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Niche separation in flycatcher-like species in the lowland rainforests of Malaysia

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ABSTRACT

Niche theory suggests that sympatric species reduce interspecific competition through segregation of shared resources by adopting different attack manoeuvres. However, the fact that flycatcher-like bird species exclusively use the sally manoeuvre may thus challenge this view. We studied the foraging ecology of three flycatcher-like species (i.e. Paradise-flycatcher *Terpsiphone* sp., Black-naped Monarch *Hypothymis azurea*, and Rufous-winged Philentoma *Philentoma pyrhoptera*) in the Krau Wildlife Reserve in central Peninsular Malaysia. We investigated foraging preferences of each bird species and the potential niche partitioning via spatial or behavioural segregation. Foraging substrate was important parameter that effectively divided paradise-flycatcher from Black-naped Monarch and Rufous-winged Philentoma, where monarch and philentoma foraged mainly on live green leaves, while paradise-flycatcher foraged on the air. They also exhibited different foraging height preferences. Paradise-flycatcher, for instance, preferred the highest studied strata, while Black-naped Monarch foraged mostly in lower strata, and Rufous-winged Philentoma made use of the lowest strata. This study indicates that niche segregation occurs among sympatric species through foraging substrate and attack manoeuvres selection.

1. Introduction

Differences in microhabitat and resource utilization among closely-related bird species that inhabit the same geographical area have been widely reported in ornithological studies (e.g. Lara et al., 2011; Cloyed, 2014; Mansor et al., 2015; Styring et al., 2016). Coexistence of related species of similar sizes may result in specialization via fine-scale niche separation (May, 1974). Understanding how sympatric species employ unique foraging tactics from one another can assist in understanding how they co-exist in the same habitat (Robertson et al., 2013), particularly in tropical region that comprises of many species (Wells, 1976). Forest birds have adopted different ecological strategies in partitioning available resources, potentially shedding light on how birds' guilds respond to disturbances (Styring and Hussin, 2004). Habitat structure has previously been highlighted as important for forest birds as it provides many foraging opportunities (Whelan, 2001), which have subsequently shaped birds' foraging patterns (Robinson and Holmes, 1982).

Niche theory suggests that coexisting species in the same habitat will reduce interspecific competition through partitioning of shared resources (Lack, 1971; Chesson, 2000), and consequently important in structuring animal communities (Elton, 1927). Long-term competitive adaptation over evolutionary time may define the foraging strategies of a species with regards to resource exploitation. Sympatric species that adopt specific foraging tactics may result in targeting different prey items (Pulliam, 1985; Chapman and Rosenberg, 1991), consequently resulting in specialization. Specialization is associated with high foraging success based on the consistent use of selected foraging tactics over a period of time (Svanbäck and Eklöv, 2003) and morphological adaptation (Moermond, 1990). Any small differences in birds' morphological traits (e.g. wing shape and tarsus length) could mean the adoption of particular attack manoeuvres (Moermond, 1990). Birds' morphology is considered the main feature for limiting the type of attack manoeuvre they can employ that associated in substrate selection which generally leads to niche separation (Rolando and Robotti, 1985; Martin and Karr, 1990).

This study examines the foraging ecology of three flycatcher-like species (i.e., Paradise-flycatcher (*Terpsiphone* sp.), Black-naped Monarch (*Hypothymis azurea*), and Rufous-winged Philentoma (*Philentoma pyrhoptera*) that coexist in central Peninsular Malaysia by analyzing their foraging heights, foraging substrates, attack manoeuvres and foliage density use. The paradise-flycatcher, monarch,

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and philentoma are, however, considered sallying bird species (Wells, 2007), thus challenge the above view. These three flycatcher-like species use the sally manoeuvre for flycatching food items from one perch to another. Previously, these three species were grouped together within the family Monarchidae, generally consisting of large and robust flycatcher-like birds with bright plumage (Lekagul and Round, 1991; Fuchs et al., 2006). However, Rufous-winged Philentoma was reclassified due to their complexity and being closest relatives of the Malagasy Vangidae that consist of species from Africa and Asia (Moyle et al., 2006; Fuchs et al., 2012; Reddy et al., 2012). The former two species remain placed within the Old World Monarchidae that comprises three well-supported monophyletic clades including *Terpsiphone*, *Hypothymis* and *Trochocercus* (Pasquet et al., 2002; Fabre et al., 2012). Despite their phylogenetic dispersion, the three flycatcher-like species are having fairly similar morphology, voice and social behaviour (Wells, 2007). They show fairly similar morphology with respect to their body size, and have relatively long and slender bills with strong rictal bristles (Robson 2008; Jeyarajasingam and Pearson, 2012) that may help in aerial flycatching (Cunningham et al., 2011). Sympatric species with similar morphology are most likely employs different foraging strategies to stably coexist (Styring et al., 2016). Similarity in the usage of attack manoeuvres and frequently seen foraging together have given rise to the question of how these three flycatcher-like species partition their resources during the presence of other species in the same habitat.

Resident population of Asian Paradise-flycatcher (*Terpsiphone paradisi affinis*) is seasonally augmented by northern wintering subspecies (i.e. *T. paradisi incei*) and uncommon wintering migrant from continental Asia (i.e., Japanese Paradise-flycatcher *Terpsiphone atrocaudata*) (Wells, 2007). To avoid complication in distinguishing of these alike migratory subspecies and sister species (especially the females), we considered these birds as Paradise-flycatcher (*Terpsiphone* sp.). Previous studies have shown that the Asian Paradise-flycatcher (*Terpsiphone paradisi*) usually forages at higher levels and primarily flycatches their prey items in air, while Black-naped Monarch frequently sally on the underside of leaves (Mansor and Sah, 2012). We hypothesized that the use of attack manoeuvres and substrates by Asian Paradise-flycatcher and Black-naped Monarch are restricted by their similar morphological traits across different geographical area. In this context, differences in the use of foraging substrates to obtain food items definitely facilitate niche separation between the monarch and paradise-flycatcher. This niche partitioning allows them to stably coexist in the same geographical area (Hon-kai, 2009). However, more information is needed to gain further insight into their niche partitioning strategies, especially when the presence of other potential competitor species (such as Rufous-winged Philentoma) that occupy similar environments. Morphological similarities and sympatry of the studied species have also led us to hypothesize that these three flycatcher-like species should have different microhabitat preferences to coexist. Therefore, our study addresses the following questions: (1) how do these species forage in the wild and use vegetation to obtain their food items? and (2) how do these trophically similar species partition their resources by spatial dimensions?

2. Methods

2.1. Study area

Observations were made at Bukit Rengit area (3°35′40.02″N, 102°10′43.24″E), southern part of the Krau Wildlife Reserve, a protected area located in Pahang, central Peninsular Malaysia (Fig. 1). The reserve is the second largest protected area in Peninsular Malaysia (with an approximate size of 63,000 ha) after Taman Negara. Study sites comprised of a large area of old-growth forest (Clark, 1996) and can be considered lowland dipterocarp forest that is associated with dominant tree species including *Anisophyllea corneri*, *Mallotus penangensis*, *Gymnacranthera forbesii*, *Shorea macroptera*, *S. maxwelliana*, *S. lepidota*, and *Elateriospermum tapos* (Nizam et al., 2006). The reserve elevation ranges from 50 m at Kuala Lompat and about 80 m at Bukit Rengit to over 2000 m at the summit of Gunung Benum (Raemaekers et al., 1980). The reserve is drained by three main river systems – Sungai Krau, Sungai Lompat and Sungai Teris. The annual mean temperature is 26 °C, and average rainfall is roughly 2000 mm, with maximum rainfall between September and December and March and May, separated by two periods of minimum rainfall (Yusof and Sorenson, 2000).

2.2. Observations on foraging strategies

Focal species were located visually and randomly along several forest trails and followed opportunistically. Observations were made for 10 days/month for a period of 20 months, from February 2014 to September 2015. Birds were observed throughout the day (from 0730 h to 1830 h) but, for the most part, the observations were conducted in the early morning and late afternoon when most forest birds are actively seeking food. Birds were observed as long as they could be kept in view, but only the initial (independent) foraging observations, first sighting of an individual bird, were used for statistical analysis to avoid problems with non-independent data. At least 30 independent observations were recorded for each bird species in order to represent the observed behaviour accurately (Morrison, 1984; MacNally, 1994). Incidental observations of focal species joining mixed-species flocks were also recorded.

The following data were noted on each foraging bird encountered, namely foraging height, foraging substrate, attack manoeuvre, and foliage density.

Foraging height - the level from which a food item is taken by birds. The height of selected trees was marked for references. This was estimated to 2 m intervals and grouped into five height categories (FH1: > 0–2 m; FH2: > 2–4 m; FH3: > 4–6 m; FH4: > 6–8 m; FH5: > 8–10 m).

Foraging substrate – the material (microhabitat) from which a food item is taken by birds. These substrates were the leaf surface, the underside of the leaf, the branches, aerial leaf litter, and air. The term 'leaf surface' is used to denote the morphological upper side of a leaf, while 'underside of the leaf' indicates the morphological underside. Attack manoeuvre – the method for how food items were taken (attacked) by birds. This manoeuvre was categorized as follows: (i) stretch – birds completely extend the legs or neck to reach food items; (ii) hover – birds maintain an airborne position by flapping wings and spreading tail; and (iii) sally – birds fly from a perch to attack a food item and then return to a perch. The terminology and strategy used to characterize attack manoeuvres follows Remsen and Robinson (1990).

Foliage density – this parameter was measured on a subjective scale from 1 to 5 in a 1-m diameter sphere around the bird. A series of numbers from 1 to 5 denoting the proportion of area covered by vegetation (e.g. leaves, bushes), ranging from 1 (covering less than 5% of the area) to 5 (covering more than 75% of the area) following an adapted approach from Braun-Blanquet (1932) covered the abundance scale as described by Allen and McLennan (1983), Allen (1993), Bowes et al. (1994), and Hurst and Allen (2007).

2.3. Statistical analyses

Correspondence analysis (CA) was performed on raw data to extract foraging patterns of focal bird species in each niche dimension. CA is effective in analysing the categorical data and detecting similarities between the rows and columns of a data matrix (Miles, 1990). A hierarchical cluster analysis using correlation coefficients was applied to group the species into distinctive guilds based on the frequency of all foraging parameters. Both analyses were performed using the PAST software package (PAleontological STatistics) ver. 2.17 (Hammer et al., 2001).