

# ECOLOGICAL RELATIONSHIPS OF SMALL ANTIBIRDS IN AMAZONIAN BIRD COMMUNITIES

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**ABSTRACT.**—Seven species of small antbirds were used to test predictions concerning the effects of physical factors in the form of foliage and sunlight and competitive interactions among themselves on three Amazon forest plots. Morphological adaptations of tarsus and wing length showed a correlation to foraging behavior and foliage use. Increased midday sunlight apparently caused a downward movement of the small antbirds. Evolutionary minimization of interactions within the small antbird populations on each plot was inferred from vertical stratification and a complementary cycle of diurnal broadening and narrowing of breadth in substrate and vertical foraging height.—*Department of Zoology, University of Washington, Seattle, Washington 98195. Present address: Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802. Accepted 27 October 1975.*

SOME aspects of theories of diversity, stability, and community structure are most readily tested in the tropics (see MacArthur 1972). Studies of tropical bird communities (Harrison 1962, Orians 1969, Terborgh 1971, Karr 1971, Fogden 1972, Diamond 1973, Lovejoy 1974, Willis 1974, Pearson 1975a, and others) provide a foundation of knowledge upon which some general ecological questions and hypotheses can be formulated. In earlier studies (Pearson 1971, 1975a), I found that the species equilibrium assumption used in much of community structure theory (MacArthur and Wilson 1967, MacArthur et al. 1972, and many others) had little predictive value for the bird species on my study plots. As a result, I dealt primarily with the number and proportion of ecologically similar individuals and the distribution of bird biomass on these plots.

Here I look at the question of why each species uses only a small portion of the forest. I tested predictions from the hypothesis that for any one phenotype, an optimal part of the forest is determined by such factors as branch density, substrate stability, and lighting within which foraging is most efficient. I then tested predictions of behavioral and morphological adaptations that can be interpreted as evolutionary consequences of competition. Because of the large number of variables affecting communities containing hundreds of species, I concentrated on a group of small ecologically similar antbirds (*Myrmotherula* spp. and *Hypocnemis cantator*). These antbirds are good test organisms in that 1) they are limited to a similar and narrowly defined resource, 2) they are restricted in foraging technique, and 3) at least one species was common enough on each study plot to obtain sufficient data.

## METHODS

**Study plots.**—Studies were made in three similar looking 15-ha study plots of lowland primary forest in Amazonian South America. Pearson (1972, 1975b) and O'Neill and Pearson (1974) surveyed the avifauna on each site, including abundance and habitat preference for each species. The localities and periods of observation were as follows:

(1) Limoncocha, Province of Napo, Ecuador (0°24'S, 76°38'W), 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) had a mean annual rainfall of 2978 mm and is classified by Holdridge (1967) as a tropical moist forest. The longest period without rain here during the study period was 9 days in February 1972.

(2) Yarinacocha, Department of Loreto, Peru (8°17'S, 74°37'W), in the east central part of the country near the Ucayali River (el. = 150 m), 15 km northwest of Pucallpa (2 June to 5 September 1972) had a mean annual rainfall of 1625 mm and is classified by Holdridge (1967) as a tropical dry forest. The period

TABLE 1  
MEASUREMENTS OF MORPHOLOGICAL CHARACTERS FOR SPECIES OF THE GENERA *HYPOCNEMIS* AND *MYRMOTHERULA*<sup>1</sup>

	Weight (g)		Culmen Length (mm)	Culmen Width (mm)	Wing Chord (mm)	Tarsus Length (mm)	N
	$\bar{x}$	N	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	
<i>H. cantator</i>	13.5	3	16.8 (0.6)	4.4 (0.2)	54.2 (2.2)	20.1 (0.6)	33
<i>M. axillaris</i>	9.1	7	15.1 (0.4)	3.2 (0.2)	52.9 (2.9)	15.6 (0.6)	41
<i>M. brachyura</i>	7.3	9	14.7 (0.6)	3.1 (0.2)	42.9 (1.7)	16.2 (0.4)	28
<i>M. erythrura</i>	12.4	3	14.9 (0.6)	3.7 (0.2)	51.2 (1.5)	16.0 (0.5)	20
<i>M. hauxwelli</i>	11.1	7	15.1 (0.5)	3.4 (0.2)	51.0 (1.4)	19.5 (0.6)	32
<i>M. menetriesii</i>	9.3	7	15.5 (0.7)	3.3 (0.2)	53.6 (2.4)	15.8 (0.7)	41
<i>M. ornata</i>	9.6	7	15.4 (0.4)	3.9 (0.2)	51.0 (1.7)	16.4 (0.6)	27

<sup>1</sup> Standard deviation in parentheses.

of observation here included the end of one rainy season, an extreme dry season, and the beginning of the next rainy season.

(3) Tumi Chucua, Department of Beni, Bolivia (11°8'S, 66°10'W), 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) had a rainfall pattern similar to that of Yarinacocha but was somewhat wetter (about 1995 mm/year). The annual mean for this site was based on incomplete records over only a 4-year period. My observations were made through the end of the dry season and beginning of the wet season.

**Data gathering.**—A few birds were collected to determine their identities, weights, and stomach contents. To gather observational data, I moved slowly along a roughly circular path, 3 km in length on each plot. For each foraging individual seen, I recorded its species, sex when determinable, time of day, location on the plot, vertical height at which it was foraging, foraging substrate, foraging technique, and food item. Because of the high rainfall at the Ecuador site, I censused only an average of 6 hours per observation day (total = 714 hours of observation). On the Peru and Bolivia plots, I spent 8 hours each observation day for a total of 448 hours and 208 hours, respectively. I censused all daylight hours between 0700 and 1700 by beginning alternate days early and late in the morning.

**Foliage measurement.**—To obtain quantitative measurements of the foliage profile on each plot, I used the MacArthur and Horn (1969) method of leaf density measurement with some modifications, all of which have been described in detail elsewhere (Pearson 1975a). I initially chose the study plots to minimize differences in vegetation structure. The foliage height profiles (Fig. 1) were not significantly different on the three plots ( $p > 0.01$ ; Wilcoxon matched-pairs signed-ranks test).

**Small antbirds as the test group.**—The seven species of small antbirds on the plots were morphologically very similar (Table 1). Stomach contents and field observations indicated that they all fed most frequently on small ( $\leq 1$  cm long) arthropods, mainly spiders and insects (Orthoptera, Lepidoptera larvae, Heteroptera, Hymenoptera, Coleoptera, Diptera). Although Wiley (1971) found that several species of *Myrmotherula* in Panama, including one of the same species as on my plots, regularly foraged by flying out and snatching insects resting on the undersides of leaves, I found, as did Orians (1969) in Costa Rica, that they foraged almost entirely by gleaning.

These antbirds occurred in mixed-species feeding flocks in frequencies from 10.2% of all observations for *M. hauxwelli* to 89.2% of all observations for *M. menetriesii*. Of these mixed species flocks ( $N = 226$ ) only 17.7% had two species of small antbirds, and only 1.6% of mixed species flocks had more than two species. This infrequent occurrence of more than one species of small antbirds in a flock is also in contrast to Wiley's (1971) results, which were made on the abnormally high populations of antwrens at Barro Colorado Island (Morton, pers. comm.).

The antbirds used a variety of foraging substrates and each species foraged in a characteristic vertical range (Fig. 1). Leaves or small inner branches were the major foraging substrate except for two species on the Ecuador plot. *M. ornata* foraged more frequently in tangles of dead leaves and vines and *M. hauxwelli* foraged mainly on the ground or from small vertical stems.

## RESULTS AND DISCUSSION

**Foraging behavior and morphology.**—Complexities and densities of foliage may influence the differences that evolve between populations (guilds) using the same foraging technique. Because of the limitations on body size within a guild (Karr and

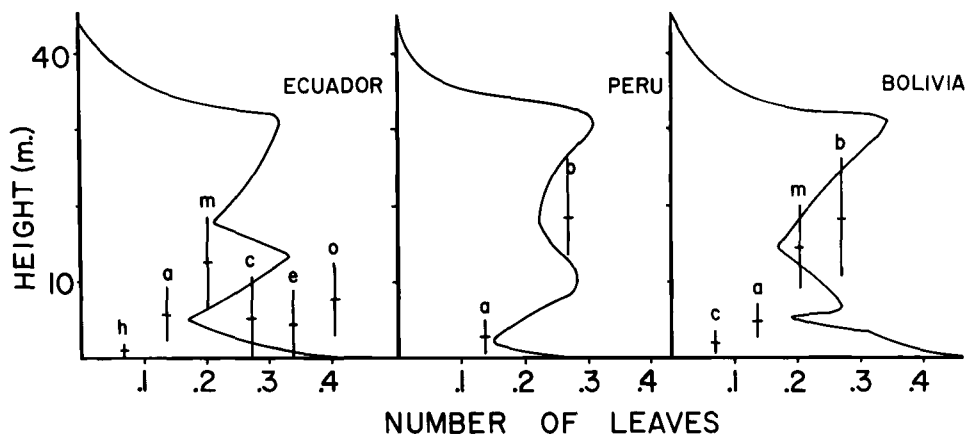


Fig. 1. Standard deviation (vertical line) around the mean (horizontal line) foraging height for species of the genera *Hypocnemis* and *Myrmotherula* (a = *M. axillaris*; b = *M. brachyura*; c = *H. cantator*; e = *M. erythrura*; h = *M. hauxwelli*; m = *M. menetriesii*; o = *M. ornata*) in relation to the average foliage profile on each plot.

James 1975, Pearson 1975a) adaptations to specific substrate conditions can involve additional morphological characteristics. For birds, bill size has been used extensively to test the effects of such adaptations (Vaurie 1951, Schoener 1965), but bill dimensions alone may be inadequate to specify foraging adaptations. For example, wing length (Hamilton 1961, Root 1967) and relative tarsal length (Dilger 1965; Grant 1965, 1966, 1971; Root 1967; Fretwell 1969) influence efficiency of use of various foraging substrates. Individuals may "recognize" their appropriate habitat by a combination of their foraging success dictated by the efficiency of their morphology in different habitats and innate habitat selection mechanisms.

On the basis of foraging characteristics such as foraging substrate density and stability (ground, large branches, twigs, etc.), vertical foraging range, and percent participation in foraging flocks, I predicted morphological characters for the small antbirds (Table 2). For example, individuals that forage on solid substrates such as the ground or large branches should have a longer relative tarsus length than individuals foraging on unstable substrates like small twigs (Grant 1965, 1966). Also, long tarsi should be disadvantageous for foraging in dense tangles regardless of stability of the substrate because the small spacing between twigs and leaves requires a foraging bird to crouch constantly to maneuver among obstacles. Long tarsi would inhibit the crouching movements and increase chances for entanglement.

Wing length as a foraging adaptation is not so well understood as bill or tarsus, but some correlations can be predicted for this group of extremely similarly sized and shaped species. Assuming that longer, narrower wings decrease drag and thus presumably increase flight efficiency, individuals that use a relatively broad vertical range should fly longer distances and have longer wings than those individuals using a narrow vertical range. Mixed-species foraging flocks tend to move rapidly through the forest and considerable flying is necessary to keep up with them. Those species that are most often in these flocks should also have relatively long wings. Those species in which individuals have a relatively short wing should be limited to a narrow vertical range, concentrate their foraging at levels where branch density is high, seldom travel in foraging flocks, and move through the foliage principally by short flights or by hopping from branch to branch in dense foliage.

TABLE 2  
PREDICTED AND ACTUAL DIFFERENCES IN ADAPTIVE MORPHOLOGY OF SEVEN SPECIES OF THE GENERA  
*HYPOCNEMIS* AND *MYRMOTHERULA*

	Relative stability of foraging substrate	Relative density of foraging substrate	Vertical range	Participation in flocks (%)	Predicted (P) and actual (A) morphological characters ( $\bar{x}$ length/ $\bar{x}$ weight) <sup>1</sup>			
					Tarsus		Wing	
					P	A	P	A
<i>H. cantator</i>	medium	open	narrow	68.5	med.	1.5	med.	4.0
<i>M. axillaris</i>	unstable	open	narrow	78.9	short	1.7	long	5.8
<i>M. brachyura</i>	stable	open	broad	65.0	long	2.2	long	5.9
<i>M. erythrura</i>	unstable	dense	narrow	86.3	short	1.3	med.	4.1
<i>M. hauxwelli</i>	stable	open	narrow	10.2	long	1.8	short	4.6
<i>M. menetriesii</i>	unstable	medium	broad	89.2	med.	1.7	long	5.8
<i>M. ornata</i>	unstable	medium	narrow	59.2	med.	1.7	med.	5.3

<sup>1</sup> Spearman Rank Correlation Coefficient ( $r_s$ ) corrected for ties for P and A of each character (\* $P < 0.05$ ). 0.87\* 0.74\*

Using a ratio of wing and tarsus length to body weight for comparisons (Table 2), the relative tarsus lengths were generally as predicted above. The ratios for wing length to body weight appear to follow the predictions except for *H. cantator* and *M. erythrura*, which have relatively shorter wings than expected. A cause for variations for all these morphological characters is that I combined measurements from many different geographical areas. As some of these antbirds forage in different strata and substrates in different regions, geographical variations in morphological characters would be expected but obscured by pooling the data (Willson 1969).

Although the differences in these few characters do not completely explain how the antwren species are adapted to specific portions of the physical structure of the foliage, they do reinforce the hypothesis that complexity of foliage favors differences in morphological characters among species to utilize different parts of the resource spectrum. In addition, measurements of more subtle characters like tail length, tendon width, or muscle arrangement in legs (Richardson 1942) and wings might better show how the foliage foraging substrate is partitioned. Displacement of characters in addition to the bill dimensions has probably been favored in these antwrens because of the relative uniformity of the size distribution of small insects in all parts of the foliage profile, but further studies are needed. Later I will consider whether these data can be used to infer competition.

*Effects of sunlight on foraging behavior.*—Frequent heavy rainfall inhibits foraging activity of many birds (Foster 1974, Leck 1972, pers. obs.), while extended dry sunny periods are associated with reduced numbers of insects (Janzen and Schoener 1968, Janzen 1973) and fruiting trees (Janzen 1967, Frankie et al. 1974). The Ecuador plot had only 3 months of typically intense and frequent rain storms (mid-March to mid-June) and no extended dry periods. The Bolivia plot had 4 months during which rainstorms were frequent (mid-November to mid-March) and also had 2½ months of extended dry sunny periods (June to mid-August). The Peru plot had 6 months of heavy and frequent rainstorms (mid-September to mid-December and February to April) and 4 months of extremely dry and sunny weather (mid-May to mid-September).

Although both extremes adversely affect birds, the extended dry, sunny periods are probably more severe. Not only is the general resource level lowered, but contrasting light-dark patches are more common. This latter factor may affect the foraging efficiency of many diurnal birds. Young (1971) and Papageorgis (1975) have

suggested that the flashing wing color of many tropical butterflies may have evolved because of the inability of birds' eyes to respond rapidly to sudden changes in illumination levels. Sallying birds often lose track of the butterfly when it changes direction between wing flashes.

At any time of the day the upper strata have more light-dark patches than the lower strata, but these patches also increase in frequency toward midday in all strata when sunlight is more likely to reach lower levels. During extended sunny seasons, the birds must often locate, pursue, and capture prey when the forest consists of alternating light and dark patches. Some birds, such as *Bucco capensis*, *Myiornis ecaudatus*, and *Platyrinchus coronatus* that forage by sitting for long periods and snatching prey from the ground or leaves, can choose places with consistent light for watching and be little affected by the midday increase of contrasting light, but sallying species and gleaning species should encounter more dark and light patches toward midday. In addition, gleaners are dependent to a large degree on insects hiding or resting on the underside of leaves. This position of the prey frequently forces the bird to look toward the light in its search, which may increase the effect of the contrast between dark and light patches on the light-adapting abilities of the bird eye.

Associated with the differences in total cloud cover and extended sunny season on the three plots (Ecuador = no sunny period, Peru plot = most extended sunny period, and Bolivia plot = intermediate), I predicted quantitative differences in the behavior of antbirds. The possible means of avoiding the increased dark and light patches include 1) migration from the area, 2) decreasing foraging activity at midday, and 3) moving to lower levels at midday. Though such birds as parrots, pigeons, and toucans make local migratory movements, most tropical forest birds are sedentary. The antbirds on the Peru plot should thus show either the greatest decrease in midday foraging activity or the most significant movement to lower strata at midday or a combination of both. The Ecuador plot should show the least change at midday and the Bolivia plot should be intermediate. In addition, these changes should be greatest in the small antbirds typical of the upper strata on all plots.

Antbirds do not decrease their foraging activity significantly at midday. After 0700 on the Peru plot, the antbirds foraged at about the same level of activity all through the day with only a small decrease from 1100–1300 and another general decline from 1300–1600. Both the Ecuador and Bolivia plots showed a gradual increase in number of foraging individuals until 1100–1200, after which the numbers slowly declined during the afternoon.

The small antbirds on the Peru plot had the greatest difference between mean foraging height at midday and morning and afternoon, those on the Ecuador plot the least difference, and those on the Bolivia plot intermediate differences as predicted. *M. axillaris*, a species occurring commonly on all three plots, showed the most significant difference between morning/afternoon and midday (1.8 and 3.2 m) levels on the Peru plot, less on the Bolivia plot (0.7 and 0.6 m) and no significant difference on the Ecuador plot. The species of the upper strata (*M. brachyura* and *M. menetriesii*) tended to show the greatest movement to lower levels at midday on all three plots. Species that typically foraged near the ground level (*H. cantator* and *M. hauxwelli*) showed no vertical movement at midday.

*Effects of antbird species on each other.*—In more than 1500 hours of observation, I saw only four direct interactions between individuals of different species of small antbirds. These involved short chases within large mixed-species feeding flocks.

Direct interactions consume both time and energy and should be engaged in only when the benefits exceed the costs. If competitors are reducing resource levels in parts of the environment more than in others, then increased foraging efficiency in the less affected spots may be favored. The species differences in morphology and habitat usage can be interpreted as the outcome of selection to reduce negative interactions.

MacArthur (1972) in looking at the relation of overlap to the subdivision of resources predicted that the distance separating the centers of distribution of two species on a resource continuum should be about equal to one standard deviation. As an example, MacArthur (1972) used Terborgh's data on the vertical foraging height segregation of four species of *Myrmotherula* (*M. brachyura*, *M. menetriesii*, *M. axillaris*, and *M. haematonota*) from another Peruvian site. On my plots none of the small antbirds foraged over the entire vertical range of ground to canopy, and the species on each plot tended to forage in separate strata (Fig. 1). For most species, fewer individuals were observed at the extremes of their foraging height distribution than in the center. If, as stomach contents, body size, and field observations indicate, individuals of these species feed on virtually the same range of prey size, competition has likely been the factor favoring vertical segregation.

To determine why the apparent availability of prey items changes with vertical level and to look more critically at MacArthur's (1972) interpretations, I compared the foliage profile and vertical distribution of the antbirds in each plot (Fig. 1). On the Ecuador plot where *H. cantator* was rare and *M. hauxwelli* was common, the former fed higher than in Bolivia and largely in tangles and smaller inner branches. In Bolivia, where the abundance of these two species was reversed, *M. hauxwelli*, now the rare species, occurred in the same low strata and on the same substrate as in Ecuador, but *H. cantator*, a common species here, foraged in the lower strata and to a large degree on the preferred substrate of *M. hauxwelli*, small vertical stems and forest floor. Probably because this stratum had a greater vertical range in Bolivia, *H. cantator* also had a wider vertical range in this habitat than *M. hauxwelli* in Ecuador. *H. cantator* was uncommon in Ecuador and foraged in both the dense understory stratum and lower part of the dense midstory but not in the intervening open area. *M. axillaris* was most common vertically in the open area separating the dense understory and dense midstory strata. In Bolivia and Ecuador, this open area was at about 5 m while in Peru it was at 3 m. *M. axillaris* adjusted its most commonly used foraging height interval accordingly. *M. menetriesii* and *M. brachyura* had the greatest vertical range of all the antwrens but did not include the area below the dense midstory. This extensive vertical range may reflect the relative uniformity of the foliage within the upper levels (Orians 1969) and indicate that the open area separating upper- and midstory dense foliage strata is much less important to the birds than the open area separating under- and midstories. Both *M. erythrura* and *M. ornata* occurred only on the Ecuador plot where they foraged largely in tangles of dead leaves and vines. This association is reflected in their commonly feeding immediately above and below the open area separating under- and midstories but rarely or not at all in the open area itself.

Except for the bimodal vertical distribution of *M. erythrura* and *M. ornata* on the Ecuador plot, the means for all the species were well within either an open or dense stratum, and their standard deviations extended approximately to the limits of that stratum. Thus whether or not competition has favored differences in bill size and prey size, each antwren primarily occupied a distinct substrate zone. MacAr-

thur's theoretical model may offer an adequate explanation of the situation, the deviations resulting from the nonuniformity of the foliage in this and Terborgh's study. On the other hand, the physical structure of the foliage may have determined how specialized an individual could become and still have sufficient space in which to find adequate resources.

That species are found most commonly in a specific physical habitat where vertical range is delimited by the differential physiognomy of the foliage (see Horn 1971) indicates that the birds are sensitive to subtle changes in the vertical structure of vegetation. It also suggests that if a species is specialized to forage most efficiently on a particular substrate, individuals would become less efficient as they approached the vertical limits of that substrate, thus explaining why one species did not occur from ground to canopy.

Both vertical foraging height and foraging substrate differences are important in determining differences in resource utilization by small antbirds (see May 1975). As there are diurnal shifts in mean vertical foraging height, vertical segregation is less pronounced at some times of the day, which might lead to increased competition unless segregation in another dimension, such as foraging substrate, increases at the same time.

Using foraging height diversity or breadth ( $H'_h = -\sum p_i \ln p_i$  where  $p_i$  = proportion of individuals in the  $i$ th height interval) and foraging substrate diversity or breadth ( $H'_s = -\sum p_i \ln p_i$  where  $p_i$  = proportion of individuals in the  $i$ th substrate type), I tested the following predictions by comparing the difference in  $H'_h$  and the difference in  $H'_s$  for each species between morning (0700–1059) and midday (1100–1359) and the difference between midday and afternoon (1400–1700) on each plot:

(1) If competition is not important, there should be a positive correlation between the direction of change in breadth of the two dimensions. For example, if vertical foraging height diversity increases, the chance of encountering and using a greater range of appropriate substrate types also increases, and vice versa.

(2) If competition is important, there should be a negative correlation between the direction of change in breadth along the two dimensions. The restrictions imposed by a narrower range in one dimension could be offset by a broadening in the other dimension. The degree of this concomitant change would be modified from species to species by the degree of morphological specialization to types of substrates and height intervals.

Except for three cases, there was a general negative correlation between  $H'_h$  and  $H'_s$  differences ( $X^2$ ;  $p < 0.01$ ) and none of the antbirds showed a simultaneous increase in  $H'_h$  and  $H'_s$  (Fig. 2). It is interesting to note that two of the three exceptions (quadrant III in Fig. 2), *M. hauxwelli* on the Ecuador plot and *H. cantator* on the Bolivia plot, were earlier described as essentially replacing one another on these two plots. These two species tend to decrease  $H'_h$  by spending more time on the ground, which reduces the number of available substrate types more severely than for the other antbirds, decreasing  $H'_h$  by a similar value above the ground.

#### DIRECTION FOR FUTURE STUDIES

With the high diversity and many possible combinations of subtle interactions in tropical lowland forest, preliminary generalizations as presented here must rely on many assumptions and exclude potentially important factors as yet unmeasured. One of the most important conclusions of this study of small antbirds rests on the assump-

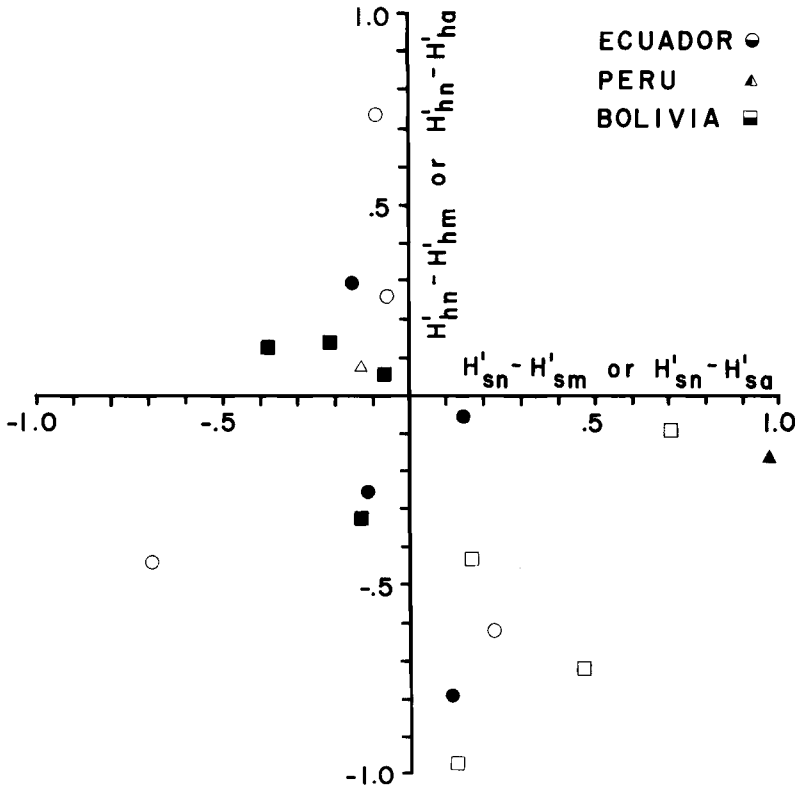


Fig. 2. Correlation of the differences between vertical foraging height diversity ( $H'_h = -\sum p_i \ln p_i$  where  $p_i$  = proportion of individuals in the  $i$ th height interval) and substrate diversity ( $H'_s$  where  $p_i$  = proportion of individuals in the  $i$ th substrate class) between morning (0700-1059) and midday (1100-1359; solid symbols) and between midday and afternoon (1400-1700; open symbols) for species of the genera *Hypocnemis* and *Myrmotherula*. Subscript m = morning; n = midday; a = afternoon.

tion of the evolutionary importance of competition. Comparing concomitant changes in two of the most important antbird dimensions (Fig. 2) approaches testing the assumption of competition itself. The results provide reassuring evidence that this assumption is probably valid.

Other assumptions and important factors must be faced in future investigations. 1) The diurnal vertical movement of birds may be totally or in part a response to vertical movements of insects. 2) The resources used by antbirds also support other bird species as well as individuals in non-avian taxa. 3) Another factor not assessed is the effect of predation on the bird community structure. Bird-eating snakes and hawks were regular on the plots, and their presence elicited conspicuous behavioral responses on the part of the small birds (mobbing or freezing in position). In 1500 hours of observation I saw only three active pursuits by predators, none of them successful. Obviously these predators influence the evolution of the birds and their ecological relations, and the difficulty of measuring this influence or its results must be overcome. 4) The problem of measuring quantity and spatial distribution of base resources within the context of diurnal and seasonal changes must be undertaken. 5) More accurate data on the range and types of resources that each bird species exploits are necessary. Differences in foraging behavior between sexes and between individu-



als of the same species in different parts of the range should also prove to be important in refining these theories. In addition, foraging efficiency should be measured for each species in a continuum of optimal to suboptimal parts of the forest. Some other promising approaches include further geographical comparisons. For example, the relation of foliage and climate as well as the influence of biotic interactions could be tested in Amazonian sites with different foliage structure, trees species diversity, and seasonal variation. Application of these theories to bird communities in Old World tropical lowland forests could also be undertaken to provide rigorous tests and to help establish their generality.

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