

TROPHIC ORGANIZATION OF UNDERSTORY BIRDS IN A MALAYSIAN DIPTEROCARP FOREST

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ABSTRACT.—Single-sample studies suggested that understory flowers and fruits and their avian consumers are scarce in the Malaysian rain forest as compared with African and Central American rain forests. Results from my longer-term studies at Pasoh Forest Reserve (Negeri Sembilan, Peninsular Malaysia) established that flowers and fruits were consistently rare as food for birds. A comparison of two forest types at Pasoh revealed the effect of lower food availability on avian trophic organization. Food resources (e.g. flowers, fruits, arthropods) were less abundant in the regenerating than in the virgin forest, and bird species richness and individual abundance were also lower in the regenerating forest understory. However, the two forests did not differ significantly in the relative importance of the various foraging guilds, suggesting that similar types of resources were present in similar proportions. None of the birds sampled in the Malaysian rain-forest understory was a specialized consumer of understory flowers or fruit, whereas birds feeding mainly on foliage-dwelling arthropods were abundant and were represented by many species. This trophic organization is contrary to that reported for rain forests in other tropical regions but may simply reflect an allocation of harvestable productivity that is different rather than lower. *Received 16 January 1985, accepted 23 July 1985.*

THE absence of avian frugivores in short-term mist-net samples from the Malaysian rain-forest understory (Karr 1980) hinted at a departure from the trophic organization observed in similar short-term studies in African and Central American rain forests, where frugivorous birds comprised 25–33% of mist-net captures (Karr 1980). Similar short-term work prompted Janzen (1977) to comment on the unusually low density of plants flowering or fruiting in the Malaysian rain-forest understory as compared with similar vegetation in Costa Rica. Janzen (1977) independently suggested that frugivores were not likely to be an important component of the Malaysian understory fauna because there would be little for them to eat.

However, such observations of low frugivore density and low reproductive activity of plants based on single visits can arise from one of two rather different ecological situations. Reproductive activity of understory plants and frugivore density may indeed be consistently low. Alternatively, frugivores may have been absent temporarily from the area because the lo-

cal availability of seasonally abundant flowers and fruits was low during the short sampling period.

Certain attributes of the Malaysian rain forest promote the expectation that understory flowers and fruits, and their consumers, are consistently low in abundance. The tree family Dipterocarpaceae dominates the canopy of the Malaysian rain forest. A compilation of surveys covering 7,900 acres of lowland and hill forest in peninsular Malaysia revealed that dipterocarps comprise 30% of the trees (≤ 30 cm in diameter) by number and 55.5% by volume (Symington 1974). In a given forest, there may be 10–40 dipterocarp species (Symington 1974) that reproduce synchronously at irregular intervals of 2–8 yr (Burgess 1972, Medway 1972, Janzen 1974, Ng 1977). Many tree species from other families (e.g. Bombacaceae, Guttiferae, Sapindaceae) also follow this reproductive cycle and either will only fruit or will fruit more heavily during dipterocarp mast years (Whitmore 1984). Although as yet undocumented, the amount of harvestable productivity (the portion of primary productivity that goes into the production of flowers, fruits, and new leaves and that is consumable by animals) in the canopy of dipterocarp forests must vary in accordance

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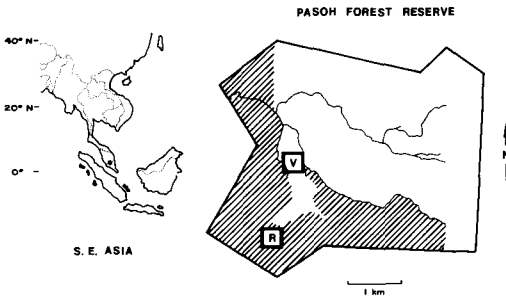


Fig. 1. Pasoh Forest Reserve in West Malaysia is indicated by an asterisk in the regional map of Southeast Asia. The map of Pasoh Forest Reserve (after Becker 1980) shows the extent of virgin (unhatched) and regenerating (hatched) habitats and the location of the two study areas (V and R). Because of swampy conditions, the southwestern corner of the virgin-forest study area was not logged even though it was within a compartment that was selectively logged.

with this supra-annual reproductive cycle (Janzen 1974, 1977, 1980). Resources reach a maximum level during mast years, when a large portion of the canopy of dipterocarps and non-dipterocarps produce massive crops of flowers and fruits, and fall to much lower levels during nonmast years, when little reproductive activity occurs. Remarkably, dipterocarps in general do not appear to be an important food source for vertebrate animals (Medway 1972). Whitmore (1984) suggested that the low primate biomass in dipterocarp forests may be due to the unpalatability of the dominant tree family.

It is not known to what extent understory plants in dipterocarp forests participate in or are affected by the gregarious reproductive cycle in the canopy, because long-term phenological studies in the region have concentrated on commercially valuable canopy trees. Janzen (1977, 1980) hypothesized that a low level of reproductive activity prevails in understory plants because of the synergistic interactions between the persistently high densities of dipterocarp seedlings and saplings that tie up resources otherwise available to nondipterocarps, and the low fertility of Malaysian soils in the light-poor understory environment. I found that in poor soils a high density of dipterocarp seedlings depresses significantly the reproductive activity and biomass of at least one herbaceous understory species (*Labisia pumila*, Myrsinaceae) (Wong 1981). Although the above observations and conjectures suggest why fruits

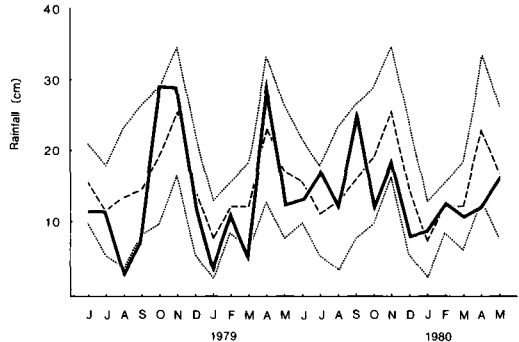


Fig. 2. Rainfall pattern at Pasoh Forest Reserve. Monthly accumulation is shown for the bird-netting period, June 1978 through May 1980 (bold line). Mean monthly accumulation (dashed line) \pm 1 SD (dotted lines) is shown for data from 1972 through 1979.

and their consumers might be consistently low in abundance in the Malaysian rain-forest understory, they do not confirm the existence of long-term scarcity.

I present here the results of a 2-yr study of food availability (flowers, fruits, and arthropods) and understory birds in a lowland Malaysian rain forest. I collected comparative data from virgin and regenerating forest habitats that differed in resource availability to test the response of avian trophic organization to different food levels.

STUDY AREA AND METHODS

The study was conducted at two sites during non-masting years in Pasoh Forest Reserve (Negeri Sembilan, Peninsular Malaysia, 2°58'N, 102°17'E), which consists of a core of virgin lowland dipterocarp forest (600 ha) ringed by a buffer zone of regenerating forest (1,400 ha) that was partially and selectively logged from 1955 to 1956 (Fig. 1). Each study site consisted of 16 ha of similar topography. Within each site, access trails were cut as parallel transects 50 m apart with one set oriented north-south and another set oriented east-west. Each of the 64 resulting subplots contained at least one uniquely numbered netting lane, placed whenever possible in a natural opening in shaded undergrowth.

The canopy vegetation and soils in the virgin forest were described briefly (Soepadmo 1978). Rainfall during the study period June 1978 to May 1980 is presented in Fig. 2. The selectively logged portions of the buffer zone are expected to be floristically similar to the virgin forest, but proportionately different in species representation and age structure because all the large timber trees (dipterocarps and legumes) have been extracted. Although the regenerating-for-

est study site has a generally lower canopy than the virgin forest site, a cluster analysis of 42 characters (e.g. composition and density of understory vegetation, prevalence of climbers, size distribution of stems, presence or absence of gap in canopy) scored at 20 randomly chosen points within each site failed to separate them on the basis of structural features in the vegetation (Wong unpubl. data). The two sites did not differ in the number of gaps present, but gaps in the virgin forest were significantly larger than those in the regenerating forest (Wong 1983). Smaller gaps in the regenerating forest can be related to the smaller crowns of trees present in that habitat.

Monthly data on the phenology of understory plants (≤ 10 m in height) were collected during December 1978 to May 1980 along the east-west transects. The exclusion of areas within light gaps resulted in a census route of 3.3 km in both sites. Each month, new plants observed flowering or fruiting were tagged and were examined in all subsequent censuses. The study population thus increased in size over time as different plants along the transect entered reproductive condition. Variation in the abundance of understory foliage arthropods was monitored by sweep-sampling the vegetation along the north-south transects in both forest sites from January 1979 through May 1980. The 10 subsamples (100 sweeps/subsample) collected each month provided the statistical basis for within- as well as between-habitat comparisons of arthropod abundances. Because the procedures used and the results of the above two studies have been presented in detail elsewhere (Wong 1983, in press), only those aspects pertinent to the discussion of avian trophic organization are included in this paper.

Mist nets were used at ground level to census birds monthly from June 1978 through May 1980. This method provides the most efficient and reliable estimate of relative density and ranging movements of birds in tropical-forest understory (Okia 1976, Greig-Smith 1980, Karr 1981). Monthly netting in the virgin forest was followed by a similar effort in the regenerating forest. Thirty mist nets (12×2.5 m, 35-mm mesh) were operated first in the southern half of the study area for 2 days (0630–1630) and then were moved to netting lanes in the northern half of the study site for 2 days. Preliminary efforts indicated that netting for more than 2 days in the same area led to a drastic reduction in the number of captures (see also Karr 1979, 1981; Schemske and Brokaw 1981) and to an increase in the number of birds rehandled, suggesting that the birds caught were sedentary (Greig-Smith 1980, Faaborg 1982). A monthly netting schedule was established on the assumption that birds forgot the position of nets after one month. By the end of the 24-month study period, at least 28,000 net-hours were logged for each study site. Nets were checked every 2 h to reduce mortality due to predators (monitor lizards, ground squirrels, macaques, and

mongooses), which quickly learned the position of nets. Captured birds were weighed, banded with uniquely numbered metals bands, and released at the place of capture to minimize disruption of their normal movements.

I distinguished 10 avian foraging guilds in the Malaysian rain-forest understory by criteria listed in Appendix 1. The guild assignments of bird species (Appendix 2) were based on personal observations and on published reports (Delacour 1947, Fogden 1972, Medway and Wells 1976, Wells 1978).

RESULTS

Phenology of understory vegetation and availability of flowers and fruits for birds.—More individuals (188 vs. 60), species (75 vs. 42), and families (25 vs. 20) of plants reproduced in virgin- than in regenerating-forest understory during December 1978 to May 1980 (Table 1). Furthermore, the monthly abundance of reproductive plants was significantly higher in the virgin than in the regenerating forest (Wilcoxon matched-pair rank-sum test, $P < 0.001$). Eleven of 13 species present in both habitats were represented by more reproductive individuals and reproduced more frequently in the virgin than in the regenerating forest. In both habitats, higher peaks of flowering, fruiting, and leafing activity occurred in the first half of the calendar year. A general impression of nonseasonality results for both communities, because smaller peaks of activity also occurred in the second half of the year and because there appeared to be no correlation between phenological events and rainfall. Most species were represented by only one reproductive plant, although nonreproducing conspecifics of similar size were often present. Species represented by more than one reproductive individual tended to be intraspecifically asynchronous in flowering. Most individuals censused (79% in virgin and 75% in regenerating forest) flowered or fruited only once during the 18-month study period.

Of the reproductive individuals censused, only 31% (59) in the virgin forest and 35% (21) in the regenerating forest produced flowers or fruits used by birds. Only 4 families (Melastomataceae, Myrsinaceae, Rubiaceae, Sterculiaceae) of 31 censused produced fruits eaten by birds, and only 1 family (Rubiaceae) produced flowers visited by birds (Table 1). The phenological profiles of these plant species are presented in Appendix 3. Consistent with the dif-

TABLE 1. Reproductive plants censused in the understory of Pasoh Forest Reserve during December 1978 to May 1980.

	Virgin forest		Regenerating forest	
	No. of species	No. of individuals	No. of species	No. of individuals
Acanthaceae	1	1		
Anacardiaceae	1	1		
Annonaceae	3	4	4	4
Celastraceae	1	1		
Convolvulaceae			1	1
Dilleniaceae			1	1
Ebenaceae	2	3		
Euphorbiaceae	7	7	1	1
Flacourtiaceae			1	1
Gnetaceae	1	2	1	1
Guttiferae	3	4	1	3
Icacinaceae	1	1		
Lauraceae	2	6	2	2
Lecythidaceae	1	1		
Melastomataceae ^a	6	7	2	4
Meliaceae	1	2		
Moraceae	2	2	2	2
Myristicaceae	2	5	1	1
Myrsinaceae ^a	6	7	1	1
Myrtaceae			3	4
Oleaceae	1	1		
Opiliaceae	2	2		
Palmae	3	44	3	3
Rosaceae	1	1		
Rubiaceae ^{a,b}	14	41	7	8
Rutaceae			1	1
Sapindaceae	3	3	2	2
Sterculiaceae ^a	1	4	1	8
Tiliaceae	1	1		
Urticaceae			1	4
Violaceae	2	26	3	5
Unidentified	7	11	3	3
Total	75	188	42	60

^a Produced fruits eaten by birds.

^b Produced flowers visited by birds.

ferences for overall reproductive activity, the number of individuals that produce flowers or fruits used by birds were, respectively, 3 and 5 times greater in the virgin than in the regenerating habitat. Not surprisingly, the monthly availability of these plants was also greater in the virgin than in the regenerating forest (Fig. 3). Refer to Wong (1983) for a detailed discussion of understory plant phenology at Pasoh Forest Reserve.

Abundance of understory foliage arthropods.—Arthropod abundance fluctuated gradually and showed no significant difference between consecutive months in either habitat (Fig. 4). Al-

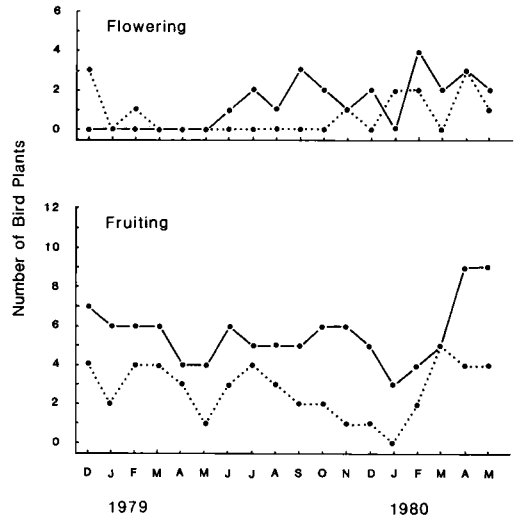


Fig. 3. Monthly number of understory plants that produce flowers or fruits used by birds in the virgin (solid line) and regenerating (dotted line) forests. Each census route = 3.3 km.

though the two forest habitats did not differ significantly from each other in a month-by-month comparison of arthropod abundance [ANOVA, $P = 0.25$, $F(1,15)$], the period of significantly lower arthropod abundance (Scheffé test, $P = 0.05$) was 4 months longer in the regenerating forest (November 1979 to May 1980) than in the virgin forest (September–November 1979).

In both habitats, ants consistently contributed the largest proportion of individuals to the monthly totals (Fig. 5). Beetles were usually

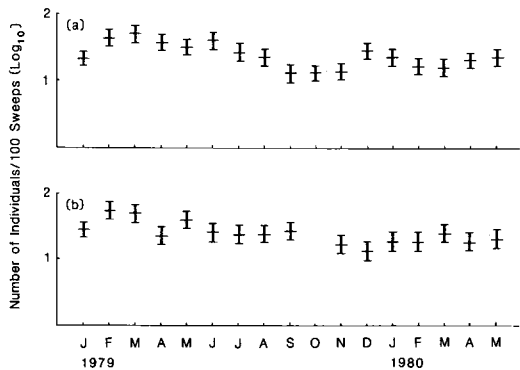


Fig. 4. Monthly variation in arthropod abundance (mean \pm 95% confidence limits) in (a) the virgin forest and (b) the regenerating forest.

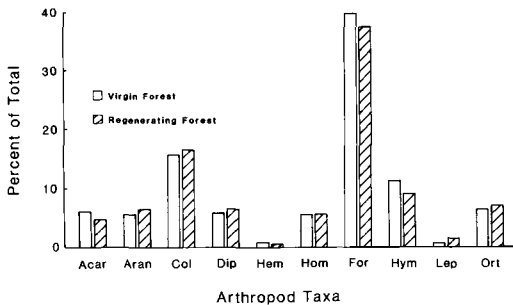


Fig. 5. Taxonomic distribution of all arthropods collected. Taxa represented are Acari (Acar), Araneida (Aran), Coleoptera (Col), Diptera (Dip), Hemiptera (Hem), Homoptera (Hom), Formicidae (For), nonformicine Hymenoptera (Hym), Lepidoptera (Lep), and Orthoptera (Ort).

second and the nonformicine hymenopterans were usually third in abundance. Of the remaining groups sampled, Acari, Araneida, Diptera, Homoptera, and Orthoptera were about equal in their relatively small contribution to the monthly total, and Hemiptera and Lepidoptera were the least represented of the arthropod groups considered. The three most abundant arthropod groups showed only a

moderate degree of population fluctuation, thus accounting for the moderate level of total fluctuations observed in the monthly totals. Wong (in press) provided a detailed account of understory foliage arthropods in Pasoh Forest Reserve.

Ants and beetles were also the two most frequent arthropod groups in 21 bird stomachs (from net casualties) examined (Table 2). However, this method of sampling food is strongly biased toward adult arthropods with hard bodies because soft-bodied arthropods and immature forms disintegrate quickly in the digestive process.

Species richness and abundance of understory birds.—Fewer species (73 vs. 83) and fewer individuals (575 vs. 703) were captured in the regenerating forest than in the virgin forest (refer to Wong 1985 for more detailed demographic comparisons of the understory bird communities in these forest habitats). However, the abundance distribution of understory bird species in the two habitats appeared similar (Fig. 6). Rare species [those representing less than 2% of the number of individuals in the census total (Karr 1971)] comprised 77% (57 and 64, respectively) of the species netted in

TABLE 2. Stomach contents of net casualties.

Species ^a	Date collected	Arthropod groups present ^b			
		Aran	Col	For	Hom
Podargidae					
<i>Batrachostomus stellatus</i>	6 Jan 1980		X		
Pittidae					
<i>Pitta granatina</i>	13 Dec 1978			X	
Timaliidae					
<i>Pellorneum capistratum</i>	5 Mar 1980			X	
<i>Trichastoma malaccense</i>	8 Jul 1978	X	X	X	
<i>Trichastoma bicolor</i>	10 Jun 1978		X		
	3 May 1980			X	X
<i>Malacopteron cinereum</i>	16 Jul 1978		X		
<i>Malacopteron albogulare</i>	12 Jun 1979		X	X	X
<i>Stachyris leucotis</i>	12 Jun 1978			X	
<i>Stachyris erythroptera</i>	5 May 1979			X	
Turdidae					
<i>Copsychus malabaricus</i>	3 Jun 1978				X
Muscicapidae					
<i>Philentoma pyrropterum</i>	19 Jun 1979				X
Nectariniidae					
<i>Hypogramma hypogrammicum</i>	1 Jul 1978	X			

^a Only 13 of 21 stomachs contained recognizable arthropod body parts.

^b Aran = Araneida, Col = Coleoptera, For = Formicidae, Hom = Homoptera.

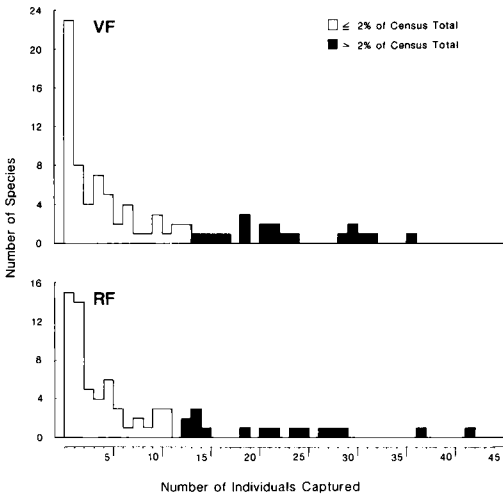


Fig. 6. Abundance distribution of understory bird species mist-netted in the virgin (VF) and regenerating (RF) forests.

the regenerating and virgin study sites. This preponderance of rare species also was noted in bird communities of other tropical forests (Karr 1971, Lovejoy 1974, Pearson 1977) and appears to be characteristic of mature tropical rain forests. Babblers (Timaliidae) provide a notable contrast to this pattern because they contributed nearly half of all the individuals, and about 25% of the species banded in both habitats. This pattern of numerical dominance has not been reported for any other tropical rain-forest avifauna, and the circumstances contributing to the success of this family merit further investigation.

DISCUSSION

The comparatively lower level of resources in the regenerating forest suggests that less food is available for consumers than in the virgin forest. Congruently, fewer birds are supported by the regenerating-forest than by the virgin-forest understory. A decline in harvestable productivity also may lead to lower availability of each food type, so that species richness also would fall in a poorer habitat because the different food types individually cannot support a specialized consumer (Janzen 1977). The regenerating-forest understory also sustains fewer bird species.

Trophic organization of understory birds.—The virgin and regenerating forests did not differ

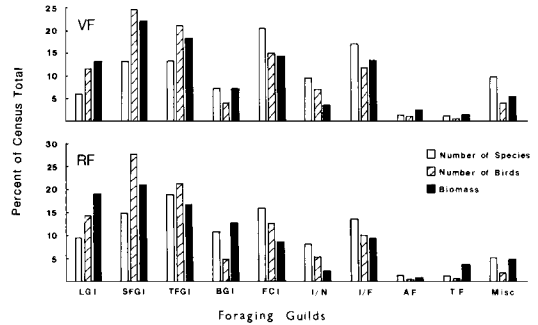


Fig. 7. Guild signatures (based on census total) of the understory bird community in the virgin- (VF) and regenerating-forest (RF) sites at Pasoh. Abbreviations are defined in Table 3.

significantly in the relative importance of guilds (Fig. 7) either in terms of species richness ($\chi^2_1 = 4.5$, $P = 0.87$) or in terms of individual abundance ($\chi^2_1 = 1.35$, $P = 0.99$). This similarity in guild signature (Karr 1980) suggests that similar resource types are available in similar proportions. Although only flycatching insectivores ($\chi^2_1 = 5.75$, $P < 0.02$), insectivore-nectarivores ($\chi^2_1 = 4.05$, $P < 0.05$), and members of the miscellaneous guild ($\chi^2_1 = 4.12$, $P < 0.05$) were significantly more numerous in the virgin forest (Table 3), the generally higher number of individuals in most guilds agrees with the observations that resource levels were generally higher in virgin forest. One exception was the Emerald Dove (*Chalcophaps indica*), which was more abundant in regenerating than in virgin forest (Appendix 2). However, because birds of this species feed primarily on fallen canopy fruits rather than on the fruits of understory plants, its abundance clearly would not be related to the availability of fruits from understory plants.

There is not always a correlation between the relative importance of guild species richness and guild individual abundance (Fig. 7). Whereas in the virgin forest flycatching insectivores ranked highest in species richness, they ranked only third in individual abundance. Conversely, shrub foliage-gleaning insectivores were most abundant in both habitats but ranked only third in species richness. The relative importance of guild biomass is correlated in general with relative abundance, except when the species considered are either relatively large (pheasants, woodpeckers, doves, kingfishers) or small (sunbirds, spiderhunters,

TABLE 3. Distribution by guild of all birds captured in the understory.^a

Guild type	Number of species		Number of individuals		<i>P</i> ^b	Biomass (kg)	
	VF	RF	VF	RF		VF	RF
Litter-gleaning insectivore (LGI)	5	7	81	82	<0.91	2.39	3.12
Shrub foliage-gleaning insectivore (SFGI)	11	11	172	157	<0.44	3.95	3.40
Tree foliage-gleaning insectivore (TFGI)	11	13	148	123	=0.14	3.24	2.70
Bark-gleaning insectivore (BGI)	6	8	29	28	=0.90	1.28	2.05
Flycatching insectivore (FI)	17	12	105	73	<0.02*	2.59	1.43
Insectivore-nectarivore (I/N)	8	6	49	31	<0.05*	0.62	0.37
Insectivore-frugivore (I/F)	14	10	82	59	<0.06	2.37	1.51
Arboreal frugivore (AF)	1	1	7	3	<0.20	0.41	0.17
Terrestrial frugivore (TF)	1	1	2	5	<0.26	0.24	0.59
Miscellaneous (Misc)	8	4	27	14	<0.05*	0.95	0.79
Total	82	73	702	575		18.03	16.13

^a VF = virgin forest, RF = regenerating forest.
^b * = significant difference between virgin and regenerating forests.

flowerpeckers). These discrepancies show clearly that all three measures should be considered whenever possible in evaluating the relative importance of a particular guild (Karr 1976).

Interguild differences in species richness and abundance.—The number of individuals in a guild reflects the availability of the resource supporting it, whereas the number of species included suggests how finely this resource can be divided. Karr (1980) hypothesized that the cryptic nature of foliage insects has been a selective factor in the specialization of foraging techniques in foliage-gleaning birds that has resulted in a diverse assemblage of bird species. Consistent with Karr's hypothesis is the prediction that specialization will result in lower resource quantity per species and fewer individuals supported per species. In contrast, un-

dergrowth fruits are conspicuous and fairly uniform in morphology compared with foliage insects and hence provide fewer opportunities for diversification in their consumers. Moreover, because fruits are one or more trophic levels lower than foliage insects, their greater biomass accounts for the greater species-specific abundance as well as the total abundance of frugivores.

Although the above pattern of species richness and individual abundance is apparent for frugivores and foliage-gleaning birds in Afro-tropical and neotropical rain-forest understories, it was not observed at Pasoh. In both the virgin and regenerating forests, foliage-gleaning insectivores (shrub and tree combined) had higher species richness, greater species-specific abundance, and greater total abundance than frugivores (Table 4). Even if the primarily in-

TABLE 4. Species richness and number of individuals per species by guild and by habitat (based on census total).

Guild type	Virgin forest		Regenerating forest	
	No. of species	No. of individuals per species	No. of species	No. of individuals per species
Litter-gleaning insectivore	5	16.2	7	11.7
Foliage-gleaning insectivore ^a	22	14.5	24	11.7
Bark-gleaning insectivore	6	4.8	8	3.5
Flycatching insectivore	17	6.2	12	6.1
Insectivore-nectarivore	8	6.1	6	5.1
Insectivore-frugivore	16	5.7	12	5.6
Frugivore ^b	2	4.5	2	4.0
Miscellaneous	8	3.4	4	3.5

^a Shrub and tree foliage-gleaning insectivores combined.
^b Arboreal and terrestrial frugivores combined.

sectivorous insectivore-frugivores (e.g. bulbuls) are counted as frugivores, the species-specific abundance and total frugivorous-bird abundance remain low.

Flycatching insectivores at Pasoh conform better to the model of species diversification suggested by Karr (1980). Different flying insects have different flight and predator-avoidance behaviors. Consequently, foraging efficiency in flycatching birds might be enhanced by specializing on a particular type of flying insect. However, improved skills for feeding on one flying-insect group will likely reduce the skills necessary for catching other insect groups, thereby effectively reducing the resource base available for each specialized species. Flying insects also tend to be more seasonal in abundance than sedentary foliage-dwelling insects (pers. obs.), and this would further reduce the food available to flycatching birds at various times of the year. This slim resource base may explain why flycatchers have the lowest survivorship among understory birds studied in a Panamanian forest (Karr pers. comm.). Predictably, the species-specific abundance of flycatching insectivores is low in both habitats compared with foliage-gleaning insectivores (Table 4). However, this lower abundance is still higher than that of frugivores. Only kingfishers (included in the miscellaneous guild), which feed on rare food items (large insects and small vertebrates), and woodpeckers, which either excavate wood for rare food items or feed on patchily distributed trail-forming ants and termites, have lower species-specific abundances than frugivores.

Food availability and fluctuation in abundance of birds in mist-net samples.—Short-term changes in the abundance of birds sampled in a given area largely reflect the movement of birds in response to the shifting spatial and temporal patterns of food availability. In the Malaysian rainforest understory, foliage arthropods are fairly evenly dispersed over time and space in contrast to flowers and fruits, which are patchily distributed and occur asynchronously. The replacement time (turnover) of these two resources also differs. Whereas it is relatively certain that a particular volume of vegetation recently gleaned by birds will be repopulated within a short time by the immigration of arthropods from surrounding vegetation (pers. obs.), flowers or fruits used by birds are produced only in small quantities and at long in-

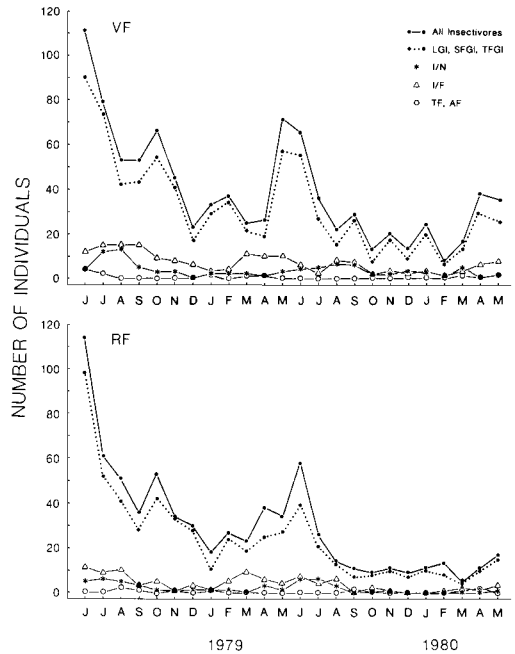


Fig. 8. Monthly abundance of understory birds by guild in the virgin (VF) and regenerating (RF) forests. Abbreviations are defined in Table 3.

tervals by understory plants (Wong 1983). Birds that primarily consume flowers or fruits would have to range over larger areas than insectivores to meet nutritional requirements. Consequently, compared with frugivores, birds that rely on foliage arthropods are likely to maintain a more stable population in a given area, have smaller home ranges, and fluctuate less numerically as judged by mist-net samples.

In both the virgin and regenerating forests, insectivores were consistently highest in abundance and frugivores were lowest (Fig. 8). The coefficients of variation [$CV = (SD/\bar{x}) \times 100$] of monthly abundance in these guilds (Table 5) further indicate that in both habitats, insectivore abundance was least variable (small CV) and frugivore abundance was most variable (large CV). Variability in the abundance of the insectivore-frugivore guild was similar in magnitude to that of insectivores, which is attributed to their general reliance on insects and their feeding on fruits only opportunistically. Although more variable than the other insectivorous groups, the insectivore-nectarivores were less variable than the specialist frugivores captured in the understory. All guilds except frugivores were more variable in monthly

TABLE 5. Coefficients of variation in the monthly abundance and species richness of selected guilds.

Guild type	Monthly abundance ^a		Monthly species richness ^a	
	VF	RF	VF	RF
All insectivores	63.3	82.3	30.2	45.0
Litter- and foliage-gleaning insectivores ^b	60.4	85.3	31.6	42.3
Insectivore-frugivore	63.5	87.3	43.5	73.7
Insectivore-nectarivore	88.6	121.7	48.4	100.8
Frugivore ^c	203.2	191.1	159.2	191.1

^a VF = virgin forest, RF = regenerating forest.

^b Shrub and tree foliage-gleaning insectivores are combined here with litter-gleaning insectivores because these three guilds represent the likely consumers of the arthropods collected in the sweep samples.

^c Arboreal and terrestrial frugivores are combined to increase size of monthly samples.

abundance in the regenerating than in the virgin forest, suggesting that, in general, birds netted in the regenerating forest have larger home ranges, possibly because of the lower resource availability per unit area relative to the virgin forest.

Interguild comparisons of monthly species richness (Fig. 9) and the associated coefficients of variation (Table 5) yield differences that are comparable to the interguild comparisons of individual abundance. It is clear that insectivores are represented by the highest number of species each month as well as by the highest abundance.

Absence of birds that specialize on understory flowers and fruits in the Malaysian rain forest.—The Emerald Dove, the only terrestrial frugivore species caught, gleans the forest floor for the fallen fruits of canopy trees. Because no individual banded in either habitat was ever recaptured, I conclude that this species must range over large areas to locate the isolated fruiting canopy tree (recall that this study occurred during nonmasting years). The only arboreal frugivore netted, the Lesser Green Broadbill (*Calyptomena viridis*), was most often observed feeding on the fruits of canopy or subcanopy trees, and its occurrence in the lower strata of the forest probably is not related to feeding on fruits from understory plants. A few individuals were once observed on the ground, feeding on termite alates emerging from a subterranean nest (J. O. Caldecott pers. comm.).

Only one or two individuals of the nectarivorous sunbird species (*Anthreptes* spp. and *Aethopyga mystacalis*) were caught in the understory. Because these primarily canopy birds were caught most often at midday or in early afternoon, their presence in the understory

might be interpreted as avoidance of high canopy temperatures. The more abundant insectivore-nectarivore species, such as the Least Spiderhunter (*Arachnothera longirostra*) and the Purple-naped Sunbird (*Hypogramma hypogrammicum*), fed mostly on arthropods and fed only opportunistically on nectar from flowers. This behavior is similar to that of bulbuls (*Pycnonotus* spp., *Criniger* spp., and *Hypsipetes* spp.), insectivore-frugivores that usually fed on insects and added fruits to their diet only when available. The scarcity of understory fruits did not reduce their desirability. The few fruits that ripened each day on the infrequently fruiting shrubs usually were taken by bulbuls in the morning before full light (pers. obs.), which suggests that the locations of fruiting plants were known in advance and fruits were anticipated and consumed at the earliest opportunity.

Impact of masting cycle on Malaysian rain-forest understory.—Food resources may reach superabundant levels during mast years in dipterocarp forests, but the population density of long-lived organisms such as birds is more likely regulated by the low level of resources during the more frequent nonmasting years. Comparisons between the virgin and regenerating forests indicate that a lowering of resources in the Malaysian rain-forest understory leads to a general depression in avian species richness, abundance, and biomass. Over evolutionary time, should the Malaysian rain-forest understory have a lower level of harvestable productivity during nonmasting years than understory habitats in other tropical forests have, then overall species richness, abundance, and biomass of understory animals ought to be lower than those of comparable samples from other tropical forest regions. Inger (1980) showed that

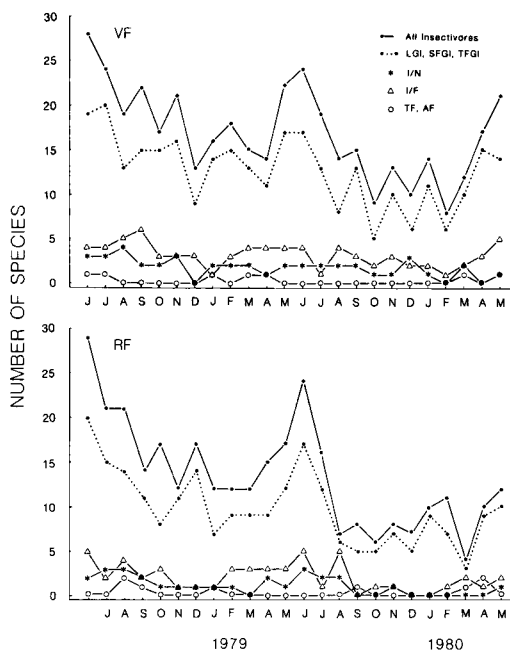


Fig. 9. Monthly species richness of understory birds by guild in the virgin (VF) and regenerating (RF) forests. Abbreviations are defined in Table 3.

the density of nonriparian frogs and lizards in Indo-Malaysian forests is an order of magnitude lower than that of lowland forests in Central America. However, the high total and species-specific abundances of foliage-gleaning insectivores in my samples suggest that understory bird biomass may not be analogously lower.

If Malaysian understory plants participate in the dipterocarp mast cycle, as do many nondipterocarp tree species in the canopy, then it is likely that photosynthate would be channeled preferentially into vegetative growth or storage tissues during "off" years. For an understory plant, an increase in photosynthetic surface area in the light-poor understory environment would increase reproductive potential in the next mast year, whereas reproduction out of synchrony would have little or no chance of success because of the relatively high rates of seed predation that occur in dipterocarp forest during nonmasting years (Chan 1980). Although the biomass of frugivores and nectarivores is reduced as a consequence, a high biomass of insectivorous birds may be sustained in the understory because the emphasis in foliage production enlarges the resource base

and, thus, the biomass of foliage-dwelling arthropods. Hence, the productivity that is harvestable by birds from understory plants may not be any lower in dipterocarp forest than in the forests of other tropical regions but simply may be allocated differently. The relevant comparison of bird densities awaits suitable data from other tropical forests.

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APPENDIX 1. Feeding guilds represented in mist-net samples of understory birds from Pasoh Forest Reserve.

Feeding guild ^a	Food type	Place or manner of foraging
Litter-gleaning insectivore (LGI)	Insects	Turns over litter, gleans low-lying foliage
Shrub foliage-gleaning insectivore (SFGI)	Insects	Gleans leaves and twigs of shrubs (≤ 3 m)
Tree foliage-gleaning insectivore (TFGI)	Insects	Gleans leaves and twigs of shrubs and foliage of understory trees (≤ 10 m)
Bark-gleaning insectivore (BGI)	Insects	Gleans surface of trunk and large branches of trees; some species also excavate food from bark and wood
Flycatching insectivore (FCI)	Insects	Sallies from perch on branch to capture flying insects
Insectivore-nectarivore (I/N)	Insects, spiders, nectar	Feeds on insects in flowers, spiders and insects in spider webs, nectar from flowers
Insectivore-frugivore (I/F)	Insects, fruits	Gleans understory trees for insects and fruits
Arboreal frugivore (AF)	Fruits	Gleans canopy or tall understory trees (> 10 m)
Terrestrial frugivore (TF)	Fruits	Gleans fruits fallen to ground from canopy
Miscellaneous (Misc)	Various	Includes other methods of capturing large insects or small invertebrates

^a See also Karr (1980).

APPENDIX 2. Guild assignments and abundance of bird species netted in the understory of Pasoh Forest Reserve during June 1978 to May 1980.

Species ^a	Guild type ^b	Mean weight (g)	Number of individuals banded ^c	
			VF	RF
Accipitridae				
<i>Accipiter trivirgatus</i>	Misc	—	2	
Phasianidae				
<i>Polyplectron malacense</i>	LGI	586.0		1
Columbidae				
<i>Chalcophaps indica</i>	TF	118.6	2	5
Strigidae				
<i>Otus rufescens</i>	Misc	77.0	1	
<i>Otus bakkamoena</i>	Misc	117.0		2
Podargidae				
<i>Batrachostomus stellatus</i>	FCI	44.0	1	
Caprimulgidae				
<i>Eurostopodus temminckii</i>	FCI	87.8	3	
Trogonidae				
<i>Harpactes diardii</i>	FCI	102.8	2	2
<i>Harpactes orrhophaeus</i>	FCI	52.7	10	2
<i>Harpactes duvaucelii</i>	FCI	36.3	4	
Alcedinidae				
<i>Alcedo meninting</i>	Misc	18.9	4	
<i>Ceyx erithacus</i>	Misc	16.9	4	5
<i>Ceyx rufidorsus</i>	Misc	17.9	6	
<i>Lacedo pulchella</i>	Misc	48.3	4	2
<i>Halcyon coromanda</i>	Misc	85.0	1	
<i>Halcyon concreta</i>	Misc	73.6	5	5
Capitonidae				
<i>Calorhamphus fuliginosus</i>	I/F	45.0	1	

APPENDIX 2. Continued.

Species ^a	Guild type ^b	Mean weight (g)	Number of individuals banded ^c	
			VF	RF
Indicatoridae				
<i>Indicator archipelagicus</i> ^d	BGI	38.5	1	1
Picidae				
<i>Sasia abnormis</i>	BGI	9.2	9	3
<i>Picus puniceus</i>	BGI	77.0		1
<i>Picus mentalis</i>	BGI	109.2		6
<i>Picus miniaceus</i>	BGI	102.0	1	
<i>Dinopium rafflesii</i>	BGI	98.0	1	1
<i>Meiglyptes tukki</i>	BGI	53.1	13	11
<i>Dryocopus javensis</i>	BGI	250.0		1
<i>Blythipicus rubiginosus</i>	BGI	84.2	4	4
Eurylaimidae				
<i>Calyptomena viridis</i>	AF	58.0	7	3
Pittidae				
<i>Pitta granatina</i>	LGI	59.3	3	2
<i>Pitta guajana</i>	LGI	90.0	1	
<i>Pitta sordida</i>	LGI	69.5		1
Pycnonotidae				
<i>Pycnonotus eutilosus</i>	I/F	35.8	3	2
<i>Pycnonotus plumosus</i>	I/F	41.5	1	
<i>Pycnonotus simplex</i>	I/F	22.0	2	2
<i>Pycnonotus erythrophthalmos</i>	I/F	18.0	2	4
<i>Criniger bres</i>	I/F	35.9	16	9
<i>Criniger phaeocephalus</i>	I/F	30.1	23	22
<i>Criniger finschii</i>	I/F	21.8	1	1
<i>Hypsipetes criniger</i>	I/F	15.0	19	13
<i>Hypsipetes charlottae</i>	I/F	24.0	1	
Dicruridae				
<i>Dicrurus paradiseus</i>	TFGI	67.5	2	6
Oriolidae				
<i>Oriolus xanthonotus</i>	I/F	31.0	1	
Corvidae				
<i>Platylophus galericulatus</i>	I/F	103.0	4	1
Timaliidae				
<i>Pellorneum capistratum</i>	LGI	27.8	33	25
<i>Trichastoma malaccense</i>	LGI	22.9	37	37
<i>Trichastoma rostratum</i>	TFGI	17.8	4	2
<i>Trichastoma bicolor</i>	TFGI	27.2	24	24
<i>Malacopteron magnum</i>	TFGI	25.5	22	10
<i>Malacopteron cinereum</i>	TFGI	15.9	31	28
<i>Malacopteron magnirostre</i>	SFGI	20.1	22	29
<i>Malacopteron affine</i>	TFGI	20.1	5	4
<i>Malacopteron albogulare</i>	SFGI	15.0	10	8
<i>Pomatorhinus montanus</i>	TFGI	30.2	3	1
<i>Kenopia striata</i>	SFGI	18.1	12	6
<i>Napothera macrodactyla</i>	LGI	53.6	7	11
<i>Macronous gularis</i>	TFGI	11.5		1
<i>Macronous ptilosus</i>	SFGI	19.1	12	10
<i>Stachyris poliocephala</i>	SFGI	22.6	17	8
<i>Stachyris nigricollis</i>	SFGI	23.4	14	14
<i>Stachyris leucotis</i>	SFGI	26.7	8	5
<i>Stachyris maculata</i>	TFGI	26.8	31	19
<i>Stachyris erythroptera</i>	TFGI	13.2	19	21
<i>Alcippe brunneicauda</i>	TFGI	14.7	5	5

APPENDIX 2. Continued.

Species ^a	Guild type ^b	Mean weight (g)	Number of individuals banded ^c	
			VF	RF
Turdidae				
<i>Erithacus cyane</i> ^e	SFGI	15.1	31	43
<i>Copsychus pyrrropygus</i>	SFGI	41.6	11	4
<i>Copsychus saularis</i>	LGI	41.4		5
<i>Copsychus malabaricus</i>	SFGI	32.3	30	27
<i>Enicurus leschenaulti</i>	SFGI	30.8	5	3
Sylviidae				
<i>Phylloscopus borealis</i> ^e	TFGI	8.0	1	1
<i>Orthotomus sutorius</i>	TFGI	7.0		1
Muscicapidae				
<i>Rhipidura perlata</i>	FCI	13.2	1	2
<i>Culicicapa ceylonensis</i>	FCI	7.8	2	
<i>Cyornis rubeculoides</i> ^e	FCI	16.8	1	1
<i>Cyornis tickelliae</i>	FCI	9.0	1	
<i>Ficedula dumetoria</i>	FCI	9.8	7	3
<i>Ficedula narcissina</i> ^e	FCI	11.0	1	
<i>Rhinomyias brunneata</i> ^e	FCI	18.1	15	7
<i>Rhinomyias olivacea</i> ^e	FCI	15.8	1	1
<i>Rhinomyias umbratilis</i>	FCI	18.0	10	15
<i>Philentoma pyrrhopterum</i>	FCI	16.9	18	14
<i>Philentoma velatum</i>	FCI	23.1		2
<i>Hypothymis azurea</i>	FCI	11.4	6	13
<i>Terpsiphone paradisi</i>	FCI	19.7	22	11
Nectariniidae				
<i>Anthreptes simplex</i>	I/N	8.5	1	2
<i>Anthreptes malacensis</i>	I/N	7.5	1	
<i>Anthreptes singalensis</i>	I/N	7.8	2	2
<i>Hypogramma hypogrammicum</i>	I/N	11.0	13	10
<i>Aethopyga mystacalis</i>	I/N	10.0	1	
<i>Arachnothera longirostra</i>	I/N	12.9	25	14
<i>Arachnothera crassirostris</i>	I/N	20.5	1	
<i>Arachnothera robusta</i>	I/N	20.0		1
<i>Arachnothera affinis</i>	I/N	20.0	5	2
Dicaeidae				
<i>Prionochilus percussus</i>	I/F	7.8	1	3
<i>Prionochilus maculatus</i>	I/F	7.8	7	2
Ploceidae				
<i>Lonchura leucogastra</i> ^f		9.0	1	
Total			703	575

^a Nomenclature of bird taxa as in King et al. (1975).^b See Appendix 1.^c VF = virgin forest, RF = regenerating forest.^d Not a typical bark-gleaning species; feeds on beeswax and bees from hives suspended on large tree branches.^e Winter resident.^f Not typically a forest species; no guild assignment was made.

APPENDIX 3. Phenological profiles of plant species that produced flowers and fruits used by birds for December 1978 through May 1980. Leaf production was monitored only from June 1979 through May 1980. Numbers in parentheses represent morphospecies identification numbers. The abbreviations and symbols used are as follows:

H = habitat
V = virgin forest
R = regenerating forest
n = number of reproductives censused
Fl and * = flowering
Fr and O = fruiting
Lf and § = leafing
? = degree of intraspecific synchrony undetermined
A = conspecifics asynchronous
O = conspecifics overlap
S = conspecifics synchronous

Species	H	D J F M A M J J A S O N D J F M A M	n	Fl	Fr	Lf
Melastomataceae						
<i>Dissochaeta hirsuta</i>	R	----- * * * ----- O O O ----- O O ----- § --- § --- § § § ---	3	?	O	?
<i>Memecylon dichotum</i>	V	----- O ----- § --- § §	2	A	?	O
<i>M. garcinioides</i>	R	----- O --- O ----- § --- § § § ---	1	?	?	?
<i>M. minutiflorum</i>	V	----- --- O O O O O ----- § ---	1	?	?	?
<i>M. oleaeifolium</i>	V	- * * * ----- * ----- * O O O O ----- § --- § ---	1	?	?	?
<i>M. pulchrum</i>	V	----- O ----- § § § --- § ---	1	?	?	?
<i>Memecylon</i> sp. (110)	V	----- * * * - * * * * * * ----- O O - O O ----- § ---	1	?	?	?
<i>Memecylon</i> sp. (124)	V	----- * * * - * ----- ----- O O ----- § --- § §	1	?	?	?
Myrsinaceae						
<i>Ardisia</i> sp. (83)	V	--- * ----- * --- --- O O ----- O --- § ---	1	?	?	?
<i>Ardisia</i> sp. (84)	V	----- ----- § ---	1	?	?	?
<i>Ardisia</i> sp. (127)	V	- * ----- * ----- * ----- - O O O ----- O ----- § ---	1	?	?	?

APPENDIX 3. Continued.

Species	H	D J F M A M J J A S O N D J F M A M	n	Fl	Fr	Lf
<i>Ardisia</i> sp. (134)	V	-----* *----- ----- -----	2	A	?	?
<i>Ardisia</i> sp. (147)	V	-----* -----O -----	1	?	?	?
<i>Ardisia</i> sp. (151)	R	-----*----- ----- -----§-----	1	?	?	?
<i>Ardisia</i> sp. (156)	V	----- -----O----- -----	1	?	?	?
Rubiaceae						
<i>Chasalia pubescens</i>	V	-----*-----* -O-----OO-----OOO- --§§§-----	3	A	A	A
<i>Chasalia</i> sp. (100)	R	----- -----OOOO----- -----	1	?	?	?
<i>Gardeniopsis longifolia</i>	V	-----*----- ----- -----§§-----	2	S	?	O
<i>Ixora</i> sp. (128)	R	-----* *----- -----O----- -----	1	?	?	?
<i>Ixora</i> sp. (157)	V	----- -----O -----§	1	?	?	?
<i>Lasianthus maingayi</i>	R	*----- ----- -----	1	?	?	?
<i>Pavetta indica</i>	V	-----*-----* -----OOO----- -----§-§§§-----	6	A	O	O
	R	---*-----* * -OOOOOOOOO-----O- -----	1	?	?	?
<i>Pavetta</i> sp. (132)	V	-----*----- -----OOO----- -----	1	?	?	?
<i>Pavetta</i> sp. (135)	V	-----*----- -----OOO----- -----	1	?	?	?
<i>Psychotria cantleyi</i>	R	*-----*-----*----- O-O-O-O-O-O-O-O-O-O-O-O-O --§§-§-----	2	A	A	?

APPENDIX 3. Continued.

Species	H	D J F M A M J J A S O N D J F M A M	n	Fl	Fr	Lf
<i>Psychotria</i> sp. (148)	R	----- -----O -----	1	?	?	?
<i>Randia macrophylla</i>	V	----- O-O----- -----	2	?	S	?
<i>Randia pinangiana</i>	V	-----*-----*----- OOOOOOOOOOO-----OO -----§§§§§§§§§§	6	A	O	O
<i>Urophyllum glabrum</i>	V	-----*-*----- OOOOOOO-O-O-C-O-O-O-O-O §-§§§§§§§§§§§§§§	11	?	O	O
	R	-----*----- --OOO-----OO -----	1	?	?	?
<i>Urophyllum</i> sp. (5)	V	----- OO-----O -----§-----	4	?	S	?
<i>Urophyllum</i> sp. (108)	V	-----*-----* * * *-----* * * -----OOOO----- §-----§-----§	1	?	?	?
<i>Urophyllum</i> sp. (145)	V	-----*----- -----O----- -----	1	?	?	?
<i>Urophyllum</i> sp. (155)	V	-----*----- ----- -----	1	?	?	?
(9)	V	-----*-----* *----- --OOO-----OOOOO----- -----§-----§-----	1	?	?	?
Sterculiaceae						
<i>Leptonychia glabra</i>	V	-----*-----* *----- O-----O-----OO-O-O-O-O- -----§§-----§§	4	O	O	?
	R	-----* *-----*-----* -----O-O-O-O- -----§-----	8	S	O	S