

PHENOLOGY OF TROPICAL BIRDS IN PENINSULAR MALAYSIA: EFFECTS OF
SELECTIVE LOGGING AND FOOD RESOURCES

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Abstract

The increasing prevalence of human disturbance to the rainforests of tropical Southeast Asia through selective logging compels studies that examine the effects of such forest degradation on the vital life cycle events of their resident understory birds, which are especially sensitive to such degradation. Over 70% of the remaining rainforests in Peninsular Malaysia are earmarked for selective logging regimes, which are often considered alternatives to clear-cut logging. Phenological cues such as rainfall and food abundance can be important determinants of decisions to breed and molt among birds. Food abundance may be affected by forest degradation from selective logging, hence studies that compare food abundance, and breeding and molting simultaneously at the same sites are important for the ecological monitoring of such logging regimes. Correlation studies of the seasonal variation of avian diet and phenology with food abundance corroborate the observed effects of logging on avian life cycles.

Tropical avian seasonal patterns, phenological cues (i.e. environmental factors), and changes in food exploitation are not well studied in Southeast Asia. My study reveals no difference in the overall understory resident bird abundance, relative species richness, breeding and molting occurrence, and food abundance (i.e. arthropod, fruit and flower) between unlogged and 30-year-old selectively logged forests in two equatorial rainforest areas in Peninsular Malaysia, Southeast Asia. The understory birds from the selectively logged forests perform important life cycle events (i.e. breeding and molting) similarly to birds from unlogged forests. Seasonal variation and frequency of occurrence of breeding and molting are comparable for understory birds in both selectively logged and unlogged

forests. The similar abundance of potential food resources observed in both forest types could have contributed to the similarity in avian phenological characteristics.

My study also demonstrates strong seasonality in avian phenology, and their potential food resources in both forests types. The breeding season generally coincides with an increased abundance of the main food for each feeding guild and diet data corroborate these findings. Breeding usually begins near the start of the half-yearly monsoon season. Hence, food abundance and rainfall during monsoons are possible cues for breeding in tropical Southeast Asian understory birds. Molting shows little correlation with rainfall or food abundance and occurs outside the breeding season for most individuals. Energy requirements may be more critical for breeding than for molting, and can constrain the timing of molt to periods of lower food abundance. Phenological cycles of sensitive indicator groups such as understory resident birds are dependent on food abundance and forest structure, and hence on human activities such as selective logging. Such data on avian breeding, molting and diet, and food abundance may be important indicators of forest regeneration and useful tools in the ecological monitoring of selectively logged forest habitats.

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1. Introduction

Polycyclic selective logging is the prevalent form of forest exploitation in the tropics, and is often proposed as a feasible alternative to clear-cut logging (Wong 1985, Lambert 1992, Johns 1996, Whitmore 1998, Hamer et al. 2003). Selective logging is particularly widespread in the Malay archipelago (Hamer et al. 2003). For example, over 70% of the remaining rainforests in Malaysia are earmarked for selective logging regimes (Nectoux and Kuroda 1989). Contrary to clear-cutting, selective logging in which collateral damage is minimized, retains much of the original floral structure capable of regeneration (Whitmore 1998). Studies of different faunal communities (e.g. butterflies, mammals and bird) have also shown long-term persistence and recolonization of selectively logged forests (e.g. Johns 1992, Hamer et al. 2003).

Whereas selective logging effects on avian community structure have been well documented, their impacts on critical avian phenology (e.g. breeding and molting) through changes in the food resource abundance are not so. Selective logging and other human activities can alter forest structure, community and phenology, and thus change the abundance of food resources utilized by different feeding guilds (Johns 1988, Whitmore 1991, Lambert 1992). Food resources are suggested to affect birds' decisions to breed and molt (Lack 1954, Perrins 1970, Stiles 1980, Poulin et al. 1992, Wikelski et al. 2000). Owing to rapidly changing land use by humans, reproduction of avian populations in selectively logged forests is key to their continuing survival, and the nature of the threat of such logging on this aspect of their ecology is thus worth investigating. This aspect can be examined through studies comparing the abundance of foods such as

arthropods, fruits and flowers, and the occurrence of breeding and molting of birds in logged versus unlogged forests.

The plethora of possible confounding factors affecting the breeding and molting of birds necessitates the corroboration of these data with correlative studies on avian phenology, diet and food abundance (Sodhi 2002a). The few studies in Southeast Asia that address this topic (e.g. Gibson-Hill 1952, Fodgen 1972) do not compare data collected from the same locations over the same period (Stiles 1980, Ahumada 2001, Stutchbury and Morton 2001). Because the seasonal variation in rainfall and food abundance may be different between years (Karr 1976), it is essential to measure all these variables at the same location over the same period. The partitioning of breeding and molting, which can be an indication of food resource abundance, is also not well understood in tropical Asian birds (Foster 1975).

Because understory tropical birds in Southeast Asia are especially sensitive to forest degradations, they have been considered indicators of forest quality (Wong 1985, Peh et al. 2005). Hence, data from this group of birds can be useful tools for the monitoring of the quality of habitats such as regenerating selectively logged forests. For this reason, my study focuses on these birds. I studied birds in two lowland humid rainforest areas of Peninsular Malaysia in equatorial Southeast Asia. I chose these locations because: 1) there has been little research on avian phenology there (Sodhi 2002a); 2) this region is rich in biodiversity (Sodhi et al. 2004a); and 3) the lowland rainforests and their rich

biodiversity are disappearing rapidly due to land use changes by humans (Brook et al. 2003, Sodhi et al. 2004a, b).

My specific objectives are:

1) To compare the food abundance (i.e. arthropods, fruits and flowers), and the frequency of occurrence of breeding and molting in resident understory tropical rainforest birds in unlogged and 30-year-old selectively logged forests. My hypothesis is that the avian breeding and molting occurrence would be similar in both forest types if food abundance was similar, since it has been shown elsewhere in Peninsular Malaysia that the avian breeding occurrence in 25-year-old regenerating selectively logged forests were not significantly different from those of virgin forests (Wong 1985, 1986).

2) To determine whether there is temporal variation in the breeding and molting of these birds, their main food resources and rainfall. My hypothesis that food abundance, rainfall, breeding and molting are seasonal stems from the occurrence of the biannual monsoon (Malaysian Meteorological Services, <http://www.kjc.gov.my/>).

3) To determine whether there is correlation of breeding, molting and diet of birds belonging to different feeding guilds, with rainfall and food resources. Information on diet changes during breeding and molting are important indicators of food exploitation strategies adopted by birds during periods of high-energy requirements (Recher 1990). My hypothesis is that the seasonal abundance of the main food of adult birds should

coincide with their breeding seasons, since this is the most commonly observed strategy adopted by tropical birds such as frugivores (Morton 1973).

4) To determine whether there is an overlap of molting and breeding at the guild and individual levels. My hypothesis is that there should be little overlap, because there are very few records of breeding and molting overlap in Asian tropical birds (Foster 1975).

2. Methods

2.1 Study areas

The study areas are located in Johor, Peninsular Malaysia, which lies mostly within the humid equatorial belt (Whitmore 1988). The study areas are called Bekok (2.38°N, 103.2°E) and Belumut (2.03°N, 103.6°E) (Fig. 1). Bekok (which is contiguous with Endau Rompin National Park) and Belumut, consist of lowland to hill dipterocarp primary tropical rainforests (80,000 ha and 30,000 ha, respectively) surrounded peripherally by secondary rainforests selectively logged at least 30 years ago (Whitmore 1984; Department of Wildlife and National parks, Peninsular Malaysia, <http://www.wildlife.gov.my/>; Richard Aldrich, Johor State Forestry Department, pers. comm.). I chose 30-year-old selectively logged forests because there have been few studies of mid-succession forests (e.g. Wong 1985, 1986), whereas most such studies have been performed on younger forests (e.g. Johns 1988, 1989). Under the Selective Management System (SMS) system adopted throughout Peninsular Malaysia since 1977, logging is only permitted on trees with a certain minimum diameter, such as 45 cm (Salleh 1988). Approximately 150 tree species, for example *Shorea curtisii* and *Dryobalanops aromatica*, are exploited for timber in these forests (Burgess, 1971). Most of the tall trees left in the sites are either of unsuitable species or trunk quality for the timber industry (Peh et al. 2005). While information on the exact size of the selectively logged forest is not available, each logged forest site is estimated to be several thousand hectares in area, based on the premise that the logged forests constitute the circumference of the unlogged forests (Peh et al. 2005). The areas are chosen because the selectively logged forests are contiguous with the unlogged forests in each study area, hence

allowing comparisons between forests with likely similar species composition. Further, the study areas are situated geographically close to each other, so comparisons between the study areas or pooling of data from both areas would be minimally affected by latitudinal and longitudinal effects.

2.2 Fieldwork

Four study sites were established: one each in the unlogged and 30-year-old selectively logged forests in Bekok and Belumut. The study sites were given these acronyms: Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL) and Belumut logged (SBL). For correlation studies between phenology and food abundance, pooled unlogged and logged sites at Bekok and Belumut were referred to as Bekok and Belumut, respectively. In this thesis, the term “selectively logged forest” is occasionally abbreviated to “logged forest”.

The unlogged and selectively logged forest sites within each study area were located at least 1.7 km apart. All the study sites were situated less than 110 m above sea level in elevation (Peh K. S.-H., pers. comm.). Data were collected between 22 January 2003 and 26 February 2004 on alternate months from Bekok (23-31 January 2003; 22-30 March 2003; 22-29 May 2003; 22-30 July 2003; 1-9 October 2003; 4-11 November 2003; 5-12 February 2004) and Belumut (25 February-6 March 2003; 22 April-1 May 2003; 22-31 June 2003; 21-29 August 2003; 23-30 October 2003; 16-22 December 2003; 19-26 February 2004). Plant, arthropod and bird data were collected concurrently in the unlogged and selectively logged forests during each sampling trip lasting from nine to 11

days. One 700-m fixed line transect was established from existing human trails at each site for all data collection. In some locations where the human trails were overgrown, a minimal clearing was made to allow for the setting up of mist-nets. Altogether, seven sampling trips were made each to Bekok and Belumut. Monthly rainfall data were compiled from the Malaysian Meteorological Service (www.kjc.gov.my).

2.3 Fruit and flower data

Fruit and flower abundance were evaluated through the number of fleshy fruits and flowers observed within 5 m along each transect. From the frugivorous bird's perspective, the absolute fruit abundance was probably more important than the number of fruiting individual plants or species (Levey 1988), and the same was assumed for flowers, because fruit from most plant species were fed on by more than one bird species and vice versa (McClure 1966, Corlett 1990). The lack of a complete published plant species list for any rainforest area in Southeast Asia (Corlett 1990) made the identification of potential food plant species impractical. Instead, I applied the fruit dispersal syndrome according to Van der Pijl (1982), whereby a bird-dispersed fruit was identified by its fleshiness and red, blue or black color when ripe. All flowers were assumed to be potential nectar sources for birds. Although this method did not represent the precise amount of plant food available to birds, it was taken as an index of the relative fruit and flower abundance between months and between study sites, because the sampling methods and transects were standardized for the study period and for each study site.

2.4 Arthropod data

Arthropod biomass was evaluated using three trapping methods: baffle traps, window traps and yellow pan traps (for details on trap design, see Upton 1991). Three trapping methods were used simultaneously to reduce bias in the trapping efficacy of different arthropod orders by different methods, because the aim was to trap a wide variety of arthropods, based on the assumption that more than one order of arthropod was eaten by birds. Baffle traps were suspended between 3 and 5 m from branches. Window traps (similar in operation to the Malaise trap) were set up at ground level and were 1 m tall. Yellow pans were combined with window traps and served as collecting pans for the window traps. Baffle and window traps targeted mostly flying arthropods at different heights, whereas yellow pans targeted both flying and ground arthropods. Four baffle traps, five window traps and 25 yellow pans were set up at 100-m intervals along each transect and operated for 72 hours during sampling months at each site; i.e. seven times during the study period. Arthropods caught were collected after every 24 hours and preserved in 70% alcohol. All arthropods were counted, sorted to order level (following Borror et al. 1989), measured for body length (<5mm long individuals were excluded), dried at 70°C, and weighed. Although my sampling protocol did not indicate the absolute arthropod availability to birds, the arthropod biomass was taken as an indication of the relative arthropod abundance between months and study sites because the trapping methods were standardized for the study period and for each site. The arthropod biomass from the three trapping methods was pooled for the statistical analyses to reduce bias from the different trapping methods.

2.5 Avian phenology

Avian phenology was assessed using mist-nets. This method introduced bias in estimates of bird community structure and dynamics, and under-represented canopy and less active species (Karr 1981). However, it was chosen because it reduced observer bias and skills, allowed identical sampling of different habitats (Karr 1981, Schemske and Brokaw 1981), and allowed close examination of the breeding, molting and age conditions of the birds (Sodhi 2002b). Mist-nets also enabled the collection of bird fecal samples. Because of the nature of the mist-net method, the focal species of this study were understory birds, fruits, flowers and arthropods. Understory tropical forest birds, being sensitive to forest disturbance, are considered useful indicator groups of the regeneration status of disturbed forests (Wong 1985), and hence are the ideal group for studies of the effects of selective logging. It has been suggested that ground- and understory-dwelling forest birds are more sensitive to disturbance such as logging and have a higher extinction risk compared with species that occupy other vertical forest strata (discussed in Marsden 1998, Peh et al. 2005). Migratory birds were excluded from analyses.

Along each transect, ten mist-nets (12 m long; 30-mm mesh) were set up 2.5 m high, while four more mist-nets of the same dimensions were set up 5.0 m high, which was the upper limit of the lowerstory of tropical rainforests in Malaysia (Jeyarajasingam and Pearson 1999). Nets were operated for two days from 0730 hr to 1730 hr at each study site during each of seven visits. The total mist-net hours were 1880.0 (PB), 1890.5 (SB), 1887.0 (PBL) and 1888.5 (SBL). All captured birds were immediately placed in plastic boxes lined with paper towels to collect their fecal droppings. All birds were marked with

metal numbered and uniquely colored bands, weighed to the nearest milligram, and examined for age (using skull pneumatization, plumage and iris coloration, and presence of yellow skin on gape), sex and breeding (using presence of brood patch) and molting condition (Ralph et al. 1993). Molting condition was indicated by the presence of molting primary flight feathers on both wings (to rule out adventitious molting). The molt of primary flight feathers was chosen as it spanned almost the entire molting period (Avery 1985). Left and right tarsus and wing lengths were also measured to the nearest millimeter. Fecal droppings were preserved immediately in 70% alcohol. Fecal droppings were used as indicators of avian diet because the collection of stomach contents from killed birds or birds treated with emetics (which were not reliable and could stress or kill the birds) (Ford et al. 1982, Ralph et al. 1985) was not ideal for my study, because the study areas were gazetted as protected sites. Although fecal droppings were biased against more easily digested food items such as soft-bodied insects, they were considered an efficient alternative because the droppings could be collected easily from a larger sample of birds with little stress to them, hence minimally disrupting their normal cycles (Ford et al. 1982, Ralph et al. 1985). Although arthropods may be broken into small fragments, they may be identified easily to order level with sufficient practice and with reference to illustrations from entomological texts (Ford et al. 1982, Ralph et al. 1985). Fecal samples were analyzed under a dissecting microscope. Food items were counted following the method by Ralph et al. (1985). For arthropods, I compared the number of body parts of distinct size, shape and color and categorized them into the minimal possible number of arthropods based on characteristic structures (e.g. the distinct comb shape of the Lepidopteran larval anal comb and the distinct double-hooked shape of the

Carabid larval mandible) (with reference to illustrations from Borror et al. (1989) and Ralph et al. (1985)). The number of a particular fragment, or one-half that if it occurred in a matched pair, was the estimate of the number of individuals represented (for more details, see Ralph et al. 1985). Seeds and fibrous tissue were taken to represent fruit intake (Poulin et al. 1992). Because nectar was completely assimilable (Remsen et al. 1986), its consumption was evaluated through the presence of pollen grains in the fecal samples (Poulin et al. 1994). The “enumeration of occurrences or frequencies” method based on the number of fecal samples in which each food type was found, was used to assess quantitatively the diet of the birds (Hartley 1948).

2.6 Statistical analyses

Scatterplots of mass versus number of individuals were plotted of the arthropod data to identify outliers, which were excluded from subsequent analyses, because a small number of outliers with extremely high mass would bias the correlation results (StatSoft, Inc. 2004). Five outliers were identified and excluded. All data on arthropod, fruit and flower abundance, and proportion of breeding and molting adults, and juveniles were tested for normality using Kolmogorov-Smirnoff; non-normal data were log-transformed or arcsin-square-root-transformed. All data were tested for temporal autocorrelation (i.e. non-independence) by calculating their sample autocorrelation coefficients (rk) and plotting them on autocorrelograms (Legendre and Legendre 1998). The coefficient rk was a representation of the correlation between samples in a time series, separated by k time units. The rule of thumb method ($2/\sqrt{n}$) was used to determine the significance of each autocorrelation coefficient at alpha 0.05. All the data tested for temporal autocorrelation

using this method were found to be independent. The recapture rates (mean \pm standard deviation) for individual birds were 0.3 ± 0.7 (PB), 0.3 ± 0.6 (SB), 0.4 ± 0.8 (PBL), and 0.3 ± 0.6 (SBL). The data from recaptured birds were treated as independent data because the recapture rates were low and the autocorrelation tests established their independence.

2.6.1 Species richness estimation

Coleman curves were plotted using EstimateS 7 (Colwell 2004) and compared with nonparametric incidence-based estimators Chao2 and ICE, and Michaelis-Menten model-based estimator MMMean, for indications of bird-sampling completeness and estimated species richness at each site (Chao 1987, Raaijmakers 1987, Lee and Chao 1994). These estimators have been found to perform best for tropical bird species (Walther and Martin 2001, Herzog et al. 2002, Matlock et al. 2002).

2.6.2 Guild classification

A hierarchical agglomerative clustering method based on the percentage occurrence of food items in 394 fecal samples was used to categorize the birds into three major feeding guilds: insectivores, frugivore-insectivores and nectarivore-insectivores. The guild definition followed the original definition by Root (1967), which defined a guild as a group of species that fed on the same food type in the same way. The method using percentage of food occurrence reduced size and mass bias between different food types (Poulin et al. 1992). I chose species with at least five fecal samples for this analysis because this satisfied the minimum sample size recommendations (i.e. four) for adequate diet representation within each bird species (Cooper et al. 1990).

2.6.3 Food abundance, and breeding and molting occurrence analyses

Two-sample t-tests were performed to test for differences in the abundance of arthropods, fruits, flowers and birds (excluding recaptures) between pooled selectively logged and unlogged sites, and between Bekok and Belumut study areas. Because many small arthropods could have less nutritional value than that of fewer large arthropods of the same dry mass, I compared the size class distribution of arthropods between the pooled selectively logged and unlogged sites using a chi-squared test of goodness-of-fit. Chi-squared contingency tests were performed to test for differences in the proportions of breeding versus non-breeding adults, molting versus non-molting adults and juveniles versus adults, and in the number of individuals in each feeding guild between these sites.

2.6.4 Seasonality analyses

Chi-squared tests of goodness of fit were performed to test for differences in breeding and molting seasonality between the study sites for each feeding guild. The unlogged and 30-year-old selectively logged forest sites at Bekok and Belumut, respectively, were not found to be significantly different ($P > 0.05$, Table 1); hence, they were pooled for subsequent analyses. Data pooling was performed for the seasonal analyses because of the small bimonthly sample sizes. However, the difference in seasonality of breeding, and molting adults, and juveniles between Bekok and Belumut was significant ($\chi^2 = 25.75$, $\chi^2 = 13.98$, $\chi^2 = 19.13$, $P < 0.001$, $P = 0.03$, $P = 0.004$, $df = 6$), so they were analyzed separately. All subsequent analyses were performed on pooled data from Bekok unlogged and selectively logged sites and pooled data from Belumut unlogged and selectively logged sites, respectively.

Kruskall-wallis tests were performed to determine whether the abundance of arthropods varied over different sampling months at Bekok and Belumut study areas. Chi-squared tests of goodness of fit to a uniform distribution were performed to determine whether fruit and flower abundance and the proportion of breeding and molting adults and juveniles were significantly variable over different sampling months at Bekok and Belumut study areas for each feeding guild.

All data for seasonal analyses were detrended using autoregressive integrated moving average (ARIMA) trend analysis, and the residuals were used for temporal cross-correlation analyses (Legendre and Legendre 1998). Temporal cross-correlation tests were performed on the bimonthly data for rainfall, arthropod biomass, and fruit and flower abundance, and the proportion of breeding and molting adults and juveniles in each feeding guild. The cross-correlation coefficient (r) was a representation of the correlation between variables. The rule-of-thumb method ($2/\sqrt{n}$) was used to determine the significance of each correlation test at alpha 0.05. No correction for multiple testing was carried out because the number of tests for each set of data was less than 20, at the alpha level of 0.05 (Bland and Altman 1995).

The seasonal variation in the diet of birds in each feeding guild was calculated using the percentage occurrence of different food categories in bimonthly fecal samples in each guild. This method reduced size and mass bias between different food items (Poulin et al. 1992). No statistical analysis was performed on the diet data because of the small bimonthly sample sizes (a total of 394 fecal samples).

2.6.5 Body condition index

The body condition indices (BCI) of insectivores in Bekok and Belumut were calculated using the mean measurements of tarsus and wing lengths, and body mass, following the method by Kanuscak et al. (2004). First axis scores from principal components analyses (PCA) on normal or log-normal mean tarsus and wing lengths were used to generate a body size index for each species. The axis scores were then regressed against body mass. Regression residuals formed an index of body condition, with larger values indicating better condition. Only eight species with at least five individuals each in Bekok and Belumut were selected for this analysis. The BCI of insectivores from Bekok and Belumut were compared using a Mann-Whitney test for non-normal data.

2.6.6 Breeding and molting overlap

Breeding and molting overlap at the individual level was determined by calculating the proportion of individuals exhibiting both conditions from the pooled total number of individuals at the four study sites.

All analyses were performed using Minitab release 14.1 (2003) and EstimateS 7 (Colwell 2004). Graphs were prepared using GraphPad Prism version 4.02 (2004). Appendix 1 lists the arthropod, fruit and flower abundance at each study site. Appendix 2 lists the bird species, guild membership, and number of juveniles, adults and actively breeding and molting adults caught at each site. Appendix 3 lists the number of birds in each guild at each site. Appendix 4 lists the percentage of each food category in the fecal samples of each guild. Appendix 5 lists the size class distribution of arthropods caught in each site.

3. Results

3.1 Bird sampling completeness

A total of 465 individuals representing 48 resident species was caught over 7546 mist-net hours at the four study sites. No individual bird was caught in more than one study site. Coleman curves showed that asymptotes were apparently reached in PB, SB and SBL (Fig. 2). Sampling completeness was estimated to range from 64-75% (for PB), 70-82% (for SB), 68-80% (for PBL) and 66-74% (for SBL) (Table 2). Estimated species richness was similar between unlogged and selectively logged sites (Table 2). Because my data were collected from only one transect at each study site, the estimated species richness values were not taken as absolute representations of the study sites. Rather, they were taken as indications of the relative bird species richness between study sites, because the sampling methods were standardized for each site.

3.2 Bird feeding guild membership

Diet analysis using hierarchical agglomerative clustering analysis revealed three guilds: insectivores, frugivore-insectivores and nectarivore-insectivores (Fig. 3). The mean percentage of each food category in the fecal samples was similar within, and different between guilds, as shown by the generally low standard deviation values (Appendix 4) (Poulin et al. 1994). Insectivores ate mostly arthropods (91%), frugivore-insectivores ate fruits (56%) and arthropods (43%) in similar proportions, and nectarivore-insectivores ate nectar (47%) and arthropods (45%) in similar proportions. There was no difference in the relative proportion of individuals in each avian feeding guild in the pooled unlogged forests and pooled selectively logged forests ($\chi^2 = 4.85$, $df = 2$, $P = 0.09$). However, the

proportion of individuals in each feeding guild in Bekok (pooled unlogged and selectively logged forests) was different from that in Belumut (pooled unlogged and selectively logged forests) ($\chi^2 = 83.83$, $df = 2$, $P < 0.001$, Appendix 3). Because the number of frugivore-insectivores and nectarivore-insectivores was low, the avian phenology of Belumut was assessed using only insectivores.

3.3 Overall bird and food abundance of unlogged forests and selectively logged forests

The bird, arthropod, fruit and flower abundance were not different between the unlogged and selectively logged forests ($T = 0.49$, $T = -0.33$, $T = -0.85$, $T = -1.8$, $P = 0.63$, $P = 0.74$, $P = 0.41$, $P = 0.10$, $df = 12$). There was no significant difference in the arthropod size-class distribution between the unlogged and selectively logged forests ($\chi^2 = 29.18$, $df = 21$, $P = 0.11$, Appendix 5). There was also no difference in the proportion of juveniles, breeding and molting adults for all birds and for individual guilds between the unlogged and selectively logged forests (Table 3).

3.4 Rainfall seasonality

The rainfall data showed highest rainfall in January and October 2003, and lowest rainfall in February 2003 and 2004 (Fig. 4). Peninsular Malaysia and other parts of Southeast Asia experienced biannual monsoon seasons. The North-East monsoon (November to March) made up the major rainy season in Malaysia, and brought heavy rainfall with it, whereas the South-West monsoon (from late May to September) was associated with drier weather (Malaysian Meteorological Service, www.kjc.gov.my).

3.5 Avian phenology

Because there was no difference in the overall bird and food abundance, and in the seasonality of juveniles, and breeding and molting adults between the selectively logged and unlogged forests in Bekok and Belumut (Tables 1 and 3), they were pooled for seasonal analyses and referred to as Bekok and Belumut, respectively. However, the seasonality of juveniles, and breeding and molting adults in Bekok and Belumut was significantly different (statistical results in Section 2.6.4), therefore they were analyzed separately. Because the phenological cycles and characteristics, and food abundance were similar in the unlogged and selectively logged forests, and because the seasonal data were collected in order to examine the relationship between phenology, diet and food resource abundance, no distinction was made between selectively logged and unlogged forests for that part of the study.

There was seasonality in the breeding and molting for birds in Bekok and Belumut study areas. The two peak breeding periods were from April to June and November to December. The molting period was from July to August (Fig. 5). Bekok showed a significant seasonality in the occurrence of breeding and molting adults for all guilds combined ($\chi^2 = 26.38$, $\chi^2 = 55.88$, $P < 0.001$, $P < 0.001$, $df = 6$), but not for juveniles ($\chi^2 = 7.00$, $df = 6$, $P = 8.14$). Belumut showed a seasonality in the occurrence of juveniles, breeding and molting adults ($\chi^2 = 21.60$, $\chi^2 = 22.80$, $\chi^2 = 59.00$, $P < 0.001$, $df = 6$).

3.6 Seasonality of food resources

Bekok showed significant seasonal variation in arthropod abundance, with an increased abundance in May and February ($H = 13.54$, $df = 6$, $P = 0.04$, Fig. 6). Although there was a small increase in arthropod biomass in December in Belumut, there was no apparent seasonality in arthropod biomass for this study area ($H = 9.67$, $df = 6$, $P = 0.14$; Fig. 6).

Bekok showed significant seasonal variation in fruit abundance, with an increased quantity in January, July and November ($\chi^2 = 4231.30$, $df = 6$, $P < 0.001$; Fig. 6).

Belumut also showed significant seasonal variation, with increases in April and June 2003 and February 2004 ($\chi^2 = 3739.30$, $df = 6$, $P < 0.001$; Fig. 6). Bekok showed significant seasonal variation in flower abundance, with an increased quantity in January and May 2003 and February 2004 ($\chi^2 = 2939.90$, $df = 6$, $P < 0.001$; Fig. 6). Belumut also showed significant seasonal variation, with an increased quantity in January and August 2003 and Feb 2004 ($\chi^2 = 5105.80$, $df = 6$, $P < 0.001$; Fig. 6).

3.7 Correlation of avian guild phenology with food resources and rainfall

Insectivores in Bekok showed a significant positive correlation of the seasonal variation in the proportion of breeding adults with arthropod biomass (Table 4; Figs. 5 and 6).

Frugivore-insectivores in Bekok showed a significant positive correlation of the seasonal variation in the proportion of breeding adults and juveniles with fruit abundance (Table 4; Figs. 5 and 6). Insectivores in Belumut showed a significant positive correlation of the seasonal variation in the proportion of breeding adults with fruit abundance (Table 5; Figs. 5 and 6). Although there was no significant correlation of the seasonal variation in breeding and molting of all guilds with flower abundance in Bekok and Belumut (Tables

4 and 5), Figure 5 shows that the first peak in the proportion of breeding adult and juvenile nectarivore-insectivores in Bekok in May corresponded with a peak in flowering. There was no significant and positive correlation for all other variables (Tables 4 and 5).

3.8 Seasonality of avian guild diet

There was 100% occurrence of arthropods in the diet of insectivores in both Bekok and Belumut throughout the year (Fig. 7). Fruit contributed less than 50% to their diet throughout the year, but showed increased intake in July and February in Bekok, and increased intake from April to August and February 2004 in Belumut. Fruit occurrence was higher than that of arthropods in the diet of frugivore-insectivores for most of the year (Fig. 7), with increased intake in March, July and November. Pollen occurrence was higher than that of arthropods or fruits for nectarivore-insectivores for most of the year (Fig. 7), with increased intake in May and November.

3.9 Breeding and molting overlap

At the guild level, the seasonality of breeding and molting showed some overlap (Fig. 5). The proportion of individuals actively breeding and molting at the same time in my study was low (2%).

4. Discussion

4.1 Understory avian abundance and composition, and food abundance in selectively logged and unlogged forests

There was no difference in the overall understory bird abundance, relative species richness, breeding and molting occurrence, and food abundance (i.e. arthropod, fruit and flower) between the unlogged and selectively logged forests in Bekok and Belumut. A concurrent point-count survey in the same study areas by Peh et al. (2005) also did not find significant differences in the overall bird abundance and species richness between the selectively logged and unlogged forests. Most other studies in Malaysian forests have also found that most forest species were able to use selectively logged forests, and many species were able to survive in these habitats (review in Lambert 1992). For example, in Pasoh Forest Reserve, Peninsular Malaysia, Wong (1985) reported that the regeneration of a 25-year-old selectively logged forest was well advanced, and that the occurrence of breeding adults, juveniles and food abundance (i.e. arthropod, fruit and flower) was not significantly different from that of an adjacent unlogged forest. However, she found that the overall bird abundance and species richness was lower in the logged forest. Another study in Sabah, East Malaysia, by Johns (1996) also showed that there was higher bird abundance in the unlogged forests compared with 6- and 12-year-old selectively logged adjacent forests. The longer (by five to 24 years) logging cycle in Bekok and Belumut (compared to that in Pasoh and Sabah) could be long enough to allow further regeneration of the vegetation and its associated fauna (Lambert 1992). Another likely important factor was the contiguity of the selectively logged forests in Bekok and Belumut with extensive areas of unlogged forest, a factor considered critical in the

recolonization of selectively logged forests (Lambert 1992). The unlogged forests in Bekok (80,000 ha) and Belumut (30,000 ha) were at least 50 times larger than that in Pasoh (600 ha).

There was no difference in the guild composition (i.e. individual abundance) between the unlogged and selectively logged forests in Bekok and Belumut. In the study of Wong (1986) in Pasoh, the unlogged and selectively logged forests were also not found to differ significantly in the relative importance of the various avian feeding guilds. However, in another study in eight-year-old selectively logged forests in Sabah, Lambert (1992) observed that certain guilds, such as nectarivores, were more abundant, whereas some insectivores were fewer, in the selectively logged forests than in the unlogged forests. The similarity in guild signature (Karr 1980) could suggest that resource types were available in similar proportions in both unlogged and selectively logged forests in my study and that of Wong (1986), and could indicate a more advanced regeneration of forest structure and composition in the 25- and 30-year-old logged forests, compared to that of the eight-year-old forests (Wong 1986). Nevertheless, more comprehensive data on the nectar and fruit quality and quantity could be useful in studies like mine, because although I did not distinguish between plant species, there could still be important differences in the suitability of these plants as food for birds. For example, there were 56 and 72 different species of flowering plants encountered in my unlogged and selectively logged forest sites respectively, of which only six were shared between the two habitats. It is possible that these common species were used by birds as food and hence their

presence in both habitats contributed to the similarity in nectarivore diversity and abundance.

4.2 Avian phenology and rainfall

There was no difference in avian phenology in the unlogged and selectively logged forests in Bekok and Belulut. There was a strong seasonality in the overall phenological cycle of the forest birds. The breeding seasons of the birds began near the start of each monsoon season. Fogden (1972) observed that forest birds in Sarawak started breeding with the Northeast monsoon in December. Biannual breeding seasonality was also observed for other tropical bird species such as the white-starred bush robin *Pogonocichla stellata* and the variable sunbird *Nectarinia venusta* (Cunningham-van Someren 1976) in regions with bimodal rainfall regimes (Wilkinson 1983).

4.3 Avian guild phenology and food seasonality

The guild classification was tested for its robustness by comparing the list of species comprising the three guilds with the feeding guild list for Malaysia by Wells (1988); all except for the green broadbill *Calyptomena viridis* and the Abbott's babbler *Malacocincla abbotti* had been classified similarly. The green broadbill and babblers in general were classified as frugivores and insectivores, respectively by Wells (1988).

There was strong seasonality in the fruit and flower abundance in both Bekok and Belulut study areas. A strong arthropod seasonality was observed only in Bekok. Fodgen (1972) and Wong (1986) recorded seasonality in plant phenology, but relatively

stable arthropod abundance throughout the year in Sarawak and Pasoh, respectively. Nevertheless, there was a few-fold fluctuation in the arthropod abundance in Sarawak (Fogden 1972).

The breeding season of the birds in the various guilds in Bekok appeared to coincide with an increased abundance of their main food resources, i.e. insectivores to arthropods, frugivore-insectivores to fruits, and nectarivore-insectivores to flowers. Many similar observations have been reported for humid tropical areas such as Sarawak, Africa, New Guinea and Costa Rica (Fogden 1972, Sinclair 1978, Bell 1982, Stiles 1980). However, the main guild in Belumut, the insectivores, showed a different pattern. Their breeding seasonality coincided with fruit abundance. Molting showed no correspondence with food abundance.

4.4 Insectivore breeding season and food abundance

The strong positive correlation of the insectivore breeding season in Bekok with arthropod biomass suggested that the seasonal increase in arthropod biomass sufficiently met the higher energy requirements of adults and nestlings during the breeding season. The diet data showed that arthropods indeed were the constant food source for the insectivores. Intake of vegetable matter did not increase during the breeding seasons. Similarly, insectivores were found to breed at a time of high arthropod abundance in Sarawak (Fogden 1972).

The main guild in Belumut, the insectivores, showed a different relationship. Their breeding season correlated with fruit abundance. The species composition of the insectivorous feeding guild in Bekok and Belumut was the same (Appendix 2). Therefore, the differences in food exploitation and food correlation in the two study areas were not the result of different guild species composition. I suggest possible reasons to explain the correlation of the breeding season in Belumut insectivores with fruit abundance. The diet data showed that although the arthropod intake throughout the year was 100%, the fruit intake increased during the breeding season (Fig. 7). This suggested that perhaps the arthropod biomass in Belumut was inadequate to support the energy requirements of both adults and the nestlings, and that the adult insectivores possibly had to supplement their diet with fruits. Many sedentary tropical insectivorous bird species are known to eat fruit as it becomes periodically available within their home range (Morton 1973) and to modify their diets with changes in food abundance (Recher 1990). Food exploitation by many tropical bird species varies over time (Poulin et al. 1992), and between habitats, and many show feeding plasticity (Poulin et al. 1994, reviewed in Corlett 1998). Laboratory experimental data have also shown that tropical birds such as spotted antbirds *Hylophylax naevioides* can adjust their breeding to changes in food abundance (Hau et al. 2000). My data showed that the arthropod biomass in Belumut was indeed significantly lower than that in Bekok ($T = 2.67$, $df = 12$, $P = 0.02$, Appendix 1), and that there was no seasonal peak in the arthropod biomass in Belumut, unlike in Bekok, which had significant seasonal peaks. The difference between the highest and lowest recorded arthropod biomass was almost 5-fold for Bekok and only 2-fold for Belumut (Appendix 1). The constant supply of arthropods in Belumut could have

contributed to the predominance of insectivores and the significantly fewer frugivore-insectivores and nectarivore-insectivores in Belumut (Appendix 3) (Karr 1976, Wong 1986). Wong (1986) found a higher insectivore abundance and species richness compared to frugivores in the Pasoh forests, where the arthropod abundance was relatively stable and the fruit and flower abundance fluctuated. The scarcity of frugivore-insectivores and nectarivore-insectivores could have reduced the competition for fruits for the insectivores, allowing them to exploit this food resource more easily as a supplement during their breeding season and giving them more time to catch arthropods for their nestlings. The body condition index of Belumut insectivores was lower than that of Bekok insectivores and approached statistical significance ($W=10381.50$, $P=0.06$). This could be circumstantial support for the higher fruit diet of Belumut insectivores, which would be lower in proteins and hence would result in slower growth (Ward 1969).

The lower arthropod biomass in Belumut could be due to factors such as a lower tree cover, perhaps due to higher human disturbance. Belumut was a more popular recreational area with hikers and campers than Bekok (Malaysia Tourism Portal, <http://www.virtualmalaysia.com/>). A Kruskal-Wallis test using tree cover data from the same study areas and study period (Peh K. S.-H. unpublished data; methodology in Peh et al. 2005) showed that tree cover was indeed lower in Belumut than in Bekok ($H = 40.83$, $P < 0.001$). The fuller sunlight and reduced vegetation cover could have promoted high soil and air temperatures (Ash and Barkham 1976, Collins et al. 1985), and higher moisture loss (Marquis 1973) from the litter and upper soil surfaces, and perhaps resulted in lower arthropod abundance (Shure and Phillips 1991).

4.5 Frugivore-insectivore breeding season and food abundance

My study found that the frugivore-insectivores bred during periods of high fruit abundance. This correlation of the breeding season with fruit abundance was supported by the diet data that showed a higher intake of fruits during the breeding seasons. This strategy followed the most common food exploitation model proposed for tropical fruit-eating birds, whereby the adults ate mostly low protein but high energy fruits during their breeding season and fed their nestlings arthropods (Morton 1973). The breeding seasons of other tropical frugivores are also known to correspond to a time of increasing fruit availability (e.g. Worthington 1982, Wheelwright 1983, Murray 1986). Fruit is energy-rich and easily obtained, and if the energy demands of the adults are met this way, only a small amount of high protein food such as arthropods is required by the adults for growth, leaving time to hunt arthropods for nestlings (Fogden 1972). This breeding strategy would decrease their competition with the insectivores for arthropods, with whom they were at a competitive disadvantage since they were not specialized insectivores (Fogden 1972). In Sarawak, although frugivores bred at a time of high arthropod abundance, the observation of genera such as *Pycnonotus* feeding on fruits even though arthropods were abundant, suggests that they were unable to breed successfully while feeding solely on arthropods (Fogden 1972). Further, the breeding season in that study was determined from nesting records from scientific literature from different years, and other records from Sarawak, and was likely inconclusive since the fruit and breeding data were not collected concurrently, and could have varied over the different years.

4.6 Nectarivore-insectivore breeding season and food abundance

Correlation tests showed no significant results for the Bekok nectarivore-insectivores, possibly due to small sample sizes. However, the graphical results showed that the first breeding season in May occurred during a peak in flowering and the diet data supported this result (Figs. 5, 6 and 7). The first breeding season could reflect the same strategy I had suggested for the frugivore-insectivores. However, the second breeding season did not suggest any clear-cut strategy. Although the diet data still showed an increased nectar intake, the flower abundance for that month was low. It was possible that the nectarivore-insectivores could be taking nectar from canopy flowers, which I did not sample due to inaccessibility.

4.7 Molting seasons, food abundance, rainfall and overlap with breeding seasons

There was no significant correlation of the molting season with food abundance or rainfall for all guilds in Bekok and Belumut. At the guild level, the seasonality of breeding and molting appeared to have some overlap. However, at the individual level, the molting period generally occurred outside the breeding season. There were very few known cases of breeding and molting overlap of individuals in Asian birds (Foster 1975). Data by Fogden (1972) in Sarawak also found that the molting season in July occurred between the breeding seasons. Tropical birds generally initiated molting outside the breeding season, and completed it at a time of decreasing food resources (Poulin et al. 1992). Hence, it was possible that the energy requirements for breeding were more crucial than that for molting, given that food was required for both nestlings and adults during breeding, but required only for adults during the molting season. It was also

possible that the timing of molting was constrained by the timing of breeding and consequently occurred in periods of lower food abundance than that of the breeding season. The lack of breeding and molting overlap suggests that food may be limiting in the Malaysian forests. Relative stable tropical environments could have bird populations near carrying capacity due to high adult survival (Cody 1966). This is in contrast to temperate regions, where overlap can occur during a period of superabundant food (Foster 1975).

5. Conclusions

Potential food resources (i.e. arthropods, fruits and flowers) for birds in two 30-year-old selectively logged forests were found to be comparable to those of adjacent large unlogged forest areas in two tropical rainforests of Peninsular Malaysia. The individual abundance, relative species richness, breeding and molting occurrence, and guild composition of understory resident birds were found to be similarly abundant in both forest types. The regeneration of the logged forests could be sufficiently advanced to support an understory avifauna similar to that of the unlogged forests, and the comparable abundance of food resources in both forest types could have contributed to the similarity in phenological characteristics.

There was strong seasonality of avian phenology and potential food resources. There was similar seasonal variation of breeding and molting for understory birds in both forest types. Breeding was generally initiated near the start of the biannual monsoon seasons. Biannual monsoons bringing rainfall may be the long-term cues for breeding in birds.

A strong positive correlation of phenology with food abundance corroborated the findings on the effects of logging on avian life cycles. Breeding generally coincided with an increase in the main food type for each feeding guild, and diet data supported these findings. Food availability may be the proximate cue for breeding in tropical Southeast Asian birds. The breeding seasonality of insectivores in habitats that lacked seasonality in their main food source (i.e. arthropods) could breed at a time of increased abundance of a secondary food source (e.g. fruits) that did have a strong seasonality. This could occur in

areas where the biomass of their main food source was inadequate to support the increased nutritional needs of both adults and nestlings during the breeding season. Habitat degradation could be a factor for such poor resource potential. Molting occurred outside the breeding season for most individuals in the study areas. Molting showed little correlation with rainfall or food abundance. It is possible that energy requirements are more critical for breeding than molting, given that food is required for both nestlings and adults during breeding, but required only for adults during the molting season. It is also possible that the timing of molting is constrained by the timing of breeding, and consequently occurs in periods of lower food abundance than that of the breeding season.

The lack of breeding and molting overlap suggests that food may be limiting in the Malaysian forests. This is in contrast to temperate regions, where overlap can occur during a period of superabundant food. The degree of molting and breeding overlap can be a useful indicator of food resource availability and reflect strategies for food resource allocation for the different energy-demanding stages in the avian annual cycle.

Because most of the remaining forests in Peninsular Malaysia are slated for logging regimes, it is important to monitor the effects of these habitat degradations on the forest community. Large areas of polycyclic selectively logged forests connected to extensive unlogged forests are found to regenerate well and to be important for bird conservation. Important life cycle events such as breeding are dependent on food availability and forest structure, which are in turn affected by human activities such as logging and recreation. Because understory resident birds can be important indicators of the regeneration

progress of logged forests, data on their breeding, molting and diet, and food abundance may be important habitat quality indicators and useful tools in the ecological monitoring of habitats such as selectively logged forests.

6. Caveats and future research directions

The data for my study are not exhaustive, and shortfalls include:

- 1) short period of study (14 months);
- 2) small number of replicate study sites (4);
- 3) use of data from recaptured birds;
- 4) use of fecal samples instead of emetic samples;
- 5) under-representation of mid-story and canopy birds, and birds from other feeding guilds;
- 6) absence of nesting and nestling data;
- 7) absence of genetic diversity data; the long-term viability of selectively logged forest avifauna is also affected by genetic factors related to small population sizes, such as loss of genetic diversity, mutational accumulation and inbreeding depression, which may threaten endangered species with an earlier extinction (Frankham 1995, Frankham et al. 2002, Brook et al. 2002); and
- 8) absence of nectar data because the nectar quantity and quality could be different in different plant species.

Possible future investigations suggested to address these shortcomings are:

- 1) a long-term monitoring study beginning in unlogged forests and continuing while the forest undergoes logging and subsequent regeneration for several years, carried out in several study sites;
- 2) a study of avian diet from stomach contents using less destructive methods than emetics;

- 3) a study of nesting characteristics of resident birds that includes data on nest initiation and success, and clutch size and diet;
- 4) experimental studies on diet preferences of birds from different guilds during different stages of their life cycles;
- 5) a study of the genetic diversity of conspecifics in both habitats; and
- 6) a study of the nectar quantity and quality between the two habitats.

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Table 1: Differences in seasonality of breeding and molting for each guild among the four study sites: Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL), and Belumut logged (SBL). Feeding guilds: I (insectivore); FI (frugivore-insectivore); NI (nectarivore-insectivore). Proportion of juveniles (J); breeding adults (BP); molting adults (M). * indicate no value due to low sample sizes.

	Study sites					
	PB and SB			PBL and SBL		
	χ^2	p value	df	χ^2	p value	df
I J	11.13	0.08	6	4.03	0.67	6
I BP	11.48	0.08	6	4.17	0.65	6
I M	4.00	0.68	6	7.50	0.28	6
FI J	5.00	0.54	6	*		
FI BP	11.63	0.07	6	*		
FI M	5.50	0.48	6	*		
NI J	5.00	0.54	6	*		
NI BP	5.58	0.47	6	*		
NI M	4.50	0.61	6	*		

Table 2: Estimated bird species richness for the four study sites: Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL), Belumut logged (SBL). Standard deviations in parentheses.

Study site	Coleman rarefaction (\pm SD)	Chao2 (\pm SD)	ICE (\pm SD)	MMMean
PB	32.8 (\pm 1.0)	43.9 (\pm 8.8)	46.9 (\pm 0.0)	51.3
SB	31.2 (\pm 0.9)	38.2 (\pm 6.0)	42.6 (\pm 3.0)	44.6
PBL	25.7 (\pm 1.1)	37.3 (\pm 5.2)	32.1 (\pm 0.0)	38.1
SBL	23.1 (\pm 0.9)	33.3 (\pm 12.5)	31.0 (\pm 3.0)	34.9

Table 3: Differences in proportion of juveniles, breeding and molting adults for each guild in the pooled unlogged forests of Bekok and Belumut, and pooled selectively logged forests of Bekok and Belumut.

	Insectivores			Frugivore-insectivores			Nectarivore-insectivores		
	Juveniles	Breeding adults	Molting adults	Juveniles	Breeding adults	Molting adults	Juveniles	Breeding adults	Molting adults
χ^2	0.24	0.29	0.39	0.67	1.69	0.06	3.11	0.49	0.03
p-value	0.63	0.59	0.53	0.41	0.19	0.81	0.08	0.48	0.86

Table 4: Temporal cross-correlations (r) between the proportion of juveniles, breeding and molting adults and environmental variables for Bekok unlogged and selectively logged sites pooled. Temporal cross-correlation coefficient values (r) are for lag = 0, values significant at alpha 0.05 are denoted with *. Feeding guilds: I (insectivore); FI (frugivore-insectivore); NI (nectarivore-insectivore).

Variables	Guild	r			
		Arthropods mass (mg)	Number of fruits	Number of flowers	Rainfall
Juveniles	I	-0.35	-0.35	-0.65	0.41
	FI	0.21	0.85 *	-0.20	-0.17
	NI	0.35	0.57	-0.53	0.17
Breeding adults	I	0.80 *	0.16	-0.04	-0.50
	FI	-0.01	0.85 *	-0.38	0.39
	NI	0.52	0.26	-0.34	-0.09
Molting adults	I	0.15	0.42	-0.36	0.10
	FI	0.04	-0.48	-0.25	0.16
	NI	0.26	0.44	-0.47	0.18

Table 5: Temporal cross-correlations (r) between the proportion of juveniles, breeding and molting adults and environmental variables for insectivores in Belumut unlogged and selectively logged sites pooled. Temporal cross-correlation coefficient values (r) are for lag = 0, values significant at alpha 0.05 are denoted with *.

Variables	Guild	r			
		Arthropods mass (mg)	Number of fruits	Number of flowers	Rainfall
Juveniles	I	0.44	0.45	-0.17	-0.26
Breeding adults	I	0.08	0.92 *	-0.12	-0.11
Molting adults	I	0.34	0.16	-0.62	0.45

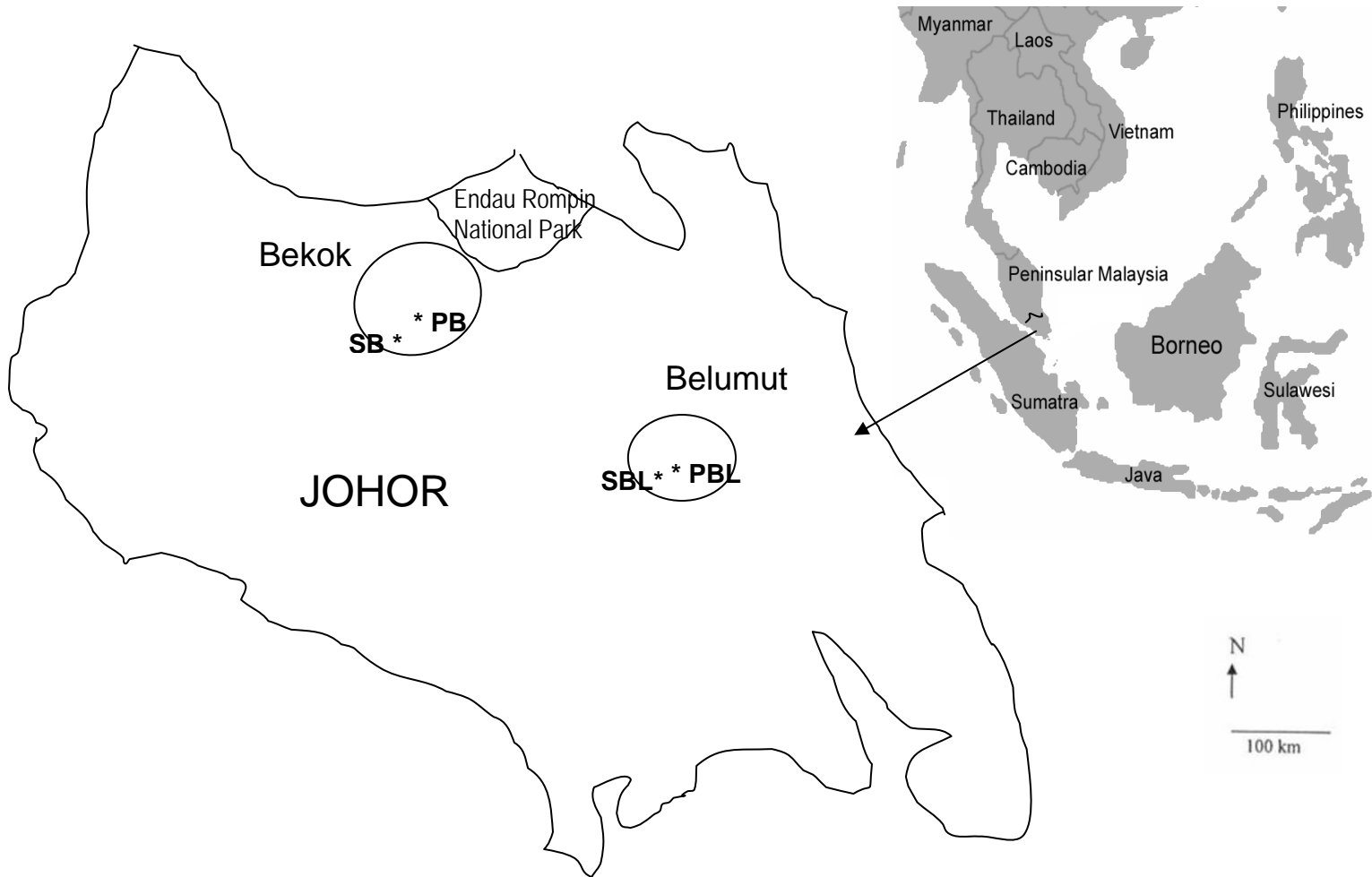


Fig. 1. Map of Southeast Asia showing Peninsular Malaysia and the location of the study areas Bekok and Belumut (denoted by ovals), and the study sites Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL), and Belumut logged (SBL) (denoted by asterisks).

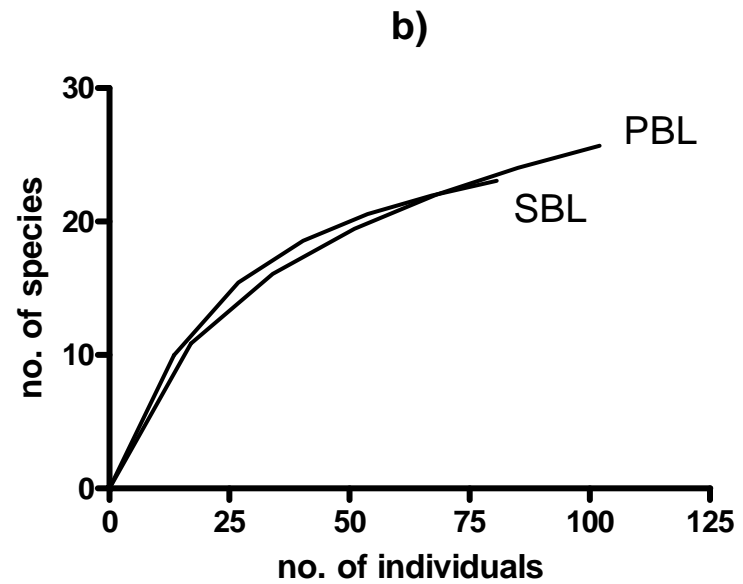
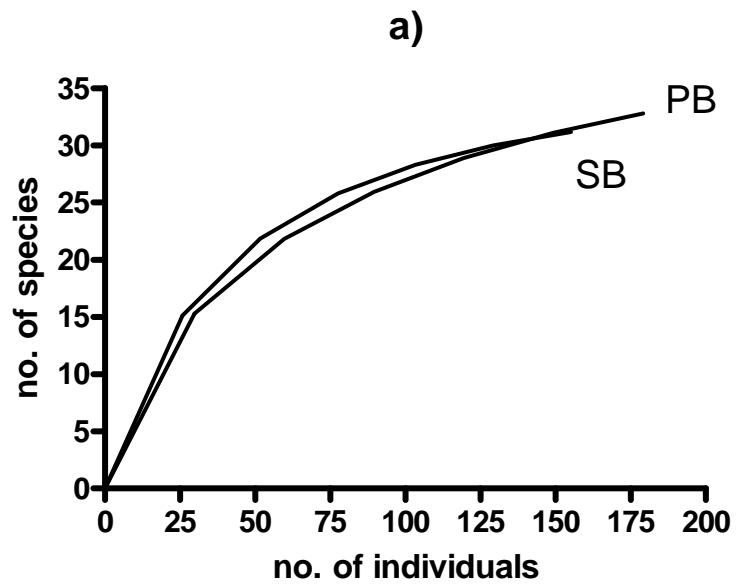


Fig. 2. Coleman curves for resident understory birds caught at the four study sites: (a) Bekok unlogged (PB) and logged (SB); and (b) Belumut unlogged (PBL) and Belumut logged (PBL).

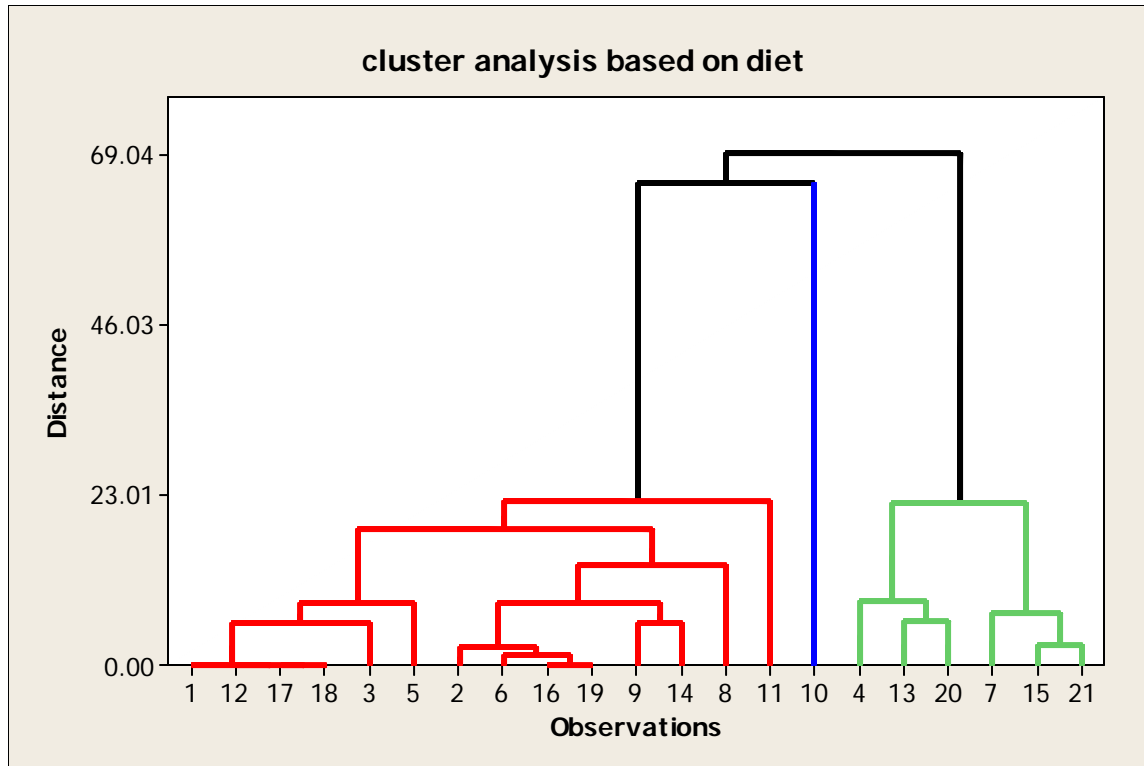


Table of code numbers and common names for bird species in dendrogram		
Species code	Species common name	Guild
1	scaly-crowned babbler	I
2	short-tailed babbler	I
3	rufous-winged philentoma yellow-breasted flowerpecker	I
4	flowerpecker	FI
5	white-rumped shama	I
6	moustached babbler	I
7	hairy-backed bulbul	FI
8	purple-naped sunbird	I
9	grey-throated babbler	I
10	little spiderhunter	NI
11	white-bellied yuhina	I
12	grey-chested flycatcher	I
13	grey-cheeked bulbul	FI
14	grey-headed babbler	I
15	yellow-bellied bulbul	FI
16	buff-necked woodpecker	I
17	banded kingfisher	I
18	chestnut-rumped babbler	I
19	chestnut-naped forktail	I
20	green broadbill	FI
21	abbott's babbler	FI

Fig. 3. Dendrogram of feeding guild membership for 21 resident understory bird species in the four study sites: Bekok unlogged, Bekok logged, Belumut unlogged, Belumut logged. Species names encoded on appended table. Feeding guilds: I (insectivore); FI (frugivore-insectivore); NI (nectarivore-insectivore).

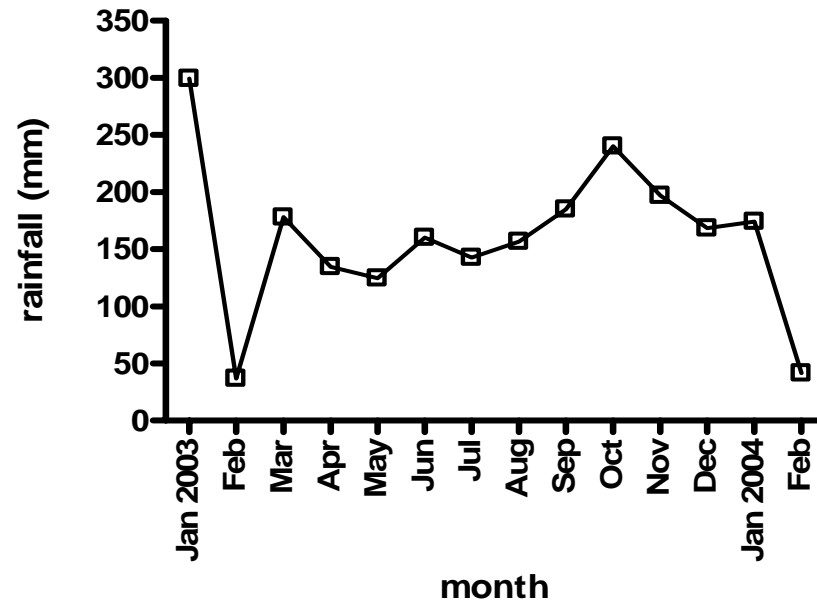


Fig. 4. Total monthly rainfall from January 2003 to February 2004 for Johor, Peninsular Malaysia.

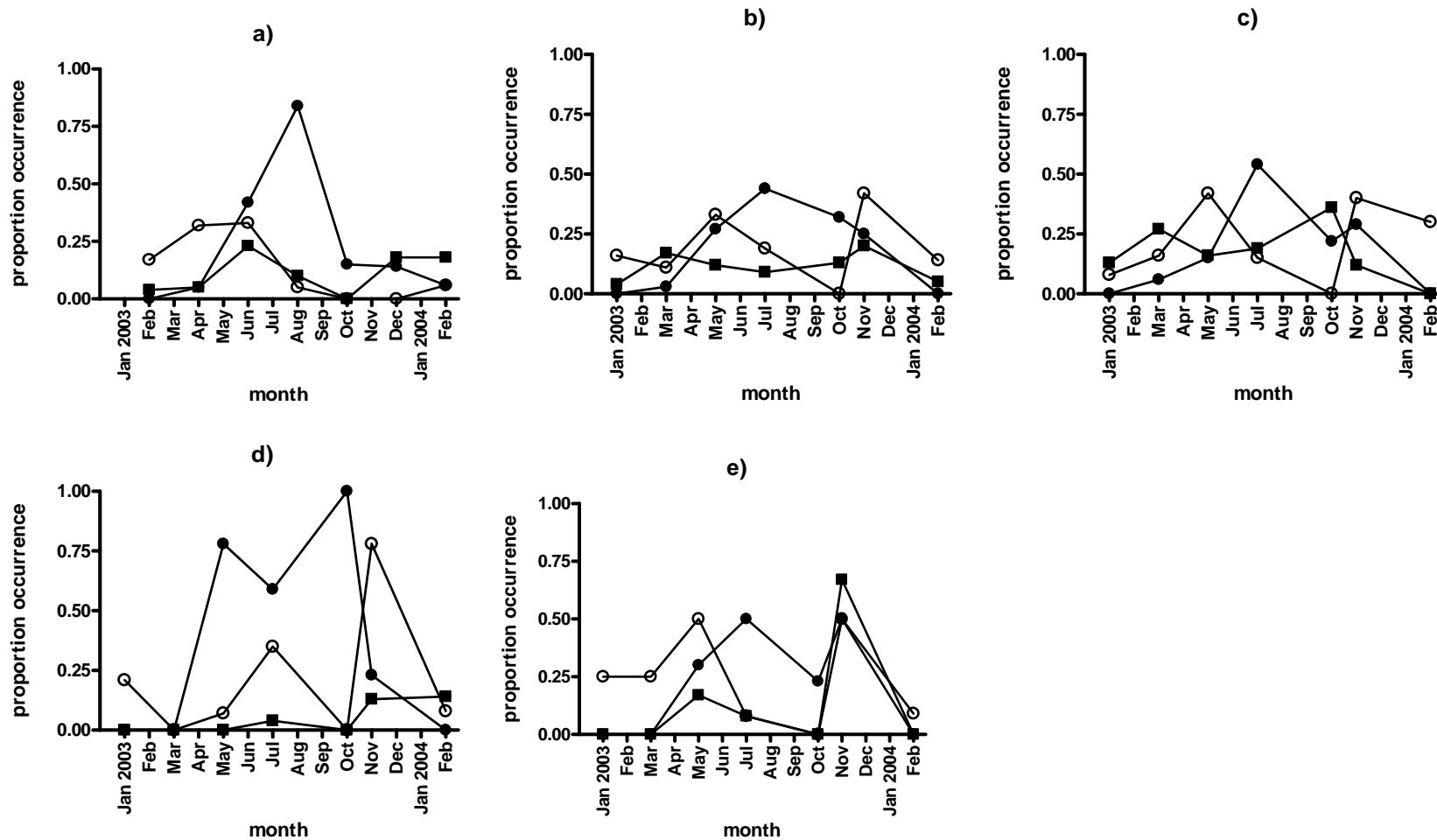


Fig. 5. Seasonal variation in the proportion of juveniles (solid squares), adults having brood patch (open circles), and adults in primary molt (solid circles) among (a) insectivores in Belumat, (b) all guilds combined in Bekok, (c) insectivores in Bekok (d) frugivore-insectivores in Bekok, and (e) nectarivore-insectivores in Bekok.

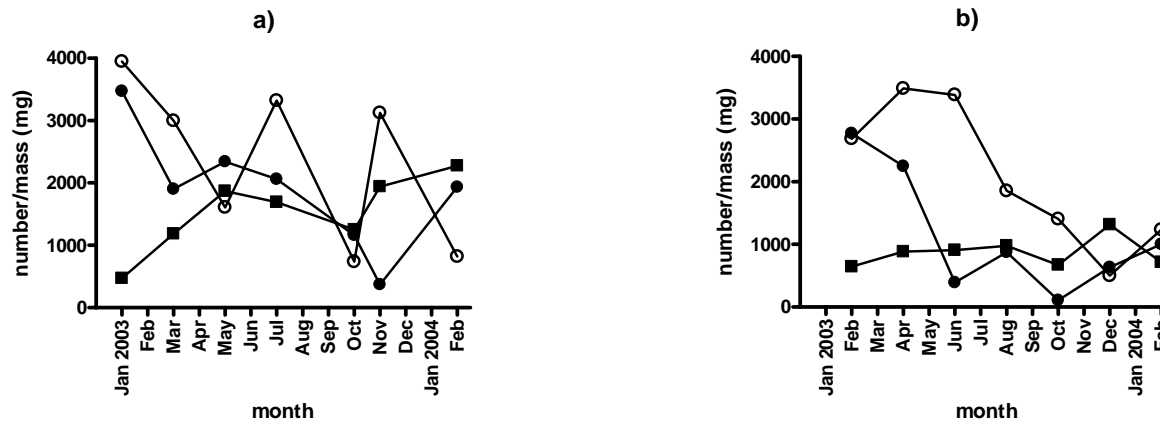


Fig. 6. Seasonal variation in arthropod biomass (solid squares), fruit abundance (open circles), and flower abundance (solid circles) in (a) Bekok and (b) Belumut study areas.

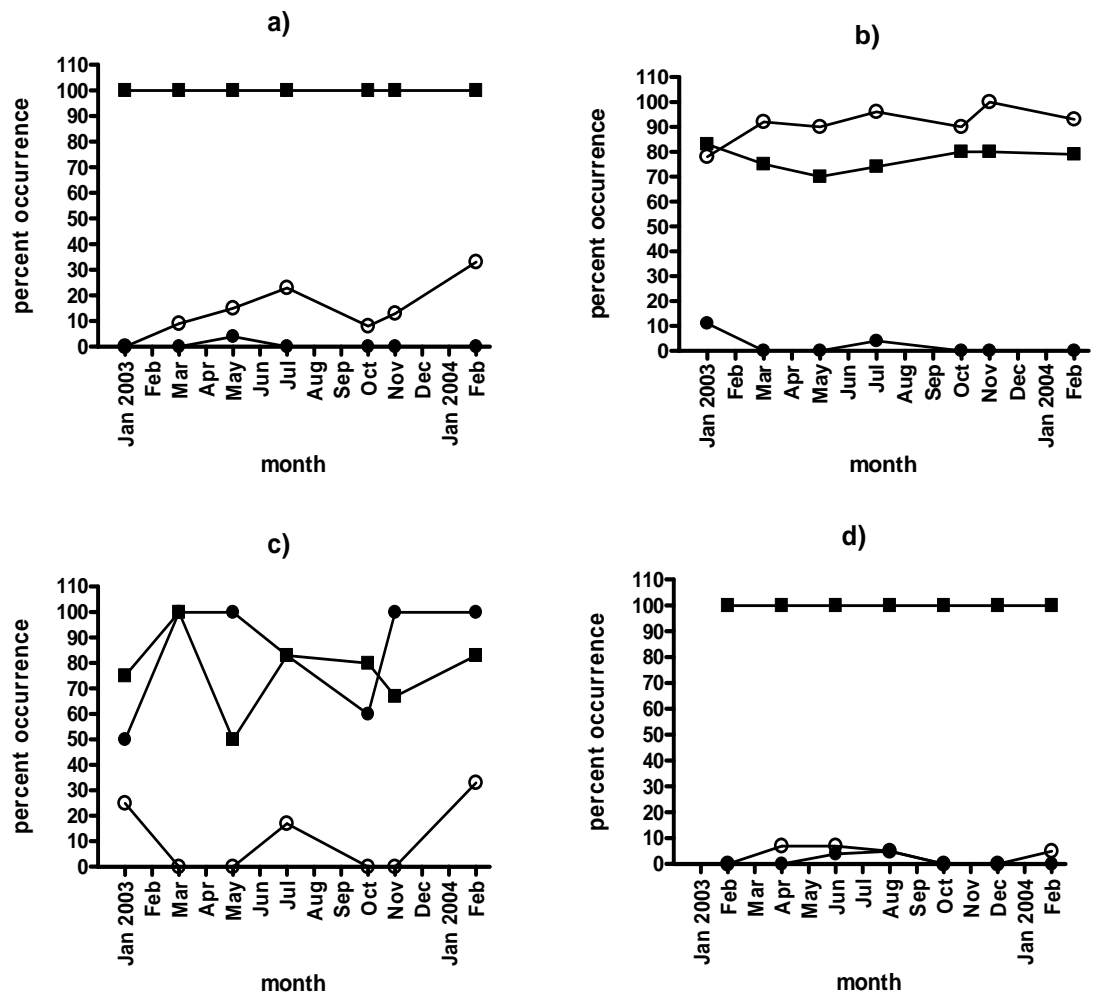


Fig. 7. Seasonal variation in the percent occurrence of arthropods (solid squares), fruits (open circles) and nectar (solid circles) in the fecal samples of (a) insectivores (b) frugivore-insectivores and (c) nectarivore-insectivores in Bekok, and (d) insectivores in Belulut.

Appendix 1: Total arthropod biomass, and flower and fruit abundance in the four study sites: Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL), Belumut logged (SBL).

Sample no.	Arthropod biomass (mg)				Number of flowers				Number of fruits			
	PB	SB	PBL	SBL	PB	SB	PBL	SBL	PB	SB	PBL	SBL
1	206	264	309	337	960	2510	26	2746	1423	2526	2034	651
2	399	786	335	551	1225	675	1515	732	524	2474	2308	1180
3	1361	506	422	487	278	2063	359	34	411	1196	2256	1129
4	766	924	658	320	241	1820	842	33	1346	1976	1296	558
5	556	697	474	198	114	1048	50	58	215	524	1100	305
6	944	997	756	559	5	368	563	72	274	2850	500	0
7	650	1625	262	453	231	1704	0	1000	52	768	84	1150

Appendix 2: Resident understory bird species, and the number of juveniles (J), adults (A), and adults with brood patch (BP) and primary molt (M) caught in the four study sites: Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL), Belumut logged (SBL). Feeding guilds: I (insectivore); FI (frugivore-insectivore); NI (nectarivore-insectivore). Scientific names follow the nomenclature and taxonomic sequence in Inskipp et al. (1996).

No.	Scientific name	Common name	Guild	Study site															
				PB				SB				PBL				SBL			
				A	J	BP	M	A	J	BP	M	A	J	BP	M	A	J	BP	M
1	<i>Sasia abnormis</i>	rufous piculet		1	1	0	0	1	0	0	0	2	0	0	0	0	0	0	0
2	<i>Picus mineaceus</i>	banded woodpecker		0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
3	<i>Blythipicus rubiginosus</i>	maroon woodpecker		0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0
4	<i>Meiglyptes tristis</i>	buff-rumped woodpecker		2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
5	<i>Meiglyptes tukki</i>	buff-necked woodpecker	I	1	0	0	0	7	1	3	1	2	0	1	0	3	0	0	2
6	<i>Alcedo euryzona</i>	blue-banded kingfisher		2	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0
7	<i>Ceyx rufidorsa</i>	rufous-backed kingfisher		1	0	0	0	6	0	0	0	1	0	0	0	6	0	1	0
8	<i>Lacedo pulchella</i>	banded kingfisher	I	2	0	0	1	2	0	0	0	0	0	0	4	0	0	0	0
9	<i>Chalcophaps indica</i>	emerald dove		4	0	2	0	7	0	4	0	0	0	0	0	0	0	0	0

No.	Scientific name	Common name	Guild	Study site															
				PB				SB				PBL				SBL			
				A	J	BP	M	A	J	BP	M	A	J	BP	M	A	J	BP	M
10	<i>Calyptomena viridis</i>	green broadbill	FI	2	0	0	1	2	1	0	1	1	0	0	0	0	0	0	0
11	<i>Platylophus galericulatus</i>	crested jay		0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
12	<i>Rhipidura javanica</i>	pie'd fantail		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	<i>Rhipidura perlata</i>	spotted fantail		2	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0
14	<i>Dicrurus paradiseus</i>	greater racquet-tailed drongo		2	0	1	1	3	0	3	0	0	0	0	0	0	0	0	0
15	<i>Hypothymis azurea</i>	black-naped monarch		0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	0
16	<i>Philentoma pyrropterum</i>	rufous-winged philentoma	I	7	2	2	1	0	0	0	0	12	0	2	2	3	2	0	1
17	<i>Zoothera interpres</i>	chestnut-capped thrush		0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
18	<i>Rhinomyias umbratilis</i>	grey-chested flycatcher	I	5	1	0	1	0	0	0	0	13	0	1	1	5	0	1	1
19	<i>Cyornis unicolor</i>	pale-blue flycatcher		0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0
20	<i>Culicicapa ceylonensis</i>	grey-headed flycatcher		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	<i>Copsychus malabaricus</i>	white-rumped shama	I	7	1	0	1	4	0	3	0	1	1	0	1	4	0	2	0

No.	Scientific name	Common name	Guild	Study site															
				PB				SB				PBL				SBL			
				A	J	BP	M	A	J	BP	M	A	J	BP	M	A	J	BP	M
22	<i>Enicurus ruficapillus</i>	chestnut-naped forktail	I	2	0	0	1	2	0	1	0	2	0	1	1	0	0	0	0
23	<i>Pycnonotus cyaniventris</i>	grey-bellied bulbul		2	0	0	2	0	0	0	0	1	0	0	1	0	0	0	0
24	<i>Pycnonotus erythroptalmos</i>	spectacled bulbul		2	0	0	1	1	0	0	0	0	0	0	2	0	0	0	0
25	<i>Alophoixus bres</i>	grey-cheeked bulbul	FI	11	0	3	2	8	1	0	2	5	0	0	1	0	0	0	0
26	<i>Alophoixus phaeocephalus</i>	yellow-bellied bulbul	FI	20	0	4	6	14	0	0	3	4	0	0	7	0	1	0	0
27	<i>Tricholestes criniger</i>	hairy-backed bulbul	FI	16	1	3	1	23	0	3	4	8	0	2	2	4	0	0	1
28	<i>Hemixos flava</i>	ashy bulbul		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	<i>Malacocincla abbotti</i>	abbott's babbler	FI	0	0	0	0	3	2	2	0	0	0	0	1	0	0	1	0
30	<i>Malacocincla malaccensis</i>	short-tailed babbler	I	7	0	1	0	3	1	0	1	6	0	1	2	5	2	1	1
31	<i>Pellorneum capistratum</i>	black-capped babbler		1	0	0	1	4	0	2	0	2	0	0	2	2	0	1	0
32	<i>Malacopteron magnirostre</i>	moustached babbler	I	9	10	1	0	5	3	1	2	10	6	0	6	5	1	0	1
33	<i>Malacopteron cinereum</i>	scaly-crowned babbler	I	2	0	0	0	0	0	0	0	8	0	0	0	9	0	2	1

No.	Scientific name	Common name	Guild	Study site															
				PB				SB				PBL				SBL			
				A	J	BP	M	A	J	BP	M	A	J	BP	M	A	J	BP	M
34	<i>Malacopteron magnum</i>	rufous-crowned babbler		0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
35	<i>Pomatorhinus montanus</i>	chestnut-backed scimitar babbler		3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
36	<i>Napothera epilepidota</i>	eyebrowed wren babbler		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
37	<i>Stachyris nigriceps</i>	grey-throated babbler	I	4	0	1	1	3	0	1	1	12	0	5	2	6	0	1	3
38	<i>Stachyris poliocephala</i>	grey-headed babbler	I	7	2	3	2	8	1	4	0	1	1	1	0	4	2	1	2
39	<i>Stachyris leucotis</i>	white-necked babbler		0	0	0	0	0	0	0	0	4	0	2	1	0	0	0	0
40	<i>Stachyris maculata</i>	chestnut-rumped babbler	I	5	0	4	1	0	0	0	0	0	0	0	0	7	0	0	3
41	<i>Macronous pilosus</i>	fluffy-backed tit-babbler		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	<i>Yuhina zantholeuca</i>	white-bellied yuhina	I	0	0	0	0	3	1	0	3	1	0	0	1	0	0	0	0
43	<i>Prionochilus maculatus</i>	yellow-breasted flowerpecker	FI	10	0	3	2	12	0	2	4	0	0	0	0	2	0	1	0
44	<i>Prionochilus thoracicus</i>	scarlet-breasted flowerpecker		0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
45	<i>Dicaeum trigonostigma</i>	orange-bellied flowerpecker		0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0

No.	Scientific name	Common name	Guild	Study site															
				PB				SB				PBL				SBL			
				A	J	BP	M	A	J	BP	M	A	J	BP	M	A	J	BP	M
46	<i>Hypogramma hypogrammicum</i>	purple-naped sunbird	I	4	1	1	1	6	0	0	0	6	1	0	1	1	2	0	0
47	<i>Arachnothera longirostra</i>	little spiderhunter	NI	35	7	5	8	25	0	6	5	2	0	1	0	1	0	0	1
48	<i>Arachnothera affinis</i>	grey-breasted spiderhunter		0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0

Appendix 3: Numbers of individuals in each feeding guild caught in the four study sites: Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL), Belumut logged (SBL). Feeding guilds: I (insectivore); FI (frugivore-insectivore); NI (nectarivore-insectivore).

Guild	PB	SB	PBL	SBL
I	79	50	83	65
FI	60	66	18	14
NI	42	25	2	1

Appendix 4. Mean percentages (\pm standard deviation) of items from each food category found in all fecal samples of species belonging to each feeding guild in the four study sites: Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL), Belumut logged (SBL). Nectarivore-insectivore guild comprises 1 species.

Feeding guild	Arthropod	Fruit	Pollen
Insectivore	91.0 (± 7.4)	7.1 (± 7.6)	1.9 (± 4.7)
Frugivore-insectivore	42.5 (± 9.5)	55.8 (± 7.4)	2.0 (± 3.3)
Nectarivore-insectivore	45.0 (-)	8.0 (-)	4.0 (-)

Appendix 5. Size class distribution of arthropods caught in the four study sites: Bekok unlogged (PB), Bekok logged (SB), Belumut unlogged (PBL), Belumut logged (SBL).

Size Class (mm)	PBL	PB	SB	SBL
5-10	807	905	1101	805
10-15	67	215	210	38
15-20	18	28	10	27
20-25	1	4	2	3
25-30	1	2	3	1
30-35	1	1	1	1
35-40	0	0	0	0
40-45	0	0	0	0
45-50	0	0	0	0
50-55	0	0	0	0
55-60	0	0	0	0
60-65	0	0	0	0
65-70	0	0	0	0
70-75	0	0	0	0

Size Class (mm)	PBL	PB	SB	SBL
75-80	0	0	0	0
80-85	0	0	0	0
85-90	0	0	0	0
90-95	0	0	0	0
95-100	0	0	0	0
100-105	0	1	0	0
105-110	0	0	1	0
110-115	0	0	0	0
