

THE RELATION OF FOLIAGE COMPLEXITY TO ECOLOGICAL DIVERSITY OF THREE AMAZONIAN BIRD COMMUNITIES

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The relation between foliage complexity and bird species diversity has been studied by several investigators. Some (MacArthur and MacArthur 1961, MacArthur et al., 1962, Recher 1969, Karr 1971, Karr and Roth 1971) found that the complexity of the vertical distribution of leaves, as measured by foliage height diversity (FHD), was a good predictor of bird species diversity (BSD). Other investigators (Terborgh 1967, Balda 1969, Lovejoy 1972) have found little correlation between FHD and BSD. BSD, as measured by a statistic derived from information theory, necessitates knowledge of the number of individuals of each species as well as number of species. In mature tropical forests, estimates of population size are difficult because such a large proportion of the bird species do not typically occur in low strata where they can be readily netted and marked. Orians (1969) avoided this problem in Costa Rican forests by comparing only the number of bird species (bird species richness, BSR) to FHD. He suggested that the range of resource types permanently above threshold values in tropical forests was the major factor determining bird species richness. However, in all these relations between foliage complexity and the number of bird species inhabiting the foliage, the assumption is made that the community is in an equilibrium or saturated state, that is, new species can enter the community only if they exclude a species already present.

The Amazon Basin presents a distinct difficulty in applying FHD-BSD (BSR) correlations. Due to numerous historical changes in climate, continuous forest apparently alternated with forest islands (refugia) surrounded by non-forest vegetation throughout the Pleistocene and post-Pleistocene (Haffer 1969, Vanzolini 1973). It is now generally recognized that islands with similar habitat harbor different numbers of species depending on the area and distance of the island from the mainland species pool (MacArthur and Wilson 1967). Island-like effects are also recognized for continental habitats that occur in patches

(Vuilleumier 1970, Willis 1974) and island-like areas of continents (Cody 1970). In addition, displaced immigration-extinction equilibria and relaxation effects (Diamond 1972), in which the former area of islands differed from the present area, have been shown to affect species richness and diversity of otherwise similar islands (Brown 1971) and are likely applicable to the Amazon area. These island differences, island-like effects, and relaxation effects all mean that habitats with similar FHD at separate sites may not have the same BSD if there has been insufficient time for equilibrium to have been re-established.

The precise location of these refugia, their minimum size, and the time span involved between climatic changes are not known. Unfortunately, this information is vital to our interpretation of present ecological data. If, for instance, the time span between the present and the last isolation of the refugia has been relatively long, then one could safely assume that the bird communities throughout the Amazon are at equilibrium. Differences in the bird community observed from site to site could then be attributed largely to local differences in physical factors such as weather and foliage structure. If, on the other hand, the time span between the present and the last isolation of the refugia has been relatively short, then differences in bird communities at different sites could be the result of non-equilibrium and non-saturation.

To disentangle the roles of historical influences and equilibrium assumptions, I have made a series of predictions on the basis of different postulates concerning the time continuous forest has existed in the Amazon Basin. First, assuming equilibrium, i.e., a long time span since the last isolation of the refugia, I predict the following:

1. Similar foliage structure at different sites will be found to support similar numbers of bird species (MacArthur and MacArthur 1961).
2. Similarly structured sites with larger numbers of non-avian potential competitors

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will be found to have fewer bird species and vice versa.

On the other hand, assuming that only a short time span has occurred between the present and the last isolation of the refugia and that equilibrium has not generally been reached, I predict the following:

1. Similarly structured sites will be found to have the number of bird species inversely proportional to the distance from historical refugia.

2. The number of common and rare species on sites at various distances from refugia will be found to vary in a distinct pattern. Sites in or close to refugia will be found to have the greatest number of rare species and the fewest number of common species. Sites far from refugia will be found to have the greatest number of common species and the fewest number of rare species (MacArthur 1972).

The presence of many complicating factors, such as weather and resource base differences, partial congeneric replacements, and differential influences of non-avian members of the community, as well as the question of equilibrium, make still another set of predictions concerning the relation of foliage structure and the bird community desirable, especially if they can eliminate the necessity of making any assumptions about equilibrium. By looking at the relation and influence of the foliage structure on the distribution of bird biomass, the number of individuals, and the use of certain foraging strategies without regard to species, the following set of predictions can be made (with the one assumption that any forest site will be sustaining the maximum possible total number of individuals and biomass):

1. Foliage type and density at different vertical intervals will be found to be major determinants of the foraging technique used by birds in each vertical interval.

2. Foraging technique together with foliage density will be found to determine optimum size of birds as well as total biomass supported in each vertical interval.

3. The biomass of non-avian potential competitors will be found inversely proportional to the biomass of birds in corresponding vertical intervals of similarly structured sites.

If the foliage structure does influence important aspects of the bird community, such as amount and distribution of total biomass, and size and foraging technique of individuals, bird communities in areas with similar foliage complexity and structure will be found to have many similar attributes. Using these predictions and testing for similarities on different sites, I will attempt to determine the relation



FIGURE 1. Map of northwestern South America indicating location of study sites.

between foliage complexity and the structure of the bird community inhabiting primary lowland forest in Amazonian South America. I will generalize about the hypothesis that foliage complexity is a major determinant of the number of ecological roles or niches available to the birds, which in turn affects the ecological diversity of the bird community. Ecological diversity will be largely interpreted not in terms of species and taxonomic diversity but in terms of adaptive morphology and foraging techniques of individuals and biomass.

METHODS

STUDY PLOTS

I chose three locations in Amazonian South America (fig. 1) to make my observations. Pearson (1972, 1975) and O'Neill and Pearson (1974) provide a survey of the avifauna for each site, including abundance and habitat preference for each species. The localities and periods of observation were:

(1) Limoncocha, Province of Napo, Ecuador ($0^{\circ} 24'S$; $76^{\circ} 38'W$), located in the northeastern part of the country near the Napo River (el. = 300 m) about 15 km south of the town of Coca (19 July 1971 to 19 April 1972).

(2) Yarinacochoa, Department of Loreto, Peru ($8^{\circ} 17'S$; $74^{\circ} 37'W$) located in the east central part of the country near the Ucayali River (el. = 150 m) 12 km northwest of Pucallpa (2 June to 5 September 1972).

(3) Tumi Chucua, Department of Beni, Bolivia ($11^{\circ} 8'S$; $66^{\circ} 10'W$) located in the extreme northeastern part of the country near the Beni River (el. = 176 m) about 20 km south of Riberalta (14 September to 15 November 1972).

At each of the three locations, I selected a study plot from representative primary forest on flat terrain. Each plot consisted of a roughly circular path 3 km in length. I attempted to census foraging birds for a distance of 25 m on either side of the path. For each 200 m of trail I was thus censusing 1 ha

of forest, for a total of 15 ha per plot. Mean monthly temperatures varied less than 5°C throughout the year at all three locations. Figure 2 indicates the mean monthly and annual rainfall for each of the sites. Limoncocha had the greatest total rainfall and the least degree of seasonality; Yarinacochoa had the least total rainfall and the most extreme seasonality; Tumi Chucua was intermediate in total rainfall but showed a seasonality approaching that of Yarinacochoa.

A few birds were collected to determine the identity, weight, and stomach contents of the bird species present on each plot. To gather observational data, I moved slowly along the path with frequent stops. For each foraging individual observed, I recorded its species; sex, when determinable; time of day; location on the plot; vertical height at which the individual was foraging; foraging substrate; foraging technique; weather at time of observation; type of foliage column (as discussed in the next section); and flock association. (Total number of hours of observation on the Ecuador plot = 714; Peru plot = 448; Bolivia plot = 208.)

FOLIAGE MEASUREMENT

As an estimate of the physical complexity of the vegetation, I measured the foliage profile of each plot. I found that I could most finely divide the foliage into the following 12 height intervals with some degree of accuracy: ground, 0–1 m, 1–2 m, 2–4 m, 4–6 m, 6–10 m, 10–14 m, 14–18 m, 18–22 m, 22–26 m, 26–33 m, > 33 m. The lower strata are narrower both because the birds appear to be more sensitive to slight changes in height at lower levels (Willis, pers. comm.; Orians 1969; Pearson 1971) and because my height measurements, accurate to within $\pm 10\%$, allowed more precision for the lower strata than for the canopy.

I subjectively divided the forest in each plot into general foliage column types. The forest in most areas is made up of a combination of canopy, mid-story, and understory components. At any point, each of these three components can be quickly classified as open, with few leaves and branches, or closed, with dense leaves and branches. By checking many spots for all possible combinations of these three components, I found that some combinations, such as closed canopy, closed midstory, closed understory, were very rare, while other combinations, such as open canopy, open midstory, open understory, were non-existent. Only seven foliage column types were common enough to make any significant contribution to the structure of the forest on the plots.

To obtain quantitative measure of these subjective divisions of the forest, I used the MacArthur and Horn (1969) method of leaf density measurement. I placed an acetate sheet marked with eight intersecting lines on the viewfinder of a single lens reflex camera with a 135 mm lens. With the camera mounted on a tripod, I measured the vertical distance to the first leaf above an intersection of two of the lines by focusing on the leaf and reading the distance on the lens range finder. I measured 30 points (16 sightings for each point) within each of the foliage column types on each plot. The results indicate that each of the seven foliage column types is similar on all three plots. Figure 3 shows the mean foliage profile from all three plots for each foliage column type. To estimate an average profile for each plot, I weighted the proportion of the representation of each foliage column type on each plot (fig. 4). The average profiles are not significantly different ($p > 0.01$;

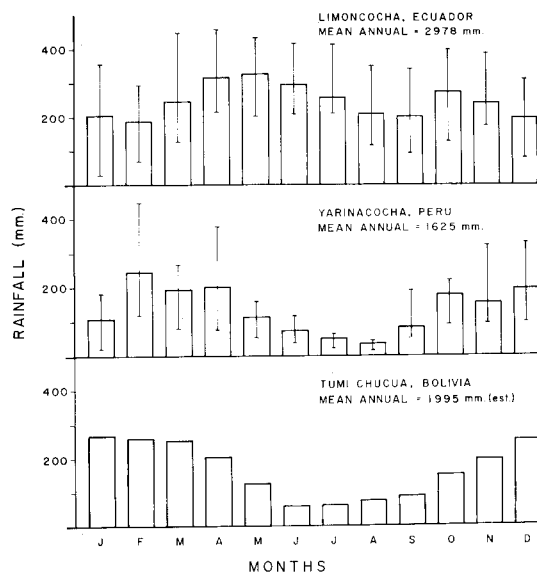


FIGURE 2. Mean monthly rainfall (bars) and range (vertical lines) for the study sites. Eleven years of weather data available for Limoncocha, Ecuador; 16 for Yarinacochoa, Peru; and four for Tumi Chucua, Bolivia.

Wilcoxon matched-pairs signed-ranks test), and the FHD calculated using information theory index of diversity ($H' = -\sum p_i \ln p_i$ where p_i = proportion of foliage in the i^{th} interval) with 12 strata is virtually identical (Ecuador plot = 2.36, Peru plot = 2.37, Bolivia plot = 2.36). Seasonal variability in these foliage profiles was not compared quantitatively. The profile measurements used for figure 3 and figure 4 were taken during the drier months on each plot (21–23 December 1971 for Ecuador, 2–4 September 1972 for Peru, 1–3 October 1972 for Bolivia). Qualitative seasonal differences were evident in the number of leaves accumulated on the ground on the Peru and Bolivia plots and undoubtedly the foliage profiles for Bolivia and Peru were somewhat different during the wet season. That the foliage profiles were so similar in the dry season when the greatest difference would be expected suggests that in the wet season when the climate was very similar on all three plots, the profiles would be even more similar. Foliage profile measurements at different seasons should be made to quantify seasonal differences, but I suspect that these differences on my study plots are too subtle to be detected by the MacArthur-Horn method of foliage profile measurement. The similarity of these plots, however, should not be taken as an indication that the entire Amazon Basin has the same or even similar foliage profile. I had chosen the plots carefully to yield profiles as similar as possible. In general though, each of the plots was representative of the general forest surrounding it.

Why such similarly structured foliage should be available among the three plots with such differences in total rainfall is puzzling. Although epiphytes were somewhat more obvious on the Ecuador plot, the number of most plant types such as palms was similar from plot to plot. In the long range cyclic changes of Amazonian weather patterns (Haffer 1969) the forests may be able to maintain themselves longer than ex-

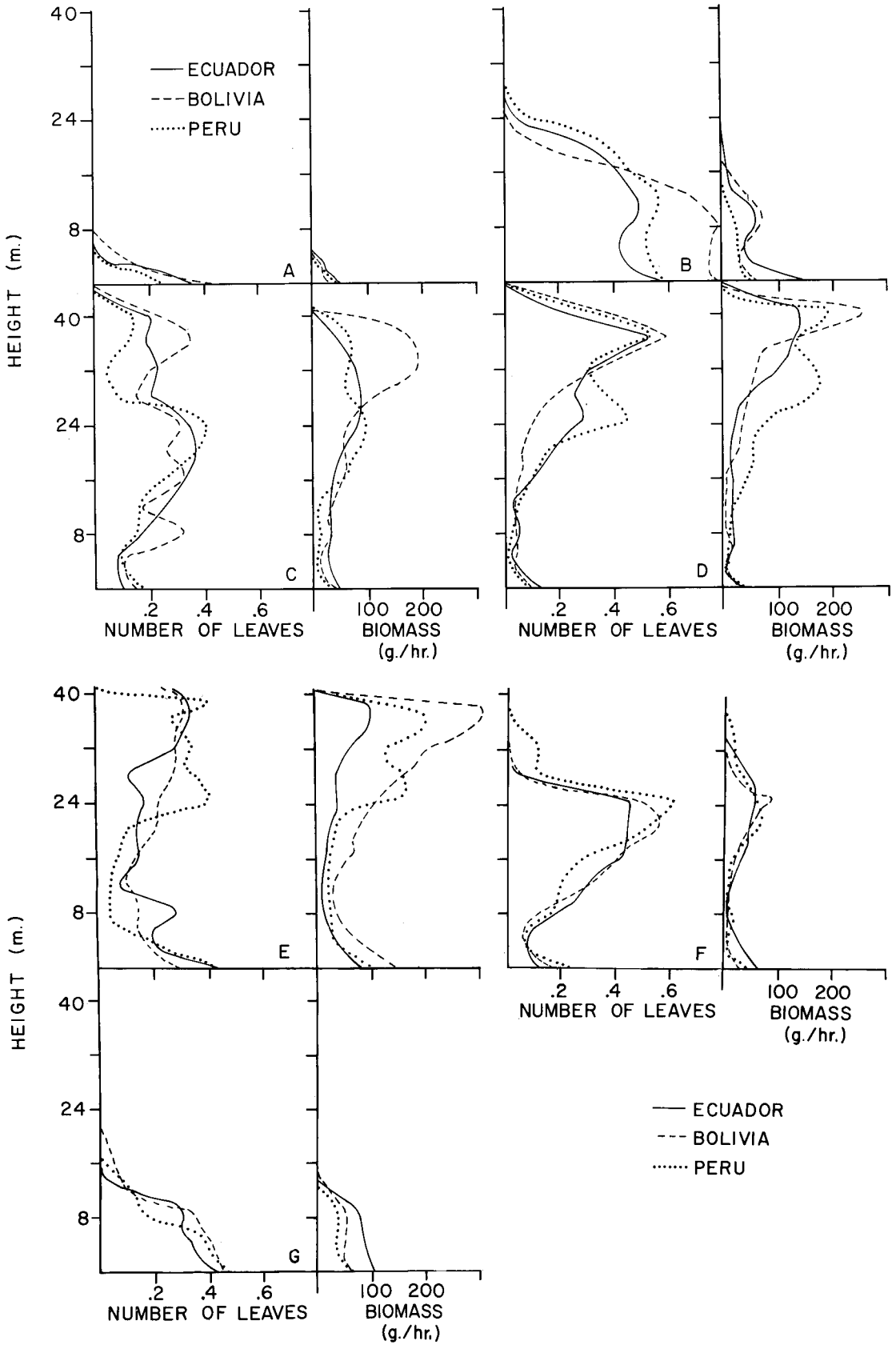


FIGURE 3. Foliage column profiles (A = tree fall; B = open canopy, closed midstory, closed understory; C = closed canopy, closed midstory, open understory; D = closed canopy, open midstory, open understory; E =

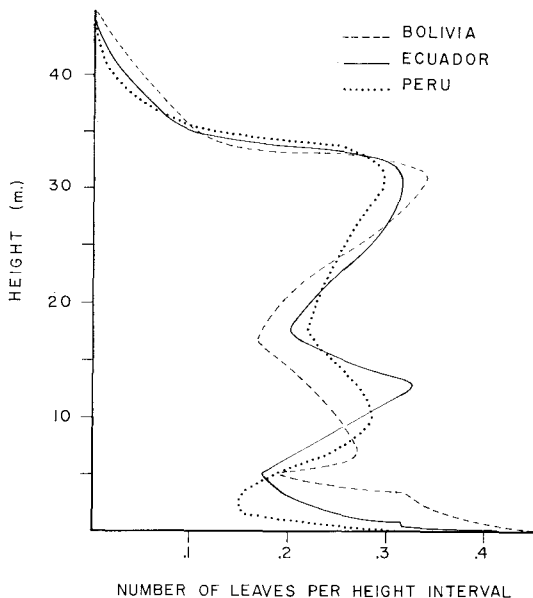


FIGURE 4. Average foliage profiles for each of the study plots.

pected into dry periods at a structural level attained in earlier wet periods (Killick 1959). Evidently the foliage, especially of dense primary forest, can effectively modify the local climate so that gradual changes in the regional climate do not affect forest structure immediately. When these forests are disturbed, however, by extensive tree falls, fires, cutting, and the like, the change in general climate may not permit the forest to proceed through the former successional seres so that a forest similar to the one previously present cannot be reestablished.

RESULTS

TESTING EQUILIBRIUM PREDICTIONS

The first set of predictions I made assumed an equilibrium of species on these three plots. If this is true, then according to MacArthur and MacArthur (1961), Recher (1969), Karr (1971), and others, the similarity in the foliage complexity (as measured) should provide approximately the same number of ecological roles or niches on each plot, and accordingly, the number of bird species should be similar from plot to plot. This is not the case, however, as the Ecuador plot had many more species than the others (fig. 5).

If these plots are truly at equilibrium, the difference in number of bird species might be offset by non-avian potential competitors. As will be discussed in more detail in a later section, monkeys appear to be the most obvious

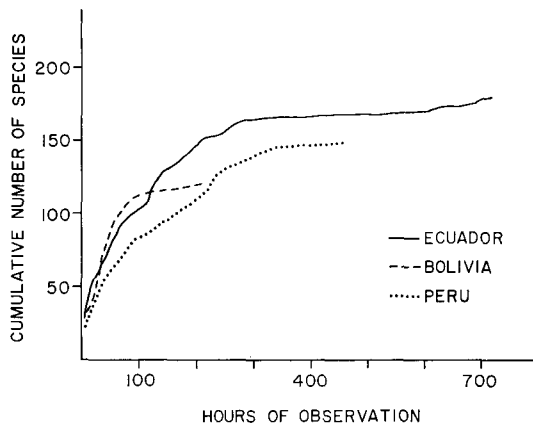


FIGURE 5. Cumulative number of bird species seen on each plot (excluding raptors and nocturnal species).

non-avian group to have a potential competitive influence on the number of bird species. Plots with the smallest number of bird species should have the greatest monkey population and vice versa. Table 1 indicates that this prediction is not valid. Indeed, the opposite is true; there is a direct rather than an inverse correlation between numbers of monkeys and bird species.

Therefore, in terms of predictions from foliage profiles and presence of potential competitors, these three plots are not all at equilibrium. If this is the case, then differences in BSD on the plots could be the result of either local physical differences, historical differences, or a combination of both. The ambiguity of these conclusions makes an alternate set of predictions necessary.

TABLE 1. Insectivorous/frugivorous monkey species and estimated population sizes present on the three study plots.

	ECUADOR	PERU	BOLIVIA
<i>Saimiri sciureus</i> (Squirrel Monkey)	130	50	—
<i>Aotus trivirgatus</i> (Night Monkey)	15	15	10
<i>Pithecia monachus</i> (Saki Monkey)	—	5	—
<i>Saguinus</i> sp. (Tamarin)	75	60	—
<i>Cebuella pygmaea</i> (Pygmy Marmoset)	30	—	—
Total	250	130	10

←

closed canopy, open midstory, closed understory; F = open canopy, closed midstory, open understory; G = open canopy, open midstory, closed understory) within each plot compared to vertical bird biomass distribution within each foliage column type.

TABLE 2. The number of common, uncommon, occasional, and rare species on each study plot. The common species are listed in descending order of abundance. (*species for which at least 30% of observations were recorded as foraging on fruits)

ECUADOR	PERU	BOLIVIA
Common (> 0.12 sightings per hour of observation)		
1. *Tangara schrankii	1. *Tangara chilensis	1. *Brotogeris cyanoptera
2. Myrmotherula axillaris	2. *Pionites melanocephala	2. *Pionites leucogaster
3. *Cacicus cela	3. *Cacicus cela	3. *Tachyphonus luctuosus
4. Habia rubica	4. *Hemithraupis flavicollis	4. Pygiptila stellaris
5. Thamnomanes ardesiacus	5. *Thraupis palmarum	5. Myrmotherula menetriesii
6. Thamnomanes caesius	6. Myrmotherula axillaris	6. *Leptotila rufaxilla
7. Monasa morphoeus	7. *Melanerpes cruentatus	7. Hypocnemis cantator
8. *Brotogeris cyanoptera	8. *Tangara mexicana	8. *Cacicus cela
9. Myrmotherula huxwelli	9. *Dacnis cayana	9. Phlegopsis nigromaculata
10. *Pyrrhura melanura		10. *Pteroglossus castanotis
11. Xiphorhynchus guttatus		11. Xiphorhynchus guttatus
12. *Capito niger		12. Monasa nigrifrons
13. Gymnopithys leucaspis		13. Thryothorus guarayanus
14. Piaya cayana		14. Myrmotherula brachyura
		15. Myrmotherula axillaris
		16. Cranioleuca gutturata
		17. Myrmeciza hyperythra
		18. Piaya cayana
		19. Veniliornis affinis
Uncommon (0.12–0.08 sightings per hour of observation)		
8 species	8 species	11 species
Occasional (0.08–0.04 sightings per hour of observation)		
30 species	22 species	18 species
Rare (<0.04 sightings per hour of observation)		
130 species	113 species	74 species
Total	182	152
	182	122

TESTING NON-EQUILIBRIUM PREDICTIONS

These three study plots lie in historically different parts of the Amazon. According to both Haffer (1969) and Vanzolini (1973), the Ecuador plot is in the largest and most persistent of all the forest islands (Napo refuge). The Peru plot itself is in an area of long term weather fluctuation, and probably the only forest present in dry periods was gallery forest along the Ucayali River; the East Peruvian refuges, however, were within 100 km. The Bolivia plot is the farthest from any forest refuges, and gallery forest along the Beni River was probably the only forest present in dry periods.

If the time span between the present and the last forest island period is relatively short, and equilibrium has not been generally attained, then one would predict the largest species pool for the Ecuador plot, intermediate for the Peru plot, and smallest for the Bolivia plot. The sizes of the species pools as recorded in figure 5 support this prediction.

MacArthur (1972) cited evidence from comparisons of mainland and offshore island bird surveys that indicates, in addition, that

areas below equilibrium will have fewer species but more of them common than areas near or at equilibrium. If the Ecuador plot is closest to equilibrium, the Peru plot intermediate, and the Bolivia plot farthest from equilibrium, then the Ecuador plot should have the greatest number of rare species and the fewest common species; the Bolivia plot should have the fewest rare species and the greatest number of common species; and the Peru plot should be intermediate.

To test this prediction, I corrected for the difference in time spent on each plot by calculating abundance in terms of number of sightings per hour of observation and then divided the bird species into four abundance classes: common (> 0.12 sightings per hour of observation); uncommon (0.12–0.08 sightings per hour of observation); occasional (0.08–0.04 sightings per hour of observation); and rare (< 0.04 sightings per hour of observation). Table 2 compares the number of species in each of these four classes of abundance and lists the names of the common species on each plot in descending order of abundance. All the totals for the abundance classes except the rare

class were reached by 150 hours of observation on each plot. After this time, I added only rare species; any comparison of species in the rare class must be interpreted in the light of the greater number of hours spent on the Ecuador plot. The "occasional" class of abundance, however, is much less sensitive to the difference in total hours of observation.

Of the three plots, the Bolivia plot, as predicted, had the greatest number of species in the common and uncommon classes and the fewest in the rare and occasional classes. The Ecuador plot had the greatest number of occasional and rare species as predicted, but the Peru plot, not the Ecuador plot, had the least number of species in the common and uncommon classes.

Both the Peru and Bolivia plots had a regular synchronized fruiting season during the corresponding periods of observation. The Ecuador plot had a relatively asynchronous fruiting pattern. During the extreme dry season on the Peru and Bolivia plots, both plots showed a qualitatively noticeable decrease in the insect abundance; both the seasonality and change in insect and fruit abundance were most extreme on the Peru plot. The Ecuador plot showed little fluctuation or evidence of what Fogden (1972) referred to as the "lean" period. On the Peru plot 89% of the common species foraged at least 30% of the time on fruit; on the Ecuador plot 36% of the common species did so, and only 32% of the common species on the Bolivia plot foraged to this degree on fruit (table 2). Perhaps a difference in the insect and fruit resource permanently above a threshold value had an influence at least partially independent of foliage structure and "normal" processes of equilibration.

TESTING SUSTAINED MAXIMUM NUMBER OF INDIVIDUALS AND BIOMASS PREDICTIONS

For more detailed predictions and generalizations concerning the relation of bird species numbers to foliage structure, quantitative investigations of resource base in the form of general insect and fruit seasonality, specific food preference of each bird species, and microhabitat preference of insect and fruit species are necessary. These detailed investigations, as desirable as they may be, are not within the scope of the present study. This set of predictions will thus switch emphasis to the overall relation of bird individuals and bird biomass to the complexity of the foliage. These predictions will assume that the foliage on each plot is sustaining the maximum amount of individuals and bio-

mass, whether or not the number of species is at equilibrium. This assumption is reasonable since abundances of individual species can change quickly relative to Pleistocene climatic changes.

Role of foliage structure in foraging strategies. A particular type of foliage structure is a strong determinant of the behavior and size of birds capable of successfully foraging in that part of the foliage. Foraging from trunks and large branches by pecking and probing has an obvious influence on the behavioral and morphological characteristics of the type of birds that can use this substrate. It is also obvious that large birds cannot readily forage on small outer branches. The development of characteristics such as long bills in toucans, strong and dexterous feet and bills of parrots, and modification in flight structure of trogons and fruitcrows for hovering are evolutionary adaptations in the larger species to reach some of the smaller branches. Hovering flight in large birds such as trogons and fruitcrows limits them to open areas. Dense areas will also inhibit birds like jacamars, nunbirds, and many flycatchers that sally out after flying insects. The dense foliage will both reduce their ability to see flying insects at a sufficient distance and interfere with pursuit flights. The requirements for maneuverability will also limit the size of salliers. Too large a size would make it difficult to change direction rapidly, but too small a size would make a large proportion of the larger insects unavailable.

Birds that move through the foliage, glean-ing insects from leaves, will be most limited to areas that offer sufficient return in energy for the constant drain on energy this strategy of searching entails. Open areas with few leaves offer reduced insect densities. One would expect gleaners to forage in moderate to dense foliage where large size would be disadvantageous both because of hindrance to mobility and perching on the small twigs common in this type foliage.

Birds that use the strategy of flying out from perches and snatching insects from leaves need fairly dense foliage so that they will see and capture prey often enough to maintain a positive energy balance. Because of the nature of the leaf substrate and the chance that most insects moving on a leaf within the observational and effective flight range of the bird will be small, together with the advantage of maneuverability in dense foliage, there should be selection for small size. This strategy, while enabling them to use insects that are often too

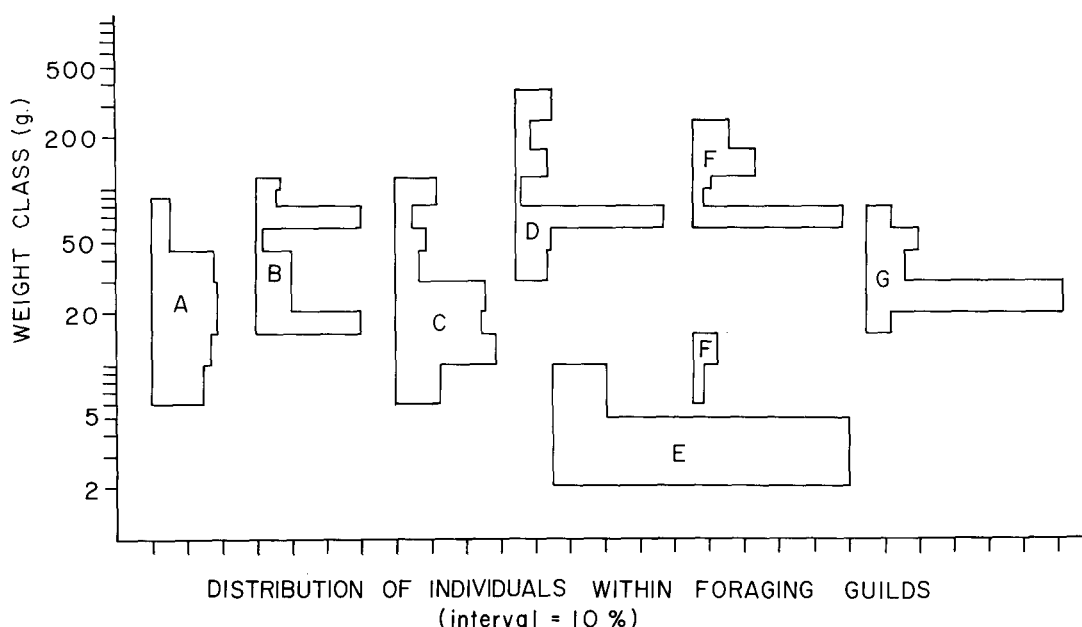


FIGURE 6. Weight class distribution of individuals observed foraging in each of seven guilds (A = insect-gleaning, B = sallying, C = snatching, D = pecking and probing, E = hovering, F = fruit-eating, G = army following). Weight classes with one percent or less representation in a guild are not included.

far out on the underside of leaves for the gleaners to reach, has the disadvantage that the increased metabolic rate typical of smaller size makes the long wait between prey captures especially crucial.

More subtle factors such as consistent or uniform lighting affect some species. Insects flying through alternate light and shaded patches of the forest are probably very difficult for salliers to pursue successfully (Young 1971b). Several southern migrants on the Peru plot sallied in the upper canopy and emergents throughout the day. These migrants and resident species such as *Sirystes sibilator* were the major full-time salliers. They foraged where the light intensity was uniformly high all day long. *Thamnomanes caesioides* is an example of another full-time sallier that operated in uniform light intensity but in the shady portions of the lower strata. Perhaps because these areas of uniform shade all day were relatively uncommon, very few other full-time salliers operated in the lower strata. Ecuador, however, with the greatest cloud cover all year-round of the three plots, supported two species of *Thamnomanes*, both of which were common salliers in the lower strata. Peru had one very rare species of *Thamnomanes* and Bolivia had no species that regularly sallied in the lower strata.

Among the many influences that foliage structure exerts on the morphology and be-

havior of foraging birds, size appears to be especially important. Fig. 6 summarizes the weight class distribution of all individuals using each of seven foraging strategies on the Ecuador plot. Except for the hovering guild that includes only hummingbirds, each of these foraging strategies includes many species of different families. Gleaners feeding on small branches and outer leaves are, as expected, small to medium sized. The salliers are mostly confined to a narrow range of weights between 18–40 g. The larger-sized group of salliers is composed of *Monasa* spp. that also occasionally snatch lizards from ground and trees.

The snatchers tend to fall into three groupings of body size. Only the smallest individuals (8–20 g) follow the expectation, and only the smallest individuals forage on small prey from leaves in dense foliage. Larger birds, such as trogons and fruitcrows, also use this method of foraging, but by using fruit as an alternate food source, they are able to avoid the necessities and disadvantages of small size. These large snatchers can energetically afford to ignore small prey and wait longer for a large prey to move. This latitude in choice of prey size and type releases them from the necessity of foraging in dense foliage and from selection for small body size. The medium-sized snatchers like puffbirds and motmots also fail to follow the prediction for

TABLE 3. Diversity of foraging individuals within nine foraging guilds ($H' = -\sum p_i \ln p_i$ where $p_i =$ proportion of individuals in the i th guild).

	Glean insects	Sally	Snatch	Peck & probe	Flower hover	Fruit	Ant follower	Glean & sally	Glean & snatch	
ECUADOR										
no. of indiv.	2458	509	231	452	46	937	204	26	11	Total = 4874
%	50.4	10.4	4.7	9.3	0.9	19.2	4.2	0.5	0.2	$H' = 1.48$
PERU										
no. of indiv.	966	264	122	304	25	658	38	123	39	Total = 2539
%	38.0	10.4	4.8	11.9	1.0	25.9	1.5	4.8	1.5	$H' = 1.67$
BOLIVIA										
no. of indiv.	693	146	75	145	32	580	75	72	9	Total = 1827
%	37.9	8.0	4.1	7.9	1.7	31.7	4.1	3.9	0.5	$H' = 1.62$

small body size. These birds, however, feed to a great degree by dropping from their perch and snatching prey from the ground or large branches and trunks. Because of the stable nature of these substrates, more larger prey are present than on leaves.

Members of the pecking and probing guild are made up mainly of a narrow size class from 40–70 g; too large a size eliminates the availability of many medium and small branches and trunks, while too small a size reduces the leverage and physical ability to pry out prey from bark and crevices. Ant-followers are concentrated in size between 25–50 g. This size range is likely an evolutionary response to size and types of insects frightened up by the army ants. Also, a small ant-follower would probably be too low in the dominance hierarchy to regularly capture sufficient food (E. O. Willis, pers. comm.).

The weights of the fruit-eating individuals are bimodally distributed. The small-sized individuals are mainly the manakins that hover for the small fruits typical of the dense lower strata; the large-sized individuals are made up mainly of pigeons, parrots, and toucans, all of which feed principally in the canopy. Large size may be advantageous for longer and faster flights by the individuals that feed on fruits in the canopy and are constantly searching for the often distantly-spaced fruiting trees. In addition, exposure to predation may be higher in the upper strata. Large size would reduce the number of potential predators by eliminating the danger from all but the largest predators.

Ecological diversity. If the effect of foliage structure on foraging technique is consistent, then similar foliage complexities should have a similar composition of foraging techniques represented. If each plot is sustaining the maximum number of individuals possible, then

the proportion of foraging individuals, regardless of species, using each of the nine major combinations of foraging techniques or guilds should be similar from plot to plot. The only category that might be expected to differ significantly is the fruit-eating guild. With the greater number of monkeys on the Ecuador and Peru plots and the greater chance for negative interactions associated with the increased numbers, the proportion of fruit-eating birds should be inversely correlated with monkey population size. Table 3 lists for each plot the number and percent observations of the individuals within each of the nine foraging guilds. The similarity from plot to plot of percent distribution within each guild is striking. The most apparent differences are in the percent of fruit-eating and insect-gleaning individuals as anticipated. These differences, however, may be greater than can be attributed to differential monkey populations. A concentrated fruiting season, which coincided with my observation periods on both the Peru and Bolivia plots, probably explains part of the greater number of fruit-eating birds on these two plots. Not only do many typically insect-gleaning individuals temporarily switch a part of their foraging to fruits, but several species of parrots and aracaris moved into the Peru and Bolivia plots in large numbers, mainly from mountains west of the plots. Conservative adjustment to allow for these fruit-eating migrants (15% of all fruit-eating individuals on the Peru plot and 25% on the Bolivia plot) brings the percent of individuals in the fruit-eating category on each plot to values that reflect more accurately the presence of different numbers of monkeys on each plot.

As another test of the relation of foliage complexity to structure of the bird community, I predicted that with similar vertical foliage structure and similar proportion of individuals

TABLE 4. The number of individual birds observed using one of seven foraging techniques in each of seven vertical strata (A = upper canopy and emergents, > 33 m; B = dense upperstory, 26–33 m; C = open area separating midstory and upperstory, 15–26 m; D = dense midstory, 6–15 m; E = open area separating understory and midstory, 2–6 m; F = dense understory, 0–2 m; G = ground).

	Foraging technique						
	glean	sally	snatch	peck/probe	hover	fruit	ant-follower
ECUADOR							
A	208	36	23	26	—	228	—
B	527	129	48	117	1	243	—
C	370	109	37	104	2	172	—
D	262	85	57	92	4	107	5
E	317	99	32	70	24	19	19
F	428	51	34	43	15	22	72
G	346	—	—	—	—	146	108
						Total = 4837	
PERU							
A	145	46	8	32	—	126	—
B	392	121	22	88	1	341	—
C	179	30	23	64	1	106	—
D	59	23	29	35	2	16	3
E	31	17	25	42	6	12	4
F	108	27	15	43	15	—	12
G	52	—	—	—	—	57	19
						Total = 2377	
BOLIVIA							
A	37	7	1	9	—	238	—
B	164	37	15	46	—	184	—
C	167	38	22	35	3	67	—
D	95	34	17	26	5	2	1
E	67	17	15	20	10	5	7
F	111	13	5	9	14	1	29
G	52	—	—	—	—	83	38
						Total = 1746	
Spearman Rank Correlation Coefficient (r_s): * $p < 0.05$; ** $p < 0.01$							
PERU and							
ECUADOR	0.46	0.50	0.84*	0.86*	0.92**	0.96**	1.00**
PERU and							
BOLIVIA	0.57	0.46	0.83*	0.77*	0.87*	0.89**	1.00**
BOLIVIA and							
ECUADOR	0.75*	0.93**	0.74*	0.95**	0.94**	0.82*	1.00**

using each foraging guild, the rank order of individuals using a particular foraging technique in each vertical stratum should be correlated between the three plots. Table 4 indicates that this prediction is generally true. Only the larger numbers of salliers and gleaners in the upper canopy and emergents on the Peru plot are significantly different from the Ecuador and Bolivia plots. The greater representation of salliers and gleaners in the upper strata of the Peru plot is due to the presence of species not well represented on the other two plots. Southern migrants such as *Empidonomus aurantioatrocristatus* and *Pyrocephalus rubinus* as well as permanent residents such as *Tyrannus melancholicus* commonly sallied for insects high in the upper canopy throughout the observation period on the Peru plot.

These species, if present in the general area of the other two plots, occurred only in open pastures or in secondary scrub forest. The greater proportion of gleaners in the upper strata is largely due to the frequent presence of "scrub" species (Pearson 1971) treating emergents and upper canopy as a scrub area. I observed these "scrub" gleaners only rarely in the upper strata of the Ecuador and Bolivia plots where wetter, cooler conditions probably made the upper strata much less similar to secondary "scrub" areas than on the Peru plot.

Biomass comparisons. Since biomass is a much more accurate reflection of energy use than number of species or number of individuals, I made another analysis of the bird

communities at the three plots by comparing the total biomass of foraging birds per hour of observation. The Bolivia plot had the greatest with 673 g per hour of observation, Ecuador second with 540 g per hour of observation, and Peru least with 460 g per hour of observation. No plot had significantly different numbers of large or small species.

One possible explanation for the differences is that the presence of large flocks of locally migrant fruit-eating species on the Bolivia plot raised the biomass above the level typical of the whole year. Recomputing the bird biomass for Bolivia excluding these migrants (principally *Brotogeris cyanoptera*), reduces the biomass of birds seen per hour of observation to 606 g, a value still considerably higher than that for Ecuador or Peru.

Another possibility is that these three plots have different primary productivities and can thus support different amounts of bird biomass. I did not measure primary productivity and cannot test this prediction. However, if productivity is correlated with total precipitation (Holdridge 1967), the Ecuador plot and not the Bolivia plot should have the highest productivity and thus support the greatest biomass.

An alternate hypothesis is that the birds on some plots have more significant competition for resources from non-avian members of the community. The influence of more distantly related organisms like bats, fruit- and insect-eating monkeys, as well as insectivorous lizards and arthropods must be included in any complete exploration of competitive pressure. I frequently watched birds (*Phaethornis* spp., *Threnetes leucurus*, *Pipra fasciicauda*) snatching insects from spider webs. With the myriad of webs present in the forest, spiders harvest a large supply of resource that would otherwise be available to the birds (Young 1971a). In addition, large (15 cm long) pseudostigmatid damselflies frequently snatched captured insects from webs and give further evidence of potentially significant competition. This potential can extend to the plant kingdom. Entomophagous fungi that attack many types of insects were common at some seasons and undoubtedly deprived birds of a considerable proportion of insects (Evans 1974). Differences in the effect of interclass and interphyletic competition between the plots may in part explain the discrepancies in bird species composition and numbers.

The influence of insects was difficult to measure, but there are reasons for believing that their competitive effect was similar on all

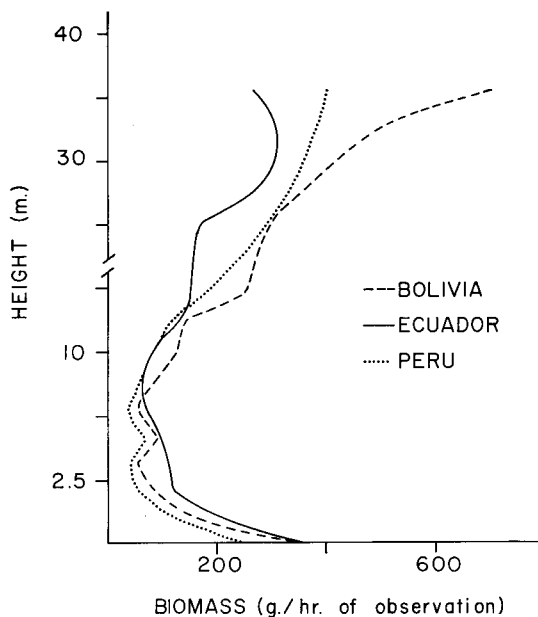


FIGURE 7. Total vertical distribution of bird biomass on each plot (excluding local migrant fruit-eating species).

plots. Predatory insects are most common when insect prey are common and rare when insect prey are rare. In addition, the predatory insects are potential prey for the birds as well as being competitors. Lizards were not common on any of the plots and most of those present rarely occurred above the ground level. Bats were not accurately censused, and thus the mammals most likely to have a measurable effect on the bird communities were the monkeys. If the sum of foraging biomass of monkeys, many of which eat both insects and fruits, combined with the bird biomass was similar on each of the plots, the influence of interclass competition could be inferred. I do not have weights for the different species and age classes of monkeys seen on the plots and must use a more indirect test. Table 1 indicates that excluding the leaf-eating species, *Alouatta seniculus*, monkeys were most common on the Ecuador plot where four species and a total of 250 individuals were present. On the Peru plot, four species and a total of 130 individuals were present. One species and a total of ten individuals were present on the Bolivia plot.

Previously (Pearson 1971), I found that the relative vertical bird biomass distribution followed very closely the vertical foliage distributions, and that the foliage in the upper canopy and the ground supports proportionately more bird biomass than other levels. Large birds on the ground use less energy by

walking rather than flying, and large birds in any stratum generally use less energy per unit weight than small birds (Kendeigh 1972). Also, proportionately more food is available in the form of fruit and associated insects in the canopy and fallen fruits on the ground. First I tested to see if this pattern held true for the different foliage column types within each plot. Fig. 3 shows this pattern to be valid for very differently shaped foliage profiles. Since the monkeys forage principally in the upper strata, I would expect their greater numbers on the Ecuador plot to reduce bird biomass more in the upper strata there than would be the case in the Peru plot. The Bolivia plot should have proportionately the least reduction in bird biomass in the upper strata. Fig. 7 shows that the Ecuador plot does have the lowest amount of bird biomass in the upper strata while Bolivia has the highest.

Thus the difference in bird biomass in the upper strata can probably be attributed largely to the higher biomass of monkeys on the Ecuador plot. The overall comparison of bird biomass observed per hour on the three plots points to the conclusion that the biomass that each plot can carry is partitioned among all potential competitors regardless of their taxonomic affinities. Why this partitioning does not result in a consistent ratio of individuals within a species or species within a class on all plots is likely the result of different historical influences on each plot (Simberloff and Wilson 1969, Haffer 1969).

The combination of monkey and bird biomass, however, does not explain why the total biomass was least for the Peru plot. The bird biomass in the upper strata is as expected; the difference in total biomass between Peru and the other two plots lies mainly in the lower strata. An additional factor in the form of major differences in seasonality and resource availability was apparently important in determining the overall carrying capacity of the plots. Peru, with the most extreme seasonality and a large monkey population, would be expected to have the least total bird biomass. In general, it appears that a certain biomass of monkeys will offset a certain biomass of birds even though no effect can be detected at the level of species richness.

DISCUSSION

Complexity of foliage structure in the form of specific combination of substrate types, dense and open areas, etc., makes predictable evolutionary demands on birds that are successful to use the foliage as refuge, substrate,

and energy supply. Parts of the foliage will have different energy potential to offer the birds, and thus not all portions of the foliage can support equivalent bird biomass per unit volume. With the foliage structure playing a major role in both the total bird biomass supported and its distribution as well as the size and foraging techniques of individuals making up this biomass in different parts of the foliage, it is not surprising that bird communities in these three areas with similar foliage complexity and structure have some similar attributes.

In addition to these similarities, however, are some obvious differences. Total biomass differences can be partially explained by non-avian competitors, but these differences affect only part of the bird community. General differences in both total number of bird species and individuals (Ecuador = 9.9 individuals per hour of observation, Peru = 6.7, and Bolivia = 9.1) are obvious on each plot. As mentioned previously, a major factor that must be considered in this analysis is the series of drastic environmental changes during the recent geological history of the Amazon Basin (Haffer 1969, Vanzolini 1973). The isolated forest refuges during the dry periods were apparently loci for speciation. Upon reconnection of the refuges and resultant interactions between individuals of bird species that had never encountered one another before, some species easily extended their ranges, while others merely managed to maintain themselves in their original refugium, and others were doubtlessly eliminated from all or part of their range.

Simberloff and Wilson (1969) have shown that being in an area first can be competitively advantageous. With this advantage added to the evolutionary restrictions imposed by the structure of the foliage on the ultimate character of the bird community compositions, the general dissimilarity of numbers of bird species and individuals between plots is more easily understood. Each vertical stratum of foliage has a maximum carrying capacity for birds. If the first species into that stratum are at one extreme or the other of an appropriate size range and foraging technique, they will exert a definite influence on the size of the successive birds that will accumulate until the total biomass allocation for the stratum is reached. If monkey species are present early, they will likely have a similar influence on the late-arriving bird species and also affect any equilibrium that takes only birds into account.

If the birds are of similar sizes, the most efficient foraging techniques determined by the characteristics of each stratum should result in a similar number of individuals in each foraging category within corresponding vertical strata on the different plots. The number of species (more rare species or a fewer common species) in each stratum and, thus, for the entire forest is in part dependent on historical factors, and although the number of individuals would be expected to be similar, the species numbers need not be expected to be similar from plot to plot. Except for the combination of extreme seasonality and large monkey population, the Peru plot would probably have had a similar number of total bird individuals to that of Ecuador and Bolivia (ca. 9.0 individuals per hour of observation).

Even if accurate censuses could be made for each bird species on these plots, it is obvious that with the question of equilibrium unanswered a correlation between FHD and BSD (BSR) is not close. What the correlation between foliage complexity and bird diversity does mean in general is that more complex foliage generally provides more, efficient ways of survival and as a result chances for more birds to co-occur in an area. Only in areas where birds compete principally with other birds, where similar foliage structure on different plots presents similar energy availability to the birds, and where historical differences are not extreme, can one expect direct correlation between FHD and BSD (BSR). These factors are likely to be more important in most tropical forests than in temperate zone areas because tropical species are much more sedentary and are hindered or stopped in their dispersal by barriers that are trivial to migratory temperate zone species.

SUMMARY

The relation between the complexity of the foliage and the structure of the bird community was compared on three Amazonian forest plots of similar foliage complexity. Predictions made by assuming equilibrium numbers of species in relation to foliage profile were not supported, and expected correlations between foliage complexity and numbers of bird species were not found. Correlations between total number of individuals and total biomass, however, were found. Similar proportions of individual birds on each plot used the same foraging technique. In corresponding vertical strata, there was a significant correlation between the rank order of number of bird individuals using a specific foraging technique on each plot. The vertical biomass

distribution was different on the three plots and different degrees of interclass competition was a possible explanation for the difference in bird biomass in the upper strata. The overall structure of the bird communities on the plots was mediated by a combination of (1) structural and energetic limitations inherent in the foliage, (2) historical patterns of foliage and bird distribution, and (3) competitive interactions among the birds and with other animals, especially monkeys.

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