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Cover: *Pipistrellus tenuis* recorded during the small mammalian fauna study, Manipur, India. © Uttam Saikia.

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COMMUNICATION

Foraging strata and dietary preferences of fifteen species of babblers in Sarawak, Malaysia

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Abstract: Babblers are the primary insectivorous birds of the tropical forests in southeastern Asia which have shown to be affected by forest disturbance. Their high diversity, microhabitat specificity and specialised feeding guilds provide a good opportunity for ecological research pertaining to niche segregation. We examined the diet and foraging strata of 15 sympatric babbler species mist-netted in nine forests in Sarawak, eastern Malaysia. Based on 222 birds captured from December 2014 to March 2016, a segregation in foraging strata was found, with half of the species captured frequenting low strata, while only three were found at mid strata and four at high strata. Both species richness and abundance were found to decrease when the foraging height increased. From a total of 136 prey items retrieved from regurgitated and faecal samples of 13 babbler species, we found that Coleoptera (41.5%), Hymenoptera (36.2%), and Araneae (12.3%) formed the major diet of the birds. Diet overlaps among the babblers were relatively low. Our study demonstrated the possible presence of spatial and trophic niche segregation among babblers, and justified their ecological role as indicators of tropical forest ecosystem health, especially in the case of specialists, that deserve further conservation attention.

Keywords: Forest fragmentation, forest health indicator, forest specialist, insectivorous birds, niche differentiation.

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Author contributions: AAT initiated the project and AFS carried out the fieldwork which was co-supervised by JMA. AFS analysed the data and wrote the masnucript with input from JMA, AAT and CLP.

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INTRODUCTION

Bird communities in the tropics can be good systems to investigate complex interactions among sympatric species (Mansor & Mohd Sah 2012; Styring et al. 2016; Mansor & Ramli 2017; Sherry et al. 2020). How communities are structured are dependent on how they partition their resources and differentiate niches. Understanding how sympatric species utilise their resources can provide evidence about the coexistence of potential competitors (Morin 1999). Coexisting species in a community separate their ecological needs by resource partitioning along temporal, spatial, and behavioural niches (Mohd-Azlan et al. 2014). In general, when resources are a limiting factor, competitive interactions between species can result in non-random pattern of resource use (Morin 1999). Some studies on closely related species have shown that birds partition food resources by utilising different vertical strata, or by differential use of microhabitats (Styring & Hussin 2004; Mohd-Azlan et al. 2014).

Insectivorous birds consume a substantial amount of arthropods, hence their ecological importance in many ecosystems is significant (Nyffeler et al. 2018). Many studies have demonstrated the effects of forest disturbance on insectivorous birds, which may be linked to the decline of insect communities particularly certain insect groups (Didham et al. 1996; Didham 1997; Şekercioğlu et al. 2002; Stratford & Stouffer 2015; Bowler et al. 2019). In the tropics, understory insectivores are characterized by high habitat specificity and lower mobility relative to other passerines (Şekercioğlu et al. 2002; Yong 2009). Thus birds of the understory strata are sensitive to forest disturbance (Thiollay 1992; Kattan et al. 1994; Stouffer & Bierregaard 1995; Canaday 1996; Stratford & Stouffer 1999) and they have adapted to occupy specialized niches when foraging for their insect prey (Sekercloğlu et al. 2002). For instance, small forest fragments have been shown to experience a decline in the number of invertebrates dwelling among the leaf litter and soil while increasing the generalist numbers at the forest edge (Didham et al. 1996; Didham et al. 1997). These changes can affect understorey insectivores that avoid relatively open or edge habitats and specialise on arthropod prey that hide within leaf litter and soil (Canaday 1996).

With the increasing reports on the effects of forest disturbance on arthropods in the tropics (Hamer et al. 1997; Chey et al. 1998; Holloway 1998; Lawton et al. 1998; Schowalter & Ganio 1999; Floren & Linsenmair 2001, 2003; Hartshorn et al. 2021), concerns over the associated effects on insectivorous birds are also raised. Equally, there is a need for more in-depth study on the foraging ecology of the tropical insectivorous birds in the tropics so as to determine which species are particularly affected by or resilient to forest disturbance.

In southeastern Asia, babblers primarily refer to two insectivorous families, namely Timaliidae (54 extant species) and Pellornidae (64 species), the majority of which rely on forest or wooded habitats. As many babbler species are sedentary, with poor ability to disperse across non-forest habitat (Yong 2009), and are associated especially to lower forest strata of forest interior, they serve as suitable indicators of the level of forest disturbance (Lambert & Collar 2002; Hamer et al. 2015). Past studies based on relative abundance have shown that certain babbler species (Hussin & Francis 2001; Lambert & Collar 2002; Moradi & Mohamed 2010) and even specific feeding guilds (Johns 1986; Yong et al. 2011) are sensitive to forest fragmentation.

In the tropical forests of Malaysia, babblers form a major portion of the diverse middle and understorey avian insectivores (38 species; Puan et al. 2020), with high numbers of congeneric and sympatric species (Lambert & Collar 2002). This makes them suitable candidates for the research on avian community ecology including trophic diversification, resource partitioning and functional morphology, all of which are essential in driving the associated biotic community assembly in the tropical forests. Such research is feasible by examining their diets, which comprises of indigestible exoskeletons of arthropods, as demonstrated in studies elsewhere on food partitioning (Kent & Sherry 2020; Sherry et al. 2020), seasonal dietary patterns in relation to changes in the environment (Poulin et al. 1992) or abundance of resources (Yard et al. 2004). In central Peninsular Malaysia, Mansor et al. (2018) found little dietary overlaps among 12 babbler species. Despite most being morphologically similar (Styring et al. 2016; Mansor & Ramli 2017; Puan et al. 2018), niche differentiation with respect to foraging tactics have been demonstrated based on opportunistic visual observations on the Malaysian babbler species (Mansor & Mohd Sah 2012; Mansor et al. 2015; Styring et al. 2016; Mansor & Ramli 2017). Owing to their diversity and specialised feeding guilds of being terrestrial, foliage and/or bark gleaning insectivores (Johns 1986; Mitra & Sheldon 1993; Yong et al. 2011), this study examined niche segregation, i.e., diet and foraging strata, of 15 sympatric babbler species found in Sarawak, Borneo.

MATERIALS AND METHODS

Study sites

A total of nine sampling sites were chosen in Sarawak, eastern Malaysia, which can be grouped according to Pelagus (three sites), Ulu Baleh (three sites), and Baram (three sites) (Figure 1). Pelagus is located about 33 km from the Kapit town and the three sampling sites were Nanga Benin (2.165°N, 113.074°E), Nanga Pelagus (2.171°N, 113.055°E) and Nanga Peraran (2.193°N, 113.118°E) located along Batang Rajang River. Ulu Baleh is located along the Baleh River which is about 176 km from Kapit town. The three sampling sites were Nanga Gaat (1.645°N, 113.133°E), Putai (1.595°N, 113.791°E) and Long Singut (1.560°N, 114.202°E). Baram is located about 120 km from the Miri city. The three sampling sites were Long San (3.293°N, 114.779°E), Selunggo (3.208°N, 115.185°E) and Lio Mato (3.174°N, 3.174°E). Except the Pelagus National Park, all sampling sites comprised logged over secondary forests located close to human settlements and some agriculture lands.

Bird sampling

From December 2014 to March 2016, three double-stacked mist-nets (measuring 9 × 4 m each) were deployed from 0600–1830 h for four consecutive days at each of the two sampling stations at each site. The distance of the two stations was 100–1000 m away from human settlement areas, so as to assess the effects of anthropogenic disturbance on birds in another study (Mohd-Azlan et al. unpubl. data). The double-stacked nets were set vertically to create six shelves representing foraging strata based on the distance from the forest floor, i.e. Shelves 1 and 2 were categorized as low strata (0–1.2 m from the forest floor), Shelves 3 and 4 as mid strata (1.3–2.4 m) and Shelves 5 and 6 as high strata (2.5–3.6 m). All birds caught were weighed, measured and had the capture shelve numbers recorded.

Diet analysis

All babbler species, except juveniles and birds caught during the first hour of the sampling (Lopes et al. 2005), were administered with tartar emetic (Poulin & Lefebvre 1995; Zduniak 2005) before being released immediately. Depending on body weight and species, careful administration of acceptable concentration of tartar emetic solution (Sing-Tyan et al. 2017) will extract stomach contents via regurgitation. For every 100 g of the body mass, a dosage of 0.8 ml of 1.2% potassium antimony tartrate was used (Durães & Marini 2003). The regurgitated items and faeces were preserved using 70% alcohol in the field before being examined under a compound microscope in the laboratory. All prey items were identified up to taxonomic order and each order

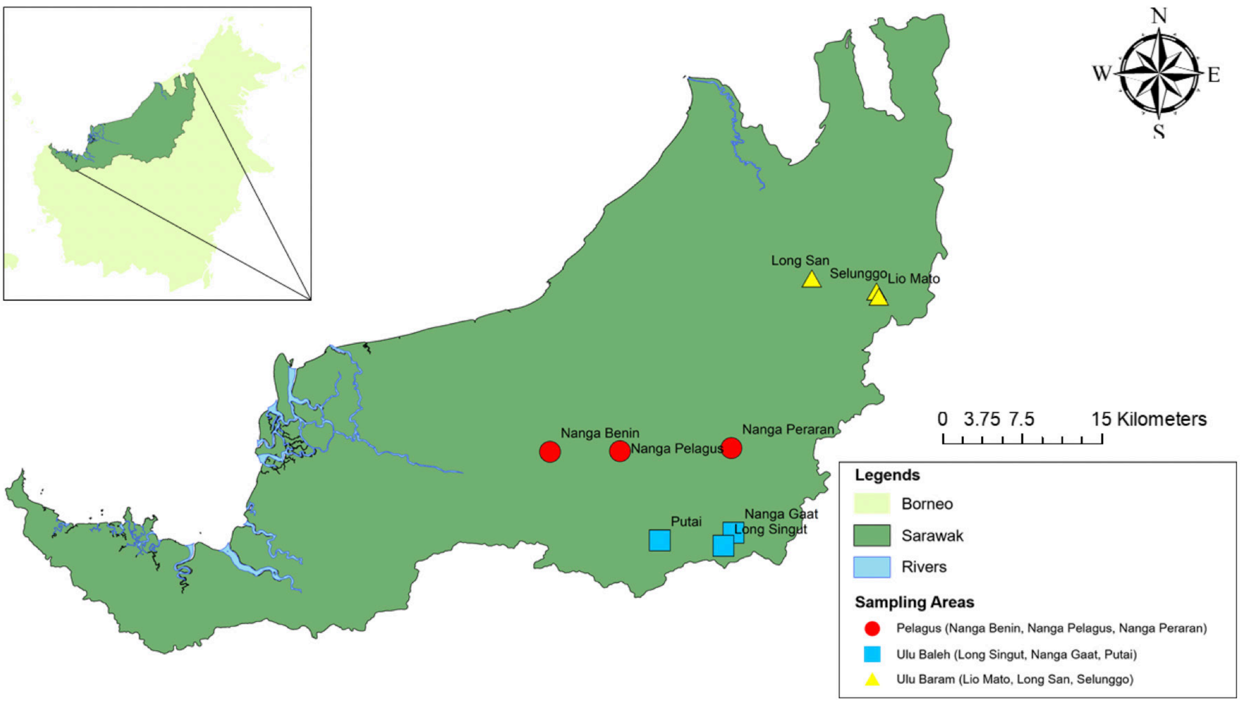

Figure 1. Mist netted areas located in the interior parts of Sarawak within the Heart of Borneo Forest Complex: A—Long San | B—Selunggo | C—Lio Mato | D—Nanga Benin | E—Nanga Pelagus | F—Nanga Peraran | G—Putai | H—Long Singut | I—Nanga Gaat.

found in an individual sample was counted as one prey item.

Data analysis

Analysis of bipartite ecological webs (Dormann et al. 2017) was performed to visualize and calculate indices representing the pattern of ecological networks among prey and predators. Berger-Parker dominance index was also calculated to determine whether babblers are specialized in food choice or polyphagous. Species diversity and evenness were assessed using Shannon (H') and Pielou's (J) evenness indices (Oksanen et al. 2013), respectively, whereas overlaps of prey items among babbler species were assessed using Pianka index (EcoSimR package; Gotelli & Ellison 2013). The outputs of prey item overlap analysis are a histogram of which its skewness represents the degree of overlap, i.e., left-skewed indicating a low overlap in the diet and right-skewed if otherwise. This is followed by two graphical plots with circles indicating the observed and simulated diet segregation pattern, i.e., a circle represents the relative consumption of prey category and its size is proportional to the level of such consumption. In other words, if there is no overlap of prey items among the babbler species, no circle will be present. Analyses were performed using R version 3.3.1 (R Core Team 2016).

RESULTS AND DISCUSSION

Species diversity and foraging strata

Over 4,800 net-hours, a total of 222 individuals representing 15 babbler species (nine from Pellorneidae and six from Timaliidae) were caught during this study (Table 1). This represents more than 50% of the babblers recorded in Sarawak. The Black-throated Babbler (*Stachyris nigricollis*, n = 32) was the most common species caught for all sites, followed by Short-tailed Babbler (*Trichastoma malaccense*, n = 25). The most common abundant species recorded for each site was White-chested Babbler (*Trichastoma rostratum*, n = 11) in Pelagus, Rufous-crowned Babbler (*Malacopteron magnum*, n = 18) in Ulu Baleh and Chestnut-winged Babbler (*Stachyris erythroptera*, n = 12) in Baram. Based on the Shannon diversity index, Ulu Baleh had the highest species diversity (*H'* = 2.314), followed by Baram (*H'* = 2.238) and Pelagus (*H'* = 2.193). The distribution of individuals among species was more even in Ulu Baleh and Baram compared to Pelagus (Table 1).

The babblers showed a segregation in foraging strata, with half of the species captured frequenting low strata while only three were at mid strata and four at high strata. Both, species richness and abundance were found to decrease when the foraging height increased. All species were found foraging mostly at a height of less than two meters, while others such as the Babbler Fluffy-backed Tit-babbler, Ferruginous, Scaly-crowned, Chestnut-rumped, Black-throated, Grey-hooded Babblers only occasionally go higher (2.5–3.6 m), whereas the Black-capped Babbler is strictly below one meter. This implies some form of niche segregation among the sympatric babbler species. It should be noted that the foraging height recorded in this study was solely based on the vertical capture location of double-stacked mist-nets, which may not entirely represent the foraging height. It also covered flying height of the babblers.

Diet composition

A total of 136 prey items were retrieved from regurgitated and faecal samples of 13 babbler species which comprised eight insect orders, plus one arachnid and one gastropod. Of those identifiable prey items, Coleoptera (41.5%), Hymenoptera (36.2%), and Araneae (12.3%) formed the major diet of babblers (Table 2). Based on analysis of bipartite ecological webs (Figure 2), Sooty-capped and Black-capped Babblers are specialists that feed solely on Coleoptera. Among all the babbler species, Fluffy-backed Tit-babbler seems to have the most generalized diet, covering seven insect orders. With respect to diet overlap analysis (Figure 3), the histogram was skewed to the left indicating that the diet overlap among the 13 babbler species was low. The prey items that heavily overlapped were from Categories 1 (for Araneae), 2 (Caterpillar), and 3 (Cicaedae). On the other hand, prey items that did not overlapped were from Categories 6 (Diptera), 9 (Hymenoptera), 10 (Orthoptera), and 11 (Phasmidae).

Being terrestrial, foliage and/or bark gleaning insectivores, the major prey groups of the babblers comprises of relatively more terrestrial (i.e., Coleoptera, Hymenopter,a and Araneae of understory level, similar to Mansor et al. (2018), except Blattodea) rather than aerial arthropods (but see Mansor et al. 2021). The abundance of Hymenoptera such as ants and Araneae (spiders) on the forest floor (Griffiths et al. 2018; Hartshorn et al. 2021) as well as those in the aerial leaf litter (Mansor et al. 2019) might be a reason that they formed a major portion of the babblers' diet. With respect to nutritional composition, Coleoptera and Araneae were found to contain higher portions of crude protein and lipids than Hymenoptera (Razeng & Watson 2015). Both protein and lipids (e.g., fats) are crucial for bird growth

Table 1. Species and number of individuals of babblers caught in Pelagus, Ulu Baleh, and Baram.

Common name	Species name	Study sites			Foraging strata		
		Pelagus	Ulu Baleh	Baram	Understorey	Mid-storey	Sub-canopy
Pellorneidae							
Rufous-crowned Babbler	*Malacopteron magnum*	3	18	0	11	10	0
Salvadori's Babbler	*Malacocincla sepiaria*	0	16	2	16	2	0
Scaly-crowned Babbler	*Malacopteron cinereum*	1	11	3	11	2	2
Sooty-capped Babbler	*Malacopteron affine*	1	4	0	2	3	0
Moustached Babbler	*Malacopteron magnirostre*	1	0	0	1	0	0
White-chested Babbler	*Trichastoma rostratum*	11	11	1	17	6	0
Short-tailed Babbler	*Trichastoma malaccense*	10	5	10	18	7	0
Ferruginous Babbler	*Trichastoma bicolor*	7	7	3	13	3	1
Black-capped Babbler	*Pellorneum nigrocapitatum*	1	0	3	4	0	0
Timaliidae							
Black-throated Babbler	*Stachyris nigricollis*	8	13	11	15	15	2
Grey-headed Babbler	*Stachyris poliocephala*	6	3	5	11	3	0
Chestnut-rumped Babbler	*Stachyris maculata*	1	2	4	4	2	1
Grey-hooded Babbler	*Cyanoderma bicolor*	1	5	12	12	4	2
Fluffy-backed Tit-babbler	*Macronous ptilosus*	3	8	5	7	8	1
Bold-striped Tit-babbler	*Mixornis bornensis*	1	0	6	6	1	0
Shannon index (*H'*)		2.193	2.314	2.238			
Species evenness (*J*)		0.867	0.941	0.919			
Total individual		55	103	65			
Total species		14	12	12			

Table 2. Prey item composition identified up to order.

Taxa	Pelagus	Ulu Baleh	Baram	Total
Coleoptera	21	14	19	54
Hymenoptera	8	24	15	47
Araneae	8	6	2	16
Orthoptera	0	2	2	4
Hemiptera	1	1	0	2
Phasmida	1	1	0	2
Dictyoptera	0	1	1	2
Diptera	1	0	0	1
Cicaedae	0	1	0	1
Gastropods	1	0	0	1
Unidentified	5	0	1	6

(Klasing 2000). Diet overlaps among babblers in this study were relatively low, consistent with reports from central Peninsular Malaysia (Mansor et al. 2018, 2021). The differences noted in foraging tactics might be one of the factors influencing the diet of the babbler species and vice versa. In addition, low diet overlaps of these birds could also be due to potential shifts in foraging behaviour when joining heterospecific feeding flocks (Mansor et al. 2020), which awaits further investigation in the case of Bornean babblers.

CONCLUSION

In the tropics where species diversity is high, resource partitioning and niche differentiation are essential evolutionary adaptions that lead to character displacement and reduce the competition among sympatric species (Wiens 1989). The use of different forest strata, either vertically or horizontally, and food resources by birds are common ecological strategies to reduce interspecific competition. Our study demonstrated the possible presence of spatial and trophic niche segregation among 15 babbler species in eastern Malaysia, some of which are likely to be specialists while others are generalists. Similar to other more localised

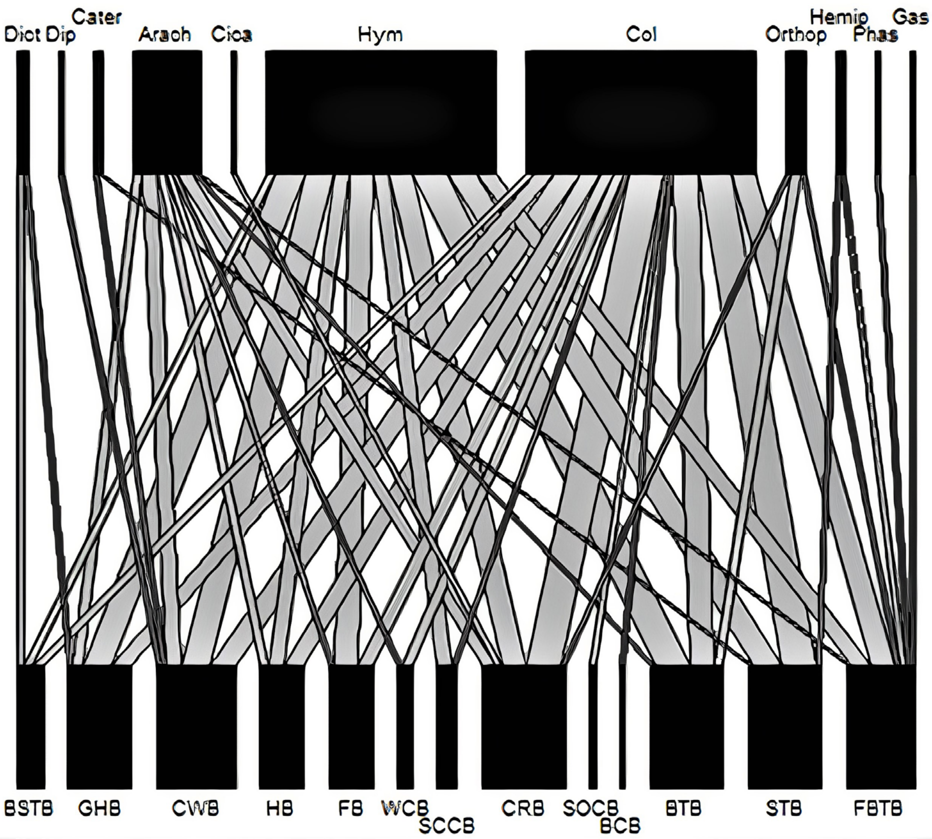

Figure 2. Analysis of babbler diets according to prey taxa. Widths of links are scaled to reflect interaction frequencies, while bar sizes indicate total interaction frequencies (Voon et al. 2014): BSTB—Bold-striped tit-babbler | GHB—Grey-headed Babbler | CWB—Chestnut-winged Babbler | HB—Horsfield's Babbler | FB—Ferruginous Babbler | WCB—White-chested Babbler | SCCB—Scaly-crowned Babbler | CRB—Chestnut-rumped Babbler | SOCB—Sooty-capped Babbler | BCB—Black-capped Babbler | BTB—Black-throated Babbler | STB—Short-tailed Babbler | FBTB—Fluffy-backed Tit-babbler | Dict—Dictyoptera | Dip—Diptera | Cater—Caterpillar | Arach—Araneae | Cica—Cicaedae | Hym—Hymenoptera | Col—Coleoptera | Orthop—Orthoptera | Hemip—Hemiptera | Phas—Phasmida | Gas—Gastropoda.

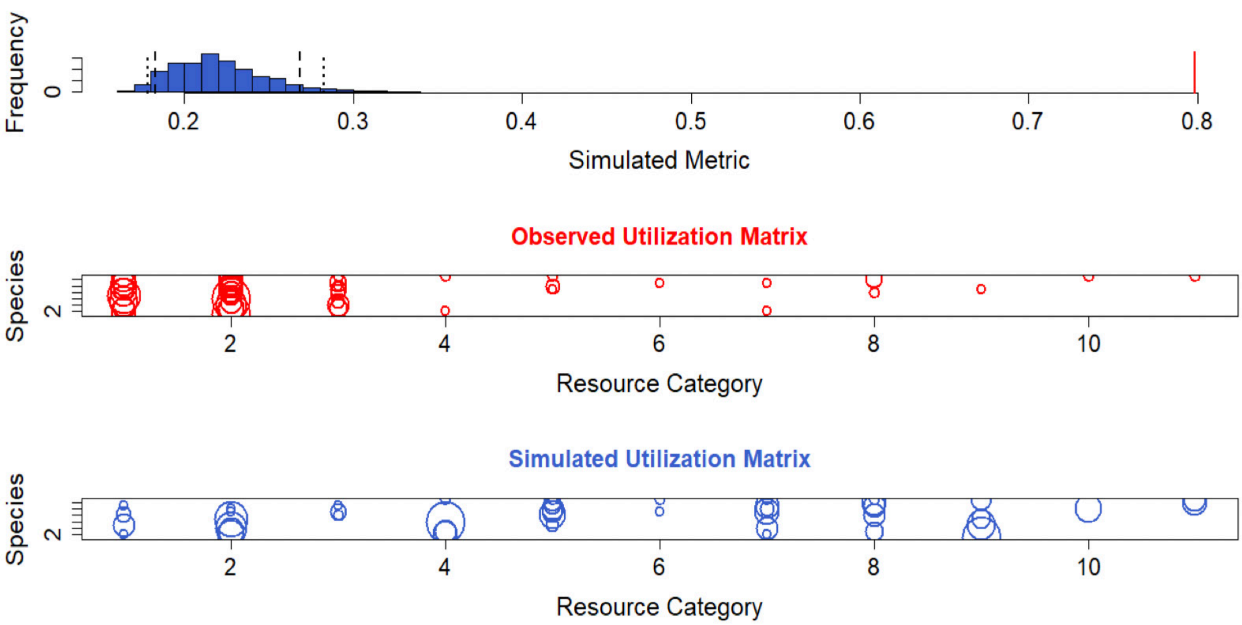

Figure 3. Diet overlap analysis (resource category input: 1—Araneae | 2—Caterpillar | 3—Cicaedae | 4—Coleoptera | 5—Dictyoptera | 6—Diptera | 7—Gastropoda | 8—Hemiptera | 9—Hymenoptera | 10—Orthoptera | 11—Phasmidae.

studies conducted in Malaysia, our study supported that different foraging tactics (Mansor & Mohd Sah 2012; Mansor et al. 2015, 2018; Styring et al. 2016; Mansor & Ramli 2017), foraging area and prey preference may have contributed to the difference in the diet of babblers (both Timaliidae and Pellornidae). Furthermore, prey size and type preference of the babblers in the Malaysian forests is believed to be influenced by predation and anti-predation strategies (Sherry et al. 2020) as well as possibly nutritional composition of the prey which deserve further investigation.

Having a feeding guild that is more terrestrial, foliage and/or bark gleaning in nature at the understory strata may render babblers, particularly those with specific spatial and trophic niches, exceptionally sensitive to habitat disturbance and fragmentation (Zakaria & Nordin 1998; Yong 2009). This implies that protection of this bird group, among others, is essential when forest management practices are being made. Their ecological role as indicators of forest ecosystem health (Lambert & Collar 2002; Hamer et al. 2015) is supported by our findings. It is also worth mentioning that two Near Threatened babbler species, i.e., White-necked Babbler (*Stachyris leucotis,* a rare slope specialist) and Grey-breasted Babbler (*Malacopteron albogulare,* an uncommon peat-swamp and heath forest specialist; Yong et al. 2014) are also found on Borneo, although not recorded in our study. Both species deserve more research and protective measures pertaining to their ecological requirements, trophic and spatial niches.

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