International Master Programme at
the Swedish Biodiversity Centre

Master theses
No. 26
Uppsala 2003
ISSN: 1653-834X

Lowland rainforest avifauna and human disturbance:

Persistence of primary forest birds in logged forest and countryside of southern Peninsular Malaysia

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Abstract

Human disturbance is constantly threatening the lowland rain forest in Peninsular Malaysia. To understanding its impact, we investigated the persistence of primary forest avifauna in selectively logged forest and countryside. We found that forests that were selectively logged at least 30 years ago have failed to complete their recovery in term of species richness and community structure. Of the 159 extant primary forest species considered in this study, only 28 – 32% persisted in the countryside. The types of microhabitat in which species inhabit seemed to influence their vulnerability to disturbance. The ground-dwelling species tended not to occur in logged forest. Frugivorous and omnivorous species in the canopy, and insectivores that feed on trunks showed a greater tendency to persist in the countryside. Resource abundance and variables that are closely related to forest disturbance such as density of large trees, density of dead trees, canopy cover density and shrub volume seemed to influence the distribution of the primary forest birds. Our results identified species that have conservation priority. Certainly, large primary forest reserves are needed to conserve the lowland rain forest avifauna of Peninsular Malaysia and other part of Southeast Asia.

Contents

Introduction

Tropical lowland rain forest biodiversity is currently facing an unprecedented decimation by human activities. This habitat loss and disturbance have resulted expiration of many lowland rain forest flora and fauna (e.g., Diamond et al. 1987; Castelletta et al. 2000; Brook et al. 2003). Deforestation in Southeast Asia is the highest among tropical areas (Achard et al. 2002). In Peninsular Malaysia, most of the pristine lowland dipterocarp forests have already been exploited for timber industry or cleared for establishment of commercial crops, and few pristine forest remnants remain (Caufield 1991). Rapid deforestation in Malaysia reached 1.8% between 1981 and 1990, which is among the highest rates in the world (World Resource Institute 1998). The main commercial crops grown in the clear-cut forest in Malaysia are oil palms (*Elaeis guineensis*) and rubber trees (*Hevea brasiliensis*), which make up about 28 % of total land use (Department of Agriculture, 1995). Little is known how the extensive disturbance in Peninsular Malaysia is affecting its forest biodiversity (e.g. Wong 1985).

Degraded habitats and landscapes can, in some cases, serve as refuges for some of the forest biodiversity (Mitra and Sheldon 1993; Hughes et al. 2002). If forests are allowed to regenerate in heavily disturbed areas, they might act as good refuges for forest biota (Castelletta et al. 2004). Past research from Peninsular Malaysia revealed that the majority of the studies on the effect of selectively logging focused on the early stages of forest regeneration (e.g., Johns 1986; 1989). Only few studies have compared the biodiversity between primary forest and mid-succession (> 20 years old) forest (e.g., Wong 1985; 1986). It is also not known how valuable the rural agricultural landscapes are for forest biodiversity.

We report the avifaunal communities in three habitat types – intact continuous primary rain forest, disturbed secondary forest that was selectively logged about 30 years ago, and human-dominated landscapes comprising home gardens and agricultural lands. We used birds as our study species group for two main reasons. First, they play important roles as predators, prey, seed dispersers and pollinators in the maintenance of ecological processes (Pimm 1986). Second, they are easy to sample and are sensitive to the habitat change that made them useful indicators of changes in ecological processes (Johns 1992). We determined the persistence of the primary forest avifauna to the change in the use of landscape in southern Peninsular Malaysia. Our main objective was to address the following questions: (1) What is the proportion of primary forest species that occur in disturbed forest that was selectively logged at least 30 years ago? (2) How many of primary forest species are present in countryside? (3) What are the ecological traits that account for the persistence and sensitivity of the primary forest birds? (4) Does the vegetation structure correlate with the primary forest bird distribution? To determined how different habitats are utilized by the primary forest birds, we also compared the avian activities and their vertical distribution among the different vegetation strata between the primary forest and disturbed areas (i.e., selectively logged and countryside). Our study shows the conservation importance of different habitat types and, we hope, it will direct avian conservation in Malaysia as well as elsewhere in Southeast Asia.

Methods

Study Areas

Study areas were located in the state of Johore, Peninsular Malaysia (Fig.1). We collected data from two areas, Sungei Bantang (hereafter we named Bekok) and Gunung Belumut (hereafter Belumut). We refer a *study area* as a contiguous habitat comprising a large, continuous tropical primary rain forest surrounded by a matrix of selectively logged forest and agricultural lands. Whereas the *study site* refers to either a primary forest, it's surrounding selectively logged forest or the adjacent rural human-dominated habitats. We conducted bird species surveys from a total of six study sites within the two study areas: two primary forests, two logged forests and two human-dominated landscapes.

The two primary forest sites were continuous hill dipterocarp forests, which have never been logged. Belumut had an area of at least 30,000 ha whereas Bekok, which joined to the Endau Rompin National Park, was more than 80,000 ha (Department of Wildlife, Malaysia, 2003). Both sites were two of the most intact primary forests in Johore and were being gazetted as protected areas. We assumed such primary forests retain most of their original avifauna. The two disturbed forest sites, surrounding the primary forest sites, consisted mainly selectively logged forests that were cut at least 30 years ago (Richard Aldrich, Johore State Forestry Department, personal communication). About 150 tree species, for examples *Shorea curtisii* and *Dryobalanops aromatica*, were being exploited for timber (Burgess 1971). Most of the tall trees left in the areas were either species not suitable for timber industry or not appropriate for timber use because of their trunks quality. The logged forests also contained a mixture of small recreational forests (< 10 ha), open gaps (< 2 ha) and forest edge overgrown with pioneer plant species such as *Trema orientalis*, *Mallotus paniculatus*, *Macaranga* spp., and wild bananas, *Musa* spp. The size of the area covered by the logged forest was not available. Judging by the fact that it surrounded the whole of the primary forests, each logged forest sites certainly encompassed several thousands of hectares.

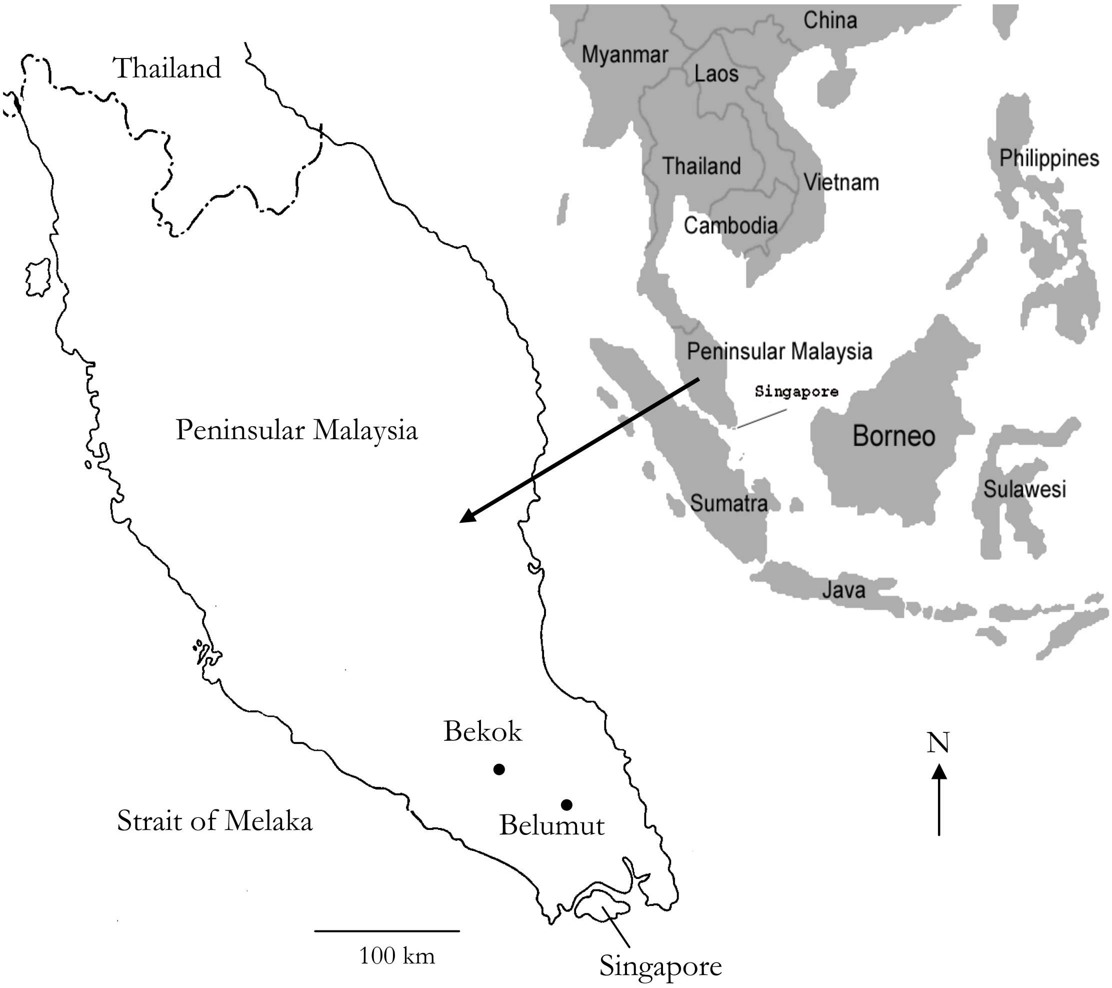


Fig. 1. Map showing location of the two study areas in Johore, Malaysia: Bekok, Sungei Batang; Belumut, Gunung Belumut.

The two human-dominated landscapes adjacent to the forests comprised villages, home gardens and a mixed array of agricultural lands. The non-arboreal crops comprised oil palm and banana plantations. The only arboreal crop was the rubber tree stands. All study sites ranged over 80 – 790 m elevation, and majority of the bird species occurred within this range. Table 1 gives a summary of forest types based on Whitmore (1984), historical and geographical information of all the study areas and sites.

Table 1. Bird species richness (S), absolute numbers of birds observed (N), Shannon's indices (H'), eveness indices (J') and measures of dominance (D) at each study sites.

Sites	S	N	H'	J'	D
Bekok					
Primary forest	157	846	4.35	1.98	0.02
Secondary forest (overall)	145	823	4.30	1.99	0.02
Secondary forest (primary forest species)	127	763	4.16	1.98	0.03
Mixed-rural habitat (overall)	85	903	3.63	1.88	0.04
Mixed-rural habitat (primary forest species)	51	249	3.27	1.92	0.06
Belumut					
Primary forest	148	779	4.39	2.02	0.02

Secondary forest (overall)	140	737	4.22	1.97	0.03
Secondary forest (primary forest species)	123	654	4.14	1.98	0.03
Mixed-rural habitat (overall)	74	1139	3.29	1.76	0.06
Mixed-rural habitat (primary forest species)	42	227	2.91	1.79	0.10

Bird point count

We conducted actual bird surveys using the bird point count technique to determine the resident bird communities in all the six study sites from 14 January to 3 June 2003. All bird samplings always involved the same observer (K.S.-H.P.). Our sampling regime was designed in such a way that all study sites were censused with the same intensity and randomness. All forest sites had extensive networks of animal trails. Although the bird sampling points were not restricted only to the trails, some study sites were surveyed along the selected trails due to a variety of constraints that pertain in the area such as inaccessible steep ridges. The sampling points were at least 200 m apart to make sure that each of them was independent. All sampling points in human-dominated landscapes were < 10 km from the primary forests. We conducted a total of 120 sampling points for each study site. We recorded birds that were seen or heard for 10 minutes within 25 m radius of each sampling point. All bird surveys were conducted between 0700 h and 1030 h on days with no precipitation or strong wind. If a bird was heard and could not be identified, we documented the call using a voice recorder and a parabolic microphone, and then compared with the CD-ROM of local bird vocalizations (Scharringa 2001). We took care as to minimize double counting the same individual. Species with both resident and migrant populations, crepuscular species, birds with limited altitudinal distribution (< 200 m), non-natives, migrants, aerial feeders and raptors were excluded. We followed Inskipp et al. (1996) for the bird scientific names. Birds were classified as primary forest species according to Wells (1985).

Following Hughes et al. (2002), we recorded the vertical vegetation strata in which birds were seen to determine the use of each stratum by bird communities within each study site. We defined emergent as the tree crown > 25 m; canopy, the crown of the trees >10 m tall; middle, the understory layer between the shrub and main canopy; shrub, any woody vegetation < 2 m tall; and ground, the leaf litter and herb layer. To determine the activities associated with a certain habitat, we also recorded the type of activities (foraging, nesting, moving, or perching) in which every observed individual engaged. Foraging referred to actual feeding or movement executed to obtain food. Nesting included courtship display, collection of nesting materials or the flights to and from the nests. Moving included the locomotion of birds in the midst of vegetation. Perching comprised all activities observed while sitting such as preening and vocalization. To determine if primary forest birds associated with certain countryside sub-habitats, we classified our bird count points in the countryside as either 'plots' or 'edges'. We defined plots as areas for crop production and included stands of rubber trees, oil palm and banana plantations. Edges were the second growth of pioneer tree or shrub species that found within or bordered plots and villages.

While it is true that longer duration of bird point count will invariably render larger number of bird species, there is a risk of double counting. We performed bird count in primary forest, logged forest and countryside to reconfirm that our sampling technique was optimized in each of these habitat types. Five bird point counts for a period of 30 min each were conducted between 0700 h and 1030 h in each habitat types at Belumut. The bird species seen or heard within a radius of 25 m was recorded at every 5 min interval to obtain the cumulative number of bird species. It was found that the cumulation curves at all habitat types increased sharply by the first 10 min of observation and then started to level off. The average numbers of bird species observed or heard during each thirty-minutes count were 11.8 ± 0.9, 9.2 ± 1.0 and 12.0 ± 1.5 for primary forest, logged forest and countryside, respectively. By the tenth minutes of sampling, approximately 9.2 ± 0.9 bird, 6.8 ± 0.9 and 10.2 ± 1.0 birds were counted for the primary forest, logged forest and countryside, respectively. This suggests that most species (80%) within a sampling plot were recorded during the 10 min count.

Vegetation sampling

To determine if resource abundance affected the primary forest frugivore distribution, we scanned a circular area of 8 m in radius within every bird sampling point and estimated the fruiting intensity of vegetation bearing bird-dispersed fruits. The bird-dispersed fruits were defined as fleshy, bright colored, and of small or medium size (Hamann and Curio 1999). A fruiting index was used to describe the estimated fruiting intensity. Each sampling plot was given a score based on the number of bird-dispersing fruits observed: individuals that bore one to 50 fruits = 1, 51 to 500 fruits= 2 and > 500 fruits= 3. In addition to recording fruiting trees and shrubs, we also recorded their flowering intensity based on the same method as fruiting index. Each plot was given a score according to the flowering intensity within: trees or shrubs that bore one to 50 flowers = 1, 51 to 500 flowers = 2 and > 500 flowers = 3. The addition of flowering and fruiting intensity indices deduced the resource abundance index.

To determine if bird communities associated with certain vegetation structure within each habitat type, we quantified the following variables within a 5 m radius circular area in the same bird count plots: (1) the percentage of tree (> 10 m in height) canopy density using spherical densiometer following Lemmon (1957), (2) the percentage shrub (woody vegetation < 2 m in height) cover, (3) the percentage of herb (non-woody vegetation < 1m) cover, (4) the number of trees < 10 m in height, (5) the diameter at breast height (d.b.h.) of trees, (6) the number of trees with d.b.h. < 2 cm, (7) the number of dead trees, (8) the leaf litter depth and (9) the understory vegetation volume. For measurement of vegetation volume, see Mills et al. (1991).

Statistical Analyses

We graphed cumulation curves for all study sites to assess inventory completeness. To estimate the 'true' primary forest bird species richness for each study sites, we used EstimateS version 6.0 (Colwell 2000) to calculate the abundance- and incidence-based estimator Chao2 (Chao 1987), incidence-based coverage estimator ICE (Lee and Chao1994) and MMMean that based on Michaelis-Menten model (Raaijmakers 1987). These three estimators were found to have the best performance predicting tropical bird species richness (Herzog et al. 2002; Matlock et al. 2002; Walther and Martin 2001). EstimateS version 6.0 was also used to graph smoothed rarefaction curve for comparison of species richness among the study sites.

For each species, we calculated the frequency of occurrence, which was the proportion of sampling plots where the species was detected. We calculated the index of similarity to measure the degree of resemblance when comparing two study sites in species assemblage. We used Jaccard (IsJ) to determine the qualitative index of similarity:

$$IsJ = C(A, B)/[N(A) + N(B)]$$

where C(A, B) is the number of species shared by study sites A and B, and N(A) + N(B) are the total number of species in study site A and B.

Primary forest bird diversity indices, Shannon-Wiener (H') and Simpson's ($1/\Sigma p_i^2$), were calculated using EstimateS and were used to derive the evenness index ($J' = H'/\text{Log } S$), that determined the degree of equitability of species abundances, and the inverse of Simpson's index ($D = \Sigma p_i^2$), that measured the relative importance of dominant species. We applied chi-squared test to determine if the use of vegetation strata and avian activities among the study sites were significantly different. Due to the small sample size, we pooled the data from the two study areas so that no more than one fifth of the total number of expected frequencies in the chi-squared tests had the value below five. Admittedly, the data from the two study areas should ideally be analyzed separately. However, combining the data was justifiable here given that both areas were used to be one large, contiguous primary forest; and shared the same management history. We performed the tests using SAS version 6.12 (SAS Institute Inc. 1990).

We used the nonparametric, univariate classification trees to distinguished the ecological traits of the primary forest birds that account for vulnerability to disturbance. The response variables were represented by categorizing species as 'persistent' to disturbance if they were present in the countryside and 'non-persistent' if absent. Those were also classed as 'vulnerable' if only present in primary forest and 'non-vulnerable' if detected in selectively logged forest as well. The continuous explanatory variable was the body length. Geographical distribution (narrow [restricting only within Sunda region] or wide [occurring beyond Sunda region]), diet (frugivory [feeding mostly on fruits], insectivory [feeding mainly on insects], omnivory [mixed diet of both fruits and insects] or nectarivory [feeding on nectar although insects are also part of the diet]) and microhabitat (ground-dwelling, understory, canopy or trunks) were specified as categorical explanatory variables. The grouping of each species for each explanatory variable was assessed by field observations or data obtained from literature (e.g., Smythies 1981; Thiollay 1995; Jeyarajasingam and Pearson 1998; Robin 2000). Tree classifications were performed using the tree function in S-Plus

Version 6.1 (Insightful Corp. 2002). The minimum group size for data splitting was set at 10. To improve classification efficacy, the trees were 'pruned' based on optimizing misclassification errors. A 10-fold cross validation process, repeating 500 times, was used to determine the tree size.

We calculated the Pearson correlation coefficients using SAS for 20 environmental variables (the mean d.b.h. and number of trees < and > 10 m height plot^{-1}; the mean density of trees < 2 cm d.b.h. plot^{-1}; the mean number of dead trees plot^{-1}; tree canopy, herb and shrub cover; litter depth; the density of trees with d.b.h. < 10 cm, between 10 and 20 cm, 20 and 30 cm, 30 and 40 cm and > 40 cm, flowering intensity index, fruiting intensity index; resource abundance index; shrub volume index; understory tree volume index and total understory vegetation volume index). These correlated variables (Pearson Correlation coefficient > 0.5) formed five groups and only the most biologically meaningful variable from each group was retained. The retained variables were the mean number of dead trees plot^{-1}, mean density of trees between 30 and 40 cm, canopy cover, resource abundance index and shrub volume index. To determine the relationship between the primary forest bird species distribution and the retained environmental variables, we constrained the ordination of a matrix of primary forest bird species abundance by a multiple linear regression on the five retained, log-transformed environmental variables in a second matrix using canonical correspondence analysis (CCA; ter Braak 1986) in PC-ORD version 2.0 (McCune and Melford 1995). Outlier analysis was performed with the cutoff set at 2.0 standard deviations. Axis scores were rescaled using Hill's (1979) scaling method and the representation of species was optimized. Statistical significance for all analyses was set at 0.05.

Results

Overall species richness

We detected 5227 individuals representing 188 species and 26 families. The total number of species detected at each site ranged from 74 in Belumut countryside to 157 in Bekok primary forest. The total number of individuals recorded ranged from 737 in Belumut logged forest to 1139 individuals in Belumut countryside. According to Shannon-Wiener index, the primary forests at Bekok and Belumut are the two most diverse sites whereas the least diverse site was the countryside at Belumut (Table 2)

Table 2. Frequencies of occurrence for primary forest birds in the two study areas (see Methods for frequencies of occurrence). Each species is broadly grouped based on canonical correspondence analysis (see Fig.8). Chi-squared tests with Yates' correction for continuity, for bird abundance between the primary forest and its corresponding disturbed habitats, are performed for species with ample sample sizes. The level of significance is set at alpha 0.05.

Scientific name	Common name	Group class	Frequency of occurrence					
			Bekok			Belumut		
			Primary	Secondary	Mixed-rural	Primary	Secondary	Mixed-rural
Rhizothera longirostris	Long-billed partridge	4	0.008	0	0	0.017	0	0
Melanoperdix nigra	**Black partridge**	**4**	**0.008**	**0**	**0**	**0.008**	**0**	**0**
Rollulus rouloul	Crested partridge	4	0.008	0	0	0.017	0	0
Lophura erythrophthalma	**Crestless fireback**	**4**	**0.008**	**0**	**0**	**0.008**	**0**	**0**
Argusianus argus	Great argus	3	0.025	0	0	0.058	0.033	0
Sasia abnormis	Rufous piculet	3	0.017	0.008	0	0.008	0.008	0
Celeus brachyurus	Rufous woodpecker	1	0.017	0.042	0.017	0.017	0.008	0.067
Dryocopus javensis	White-bellied woodpecker	2	0.008	0.017	0	0.017	0.017	0.017
Picus miniaceus	Banded woodpecker	2	0.008	0.042	0.033	0.017	0.042	0.017
Picus puniceus	Crimson-winged woodpecker	2	0.017	0.017	0.017	0.025	0.075	0.008
Picus mentalis	Checker-throated woodpecker	2	0.017	0.025	0.017	0.050	0.025	0.008
Blythipicus rubiginosus	Maroon woodpecker	5	0.008	0.042	0	0.008	0.017	0
Reinwardtipicus validus	Orange-backed woodpecker	2	0.017	0.017	0	0.008	0.008	0.017
Meiglyptes tristis	Buff-rumped woodpecker	1	0.058	0.017	0.042 n.s.	0.017	0.008	0
Meiglyptes tukki	Buff-necked woodpecker	5	0.008	0.042	0	0.025	0.008	0
Hemicircus concretus	Grey-and-buff woodpecker	3	0.008	0	0	0	0.008	0
Magalaima chrysopogon	Gold-whiskered barbet	#	0.050	0.008	0.025	0.067	0.033	0.008
Megalaima rafflesii	**Red-crowned barbet**	**4**	**0.017**	**0**	**0**	**0.008**	**0**	**0**
Megalaima mystacophanos	Red-throated barbet	3	0.025	0.017	0	0.042	0.008	0
Megalaima henricii	Yellow-crowned barbet	3	0.058	0.008	0.008	0.142	0.025	0
Megalaima australis	Blue-eared barbet	3	0.150	0.058*	0.008*	0.125	0.067	0
Calorhamphus fuliginosus	Brown barbet	2	0.042	0.017	0	0.008	0.025	0.025

Anthracoceros malayanus	**Black hornbill**	**2**	**0.008**	**0.025**	**0**	**0.017**	**0.008**	**0.025**
Buceros rhinoceros	Rhinoceros hornbill	3	0.075	0.025	0	0.058	0.042	0
Rhinoplax vigil	**Helmeted hornbill**	**3**	**0.033**	**0.008**	**0**	**0**	**0**	**0**
Anorrhinus galeritus	Bushy-crested hornbill	3	0.033	0	0	0.067	0.017	0
Aceros comatus	White-crowned hornbill	2	0.025	0.025	0.017	0.017	0.017	0.017
Aceros undulatus	Wreathed hornbill	5	0.025	0.050	0	0.017	0.017	0
Harpactes kasumba	Red-naped trogon	3	0.017	0	0	0.008	0.008	0
Harpactes diardii	Diard's trogon	3	0.025	0.025	0	0.033	0	0
Harpactes duvaucelii	Scarlet-rumped trogon	3	0.017	0.008	0	0.025	0.017	0
Harpactes oreskios	Orange-breasted trogon	4	0.008	0	0	0.017	0	0
Alcedo meninting	Blue-eared kingfisher	#	0.008	0.008	0	0.008	0.008	0.008
Alcedo euryzona	Blue-banded kingfisher	3	0.008	0.008	0	0.008	0	0
Ceyx erithacus	Oriental dwarf kingfisher	2	0.008	0.017	0.017	0.017	0.008	0.008
Lacedo pulchella	Banded kingfisher	3	0.050	0.075	0.008	0.033	0.017	0
Actenoides concretus	Rufous-collared kingfisher	4	0.017	0	0	0.017	0	0
Nyctyomis amictus	Red-bearded bee-eater	#	0.008	0.033	0	0.017	0.017	0.008
Hierococcyx vagans	Moustached hawk cuckoo	3	0.008	0.008	0	0.017	0	0
Cacomantis sonneratii	Banded bay cuckoo	#	0.017	0	0.008	0.017	0.017	0
Cacomantis variolosus	Brush cuckoo	#	0.008	0.008	0.008	0.017	0.017	0
Chrysococcyx xanthorhynchus	Violet cuckoo	3	0.008	0.017	0	0.017	0.008	0
Phaenicophaeus diardii	Black-bellied malkoha	5	0.008	0.025	0	0.008	0.008	0
Phaenicophaeus sumatranus	Chestnut-bellied malkoha	2	0.008	0.008	0.008	0.008	0.017	0.008
Phaenicophaeus chlorophaeus	Raffles's malkoha	5	0.017	0.058	0	0.017	0.017	0
Phaenicophaeus javanicus	Red-billed malkoha	4	0.017	0	0	0.008	0	0
Phaenicophaeus curvirostris	Chestnut-breasted malkoha	2	0.008	0.033	0.008	0.017	0.008	0.008
Centropus rectunguis	**Short-toed coucal**	**4**	**0.017**	**0**	**0**	**0.008**	**0**	**0**
Psittinus cyanurus	**Blue-rumped parrot**	**1**	**0.025**	**0.008**	**0.058 n.s.**	**0.017**	**0.017**	**0.050**
Loriculus galgulus	Blue-crowned hanging parrot	#	0.625	0.425*	0.175*	0.483	0.492	0.483 n.s.
Psittacula longicauda	Long-tailed parakeet	2	0.008	0.008	0.033	0.017	0.150**	0.075 n.s.

Chalcophaps indica	Emerald dove	2	0.017	0.058	0.042	0.017	0.008	0.025
Treron olax	Little green pigeon	2	0.058	0.050	0.075 n.s.	0.017	0.058	0
Treron curvirostra	Thick-billed green pigeon	5	0.008	0.058	0.008	0	0.017	0
Treron capellei	**Large green pigeon**	**4**	**0.025**	**0**	**0**	**0**	**0**	**0**
Ptilinopus jambu	Jambu fruit dove	#	0.008	0	0	0	0	0.017
Ducula aenea	Green imperial dove	2	0.017	0.008	0	0.008	0.025	0.008
Pitta caerulea	Giant pitta	3	0.008	0	0	0.008	0.008	0
Pitta guajana	Banded pitta	3	0.008	0	0	0.008	0.008	0
Pitta granatina	Garnet pitta	5	0.008	0.008	0	0	0.008	0
Corydon sumatranus	Dusky broadbill	3	0.083	0.042	0	0.008	0	0
Cymbirhynchus macrorhynchus	Black-and-red broadbill	5	0.017	0.025	0.008	0.025	0.058	0
Eurylaimus javanicus	Banded broadbill	3	0.100	0.025	0	0.017	0.050	0
Eurylaimus ochromalus	Black-and-yellow broadbill	5	0.042	0.033	0	0.017	0.025	0
Calyptomena viridis	Green broadbill	5	0.017	0.042	0	0.017	0.017	0
Gerygone sulphurea	Golden-bellied gerygone	1	0.008	0.008	0.033	0	0.008	0.008
Irena puella	Asian fairy bluebird	3	0.158	0.075	0.025*	0.225	0.258	0
Chloropsis sonnerati	Greater green leafbird	#	0.008	0.017	0	0.008	0.017	0
Chloropsis cyanopogon	Lesser green leafbird	2	0.008	0.008	0	0.017	0.008	0.008
Chloropsis cochinchinensis	Blue-winged leafbird	5	0.033	0.075	0.008	0.075	0.125	0.017 n.s.
Eupetes macrocerus	Rail-babbler	4	0.017	0	0	0.008	0	0
Platylophus galericulatus	Crested jay	3	0.025	0.008	0	0.008	0	0
Platysmurus leucopterus	**Black magpie**	**5**	**0.025**	**0.025**	**0**	**0.008**	**0.033**	**0**
Corvus enca	Slender-billed crow	4	0.017	0	0	0.017	0	0
Oriolus xanthonotus	Dark-throated oriole	#	0.008	0.008	0	0.017	0.050	0
Coracina striata	Bar-bellied cuckooshrike	4	0.008	0	0	0.017	0	0
Coracina fimbriate	Lesser cuckooshrike	3	0.017	0.017	0	0.008	0.008	0
Pericrocotus igneus	Fiery minivet	3	0.008	0.008	0	0.017	0.008	0
Pericrocotus flammeus	Scarlet minivet	5	0.017	0.067	0	0.033	0.083	0
Hemipus hirundinaceus	Black-winged flycatcher-shrike	3	0.017	0.008	0	0.017	0.008	0

Rhipidura perlata	Spotted fantail	3	0.033	0.008	0	0.092	0.008*	0
Dicrurus aeneus	Bronzed drongo	3	0.008	0.008	0	0.008	0	0
Dicrurus paradiseus	Greater racket-tailed drongo	#	0.250	0.708**	0.242 n.s.	0.242	0.442**	0.067*
Hypothymis azurea	Black-naped monarch	#	0.050	0.025	0.008	0.008	0.017	0
Terpsiphone paradisi	Asian paradise-flycatcher	5	0.008	0,025	0	0.017	0.025	0
Aegithina viridissima	Green iora	3	0.017	0.025	0	0.025	0.008	0
Aegithina lafresnayei	Great iora	5	0.008	0.017	0	0.017	0.025	0
Philentoma pyrhopterum	Rufous-winged philentoma	3	0.033	0.033	0	0.033	0.025	0
Philentoma velatum	Maroon-breasted philentoma	4	0.008	0	0	0.008	0	0
Tephrodornis gularis	Large woodshrike	#	0.075	0.025	0.025	0.025	0.092	0
Rhinomyias umbratilis	Grey-chested jungle flycatcher	3	0.025	0.008	0	0.033	0.025	0
Eumyias thalassina	Verditer flycatcher	3	0.008	0.008	0	0.008	0	0
Cyornis concertus	White-tailed flycatcher	4	0.017	0	0	0	0	0
Cyornis tickelliae	Tickell's blue flycatcher	3	0.017	0.008	0	0.017	0.008	0
Culicicapa ceylonensis	Grey-headed canary flycatcher	3	0.117	0.033*	0	0.033	0.008	0
Copsychus malabaricus	White-rumped shama	#	0.125	0.142	0.042*	0.167	0.067*	0
Trichixos pyrropyga	Rufous-tailed shama	4	0.008	0	0	0.008	0	0
Enicurus ruficapillus	Chestnut-naped forktail	3	0.033	0.017	0	0.008	0.008	0
Enicurus leschenaulti	White-crowned forktail	3	0.008	0.008	0	0	0	0
Gracula religiosa	Hill myna	2	0.008	0.067	0.033	0.050	0.208**	0.058 n.s.
Sitta frontalis	Velvet-fronted nuthatch	3	0.008	0.008	0	0.017	0.017	0
Melanochlora sultanea	Sultan tit	5	0	0.067	0	0.008	0.008	0
Pycnonotus zeylanicus	**Straw-headed bulbul**	**2**	**0.008**	**0.025**	**0.025**	**0.017**	**0.042**	**0.025**
Pycnonotus atriceps	Black-headed bulbul	4	0.008	0	0	0.008	0	0
Pycnonotus squamatus	Scaly-breasted bulbul	4	0	0	0	0.008	0	0
Pycnonotus cyaniventris	Grey-bellied bulbul	3	0.033	0.100	0.017	0.100	0.025	0
Pycnonotus eutilotus	Puff-backed bulbul	3	0.067	0.042	0	0.058	0.008	0
Pycnonotus finlaysoni	Stripe-throated bulbul	4	0.008	0	0	0.008	0	0
Pycnonotus simplex	Cream-vented bulbul	#	0.075	0.067	0.008	0.108	0.042	0.017*

Pycnonotus brunneus	Red-eyed bulbul	2	0.042	0.058	0.05	0.158	0.125	0.033*
Pycnonotus erythropthalmos	Spectacled bulbul	2	0.050	0.108	0.042	0.058	0.042	0.017
Alophoixus bres	Grey-cheeked bulbul	3	0.017	0.042	0	0.083	0.058	0
Alophoixus phaeocephalus	Yellow-bellied bulbul	3	0.108	0.042	0	0.067	0.042	0
Tricholestes criniger	Hairy-backed bulbul	3	0.083	0.100	0	0.083	0.075	0
Iole olivacea	Buff-vented bulbul	3	0.033	0.008	0	0.025	0.025	0
Ixos malaccensis	Streaked bulbul	3	0.133	0.008*	0.008*	0.125	0.058	0.008*
Hemixos flavala	Ashy bulbul	#	0.392	0.075*	0.017*	0.258	0.175	0.017*
Orthotomus atrogularis	Dark-necked tailorbird	1	0.133	0.083	0.150 n.s.	0.083	0.033	0.208
Trichastoma rostratum	White-crested babbler	3	0.050	0.025	0	0.033	0	0
Malacocincla abbotti	Abbott's babbler	#	0.025	0.017	0.017	0.067	0.017	0.008
Malacocincla sepirium	Horsfield's babbler	3	0.075	0.017	0	0.025	0.042	0
Malacocincla malaccense	Short-tailed babbler	3	0.033	0.100	0	0.133	0.083	0
Pellorneum capistratum	Black-capped babbler	3	0.042	0.008	0	0.017	0.017	0
Malacopteron magnirostre	Moustached babbler	3	0.142	0.158	0	0.108	0.058	0
Malacopteron affine	Sooty-capped babbler	3	0.017	0.008	0	0.025	0.008	0
Malacopteron cinereum	Scaly-crowned babbler	3	0.017	0.025	0	0.033	0.025	0
Malacopteron magnum	Rufous-crowned babbler	3	0.150	0.108	0	0.108	0.058	0
Malacopteron albogulare	**Grey-breasted babbler**	**4**	**0.008**	**0**	**0**	**0.017**	**0**	**0**
Pomatorhinus montanus	Chestnut-backed scimitar babbler	3	0.033	0.017	0	0.025	0	0
Kenopia striata	Striped wren babbler	4	0.008	0	0	0.008	0	0
Napothera macrodactyla	**Large wren babbler**	**4**	**0.008**	**0**	**0**	**0.008**	**0**	**0**
Napothera epilepidota	Eyebrowed wren babbler	4	0.008	0	0	0.017	0	0
Stachyris rufifrons	Rufous-fronted babbler	3	0.033	0.025	0	0.017	0.017	0
Stachyris nigriceps	Grey-throated babbler	3	0.025	0.017	0	0.033	0.042	0
Stachyris poliocephala	Grey-headed babbler	3	0.033	0.042	0	0.017	0.017	0
Stachyris leucotis	White-necked babbler	4	0.025	0	0	0	0	0
Stachyris nigricollis	Black-throated babbler	3	0.208	0.258	0	0.108	0.083	0
Stachyris maculata	Chestnut-rumped babbler	3	0.050	0.067	0	0.058	0.033	0

Stachyris erythroptera	Chestnut-winged babbler	5	0.017	0.108**	0	0.017	0.033	0
Macronous gularis	Striped tit babbler	2	0.100	0.175	0.075 n.s.	0.017	0.067	0.158**
Macronous ptilosus	Fluffy-backed tit babbler	3	0.008	0.017	0	0.017	0.008	0
Yuhina zantholeuca	White-bellied yuhina	3	0.042	0.017	0	0.033	0.033	0
Prionochilus maculatus	Yellow-breasted flowerpecker	5	0.058	0.083	0.008	0.033	0.075	0
Prionochilus percussus	Crimson-breasted flowerpecker	2	0.033	0.042	0.008	0.017	0.008	0.017
Prionochilus thoracicus	Scarlet-breasted flowerpecker	3	0.058	0.008	0	0.083	0.017*	0
Dicaeum agile	Thick-billed flowerpecker	3	0.025	0	0	0.025	0.008	0
Dicaeum chrysorrheum	Yellow-vented flowerpecker	2	0.008	0.017	0.008	0	0.008	0
Dicaeum trigonostigma	Orange-bellied flowerpecker	#	0.283	0.267	0.358 n.s.	0.283	0.150*	0.183 n.s.
Dicaeum concolor	Plain flowerpecker	2	0.067	0.100	0.067	0.050	0.025	0.025
Dicaeum cruentatum	Scarlet-backed flowerpecker	2	0.008	0.033	0.033	0.025	0.017	0.008
Anthreptes simplex	Plain sunbird	3	0.017	0.008	0	0.017	0.008	0
Anthreptes rhodolaema	Red-throated sunbird	3	0.058	0.017	0	0.050	0.033	0
Anthreptes singalensis	Ruby-cheeked sunbird	#	0.125	0.117	0.042*	0.050	0.083	0
Hypogramma hypogrammicum	Purple-naped sunbird	3	0.200	0.142	0.008*	0.150	0.208	0
Aethopyga temminckii	Temminck's sunbird	3	0.058	0.008	0	0.042	0.008	0
Arachnothera longirostra	Little spiderhunter	#	0.250	0.250	0.042*	0.217	0.133	0.042*
Arachnothera flavigaster	Spectacled spiderhunter	5	0.042	0.050	0	0.025	0.042	0
Arachnothera chrysogenys	Yellow-eared spiderhunter	2	0.008	0.017	0.008	0.008	0.017	0
Arachnothera affinis	Grey-breasted spiderhunter	#	0.017	0.025	0.025	0.067	0.033	0.017 n.s.

Scientific and common names follow Inskipp et al. (1996). The species in bold are globally threatened or near threatened.
# denotes species that were not grouped in Fig. 8.
* denotes a significant change in abundance whereby the occurrence was lower.
** denotes a significant change in abundance whereby the occurrence was higher.
n.s. indicates no significant change in abundance.

The cumulation curves illustrated the completeness of point count inventories (Fig. 2). All graphs appeared to have reached their asymptotes during this study. However, the various estimators suggested that 20-30% and 10-20% of the true avifauna remained undetected in the primary forest at Bekok and Belumut, respectively. In the logged forest, 20-30% primary forest species remained undiscovered at both Bekok and Belumut. We might have missed 20-30% of the primary forest species in Bekok countryside and may also have underestimated species richness by 20-50% in Belumut countryside.

At first glance, higher overall species richness in the primary forest at Bekok (157 species) and Belumut (148) were observed than in the logged forest at Bekok (145) and Belumut (140). But chi-squared test with Yates' correction for continuity showed that the differences were not significant (Bekok: $\chi^2 = 0.4$, d.f. = 1, $P > 0.05$; Belumut: $\chi^2 = 0.17$, d.f. = 1, $P > 0.05$). Their 'true' overall species richness, estimated using ICE, also did not differ (Bekok: $\chi^2 = 1.18$, d.f. = 1, $P > 0.05$; Belumut: $\chi^2 = 0.72$, d.f. = 1, $P > 0.05$). Similarly, there was no significant difference in the number of individuals detected between primary and secondary forest at each study area (Bekok: $\chi^2 = 0.29$, d.f. = 1, $P > 0.05$; Belumut: $\chi^2 = 1.11$, d.f. = 1, $P > 0.05$). The numbers of species recorded in countryside were significantly lower than those in the primary forest at each study area (Bekok: $\chi^2 = 20.83$, d.f. = 1, $P < 0.01$; Belumut: $\chi^2 = 24.00$, d.f. = 1, $P < 0.01$).

Overall species richness of each corresponding sites between Bekok and Belumut did not differ significantly (Primary forest: $\chi^2 = 0.21$, d.f. = 1, $P > 0.05$; Logged forest: $\chi^2 = 0.06$, d.f. = 1, $P > 0.05$; Countryside: $\chi^2 = 0.63$, d.f. = 1, $P > 0.05$). However, the relative abundance of individuals between the corresponding sites had significant differences (Logged forest: $\chi^2 = 4.63$, d.f. = 1, $P < 0.05$; Countryside: $\chi^2 = 27.04$, d.f. = 1, $P < 0.01$) except those of the primary forest sites ($\chi^2 = 2.68$, d.f. = 1, $P > 0.05$). The three most abundant primary forest species in the three sites combined at Bekok were *Loriculus galgulus*, *Dicrurus paradiseus* and *Dicaeum trigonostigma* with 147, 144 and 109 individuals recorded, respectively. In remarkable agreement with Bekok, these species were also the most abundant primary forest birds at Belumut in the same ranking order with 175, 74 and 90 individuals, respectively. The two most abundant species constituted 14% and 12% of the total individuals recorded in Bekok and Belumut primary forest, respectively.

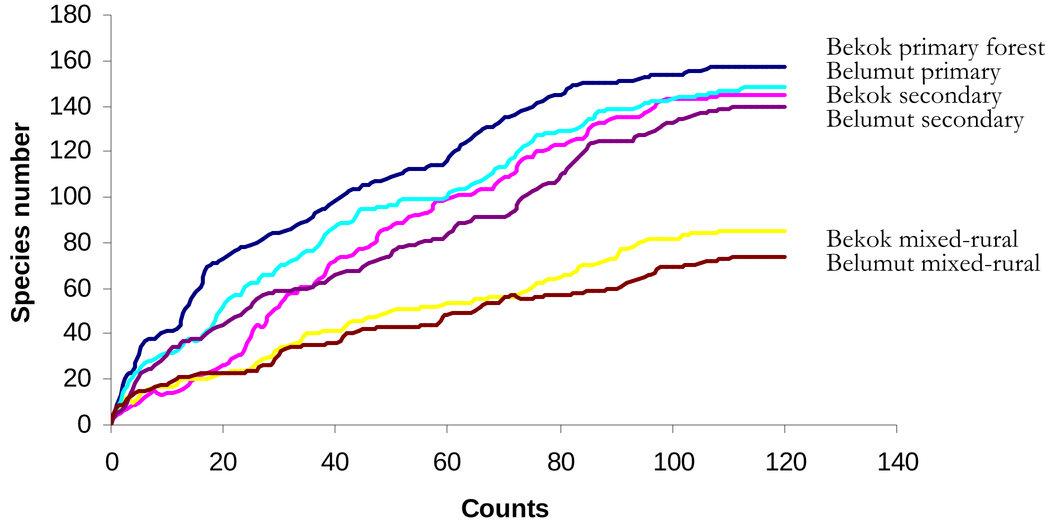


Fig. 2. Species accumulative curves of bird species detected in the six study sites.

Primary forest avian use of selectively logged forest

The various estimators suggested that the logged forests at both Bekok and Belumut were less diverse in primary bird species richness than their undisturbed counterparts (Fig. 3). The rarefaction curves also suggested that there were less primary forest birds in the logged forests (Fig.4). The total number of species shared between the primary and logged forest was 127 and 123 at Bekok and Belumut, respectively. The similarity in species composition between primary and logged forest at Bekok was 73% while that at Belumut was 75%. Thirty (19% of all species recorded at primary forest) primary forest species were not detected in the logged forest at Bekok. In Belumut logged forest, 25 interior forest species (17%) were not recorded.

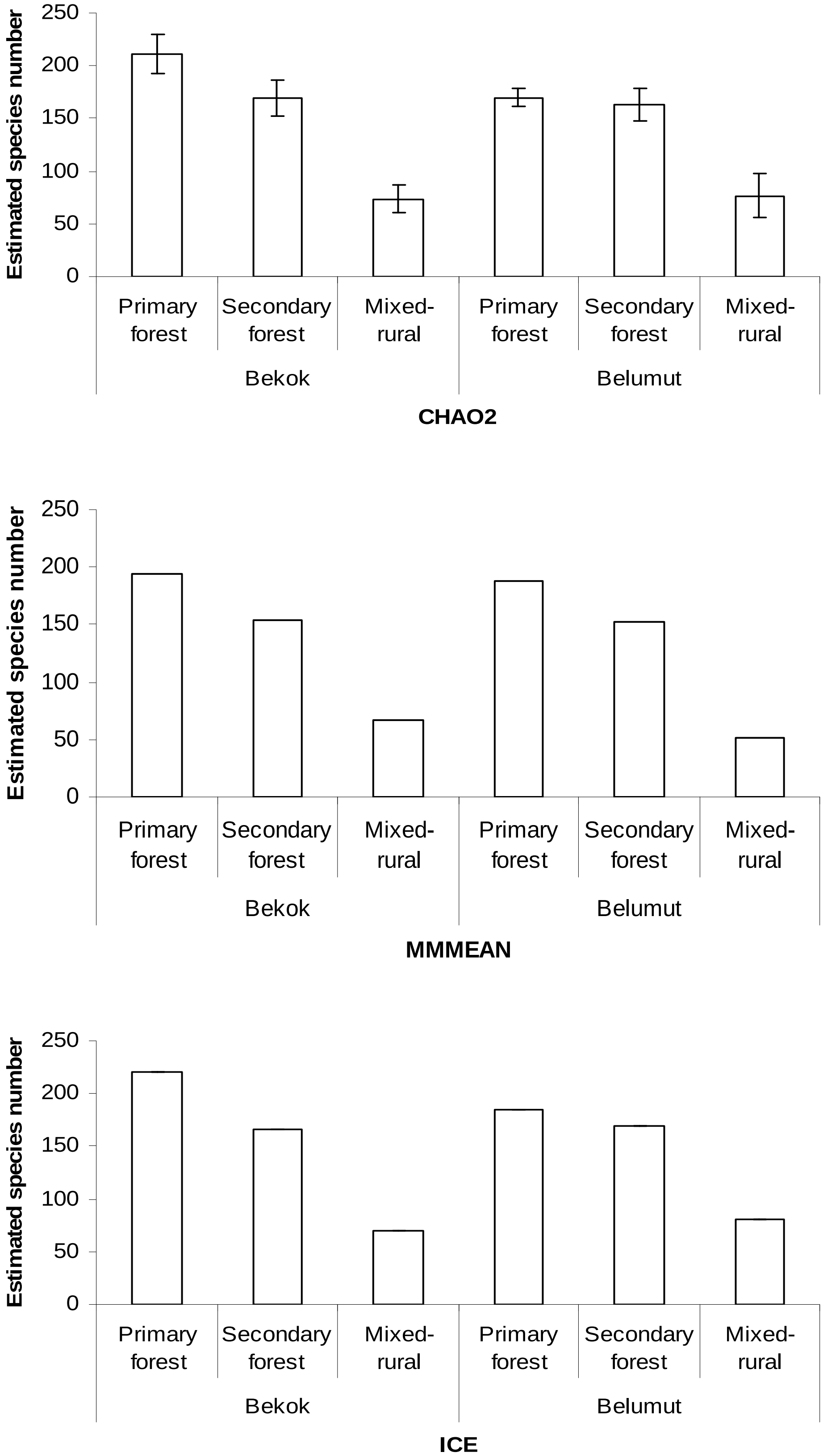
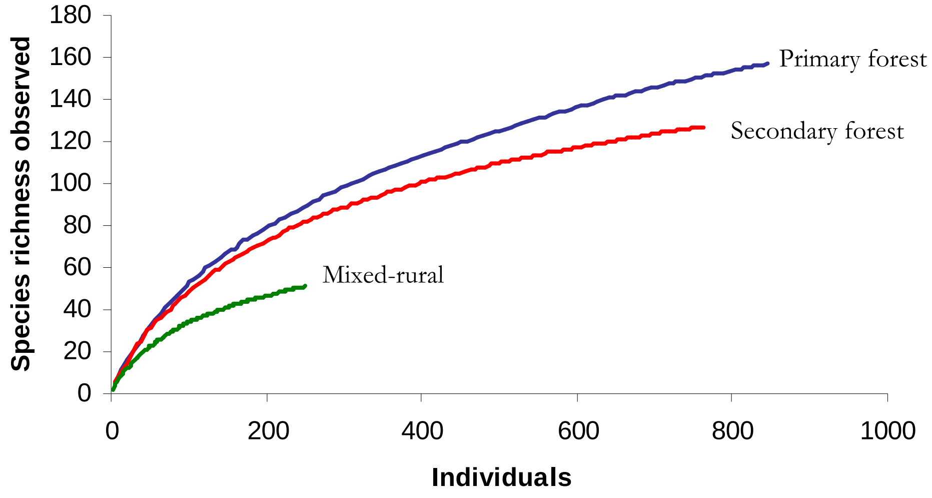


Fig. 3. Estimated primary forest bird species richness of the six study sites using three estimators. Bars represent standard errors. Standard errors for ICE are negligible.

(a) Bekok



(b) Belumut

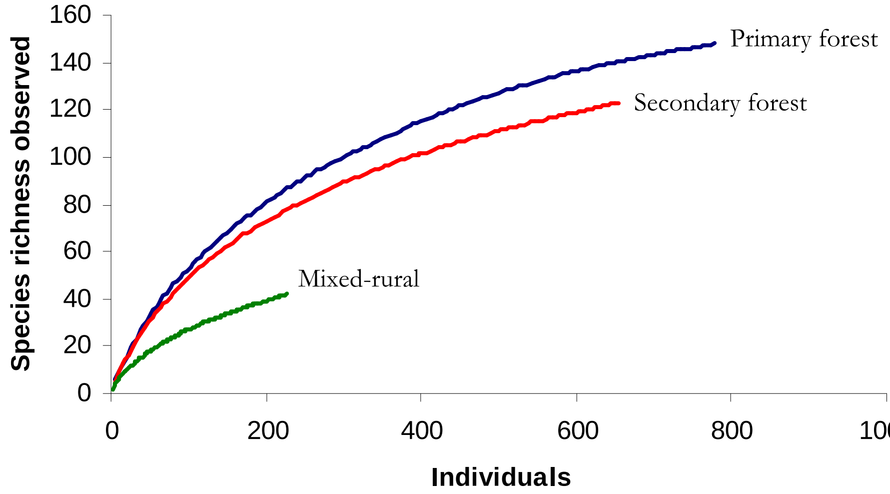


Fig. 4. Sample-based rarefaction curves displaying estimated primary forest bird species richness at the six study sites. X-axis is rescaled to the number of individuals observed.

The evenness indices among the primary and logged forests were comparatively similar (Table 1). However, the measure of dominance showed that there was an increased dominance of the commonest species in the logged forests at both study areas. The two most abundant species, which are primary forest birds, made up 17% and 15% of all birds recorded in logged forests at Bekok and Belumut, respectively. Individual taxa varied considerably in their use of logged forest, and also might response differently to the same logged forest in different area (Table 2). When compared to the primary forest, the number of *Loriculus galgulus* was lower in the logged forest at Bekok but did not differ significantly in abundance in that of Belumut. The direct opposite trend was observed for *Dicaeum trigonostigma* that remained ubiquitous in Bekok logged forest but had lower abundance in

Belumut logged forest. However, *Dicrurus paradiseus* seemed to favor both logged forests.

The classification tree (Fig. 5) showed that the microhabitat was the best-explained variables for the primary forest bird vulnerability. The ground-dwelling species tended to be vulnerable to logging disturbance with a classification success of 59%. Primary forest species that inhabited in understory, canopy and on trunks at any height, were classified as 'non-vulnerable' (89%). The misclassification error rate of the tree was 13%.

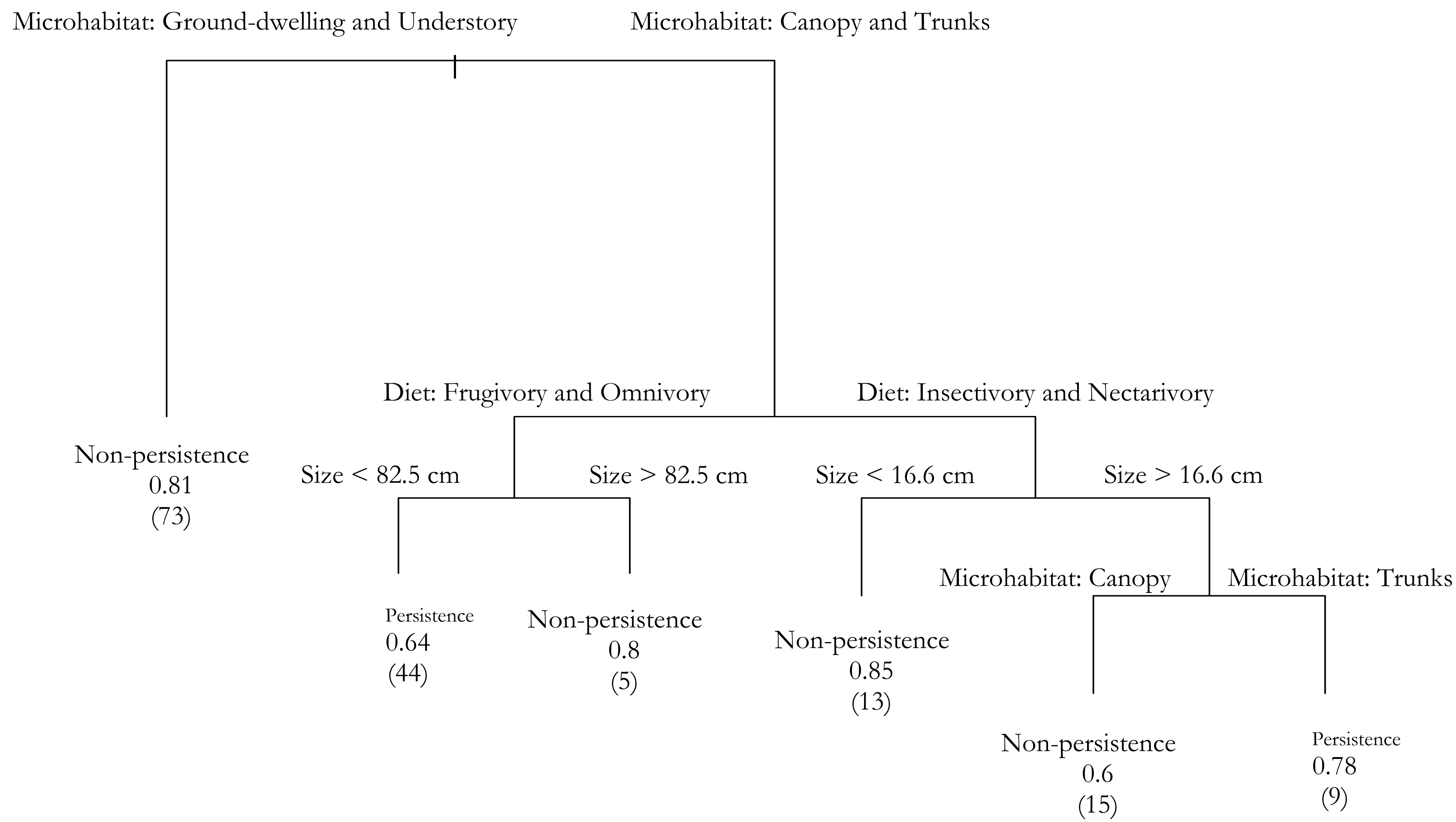


Fig. 5. Classification tree relating the ecological variables (microhabitat; size; distribution; diet) to primary forest bird persistence in mixed-rural habitat (persistence; non-persistence). At the end of each node are the probability of correct classification and number of species correctly classified.

Use of countryside by primary forest species

The estimators and rarefaction curves showed that the primary forest bird species richness in countryside at both Bekok and Belumut was comparatively poor (Fig 3 and 4). The point count surveys recorded 51 (32% of all primary forest species detected at Bekok) species of primary forest birds in the countryside at Bekok. Only 42 primary forest species, representing 28%, were shared between the primary forest and countryside at Belumut. The countryside, at both Bekok and Belumut, processed a different avifaunal community structure with only 27% and 23% of the species composition being similar to that of the primary forest, respectively.

The primary forest bird communities in the countryside at both Bekok and Belumut had the overall lowest evenness of abundance and highest dominance of the most common species (Table 1). The two most common primary forest species in the countryside at Bekok, *Dicaeum trigonostigma* and *Dicrurus paradiseus*, comprised 29% of the total primary forest species individuals detected. For Belumut countryside, *Dicrurus paradiseus* and *Orthotomus atrogularis* constituted 37% of all the recorded primary forest species individuals. The frequency of occurrence in both countryside at Bekok and Belumut, as compared to their corresponding undisturbed forest, showed contradictory results in species-level response to the use of human-dominated landscape. *Loriculus galgulus* had lower abundance in Bekok countryside but appeared to remain unaffected in that of Belumut. On the contrary, *Dicrurus paradiseus* had not changed in its abundance in Bekok countryside but was less common in the same habitat at Belumut. On the other hand, the abundance of *Dicaeum trigonostigma* remained unchanged in both sites.

The classification tree (Fig. 6) showed that the microhabitat and diet were the more important variables that associated with the birds that persist in the countryside. The relatively smaller primary forest frugivores and omnivores that occurred in canopy were more likely to be persistent of which 64% was correctly classified. The insectivores that feed on the trunks, were also tend to be persistent in the countryside (78%). However, the ground-dwelling and understory species were less persistent to the human-dominated landscaped (81%). The misclassification error rate of the tree was 25%. The variable, 'microhabitat', appeared twice along the branch and this implied the nonlinear responses to this variable. This justified the use of the classification tree that is amenable to nonlinear relationships (De'ath et al. 2000).

(a)

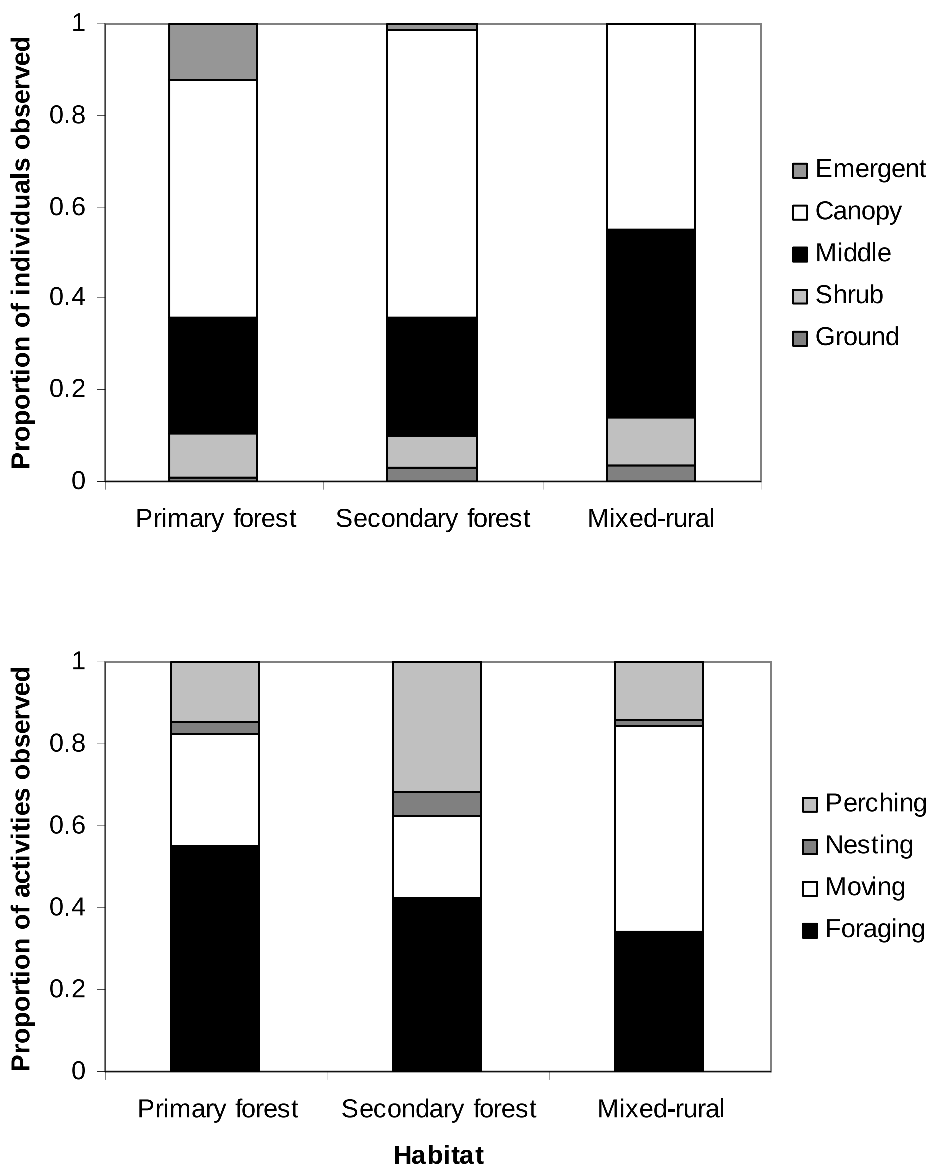


Fig.6. (a) Proportion of individuals observed in each vertical stratum in the three habitat types, and (b) proportion of individuals observed engaging in each activity.

Vertical stratum and resource use

The total number of individuals of primary forest species sighted among the three habitat types differed significantly ($\chi^2 = 46.96$, d.f. = 2, $P < 0.01$) with more individuals in primary forest and fewer in countryside observed than expected. The use of a particular vertical stratum and habitat type was not independent (χ^2 = 78.87, d.f. = 8, $P < 0.01$). More individuals were observed in the emergents than expected in primary forest and fewer than expected in selectively logged forest. In addition, there are more individuals utilizing understory in the countryside. Certain activity of an individual was significantly associated with a particular habitat type (χ^2 = 99.87, d.f. = 6, $P < 0.01$). More individuals were observed foraging in the primary forest, perching in the logged forest and moving in the countryside than expected.

The number of each sub-habitat types (edges or plots) sampled in countryside did not differ significantly (Bekok: χ^2 = 0.01, d.f. = 1, $P > 0.05$; Belumut: χ^2 = 2.41, d.f. = 1, $P > 0.05$). Although there was no significant association between certain activity of an individual and a particular sub-habitat type in the countryside for both study areas (Bekok: χ^2 = 3.45, d.f. = 2, $P > 0.05$; Belumut: χ^2 = 5.85, d.f. = 2, $P > 0.05$), there were significantly more individuals observed foraging and moving in edges (Foraging: Bekok, χ^2 = 17.45, d.f. = 1, $P < 0.01$, Belumut, χ^2 = 10.02, d.f. = 1, $P < 0.01$; moving: Bekok, χ^2 = 4.69, d.f. = 1, $P < 0.01$, Belumut, χ^2 = 37.87, d.f. = 1, $P < 0.01$). Data on primary forest bird nesting in the countryside was insufficient for analysis.

Primary forest bird communities

CCA was applied to pair the main matrix of species abundance for 154 primary forest bird species with second matrix of five log-transformed environmental variables. Five species (*Loriculus galgulus*, *Ptilinopus jambu*, *Dicrurus paradiseus*, *Dicaeum trigonostigma* and *Arachnothera longirostra*) were identified as outliers, which may have profound negative effect on the CCA results and were removed. The first two axes were used for interpretation and those explained 44.4% and 18.3% of the variance in species data, respectively The biplot scores and intraset correlations for the environmental variables with the ordination axes in Table 4 showed that first axis was related to all environmental variables. However, the mean density of dead trees, canopy cover and mean density of trees with d.b.h. between 30 and 40 cm had relatively stronger relationships to the species data. The ordination diagram from the CCA used LC scores, which were linear combinations of environmental variables (Fig.7).

Five distinct groups of primary forest bird species were formed in relation to the five environmental variables (Fig. 7). Group 1 represented the primary forest species (e.g., *Psittinus cyanurus*) that were highly persistent in countryside and tolerated fewer big trees (number of trees with d.b.h. between 30 and 40 cm), less canopy cover and lower density of dead trees. Group 2 was another cluster of primary forest species (including four species of *Dicaeum*) that increased in number with the increase in resource abundance. Groups 3 and 4 were the species that were not sensitive to resource abundance but increased in abundance with the increase in number of dead trees, canopy cover and density of larger trees. However, group 4 comprised the true forest species (e.g., all species of *Kenopia* and *Napothera*) that were highly associated with primary forest. Members of group 5 (e.g., *Stachyris erythroptera*) were relatively more associated with the logged forest and increased in abundance with increasing shrub volume.

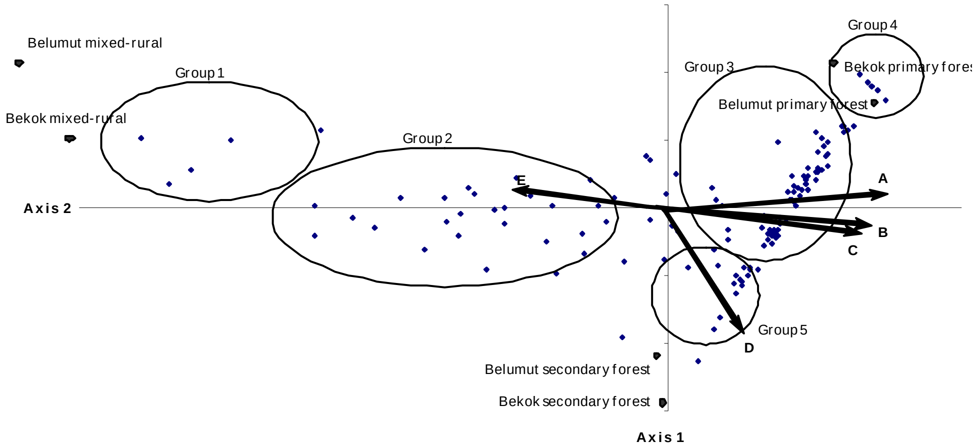


Fig. 7. Ordination diagram from the CCA of a primary matrix of the primary forest bird species abundance and a secondary matrix of five environmental variables. Large dots represented the study sites. Arrows A, B, C, D and E refer to environmental variables. A, density of trees with d.b.h. between 30 cm and 40 cm; B, tree canopy cover; C, density of dead trees; D, shrub volume; E, resource (fruit and flower) abundance. Smaller dots refer to primary forest bird species and are broadly classified into five groups.

Discussion

Acoustical and visual observations were employed for rapid assessment of lowland birds in three habitats. This method is more time efficient and enable us to detect a larger portion of avifaunas than other methods (Whitman et al. 1997). A weakness of such auditory –visual method is that it tends to underestimate richness and abundance of cryptic species (Bibby et al. 2000). However, our cumulation curves reaching asymptotes in all study sites indicated that our surveys were quite extensive. Our data when compared with another on-gong mist netting survey (C.A.-M.Y., personal communication), also show that we had recorded most of the understory species (except *Cyornis unicolor* and *Zoothera citrina*). Moreover, mist-netting in the logged forests failed to catch any of the cryptic, ground-dwelling species that we detected in the primary forest further confirmed their rarity in the disturbed forests. This attests that our survey data could accurately show the primary forest avian composition in disturbed habitats.

Our assessment clearly shows that primary forest avifaunas in Bekok and Belumut differ among disturbed and undisturbed sites in species richness and community structure. Fewer primary forest bird species were being detected in the disturbed sites such as the logged forest and countryside. It is also true that many primary forest species affected by logging initially are capable of recolonizing the logged forest over time. Species, that were absent in one and 12 year-old logged forests from the studies by John (1986; 1989) in Peninsular Malaysia, were being detected in our logged sites (e.g., *Rhinomyias umbratilis*; *Culicicapa ceylonensis*). However, the higher proportion of total individuals represented by few common species and species composition similarity of only 73 – 75% suggested that the recovery of the primary forest avian community structure in the logged forest was far from completion. Also, the vertical distribution of primary forest birds among the vegetation strata in logged forest was different when compared to pristine forest due to the lack of tall emergents. In addition, a bulk of the overall avian diversity in the logged forest was made up of birds of second growth (e.g., *Prinia rufescens*), forest edge (e.g., *Pycnonotus plumosus*) and countryside (e.g., *Copsychus saularis*). We are not certain if the interactions with birds from the disturbed habitats hinder the recovery of the original primary forest species composition and community structure. The invasive, non-native birds such as *Acridotheres cinereus*, were present in the logged forest and their influence (e.g., interspecific competition) on the primary forest avifauna also remains unknown.

Most ground-dwelling primary forest species in our study areas were still depauperate in the relatively old logged forest despite there was no barrier for movement between sites as the logged forest was contiguous with the undisturbed forest. Only few individuals of *Rhizothera longirostris*, *Melanoperdix nigra*, *Rollulus rouloul*, *Lophura erythrophthalma*, *Centropus rectunguis*, *Eupetes macrocerus*, *Trichixos pyrropyga*, *Kenopia striata*, *Napothera macrodactyla* and *Napothera epilepidoata* were observed in the primary forest and this implies that even if these ground-dwelling species occurred in the logged forest, their presence must be negligible. These species also tended to have the least tolerance for smaller trees and more open canopy (Fig. 8). This may suggest that the ground-dwelling primary forest birds are more sensitive to disturbance and have relatively higher extinction risk as compared with species that occupied other strata. Many of the vulnerable ground-dwelling species are associated with ground-nesting. Although our study does not reveal the mechanisms responsible for species vulnerability in the logged forest, there is evidence in the temperate region that nest predation rates for ground-nesting species varied among different habitat types (Martin 1993). Other workers have found higher predation of artificial eggs in the logged forest (Cooper and Francis 1998; Sodhi et al. 2003), hinting that ground-dwelling primary forest birds may suffer higher nest predation in the logged forest. Clearly, further studies of ecological mechanisms that underlie ground-dwelling primary forest bird vulnerability are needed.

Our results demonstrate that the countryside had the lowest species richness and absolute abundance of primary forest birds in Bekok and Belumut. Even pooling all birds in the countryside together and comparing species richness, the primary and logged forests still tended to have higher alpha-diversity. The majority of primary forest avifauna is clearly confined within the forested habitats. This can be explained by the vegetation structure, as countryside lacked large trees, dead trees and dense canopy (Fig. 8). However, the primary forest frugivorous and omnivorous species that are relatively smaller in sizes, tended to persist in the countryside. Higher resource abundance (i.e. fruiting intensities) in the countryside might be the attractant for the primary forest frugivores and omnivores that do not reside within the human-dominated landscapes and those with potentially large foraging range (Fig. 8). Most avian frugivores and omnivores consume fruit from several plant species. Therefore, the food resource in the countryside can replace the lack of suitable fruits caused by periodic mast of the dominant plant species in the forest. We are uncertain as to why the smaller body size is a favorable ecological trait for the primary forest species that persist in the countryside, and this raises the possibility that those smaller species in the countryside, where the anthropogenic disturbance is higher, were able to avoid human persecution and increase survival success (Owens and Bennett 2000). Another group that persisted in the countryside were the insectivores that feed on the trunks (i.e. woodpeckers). Apparently, the arboreal crop such as rubber trees and strands of pioneer trees in the countryside provided foraging opportunities for these birds (personal observation).

The interpretation of the changes in abundances of primary forest species in logged forest and countryside requires caution because of the small sample sizes for most of the taxa and therefore, we only focused on some of the more abundant species. The data on the three most common primary forest species in both study areas show individual taxa responded differently to the disturbance, and the frequency of occurrence of individual taxa in a particular habitat also varied in different locations.

Conservation Implications

The logged forests in our study areas have not quite recovered to its original avifaunal diversity despite they were selectively logged more than 30 years ago. This finding is consistent with similar comparative long-term studies in Peninsular Malaysia by Wong (1985; 1986), which showed that the species richness was lower in the 25 year-old regenerating logged forest than in virgin forest. This clearly implies that the complete regeneration of the logged forest would need a longer time (also see Huth and Ditzer 2001). Hence, the logging cycles of < 40 years in Peninsular Malaysia might impede the recovery for some interior forest species. The regime of the logging cycle must therefore be revised so that a compromise between economic and ecological interest can be achieved. The use of the logged forest by more perching birds illustrates the conservation value of this regenerating habitat. This logged matrix, if left untouched, can play a role in the conservation of widely distributed primary forest species (Lindenmayer and Franklin 2000).

A fraction of primary bird faunal (28 –32%) occurred in the countryside evinces the fact that some primary forest birds might be able to persist in the agricultural landscapes. The presence of small remnants of pioneer shrubs and trees in the countryside no doubt contributed to persistence of some primary forest species. However, we have to believe that the number of primary forest avian species that can truly survive in the agricultural landscapes is even lower for several reasons. First, since our survey sites were near the primary forest, it is likely that some species that spend most of the time in the forest use the countryside only because of its close proximity to the primary forest. Some species may commute to the countryside to exploit food resource but have all other aspects of their lifecycles dependent on the forest (Jeyarajasingam and Pearson 1999). Second, constant attempted use of countryside by forest species present in neighboring primary forest communities may be damped by the intense competition from the extant open countryside birds. Last, the countryside may still be undergoing the process of primary forest avifaunal relaxation to a new, lower number of species (Tilman et al. 1994). However, we have no knowledge of how long and how fast this relaxation takes. Clearly, more studies is needed because knowing the answer would help in the conservation action and active management for, particularly, globally threatened primary forest species in countryside (e.g., *Pycnonotus zeylanicus*).

For many primary forest avian species, undisturbed forest is clearly of critical importance for long-term survival. We studied the change in species richness of avifaunal communities in habitats subjected to logging and clearance for agriculture. We also showed how vegetation structure affected the distribution of primary forest birds. We identified rare habitat specialists, of which 29% are listed by Collar et al. (1994) as globally threatened or near threatened (Table 3). Those should therefore be priorities for conservation and monitoring. Our inventories of birds in the logged forest and countryside may be used as forecasts of primary forest avifaunal change under various human disturbances. This might be useful in management for the protection of Southeast Asian rain forest avian communities.

Acknowledgements

We thank the Economic Planning Unit, Malaysia, for granting K.S.-H.P. permission to carry out research in Johore. We are grateful to Allan Carlson, Malcolm Soh, Koh Lian Pin, Lee Tien Ming and Mary Rose Posa for their criticisms and literature. Further thanks go to many staff members and students of the Swedish Biodiversity Center for their comments, discussions and insight. Finally, we extend many thanks to the local communities at Bekok and Belumut for teaching K.S.-H. P. the know-how for survival in tropical rain forest. This research was funded by the Swedish Biodiversity Center to K.S.-H.P. and the National University of Singapore research grant no. R145000144112 to N.S.S.

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