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UNDERSTORY AVIFAUNA OF A BORNEAN PEAT SWAMP FOREST: IS IT DEPAUPERATE?

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ABSTRACT.—Southeast Asian peat swamp forests support fewer birds than dipterocarp forest. Habitat preferences appear to exist; seven species were captured significantly more often in the dipterocarp forest, and two species were represented by significantly more captures in the peat swamp forest. An increase in number of frugivorous birds in the peat swamp forest in June was correlated with a large fruit crop of *Callocarpa* sp. The difference in abundance of understory birds between the peat swamp forest and the dipterocarp forest resulted largely from three insectivorous guilds. Rare species constituted a large portion of captures, and a single family of insectivores (Timaliidae) were particularly rich in number of individuals and number of species. Peat swamp forests, although they may support a reduced understory avifauna relative to lowland dipterocarp forest, appear important in the ecology of Southeast Asian avian communities because they support specialized species and attract frugivores at sporadic intervals. *Received 4 May 1993, accepted 2 Nov. 1993.*

Our knowledge of Southeast Asian bird communities is based primarily on research conducted in pristine and regenerating lowland dipterocarp forest (Fogden 1972, Pearson 1977, Karr 1980, Wong 1986). The avifaunas of other forest formations, such as freshwater swamp forest, heath forest, mangrove forest, montane forest, and peat swamp forest (Whitmore 1984), remain largely unexplored. The avifauna of peat swamp forests is particularly worthy of investigation because such forests are widespread in Southeast Asia and are thought to support a depauperate animal community. Peat swamp forests cover 14,660 km^2 (12% of the total land area) of Sarawak, Malaysia, and in Brunei, peat swamp forests occupy 980 km^2 (23% of the total land area) (Anderson 1964). Peat swamp forests are thought to support depauperate animal communities because of the cascading influence of poor soil characteristics (Janzen 1974). The soils of peat swamp forests are rich in organic matter, acidic (pH $\leq$ 4.0), deficient in mineral nutrients, and often water-logged (Whitmore 1984:180). Janzen (1974) suggested these poor soil characteristics are responsible for structurally simplistic, slow growing, and chemically well-defended vegetation. Under this line of reasoning, plant biomass production is extremely limited and most of what is produced is toxic, creating a dramatic limitation to the productivity of higher trophic levels including birds.

I used mist nets to compare the understory bird community in a peat swamp forest with the understory bird community of an adjacent lowland

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dipterocarp forest growing on the fertile soils of an alluvial terrace in Borneo. Here, I examine the composition and dynamics of foraging guilds and test the predictions that (1) the number of individual understory birds is lower in the peat swamp forest than the dipterocarp forest within the area of study and (2) the number of species of understory birds is lower in the peat swamp forest than the dipterocarp forest within the area of study.

STUDY AREA AND METHODS

I conducted this research in the Cabang Panti Research Site in the Gunung Palung Nature Reserve (now National Park) (1°13′S, 110°7′E) in West Kalimantan (Borneo), Indonesia. The study area lies just above sea level and contains a 17-ha tract of peat swamp forest adjacent to a 48-ha tract of lowland dipterocarp forest on alluvial terrace. The study area is bounded on the north by extensive dipterocarp forest on the slopes of Mount Palung (1160 m), and on the south by peat swamp forest and freshwater swamp forest on a broad coastal plain.

Total rainfall was 4715 mm during the year in which this research took place, August 1986 to July 1987. The driest month was August with only 11 mm. February, June, and July were relatively dry with 120 mm, 275 mm, and 118 mm of rain, respectively. All other months were very wet with rainfall from 371 mm to 669 mm per month. Temperature records are unavailable, but no extremes were noted.

Vegetation structure of lowland dipterocarp forest and peat swamp forest differ greatly. The dipterocarp forest in which this study took place, is the classic, cathedral-like Southeast Asian tropical lowland evergreen rain forest, which is dominated by trees in the Dipterocarpaceae. Emergent trees exceed 60 m in height over a multi-layered and dense canopy. Mean diameter of trees is very large, with many trees exceeding 2 m in diameter. Lianas, epiphytes, and hemiepiphytes are abundant in the canopy. Compared to the dipterocarp forest, the peat swamp forest structure is stunted and sparse. Emergent trees, where present, reach heights of 20–30 m over a single-layer canopy. Mean size of trees is small; few trees exceed 0.5 m in diameter. The canopy is thin and supports relatively few lianas, epiphytes, and hemiepiphytes. Brunig (1983), Anderson (1964, 1983), and Whitmore (1984) provide more information on vegetation.

From December 1986 to July 1987, I operated ten mist nets (12 m long, 2.6 m high, 36 mm mesh, 4 shelf) at ground level for two days per month in each habitat. Mist nets are widely used in studies of tropical understory bird communities (Karr 1980, Schemske and Brokaw 1981, Wong 1986, Levey 1988, Loiselle and Blake 1991). I did not sample both habitats simultaneously; I netted for two days in one habitat, spent one day moving the nets, and then netted for two days in the other habitat. I opened the nets at dawn (06:30) and closed them after a minimum of 10 h (16:30–18:00) unless rain forced an early closure. Rain forced early net closing five times in the dipterocarp forest and three times in the peat swamp forest. In all cases, the rain fell after 14:00. There was very little variation in weather conditions between netting days in the two habitats. I accumulated 1509 net-h in the peat swamp forest and 1512 net-h in the dipterocarp forest (1 net-h = 1 mist net open for one hour).

There were 20 mist-net sites in each habitat. I used ten sites one month and the other ten sites the next month. Each mist-net site was randomly placed along a pre-existing trail system with 10 m to 50 m distance between each site. Twenty sites were used in each habitat, as opposed to just ten, to maximize the number of different patch types sampled.

Patch types range from recent tree fall gaps to mature canopy, and it is possible that as a patch of forest changes through time, the bird assemblage that utilizes the patch may also change (Schemske and Brokaw 1981). I strove to maximize the number of different patches in which I placed mist nets, so as to increase my chances of sampling all bird species present in each forest habitat.

I identified each captured bird following the nomenclature of King et al. (1975), and I released all birds at the capture location. I assigned each species to one of ten foraging guilds, using the guild classifications of Wong (1986). For some analyses, I lumped foraging guilds into guild categories of insectivore, frugivore, and nectarivore. The sample size determined the appropriate statistical test. If $N > 200$, I used Chi-square, if $200 \geq N \geq 25$ I used Chi-square adjusted for small sample sizes, and if $N < 25$ I calculated the expected binomial probabilities (Sokal and Rohlf 1981:708). I used the Wilcoxon signed-ranks test to evaluate some data on a month by month basis.

Because numbers of birds increased in the peat swamp forest in June, I conducted fruit tree watches, and I censused the standing fruit crop in both habitats during the same week in which I mist netted. Fruit tree watches consisted of standing at a distance of 10 to 20 m from *Callocarpa* sp. (Verbenaceae) trees and observing all bird feeding activity with binoculars (10 × 40). I kept a tally for all bird species observed and of all instances in which I observed a bird swallowing a fruit. I accumulated 5.2 h of observation over five consecutive mornings between 06:30 and 09:30. These observations were not incorporated into the mist net capture record. The fruit crop census consisted of quantifying the fruit crop available in both habitats in June. I searched two 20 m × 250 m randomly chosen transects in each habitat for any plants (including lianas and epiphytes) bearing ripe fruit. Where fruit was present, I determined the species of plant if possible and estimated the size of the fruit crop.

RESULTS

The data support the first prediction that the number of individual understory birds should be lower in the less productive peat swamp forest than in the dipterocarp forest sampled in this study. The total number of individuals captured in the peat swamp forest (230) was significantly lower than in the dipterocarp forest (301) ($\chi^2 = 9.49$, $P = 0.002$). The data do not support the second prediction that the number of species of understory birds should be lower in the peat swamp forest than the dipterocarp forest. There was no significant difference between the total number of species in the peat swamp forest (34) and the dipterocarp forest (39) ($\chi^2_{adj} = 0.21$, $P = 0.558$).

There was a strong tendency towards fewer individuals and fewer species in the peat swamp forest on a month by month basis (Fig. 1). In all months except June, I captured fewer individuals in the peat swamp forest than in the dipterocarp forest (Wilcoxon signed-ranks test, $T_s = 6$, $P = 0.0547$). In all months except June and July, I captured fewer species in the peat swamp forest than in the dipterocarp forest (Wilcoxon signed-ranks test, $T_s = 6$, $P = 0.0547$).

The data suggest that habitat preferences do exist among the understory birds sampled in this study. To determine whether there were significant between-habitat differences in capture frequency for any given species, a

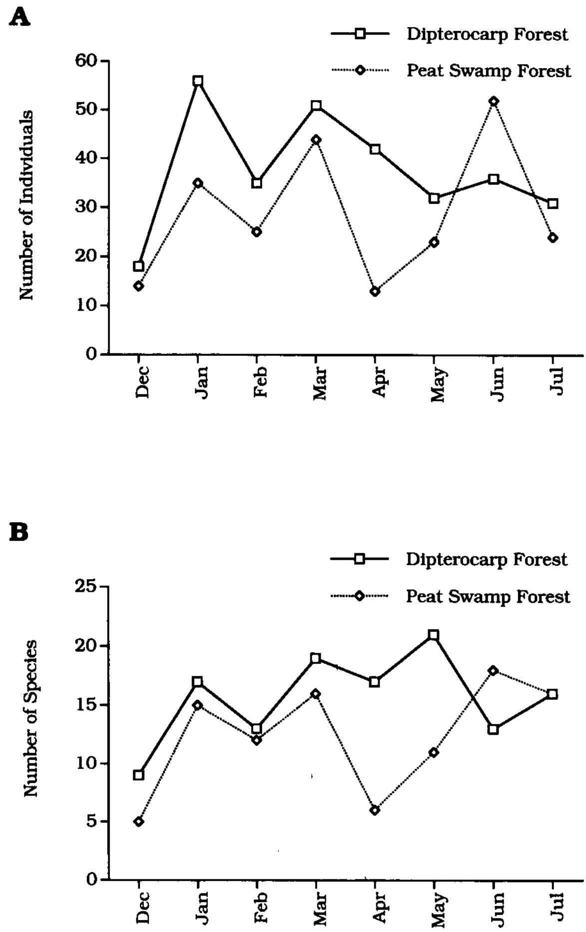

FIG. 1. Number of individual understory birds (A) and number of species of understory birds (B) captured per month in the dipterocarp forest and the peat swamp forest.

minimum of six captures is required to attain the 5% level of significance. Of the 47 species captured in this study (species list and data set available on request from JCG), 22 fulfill this criterion. Based on random processes, we expect 5% of the 22 species (=1.1) to show a significant difference in capture frequency between the two habitats. Of the 22 species, nine showed significant differences in capture frequency at the 0.05 level (Table 1), suggesting that the assemblage of understory bird species that occupied the peat swamp forest was distinct from the assemblage in the dipterocarp forest.

TABLE 1
SPECIES WITH SIGNIFICANT BETWEEN-HABITAT DIFFERENCES IN CAPTURE FREQUENCY[a]

	Number of individuals			Guild type[b]
	PSF	DF	*P*	
White-rumped Shama (*Copsychus malabaricus*)	3	10	=0.035	SFGI
Yellow-bellied Bulbul (*Criniger phaeocephalus*)	15	37	<0.005	I/F
Hairy-backed Bulbul (*Hypsipetes criniger*)	1	7	=0.031	I/F
Gray-breasted Babbler (*Malacopteron albogulare*)	14	1	<0.001	SFGI
Scaly-crowned Babbler (*M. cinereum*)	20	46	<0.005	TFGI
Buff-necked Woodpecker (*Meiglyptes tukki*)	0	6	=0.016	BGI
Yellow-breasted Flowerpecker (*Prionochilus maculatus*)	25	11	<0.05	I/F
Ferruginous Babbler (*Trichastoma bicolor*)	0	8	=0.004	TFGI
Short-tailed Babbler (*Malacocinela malaccensis*)	3	23	<0.001	LGI

[a] PSF = peat swamp forest; DF = dipterocarp forest.
[b] See Table 2 for guild codes.

The only month in which I recorded more individuals and more species in the peat swamp forest than in the dipterocarp forest was June (Fig. 1). The increased number of understory birds in the peat swamp forest in June consisted primarily of insectivore-frugivores, which are in the frugivore guild group (Fig. 2). The number of individual insectivore-frugivores captured in the peat swamp forest in June (25) significantly exceeded the number of insectivore-frugivores captured in the dipterocarp forest in June (7) (χ^2_{adj} = 9.03, P < 0.005). The insectivore-frugivore guild is dominated by bulbuls (Pycnonotidae). In the peat swamp, the mean number of individual bulbuls captured in each of the previous six months was 2.3, whereas in June 1987 I captured 19 individual bulbuls and added two new bulbul species to the capture record.

In June in the peat swamp forest, I noticed mixed species flocks, predominantly bulbuls, feeding on the fruit of a single tree species, thought to be in the genus *Callocarpa* (Verbenaceae). During fruit tree watches of *Callocarpa* sp. trees, I recorded 132 observations of insectivore-frugivores and arboreal frugivores eating *Callocarpa* sp. fruit; 78% of those observations were of bulbuls.

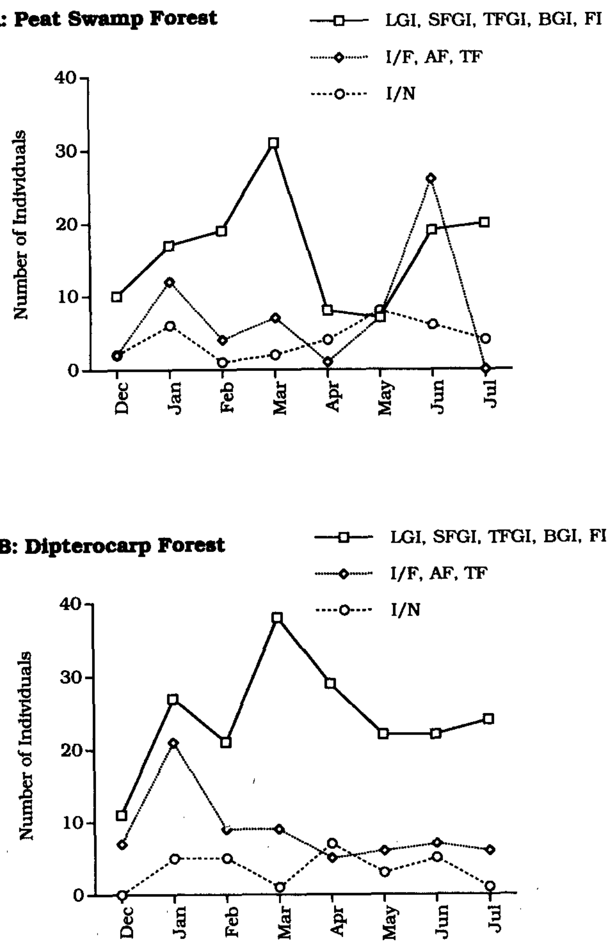

FIG. 2. Monthly captures of understory birds by guild groupings, insectivore (LGI, SFGI, TFGI, BGI, FI), frugivore (I/F, AF, TF), and nectarivore (I/N) in the peat swamp forest (A) and the dipterocarp forest (B). Guild abbreviations are defined in Table 2. Note the peak of frugivore abundance in June in the peat swamp forest.

Fruit was more abundant in the peat swamp forest in June. Within the peat swamp forest transects, I found 18 *Callocarpa* sp. trees each with abundant quantities of ripe fruit (estimated mean crop size of 2500 fruits) and one *Medinilla* sp. (Melastomataceae) epiphyte bearing 5–10 ripe fruits. Within the dipterocarp forest transects, I found one unidentified liana bearing 40–60 ripe fruits and two *Pternandra* sp. (Melastomataceae) trees each with 20–30 ripe fruits.

TABLE 2

DISTRIBUTION BY GUILD OF ALL BIRDS CAPTURED IN THE UNDERSTORY. PROBABILITY VALUES ARE LISTED FOR COMPARISONS OF NUMBER OF INDIVIDUALS BETWEEN HABITATS[a]

	Number of individuals			Number of species	
Guild type	PSF	DF	*P*	PSF	DF
Litter-gleaning insectivore (LGI)	13	37	<0.005	4	3
Shrub foliage-gleaning insectivore (SFGI)	31	28	<0.9	7	8
Tree foliage-gleaning insectivore (TFGI)	54	83	<0.025	5	5
Bark-gleaning insectivore (BGI)	3	12	=0.013	2	4
Flycatching insectivore (FI)	30	34	<0.9	3	3
Insectivore-nectarivore (I/N)	33	27	<0.9	3	2
Insectivore-frugivore (I/F)	58	68	<0.5	8	8
Arboreal frugivore (AF)	1	1	=0.5	1	1
Terrestrial frugivore (TF)	0	1	=0.5	0	1
Miscellaneous (Misc)	7	10	=0.148	1	14
Total	230	301		34	39

[a] PSF = peat swamp forest, DF = dipterocarp forest.

DISCUSSION

The reduced number of individuals, and the trend towards fewer species of understory birds in the peat swamp forest relative to the dipterocarp forest, is consistent with the hypothesis that peat swamp forests support a depauperate animal community (Janzen 1974). More research is required to understand the mechanisms responsible, particularly the possible connection between soils, vegetation, and fauna hypothesized by Janzen. A productive avenue of future study might be to study insectivorous birds because the difference in total number of captures between the peat swamp forest and dipterocarp forest consisted primarily of insectivores. Of nine guilds represented by captures in both habitats, only three guilds showed significant differences in total number of captures, and they were all insectivore guilds. Litter-gleaning insectivores, tree foliage-gleaning insectivores, and bark-gleaning insectivores were caught in significantly lower numbers in the peat swamp forest than in the dipterocarp forest (Table 2).

The general composition of the understory bird community sampled in this study is consistent with that of a virgin lowland dipterocarp forest in the Pasoh Forest Reserve, Peninsular Malaysia (Wong 1986). Rare species, defined as species whose cumulative number of individual captures is less than 2% of the total number of individual captures for all species (Karr 1971), constituted 62% of the species netted in the peat swamp

TABLE 3
SPECIES TABULATED BY THEIR NUMBER OF CAPTURES[a]

Species represented by	Number of species	
	PSF	DF
>21 Captures	3	5
10–20 Captures	5	2
2–10 Captures	16	17
1 Capture	10	15

[a] PSF = peat swamp forest, DF = dipterocarp forest.

forest and 56% of the species netted in the dipterocarp forest (Table 3). In the Pasoh Forest Reserve, 77% of the species captured in virgin dipterocarp forest were rare (Wong 1986). In the Gunung Palung Nature Reserve, 62% of all species recorded in the peat swamp forest were insectivores; likewise, 59% of all species netted in the dipterocarp forest were insectivores. This is similar to the virgin dipterocarp forest in the Pasoh Forest Reserve, where 61% of all species netted were insectivores (Wong 1986). Of the insectivores, the preponderance of babblers (Timaliidae) is particularly striking in the Gunung Palung Nature Reserve and in the Pasoh Forest Reserve. In the peat swamp forest, 29% of the species captured were babblers, and in the dipterocarp forest 31% of the species captured were babblers. In the virgin dipterocarp forest of the Pasoh Forest Reserve, 24% of the species captured were babblers (Wong 1986). The Gunung Palung Nature Reserve and the Pasoh Forest Reserve also show similarity in the proportion of frugivores in the capture record. In both the peat swamp forest and the dipterocarp forest, 26% of the species netted were frugivores. At the Pasoh site, 19% of the species netted were frugivores (Wong 1986).

The data presented here suggest that peat swamp forests are important in the ecology of understory avian communities in Southeast Asia, even though the peat swamp forest under study produced fewer individual captures and tended towards fewer species. The peat swamp forest I sampled supported at least 34 understory bird species, including two, Gray-breasted Babbler (*Malacopteron albogulare*) (Timaliidae) and Yellow-breasted Flowerpecker (*Prionochilus maculatus*) (Dicaeidae), that strongly preferred the peat swamp forest over adjacent lowland dipterocarp forest (Table 1). There was an increase of frugivorous understory birds in the peat swamp forest in June that was correlated with an abundance of ripe fruit produced by a single tree species, *Callocarpa* sp. Without having monitored plant phenology, I cannot assume causation from this correlation, but the data are suggestive. In Southeast Asian forests fruit abundance fluctuates temporally and spatially (Fogden 1972, Leighton and Leighton 1983, Wong 1986, Fleming et al. 1987), and frugivorous birds respond to these fluctuations. There is generally a positive correlation between fruit abundance and frugivorous bird abundance (Leighton and Leighton 1983, Wong 1986). The correlation between frugivorous bird abundance and fruit abundance in June in the peat swamp forest is consistent with the hypothesis that Southeast Asian peat swamp forests may act as a refuge for frugivorous animals during periods when fruit is not available in other forest habitats (Leighton and Leighton 1983). To substantiate this hypothesis, future investigators must monitor plant phenology, fruit abundance, and bird abundance simultaneously across a diversity of forest habitats.

This work is a first attempt to characterize the understory avifauna of Southeast Asian peat swamp forests, and there are limitations to the data and its analysis. First, the study is not replicated; I sampled one small stand of peat swamp forest and one small stand of lowland dipterocarp forest. Second, since I did not mark or band birds, individuals may have been captured more than once, thus violating assumptions of independence for statistical tests. Third, the reduced height of the canopy in the peat swamp forest could compress the vertical distribution of birds and result in an increase in captures of birds which dwell in the middle and upper layers of the canopy as compared to the dipterocarp forest. Finally, this study covered a brief time period and limited net hours. For example, in my study I captured 39 species during 1512 net-h over an eight-month period in the dipterocarp forest. In contrast, Wong (1986) captured 82 species of understory birds during 28,000 net-h during a 24-month period in lowland dipterocarp forest in Malaysia. To overcome such limitations in developing broad generalizations regarding the nature of peat swamp forest understory bird communities, I suggest long term studies of banded birds in the center of large tracts of peat swamp forest.

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