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Foraging patterns reveal niche separation in tropical insectivorous birds

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Abstract. The study examines the uses of attack maneuvers and foraging substrates by ten insectivorous passerine birds to explain how these trophically similar species can coexist in the same habitat, a central question in ecology. Information on the foraging height, attack maneuvers, substrate and foliage density was collected independently for each foraging bird. Sallying was the most frequently used attack maneuver, and leaves were the most frequently used substrate. Statistical analyses showed that the variation in the foraging data was significantly influenced by foraging height, followed by attack maneuver, substrate, and lastly foliage density. The foraging height, the parameters of the attack maneuvers and substrate effectively divided the birds into three foraging guilds: (1) 'High-sally insectivores' — birds that foraged in higher strata using sallying tactics, namely Arctic Warbler *Phylloscopus borealis*, Black-naped Monarch *Hypothymis azurea*, Asian Paradise-flycatcher *Terpsiphone paradisi* and Asian Brown Flycatcher *Muscicapa dauurica*; (2) 'High-foliage insectivores' — birds that foraged in higher strata using glean-stretch-hang tactics, namely White-bellied Erpornis *Erpornis zantholeuca*, Green Iora *Aegithina viridissima*, and Pin-striped Tit-babbler *Macronous gularis*; and (3) 'Understory insectivores' — birds that foraged in lower strata, namely Abbott's Babbler *Malacocincla abbotti*, Chestnut-winged Babbler *Stachyris erythroptera*, and Rufescent Prinia *Prinia rufescens*. Except for Asian Paradise-flycatcher and Asian Brown Flycatcher, no other two species used similar foraging heights, substrates and attack maneuvers at the same time. However, the use of foliage density differed significantly between these two species. Therefore this parameter should also be taken into consideration in analysis of foraging niche in tropical birds.

Key words: behaviour, feeding ecology, insectivores, limestone habitats, tropical forest

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INTRODUCTION

The loss of tropical forests represents one of the greatest threats to the global bird diversity (Niesten et al. 2004). Removal of some microhabitat components, such as curled leaves, dead trees and ant swarms, owing to forest destruction may affect insectivorous birds, particularly their foraging patterns (Ford et al. 2001). Studies of foraging ecology provide an understanding of the ways in which ecologically different species partition their resources in a habitat and may reveal how guilds of forest birds respond to disturbance. Resource partitioning reduces the competition rates by decreasing the amount of niche overlaps between the competitor species (Wiens 1989) and thus allows for the existence of the great species diversity. This niche partitioning allows them to coexist in the same geographical area (Kwok 2009).

Generally, insectivorous birds have high habitat specificity and are more confined to the forest interior than other avian feeding guilds, especially in the tropical forest (Canaday 1996). In addition, insectivorous birds are more specialized (Snow 1976) and sensitive to microclimate changes (Karr & Freemark 1983). Unlike fruits, flowers and seeds, insects actively avoid the birds and, as a result, insectivorous birds have developed numerous specialized niches and seek prey on preferred microhabitats (Sekercioglu et al. 2002). The use of foraging substrate and the attack manoeuvres may be different by trophically similar, specialized species (Holmes & Robinson 1988).

The foraging ecology of birds has been intensively studied since the beginning of 1980s (Robinson & Holmes 1982). However, the knowledge on the foraging ecology of tropical birds is incomplete, particularly in the Southeast Asia. Tropical birds vary in size and are easy to detect owing to their often loud vocals and distinctive colours. The babblers (Timaliidae), crows (Corvidae), flycatchers (Muscicapidae), woodpeckers (Picidae), and trogons (Trogonidae) are the keys of Malaysian insectivorous birds (Yong et al. 2011). Perch size, substrate, attack maneuvers and foraging height were important variables to separate the foraging niche of Malaysian woodpeckers (Styring & Zakaria 2004). Foraging tactics of non-passerine insectivores like woodpeckers may differ from passerine insectivores (Hartung & Brawn 2005). The objective of this study is to determine the foraging patterns of common insectivorous passerine birds in Malaysian tropical forest, to understand how they can coexist in the same habitat.

MATERIALS AND METHODS

Study sites

The field work was conducted on ordinary soils near the Bukit Kepala Gajah limestone area in Lenggong, Perak in northern of Peninsular Malaysia from July 2010 to July 2011. This study includes both breeding and migrating seasons. The area is located between 5°7.957'N 100°58.432'E and 5°7.728′N 100°58.410′E (Fig. 1). Bukit Kepala

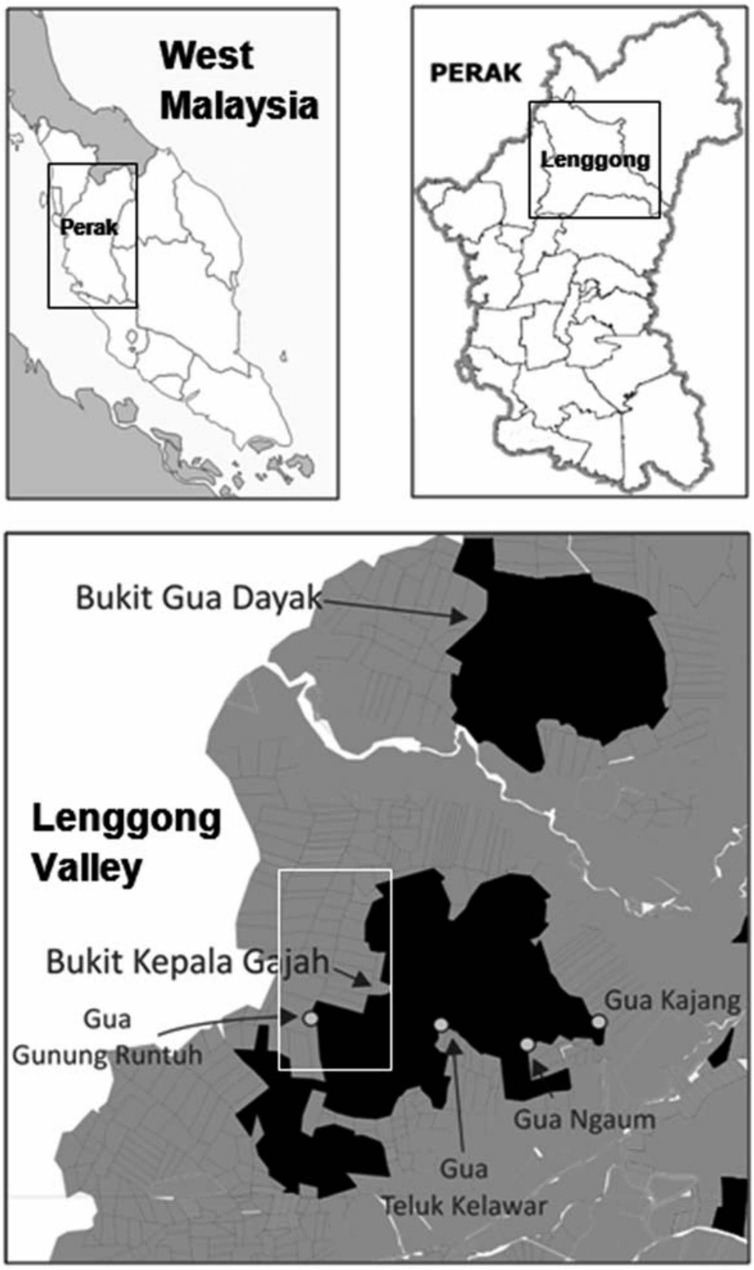

Fig. 1. Location of Lenggong Valley, Perak and the study site Bukit Kepala Gajah area. Black — limestone outcrop.

Gajah, one of eight limestone hills in the Lenggong Valley, is approximately 150 m above sea level and approximately 3 km north of Lenggong town. The climate is hot and humid throughout the year with very little variation, with temperatures of about 30 °C to 33 °C and high relative humidity of between 80% and 90% (Chia & Majid 2002). The vegetation of the study area represents a mixture of lowland dipterocarp forest, orchards, secondary forest, and includes limestone habitat, which is believed to be relatively untouched area used by the birds as roosting or refuge site. The Sungai Gelok river and several caves are found in the area. The wild ginger *Etlingera littoralis* and banana plants *Musa acuminata* are widespread along the forest edge. Some clearing occurred in the forest edge, and the area is adjacent to the rubber plantation and orchard habitat, but the interior zone consists of a dense tropical forest.

Field methods

Ten common species of insectivorous birds were located visually and randomly along a forest trail, and followed opportunistically. Observations were performed between 0730 and 1830 h. Birds were observed as long as they could be kept in view, but only the initial (independent) observations, first sighting of an individual bird, were used for statistical analysis to avoid problems with non-independent data. Observations for each foraging bird were made using 8 × 42 binoculars, recorded on voice recorder, and later transcribed to data spreadsheets. At least 30 independent observations were taken for each bird species to represent the observed behavior accurately (Morisson 1984, MacNally 1994). Observations were not made on mixed-species flocks because membership in a mixed-species flock affects the independence of data on the foraging ecology of birds (Sridhar et al. 2009).

The following data were recorded on each foraging bird encountered opportunistically: estimated height above the ground, foraging substrate, attack maneuver, and foliage density.

Foraging height. The study defined eight height categories (strata): ground, 0–2 m, 2–4 m, 4–6 m, 6–8 m, 8–10 m, 10–12 m and > 12 m. A foraging height is the height level from which a food item is taken by the birds. Selected trees were height-marked for use as references for standardization, following Somasundaram & Vijayan (2008).

Foraging substrate. A foraging substrate is the material (microhabitat) from which a food item is taken by the birds. A total of 11 substrates were identified in the study area. These substrates were the leaf surface, the underside of the leaf, the surface of branches > 2 cm in diameter, the underside of branches > 2 cm in diameter, the surface of branches < 2 cm in diameter, the underside of branches < 2 cm in diameter, the trunk, twigs, dead tree parts (dead leaves, dead branches), leaf litter, and air.

Attack maneuver. The attack maneuver is a method on how the food items taken (attack) by the birds (Table 1). The terminology and strategy used to characterize attack maneuvers follows Remsen & Robinson (1990).

Foliage density. This parameter was measured on a subjective scale from 0–5 in a 1-m diameter sphere around the bird, following modified Braun-Blanquet (1932) cover abundance scale as described by Allen & McLennan (1983), Allen (1993), Bowes et al. (1994), and Hurst a& Allen (2007). A bird in the densest foliage cover received a score of 5.

Statistical analysis

Two multivariate analyses were performed on raw foraging data to extract 'patterns' (i.e., linear combinations of raw variables that characterize foraging behaviour). PCA is a method that reduces data by forming linear combinations of variables and summarizes it into new synthetic variables (called principal components). Correspondence analysis is a technique similar to PCA, but it is effective in plotting the numerical data and detecting similarities between the rows and columns of a data matrix; correspondence analysis was found to explain more variation in foraging data than other

Table 1. Description of attack maneuvers used in this study (after Remsen & Robinson 1990).

Attack maneuvers	Description
Glean	To pick food from a nearby substrate. Can be reached without full extension of legs or neck
Stretch	To completely extend the legs and neck to reach the food items
Hang	To hang head down in order to reach food not obtainable by any other perched position
Hover	To maintain an airborne position by flapping wings and spreading tail
Sally	To fly from a perch to attack a food item and then return to a perch

multivariate methods (Miles 1990). A hierarchical cluster analysis using Pearson's correlation coefficients was used to group the species into distinctive guilds based on the frequency of use of all foraging parameters. The Pearson correlation coefficient was also used to examine niche overlap among the species studied. Ecological Simulation (EcoSim 7.71; Acquired Intelligence Inc., Jericho, USA) was used to calculate mean niche overlap of species on the foraging parameters. PCA was performed using the SPSS (ver. 17.0; SPSS Inc., Chicago, USA), while correspondence analysis was performed with the Multivariate Statistical Package (MVSP 3.13; Kovach Computing Services, Wales).

RESULTS

A total of 613 independent observations were made on 10 common passerine bird species found in the study area. The species studied were White-bellied Erpornis *Erpornis zantholeuca*, Asian Paradise-flycatcher *Terpsiphone paradisi*, Black-naped Monarch *Hypothymis azurea*, Green Iora *Aegithina viridissima*, Asian Brown Flycatcher *Muscicapa dauurica*, Arctic Warbler *Phylloscopus borealis*, Pin-striped Tit-babbler *Macronous gularis*, Chestnut-winged Babbler *Stachyris erythroptera*, Abbott's Babbler *Malacocincla abbotti*, and Rufescent Prinia *Prinia rufescens*. These species feed primarily on insects and other small invertebrates (Wells 2007, Robson 2008). Asian Brown Flycatcher and Arctic Warbler are migratory species and are present in the study area between September and May. However, foraging activity of resident species was not significantly affected by the presence of migrant species. Foraging patterns of resident species were significantly correlated throughout study periods (breeding and migrating seasons) in terms of foraging height ($r = 0.964$, $p = 0.000$), foraging substrates ($r = 0.965$, $p = 0.000$), attack maneuvers ($r = 0.991$, $p = 0.000$), and foliage density ($r = 0.948$, $p = 0.000$). Therefore, data collected over the two periods were pooled.

Foraging height

The birds used all of the selected strata. Foraging height the most frequently used by birds belongs to the class 10–12 m (25.12%), followed by 0–2 m (23.98%), > 12 m (23.82%), 8–10 m (14.03%), 6–8 m (5.71%), 2–4 m (4.08%), 4–6 m (2.77%) and ground (0.49%) (Table 2). Of 10 bird species, only Chestnut-winged Babbler, Abbott's Babbler, and Rufescent Prinia always foraged in a lower stratum (0–2 m), whereas other species foraged mainly at higher levels and showed variation in the use of different strata.

Attack maneuvers

All five attack maneuvers were used by foraging birds (Table 3). Asian Brown Flycatcher, Asian Paradise-flycatcher and Black-naped Monarch consistently used sallying to obtain food. Stretching was used frequently by four species: Green Iora, Pin-striped Tit-babbler, Chestnut-winged Babbler, and Rufescent Prinia. Abbott's Babbler used gleaning frequently, White-bellied Erpornis specialized in hanging, and Arctic Warbler showed variation in the use of foraging methods (sallying, hovering, stretching, gleaning).

Foraging substrates

Six species of birds (White-bellied Erpornis, Black-naped Monarch, Green Iora, Arctic Warbler, Pin-striped Tit-babbler, and Rufescent Prinia) foraged

Table 2. Foraging height of ten studied species of insectivorous passerines. N — sample size, data are given as percentages (%).

Species	Height (m)								N
	Ground	0–2	2–4	4–6	6–8	8–10	10–12	> 12	
White-bellied Erpornis	0.00	0.00	0.00	5.00	10.00	20.00	50.00	15.00	40
Asian Paradise-flycatcher	0.00	1.79	1.79	3.57	10.71	21.43	41.07	19.64	56
Black-naped Monarch	0.00	0.00	7.69	12.82	10.26	35.90	12.82	20.51	39
Green Iora	0.00	0.00	0.00	0.00	7.04	8.45	35.21	49.30	71
Asian Brown Flycatcher	0.00	0.00	1.10	1.10	6.59	25.27	37.36	28.57	91
Arctic Warbler	0.00	3.41	3.41	2.27	0.00	13.64	20.45	56.82	88
Pin-striped Tit-babbler	0.00	3.08	3.08	4.62	15.38	15.38	43.08	15.38	65
Chestnut-winged Babbler	0.00	81.82	14.14	2.02	0.00	1.01	1.01	0.00	99
Abbott's Babbler	9.68	87.10	3.23	0.00	0.00	0.00	0.00	0.00	31
Rufescent Prinia	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	33

Table 3. Attack maneuver for ten studied species of insectivorous passerines (see Table 1 for description). N — sample size, data are given as percentages (%).

Species	Attack maneuver					N
	Glean	Stretch	Hover	Sally	Hang	
White-bellied Erpornis	17.50	12.50	2.50	12.50	55.00	40
Asian Paradise-flycatcher	0.00	0.00	16.07	83.93	0.00	56
Black-naped Monarch	2.56	2.56	5.13	84.62	5.13	39
Green Iora	33.80	54.93	0.00	4.23	7.04	71
Asian Brown Flycatcher	1.10	1.10	8.79	89.01	0.00	91
Arctic Warbler	12.50	15.91	28.41	39.77	3.41	88
Pin-striped Tit-babbler	36.92	53.85	0.00	1.54	7.69	65
Chestnut-winged Babbler	32.32	55.56	0.00	0.00	12.12	99
Abbott's Babbler	70.97	22.58	0.00	6.45	0.00	31
Rufescent Prinia	33.33	51.52	3.03	9.09	3.03	33

primarily on the undersides of leaves. Asian Paradise-flycatcher foraged mainly in the air, whereas both Chestnut-winged Babbler and Abbott's Babbler consistently used dead tree parts. Asian Brown Flycatcher fed frequently in the air and on foliage (the leaf surface and the underside of the leaf)(Table 4).

Foliage density

Intermediate-density foliage (3 on this scale) was predominantly used by most species (White-bellied Erpornis, Black-naped Monarch, Green Iora, Arctic Warbler, Pin-striped Tit-babbler, Chestnut-winged Babbler, Abbott's Babbler)(Table 5). A foliage density of 2 was frequently used by Asian Brown Flycatcher. Rufescent Prinia always used the lowest-density foliage (1 on the scale), and Asian Paradise-flycatcher showed variation in the use foliage density.

Potential niche overlap

The principal component analysis yielded three components that explained 84% of the variation in all foraging parameter data (Table 6, 7). PC1 explained 31% of the data variation and was weighted on attack maneuvers. PC2 explained 29% of the data variation and was weighted on foraging substrate. PC3 explained 24% of the data variation and was weighted on foraging height.

Correspondence analysis of the foraging parameters yielded two dimensions that together explained 64% of the variation in the data (Fig. 2). Axis 1 explained 46% of the data variation was weighted on foraging height. Axis 2 explained 18% of the data variation was weighted on foraging substrate. The Pearson's correlation coefficient grouped the bird species that were significantly correlated for any foraging parameter: Group 1: Rufescent Prinia, Chestnut-winged Babbler, and Abbott's Babbler; Group 2: White-bellied Erpornis, Green Iora, and Pin-striped Tit-babbler; Group 3: Arctic Warbler, Black-naped Monarch, Asian Brown Flycatcher, and Asian Paradise-flycatcher.

In the cluster analysis, foraging height was important at the base of the cluster diagram and divided birds that used lower strata (Chestnut-

Table 5. Foliage density classes for ten studied species of insectivorous passerines (where 5 is the most dense foliage). N — sample size, data are given as percentages (%).

Species	Foliage density class						N
	0	1	2	3	4	5	
White-bellied Erpornis	0.00	0.00	32.50	55.00	12.50	0.00	40
Asian Paradise-flycatcher	14.29	14.29	26.79	25.00	19.64	0.00	56
Black-naped Monarch	0.00	15.38	28.21	46.15	10.26	0.00	39
Green Iora	0.00	5.63	21.13	61.97	8.45	2.82	71
Asian Brown Flycatcher	12.09	18.68	41.76	21.98	5.49	0.00	91
Arctic Warbler	1.14	11.36	31.82	52.27	2.27	1.14	88
Pin-striped Tit-babbler	0.00	0.00	9.23	60.00	18.46	12.31	65
Chestnut-winged Babbler	0.00	0.00	12.12	46.46	35.35	6.06	99
Abbott's Babbler	0.00	0.00	9.68	54.84	29.03	6.45	31
Rufescent Prinia	0.00	69.70	18.18	12.12	0.00	0.00	33

Table 4. Foraging substrate of ten studied species of insectivorous passerines. N — sample size, data are given as percentages (%).

Species	substrate										
	Leaf		> 2-cm branch		< 2-cm branch		Trunk	Twigs	Dead (leaves, branches	Leaf litter	Air
	surface	underside	surface	underside	surface	underside					
White-bellied Erpornis	27.50	57.50	0.00	0.00	2.50	2.50	0.00	2.50	7.50	0.00	0.00
Asian Paradise-flycatcher	14.29	19.64	0.00	1.79	0.00	0.00	1.79	0.00	0.00	0.00	62.50
Black-naped Monarch	23.08	41.03	0.00	0.00	7.69	2.56	0.00	5.13	2.56	0.00	17.95
Green Iora	35.21	50.70	0.00	0.00	0.00	0.00	0.00	14.08	0.00	0.00	0.00
Asian Brown Flycatcher	21.98	24.18	0.00	0.00	0.00	1.10	1.10	4.40	1.10	0.00	46.15
Arctic Warbler	28.41	43.18	2.27	1.14	2.27	0.00	0.00	11.36	3.41	0.00	7.95
Pin-striped Tit-babbler	27.69	32.31	1.54	3.08	4.62	0.00	1.54	3.08	26.15	0.00	0.00
Chestnut-winged Babbler	5.05	12.12	0.00	0.00	0.00	0.00	0.00	0.00	82.83	0.00	0.00
Abbott's Babbler	12.90	9.68	0.00	0.00	6.45	0.00	0.00	6.45	58.06	6.45	0.00
Rufescent Prinia	42.42	48.48	0.00	0.00	0.00	0.00	0.00	6.06	3.03	0.00	0.00

winged Babbler, Abbott's Babbler, Rufescent Prinia) from those that used higher strata (Fig. 3). At the next set of branches in the diagram, attack maneuver was an important variable for subdividing the height-preference groups into more specific groups based on foraging-method preferences. The cluster analysis separated the species that used sallying (Asian Brown Flycatcher, Asian Paradise-flycatcher, Black-naped Monarch, and Arctic Warbler) from those that used gleaning, stretching and hanging (White-bellied Erpornis, Green Iora, and Pin-striped Tit-babbler). At the terminal branches of the diagram, both foraging height and attack maneuver were important parameters for separating the bird species. Lastly, the foliage density was useful parameter for separating the niche of Asian Paradise-flycatcher and Asian Brown Flycatcher. In general, the analyses (principal component analysis, correspondence analysis, and cluster analysis) reveal that species studied differ primarily by the foraging height, followed by the attack maneuvers, the foraging substrate, and, lastly, the foliage density.

DISCUSSION

The study showed that the insectivorous birds observed at the study site exhibited a range of foraging strategies. The degree of niche overlap among insectivores differed for many species, with respect to foraging parameters, namely foraging height, substrate and attack maneuver. The highest mean niche overlap between species on the three foraging parameters was recorded for Asian Paradise-flycatcher and Asian Brown Flycatcher. Except for these species, no other pairs of species used similar foraging heights, substrates and attack maneuvers at the same time. However, the use of foliage density differed significantly between these two species — Asian Paradise-flycatcher showed variation in the use foliage density, while Asian Brown Flycatcher preferred at low densities (2 on the scale used in this work). Most previous studies did not consider foliage density (Somasundaram & Vijayan 2008, Kwok 2009). Foliage density may not have been considered to be as important as foraging height, substrate or attack maneuvers. This parameter should be included, because species differ in their selection of dense vegetation vs. more open habitats (Sillet 1994). Different body size may also be a factor that allows Asian Paradise-flycatcher and Asian Brown Flycatcher to have highest mean niche overlap.

Table 6. Total variance explained. Eigenvalues and cumulative percentage.

Component	Initial Eigenvalues			Extraction Loadings	Sums of Squared		Rotation Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	4.124	41.236	41.236	4.124	41.236	41.236	3.105	31.052	31.052
2	2.943	29.434	70.67	2.943	29.434	70.67	2.884	28.836	59.889
3	1.306	13.058	83.729	1.306	13.058	83.729	2.384	23.84	83.729
4	0.642	6.424	90.152						
5	0.375	3.749	93.902						
6	0.284	2.837	96.739						
7	0.157	1.569	98.308						
8	0.116	1.159	99.468						
9	0.03	0.3	99.768						
10	0.023	0.232	100						

Table 7. Component variable loadings for each species based on foraging parameters (height, substrate, attack manoeuvre and foliage density).

	Component		
	1	2	3
Rufescent Prinia	0.082	0.081	0.756
Pin-striped Tit-babbler	-0.021	0.868	0.333
Asian Brown Flycatcher	0.973	0.11	-0.091
Black-naped Monarch	0.889	0.285	-0.003
Asian Paradise-flycatcher	0.942	0.035	-0.09
Green Iora	0.141	0.927	0.177
Chestnut-winged Babbler	-0.165	0.163	0.899
Arctic Warbler	0.603	0.658	0.042
Abbott's Babbler	-0.102	0.14	0.919
White-bellied Erpornis	0.23	0.831	0.002

Size of insect taken by these species varies with body size and may lead to niche separation (Johnston 1971). Additional parameters like diets and tree preferences of birds could be valuable in the foraging ecology study to provide a more complete assessment that organizes the structure of bird community.

Leaves were the substrate most frequently searched by insectivorous birds. The use of leaves as a foraging substrate is probably related to the photosynthetic products and nutrients present in the leaves (Laxton 2005, Kwok 2009) because these resources may attract more insects to forage on the leaves and thus attract more birds. However, the underside of leaves was used more frequently than the leaf surface, probably because some insects and their larvae tend to hide and feed on the undersides of leaves to protect themselves from the sun (Remsen & Parker 1984, Thiollay 1992).

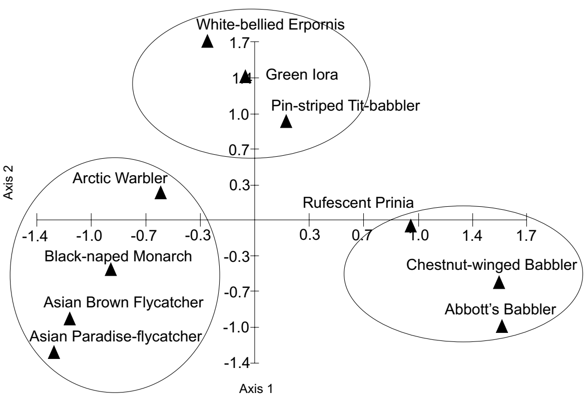

Fig. 2. Correspondence plot of foraging variables (foraging height, substrate, attack maneuver, foliage density). Ellipses indicate groups of bird species that were significantly correlated ($p < 0.01$) for any parameter according to a Pearson's correlation analysis.

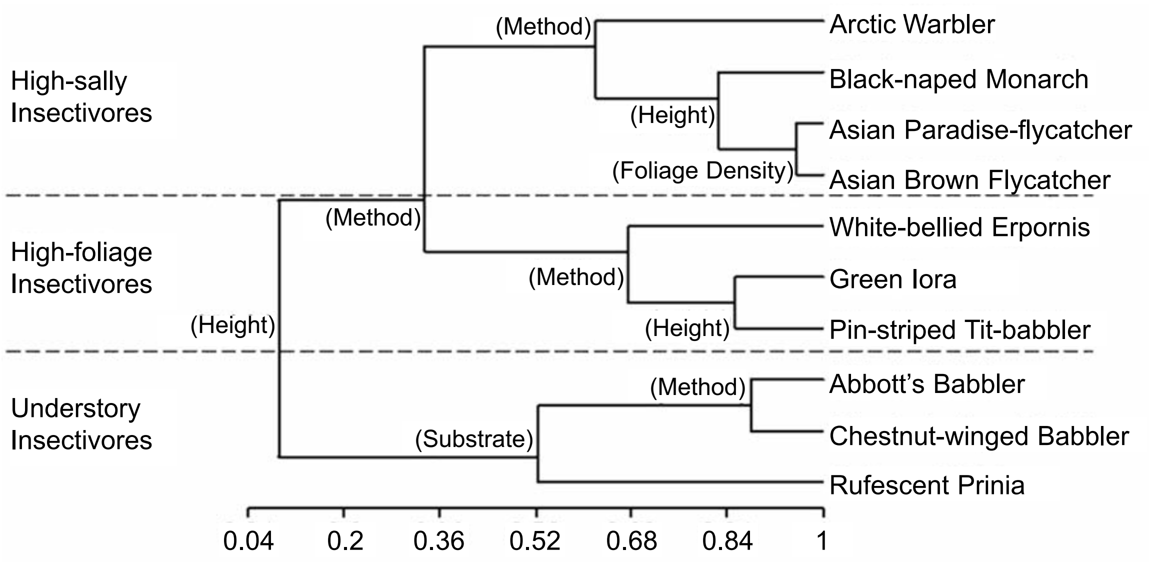

Fig. 3. Interspecific relationships of 10 insectivorous bird species, based on multivariate analyses of foraging height, attack maneuver, substrate and foliage density.

Niche separation among bird species clearly explains the groups found by the cluster analysis. These groupings illustrate the guild structure found in this study. The observed foraging heights, attack maneuvers, and foraging substrate effectively served to divide the birds into three primary foraging guilds: (1) 'High-sally insectivores' — birds that foraged in higher strata and used sallying tactics (Asian Paradise-flycatcher, Black-naped Monarch, Arctic Warbler, Asian Brown Flycatcher); (2) 'High-foliage insectivores' — birds that foraged leaves in higher strata using glean-stretch-hang tactics (White-bellied Erpornis, Green Iora, Pin-striped Tit-babbler); and (3) 'Understory insectivores' — birds that foraged in lower strata (Chestnut-winged Babbler, Abbott's Babbler, Rufescent Prinia). The presence of foraging height at the base of the cluster analysis diagram highlights the importance of this variable in the study area and stresses the importance of maintenance of a multi-level forest which provides more 'trophical space' for birds and thus allows for existence of a larger number of species. The importance of the foraging height probably reflects the distributions of insects at different heights (Gokula & Vijayan 2000). In general, the pattern of usage of foraging height by birds probably reflects the availability of food resources, the morphology of the birds and interspecific competition (Loyn 2002). The attack maneuvers and the foraging substrate effectively grouped the birds more specifically within the larger groups defined by the foraging height. Birds show special morphological adaptations that correspond to specialized attack maneuvers used to forage on particular substrates. Species-specific morphology may thus limit the usage of attack maneuvers and foraging substrates (Rolando & Robotti 1985). This information also suggests that substrate and attack maneuver parameters may contribute significantly to the specializations of certain birds.

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STRESZCZENIE

[Ekologia żerowania tropikalnych ptaków owadożernych]

Badania nad różnorodnymi zagadnieniami związanymi ze zdobywaniem pokarmu prowadzą do określenia jak różne gatunki dzielą istniejące zasoby i przez co mogą współwystępować w danym środowisku. Ekologia żerowania ptaków występujących w tropikach południowo-wschodniej Azji nie została jak dotąd dobrze zbadana, a informacje takie mogą pokazywać jak poszczególne grupy troficzne mogą reagować na zmiany zachodzące w środowisku.

Badania prowadzono w Malezji, na terenach wzgórz wapiennych doliny Lenggong (Fig. 1). Teren badań obejmował zarówno wilgotne lasy równikowe, jak i lasy wtórne, plantacje i ogrody. Obserwacjami objęto 10 gatunków ptaków owadożernych należących do rzędu wróblowych. Były to: czupurnik zielonawy, tymalia żółtobrzucha, cierniodziób modrooki, dżunglak skromny (z rodziny tymaliowatych), muchodławka rajska, monarszyk hiacyntowy (rodz. monarkowate), paskownik zielony (rodz. turkuśniki), muchołówka brunatka (rodz. muchołówki), świstunka północna i prinia rdzawa (rodz. pokrzewkowate).

Prace terenowe prowadzono od lipca 2012 do czerwca 2011, pomiędzy 7.30 a 18.30. Ptaki lokalizowano podczas wędrówek wzdłuż dróg i ścieżek. Nie zapisywano danych dla ptaków żerujących w stadach mieszanych. Tylko pierwsza obserwacja danego osobnika była wykorzystywana w dalszych analizach. Dla każdego żerującego osobnika zapisywano: szacunkową wysokość nad ziemią, miejsce żerowania, sposób zdobywania pokarmu i gęstość listowia w miejsce żerowania. Wysokość żerowania szacowano (na części drzew w terenie umieszczono oznaczenia wysokości) i zapisywano w klasach (0–2 m, 2–4, ..., 10–12, > 12 m). Miejscem żerowania określano miejsce/środowisko z którego pobierany był pokarm przez osobnika. Wyróżniono rodzajów 11 takich miejsc. Sposób zdobywania pokarmu klasyfikowano do jednej z pięciu kategorii: zbieranie, dalsze sięganie, zwisanie głową w dół, zawisanie w powietrzu i polowanie z zasiadki (Tab. 1). Dla każdego osobnika zapisywano gęstość listowia, w którym żerował (do 1 m od ptaka), przyporządkowując ją do jednej z pięciu klas, gdzie klasa 5 oznaczała najgęstsze listowie. Dla każdego gatunku zebrano co najmniej 30 niezależnych obserwacji.

Dla wszystkich gatunków zebrano łącznie 613 obserwacji. Muchołówka brunatna oraz świstunka północna są na badanym terenie gatunkami wędrownymi, ale analizy wykazały, że ich obecność nie wpływała na ekologię żerowania pozostałych, osiadłych gatunków. Ptaki żerowały najczęściej wysoko, powyżej 10 m, tylko cierniodziób modrooki, dżunglak skromny i prinia rdzawa żerowały nisko, najczęściej do wysokości 2 m (Tab. 2).

Pięć wyróżnionych technik łowieckich było wykorzystywane w różnym stopniu przez poszczególne gatunki ptaków (Tab. 3). 6 gatunków zbierało pokarm ze spodniej strony liści, muchodławka rajska i w mniejszym stopniu muchołówka brunatna łapały zdobycz w powietrzu (Tab. 4). Większość ptaków żerowała w niezbyt gęstym listowiu (klasa 3), tylko żerujące prinie rdzawe obserwowane były w miejscach najbardziej otwartych (Tab. 5).

Wykorzystując analizę składowych głównych (Tab. 6, 7), analizę korespondencyjną oraz analizę skupień badane gatunki połączono w trzy grupy (gildie)(Fig. 2, 3). Głównymi cechami, które powodowały wyróżnienie tych grup były wysokość żerowania oraz sposób polowania. Do grupy gatunków polujących z zasiadki wysoko nad ziemią zaliczono: świstunkę północną, monarszyka hiacyntowego, muchodławkę rajską oraz muchołowkę brunatną. Gatunki znajdujące pokarm wysoko w listowiu to: czupurnik zielonawy, tymalia żółtobrzucha i paskownik zielony. Natomiast grupę ptaków żerujących nisko nad ziemią stanowiły cierniodziób modrooki, dżunglak skromny oraz prinia rdzawa (Fig. 2, 3). Tylko dwa gatunki — muchołówka brunatka i muchodławka rajska — miały podobny sposób żerowania i polowały na podobnej wysokości, ale różniły się gęstością listowia, wśród którego zdobywały pokarm. Pokazuje to, że także i ten parametr, do tej pory najczęściej nie brany pod uwagę powinien być uwzględniamy w opisach niszy żerowiskowej ptaków tropikalnych.