DIVERSITY AND FORAGING BEHAVIOUR OF INSECTIVOROUS BIRDS IN LIMESTONE AREAS IN LENGGONG VALLEY, PERAK.

by

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ABBREVIATION

TREATMENTS

F	Forest
L	Logged forest
U	Unlogged forest
A	Agriculture
R	Remnant

OBSERVATION METHODS

S	Sequential observation
I	Initial observation

FORAGING PARAMETER

TP	Tree species
PT	Perch type
PS	Perch size
PH	Perch height
FH	Foraging height
AM	Attack manoeuvre
FS	Foraging substrate
FD	Foliage density
SR	Search rate
D	Diet
M	Metre

STATISTICAL ANALYSIS AND SIGNIFICANT PARAMETERS

STT	Student *t*-test
LT	Log transformation
PCA	Principal component analysis
HCA	Hierarchical cluster analysis
TT	*t*-test
CST	Chi-square test
PCC	Pearson’s correlation coefficient
DA	Discriminant analysis
GT	*G*-test
DA	Discriminant analysis
SW	Shannon-Wiener
MWUT	Mann-Whitney *U*-test
DFA	Discriminant function analysis
LA	Loglinear analysis
M	MANOVA (Multivariate Analysis of Variance)
CA	Correspondence analysis
A	ANOVA (Analysis of Variance)
KW	Kruskal-Wallis

FEEDING GUILDS

I	Insectivore
F	Frugivore
O	Omnivore
N	Nectarivore
C	Carnivore
G	Granivore

SPECIES OF INSECTIVOROUS BIRDS

WBE	White-bellied Erpornis
APF	Asian Paradise-flycatcher
BNM	Black-naped Monarch
GI	Green Iora
ABF	Asian Brown Flycatcher
AW	Arctic Warbler
PSTB	Pin-striped Tit-babbler
CWB	Chestnut-winged Babbler
AB	Abbott's Babbler
RP	Rufescent Prinia

HABITAT TYPE

GP	Gardens and parks (including wooded suburban areas)
OC	Open country (open grassy areas, scrub and tin mines)
IS	Inland freshwater swamps (mining pools, lakes and paddy fields)
MG	Mangroves
LF	Lowland rainforest (including secondary forest and forest edge)
LMF	Lower montane rainforest (including secondary forest and forest edge)
UMF	Upper montane rainforest

STATUS

R	Resident
M	Migrant
I	Introduced

INCIDENCE OF OCCURRENCE

A	Abundant
C	Common
U	Uncommon

PROTECTION BY LAW IN PENINSULAR MALAYSIA

TP	Totally protected (may not be hunted or reared in captivity)
GB	Game birds (may be hunted under license)
OPB	Other protected birds (may be reared in captivity under license)
NP	Not protected

IUCN RED LIST OF THREATENED SPECIES

LC	Least concerned
NT	Near-threatened

KEPELBAGAIAN DAN PERILAKU PENCARIAN MAKANAN BURUNG INSEKTIVOR DALAM KAWASAN BATU KAPUR DI LEMBAH LENGGONG, PERAK.

ABSTRAK

Kajian burung telah dijalankan di kawasan batu kapur Bukit Kepala Gajah di Lembah Lenggong, Perak, dari Julai 2010 hingga Julai 2011. Tujuan utama kajian adalah menerangkan corak pencarian makanan burung-burung insektivor di hutan hujan tanah rendah, dan untuk membezakan strategi pencarian makanan burung-burung insektivor di hutan berterusan dan hutan kecil yang berkelompok. Disamping itu, kajian ini juga bertujuan untuk menentukan pengaruh kaedah permerhatian awal dan berjujukan terhadap komposisi spesies burung-burung, dan mengkaji pengaruh struktur dan gangguan habitat terhadap komposisi spesies burung-burung. Kaedah persampelan jarak *point count* dan pemerhatian (awal dan berjujukan) untuk setiap burung yang mencari makanan telah digunakan dalam kajian ini. Pemerhatian untuk setiap burung-burung mencari makanan menggunakan teropong 8 × 42, direkodkan ke dalam mikro-kaset, dan kemudiannya ditranskripsikan ke dalam kertas data. Sejumlah 7789 pemerhatian telah direkodkan, mewakili 100 spesies-spesies burung daripada 28 famili. Kekayaan spesies burung-burung insektivor adalah berbeza secara signifikan antara zon-zon hutan yang dikaji, dimana burung-burung insektivor lebih banyak dijumpai di pedalaman hutan. Tiada perbezaan yang signifikan dijumpai antara kekayaan spesies di zon-zon hutan sama ada kumpulan frugivor atau gabungan kumpulan pemakanan yang lain-lain (omnivor, karnivor, nektarivor, granivor). Kajian ekologi pencarian makanan burung insektivor menyelidik bagaimana spesies-spesies yang mempunyai persamaan diet boleh wujud di habitat yang sama, soalan pusat dalam ekologi. Ketinggian dan cara serangan makanan adalah parameter penting untuk membahagikan burung-burung kepada tiga sub-persatuan utama: (1) ‘High-sally insectivores’ – burung-burung yang makan di tempat yang tinggi menggunakan cara serangan tiba-tiba; (2) ‘High-foliage insectivores’ – burung-burung yang makan di tempat yang tinggi menggunakan substrate daun; (3) ‘Understory insectivores’ – burung-burung yang makan di tempat yang rendah. Selain daripada Asian Paradise-flycatcher dan Asian Brown Flycatcher,

tiada dua spesies lain yang menggunakan sama ketinggian, substrat dan cara serangan makanan pada masa yang sama. Walaubagaimanapun, penggunaan ketumpatan dedaunan berbeza secara signifikan antara dua spesies ini. Empat spesies burung insektivor yang dikaji menunjukkan tindakbalas yang berbeza ketika mencari makanan di hutan kecil yang berkelompok, dari segi ketinggian, cara serangan makanan dan ketumpatan dedaunan. Perubahan ini mencadangkan burung-burung insektivor di Malaysia boleh bertindakbalas secara tingkahlaku terhadap kehilangan dan perubahan habitat. Pemerhatian awal memberi keputusan yang agak sama dengan pemerhatian berjujukan untuk semua parameter cara pencarian makanan. Pemerhatian berjujukan berkebolehan untuk merekod aktiviti tingkahlaku yang jarang digunakan oleh spesies-spesies ini; ketinggian dan substrat yang jarang digunakan tidak direkodkan oleh pemerhatian awal. Pemerhatian berjujukan jelas meliputi aktiviti pengambilan makanan oleh burung-burung dengan luas, tetapi hubungan antara sesi pengambilan makanan menyebabkan kaedah ini tidak bebas. Maka, hanya data pemerhatian awal sahaja yang dimasukkan dalam analisis untuk mengelakkan data yang tidak bebas. Analisis kajian ini mencadangkan sekurang-kurangnya 30 pemerhatian bebas atau 70 pemerhatian berjujukan adalah saiz sampel yang paling kurang diperlukan untuk mewakili analisis tingkahlaku pengambilan makanan.

DIVERSITY AND FORAGING BEHAVIOUR OF INSECTIVOROUS BIRDS IN LIMESTONE AREAS IN LENGGONG VALLEY, PERAK.

ABSTRACT

Bird surveys were conducted in the Bukit Kepala Gajah limestone area in Lenggong Valley, Perak from July 2010 to July 2011. The main objectives of this study were to describe the foraging patterns of insectivorous birds in lowland rainforest, and to compare the foraging strategies of insectivorous birds in the continuous and small forest patches. In addition, this study were to determine the influences of initial and sequential observation methods on foraging data of birds, and to examine the influences of habitat structure and disturbance on the bird species composition. A point-count distance sampling method and observations (initial and sequential) for each foraging bird were used in this study. Observations for each foraging bird were made using 8 × 42 binoculars, recorded on micro-cassette, and later transcribed to data sheets. A total of 7789 bird detections were recorded, representing 100 bird species belonging to 28 families. The species richness of insectivorous birds differed significantly among the forest zones sampled, with more insectivorous birds occurring in the forest interior. No significant differences were found among the zones in the species richness of either the frugivore guild or the composite of other feeding guilds (omnivores, carnivores, nectarivores, granivores). Study of the foraging ecology of insectivorous birds examines how the trophically similar species can coexist in the same habitat, a central question in ecology. The foraging height and the parameters of the attack manoeuvres effectively divided the birds into three primary subguilds: (1) ‘High-sally insectivores’ – birds that foraged in higher strata using sallying tactics; (2) ‘High-foliage insectivores’ – birds that foraged in higher strata using leaf substrate; and (3) ‘Understory insectivores’ – birds that foraged in lower strata. Except for Asian Paradise-flycatcher and Asian Brown Flycatcher, no other two species used similar foraging heights, substrates and attack manoeuvres at the same time. However, the use of foliage density differed significantly between these two species. Four focal insectivorous bird species exhibited different response in the small forest patches, in terms of foraging height, attack manoeuvres and foliage density. These changes suggest that Malaysian

insectivorous birds are able to respond behaviourally to habitat loss and alteration. Initial observation gave somewhat similar results as sequential observations for all foraging parameters. Sequential observations tends to record rare behaviour activities of studied species; infrequently used foraging height and foraging substrate were not detected by initial observation. Sequential observations apparently covered a wider range of foraging activities of birds, but the intercorrelation among foraging events cause this method are not independent. Therefore, only initial observation data can be included in analysis to avoid with non-independent data. Present analysis suggests that at least 30 independent observations or 70 sequential observations represent a minimum sample size required for analysis of foraging behaviour.

CHAPTER 1

INTRODUCTION

1.1 Background of the study

Lowland tropical rainforest supports a great proportion of bird species in the Southeast Asia (Wells, 1999; Sodhi, 2010). Over 260 of the 638 bird species recorded from both Peninsular Malaysia and Singapore are inhabitants in lowland forest, and their population may enlarge into lower montane forest (Strange & Jeyarajasingam, 1999). The cuckoos (Cuculidae), trogons (Trogonidae), hornbills (Bucerotidae), barbets (Ramphastidae), woodpeckers (Picidae), spiderhunter (Nectariniidae), flowerpeckers (Dicaeidae), bulbuls (Pycnonotidae), and babblers (Timaliidae) were key families of lowland forest birds (Wells, 1999; 2007).

However, lowland forests are currently facing massive destruction owing to agriculture and logging activities (Lambert & Collar, 2002; Peh *et al.*, 2005; Sodhi & Brook, 2006). In Peninsular Malaysia, most of the primary lowland forests have been exploited for the timber and commercial crops (Caufield, 1991). Forest biodiversity is greatly impacted by human activities such as mining operations (Clements *et al.*, 2006), agricultural colonisation (Canaday, 1997), timber extraction (Thiollay, 1992), and the hunting of wild animals (Redford, 1992). All of these impacts certainly reduce fauna diversity with degree of habitat disturbance. The loss of tropical forests represents one of the greatest threats to bird diversity globally (Niesten *et al.*, 2004).

Limestone outcrops occur infrequently throughout Southeast Asia. Approximately 400,000 square kilometres (km^2) of karst areas occur in the region (Day & Urich, 2000). Lenggong Valley, Perak consists of eight limestone hills. A great number of ecological niches provided by complex terrains (e.g., fissured cliffs and extensive caves) and variable climatic conditions in karsts area support bird's diversity (Clements *et al.*, 2006). They also stated that a unique flora species adapted to growing on karst surfaces may support bird's diversity that is somewhat different from those in non-karstic area. However, this habitat is threatened by the quarry activities, which have been identified as the primary threat to the survival of karst-associated species, and are undeniably creating problems in biodiversity conservation in Southeast Asia (Kiew, 1991; Vermeulen & Whitten, 1999; Sodhi & Brook, 2006).

Birds are good bio-indicators in the study of the impacts of forest disturbance and habitat structure on species compositions (Karr *et al.*, 1990). Tropical birds are highly diverse and their ecological niches are quite varied and reasonably well-known. Birds are also more easily detected than other types of animals due to their often loud vocals and distinctive colours. Studies on foraging ecology of birds 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 (Strying & Zakaria, 2004). Maurer and Whitemore (1981) stated that foraging patterns used by birds are affected by habitat structure. Resource partitioning reduces the competition rates by decreasing the amount of niche overlaps between the competing species (Wiens, 1989).

The foraging strategies of birds are described by the method in which species obtain the food, the types of food taken, the foraging height, and the foraging substrates used (Somasundaram & Vijayan, 2008; MacNally, 1994). However, the identification of food taken by birds is not compulsory but it can provide useful information in foraging ecology study (Remsen & Robinson, 1990). Such information and knowledge on how they share the resources among guild members would provide an indicator about the condition of the ecosystem and management needs in conservation (Loyn, 2002). The niche overlap among potential competitor species may be useful to estimate the degree of resource partitioning (Gokula & Vijayan, 2000). Studies on foraging behaviour as the base for models of coexistence among bird species have being growing since the study done by MacArthur (1958). The foraging ecology study has been standardised by Remsen and Robinson (1990).

Some bird species (e.g.: bulbuls) are generalists that will seek for food at all heights, on variety of substrates, and use different attack manoeuvres to obtain food while the others (insectivorous birds) show varying degrees of specialisation. Generally, insectivorous birds have high habitat specificity and are confined more to the forest interior than other avian feeding guilds, especially in the tropical forest (Canaday, 1997). Insectivores are sensitive to microclimate changes associated with forest fragmentation (Karr & Freemark, 1983). Impoverished invertebrates prey in the small forest patches (Canaday, 1997; Ford *et al.*, 2001), and removal of some microhabitat components, such as curled leaves, dead trees, and ant swarms owing to forest destruction may affect insectivorous birds (Ford *et al.*, 2001). In addition, insectivorous birds are more specialised (Snow, 1976) and sensitive to subtle ecological changes because the prey actively avoids the birds. Accordingly, insectivorous birds have developed numerous specialised niches and seek prey in certain microhabitats (Sekercioglu *et al.*, 2002). Such specialist species, when they are unable to adapt to the changes (particularly caused by human activities) in their habitat, will become endangered or extinct (Vijayan & Gokula, 2006), thus it is important to identify the microhabitats preferred by these specialist species. The babblers (Timaliidae), crows (Corvidae), flycatchers (Muscicapidae), woodpeckers (Picidae), and trogons (Trogonidae) are the keys of Malaysian insectivorous birds (Yong *et al.*, 2011).

1.2 Rationale

Tropical forest ecosystems are degenerating rapidly due to human impacts. Therefore, it is important to identify the bird species that are most influenced by the impacts and how far habitat disturbance has affected the biodiversity (Willis, 1984). This type of study has been intensively pursued and the question about which species are more sensitive to the rapid loss of tropical forests has received much attention (Canaday, 1997). Little is known of which feeding guilds of bird species are more sensitive to the habitat disturbance. In addition, researches conducted on the fauna of the limestone areas, particularly birds, are lacking. Studies of the bird diversity of the Lenggong limestone area can make an important contribution by offering new knowledge about the Malaysian limestone's biodiversity.

The foraging ecology of birds has been intensively studied in certain regions of the world since the 1980s. However, the available information on the foraging ecology of forest birds in Southeast Asia is not sufficient. Foraging ecology of birds has been studied in Malaysian lowland forest by Styring and Zakaria (2004) that only focused on woodpecker family. Study on oscine passerines birds (babblers, flycatchers) may differ from non-passerine insectivores (woodpeckers, trogons). Hartung and Brawn (2005) reported that the passerine birds frequently used lower height in open-canopy habitat and may foraged higher in the closed-canopy forests. Previous relevant studies in Southeast Asia regions (Noske, 1995; Sodhi *et al.*, 1997) only covered on mangrove forest. The diversity of birds in the mangrove forest is not as diverse as the rainforests and some birds are not dependent upon this forest but only use the extensive mudflats (Strange & Jeyarajasingam, 1999).

Furthermore, comparison studies between foraging ecology of bird species in different habitat types are lacking, particularly in the Southeast Asia. Foraging patterns used by birds are affected by vegetation structure (Maurer & Whitemore, 1981). This study provides an insight into resource segregation and changes in birds' foraging strategies that may respond to disturbance. Investigating the foraging ecology of sensitive species in the continuous forest and small forest patches may provide a more complete assessment that organises the structure of bird community in the wild. This study could also identify microhabitats that are important for certain birds, and tell us how the forest patches act as important tools in forest management.

Although foraging ecology of birds has been widely studied in parts of the world, almost no attention has been given to the influence of sample size or sampling method used on the foraging ecology study. Wagner (1981) reported that the observation methods in the recorded data have an effect on the results of foraging ecology of birds. This result is supported by Morrison (1984). However, Holmes *et* *al*. (1979) noted that the analysis of birds' foraging behaviour using initial observations is not different from analyses of sequential observation. Thus, further study that compares between both observation methods on foraging data is important to overcome this conflict. Figure 1.1 describes the research flow.

1.3 Objectives

The objectives of this study can be summarised as follows:

1. To examine the influences of habitat structure and disturbance, specifically the edge effects, on the bird species composition, and to determine the most sensitive feeding guilds to habitat disturbance.
2. To describe the foraging patterns and to determine the attack manoeuvres and substrates used by insectivorous birds in lowland rainforest, and to explain how these trophically similar species can coexist in the same habitat – the central question in ecology.
3. To compare the foraging strategies of insectivorous birds in the continuous forest and small forest patches in order to examine whether Malaysian insectivore species are able to respond behaviourally to habitat loss and alteration.
4. To examine and describe the influences of initial and sequential observation methods on foraging data of birds.

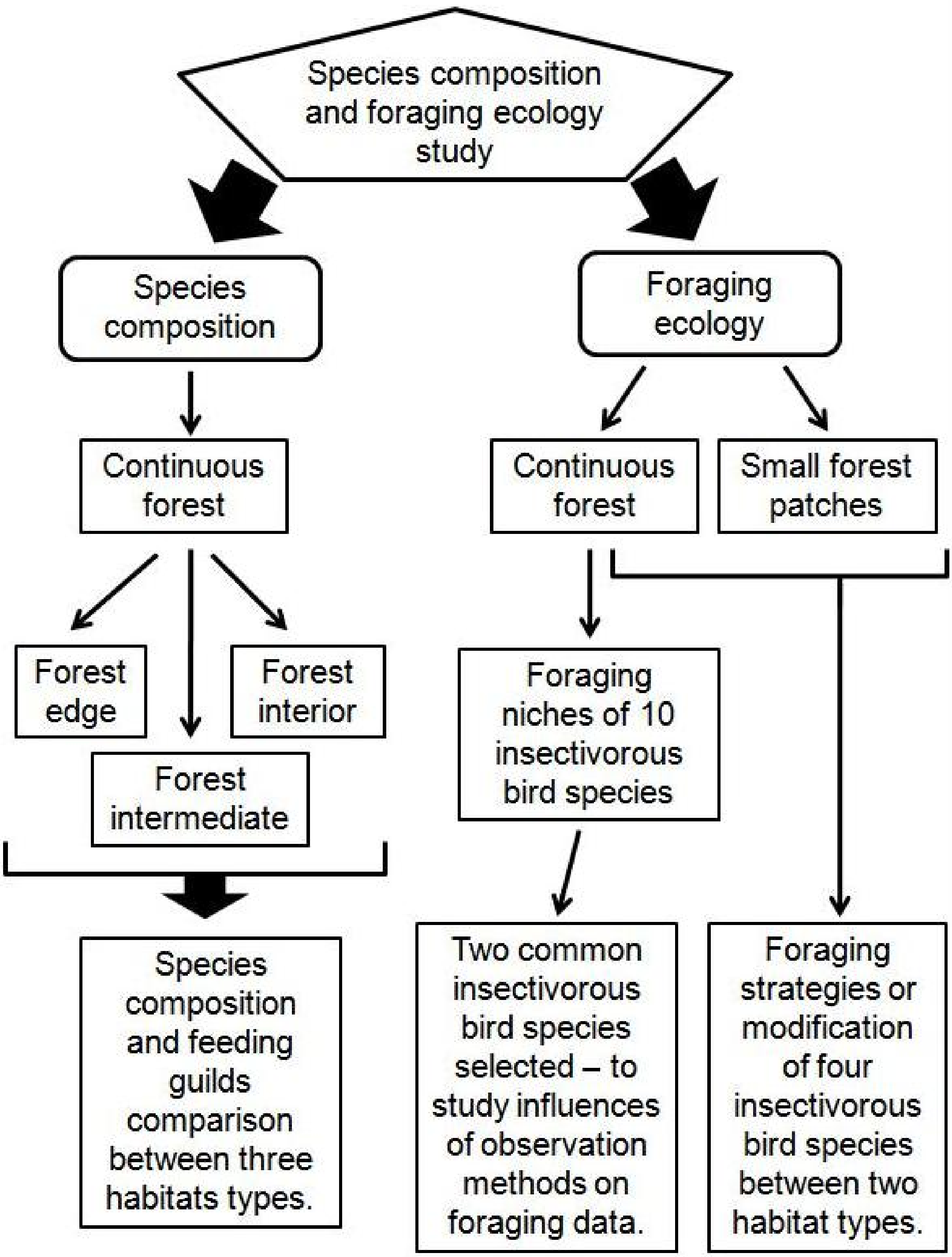

Figure 1.1 Research flow.

CHAPTER 2

LITERATURE REVIEW

2.1 Effects of habitat disturbance on birds

Bird-habitat associations tend to respond to variations of disturbance level, and it is possible to monitor the effects of habitat disturbance on the breeding-bird community (Canterbury *et al.*, 2000). Breeding cycles of understory birds are likely to depend on food resources and habitat structure (Yap *et al.*, 2007). Study done by Moradi *et al.* (2009) has divided the birds into two groups based on bird-habitat associations; arboreal foliage-gleaner and terrestrial insectivores. They reported that the species composition along edge-interior habitat was significantly different at the guild and species level. Edge effects could alter the intensity of a number of ecological processes (Ford *et al.*, 2001). Continuous habitat with high tree canopy cover contributed higher bird species diversity than edge habitat with similar levels of canopy cover (Fischer *et al.*, 2005).

In Peninsular Malaysia, about 75% of the 159 species were present in the primary forest found in the logged forests, and about 28-32% of the primary forest species occupied the mixed-rural areas (Peh *et al.*, 2005). About 37% of Javan lowland birds have also lost from the logged area (Sodhi *et al.*, 2005). Castelletta *et al.* (2000) reported that more than half of the forest birds became extinct in Singapore after extensive forest clearance. It is important to preserve the remaining forest habitats, before cleared for agriculture, as it tended to supports 15 of 16 threatened bird species (Aratrakorn *et al.*, 2006). The bird species richness increases between primary and 30-year-old regenerating secondary forest, and decreases in disturbed secondary forest (Martin & Blackburn, 2010). A well-maintained secondary forest could play a vital part in the conservation of bird species, but its potential to maintain populations over the long term is unknown (Waltert *et al.*, 2004).

In Singapore, 67% of forests bird species were found to be extinct between 1923 and 1998 due to habitat loss (Sodhi *et al.*, 2004). Species composition of birds decreased from primary forest and young secondary forest, to agroforestry systems and annual cultures (Waltert *et al.*, 2004). Endemic species was also reported to be significantly lower in young secondary forest (5-6 years old patches). Food abundance was closely related to forest conditions such as the density of large trees, density of dead trees, density of canopy cover, and shrub density that affected the forest birds (Peh *et al.*, 2005). Studies on the abundance of selected bird species in two larger forest patches also seemed to be influenced by factors such as resource availability and habitat structure (Sodhi *et al.*, 2004). Adeney *et al.* (2006) suggested that several wildfires led to the decline of birds' diversity over a large scale as birds of open country replaced interior forest specialists.

Forest fragmentation introduces ecological problems by subdividing a population into small isolated populations (Ford *et al.*, 2001). Although bird species appear to be able to move through highly fragmented area, it is possible that they suffer high death rate while moving between fragmented areas. Ford *et al.* (2001) also stated that the loss of understory vegetation is common in fragmented area and has resulted in the decline of birds' diversity. The adaptation of birds in small forest fragments may depend on their ability to use the area (Antongiovanni & Metzger, 2005). Birds' diversity was significantly correlated to vegetation parameters of the tree layer, canopy closure, and tree basal area (Thinh, 2006). Distributions of trees in the habitat were the important components that contributed to landscape connectivity and stepping stones for birds (Fischer *et al.*, 2005). Lee *et al.* (2007) reported that well-maintained forests (protected areas) recorded higher number of endemic forest bird species than in human impacted areas. Protected areas are important in bird conservations as they create a network of ecological corridors as habitats for the wildlife.

2.2 Effect of habitat types on feeding guilds

Many studies have tried to relate bird feeding guilds with habitat types in order to understand the impact of habitat disturbance on bird community. Studies on feeding guild patterns can reveal the bird population trends (Zakaria & Rajpar, 2010). In previous studies on avifauna, (Herzog *et al.*, 2003; Aggarwal *et al.*, 2008; Zakaria *et al.*, 2009; Zakaria & Rajpar, 2010), the number of insectivore species was higher than other feeding guilds. The insectivores are the most temporally stable both in terms of species richness and abundance, where the fluctuations to other diets are probably related to the availability of food resources (Herzog *et al.*, 2003). However, insectivores are highly sensitive to habitat modification (Laurance *et al.*, 2004) and they seem to be confined to less disturbed areas (Tvardikova, 2010).

Most studies have shown that the insectivores' guild was mostly affected by habitat alteration (Canaday, 1997; Sekercioglu *et al.*, 2002; Nur Munira *et al.*, 2011; Yong *et al.*, 2011). Antongiovanni and Metzger (2005) effectively grouped the insectivorous birds using *G*-tests based on their sensitivity level; highly sensitive insectivores were absent in small forest fragments and matrix habitat, moderately sensitive birds were present in small forest fragments and infrequently used matrix habitats, and least sensitive birds were present in both small forest fragments and matrix habitats. Impoverished invertebrate prey led in the decline of insectivorous birds in the forest fragments (Sekercioglu *et al.*, 2002).

Diversity of insectivorous birds declined severely after forest fragmentation, in which higher decline was found in the smaller fragments even though fragments were separated from continuous forest by only 70-650 m (Stouffer & Bierregaard, 1995). They reported that three bird species that depended on ant swarm were going to be extinct or reduced in number within the first two year after isolation. The levels of the isolation and connectivity of forest fragments were significantly correlated with the richness of insectivore species (Trollope *et al.*, 2009). The insectivorous birds were also found to be the most sensitive guild to the fragmentation in Lake Kenyir of Peninsular Malaysia (Yong *et al.*, 2011), which was probably due to the limited dispersal ability of insectivorous birds through surrounding habitat (Sekercioglu *et al.*, 2002). Insectivorous birds tended to behaviourally respond to the forest edge caused by fragmentation, and this could indicate the quality of forest conditions due to the less humidity level, tree cover, and litter depth (Moradi *et al.*, 2009).

2.3 Foraging ecology

Foraging ecology study has been intensively studied in parts of the world since 1970s, and the standardisation of foraging ecology study has been studied by Remsen and Robinson (1990). Studies on foraging ecology provide an understanding of the ways in which ecologically different bird species partition their resources in a habitat (Styring & Zakaria, 2004). Foraging ecology of birds involves five basic components; search, attack, foraging site, food, and food handling. The study by Remsen and Robinson (1990) separated the attack perch from the attack manoeuvre and further subdivided the manoeuvres into near-perch, subsurface, and aerial manoeuvres. The foraging ecology study generally involves assessing the following parameters; foraging height, foraging substrate, and attack manoeuvres (Noske, 1995; Somasundaram & Vijayan, 2008; Kwok, 2009). Standard multivariate analyses can determine the intercorrelation between these foraging parameters (Styring & Zakaria, 2004).

Although the identification of food taken by birds can provide essential information in foraging ecology study, this present study is still valuable even without this information (Gokula & Vijayan, 2000). Dietary data from stomach contents are useful in the foraging ecology study (Grim, 2006), but same diets do not indicate that two birds forage in the same way (Remsen & Robinson, 1990). In addition, dietary data are usually difficult to obtain in the field (Remsen & Robinson, 1990).

Most of the foraging ecology studies follow the standard terminologies introduced by Remsen and Robinson (1990), particularly attack manoeuvre parameter (Adamik *et al.*, 2003; Styring & Zakaria, 2004; Gomes *et al.*, 2008; Lloyd, 2008). Sillet (1994) has identified six foraging manoeuvre categories in eight species of epiphyte-searching insectivorous birds of Costa Rica; "glean", "probe" (including prying with the bill), "pull", "hang", "reach", and "acrobatic" (all sallies, lunges, leaps, and flush-pursuits). Each of the manoeuvres is described based on the standard foraging scheme. The foraging variables (foraging height, distance to canopy, attack manoeuvre, and substrate) in Dobbs *et al.* (2003) study also followed the standard scheme introduced by Remsen and Robinson (1990).

However, some modifications in Remsen & Robinson (1990) foraging scheme were noted in some studies, depending on the suitability of the study. Foraging behaviour of birds in the study by Chen and Chou (2008) followed the standard scheme, but vegetation cover parameter was modified to the density percentage of 1 m diameter sphere around the bird. Some modifications in attack manoeuvres of standard scheme were identified in the study by Hartung and Brawn (2005), where aerial manoeuvre was divided into two based on the type of substrate used (sally – on leaf or bark surfaces; flycatch –airborne insects), while the flutter-glean and flush-pursue manoeuvres were combined into one category.

Generally, the foraging ecology study reveal the most important foraging parameters that influence the foraging behaviour of birds, and provides information of the ways in which ecologically different bird species partition their resources in a habitat. Several foraging ecology studies are shown on Table 2.1.

Table 2.1 Past studies concerning foraging ecology of birds.

Source	Locality	Treatment	Observation method	Foraging parameter	Statistical analysis	Results	Significant parameters
Eckhardt (1979)	USA	F/U	S	TS/PT/FH /AM/FD /FS	STT	Eight insectivorous bird species were divided into two foraging subguilds; active searchers (gleaning) and passive searchers (sallying) guild.	AM
Holmes *et al*. (1979)	USA	F	S	TS/FH /AM/FS /FD	LT/PCA /HCA	22 insectivores' species were divided into four primary subguilds.	FH
Robinson and Holmes (1982)	USA	F	S	TS/FH /AM/FS /SR/D	TT	11 foliage-foragers bird species were divided into five foraging strategies.	AM/SR
Holmes and Robinson (1988)	USA	F	S/I	FH/AM /FS/SR/D	CST	Seven species of ground-foraging birds were divided into three foraging subguilds.	AM/SR

Table 2.1 Continued.

Source	Locality	Treatment	Observation method	Foraging parameter	Statistical analysis	Results	Significant parameters
MacNally (1994)	Australia	F/U/L	I	FH/AM /FS	HCA/PCC /DA	66 bird species were divided into 10 foraging subguilds.	AM
Sillet (1994)	Costa Rica	F/U/L	I	FH/AM /FS/FD/PT /PS/D	GT/DA	Eight species of epiphyte-searching insectivorous birds were divided into two groups.	FS
Noske (1995)	Malaysia	F/U/A	I	PS/FH /AM/FS	CST/SW/ MWUT	Four foraging guilds were distinguished among 17 bird species; obligate foliage-foraging insectivores (Guild 1), bark-foraging insectivores (Guild 2), facultative nectarivores (Guild 3), and aerial hawkers (Guild 4).	AM/FS

Table 2.1 Continued.

Source	Locality	Treatment	Observation method	Foraging parameter	Statistical analysis	Results	Significant parameters
Sodhi *et al*. (1997)	Singapore	F	I	PS/FH /AM/FS	LT/GT /HCA	The cluster analysis effectively divides the three leaf-gleaner species from the Common Flameback and Olive-backed Sunbird.	FS
Gokula and Vijayan (2000)	India	F/L	I	PS/FH /AM/FS	SW /HCA	33 bird species were divided into eight foraging subguilds.	FH
Greenberg *et al*. (2001)	Mexico	F	I	TS/FH/ AM/FD /SR	DFA	Hermit Warblers frequently used the pine trees, Townsend's Warbler showed weaker selectivity of oak trees, while Black-throated Green Warbler showed no tree-type selection.	FH/TS

Table 2.1 Continued.

Source	Locality	Treatment	Observation method	Foraging parameter	Statistical analysis	Results	Significant parameters
Recher *et al*. (2002)	Australia	F	C	FH/AM/ FS/PH/AD	LA/M/HC A/CST	The uses of attack manoeuvres, substrates and perch height were differed in foraging niches of insectivore species.	AM/FS
Styring and Zakaria (2004)	Malaysia	F/L/U	S/I	FH/DB/ AM/FS/ ST/PS/HP	PCA/CA/ HCA/A	Cluster analysis divides woodpecker species into two subguilds; (1) Conventional foragers – species that used large perches; (2) Novel foragers – species that used smaller perches and others.	PS
Lloyd (2008)	Peru	F/R	S	FH/AM/ FS/FL	HCA/ MWUT/ KW/CST/ SW	10 bird species were divided into four foraging subguilds; (1) arboreal sally-gleaners, (2) arboreal foliage gleaners, (3) arboreal bark-foliage gleaners, (4) understory bark-subsurface gleaners.	FH/FS

Table 2.1 Continued.

Source	Locality	Treatment	Observation method	Foraging parameter	Statistical analysis	Results	Significant parameters
Somasundaram and Vijayan (2008)	India	F/A	I	FH/AM/ FS	SW /HCA	26 bird species niches were divided into six foraging subguilds; (1) flower-gleaner, (2) wood-gleaner, (3) ground-forager, (4) twig-gleaner, (5) sallying birds, and (6) leaf-gleaners.	FS/AM
Kwok (2009)	Hong Kong	F	S	FH/AM/ FS	PCA/CST	The analysis revealed that except Blue-winged Minla and Japanese White-eye, no other two species used similar proportions of substrates and vertical strata at the same time.	FH/FS

Abbreviations: **Treatments;** F: forest, L: logged forest, U: unlogged forest, A: agriculture, R: remnant. **Observation methods;** S: sequential observation, I: initial observation. **Foraging parameter;** TS: tree species, PT: perch type, PS: perch size, PH: perch height, FH: foraging height, AM: attack manoeuvre, FS: foraging substrate, FD: foliage density, SR: search rate, D: diet. **Statistical analysis and significant parameters;** STT: student *t*-test, LT: log transformation, PCA: principal component analysis, HCA: hierarchical cluster analysis, TT: *t*-test, CST: chi-square test, PCC: Pearson's correlation coefficient, DA: discriminant analysis, GT: *G*-test, DA: discriminant analysis, SW: Shannon-Wiener, MWUT: Mann-Whitney *U*-test, DFA: discriminant function analysis, LA: loglinear analysis, M: MANOVA, CA: correspondence analysis, A: ANOVA, KW: Kruskal-Wallis.

The foraging niche of birds has been successfully divided based on the foraging parameters in most foraging ecology studies (Table 2.1). As identified by Holmes and Robinson (1988), the foraging substrate and the proportion of attack manoeuvres used were different for the bird species within each foraging subguild, and each species appeared to use a distinctive combination of habitat characteristics. These results may tell us how the foraging birds reduce the competition in the wild. Some of the results were different depending on the types of habitats or locality (Lloyd, 2008; Kwok, 2009), as the foraging patterns of bird may be affected by vegetation structure (Maurer & Whitemore, 1981).

2.4 Foraging behaviour in different habitat structures

Foraging ecology study provides information on resource partitioning among the bird species, and may tell us how the birds respond to habitat changes (Styring & Zakaria, 2004). Foraging niches of birds have been found to be significantly different between two structurally different habitats namely heterogeneous primary forest and homogeneous habitats (Adamik *et al.*, 2003). The cluster analysis in their study revealed four main foraging guilds in the heterogeneous primary forest comprising 23 bird species, while in the homogenous habitat only three guilds consisting of 11 species were detected. Hartung and Brawn (2005) reported that the passerine birds frequently used lower height in open-canopy habitat and they foraged higher in the closed-canopy forests. Gomes *et al.* (2008) suggested that only those species with adaptable foraging strategies are capable to expand their populations to different habitat types and structures.

The foraging tactics used by insectivorous birds between two different habitat structures are different (Lloyd, 2008) where six of 10 species tend to shift their foraging tactics in the forest patches. He suggested that insectivorous birds are able to respond behaviourally to habitat loss and alteration. Habitat structure and prey abundance could influence the potential foraging opportunities, thus affecting the foraging behaviour of birds, and finally influencing the pattern of bird habitat selection and community structure (Robinson & Holmes, 1982). Generalist bird species usually adapt in disturbed habitats, in which they may evolve in response to variations in resource availability and the habitat disturbance (Noske, 1995). The activity patterns showed by birds are influenced by moisture and vegetation type, and this activity levels change with time, suggesting that bird activity shows a dynamic process of habitat selection (Karr & Freemark, 1983). A study has also found that foraging strategies of all stork species are different with respect to habitat structure (Ishtiaq *et al.*, 2010).

The foraging behaviour study provides vital information on how guilds respond to different habitat types (MacNally, 1994). Cluster analysis in his study effectively divided the bird communities into 10 foraging guilds where species members in each foraging guild was different between the five habitat types, namely Gippsland manna gum, foothill woodlands, montane forests, red ironbark-grey box, and river red gum-grey box. The foraging patterns of birds differed between study sites, which were due to the differences in habitat types (Noske, 1995). Recher *et al.* (2002) reported that the potential foraging tactics are very wide, and can be influenced by the habitat types and resource availability. The birds tended to avoid the strongly defended plants (chemically protected) that support low insects' density

(Sipura, 1999). Therefore, the foraging ecology of birds in different habitat structures could promote the understanding in plant-insect interactions.

Gomes *et al.* (2008) reported that the foraging birds in *restinga* (humid types of Atlantic forest) habitat, Brazil were somewhat similar to other studies of the same species in other habitat types but were different in the use of foraging height and tree species preferences, and with little spatial overlap. Similar foraging tactic used by birds between two different habitats reflects a species-specific stereotypic behaviour (Martin & Karr, 1990), while the foraging differences exhibited by birds may be related to differences in plant species and types of available prey at different times of year (Holmes & Schultz, 1988). Difference in relative abundance of plant species leads birds to use different foraging strategies in different habitat types (Adams & Morrison, 1993). There were broad overlaps in foraging niches of warbler species after the removal of deciduous trees (Morrison, 1981). Most of the birds in Palni Hills, South India, fed primarily from vegetation, thus revealed the importance of plant structure in sustaining the bird community of the same area (Somasundaram & Vijayan, 2008).

The attack manoeuvres used by birds in the Talamanca Mountains of Costa Rica proved that the foraging behaviour of birds may have been restricted by habitat characteristics (Sillet, 1994). Bird foraging tactics and morphology combined with habitat structure influence bird community patterns (Holmes & Robinson, 1988). The most abundant birds in disturbed areas may be able to shift their foraging behaviour by using less substrates and attack manoeuvres (Lloyd, 2008). The homogeneous habitat leads bird to forage in narrower niches, thus increasing the niches to overlap among birds (Adamik *et al.*, 2003). Some species like flycatcher tend to sally and inhabit in an open habitat (Sherry, 1984), making them successful to reduce their diet niches with other species. There was also a significant difference in the use of attack manoeuvres by the Eastern Wood-Pewee (*Contopus virens*) and the Great Crested Flycatcher (*Myiarchus crinitus*) in open and closed-canopy forest (Hartung & Brawn, 2005). Certain habitats generally possess different tree species that support different insect diversity preferred by certain birds, thus, it is important to preserve all habitat types (Somasundaram & Vijayan, 2010).

Insectivorous birds can increase plant growth by consuming herbivorous prey and reducing the plant damage. However, different plant traits (chemical defence) may affect the insects' productivity and modify the foraging behaviour of birds (Sipura, 1999). Gabbe *et al.* (2002) reported that 12 of 13 species studied foraged selectively to tree species, where less common bird species tended to be more selective than the more abundant bird species. Selection of tree-species was different in woodpecker family in Peninsular Malaysia; Greater flameback (*Chrysocolaptes lucidus*) specialised on *Avicennia alba*, while the Brown-capped woodpecker (*Dendrocopos nanus*) preferred *Sonneratia alba* (Noske, 1995). Foraging height and tree-species were the most important variables in separating the foraging niches of three warbler species in the Eastern Highlands of Mexico. Hermit warbler frequently used the pine trees, Townsend's warbler showed weaker selectivity of oak trees while Black-throated green warbler showed no tree-species selection (Greenberg *et al.*, 2001).

The use of plant species (*Avicennia* spp.) by some bird species was significantly different compared to the use of all other plant species in Sungei Mandai mangrove forest, Singapore (Sodhi *et al.*, 1997). The bird species foraged at least eight plant species and their diversity provided foraging requirements for the resident bird species. The foraging behaviour of American redstart (*Setophaga ruticilla*) was influenced by prey type abundance, and prey escaping behaviour, which was different among tree species (Robinson & Holmes, 1984). Comparison between initial and sequential observation methods on bird foraging data by Morrison (1984) also gave similar results where the use of foraging heights and tree species was different between methods; irregularly used heights and tree species were not noticed by the initial observation method. However, the foraging ecology study is still valuable, even without tree species informations (Gokula & Vijayan, 2000; Somasundaram & Vijayan, 2008; Lloyd, 2008; Kwok, 2009).

Foliage structures are believed to influence the foraging behaviour in the north-eastern region of North America (Whelan, 2001). Two warbler species used different foraging tactics on sugar maple tree (*Acer saccharum*) that has orbicular leaves, but used similar tactics on yellow birch (*Betula alleghaniensis*) that has oblong-ovate leaves. Bird species may exhibit different foraging strategies to the leaf structure preferences (Robinson & Holmes, 1984). They also noted that although hovering and sallying birds were relatively unaffected by foliage structure, the foliage density significantly influenced the foraging patterns and prey capture success of sallying birds. Leaf-gleaners have been reported to have higher tree species preferences than species that frequently hovered for prey, and they were more influenced by foliage structure (Holmes & Robinson, 1981).

Foliage density and resource availability influences the foraging strategies of birds (Robinson & Holmes, 1984). They found that some bird species frequently foraged between perches due to the more open canopy and less dense foliage. A study done by Morrison (1981) found that the tree covers density in deciduous forest was the most important variable in separating the niches of warbler species between habitats. Orange-crowned Warbler was able to shift their foraging tactic by using shrub (denser) and undisturbed area when the deciduous tree cover was reduced. Greater foliage density in forest gap affected the foraging strategies of birds due to the steep micro-environmental conditions (Nik Fadzly, 2007). Foraging birds can respond to different environmental variable where dense vegetation cover effectively provides foraging requirement for forest-dependent birds (Lee *et al.*, 2007). Attack manoeuvres used by birds may correlate with the structure of foliage density. Sallying birds tend to forage in areas where the foliage density is lower, which are avoided by many species because a large open space is required for sally tactics (Chen & Chou, 2008).