

Niche shift in three foraging insectivorous birds in lowland Malaysian forest patches

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ABSTRACT

With the rapid growth of agricultural areas globally, forest birds increasingly encounter fragmented landscapes in which forest patches are surrounded by an agricultural plantation matrix, yet how birds respond behaviourally to this fragmentation is poorly understood. Information on microhabitat requirements of birds is scarce, but nevertheless essential to predicting adaptation of bird species to the patchy landscapes. We investigated foraging patterns of three tropical insectivorous birds, Green Iora *Aegithina viridissima*, Pin-striped Tit-Babbler *Macronus gularis* and Chestnut-winged Babbler *Cyanoderma erythropterum*, to determine whether they vary in foraging methods in different forest patches. Our study area encompassed old-logged lowland forest; one continuous forest and three forest patches. Observations were performed for 15 days every month for a period of 13 months. Information on foraging height, substrate, attack manoeuvres, and foliage density was collected independently for each foraging bird individual. All three species used different foraging substrates and attack manoeuvres in different habitat types. The Green Iora frequently used lower strata when foraging in forest patches as opposed to continuous forest, while the Pin-striped Tit-Babbler tended to forage in more dense vegetation in patches. Only Chestnut-winged Babbler displayed complete foraging plasticity across all study parameters. Different habitat features (e.g., edges, microclimates) between continuous forest and forest patches significantly influenced the foraging strategies of the study species. These changes in foraging strategies suggest that some Malaysian forest birds (e.g. generalist species) can respond behaviourally to fragmentation and habitat loss. Although continuous forest has critically important characteristics that need to be conserved, remnant forest patches are also important as ecological movement corridors and foraging grounds for birds.

1. Introduction

Over 300 bird species recorded in Peninsular Malaysia are inhabitants of lowland rainforest. This habitat is currently facing massive destruction or modification by human activities (Peh et al., 2005), and much of it exists presently as small, isolated patches within variable landscapes of heavily logged forest and agricultural plantations (Wong, 1986; McShea et al., 2009). Such fragmentation strongly influences habitat connectivity and alters the functionality of native habitats within the landscape, e.g., through changes in vegetational structure and floristic composition (Taylor et al., 1993; Fleishman et al., 2003; Ferraz et al., 2007; Boscolo and Metzger, 2011), thereby modifying microhabitats used by dependent animals (Fischer and Lindenmayer, 2007). For birds, the loss of tropical forest represents an extreme threat to global diversity (Nielsen et al., 2004), as many understory forest

species respond negatively to habitat fragmentation (Barlow et al., 2006; Sheldon et al., 2010; Mohd-Taib et al., 2016).

The value of continuous forest has been repeatedly examined in respect to the conservation of birds (Hurst et al., 1980; Freemark and Merriam, 1986; Blake and Karr, 1987), and the impact of habitat modifications on bird species richness and assemblages has been demonstrated in many studies (Ferraz et al., 2007; Flaspohler et al., 2010; Bregman et al., 2014). Island biogeography theory (MacArthur and Wilson, 1967) has been used as a basis for measuring processes of community assembly and local extinctions in continuous forest and human-modified patchy landscapes (Fischer and Lindenmayer, 2005; Tinoco et al., 2013; Styring et al., 2018). However, the significance of forest patches to bird community structure is not yet fully understood. In particular, the question of whether several small forest patches can support a diversity of sensitive species comparable to a single large

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fragment of equal area continues to be one of the most debated issues in conservation biology (Simberloff and Abele, 1976; Sodhi et al., 2010; Kormann et al., 2018).

Different species respond differently to fragmented habitat (Bélisle et al., 2001). Many tropical forest species have been found to be relatively reluctant to cross gaps, especially understory species (Stouffer and Bierregaard, 1995; Thiollay, 1997; Van Houtan et al., 2007). They may occur in a fragment immediately after it is isolated from continuous forest, but how long they remain and response behaviourally in such habitats are still unknown. Certain forest bird species are consistently found only in continuous forest, and a portion of those species do not venture more than 50 m from the forest cover (Cassady St Clair et al., 1998). The movement of species across gaps mostly takes place from smaller to larger fragments, but none prefers emigration to remaining in continuous forest (Van Houtan et al., 2007). The ability to cross a gap is a crucial component of functional connectivity within fragmented landscapes. The tendencies and differences among individual species to remain in or disperse among fragments highlights the need for more information on tropical bird foraging in a variety of habitat types and conditions (Maurer and Whitmore, 1981).

In general, tropical insectivorous birds have high habitat specificity and are confined more to the forest interior than other avian feeding guilds (e.g., frugivores, granivores). This is especially evident in tropical forests where habitat loss is heavily concentrated (Canaday, 1997). Insectivorous birds are more sensitive to subtle ecological changes because their prey actively avoids them and, accordingly, birds have evolved numerous specialized foraging niches (Snow, 1976; Şekercioğlu et al., 2002). Removal of particular microhabitat components, such as aerial leaf-litter and dead trees, in a fragmented landscape may especially affect insectivorous birds (Ford et al., 2001). Habitat structure has been highlighted as an important element for forest birds, particularly insectivores, as it provides many foraging opportunities (Whelan, 2001) and effectively shapes their community structure (Robinson and Holmes, 1982). It likely acts as a selective force shaping birds' foraging patterns and determining which species are able to occupy and exploit an area successfully (Robinson and Holmes, 1982).

The foraging ecology of birds has been intensively studied in certain regions of the world since the 1980s (Holmes and Robinson, 1981). However, information on the foraging ecology of forest birds in Southeast Asia is relatively rare, as is basic information on microhabitat requirements of rainforest birds in general. Moreover, the influence of landscape connectivity on foraging opportunities for birds has not been well considered (Lloyd, 2008; Tinoco et al., 2013; Grafius et al., 2017). Although some species are capable of modifying their foraging strategies to take advantage of opportunities in different environments (Overington et al., 2011), we do not know to what extent this occurs in Southeast Asia for insectivorous forest birds, except perhaps woodpeckers (Lammertink, 2004; Styring and Hussin, 2004). Here, we examine how foraging behaviour of three insectivorous bird species (Green Iora *Aegithina viridissima*, Pin-striped Tit-Babbler *Macronus gularis*, Chestnut-winged Babbler *Cyanoderma erythropterum*) responds to changes in forest structure and vegetation in a diverse forest landscape of patchy and continuous forest. These species are common in Malaysian rainforest, where they can easily be found in most forest types, allowing the acquisition of an adequate sample of foraging behaviour. They are similar in body size and bill morphology (slender and either straight or slightly decurved), but differ slightly in occurrence patterns (Wells, 2007; Styring et al., 2016), suggesting that they may also differ in microhabitat preferences and may respond differently to forest disturbance. For these three species, we hypothesize that continuous old-growth forest, which contains mature trees and is structurally complex, should provide greater foraging opportunities than patches of simple habitat structure (Karr and Roth, 1971). As a result, the simple vegetational structure and floristic composition of forest patches may cause

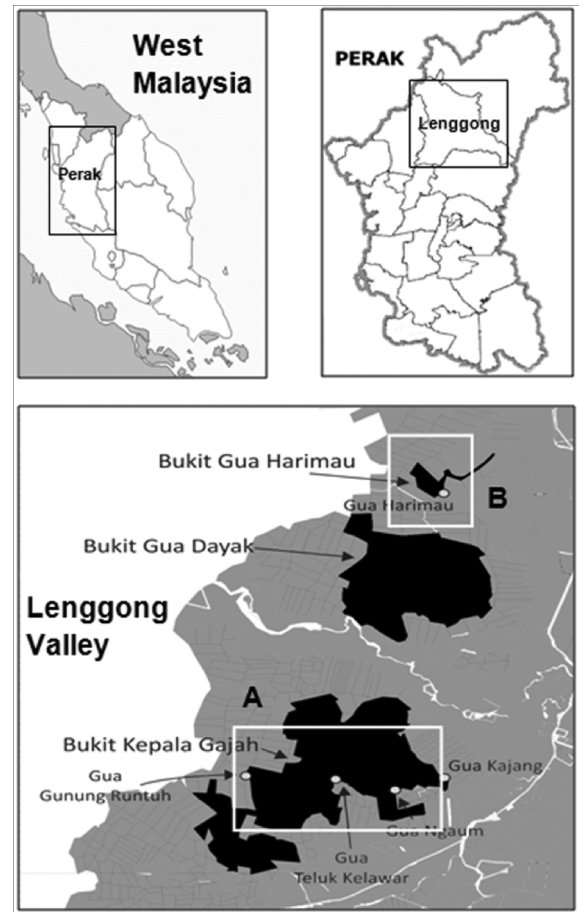


Fig. 1. Schematic showing the location of study sites in the Lenggong Valley, Perak, Peninsular Malaysia. A = continuous forest; B = forest patches.

certain bird species to forage differently than they would in continuous forest (Maurer and Whitmore, 1981; Robinson and Holmes, 1982).

2. Methods

2.1. Study area

The study was conducted in lowland forest near the Bukit Kepala Gajah limestone area, within Lenggong Valley, a UNESCO world heritage site in Perak, northern Peninsular Malaysia (Fig. 1). Bukit Kepala Gajah is one of eight limestone hills in the Lenggong Valley of Ulu Perak. It is located approximately 150 m above sea level and approximately 3 km north of Lenggong town (5°7.957'N - 5°7.728'N, 100°58.432'E - 100°58.410'E). The climate is hot and humid throughout the year with very little variation, with temperatures of about 30 °C–33 °C.

The survey sites consisted of a continuous forest (≥ 100 ha) and three small forest patches (≤ 10 ha each). The latter were separated from the continuous forest by rubber plantation, orchards, and grassy areas. Distances among the forest patches were about 80–100 m, and about 500 m away from the continuous forest. Vegetation of the study area (i.e., both continuous forest and forest patches) consisted of a mixture of lowland dipterocarp and limestone forest. The continuous forest was relatively undisturbed, and contained dominant trees including *Dipterocarpus* sp., *Koompassia* sp., *Dyera* sp., and *Shorea* sp. The forest patches generally had highly reduced tree density, smaller trees, and less canopy cover than the continuous forest, with an abundance of undergrowth and bushes.

Table 1

Foraging parameters of three insectivorous bird species in continuous forest and forest patches. Data are given as percentages (%). Abbreviations: CF, Continuous forest; FP, Forest patches.

Bird species		Green Iora		Pin-striped Tit-Babbler		Chestnut-winged Babbler	
Parameter / Habitat		CF	FP	CF	FP	CF	FP
<i>Foraging height</i>							
> 0–2 m		0	0	3.08	4.23	81.82	66.67
> 2–4 m		0	0	3.08	15.49	14.14	15.15
> 4–6 m		0	0	4.62	7.04	2.02	9.09
> 6–8 m		7.04	0	15.38	7.04	0	0
> 8–10 m		8.45	11.11	15.38	15.49	1.01	0
> 10–12 m		35.21	51.11	43.08	38.03	1.01	9.09
> 12 m		49.3	37.78	15.38	12.68	0	0
<i>Foraging substrate</i>							
Leaf	surface	35.21	26.67	27.69	11.27	5.05	12.12
	underside	50.7	62.22	32.31	54.93	12.12	15.15
> 2-cm branch	surface	0	4.44	1.54	2.82	0	0
	underside	0	0	3.08	4.23	0	3.03
< 2-cm branch	surface	0	4.44	4.62	4.23	0	3.03
	underside	0	0	0	0	0	0
Trunk		0	0	1.54	3.64	0	0
Twigs		14.08	0	3.08	0	0	0
Aerial dead leaves		0	2.22	26.15	19.72	82.83	66.67
<i>Attack manoeuvres</i>							
Gleaning		33.8	13.33	36.92	30.99	26.26	21.21
Stretching		54.93	48.89	53.85	39.44	53.54	39.39
Hanging		7.04	33.33	7.69	26.76	9.09	9.09
Probing		0	0	0	0	11.11	30.3
Sallying		4.23	4.44	1.54	2.82	0	0
<i>Foliage density</i>							
Scale 0		0	2.22	0	2.82	0	0
Scale 1		5.63	2.22	0	4.23	0	0
Scale 2		21.13	24.44	9.23	12.68	12.12	0
Scale 3		61.97	55.56	60	54.93	46.46	27.27
Scale 4		8.45	15.56	18.46	25.35	35.35	72.73
Scale 5		2.82	0	12.31	0	6.06	0

2.2. Survey methods

Birds were located visually and followed opportunistically along several forest trails. Observations were performed for 15 days every month for a period of 13 months from July 2010 to July 2011. Birds were observed throughout the day, between 0730 and 1830 h, but most observations occurred in the early morning and late afternoon. For each individual encountered, we recorded the first sighting of the bird. Subsequent observations of foraging in the same bird were assumed to be correlated, and ignored (Hejl et al., 1990; MacNally, 1994). At least 30 independent observations were made of each species to represent foraging behaviour accurately (Morrison, 1984; MacNally, 1994; Somasundaram and Vijayan, 2008). We compared foraging activities in continuous forest to activities in forest patches for the three focal species. Observations were made using 8 × 42 binoculars, recorded on a voice recorder, and later transcribed. Observations of the species were not recorded if the birds were participating in mixed-species flocks, because membership in such flocks affects foraging behaviour of birds and hence the independence of the observations (Sridhar et al., 2009). To minimize the probability of repeatedly observing the same individuals, we recorded only the first individual of a species seen on a forest trail or at an observation point each day.

The following data were recorded for each foraging observation: foraging height, foraging substrate, attack manoeuvre, and density of the foliage at the foraging site.

Foraging height was the height above the ground at which a food item is taken by a bird. This parameter was grouped into 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. Selected trees were height-marked as references for standardization.

Foraging substrates was defined as the material (microhabitat) from which a food item is taken by the birds: leaf surface, underside of the leaf, surface of branches, underside of branches, trunk, twigs, dead tree parts (dead leaves, dead branches), leaf litter, and air.

Attack manoeuvres were defined using the terminology outlined in Remsen and Robinson (1990). We used the following subset of categories: (i) glean – to pick food from a nearby substrate, reached without full extension of legs or neck; (ii) stretch – to completely extend the legs or neck to reach the food items; (iii) probe – to insert bill into softer substrate to capture hidden prey; (iv) hang – to hang the head down to reach food not obtainable from any other perched position; and (v) sally – to fly from a perch to attack a food item and then return to a perch.

Foliage density was measured on a subjective scale in the 1-m diameter sphere around the bird. The proportion of the sphere covered by vegetation (e.g. leaves, bushes) ranged from 0 (no vegetation) to 5 (covering more than 75% of the area), as adapted from the approach of Braun-Blanquet (1932) and covering the density scale described by Allen and McLennan (1983), Allen (1993); Bowes et al. (1994), and Hurst and Allen (2007).

To obtain a mobility index of the study species, we calculated a dispersal ratio (dp) for each species by dividing its mean wing length (mm) by the cube root of its mean mass (g) (Woinarski, 1989; Fischer and Lindermayer, 2005). The species were categorized as relatively mobile (dp > 33), relatively immobile (dp < 31), or ‘intermediate’ between these indices.

2.3. Statistical analyses

All foraging parameters were checked for normality using SPSS 17.0 (SPSS Inc., U.S.A.). Foraging height and foraging substrate were log

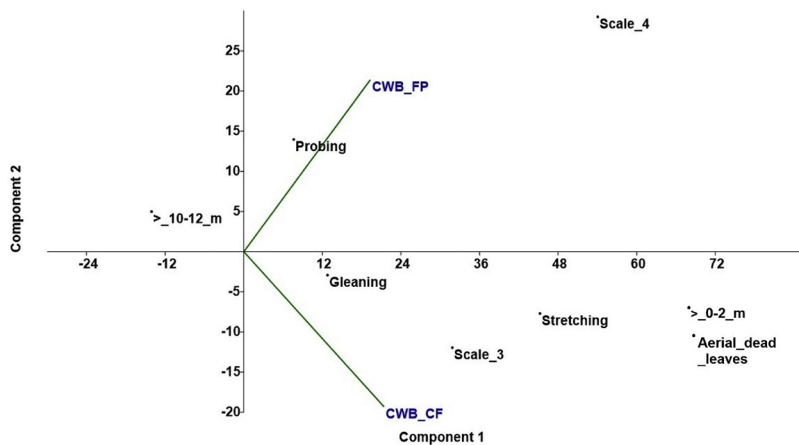


Fig. 2. Distribution of four foraging parameters (height, attack manoeuvre, substrate and foliage density) in the Chestnut-winged Babbler based on principal component analysis (PCA). Preferred parameters are indicated in the same dimension as bird species. Abbreviations; CWB: Chestnut-winged Babbler, CF: continuous forest, FP: forest patches.

transformed to meet these assumptions. We used general linear models (GLMs) to examine the effect of patches on foraging behaviour in each study bird species. GLM tests were performed using STATISTICA v.8.0 (StatSoft, 2007). Principal component analysis (PCA) was performed to extract foraging patterns (i.e. linear combinations of raw variables that characterize foraging behaviour) of bird species existing within two different habitats (i.e., forest patches versus continuous forest). We used a scree plot to define components of all foraging parameters in the analysis, and only components with eigenvalues > 1 were selected. From each of the components, high loading plots were used to determine significant parameters (e.g. foraging height). Plots were constructed using the PAST software (Paleontological Statistics, 2.17) (Hammer et al., 2001).

3. Results

We recorded 384 independent observations of the three bird species during 195 point-counts performed in both continuous forest and forest patches. The dispersal ratio of the species ranged from 24.79 to 25.91 (25.20 ± 0.62), indicating a relative lack of vagility ($dp < 31$). We obtained 235 independent observations in the continuous forest: 71 of Green Iora, 65 of Pin-striped Tit-Babbler, and 99 of Chestnut-winged Babbler. In forest patches, we obtained 149 independent observations: 45 of Green Iora, 71 of Pin-striped Tit-Babbler, and 33 of Chestnut-winged Babbler (Table 1). Grouping the species by habitat preference indicated that all were forest-edge species, sometimes entering the intermediate forest.

Of the study species, only the Chestnut-winged Babbler exhibited foraging plasticity across all study parameters (Table 1). Some

individual babblers shifted to higher strata ($F_{6,131} = 2.785$; $P = 0.032$) from the lowest stratum ($> 0-2$ m) in the continuous forest, to higher strata ($> 4-6$ m and $> 10-12$ m) in the forest patches. This babbler frequently employed the stretching manoeuvre in both habitats and adopted probing manoeuvres in the forest patches ($F_{4,131} = 2.466$; $P = 0.049$). It preferred aerial dead leaves but used them less ($F_{6,131} = 2.642$; $P = 0.038$) when foraging in forest patches. This species predominantly used intermediate-density foliage (3 on this scale) in the continuous forest, but preferred intermediate-to-highest density foliage (4 on this scale) in the forest patches ($F_{5,131} = 7.452$; $P = 0.000$). Fig. 2 illustrate the distribution of foraging parameters used by the Chestnut-winged Babbler.

The Green Iora often made use of the lower strata ($F_{6,115} = 2.569$; $P = 0.042$) when foraging in forest patches, as opposed to higher strata (> 12 m) in continuous forest. The iora foraged primarily on the live green leaves in both habitats but avoided twigs (GLM, $F_{6,115} = 3.051$; $P = 0.022$) in forest patches. The stretching manoeuvre was frequently employed by this species in both continuous and forest patches, while the hanging manoeuvre ($F_{4,115} = 3.334$; $P = 0.016$) was adopted by the Green Iora in forest patches. Fig. 3 illustrate the distribution of foraging parameters used by the Green Iora.

The Pin-striped Tit-Babbler constantly used the underside of leaves ($F_{6,135} = 3.000$; $P = 0.024$) in forest patches, while preferring various materials in continuous forest (i.e., leaf surface, underside of leaf, aerial dead leaves). Stretching and gleaning manoeuvres were frequently employed by the tit-babbler in both continuous and forest patches, although it tended to use a wider range of attack manoeuvres with the adoption of hanging manoeuvres ($F_{4,135} = 2.785$; $P = 0.032$) in forest patches. Fig. 4 illustrate the distribution of foraging parameters used by

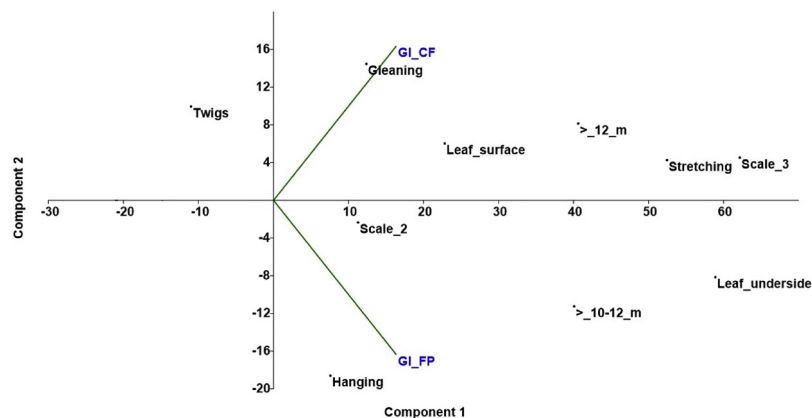


Fig. 3. Distribution of four foraging parameters (height, attack manoeuvre, substrate and foliage density) in the Green Iora based on principal component analysis (PCA). Preferred parameters are indicated in the same dimension as bird species. Abbreviations; GI: Green Iora, CF: continuous forest, FP: forest patches.

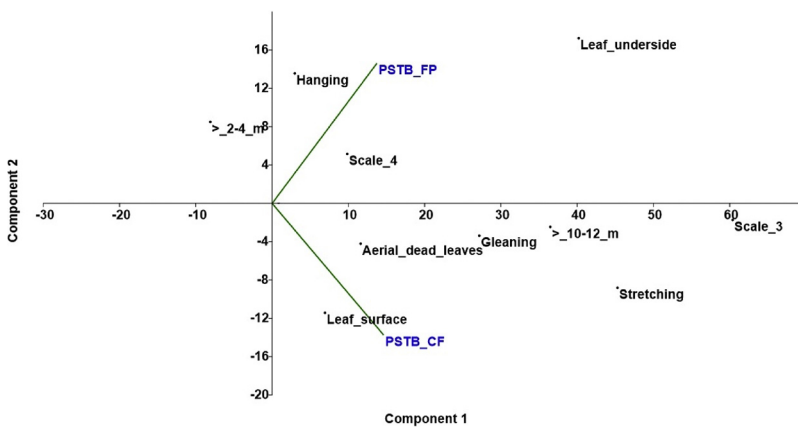


Fig. 4. Distribution of four foraging parameters (height, attack manoeuvre, substrate and foliage density) in the Pin-striped Tit-Babbler based on principal component analysis (PCA). Preferred parameters are indicated in the same dimension as bird species. Abbreviations; PSTB: Pin-striped Tit-Babbler, CF: continuous forest, FP: forest patches.

the Pin-striped Tit-Babbler.

4. Discussion

Foraging strategies of the focal species differed between forest patches and continuous forest, as has been found previously in temperate birds (Krebs et al., 1972; Alatalo, 1982; Morrison et al., 2010) and other tropical birds (Lloyd, 2008; Fink et al., 2009). This plasticity suggests that certain Malaysian insectivorous birds are able to respond behaviourally to habitat loss and alteration. Compared to continuous forest, patches generally exhibit modified habitat structure (e.g. reduced tree density, smaller trees, and less canopy cover) and microclimates (Jedlicka et al., 2006; Cahill and Matthysen, 2007), thus potentially disrupting established foraging strategies of many bird species. For example, forest degradation disrupts the abundance and distributions of insects, subsequently forcing insectivores to modify their distribution and foraging tactics (Robinson and Holmes, 1982; Wong, 1986; Peh et al., 2005). Unlike fruits, flowers, and seeds, arthropod prey actively avoid insectivorous birds, thus causing members of this feeding guild to become more sensitive and specialized hunters.

Specialisation in attack manoeuvres generally involves limited use of foraging substrates by most birds (Gradwohl and Greenberg, 1984; Rolando and Robotti, 1985). However, changes in foraging substrates appear to have caused the adoption of different attack manoeuvres by our study species in forest patches. Alteration of floristic structure in forest patches may reduce availability of certain microhabitats that offer many foraging opportunities (Styring et al., 2016; Mansor and Ramli, 2017). Tree removal and increased edge effects in forest patches will disrupt the distributions and abundance of litter-dependent arthropods (Jokimäki et al., 1998; Turner and Foster, 2009; Ruiz-Guerra et al., 2010), which may force the dead-leaf foragers to adopt additional manoeuvres (i.e., probing) to thoroughly explore scarce litter-dependent arthropods. For example, the Chestnut-winged Babbler adopted a probing manoeuvre in forest patches that requires more time and energy to search for less abundant and more patchily distributed aerial leaf-litter (than in continuous forest) and to extract prey. A high frequency of probing manoeuvres employed by Chestnut-winged Babblers in forest patches is also possibly related to their involvement in mixed-species flocks. Participating in these flocks allows birds to reduce their vigilance, thus providing more time for prey exploitation (Sridhar et al., 2009), in this case to explore aerial dead leaves more thoroughly.

The Chestnut-winged Babbler made use of other foraging strata (i.e., > 4–6 m and > 10–12 m) when foraging in forest patches. A broad range of foraging heights exhibited by study species may allow them to detect prey easily in forest patches, subsequently providing many foraging opportunities, thus contributing to high survival and fitness. Increased edge effects in forest patches (Mancke and Gavin, 2000; Matthews and Rodewald, 2010) influence birds' microhabitat selection and prey taken (Johns, 1989; Thiollay, 1992) as well as increase the risk

of predation, parasitism, and competition (Mcintyre, 1995), consequently leading certain bird species to forage in an irregular manner (Barbaro et al., 2014). Edge effects usually eliminate certain forest-dependent species (Mcintyre, 1995; Schmiegelow et al., 1997; Mansor and Sah, 2012), thus permitting other species to increase the breadth of their foraging niches. Furthermore, plasticity in vertical strata is often driven by habitat alteration (Lloyd, 2008) or participation in mixed-species flocks (Zou et al., 2011; Farine and Milburn, 2013). An abundance of undergrowth and reduced canopy in forest patches (Ariffin and Kumari, 1989) may explain the reason why certain species change their foraging strategies in forest patches. By foraging in more dense vegetation (4 on this scale) birds in forest patches would likely increase their foraging efficiency (Walther and Gosler, 2001) by increasing their scanning and hopping rates (Telleria et al., 2001) while reducing predation risk.

The present results suggest that habitat disturbance is responsible for the changes in foraging strategies by birds in forest patches. Nevertheless, forest patches still supply useful foraging opportunities for certain insectivores. Therefore, forest patches should not be excluded from forest restoration practices. Small dispersal ratio (dp) values in small passerine forest birds, indicating immobility, suggests they may only cross nearby forest patches but are reluctant to cross large gaps to continuous forests (Van Houtan et al., 2007). This highlights the importance of several forest patches acting as wildlife corridors. It is reported that the small patches of Malaysian tropical forest which have had low human disturbance and are surrounded by crop plantations contain high diversity of wildlife (Azad, 2006; Sheldon et al., 2010).

Present and previous studies (Ariffin and Kumari, 1989; Abdullah and Nakagoshi, 2007; Azhar et al., 2011) have revealed the importance of these forest patches as ecological corridors. Forest patches may lack important resources, but certain bird species might be able to shift their foraging behaviour (Matthews and Rodewald, 2010). A number of species of small passerine forest birds may be avoid and reluctant to cross between patches that have a distance as short as 100 m, which could probably create a barrier for them (Stouffer and Bierregaard, 1995). These limited dispersal capabilities may force these birds to modify their foraging strategies in disturbed habitats (Şekercioglu, 2002). Further, certain bird species may not be tolerant to the conditions of smaller fragmented habitat, subsequently may shift their foraging strategies to adapt to certain habitat quality and environment (Ghosh et al., 2011; Alström et al., 2015; Dubay et al., 2017), and resources (Hazlehurst and Karubian, 2018).

We proposed that the remnants forest patches should be protected, and conservation of species living in this area requires careful management. These habitat types could possibly have their own environmental aesthetic and social values, also known as a High Conservation Value (Jenning et al., 2003). Preserving and enhancing forest quality and understanding what vegetation remains are vital in remnant forest management (Trollope et al., 2009). The best practices are by

increasing the size of small patches wherever possible and elevating the connectivity among patches or continuous forest. Enhancing the quality and connectivity of these habitats will increase foraging opportunities of many birds (Holmes and Robinson, 1988), which act as ecological corridors for certain forest birds that could help in the dispersal of isolated populations (Thiollay, 1992; Simberloff et al., 1992). The recent ecological corridor connectivity plan, the Central Forest Spine (CFS) Master Plan for Ecological Linkages in Peninsular Malaysia (Jain et al., 2014), will be very valuable in reducing fragmentation effects on wildlife. Investigating the foraging ecology of sensitive species in different habitat types may provide a more complete assessment that organizes the structure of the bird community in the wild.

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