

A PANTROPICAL COMPARISON OF BIRD COMMUNITY STRUCTURE ON SIX LOWLAND FOREST SITES

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Because of the large number of coexisting species, tropical lowland birds probably exhibit the most complex array of ecological interactions of any bird community in the world. Ecological studies in Australia (Kikkawa 1968), Sarawak (Fogden 1972), Malaya (Harrison 1962), Gabon (Brosset 1974), Panamá (Karr 1971, Willis 1974), Costa Rica (Orlans 1969), Brazil (Lovejoy 1974), and Western Amazonia (Pearson 1971, 1975a, 1977) have begun the work of defining and interpreting general ecological patterns among birds inhabiting these forests. Only within the last few years, however, have theories and generalizations been tested by comparing lowland forest avifaunas between Old World and New World sites (Amadon 1973, Karr 1975, 1976a, 1976b, Karr and James 1975). If similar (or dissimilar) patterns of avian species assemblages relative to foliage, climate, and biotic interactions are found, generalizations about community structure are refined.

Using similar-sized study plots in Old World and New World tropical lowland forests, I examine some of the major biotic factors involved in the evolution and present state of avian community structure on these sites by comparing: 1) historical factors and island or island-like effects; 2) seasonality of rainfall and its effect on insect and fruit abundance; 3) habitat heterogeneity; and 4) the influence of avian and non-avian competition.

METHODS

This study compares three New World sites in western Amazonia (Pearson 1971, 1975a, 1977) and three Old World sites, one each in Indonesian Borneo (Kalimantan), Papua New Guinea, and Gabon in West Central Africa. Table 1 indicates the coordinates, elevation, mean annual rainfall, period of study, and hours of observation for each of the six study plots. More detailed descriptions of weather patterns and bird lists including abundance and preferred habitats for each species are available elsewhere (Pearson 1972, 1975b, 1975c, 1975d, O'Neill and Pearson 1974, Brosset in press, Tallman and Tallman in press).

Foraging height, substrate, and guild or foraging technique (gleaning, sallying, snatching, pecking and probing, fruit-eating, etc.) were recorded for each foraging individual. All sightings between 0700 and 1700 are included except for raptors and nocturnal species. Study plots were all in extensive stands of primary forest and, except for occasional

logging of single trees, were not modified by man's presence. Hunting pressure during periods of observation differed markedly from plot to plot, but only the Ecuador and New Guinea plots were hunted heavily. Some of the larger birds (*Mitu* on the Perú and Bolivia plots and *Goura* on the New Guinea plot) had been locally exterminated by hunting, but most bird life on the plots was not affected.

Each plot consisted of a roughly circular path 2.5–3 km in length. I attempted to observe all birds 25 m on either side of the path giving a total area of approximately 15 ha. I chose the plots to be as representative of the general forest in each area as possible. On plots exhibiting extreme dry periods, the end of the dry period and time into the following rainy season were included in the observations.

RESULTS

HISTORICAL FACTORS

Recent theories (Haffer 1969, 1974, Vanzolini 1973, Laurent 1973, Müller 1973, Meggers 1975, Livingstone 1975) suggest that long-term dry (interpluvial) periods in both Africa and South America may have caused invasion of grasslands into the equatorial forests. Only where local conditions resulted in high levels of ground water or rainfall did isolated islands or refugia of forest survive the interpluvial periods. Isolation of these refugia may have been sufficient for speciation to occur, and if so, when pluvial periods returned and forests expanded to reconnect, new species encountered one another. Through selection for characters that reduced the intensity of interspecific competition, exclusion, and probable extinction, the new forest bird community structure was established. Evidently more of these forest refugia were present in South America during interpluvials than in Africa (Laurent 1973, Vanzolini 1973). This pattern of speciation probably also applied to other animal groups as well as forest trees and affected the extinction and exclusion rates during reconnection phases of forest expansion. If some birds, for instance, were adapted or specialized for fruits and insects of their refugium, they would be able to expand their range along with the trees and insects while birds from other refugia, more specialized on their corresponding fruits and insects, would have some preadaptation for co-occurrence as the forests merged. These combined patterns of greater numbers of refugia for more specia-

TABLE 1. Physical aspects and period of study for each of the six study plots.

	Coordinates	Elev. (m)	\bar{x} annual Rainfall (mm)	Period of study	Hrs. of Observation
Limoncocha, Ecuador	0°24'S; 76°38'W	300	2,978	19 July 1971 to 19 April 1972	714
Yarinacocha, Perú	8°17'S; 74°37'W	150	1,625	2 June to 5 Sept. 1972	448
Tumi Chucua, Bolivia	11°8'S; 66°10'W	176	1,995	14 Sept. to 15 Nov. 1972	208
Kutai (Borneo), Indonesia	0°24'N; 117°16'E	40	2,360	25 July to 4 Sept. 1974	250
Maprik, Papua New Guinea	3°55'S; 143°2'E	45	2,037	30 Sept. to 3 Nov. 1974	225
Makokou, Gabon	0°4'S; 12°8'E	500	1,731	28 Sept. to 14 Nov. 1976	300

tion and reduced extinction and exclusion rates in South America would bring about greater numbers of species in present day Amazonian forest than in African lowland forest.

The history of lowland forests of Borneo and New Guinea is most strongly influenced by the location of each of these islands on the relatively shallow continental Sunda and Sahul shelves, respectively. Geological evidence indicates that land bridges connected them to their respective continental land masses during eustatic lowering of sea level, perhaps three to five times during the Late Quaternary (Fairbridge 1966, Van Andel et al. 1967, Flint 1971, Bloom et al. 1974). If, as appears likely, Amazonian and African refugia were formed more frequently in the same period than on Borneo and New Guinea, potential species accumulation would have been lower on the islands. In addition, the greater extinction rates of species on islands than on mainlands (MacArthur and Wilson 1967), together with the effectiveness of water barriers (lower immigration rates) to many lowland forest bird species (Willis 1974), lead one to expect fewer species on these islands than on mainland sites in Africa and South America.

The potential contribution of the Greater and Lesser Sundas, together with the Malaysian Peninsula, to species numbers on Borneo during eustatic lowering of sea level would be greater than that of the relatively species poorer forest avifauna of the Australian continent to New Guinea. This difference is theoretically offset somewhat by the larger size (lower extinction rate) of New Guinea (791,650 km²) over Borneo (725,665 km²). With islands of this magnitude, however, an 8% size difference may be insignificant in regard to immigration and extinction rates.

Berlioz (1970) has remarked on the taxonomic affinities of the tropical forest avifaunas in Africa and Asia, but no exhaustive comparison of species has been made. Moreau (1966), Amadon (1973), and others have compared bird species numbers over large geographical areas of South America and Africa. MacArthur and Wilson (1963) have compared numbers of land and freshwater bird species on various islands in the Sunda group as well as New Guinea, but these comparisons include many types of habitats. Karr (1976b) made one of the few studies comparing bird species number on similar sized plots in comparable habitats in Africa and the New World (Liberia and Panamá). Only if species numbers are compared on similar-sized plots in uniform habitat of comparable foliage complexity can historical effects on bird species numbers within habitats be assessed. Comparing large areas with many habitats does not eliminate the possibility that large geographical areas have more species at least partly because they have more habitat types.

Figure 1 compares the cumulative number of species seen within the forest on each plot, excluding raptors and nocturnal species. Both Old World island plots had fewer species than the Africa and New World plots, and the Africa plot had fewer species than any of the New World plots. On all plots, the cumulative number of species approached an asymptote. I used Rand and Gilliard (1967) for New Guinea, Smythies (1968) for Borneo, Brosset (in press) for Gabon, Meyer de Schauensee (1970) for Amazonia, and additional data from more recent field investigations on some of the plots (Tallman and Tallman in press, Bruce Wheatley pers. comm., J. Van Remsen pers. comm.), to calculate the

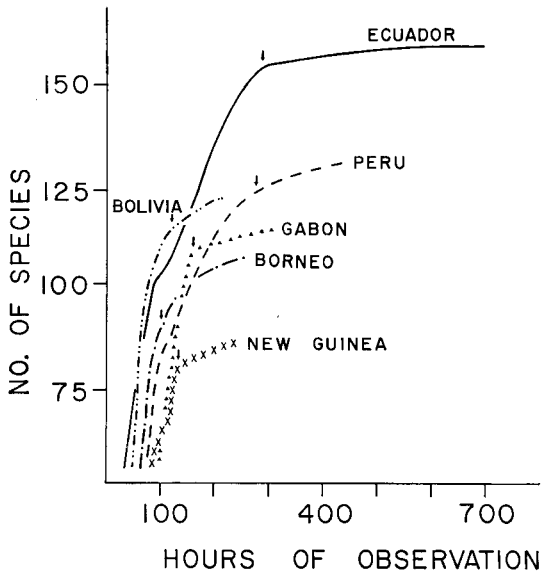


FIGURE 1. Cumulative number of bird species seen on each plot. An arrow indicates the approximate point at which each line reaches an asymptote.

percentages of the total number of forest species known to occur in each area that this plateau point represents: Ecuador = 63%, Perú = 61%, Bolivia = 53%, Borneo = 63%, Papua New Guinea = 70%, Gabon = 62%. Generally, rare and occasional species were the only ones added after this point.

SEASONALITY

Several studies in the Neotropics (Janzen and Schoener 1968, Robinson and Robinson 1970, Janzen 1973, Buskirk and Buskirk 1976), Africa (Charles-Dominique 1971), and Borneo (Fogden 1972) indicate that insect abundance in tropical forests is related to seasonality of rainfall. In forests with high annual rainfall, such as the Ecuador and Borneo plots, insect abundance generally increases in months of less rainfall, but in forests with severe dry seasons, the insect abundance decreases during the dry months (Janzen 1973). To obtain some direct comparison of the seasonal fluctuation of insect abundance on each plot, I systematically collected odonates and tiger beetles (Cicindelidae). Increases in abundance of adults of these two insect taxa were three to nine fold between dry periods (July-August on the Perú plot; September to early October on the Bolivia and New Guinea plots) and initial part of the rainy season (September on the Perú plot; October to November on the Bolivia and New Guinea plots). Similar results were obtained on the Gabon plot (Charles-Dominique 1971).

The Ecuador and Borneo plots had no months below 190 mm mean rainfall and had minimal fluctuations in abundances of these two insect groups, although species changes and replacements were evident. These insects were collected principally from the forest floor and the lowest parts of the foliage (to 3 m) where microclimatic fluctuations (seasonal and diurnal) are the least (Allee 1926, Smythe 1974). Changes in insect abundance as represented by collections of the odonates and tiger beetles in these low parts of the forest probably underestimate changes in insect abundance in mid- and upper-strata and caution must be exercised in extending their population size fluctuations to the entire insect community.

Fruiting phenology is also closely tied to dry-wet season in many tropical forests. Generally, forests with extreme dry seasons have synchronous fruiting of many plant species just prior to the onset and/or the beginning of the rainy season and again, although less significantly, just before the end of the rainy season (McClure 1966, Janzen 1967, Charles-Dominique 1971, Medway 1972, Emmons 1975). This pattern was evident for the Perú, Bolivia, New Guinea, and Gabon sites. The Ecuador site had the least synchrony of fruiting, with fruiting trees uncommonly but regularly available throughout most of the year. The Borneo site, like the Ecuador site, had no extreme dry season, but it had the synchronized, acyclic (3-9 years) fruiting pattern typical of dipterocarp-dominated forests (Janzen 1974). A few fruits such as *Ficus*, however, were available throughout the year, but they were not common in the primary forest and were patchy in distribution (Rodman 1973). In general, local migration of frugivorous species (parrots, toucans, pigeons) was most evident on sites with extreme dry seasons and synchronous fruiting. Insectivorous species, except for northern or southern migrants, showed minimal local movements.

HABITAT HETEROGENEITY

Many aspects of the general physiognomy of lowland tropical forests are similar throughout the world (Richards 1966, Leigh 1975). Convergence through adaptation to similar climates, topography, and soil have brought about striking similarities not only in broad features but also in many details such as shape and size of leaves, buttressing of roots and cauliflorous flowers (Richards 1973). However, measurable differences that do appear in the physiognomy and heterogeneity of these six forest plots may have produced dif-

TABLE 2. Horizontal heterogeneity of foliage as measured by the percentage of each of six foliage column types on each plot (A = tree fall; B = open canopy, closed mid-story, closed under-story; C = closed, closed, open; D = closed, open, open; E = closed, open, closed; F = open, closed, open). N = 1,000 random sightings for each plot.

	Foliage Column					
	A	B	C	D	E	F
Ecuador	3.2	15.9	38.1	5.7	31.8	5.4
Peru	4.1	7.2	39.6	11.6	32.1	5.5
Bolivia	1.8	10.3	41.1	3.2	31.2	12.4
Borneo	0.8	0.8	39.8	15.5	24.7	18.3
New Guinea	2.7	1.4	43.8	11.0	35.6	5.5
Gabon	2.4	10.0	41.6	3.9	32.5	9.4

ferential evolutionary adjustments among the birds inhabiting them.

To measure some of these differences and to attempt to establish their influence on the bird community, I compared three aspects of the forest that are important in determining habitat heterogeneity; a) relative plant species richness; b) horizontal foliage heterogeneity; and c) vertical foliage profile.

Africa is remarkably poor or lacking in certain families of plants generally regarded as characteristically tropical, such as palms and bromeliads. An estimate of relative floral species richness over either large or small areas of African lowland forest places Africa far below that of Amazonia and Indo-Malaysia, and the New World tropical forests are generally poorer than those of Indo-Malaysia (Richards 1973, Whitmore 1975). The number of plant species probably affects the heterogeneity of the forest in the diversity of substrates, insects, fruits, etc., available to the bird community.

For instance, the number of epiphytes was greatest on the Ecuador and Borneo plots, but they were concentrated on about 4% of the trees (mainly large emergent individuals). Epiphyte loads were noticeably less on the Perú, Bolivia, and New Guinea plots and qualitatively similar among these three seasonally dry plots. The Gabon plot was the poorest in number of epiphytes. Only the Ecuador plot had tree ferns, but these were few in number (2.3/ha). Tree-sized palms and cycads were common and present in roughly similar numbers on all the plots (20–40/ha) except Borneo, which had few (0.2/ha), and Gabon, which had none.

Horizontal heterogeneity was assessed by estimating the percent of six foliage column types on each plot. These foliage columns were classified by their sequence of relatively closed or open canopy, mid-story, and under-

story (closed canopy, open mid-story, closed under-story; closed, closed, open; closed, open, open; open, closed, open; open, closed, closed; and tree fall). Measurements were then made of each foliage column type using a modification of MacArthur and Horn's (1969) method (see Pearson 1975a), and the Wilcoxon matched-pairs signed-ranks test applied to determine that the columns were statistically different within each plot. The percentage of each column type present appear in table 2.

By combining the percent representation and the calculated value for the vertical profile of each column type, a mean overall foliage profile was determined for each plot (fig. 2). Wilcoxon matched-pairs signed-ranks tests indicate that the profiles for the three Amazonian plots are the most similar. The Borneo plot profile is significantly different from all other plot profiles as is the Gabon plot. The New Guinea plot profile is most similar to that of the Borneo plot. In addition, by adding the mean total number of leaves along a vertically-sighted line in each of the seven strata of the overall profile (0–2 m; 2–6 m; 6–14 m; 14–26 m; 26–33 m; 33–40 m; > 40 m), a simple quantitative comparison and ranking (leaf total in fig. 2) is possible between the plots.

The Borneo plot and to some extent the New Guinea plot had trees that were much taller than those elsewhere. Malaysian lowland forests, dominated by tree species of the family Dipterocarpaceae, are typically much taller than tropical lowland forest in most other parts of the world (Richards 1966). The Kutai Reserve, in which the Borneo plot was located, was on a shale-dominated substrate. As a result, it had shorter trees than most dipterocarp forest and resembled the height and profiles of the other five plots as closely as could probably be found anywhere in lowland Malaysia (Whitmore, pers. comm.). The New Guinea plot had only a few dipterocarps.

ECOLOGICAL DIVERSITY OF THE BIRD COMMUNITY

Earlier (Pearson 1975a, 1977) I discussed the apparent influence of foliage complexity in determining which foraging techniques required the least energy for birds. Such factors as foliage density, substrate stability, frequency of sun-lit patches, and others were correlated with similarities and differences in distribution of foraging techniques among birds on the Amazonian plots. I expanded this comparison to include Old World forests, where the taxonomic affinities to New World

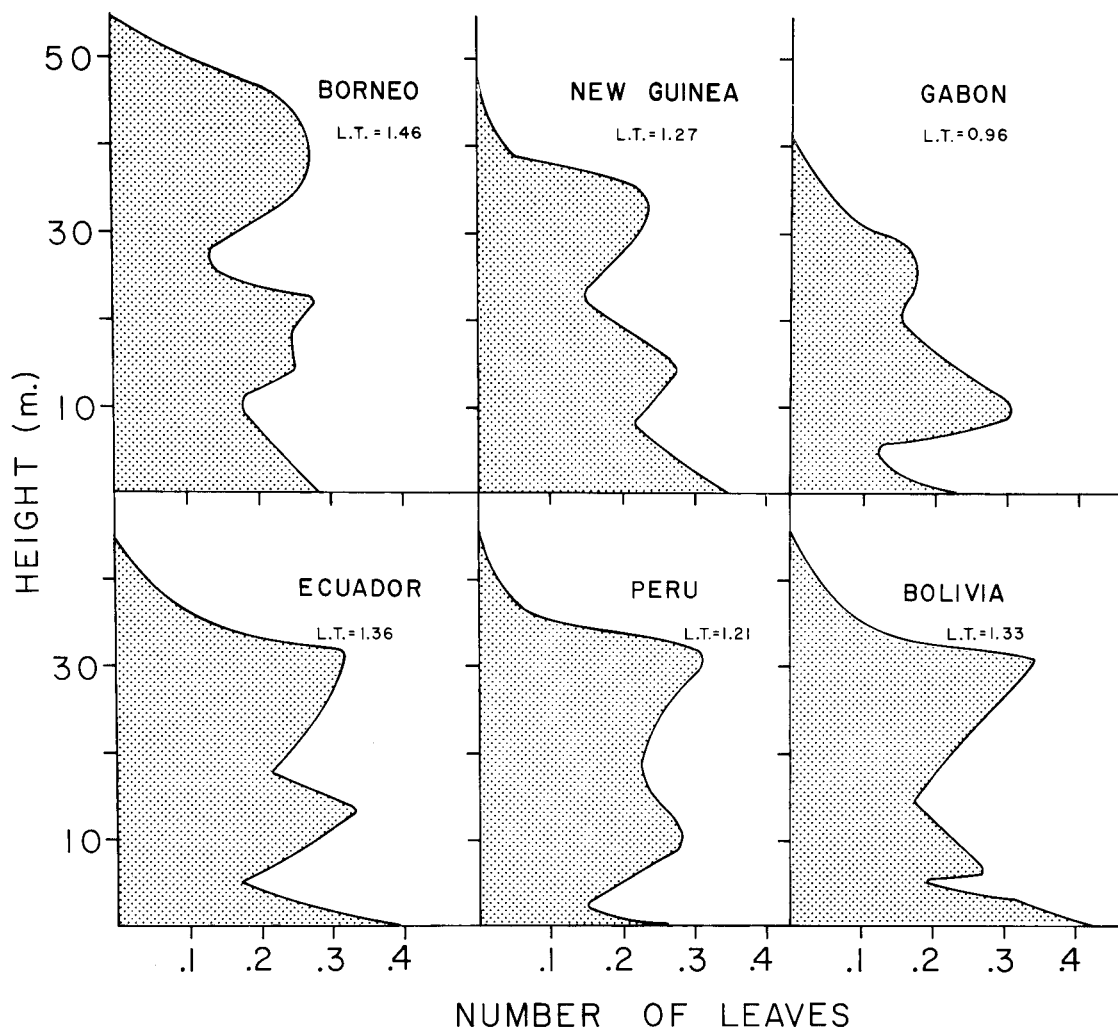


FIGURE 2. Mean foliage profile and total sum of leaves (L.T.) through a vertical sighting in seven strata (0-2 m; 2-6 m; 6-14 m; 14-26 m; 26-33 m; 33-40 m; > 40 m) on each plot.

birds are minimal. Some interesting patterns of similarity and difference appear among the number of individuals in corresponding guilds or foliage habitats (table 3).

A highly significant rank correlation in the number of individuals seen per hour of observation in each of the nine major foraging categories exists on all plots ($P < 0.01$, Spearman rank correlation). Even though species numbers differ, and despite differences in absolute numbers within several categories, this measure of ecological diversity is similar on all plots.

The most obvious differences and patterns in numbers of individuals using each foraging technique were: 1) Although gleaners were the most numerous group on each of the plots, there were almost twice as many glean-ing individuals on each of the Old World plots as on any of the New World plots. 2)

Sallying individuals were 2.2 to 1.6 times as common on the Borneo and Gabon plots as on the others. 3) Pecking and probing individuals that forage for insects on trunks and large branches were rarer on the Old World plots—half the number of individuals to almost none in comparison to the New World plots. 4) Fruit-eating is the second most frequently used foraging technique on all plots but Gabon. There is no parallel ranking or division of number of individuals between the Old World and New World plots. The New Guinea plot had the largest number of fruit-eating individuals followed closely by the Bolivia plot and then by the Borneo, Perú, Ecuador, and finally by the Gabon plot. Table 4 amplifies the frugivore pattern by listing the number of obligate and facultative frugivorous bird species on each plot. 5) Ant-following individuals were absent from

TABLE 3. Number of individuals per hour of observation recorded using each of nine foraging techniques, and the foraging technique diversity of each plot ($H' = -\sum p_i \ln p_i$, where p_i = proportion of individuals in the i th foraging class).

	Glean	Sally	Snatch	Peck Probe	Flower Hover	Fruit	Ant Follower	Glean/Sally	Glean/Snatch	Total No. Ind.	H'
Ecuador	3.44	0.71	0.32	0.63	0.06	1.31	0.29	0.04	0.01	4,874	1.48
Perú	2.15	0.59	0.27	0.68	0.06	1.47	0.08	0.27	0.09	2,539	1.67
Bolivia	3.33	0.70	0.36	0.70	0.15	2.79	0.36	0.35	0.04	1,827	1.62
Borneo	6.90	1.27	0.48	0.35	—	1.73	—	0.75	0.20	2,919	1.30
New Guinea	4.83	0.83	0.44	0.04	0.25	3.04	—	1.06	0.29	2,426	1.48
Gabon	5.12	1.30	0.57	0.28	0.02	1.21	0.16	0.38	0.12	3,307	1.42

the Borneo and New Guinea plots. 6) The number of individuals using the combined foraging strategies of gleaning and sallying or gleaning and snatching show a similar rank correlation ($r_s = 0.97$; $P < 0.01$). The Old World plots, led by New Guinea, had the largest number of individuals that used this strategy, the New World plots had the fewest individuals.

Some of these differences are most easily explained by the absence of specialized avian groups or resources. Woodpeckers (Picidae) and woodcreepers (Dendrocolaptidae) are the common foragers on tree trunks and larger branches throughout the Neotropics, but dendrocolaptids are absent from the Old World. Woodpeckers, a babbler (*Pomatorhinus montanus*) and occasionally barbets (*Megalaima* spp.) were the only birds that used this technique on the Borneo plot. Only woodpeckers used it on the Gabon plot. Woodpeckers are also absent from New Guinea, and the only bird I found foraging on tree trunks and large branches was a small parrot (*Micropsitta pusio*), which took both insects and fungi from this substrate (Rand and Gilliard 1967, Forshaw 1973).

The absence of ants that raid in diurnal columns on the Borneo and New Guinea plots explains the absence of ant-following birds there. The availability of another resource, fruit, has not been measured on these plots, but surprisingly, the density of fruit-eating individuals was greater on the Borneo plot than on the Perú, Ecuador, and Gabon plots. Janzen (1974) speculated that the paucity of obligate frugivores, such as parrots and pigeons, in Malaysia was due to the unpredictable fruiting cycles of dipterocarp forest. Indeed, the number of obligate frugivorous species was least for the Borneo plot (table 4), but the number of individuals feeding on fruits was augmented by a large number of common facultative frugivores, mostly bulbuls (Pycnonotidae) feeding on *Ficus*.

The larger number of gleaning individuals

on the Borneo and New Guinea plots may be partially due to the greater amount of foliage (L.T. in fig. 2) available as a substrate for insects. This explanation, however, does not appear to be valid for the Gabon plot, which also had many gleaning individuals but the least total amount of foliage of all the plots.

The large number of sallying individuals on the Borneo and Gabon plots may have also been influenced by foliage, but in this case by the greater availability of open areas. Sallyers evidently need open areas to both successfully search for and pursue flying insect prey (Pearson 1975a). The Gabon plot had the most open overall vertical foliage profile of all the plots. The Borneo plot had the greatest percent of predominantly open foliage column types (34.6%: columns A, D, and F in table 2) of all the plots.

SPECIES CO-OCCURRENCE

By combining the results of foliage complexity, species richness, and ecological diversity, some patterns concerning the co-occurrence of birds in the same community can be tested.

Several attempts have been made to explain how a large number of species can co-occur. Three of the more easily tested ones are: 1) species-rich communities will have more rare species and fewer common species than species-poorer communities, which will have more common species and fewer rarer spe-

TABLE 4. Percent of total number of bird species which were obligate (>90% of observations recorded as feeding on fruits) and facultative frugivores.

	Percent of observations feeding on fruit						Total no. species
	>90%	90-75%	74-25%	24-10%	9-1%	0%	
Ecuador	11.3	3.8	9.4	10.1	2.5	62.9	159
Perú	10.7	6.9	9.2	6.1	2.3	64.9	131
Bolivia	9.7	4.0	6.5	4.0	1.6	74.2	124
Borneo	5.6	2.8	6.5	4.6	3.7	76.9	108
New Guinea	19.3	2.4	13.3	6.0	8.4	50.6	83
Gabon	10.7	2.7	8.9	1.8	3.6	72.3	112

TABLE 5. Percent common (> 0.12 sightings/hour of observation), uncommon ($0.12\text{--}0.08$ sightings/hour of observation), occasional ($0.08\text{--}0.04$ sightings/hour of observation), and rare (< 0.04 sightings/hour of observation) species seen on each plot. The number of unseen but potentially occurring species included in the rare class is indicated in parentheses following the total.

	%				Total no. species
	Common	Uncommon	Occasional	Rare	
Ecuador	5.5	3.1	11.8	79.5	254 (95)
Perú	4.2	3.7	10.3	81.8	214 (83)
Bolivia	9.2	5.3	8.7	76.8	207 (83)
Borneo	14.1	5.6	20.4	59.9	142 (34)
New Guinea	23.6	8.7	17.5	49.7	114 (31)
Gabon	9.1	7.1	11.0	72.7	154 (42)

cies (Preston 1948, MacArthur and Wilson 1967, Simberloff and Wilson 1969); 2) species-rich communities will have more species that are specialized while species-poorer communities will have more species that are generalists (MacArthur 1972); and 3) the community as a whole will use a greater range of resources and microhabitats when it is species-rich (MacArthur 1972).

Table 5 indicates that the first of these theories applies to the six plots. It compares the number of common (> 0.12 sightings/hr of observation), uncommon ($0.12\text{--}0.08$ sightings/hr), occasional ($0.07\text{--}0.04$ sightings/hr), and rare (< 0.04 sightings/hr) species on each plot. Since the number of rare species is largely a function of the number of hours of observation on the plot, and assuming that most of the potentially occurring species not seen on each plot would be in the rare class when they did occur, I have added them to the rare class. In 14 additional months of intensive observation and collecting at Limoncocha in 1975–1976, Tallman and Tallman (in press) added 21 species to my list of those seen in primary forest, of which one was occasional and the rest were rare. Similar results by Bruce Wheatley on the Borneo plot, J. Van Remsen on the Bolivia plot, and André Brosset on the Gabon plot justify the inclusion of these unobserved species in the rare class.

The number of rare species shows a strong direct correlation ($r_s = 1.00$) with the total number of species on the plot, while the number of common species shows a significant ($r_s = 0.81$) negative correlation.

Quantitative tests of the second theory were impossible because I had insufficient data. However, a consistent series of examples supports the conclusion that there is a

generally positive correlation between number of species on a plot and degree of specialization. For example, several species that occurred on all three of the New World plots showed an inverse correlation between the diversity of their foraging habitat and number of species on the plot. *Taraba major*, a formicariid, and *Thryothorus leucotis*, a wren, were found only in shrubby second growth on the Ecuador and Perú sites. On the Bolivia plot, however, they also foraged commonly in the lower strata of the primary forest plot. *Phlegopsis nigromaculata*, another formicariid, occurred commonly on the Perú and Bolivia plots of primary forest as well as in nearby secondary forest, where it was one of the few regular army ant followers. On the Ecuador plot, however, where the army ants were regularly followed by six bird species including a congener (*P. erythroptera*), *P. nigromaculata* was rare in the primary forest. I found it regularly only in the late secondary growth forest.

Similarly, the New World plots had a relative paucity of individuals using the generalized foraging techniques of mixed gleaning and sallying or snatching. Among both the New World and Old World plots there is a consistent inverse correlation between the number of individuals using these mixed strategies and the total number of species per plot. Less consistent but still important as supporting evidence was the smaller number of individuals that foraged by gleaning on the New World plots as compared to the Old World plots. According to current "optimal foraging theory" (MacArthur 1972), the searching phase of gleaning costs considerable energy. Thus, a gleaning bird cannot afford to be highly selective in type or size of prey. The bird must take the prey in a proportion similar to that in which they are encountered and be a generalist. Gleaning individuals should then be expected to be most common on plots with the fewest total species. The number of gleaning individuals, however, is probably influenced by the abundance of gleaning substrate as well as species numbers and should be ultimately considered in the light of both factors.

A foraging technique too rare to be included in table 3 was palm frond gleaning. The three Amazonian plots each had at least two species that foraged on this substrate almost exclusively (*Dendrexetastes rufigula*, *Philydor pyrrhodes*) and two species that foraged there frequently but not exclusively (*Campylorhynchus turdinus*, *Thraupis palmarum*). The Borneo and Gabon plots with

TABLE 6. Number of individuals per hour of observation recorded using each of seven vertical strata and 14 substrate types ($H' = -\sum p_i \ln p_i$, where p_i = proportion of individuals in the i th stratum or substrate type).

	Vertical foraging strata (m)							N	H'
	ground	0-2	2-6	6-14	14-26	26-33	>33		
Ecuador	0.99	1.83	1.56	1.23	2.35	1.15	0.94	7,169	1.89
Perú	0.33	0.59	0.40	0.46	2.63	1.31	0.96	2,985	1.68
Bolivia	0.84	0.96	0.76	1.11	3.52	1.29	1.58	2,093	1.79
Borneo	0.65	0.58	1.28	2.19	3.19	1.13	2.30	2,960	1.89
New Guinea	0.59	0.80	0.99	1.12	3.33	1.76	2.20	2,425	1.79
Gabon	0.84	2.62	2.11	2.00	2.47	0.92	0.97	3,319	1.75

	Foraging substrate								
	Inner Branch			Out. leaf	Tangle	Flower	Vert. stem	Sml.-med. trunk	Lge. trunk
	Small	Med.	Lge.						
Ecuador	2.25	1.53	0.39	0.26	0.28	0.06	0.40	0.44	0.07
Perú	1.39	2.57	0.25	0.13	0.15	0.06	0.20	0.46	0.06
Bolivia	2.42	2.43	0.14	0.16	0.25	0.12	0.28	0.38	0.06
Borneo	2.83	2.08	1.07	0.33	0.35	0.01	0.03	0.11	0.02
New Guinea	2.08	3.91	0.23	0.22	0.53	0.24	0.08	0.02	0.02
Gabon	3.76	1.08	0.19	0.13	0.53	0.09	0.26	0.17	0.08

	Foraging substrate							
	Web	Dead leaf	Vine		Palm frond	Ground	N	H'
			Vert.	Horiz.				
Ecuador	0.02	0.28	0.06	0.16	0.17	0.68	5,043	2.12
Perú	—	0.07	0.01	0.06	0.05	0.22	2,554	1.72
Bolivia	—	0.17	0.06	0.14	0.11	0.62	1,841	1.86
Borneo	0.08	0.61	0.03	0.09	—	0.61	2,114	1.91
New Guinea	0.01	0.12	0.01	0.03	0.15	0.62	1,907	1.68
Gabon	0.02	0.30	0.55	0.40	—	0.61	2,438	1.73

few or no palms had no species that used this technique. The New Guinea plot, however, with palms as common as on the Amazonian plots had only one species (*Garritornis isidorei*) that used this foraging substrate regularly, while 13 other species rarely used palm fronds as a foraging substrate.

Other highly specialized foragers were birds who fed on epiphyte fruits. Although the Perú plot had two rare species and the New Guinea plot one species that occasionally used this technique, only the Ecuador and Borneo plots had common and regular representatives of this guild. Despite the apparent similarity in epiphyte abundances, however, the Ecuador plot had at least three species that regularly fed on epiphyte fruits (*Tyrannutes stolzmanni*, *Piprites chloris*, and *Euphonia rufiventris*) while the Borneo plot had but one (*Dicaeum agile*).

One obvious exception to the correlation between the greatest total number of species and proportion of specialized species was found in the birds that robbed spider webs. On the Amazonian plots (Pearson 1975a), several species of hummingbirds and manakins occasionally hovered in front of webs to snatch struggling insects or, rarely, the spiders

themselves. On the New Guinea plot, the dicacid, *Melanocharis nigra*, and on the Gabon plot, the muscicapid, *Platysteira castanea*, the sunbird, *Nectarinia olivacea*, and the bulbul, *Phyllastrephus icterinus*, occasionally snatched insects from webs. On the Borneo plot, however, in addition to the dicacid, *Prionochilus maculatus*, that rarely foraged in this manner, three uncommon species of sunbirds called spider-hunters (*Arachnothera longirostra*, *A. crassirostris*, and *A. robusta*) appeared to be highly adapted and specialized for this type of foraging. Several field observations (MacKay 1929, Abbott 1931) report that small birds can be caught and killed in spider webs, and this technique may be costly for birds that forage there regularly. A long, decurved bill in the spider-hunters, however, permits them to hover away from and slightly below the web to avoid entangling their wings in the sticky strands. A significant proportion of foraging observations (15–32%) for these three species was at spider webs.

For the third theory concerning species co-occurrence, a more quantified test was possible. Were more species able to co-occur on some plots because of a greater total range

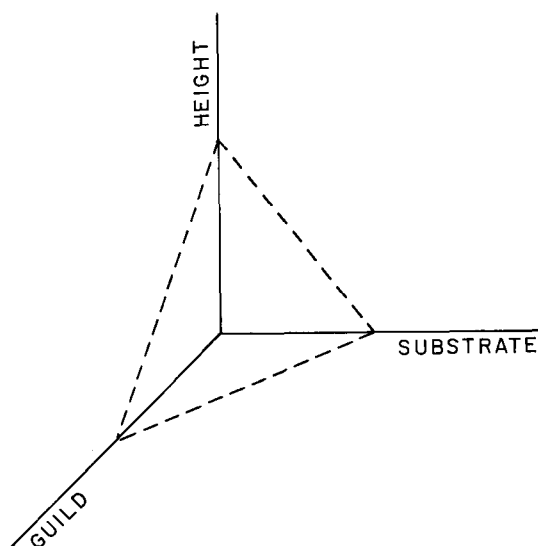


FIGURE 3. General example of a foraging volume generated by connecting the points calculated as the diversity ($H' = -\sum p_i \ln p_i$) of use of all individuals along each axis. The resultant volume is measured in H'^3 units.

of usable resources or available microhabitats than on other plots? If different habitats contain different resources, this prediction can be tested without actually measuring resources and their use by different species, though eventually such measures will be needed.

By calculating a diversity or breadth of habitat use for all the combined individuals in the bird community regardless of species (as was done for guilds in table 3), one can quantify and compare breadths from plot to plot independent of species and species richness. Breadths ($H' = -\sum p_i \ln p_i$) for each of the three most important parameters (vertical foraging range, substrate use, and guild) (table 6) were plotted on three axes as in figure 3, much as done by Cody (1974) for individual species. Each of the points on the axes describes the vertex of an irregular pyramid. I refer to the volume of this pyramid as the foraging volume of the bird community (see Ricklefs and O'Rourke 1975) and is expressed in H'^3 units. Figure 4 indicates some correlation ($r^2 = 31.6$) between species numbers and foraging volume of all individuals combined, but is not statistically significant. This insignificance is due to the unexpectedly small foraging volumes of the Perú and Gabon plots.

NON-AVIAN INFLUENCES

Historical and ecological influences have affected patterns of distribution, species rich-

ness, and community structure in non-avian taxa (Müller 1973, Vanzolini 1973, Laurent 1973). The potential influence of these other taxa on bird communities is great but has been investigated only superficially. The evolutionary response to nest predation (mainly by snakes and monkeys), for instances, has probably been a major factor in small clutch size of these tropical birds (Skutch 1949), as well as cavity nesting in frugivorous species and change in foraging habits of some frugivores to insectivory while feeding young (Morton 1973). Some behavior such as mobbing or freezing in position, and joining mixed-species flocks may also be at least partially a response to predation (Bates 1892 and many others).

In addition, suggestions have been made that non-avian species as competitors are also important selective agents in the evolution of tropical forest bird community structure. Harrison (1962), Pearson (1975a), Charles-Dominique (1975), Fenton and Fleming (1976), and Karr (1976b) suggested that foraging techniques as well as spatial and temporal distribution of birds within a forest plot are probably influenced by competing monkeys, rodents, ruminants, bats, lizards, etc.

Some of the patterns on my study plots could be interpreted to include inter-class or inter-phyletic competitive influences. Table 3, for instance, shows a gradient in abundance of fruit-eating individuals that is independent of Old World-New World relationships. A reasonable interpretation of this pattern is as an inverse correlation to the number of mammalian frugivores, excluding bats (see Fenton and Fleming 1976), on each plot. The New Guinea plot, with no primates and only a few relatively uncommon marsupial frugivores such as tree kangaroos (*Dendrolagus* sp.), had the greatest number of avian fruit-eating individuals. The Bolivia plot, with only one species of monkey and a few uncommon species of frugivorous rodents, was the next lowest plot in number of frugivorous mammals, and the second highest number of fruit-eating bird individuals. Gabon, with 8 species of frugivorous or partially frugivorous squirrels, 6 species of frugivorous ruminants, and 13 species of frugivorous primates (L. H. Emons, pers. comm.) was equaled only by the Borneo plot in richness of mammalian frugivorous species: 12 species of frugivorous or partially frugivorous primates, 5-7 species of frugivorous squirrels, and 6 species of frugivorous ruminants (P. S. Rodman and B. Wheatley, pers. comm.). The peculiar fruiting strategy of dipterocarp forest, however,

probably had some influence on fruit availability; the high number of mammalian frugivores on the Borneo plot was probably offset by the majority of them being facultative frugivore-folivores or frugivore-insectivores. The low number of bird individuals seen eating fruit on these two plots follows the inverse correlation between frugivorous mammals and birds as it also does on the Perú and Ecuador plots.

Comparisons of insectivorous bats, lizards, etc., might show similar inverse correlations to insectivorous bird abundances, but without accurate measurements of insect abundance, speculations must remain tentative. Some specific examples, however, suggest that inter-phyletic as well as inter-class competition for insects are potentially important interactions in these forest plots.

The absence of all but one uncommon species of trunk-foraging bird on the New Guinea plot and the absence or paucity of woodcreeping species other than woodpeckers on the Gabon and Borneo plots caused me to look carefully for other organisms foraging on this substrate. On the New Guinea plot, a large (2 cm), flightless species of predatory tiger beetle, *Tricondyla aptera*, was common on the trunks of trees and large branches. It foraged by capturing insects in the cracks and irregularities of the bark, the same location where dendrocolaptids and many woodpeckers on the other plots found their prey. None of the other plots had such an obvious and common trunk-foraging arthropod predator. A congener, *T. doriai*, occurred on the Borneo plot, but it was smaller (1.5 cm), rare, and foraged on small branches and leaves, not the trunk or large branches. The most obvious non-avian trunk-foraging insectivores on the Borneo plot were the small (15 cm) squirrel, *Nannosciurus melanotis*, and flying lizards (*Draco* spp.). On the Gabon plot, 5 species of insectivorous squirrels and 5 species of prosimians foraged for insects on the trunks of trees and branches (Emmons, pers. comm.). These non-avian alternatives to New World dendrocolaptids were conspicuously rare or absent on the Amazonian plots.

Further evidence for inter-phyletic possibilities of competition were found in the orb-weaving spiders. The web-robbing behavior of some bird species on each plot indicates that birds and spiders capture prey from the same size range and to some extent share a common resource base. In addition a group of highly specialized non-avian insectivores commonly robbed spider webs on the New World plots—the pseudostigmatid damsel-

flies. They were large (up to 15 cm) and common forest odonates (five common species on the Ecuador plot). Perhaps their competitive ability was significant enough to be at least partly responsible for the lack of specialized web-robbing avian species on the New World plots.

DISCUSSION

Because of the limitations of short term studies such as these, the major goal of this work lies not in detailed description and quantification but rather in preliminary formulations and in providing direction to future studies.

One major generalization, as earlier suggested by Hafter (1969), Karr (1976b), and others, involves the influence of historical factors on these communities. From theorized geological history alone one can predict the rank order of the number of bird species on the six plots. The importance of species numbers to much of community structure theory and the biotic interactions associated with co-occurring species makes historical factors a vital part of understanding these communities. Foliage complexity, physical habitat, and resource levels influence the maximum number of species capable of being supported as well as details such as how the birds present will forage, but historical factors are probably the major factor controlling how many species will be available to enter the forest. Separating these two groups of factors, however, is sometimes difficult. Seasonality is a direct abiotic force influencing the availability of resources as well as physiological adaptations to heat stress and water loss. However, present day seasonality is also probably related to the geographical location of forest refugia or grasslands during interpluvial periods. Areas with extreme dry seasons are most likely to be the areas that grasslands invaded while areas with little or no dry season were most likely the areas where forest refugia survived.

Combinations of factors, especially in complex ecosystems such as this one, need to be understood as ensembles. Looking at factors one at a time is probably an unprofitable approach since each one individually has proportionately little chance to have a major effect on the total system. For instance, both historical and ecological influences of extreme dry season are probably involved on the Perú plot. It had the most severe dry season and the lowest mean annual rainfall of all the plots. This three month dry period may have influenced the number of species and the abundance of each that could occur on the

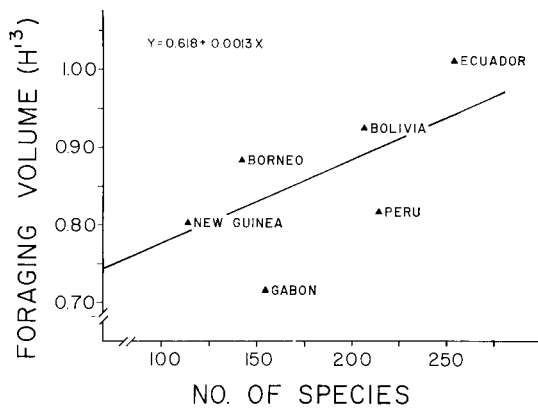


FIGURE 4. Correlation between total number of potentially occurring species and the foraging volume of all individuals on each plot.

plot for the whole year. If this is true, the significantly smaller foraging volume of the Perú plot (fig. 4) is partially explained.

A more complete understanding of this small foraging volume emerges when non-avian competition is also included. If the resource levels are already critical because of the extreme dry season, one would expect the bird community on this plot to be sensitive to even the moderate primate population present (Pearson 1975a). Similarly, the Gabon plot had a distinct and extended dry season, although the effect here was partially offset by prevailing dry season cloud cover. However, the tremendous number of individuals and species of mammalian frugivores and insectivores combined with low plant species and physical diversity may have been sufficient to explain the significantly small avian foraging volume on this plot (fig. 4). The New Guinea and Bolivia plots, also with definite dry seasons, did not have the mammalian pressure to reduce the avian foraging volume. The Borneo and Ecuador plots, on the other hand, had no significant dry season, and their resource levels could permit a large avian foraging volume yet also support large populations of mammalian competitors. The problem of a less reliable and general fruit availability on the Borneo plot may have been offset by the greater physical and taxonomic foliage diversity.

The combined effect of several theories for co-occurrence also needs to be studied. The theories discussed here are not mutually exclusive and may be directly related in many cases (specialization and rareness for instance). Greater numbers of highly specialized but rarer species could conceivably expand the potential foraging volume of a

community by efficiently exploiting substrates too rare or tenuous to support a more generalized and common species (Orians 1969). Again, the pressure from combined influences and factors emphasizes the importance of an integrated approach to understanding this ecosystem.

These preliminary results also emphasize the limitations of taxon-oriented analyses of communities. The potentially important factors influencing tropical lowland forest bird communities include so many interactions that cross class and phylum lines that the boundaries of the community by necessity extend far beyond birds. How far they extend will have to be left to detailed, long-term studies that are more ecosystem-oriented, but these initial observations have shown that ignoring non-avian influences is probably unwise. Comparisons and predictions directed at patterns that are not restricted to taxonomic levels should prove to be more general and ecologically significant.

SUMMARY

Preliminary patterns in tropical lowland forest bird communities are investigated by comparing the avifaunas of three New World (Amazonia) and three Old World (Borneo, New Guinea, Gabon) plots. The factors emphasized are: 1) historical and island or island-like effects; 2) seasonality of climate and base resources (insects and fruits); 3) habitat heterogeneity; and 4) the influence of avian and non-avian competitors.

Historical effects for species numbers are examined by comparing uniform plots of a limited area (15 ha). Species richness is correlated with number of common and rare species, amount of specialization, and to some extent the overall habitat use by the bird community. Similarities and differences in foliage complexity help explain observed similarities and differences in the number of individuals using specific foraging techniques on each plot. Initial observations indicate the potential effects of non-avian competitors ranging from damselflies and spiders to mammals.

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