, Table 4.3).

4.4 Discussion

4.4.1 Breeding time variation

Breeding activity of Germain's swiftlet varied with geographic location, with western colonies breeding earlier than eastern colonies. Breeding peaked from July to October and December to May at western sites and from January to May at eastern sites, whereas, peak was from January to March at this site as reported by Phongchoo (1985). The duration of one breeding cycle of the Germain's swiftlet in southern Thailand from this study was the same as birds breeding in central Thailand (Viruhpintu, 2002), Sarawak, Malaysia (Lim and Cranbrook, 2002), and Penang, Malaysia (Langham, 1980; Anun et.al., 2014). Most of *Aerodramus* spp. breed two times a year; similar to the breeding swiftlets in Vietnam (Phong et al., 2015) and Andaman and Nicobar islands (Manchi, 2009). However, some swiftlets can raise the third broods in wet months. Thus some birds demonstrate reproductive flexibility by extending the reproductive quiescent period in dry months but shortening it in wet months due to richer of food supply (Visser et al., 2006). Thus environmental factors

can directly influence bird breeding strategies (Lim and Cranbrook, 2002). Extended nestling period is characteristic of other species of swiftlets and may represent food limitation in these aerial insectivores (Reichel et al., 2007).

4.4.2 Breeding time, insect biomass and rainfall

The overlap between nestling feeding and peak of insect biomass suggests that swiftlets adjust the hatching time to meet the peak food period; especially important given that insect biomass fluctuates between seasons (Dunn et al., 2011). Although the synchronization was not precise, the peak food still fell within the nestling period. Optimal time for reproduction is clearly set by prey peak in other insectivorous species e.g. great tit, *Parus major* (Visser et al., 2006), Spotted Antbirds, *Hylophylax n. naevioides* (Wikelski et al., 2000). Asynchrony between chick hatch and food peaks can decrease growth rates in chicks (Mckinnon et al., 2012) and delay egg laying and fledging when rich food resources are missed (Kang et al., 1991).

In our study, high percentage of breeding occurred at beginning and closing months of wet periods because flying insect peak at that time. Insect biomass and rainfall were mainly positive predictors of breeding activities but low and very heavy rainfall showed negative effects on insect biomass that, in turn, influenced breeding. Similarly, cross-correlation results indicated that the breeding activities of Germain's swiftlet at the western colonies peaked in January, one month prior the food peak and the insect biomass peaked in February, the closing month of wet season. At the eastern colonies, the negative relationship between insect biomass and heavy rainfall > 600 mm/month in October (Wangwongchai, 2005) influence to swiftlet breeding. However, there was positively related between food peak and breeding activities. This indicated the use of short-term information on food availability for the temporal fine-tuning of reproduction (Wikelski et al., 2000). Our results provide evidence that the high percentage of breeding birds and high total insect biomass occur when rainfall is at moderate levels (100-300 mm/month). When rainfall was lower than 100 mm/month or over 300 mm/month, the breeding percentage and total insect biomass decreased. The association between swiftlet breeding and climate has also been found in in central Thailand (Viruhpintu, 2002), Penang (Langham, 1980; Anun et al., 2014) and Sarawak in Malaysia (Lim and Cranbrook, 2002; Lim, 2011) (Table 1.1). Both distribution and abundance of prey insects have been found to vary with climatic

conditions and influenced to other bird breeding. For example, insect dispersal in South America (Srygley and Dudley, 2008) and seasonal change in foraging of Pacific swallow were associated with breeding in Malaysia (Waugh and Hails, 1983).

Other studies have found that higher rainfall in wet seasons causes higher insect availability (Fukui et al., 2006) but very heavy rainfall can cause the negative effect to breeding (Öberg et al., 2015) by effecting through the insect availability and reduce the foraging time outside nest site. In contrast, dry months contain low insect availability result in low breeding activity, longer nestling period and subsequence brood. This suggests that breeding activity is related to the monsoon cycle (Manchi, 2009) and prey abundance (Srygley and Dudley, 2008).

4.4.3 Breeding success

Swiftlet may respond to food insufficiency by extending their breeding time to meet with high breeding requirements. Breeding success is also low when breeding period overlap with very heavy rainfall as demonstrated in our study on the eastern coast during the north-east monsoon period. Swiftlet is possibly not able to forage. Previous authors demonstrated that insectivorous bird fledging success was negatively related to rainfall, especially in first half of nestling period (Öberg et al., 2015).

In conclusion, breeding period variation between western and eastern sites results from variation in major food supply that is, in turn, influenced by rainfall. Germain's swiftlet appear to adjust their breeding strategies to meet with rich food resources.

4.4.4 Implication on nest harvest

For sustainable use, frequency and timing of nest harvesting should be set to counteract observed population decline of swiftlet. Given the strong geographic difference in breeding chronology found in this study, swiftlet's nest should be harvested at the end of breeding season and this timing of post fledging varied between the east and west of Thai peninsula.

In Vietnam the swiftlet populations breed two times a year and both harvest and non-harvest nests and harvesting increases the likelihood of immature birds leaving the colony (Phong et al., 2015). In Thailand, harvest in concession caves of three times a year may not enable the breeding pairs to finish their annual breeding cycle and/or result in lower breeding success (Kang et al., 1991; Nguyên Quang and

Voisin, 1998; Phong et al., 2015) and adult survival (Tompkins, 1999). From our study sites, where harvested is restrict to twice a year after birds fledge, the breeding success was not different between broods (Table 4.3). Therefore, we recommend two harvests after chicks fledge will minimize the impact and is appropriate for farmed swiftlets.

Acknowledgement

4.5 References

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Table 4.1 Breeding period and duration of each breeding stage (mean ± SD) in the west (121 nests) and east (71 nests) coast of the peninsular Thailand between July 2014 - October 2015.

Location/ Brood	Month	Nest building (days)	Egg laying to incubation (days)	Nest feeding to fledging (days)	Breeding cycle (days)
West					
1st brood	Jul-Nov	31.1±4.2	18.8±4.6	50.4±5.1	100.3±6.5
2nd brood	Dec-May	47.3±15.6	27.5±2.3	38.5±6.8	113.0±15.1
3rd brood	Jun-Sep	50.1±20.4	29.1±4.3	39.5±8.5	119.1±19.0
East					
1st brood	Sep-Dec	23.1±11.9	24.7±4.6	38.7±4.6	86.7±14.4
2nd brood	Jan-Apr	38.5±11.2	26.6±2.8	40.2±10.7	105.4±10.8
3rd brood	Jul-Oct	46.2±20.2	24.2±5.8	33.6±15.2	104.0±7.9

Table 4.2 Results of generalized linear mixed model for swiftlet breeding evidences (breed and non-breed) with binomial error distribution include three broods (192 nests) for 60 weeks from July 2014 to October 2015, fixed effect are geographic locations (west and east), insect biomass and rainfall.

Fixed variables	Estimates	Standard error	Z-value	P-value
Intercept	-1.63	0.268	-6.060	<0.001**
Geographic location	-1.25	0.194	-6.438	<0.001**
Insect biomass	0.017	0.003	4.819	<0.001**
Rainfall	0.001	<0.001	2.291	0.021*
Insect biomass×Rainfall[a]	-<0.001	<0.001	-2.720	0.006*
Insect biomass×Geographic location[a]	0.037	0.003	10.071	<0.001**

Note. *p<0.05; **p<0.001. [a] Indicates an interaction.

Table 4.3 Clutch size, hatching success, fledging success and breeding success percentage from three breeding bouts in the western and eastern colonies of peninsular Thailand.

Breeding chronology	West			East		
	1st bout (Jul-Nov14) n = 39	2nd bout (Dec14-May15) n = 41	3rd bout (Jun-Sep15) n = 42	1st bout (Sep-Dec14) n = 18	2nd bout (Jan14-May15) n = 34	3rd bout (Jul-Oct15) n = 19
Clutch size	1.41	1.70	1.75	1.65	1.74	1.50
Hatching success	91.48%	97.36%	88.31%	86.73%	88.08%	88.26%
Fledging success	93.02%	85.00%	79.41%	84.54%	87.50%	86.85%
Breeding success	84.80%	82.00%	70.12%	71.43%	81.50%	76.55%
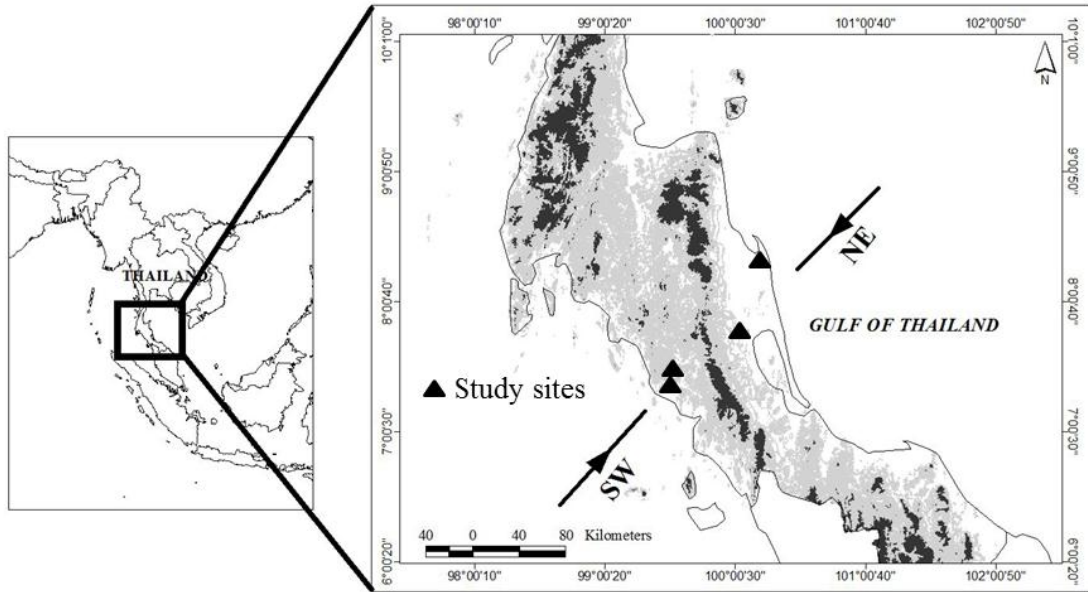
Figure 4.1 Map of study sites on the peninsular Thailand and four observation colonies of Germain's swiftlet and the direction of southwest monsoon (SW) during May to October and northeast monsoon (NE) during November-January.
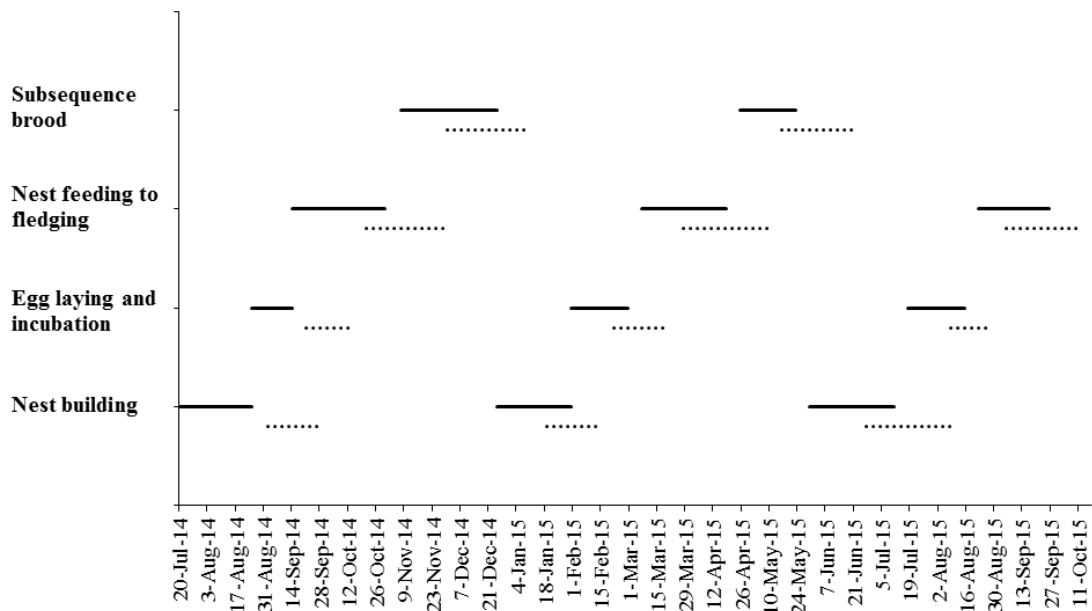
Figure 4.2 Breeding chronology of the Germain's swiftlet from three breeding bouts in the western (bold line) and the eastern (dot line) colonies of 85 breeding pairs (192 nests) in the peninsular Thailand between July 2014 to October 2015.
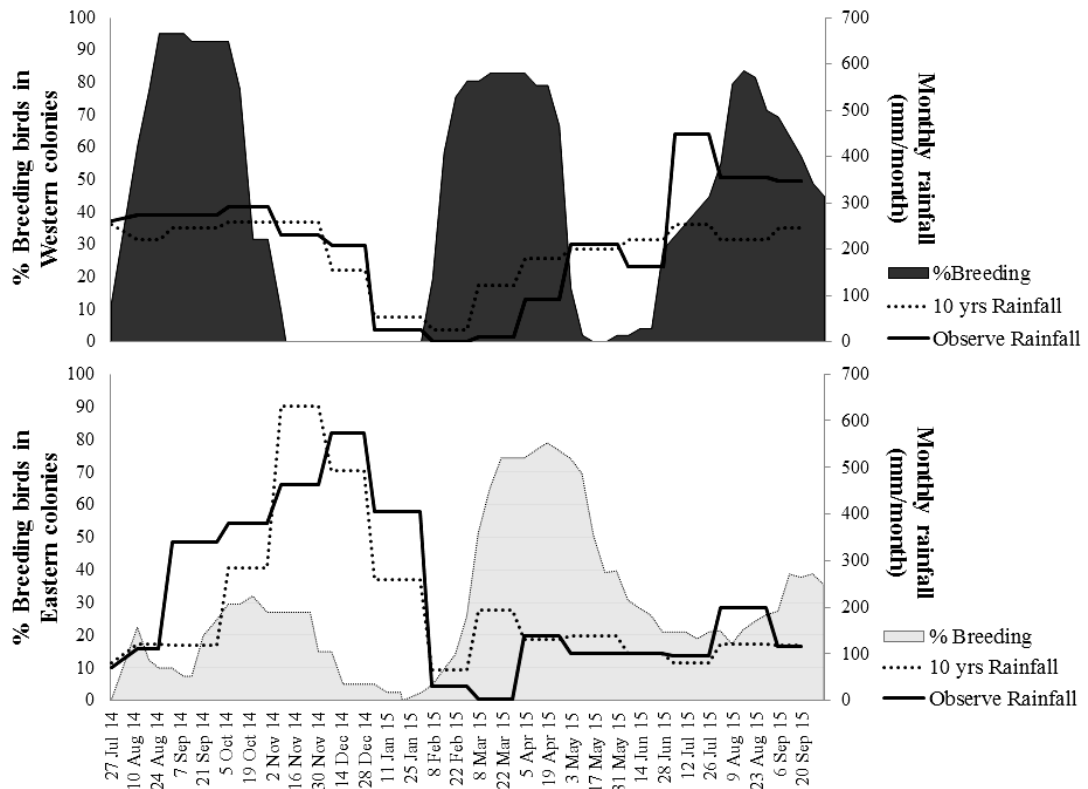
Figure 4.3 Pattern of breeding, breeding time variation (area), monthly rainfall at the latest 10 years average (dot line) and monthly rainfall at observation time (bold line) from the western and eastern colonies of 85 breeding pairs (192 nests) in July 2014 to October 2015.
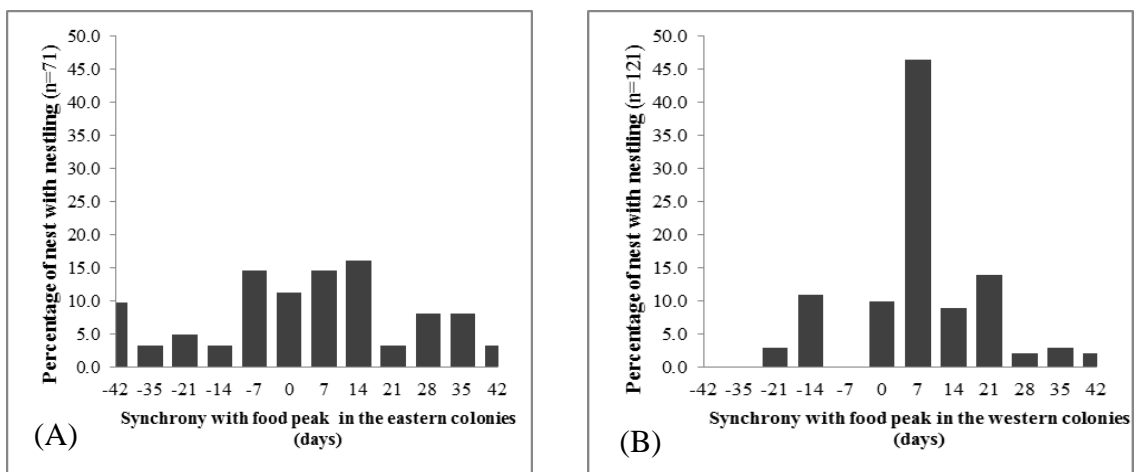
Figure 4.4 Synchronization of nest with nestling at high food demand frequency and food peak in the eastern colonies (A) and the western colonies (B).
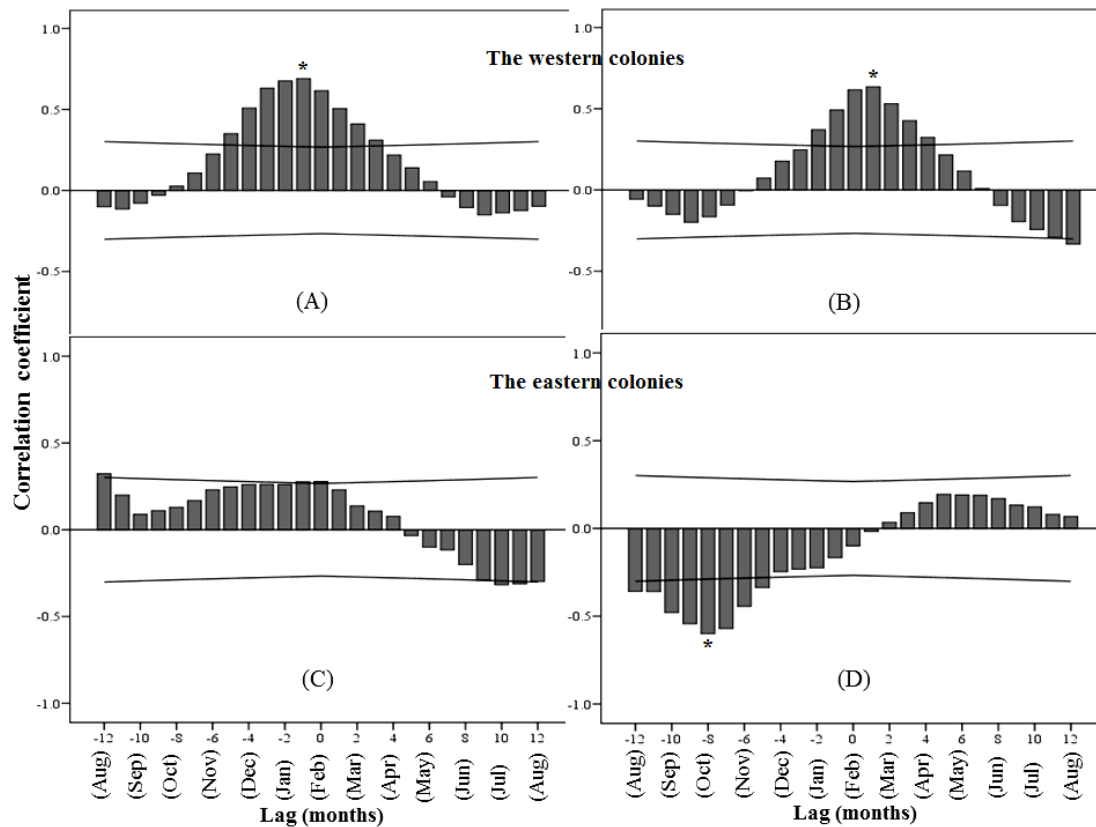
Figure 4.5 Cross-correlation analysis of the insect biomass - breeding percentage and insect biomass - rainfall (July 2014 – September 2015) at the peninsular Thailand by used every two weeks data. The western colonies: (A) insect biomass and breeding ($P < 0.001$), (B) insect biomass and rainfall ($P = 0.008$). The eastern colonies: (C) insect biomass and breeding ($P = 0.093$), (D) insect biomass and rainfall ($P < 0.001$).
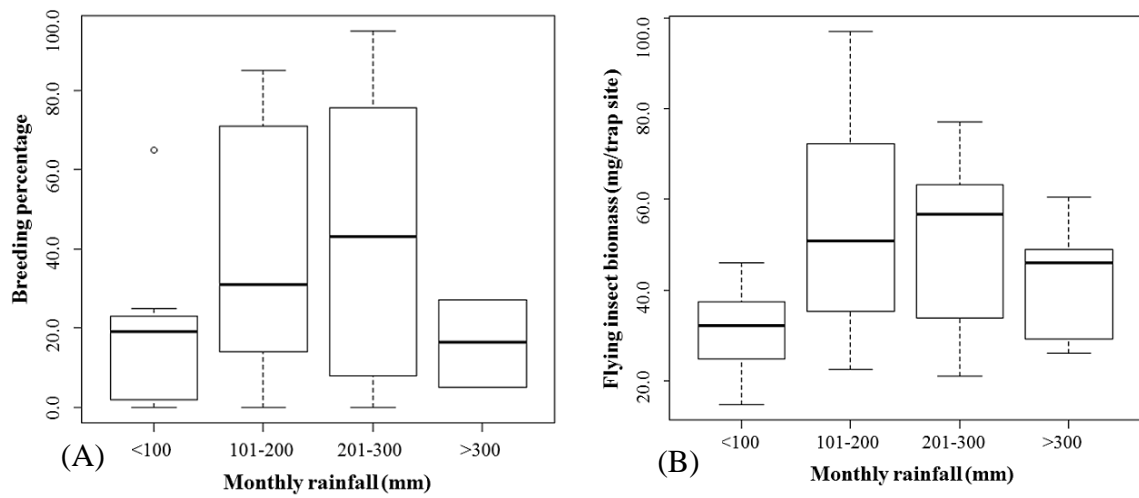
Figure 4.6 Breeding percentage (n = 192 nests) (A) and flying insect biomass in mg per trap site (1,044 trap hours) (B) at each monthly rainfall categories between July 2014 to October 2015.

CHAPTER 5

GENERAL DISCUSSION AND CONCLUSION

The foraging habitat selection of Germain's swiftlet was investigated across time, habitat types and vertical variation infer from the foraging intensity of birds by record the number of prey capture attempts per minute. Then relate the intensity of foraging with flying insect biomass and breeding period. Furthermore, breeding chronology in the west and east of peninsular Thailand was compared and determined factors affected to swiftlets breeding evidences such insect biomass and rainfall. These aspects will be discusses and concludes including implications for conservation.

5.1 Foraging habitat selection of the Germain's Swiftlet

5.1.1 Temporal variation

Germain's swiftlet exhibited variation in use in both diurnal and seasonal pattern. The explanations were the rich of insect prey at that time cause high intensity of foraging. They try to maximize the profitability according to the optimum foraging model (Stephen et al., 2007). The observation of high number of prey capture attempts in late afternoon and morning can be explained by the emergence of more flying insects during twilight, which is in accordance with patterns of insect distribution observed in lowland tropical rain forest in South-east Asia (Basset et al., 2003; Kishimoto-Yamada and Itioka, 2015).

The prey capture attempts was significantly greater during the wet season than in the dry season. This coincided with average total insect biomass per trapped site which significant 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). Seasonal variation in insect biomass could be correspond to vegetation structure which change after rainfall (Cody, 1981). Then climatic variation due to season cause changes in food supply, in turn influence foraging habitat selection for this species as also found in others insectivorous birds (Lourie and Tompkins, 2000; Wolfe et al., 2014).

5.1.2 Habitat type variation

Water bodies, forest areas and open paddy land are the major foraging habitat of the Germain's swiftlet that caused by the rich of insect availability. This suggests that birds select foraging habitat based on patches quality which provide the highest profitability (Stephens et al., 2007; Sanchez-Clavijo et al., 2016).

The most important foraging habitat for Germain's swiftlet was water bodies since the rich of both aquatic and terrestrial insect prey (Fukui et al., 2006), water bodies with green vegetation can be long-term high quality patch (Watanabe et al., 2014). Forest was the major source of Hymenoptera, which is the major diet item for swiftlets (Langham, 1980; Nguyên Quang et al., 2002). This coincided to the study on diet of Germain's swiftlet in Malaysia and the eastern of Thailand that Hymenoptera comprised the largest proportion in food boluses collected from nestlings fed by swiftlets foraging over forest canopy (Lourie and Tompkins, 2000; Ponak, 2004). Open paddy land will likely be a good choice when it is covered with green plants and flood plain patch in wet season (Kishimoto-Yamada and Itioka, 2015). The dominant insects were Diptera and Hemiptera, which are amongst major swiftlet diet component (Lourie and Tompkins, 2000; Medway, 1962). The monoculture tree-dominated agricultural land that low complexity vegetation structure was associated with lower insect biomass, Insect biomass has found to be less than twice as low in rubber plantation compared to forest habitat (Phommexay, et al. 2011). Nevertheless, this habitat was known to use during the termite-swarming period in the early wet season because of its high energy and protein (Viruhpinthu, 2002). Urban habitat which is known to be dominated by Diptera (Lourie and Tompkins, 2000) was seldom use in term of low foraging attempts. This habitat probably supplements the meal during twilight period of the day.

5.1.3 Vertical variation on foraging

When consider the vertical variation on foraging intensity of the Germain's swiftlet, the foraging height was significant related to canopy height in foraging habitat (Manchi and Sankaran, 2010). At 0-10 m above canopy level was mostly used by foraging swiftlets despite at open paddy land where was frequently used at edge space of canopy. Similarly, the flying insect biomass was highest at canopy level and slightly low at upper level (Basset et al., 2003). This was in accordance with the

dispersal level of their prey such as the breeding ants that can glide and fly over canopy and fig wasp can move and dispersal over figs tree canopy by wind (Compton et al., 2000). This suggested that vegetation flying insect availability at canopy level and space strongly influenced to vertical activity of nonstop flying swiftlets.

5.2 Breeding time variation of the Germain's Swiftlet

Breeding activity varied with geographic location, with western colonies breeding earlier than eastern colonies. Breeding peaked from July to October and December to May in western sites, similar time period to breeding time at Penang, the western Malaysia (Anun et al., 2014) and in eastern sites peaked from January to May coincided with Phongchoo (1985). These times are the transition periods between seasons when food is most abundance. Breeding activities of swiftlet was seasonal and significantly related to food supply. Previously studies showed the relationship between breeding percentage and rainfall without indicating in optimal range, i.e. the studies in central Thailand (Viruhpintu, 2002), Penang (Langham, 1980; Anun et al., 2014) and Sarawak in Malaysia (Lim and Cranbrook, 2002; Lim, 2011). Nevertheless, our results suggested that an optimal range of rainfall influence to insect availability. The dry months (<100 mm rainfall) and wet months (>300 mm rainfall) exhibited low percentage of reproductive swiftlets and the breeding success was reduce in this range. This indicating that breeding activity is related to the monsoon cycle (Manchi, 2009) and prey abundance (Srygley and Dudley, 2008).

5.3 Implications for conservation

This study highlights the need for greater protection of water bodies, forest and open paddy lands to provide natural prey insects for swiftlet populations, and consequently maintain ecosystem function. Otherwise, information on habitat use is useful for local swiftlet farmers to establish suitable nest sites for Germain's swiftlet in closer proximity to their preferred foraging habitats. This can be apply as a guideline for providing artificial food resources for birds

Given the strong geographic difference in breeding chronology found in this study, commercially exploited colonies should not be harvested until late in the breeding season and this timing will vary with location. Reducing the potential for

swiftlet populations to be overexploited should be included in the best practice for sustainable use (Kang et al., 1991; Sankaran, 2001; Hobbs, 2004).

5.4 Future studies and limitations of the study

This study can raise the significant on the foraging habitat selection of Germain's swiftlet in population level. Further studies should continue on foraging of individual birds relate to their diet and details on foraging behavior, movement patterns and home range. Although in this study the birds frequently forage close to vegetation canopy, there was lack of dispersal data at high altitude. Transmitter tracking at individual bird remains a priority for Germain's swiftlets observation at over 100 m above ground and the insect trapping at high altitude were needed for additional measurement.

Despite rainfall and insect availability that cause significantly different on breeding period between different geographic locations, it will be meaningful to measure the other factors affect the breeding activities such as competition, predation and other physical factors. Breeding chronology across its world distribution range should be map and apply for appropriated nest harvest time. According to their high valuable nest, I can observe breeding activities by record on internet protocol camera, I'm not allowed to catch and weigh the chick for follow their growth which may relate to insect availability, so this still need more intensive examination.

For the highlight results on breeding time variation between the western and the eastern swiftlet colonies of peninsular Thailand, I recommend that the further studies should focus on long term monitoring in breeding seasonality of this species throughout its distribution range to answer the question "what cue could swiftlet use to adjust annual breeding period?". Our results suggest that swiftlet can adjust the breeding period to avoid bad climate conditions. For example, in the eastern coast, the heavy rainfall cause delay egg laying while their nests were built or the breeding period was shortened. This study is the first comparison on breeding time variation between sites in Thailand and indicate significantly different in breeding chronology. New nest harvesting period should be implemented to reduce negative effect to swiftlet breeding success. This information can imply the nest harvest time both in manmade and natural habitat. As the high valuable of swiftlet's nest industry and

concession cave provide high income for government and concessionaire, conservation and sustainable use should be intensively concerned. Public sector should promote the cooperation between researchers and private sectors for long monitoring projects. In addition, researches on nest harvesting methods and their impacts on breeding strategies are needed. Complete information in breeding seasonality and harvesting methods can lead to sustain swiftlet industry in Thailand and other countries within swiftlet distribution range.

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APPENDIXES

Appendix 1 Study species : Germain's swiftlet (*Aerodramus inexpectatus germani*)

A. Topotype *A.i. germani*

   1A : Palua Condore, Vietnam, 1882, USNM

   1B : Koh Phangan, Thailand, 1912, AMNH

   1C : Satang Kechil, Sarawak, 1932, RMBR

  (Cranbrook et al., 2013)

B. Germain's swiftlet in house farm at Phattalung, Thailand

C. Germain's swiftlet in house farm at Pak Phanang, Thailand

Appendix 2 Prey capture attempts identification from field observations at the timing of insect swarming such as ant and termite, refer to Manchi and Sankaran (2010).

Foraging behaviors categories

1. *Twist* : The bird makes a sudden twist while gliding, tail open to reduce speed.

2. *Tail-wing open* : A pre-planned position to capture prey once observed. Wing and tail feathers are stretched while approaching the prey and a small twist or flutter is performed during capture.

3. *Flutter* : A hover performed with a rapid wing beat and a pause in flight.

4. *Roll* : The individual catches prey in its beak and rolls down. Birds were observed rolling down for about 2 sec.
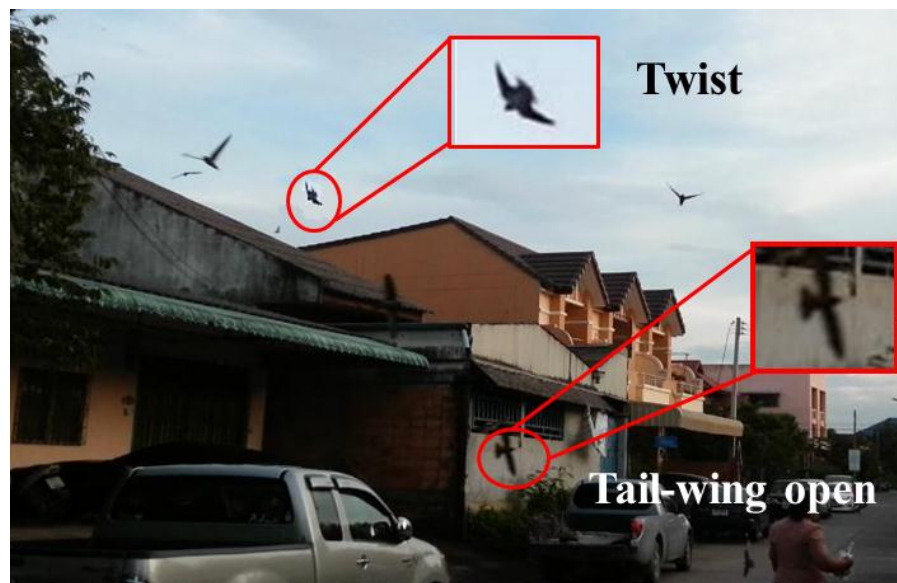
A. Twist and Tail-wing open
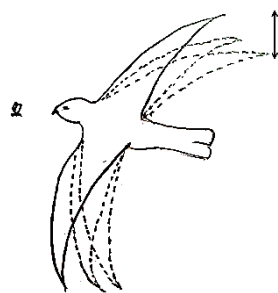
B. Flutter   C. Roll

Appendix 3 Sampling points of five habitat types for foraging observations within foraging range, Hat Yai, Songkhla.

A. Water body

B. Forest

C. Open paddy land

D. Tree-dominated agricultural land

E. Urban
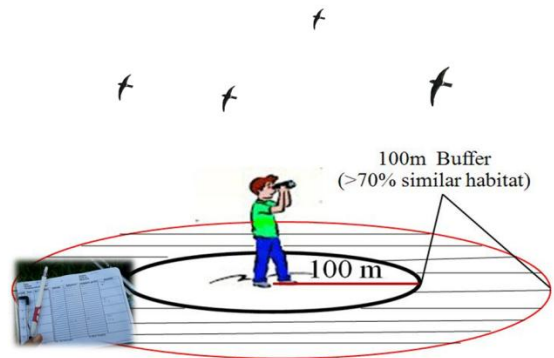
F. Foraging intensity observation

Appendix 4 Insect samplings and identifications
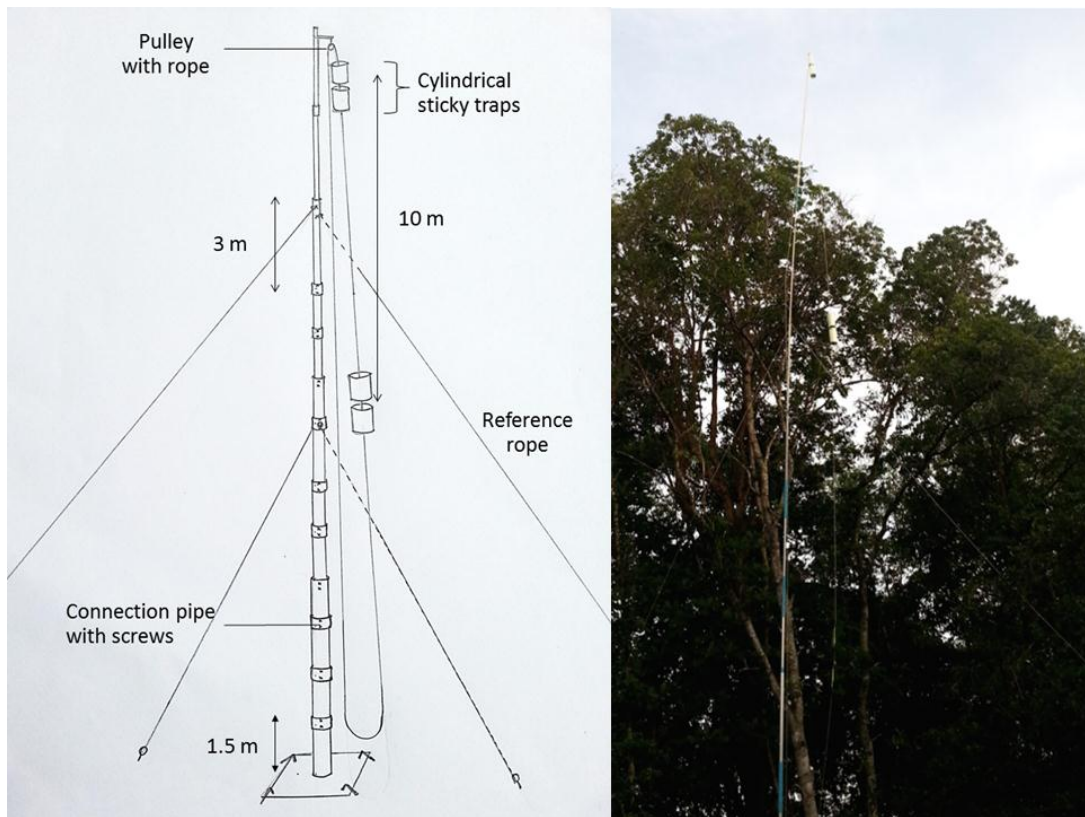
A. Pole for flying insect trapping: a series of aluminum tubes attached with a rope on a single fixed pulley on the top and attached with the cylindrical sticky traps at canopy and 5-10 m over canopy with 10 m between its. The height of the pole can adjust by push the pole up and add the aluminum tube at the bottom.

B. Insect sampling in open paddy land and near water surface using floating cylindrical sticky trap.
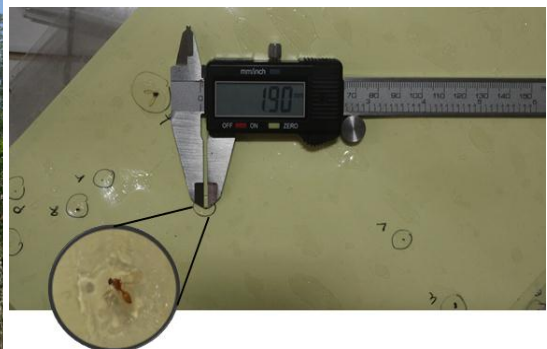
C. Measuring the body length of insect and identification under the stereo microscope.

Appendix 5 Sampling colonies and example of sampling nest patches in Trang (western coast), Phattalung and Nakhon Si Thammarat (eastern coast) province, southern Thailand.

A. Sampling colony at KanTang, Trang province.

B. Sampling colony at Pak Phanang, Nakhon Si Thammarat province.
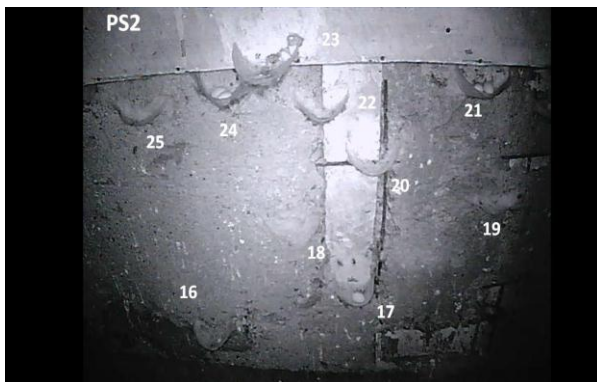
C. Sampling nest patch in Trang colony.

D. Sampling nest patch in Nakhon Si Thammarat colony.

E. Sampling nest patch in Trang colony.

F. Sampling nest patch in Phattalung colony.

Appendix 6 Number of individuals per trap site of 2,400 cm^2 sticky trap in each habitat type within swiftlet potential range at Hat Yai, Songkhla between February 2014 to March 2015.

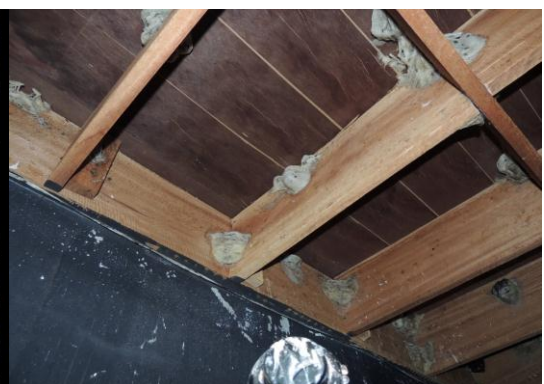| Major insects	Number of individuals per trap site (mean±SD)						
	Feb-Mar	Apr-May	Jun-Jul	Aug-Sep	Oct-Nov	Dec-Jan	Feb-Mar
Forest							
Hymenoptera	11.6±7.2	20.6±15.0	16.0±2.9	19.0±7.9	13.0±8.1	12.5±2.5	5.0±2.4
Diptera	11.0±9.2	13.0±10.4	47.2±33.2	90.6±29.0	38.5±10.1	43.0±26.8	28.7±17.8
Hemiptera	8.0±3.0	3.0±1.0	3.5±0.9	4.0±0	4.5±1.7	5.0±2.1	3.0±1.0
Coleoptera	2.0±2.0	4.0±1.2	5.2±1.7	6.0±2.6	3.0±2.0	2.0±1.2	2.0±1.0
Isoptera	0.00	3.0±1.7	1.0±0.5	0.00	0.00	0.00	0.00
Other	7.0±1.5	6.0±3.5	10.7±2.6	7.0±6.1	5.7±1.5	2.8±0.6	2.5±0.5
Open paddy land							
Hymenoptera	11.6±5.5	16.0±3.4	15.2±4.6	8.0±2.9	3.3±2.1	7.0±2.7	9.0±5.7
Diptera	15.6±3.1	42.0±15.1	67.9±29.6	106.7±115.1	77.3±32.1	47.2±28.0	39.7±16.3
Hemiptera	3.5±2.1	8.5±1.5	14.6±5.2	2.3±0.6	6.0±1.4	5.7±2.1	3.5±0.7
Coleoptera	2.3±0.6	5.5±2.2	11.8±6.8	6.0±4.8	3.3±1.5	3.5±2.4	3.5±1.9
Isoptera	0.00±	2.0±1.0	2.0±1.0	0.00	0.00	0.00	0.00
Other	10.5±7.8	8.6±1.4	14.2±2.2	7.2±1.5	7.5±0.7	7.9±3.1	8.2±1.3
Tree-dominated agricultural land							
Hymenoptera	20.7±11.6	17.5±9.5	16.0±10.4	8.5±5.4	14.7±10.3	10.7±5.4	11.5±13.7
Diptera	9.3±10.1	39.0±18.1	63.0±52.4	61.5±34.4	103.0±48.4	49.7±24.1	32.2±34.3
Hemiptera	5.0±1.4	10.0±2.1	5.2±1.5	7.8±3.1	3.5±1.0	5.0±1.4	5.5±4.9
Coleoptera	6.0±5.7	5.8±2.2	10.5±1.3	5.0±3.2	5.0±4.2	3.0±0.8	4.0±1.0
Isoptera	0.00	1.0±0.6	11.0±6.2	0.00	1.0±0.5	0.00	0.00
Other	10.6±10.7	6.6±3.6	10.8±1.0	4.7±1.3	4.7±2.2	5.6±2.1	3.3±0.6
Urban							
Hymenoptera	8.5±2.1	16.5±7.4	10.5±4.2	9.5±2.1	15.3±6.0	6.3±5.8	6.7±5.6
Diptera	28.0±1.4	47.0±23.7	47.0±18.1	37.0±29.4	66.0±55.3	35.0±24.3	30.7±17.1
Hemiptera	8.0±5.7	14.6±4.0	3.5±1.7	5.2±1.5	5.3±0.6	4.6±0.9	2.5±1.3
Coleoptera	8.0±2.8	11.9±7.8	7.0±3.3	6.3±6.7	3.6±2.9	3.0±2.8	5.0±2.6
Isoptera	0.00	1.0±0.5	1.5±1.0	0.00	0.00	0.00	0.00
Other	9.5±0.7	8.0±1.3	9.0±3.2	6.6±1.7	5.3±1.5	7.5±4.2	3.5±1.0
Water bodies							
Hymenoptera	11.5±3.9	13.2±2.9	27.75±14.1	16.5±5.6	25.7±34.2	11.7±5.7	11.7±6.2
Diptera	46.7±61.4	59.7±21.2	103.2±64.8	79.2±27.9	180.5±111.1	77.2±46.4	45.7±13.4
Hemiptera	7.0±0.0	10.3±3.1	9.0±2.4	8.3±3.7	7.3±4.2	41.0±40.2	5.5±3.4
Coleoptera	2.0±0.5	5.3±4.1	5.0±0.5	7.2±5.1	6.0±2.0	5.0±4.8	6.0±8.0
Isoptera	0.00	3.0±1.5	1.0±0.5	0.00	0.00	0.00	0.00
Other	6.5±4.0	12.0±6.4	21.3±6.7	6.0±0.6	8.5±4.3	5.4±2.8	10.2±1.8

Appendix 7 Insect biomass in mg per trap site of 2,400 cm^2 sticky trap in each habitat type within swiftlet potential range at Hat Yai, Songkhla between February 2014 to March 2015.
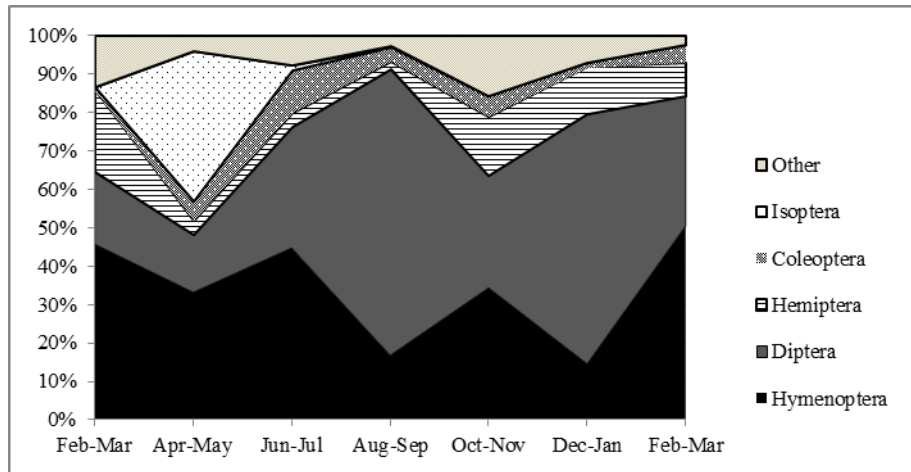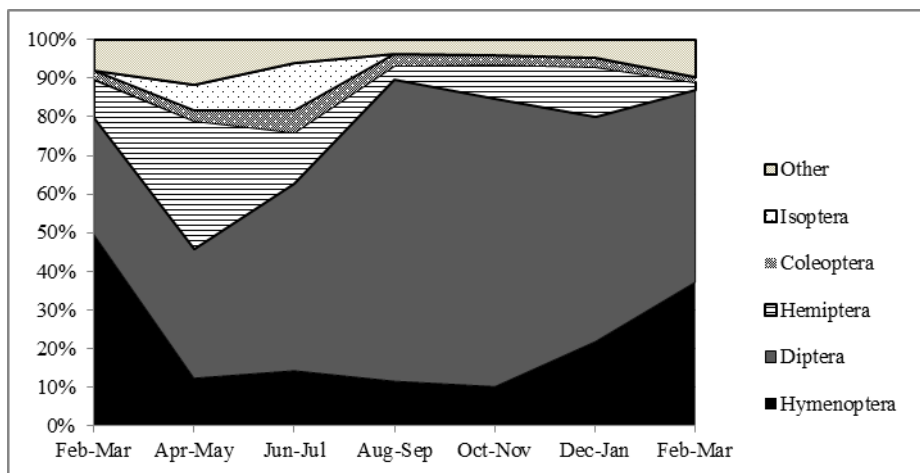
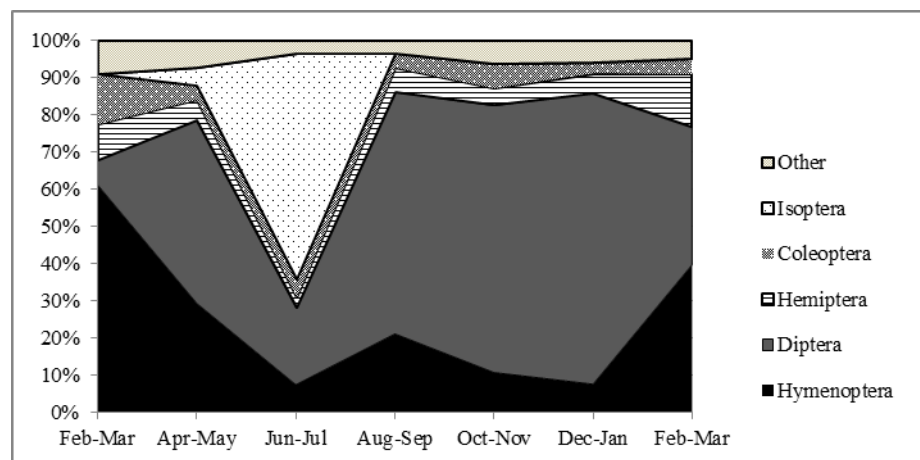| Major insects	Insect biomass in mg per trap site (mean±SD)						
	Feb-Mar	Apr-May	Jun-Jul	Aug-Sep	Oct-Nov	Dec-Jan	Feb-Mar
Forest							
Hymenoptera	13.10±3.3	18.72±11.6	18.31±7.6	11.58±6.2	10.51±3.6	5.18±3.9	8.04±6.4
Diptera	5.37±3.8	8.52±11.4	12.93±8.6	51.28±14.7	8.92±5.2	23.11±18.7	5.40±3.5
Hemiptera	6.10±0.6	1.98±0.6	1.48±0.7	1.44±0.7	4.72±2.5	4.40±2.6	1.37±1.4
Coleoptera	0.28±0.2	2.82±1.7	4.49±3.4	2.72±0.8	1.59±0.9	0.40±0.2	0.75±0.9
Isoptera	0.00	22.19±12.4	0.59±0.3	0.00	0.00	0.00	0.00
Other	3.80±3.4	2.19±1.9	3.13±0.8	1.94±1.3	4.83±3.9	2.51±0.8	0.36±0.1
Open paddy land							
Hymenoptera	14.85±9.7	7.85±3.3	7.80±3.1	5.78±5.2	3.94±2.0	5.21±3.7	8.14±13.7
Diptera	9.08±5.3	21.46±12.2	26.73±8.8	39.69±21.9	29.31±16.0	14.00±11.2	10.94±6.4
Hemiptera	3.01±0.5	21.50±6.5	7.40±4.0	1.74±0.9	3.57±2.0	3.14±2.5	0.46±0.1
Coleoptera	0.65±0.6	1.84±1.4	2.99±1.9	1.55±1.5	0.91±0.4	0.51±0.3	0.25±0.2
Isoptera	0.00	4.09±3.7	6.85±3.4	0.00	0.00	0.00	0.00
Other	2.38±0.2	7.50±5.5	3.33±2.0	1.84±0.3	1.53±0.6	1.15±0.6	2.12±1.1
Tree-dominated agricultural land							
Hymenoptera	33.37±30.7	13.99±10.0	11.79±2.4	10.22±8.8	5.84±3.5	2.16±1.1	8.18±7.8
Diptera	3.73±2.7	23.40±20.8	32.49±23.2	31.34±8.2	38.80±18.9	22.06±15.8	7.63±4.4
Hemiptera	5.17±2.4	2.61±0.6	4.36±2.3	3.14±1.0	2.54±1.5	1.48±0.5	2.87±1.7
Coleoptera	7.40±4.4	1.85±0.4	7.22±3.8	1.80±1.1	3.53±2.9	0.82±0.4	0.88±0.5
Isoptera	0.00	2.24±1.6	95.28±56.8	0.00	0.00	0.00	0.00±
Other	4.84±2.9	3.49±1.6	5.37±3.8	1.70±0.6	3.35±2.4	1.66±1.0	1.00±1.1
Urban							
Hymenoptera	5.30±0.8	12.47±9.2	2.85±2.1	4.44±0.2	5.72±4.9	1.68±0.9	2.29±2.8
Diptera	13.20±7.3	22.70±7.7	21.53±6.4	17.03±7.7	24.20±16.3	4.81±4.0	8.68±6.3
Hemiptera	3.29±1.7	9.07±7.9	1.64±0.9	5.69±2.6	1.83±0.3	1.56±1.3	2.24±3.5
Coleoptera	6.96±4.5	4.39±3.6	3.89±3.2	1.91±1.9	1.16±0.7	1.00±0.2	1.08±1.2
Isoptera	0.00	0.59±0.3	0.56±0.5	0.00	0.00	0.00	0.00
Other	2.96±2.6	11.60±7.7	1.63±0.5	5.85±2.3	2.41±1.7	1.03±0.3	1.17±0.1
Water bodies							
Hymenoptera	17.96±14.3	13.86±13.1	13.16±11.7	22.00±13.6	15.57±10.1	5.22±3.5	17.03±11.7
Diptera	22.03±15.9	35.31±17.0	49.01±16.0	35.49±12.4	86.06±55.3	68.61±54.5	19.31±6.0
Hemiptera	7.77±6.9	6.75±2.5	40.26±30.8	3.97±3.5	2.75±1.1	23.74±20.9	2.77±2.7
Coleoptera	0.41±0.1	1.71±1.0	1.43±0.7	4.68±3.7	2.17±1.3	2.04±1.5	1.68±0.3
Isoptera	0.00	7.20±3.6	3.63±1.8	0.00	0.00	0.00	0.00
Other	6.96±6.8	2.59±1.3	9.18±2.7	5.93±2.9	5.32±3.4	1.22±0.6	5.66±7.3

Appendix 8 Insect biomass in proportion of major diet group in each habitat type at Hat Yai, Songkhla between February 2014 to March 2015.
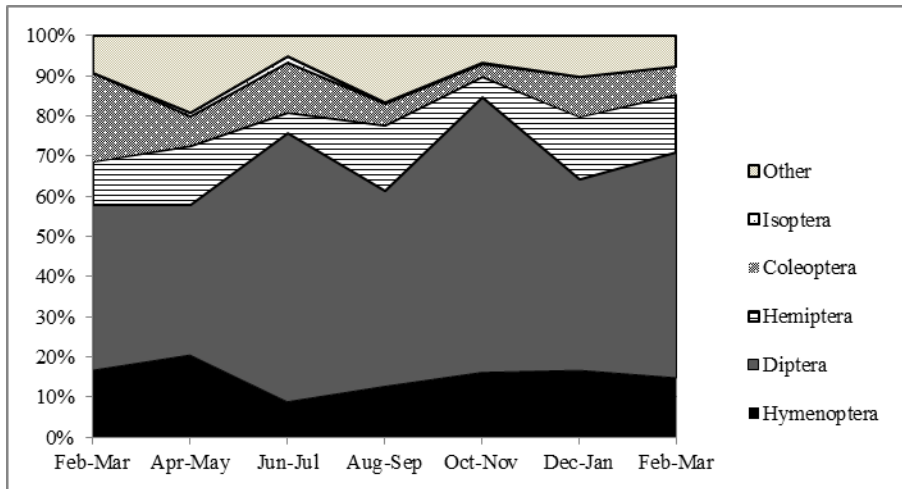

A. Forest

B. Open paddy land

C. Tree-dominated agricultural land

Appendix 8 (continue)

D. Urban
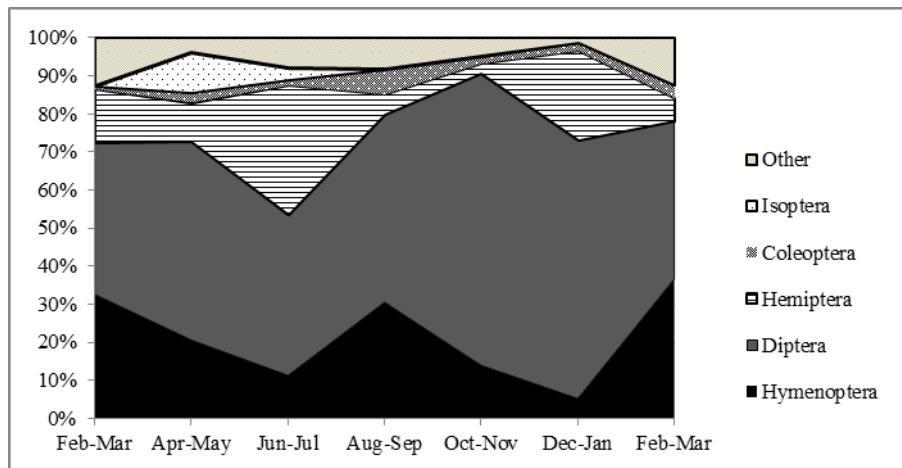
E. Water bodies

Appendix 9 Number of individuals, insect biomass per trap site of 3,000 cm^2 sticky
trap in major foraging habitat (mean±SD) and rainfall within swiftlet potential range
in the western coast and eastern coast of peninsular Thailand between August 2014 to
September 2015.

Sampling month	Isect abundance (no./trap site)		Insect biomass (mg/trap site)		Rainfall observe (mm/month)		Rainfall (2005-2014) (mm/month)	
	West	East	West	East	West	East	West	East
Aug 2014	54.0±3.6	84.8±10.3	33.8±11.1	49.2±11.9	274.8	110.7	246.9	117.2
Sep 2014	86.5±17.6	120.5±102.5	42.9±40.9	69.5±33.7	274.8	339.0	246.9	284.1
Oct 2014	113.5±7.8	128.5±5.3	71.1±5.1	42.1±36.5	292.7	379.5	260.0	478.1
Nov 2014	106.0±16.2	142.8±51.6	60.9±5.8	60.4±9.1	231.7	462.0	259.4	632.4
Dec 2014	123.0±21.5	108.8±25.1	51.1±18.3	49.0±10.1	208.3	572.3	154.5	521.1
Jan 2015	77.0±3.0	88.5±37.8	27.6±22.6	26.2±4.4	26.0	406.0	52.9	432.9
Feb 2015	96.0±28.3	109.0±43.8	42.0±19.6	33.8±26.3	0.9	31.8	25.7	124.7
Mar 2015	159.5±115.2	159.5±37.8	75.9±32.5	38.6±13.5	10.0	3.0	123.2	153.4
Apr 2015	60.0±42.4	110.8±2.8	70.4±20.9	89.2±9.5	91.6	138.4	180.1	130.1
May 2015	41.5±4.9	112.0±82.0	49.7±19.8	32.5±16.3	209.7	100.8	199.5	138.8
Jun 2015	48.0±8.2	129.0±12.0	28.5±.7	60.2±8.5	163.4	99.8	220.6	108.9
Jul 2015	79.0±8.5	73.3±57.6	65.2±26.2	35.5±13.4	449.8	95.3	252.9	89.8
Aug 2015	59.5±17.2	158.8±71.1	58.8±17.2	57.4±38.0	355.9	199.9	220.2	104.9
Sep 2015	81.3±14.8	165.5±21.3	67.5±20.4	85.8±52.0	348.3	116.8	246.9	117.2

Appendix 10 Sample of climate data was hourly recorded inside the swiftlets house farm at Trang colony throughout the study.
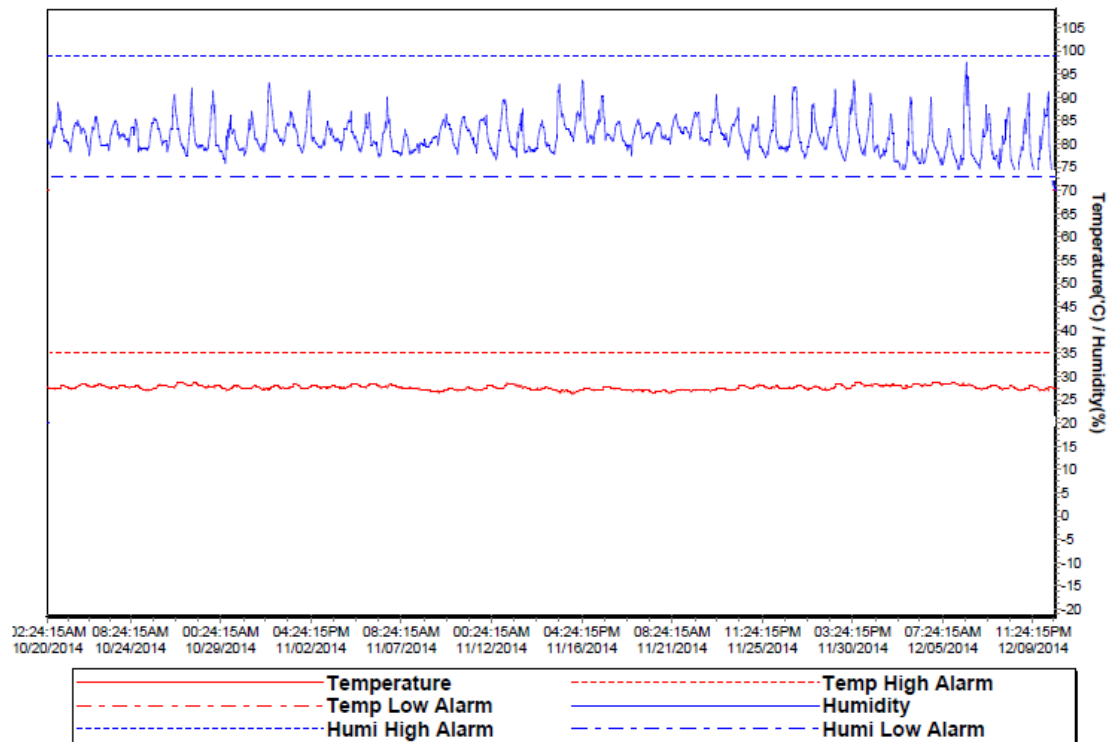
Appendix 11 Published paper.

 "Petkliang, N. Gale, G.A. Brunton, D.H. and Bumrungsri, S. (2017). Wetland, forest and open paddy land are the key foraging habitats for Germain's swiftlet (*Aerodramus inexpectatus germani*) in southern Thailand. *Tropical Conservation Science.* 10, 1-12."

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

SAGE

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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.

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 (Grüebler, 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; Nguyên 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; Grüebler 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, & Tscharntke, 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
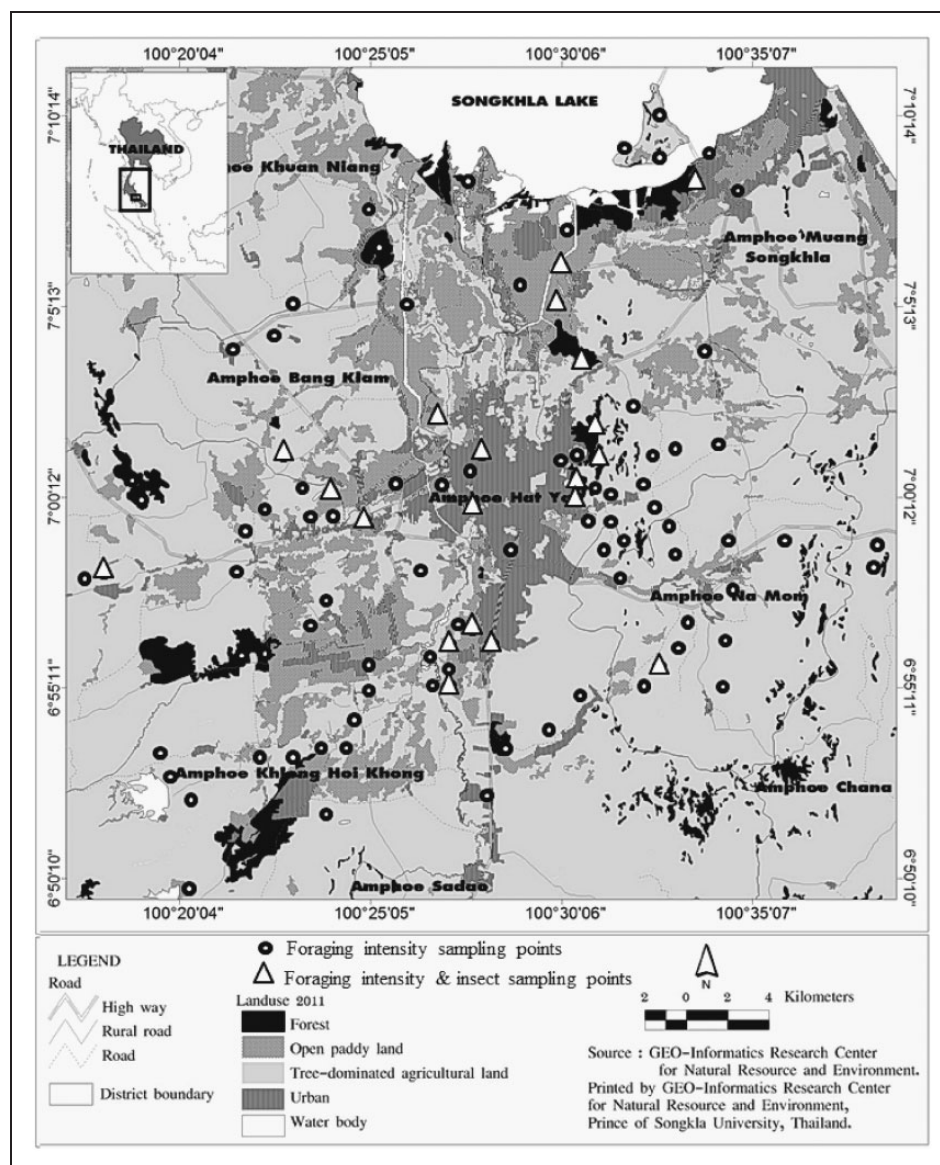
Figure 1. Map of 100 sampling points, which included 80 swiftlet foraging intensity sampling points and 20 sampling points which in addition to swiftlet foraging intensity samples, also included insect sampling, covering all five habitat types noted in the legend within a 40 × 40 km block covering the 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	$n = 12$	$n = 12$	$n = 12$	$n = 12$	$n = 12$
Prey capture attempts per habitat	$n = 12$	$n = 12$	$n = 52$	$n = 12$	$n = 12$
Insect biomass	$n = 4$	$n = 4$	$n = 4$	$n = 4$	$n = 4$

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 cm^2 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).
*$p < 0.05$; **$p < 0.001$.
[a]Indicates 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
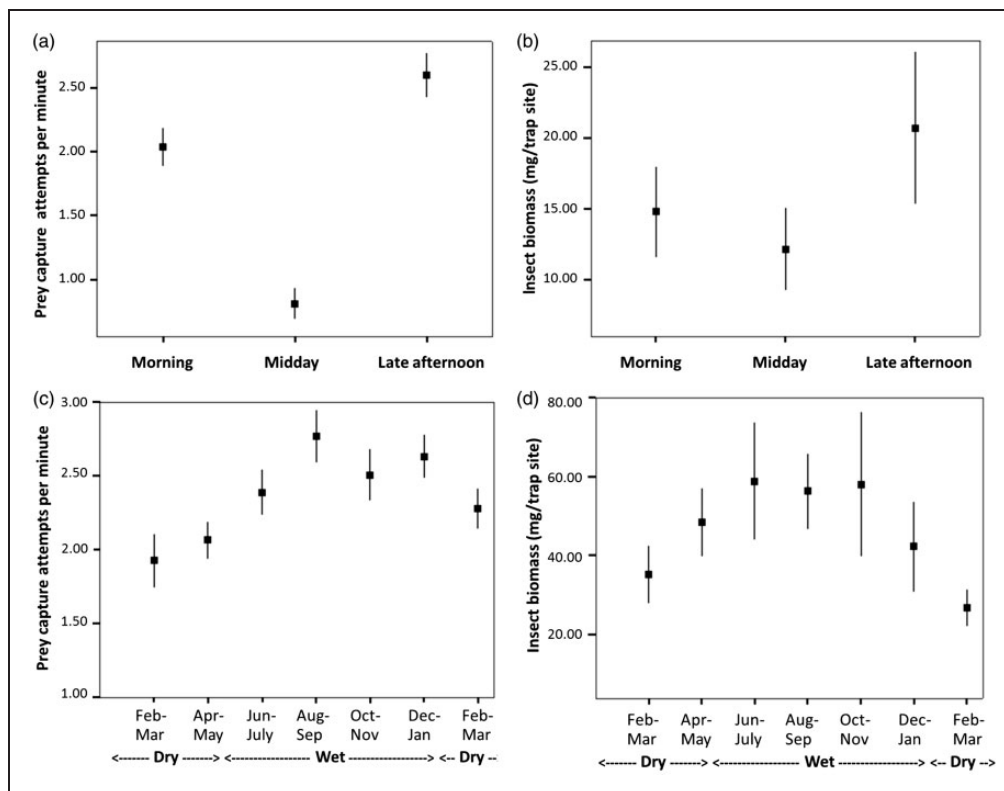
Figure 2. Temporal variation (February 2014 to March 2015) in prey capture attempts: diurnal differences in (a) average number of swiftlet prey capture attempts per minute (mean ± 2 SE) of 540 observations and (b) the average insect biomass in mg per trap site (180 traps opened for 4 hr of sampling, 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).
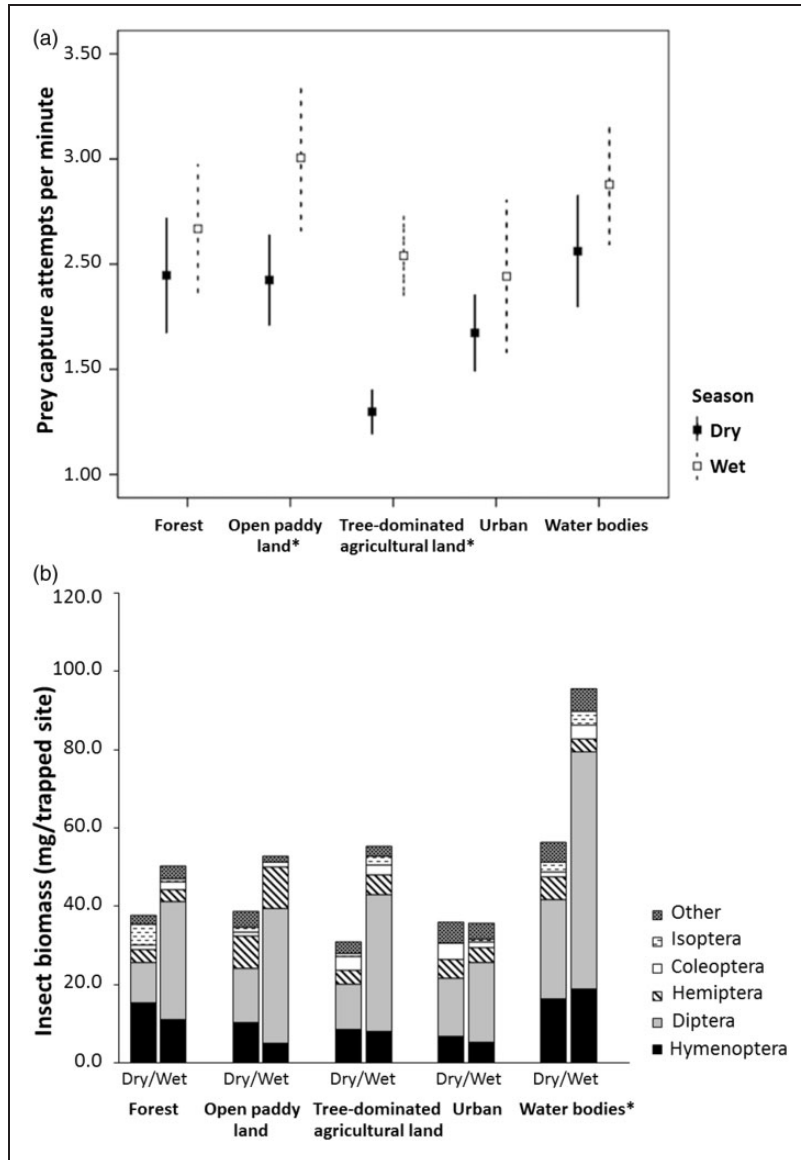
Figure 3. (a) The average number of swiftlet prey capture attempts per minute (mean ± 2 SE) showing significantly more attempts during the wet than dry in open paddy land and tree-dominated agricultural land ($p < .001$) and (b) the average insect biomass in mg per trap site (2,400 cm² trapping area) 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, Hearns, & 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 (Nguyên 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, & Tscharntke, 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-swarming 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).
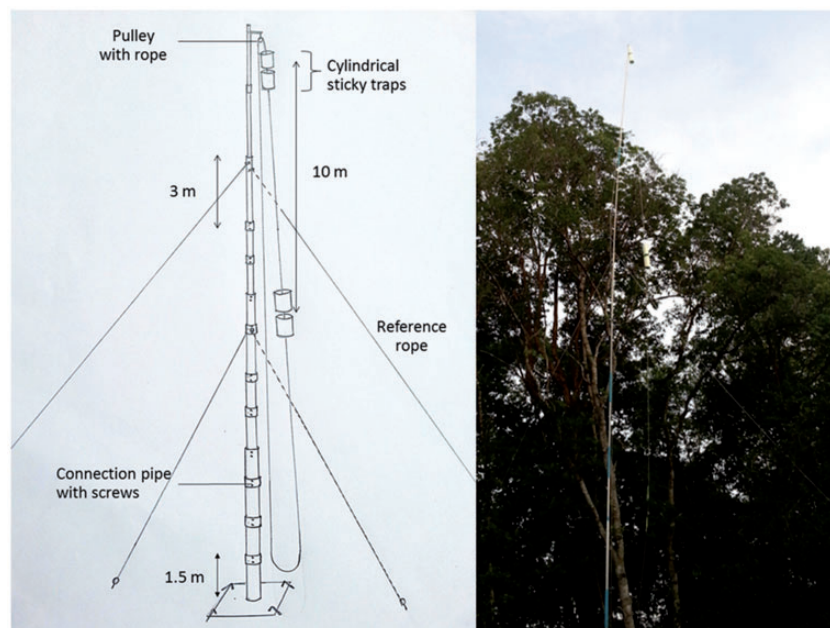
Implications for Conservation

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 cm^2 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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