

VERTICAL STRATIFICATION OF BIRDS IN A TROPICAL DRY FOREST

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Various studies of tropical ecology have included investigation of vertical stratification of both plants and animals, but few of these studies have made precise measurements of the vertical distribution of the organisms being studied. The purpose of this paper is to clarify the role of vertical stratification in relation to birds through the use of quantitative measurements. Stratification as used in this paper does not imply the presence of discrete layers of vegetation, each containing its own distinct and unique fauna. Stratification refers here to the distribution of bird species in relation to the vertical distribution of the foliage.

Among the terrestrial animals in which stratification has been investigated are the leaf hoppers (Adams 1941), mosquitoes (Bates 1944; Snow 1955; Haddow et al. 1964), ants (Wilson 1959), spiders (Gibson 1947), various arthropods (Fichter 1939), and mammals (Harrison 1962; Napier 1966). Because of their extreme vertical mobility, birds are especially sensitive to vertical stratification of vegetation and, because of their size and activity, lend themselves well to observation. Studies of bird stratification have been conducted in relation to morphological adaptations (Dilger 1956), social patterns (Moynihan 1962), nest site (Turček 1951), territory maintenance (Kendeigh 1947), predator avoidance (Dunlavy 1935), and food (Colquhoun and Morley 1943; Hartley 1953; Slud 1960; Pielowski 1961; Harrison 1962). Recent studies of species diversity (MacArthur et al. 1962; MacArthur 1964; MacArthur et al. 1966; Recher 1969) have also been concerned with vertical stratification of birds.

This investigation was undertaken to answer a series of questions concerning the vertical distribution of birds. First, how is the vertical foliage distribution related to the distribution of bird species, what factors affect this relationship, and how do these operate? Second, regarding the individual bird species, what differences in both foliage distribution and bird species make such zonation possible or mandatory? Finally, how stable over time

and season is the observed vertical stratification?

This study was carried out from June to August 1968 in central eastern Perú, Departamento Loreto, 20 km NW of Pucallpa, at Yarinacocha, base of the Instituto Lingüístico de Verano. This area of the Amazon basin lies at the north end of a belt of low rainfall that extends for about 300 km to the south-east and averages 80 km in width. It is classified by Holdridge (1967) as tropical dry forest. The average monthly rainfall totals for 1956–1963 at Yarinacocha are shown in figure 1 (mean annual rainfall = 1523 mm). During the study period, rainfall in excess of 3.5 cm occurred on only five dates: 15 June, 20 July, 6 August, 12 August, and 19 August. On all other days there was either no rainfall or only local, transitory showers lasting less than 20 min. The average monthly mean temperatures range from 21 to 24°C. The annual extreme temperatures are 15 and 37°C, both of which were recorded during the study period.

METHODS OF STUDY

I selected a 9-ha area of relatively uniform, primary forest in terrain of gently rolling hills 2 km S of Yarinacocha. By using existing survey paths or cutting new paths, boundaries were set up and access provided to the interior of the plot.

The top of the canopy averaged 25 m in height, with emergent trees rising to 40 m. A zone of primary forest 5 km wide bordered the eastern and southern boundaries, another 15 km wide bordered the northern boundary, and extensively cleared areas approached within 1 km of the west side of the study tract. A 2000-m² area of 2–4-m high secondary growth was present in the northwest corner of the study tract. This area had been created by a tree fall during a storm in April 1967. A narrow stream bed extended from the northeast corner to the southwest corner. The stream banks were 1–3 m high, but the bed contained only isolated pools of water during the study period. The study tract was approximately 200 m above sea level and 15 m above flood level.

A modification of MacArthur and MacArthur's (1961) grid method was used to determine the relative foliage density at different heights. Black lines 1 cm wide delineated nine equal squares on a white board (30 × 30 cm). My assistants first held the grid at ground level and moved it away from me until only three squares were not obscured by the

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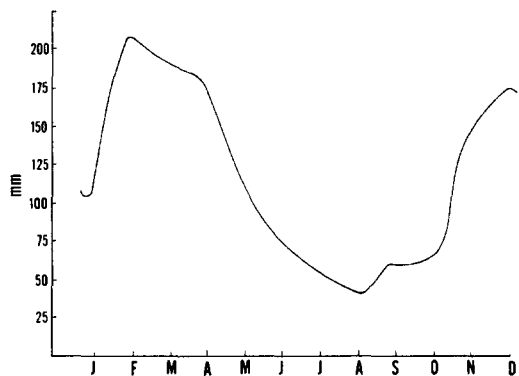


FIGURE 1. Average monthly rainfall at Yarinacocha, Perú.

foliage. This distance was then measured. The grid was raised successively to 0.3 m, 1.5 m, 3.0 m, and then at 3.0 m intervals to the canopy, and the distance at which just three of the grid squares were visible was measured or estimated at each height. Precautions were taken to avoid trampling down the vegetation in the path of vision along which we sighted. At higher levels, tree climbing made the measurements tactically difficult. Figure 2 shows the resultant foliage profile and represents an average of surveys taken to the canopy at three points, and to a height of 20 m at 15 points. These points were arbitrarily selected on a map of the study tract; the direction of the sightings were chosen by throwing a pointed stick into the air and letting it fall on the ground.

In the period 12 June–22 August 1968, I conducted 35 eight-hour surveys of the tract. I began these surveys alternately at 06:00 and 08:00 and, over the course of the study period, included all daylight hours except 16:00–18:00. Each survey consisted of moving slowly along the perimeter and interior paths and stopping for various lengths of time at various places. For each observation I recorded the time of day, the species or approximate size class, and the flock associations. Birds involved in nonforaging activities were not included. Estimates of bird heights in the foliage were probably accurate to ± 10 per cent.

Low-feeding birds (0–3 m) were extremely difficult to observe. To help offset this disadvantage, I strung 10 mist nets through the tract and checked them every 2 hr. While the catches represented a valuable addition to my limited visual observations at these levels, they revealed only the approximate height at which the birds were moving, gave no indication of feeding activity, and provided no more than a rough index of the time of activity. Another method that facilitated the observation of these low-level birds was simply to sit in one place for several hours and permit feeding activity to go on around me without scaring the birds to nonfeeding levels.

Table 1 lists all species observed on the study tract during the study period. The similarity between the bird species present in this area (see Traylor 1958) and those listed for Surinam by Haverschmidt (1968) reflects the uniformity of habitat of Amazonia. Since 65 per cent of the species identified on the study tract also occur in Surinam, similar results would probably be obtained over much of the Amazon basin.

VERTICAL DISTRIBUTION OF THE BIRD COMMUNITY

Figure 2 shows the relative vertical distribution of all individuals observed during the study period. Levels at 2 m and 25 m are utilized most, while the ground and the zone between 5 m and 10 m are least utilized. Birds at the low levels (0–2 m) present special problems, and are probably underrepresented in the survey for the following reasons. First, some birds perch in low branches but fly to the ground for food. *Gymnopithys lunulata*, *Phlegopsis nigromaculata*, *Dendrocincla merula*, and *D. fuliginosa* capture about 90 per cent of their food on the ground but fly to it from higher perches (E. O. Willis, pers. comm.). Second, in walking through the area, I scared up many birds before I could see where they were feeding. Although *Myrmeciza melanocephala* and *Myrmoborus myotherinus* obtain almost all their food on the ground, I most often saw them 50 cm or more above the ground. Third, many ground species are very timid and difficult to see. Mainly because of their timidity, the species of the genera *Crypturellus*, *Odontophorus*, *Aramides*, and *Dichrozona* were undoubtedly much more common than my records indicate. Several species would never have revealed their presence on the study tract at all, had not individuals blundered into the mist nets. Several other species would not have been observed feeding on the ground if I had not remained motionless in one location for several hours.

A comparison of the vertical distribution profiles of birds with that of the foliage reveals a similar trend at all levels except ground and canopy and indicates a direct correlation between relative foliage density and the number of feeding individuals. Because biomass is a more accurate reflection of energy utilization, I have also calculated from the average weight of each species a profile of the total vertical distribution of avian biomass over the length of the study period (fig. 2). This biomass profile resembles the profile of numbers of individuals at all intervals except the ground, where only the former profile parallels the foliage density profile.

The inverse correlation between the distribution of birds by numbers and by biomass at the ground level is due to the greater average weight of the terrestrial species (table 2). The vertical intervals with the next greatest average weights are in the more open areas of the upper canopy above 30 m and in the open area of subcanopy between 5 m and 10 m. These weight distributions may be directly

TABLE 1. Bird species present on the study tract, their mean weight, and the vertical foraging distribution of the most common species.

Species ^a	Weight \bar{x} g	% observations stratum ^b					Vertical foraging distributions ^c			
		I	II	III	IV	V	H'_c	n_c	H'_t	N
<i>Crypturellus cinereus</i>	529					100				
<i>Penelope jacquacu</i>	100									
<i>Odontophorus stellatus</i>	270					100				
<i>Aramides cajanea</i>	422					100				
<i>Columba plumbea</i>	177	16	79	5			.7492	20	.7141	53
<i>Brotogeris cyanopectera</i>	73	78	22				.5599	20	.5901	77
<i>Pionites melanocephala</i>	149	61	34	5			.6394	30	.6739	130
<i>Amazona farinosa</i>	687	81	19				.5512	20	.5376	36
<i>Piaya cayana</i>	99	5	50	35	10		.6883	20	.6913	27
<i>Piaya melanogaster</i>	104	12	84			4	.5732	20	.5695	24
<i>Phaethornis hispidus</i>	4									
<i>Phaethornis philippi</i>	5									
<i>Phaethornis longuemareus</i>	4									
<i>Hylocharis cyanus</i>	3									
<i>Trogon viridis</i>	85	5	74	14	7		.5592	50	.6180	87
<i>Trogon curucui</i>	61	3	73	24			.5038	30	.5012	42
<i>Trogon violaceus</i>	48									
<i>Momotus momota</i>	126									
<i>Galbula cyanescens</i>	24									
<i>Notharchus macrorhynchus</i>	90									
<i>Monasa nigrifrons</i> *	83									
<i>Chelidoptera tenebrosa</i> *	36									
<i>Capito niger</i>	54	24	56	12	8		.8300	40	.8471	65
<i>Pteroglossus castanotis</i>	258									
<i>Pteroglossus mariae</i>	151									
<i>Pteroglossus beauharnaesii</i>	235	44	44	10	2		.7851	30	.7940	56
<i>Ramphastos culminatus</i>	482									
<i>Ramphastos cuvieri</i>	737									
<i>Celeus</i> sp.	150									
<i>Melanerpes cruentatus</i>	53	67	33				.5356	30	.5458	63
<i>Veniliornis affinis</i>	37									
<i>Campephilus melanoleucos</i>	239									
<i>Campephilus rubricollis</i>	223	8	45	39	8		.7678	20	.7859	34
<i>Dendrocincla fuliginosa</i>	37									
<i>Dendrocincla merula</i>	46									
<i>Glyphorhynchus spirurus</i>	12			4	96		.5261	20	.5438	33
<i>Dendrozetetes rufigula</i>	69									
<i>Dendrocolaptes certhia</i>	67									
<i>Xiphorhynchus spixii</i>	35									
<i>Synallaxis rutilans</i>	18				86	14	.5497	10	.5791	27
<i>Automolus infuscatus</i>	20									
<i>Thamnophilus aethiops</i>	27									
<i>Thamnophilus schistaceus</i>	20									
<i>Pygiptila stellaris</i>	24			84	16		.5057	10	.5150	19
<i>Myrmotherula axillaris</i>	9				71	29	.6424	20	.6543	32
<i>Dichrozona cincta</i>	14									
<i>Cercomacra cinerascens</i>	17			60	40		.5301	10	.5433	21
<i>Myrmoborus myotherinus</i>	20									
<i>Myrmeciza hemimelaena</i>	16			36	64		.2831	10	.2943	20
<i>Myrmeciza hyperythra</i>	38									
<i>Myrmeciza melanoceps</i>	30									
<i>Gymnophis lunulata</i>	25									
<i>Phlegopsis nigromaculata</i>	48									
<i>Attila spadiceus</i>	29									
<i>Lipaugus vociferans</i>	85	3	40	54	3		.8532	30	.8745	48
<i>Pachyramphus polychopterus</i>	19									
<i>Pachyramphus marginatus</i>	18									
<i>Tituya semifasciata</i>	83	83	17				.5395	30	.5539	43
<i>Querula purpurata</i>	103	72	25	3			.5205	20	.5895	133

^a "Scrub" species indicated by *.^b Strata: I, upper canopy and emergents (25–40 m); II, remainder of canopy to lower extremes of tree crowns making up canopy (12–25 m); III, subcanopy (7–12 m); IV, dense low shrubs (0–7 m); V, ground level.^c H'_c = the upper limit of the first interval in which cumulative foraging height diversity does not increase more than .02 per 10 observations; n_c = number of observations necessary to reach H'_c ; H'_t = foraging height diversity based on the total number of observations for a species; N = total number of observations. All calculations based on 12 strata.

TABLE 1. Continued.

Species ^a	Weight \bar{x} g	% observations stratum ^b					Vertical foraging distributions ^c			
		I	II	III	IV	V	H' ^e	n ^e	H' ^t	N
<i>Gymnoderus foetidus</i>	256									
<i>Pipra fasciicauda</i>	18									
<i>Pipra pipra</i>	9									
<i>Pipra coronata</i>	9									
<i>Machaeropterus pyrocephalus</i>	8									
<i>Machaeropterus regulus</i>	10									
<i>Pyrocephalus rubinus</i> *	13									
<i>Tyrannus melancholicus</i>	41	76	24				.5685	20	.5466	46
<i>Myiodynastes maculatus</i>	47	21	47	22	10		.8296	40	.8598	74
<i>Sirystes sibilator</i>	32									
<i>Megarhynchus pitangua</i>	60	69	31				.5134	20	.5044	33
<i>Myiozetetes</i> sp.	35									
<i>Myiarchus ferox</i>	29									
<i>Empidonax euleri</i>	12									
<i>Terenotriccus erythrurus</i>	6									
<i>Cnipodectes subbrunneus</i>	19				100		.3617	10	.3689	49
<i>Tolmomyias assimilis</i>	14									
<i>Ramphotrigon ruficauda</i>	17									
<i>Todirostrum chrysocrotaphum</i>	8									
<i>Lophotriccus vitiensis</i>	6		6	11	83		.2266	10	.2250	27
<i>Elaenia spectabilis</i>	25									
<i>Pipromorpha oleaginea</i>	11									
<i>Microcerculus marginatus</i>	18					100				
<i>Turdus ignobilis</i> *	57									
<i>Turdus</i> sp.	70									
<i>Vireo olivaceus</i>	12									
<i>Psarocolius decumanus</i>	221									
<i>Gymnostinops yuracares</i>	287									
<i>Cacicus cela</i>	96	34	66				.5798	30	.5627	267
<i>Dacnis cayana</i>	12	32	62	6			.7151	30	.7692	52
<i>Euphonia</i> sp.	10									
<i>Euphonia chrysopasta</i>	11									
<i>Tangara velia</i>	21	52	24	24			.4472	20	.4704	36
<i>Tangara chilensis</i>	24	66	34				.5024	20	.4670	164
<i>Tangara xanthogastra</i>	14									
<i>Tangara mexicana</i>	21									
<i>Thraupis palmarum</i> *	37	59	34	7			.6928	40	.7424	129
<i>Ramphocelus carbo</i> *	27	11	34	40	15		.9079	80	.9455	102
<i>Tachyphonus rufiventer</i>	19	24	69	7			.6306	20	.6508	31
<i>Hemithraupis flavicollis</i>	14									
<i>Cissopis leveriana</i> *	77									
<i>Saltator maximus</i> *	41									

TABLE 2. Average weights of individual birds found at successive vertical intervals.

H. (m)	W. (g)
0	210
1	19
2	24
4	25
6	40
8	80
10	70
15	73
20	58
25	70
30	115
35	55

related to the physical support the different levels afford. The ground can support heavy species of such genera as *Odontophorus* and *Crypturellus*. The upper canopy and immediate subcanopy levels are made up of many large branches and can also support large species. The dense levels around 20 m, however, not only have smaller branches incapable of supporting these species, but the density of the foliage prevents larger birds from sallying or snatching prey on the wing in this area.

Another reason for the low correlation between the foliage density profile and the two profiles representing the vertical bird distribution (fig. 2) at canopy and emergent levels, may be the resource supply. Leaves at the upper levels are usually photosynthesizing at

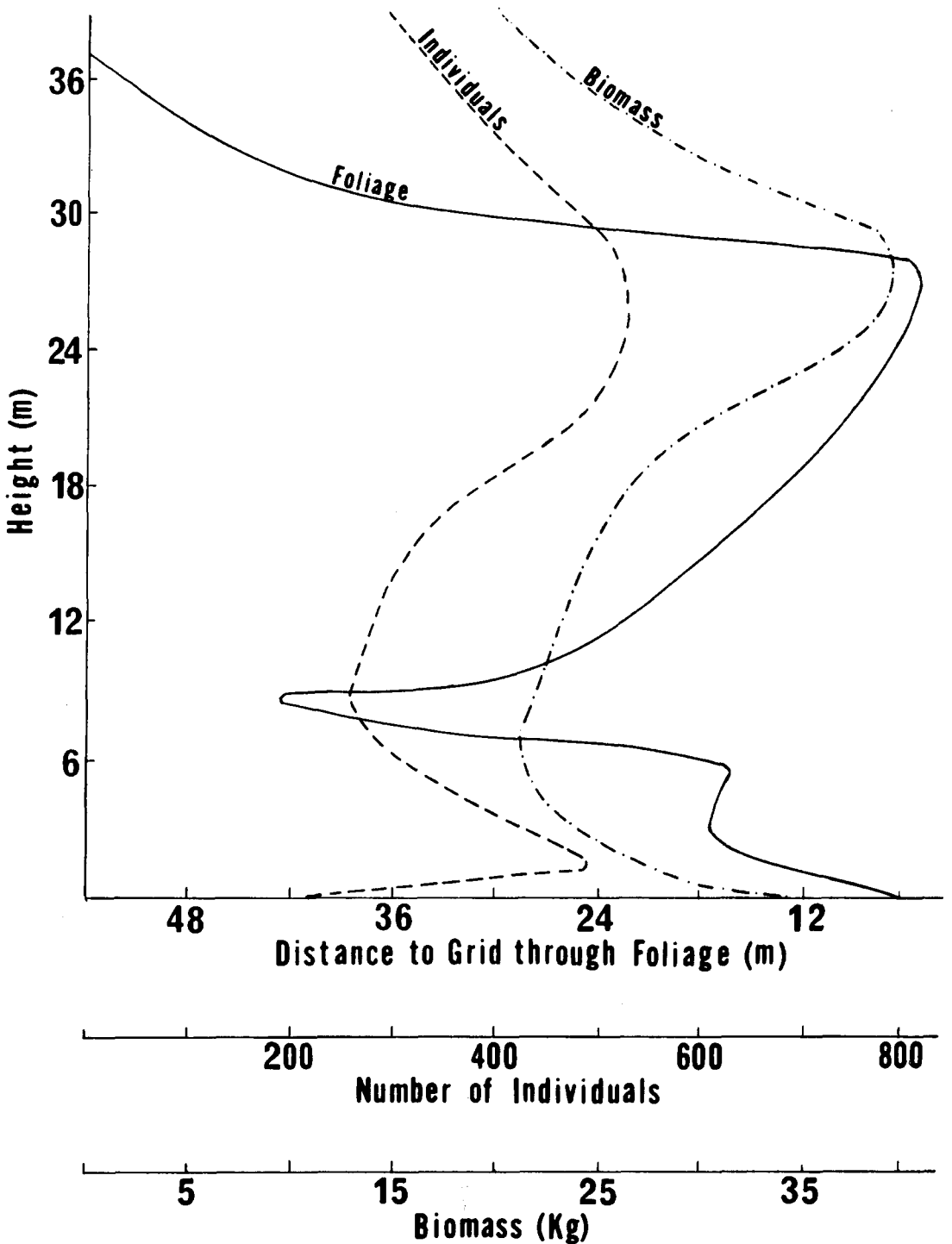


FIGURE 2. Vertical distribution of the total individual birds and biomass in relation to the vertical distribution of the foliage (determined by measuring the distance horizontally at which six of nine 10×10 mm squares on a 30×30 mm grid were obscured by the foliage).

maximum rates while the lower leaves probably operate close to the compensation point most of the time (Evans 1939). Therefore less energy per unit leaf area is being incor-

porated at lower levels in the forest. Successive levels, then, present a gradient of energy availability. Nonetheless, a large biomass can be supported on the ground level despite the

low sunlight because the majority of terrestrial species are vegetarian and expend little energy foraging in comparison to species in the upper levels. In other words, the amount of energy necessary to maintain 1 g of biomass on the ground may be considerably less than that needed to maintain 1 g of biomass in the air as the bird flies within the foliage. Furthermore, packets of extremely high energy content are easily accessible to these terrestrial species in the form of fallen fruit and seeds which often accumulate abundantly on the ground.

VERTICAL STRATIFICATION OF SPECIES

On the basis of foliage density and bird individual and biomass profiles, I arbitrarily selected five vertical strata: (I) upper canopy and emergents (25–40 m), (II) the remainder of the canopy to the lower extremes of the tree crowns making up the canopy (12–25 m), (III) subcanopy, consisting characteristically of many open spaces and low leaf density (7–12 m), (IV) dense low shrubs (0–7 m), and (V) ground level.

The bird species observed most frequently and the proportion of the times they were observed feeding in each of the strata are listed in table 1. The fact that not one of these 37 species was observed feeding in all five strata and only eight were observed feeding in four of the five strata suggests that there is a limited vertical distribution of some species. All eight of the most ubiquitous species are among the 25 most commonly observed. This might indicate that, given a sufficiently large sample, one might find almost all species at least occasionally visiting all strata.

The testing of this possibility obviously required the use of more finely divided strata. I chose 12 vertical intervals (ground, ground–1 m, 1–2 m, then 2-m intervals to 10 m, and 5-m intervals to the canopy), and, using the information theory (Shannon 1948), I calculated foraging height diversity (H') for each of the species ($H' = -\sum p_i \log p_i$, where p_i = the proportion of observations in the i th foliage height interval). If all species occur in all strata, however, values for foraging height diversity will be underestimated for the less common species. To determine the minimum number of observations necessary for a reasonably accurate H' value, I calculated cumulative foraging height diversities for several species. *Cacicus cela* and *Tangara chilensis*

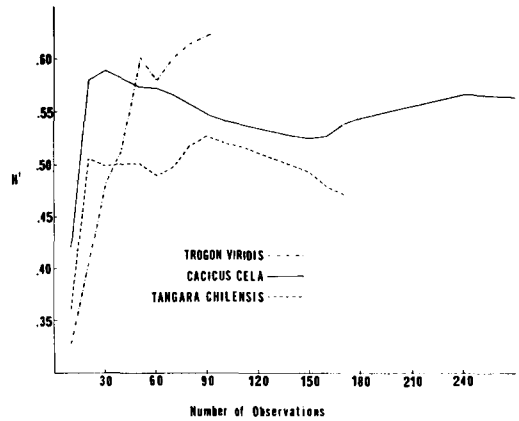


FIGURE 3. Cumulative foraging height diversity (H') for *Trogon viridis*, *Cacicus cela*, and *Tangara chilensis*.

represent species with a relatively limited vertical range. An accumulation beyond 30 observations in the case of *C. cela* and beyond 20 observations in the case of *T. chilensis* did not significantly improve the accuracy of the calculated foraging height diversity (fig. 3). *Trogon viridis*, on the other hand, represents a species with a wide vertical range and only after 50 observations did the cumulative H' become roughly constant. To determine the minimum number of observations beyond which foraging height diversity does not significantly increase, I used as a rough criterion the end of the first interval in which H' increased no more than .02 per ten observations (H'_c). The H'_c values for all species on the study tract to which this criterion could be applied and the number of observations (n_c) to reach this point are included in table 1. H'_t (the foraging height diversity based on the total number of observations of a species during the study period) is also included in table 1 as a comparison. These results support the hypothesis that many birds do distinguish vertical foraging areas.

One group of birds in particular seemed not to show any stratification. These were the so-called "scrub" or edge birds that were common in the brushy clearings and edge of the forest but occasionally turned up far back in the forest at canopy and emergent levels. Their feeding activity did not remain constant relative to fixed heights above the ground, but instead seemed to follow any area of direct exposure to light; thus they apparently treated the upper canopy and emergent trees as a "scrub" area as well. The species that appear to qualify for this classification are indicated in table 1.

TABLE 3. Some mixed species feeding flock (m.s.f.f.) members and their foraging heights.

Species	% observ. in m.s.f.f.	Foraging height (\bar{x} m)		diff.
		in m.s.f.f.	not in m.s.f.f.	
<i>Brotheris cyanoptera</i>	12	27	26	1
<i>Pionites melanocephala</i>	10	26	22	4
<i>Piaya cayana</i>	69	10	21	-11
<i>Piaya melanogaster</i>	35	23	13	10
<i>Trogon viridis</i>	9	24	13	11
<i>Capito niger</i>	36	23	15	8
<i>Pteroglossus beauharnaesii</i>	24	28	23	5
<i>Melanerpes cruentatus</i>	38	28	25	3
<i>Pygiptila stellaris</i>	12	14	9	5
<i>Lipaugus vociferans</i>	15	18	11	7
<i>Tityra semifasciata</i>	61	29	19	10
<i>Querula purpurata</i>	17	28	25	3
<i>Tyrannus melancholicus</i>	40	34	28	6
<i>Myiodynastes maculatus</i>	28	23	11	12
<i>Megarhynchus pitangua</i>	14	32	28	4
<i>Cacicus cela</i>	16	26	24	2
<i>Dacnis cayana</i>	81	26	14	12
<i>Tangara chilensis</i>	93	33	29	4
<i>Tangara mexicana</i>	78	28	24	4
<i>Thraupis palmarum</i>	81	29	24	5
<i>Ramphocelus carbo</i>	41	22	11	11

Similarly I found, as did Orians (1969) in Costa Rica, that many of the upper canopy species, such as *Tangara velia*, *Dacnis cayana*, and *Euphonia chrysopasta*, forage over a wide vertical range and often occur in clearings or tree falls where small successional vegetation is present. Orians (1969) suggests that the lighting characteristics of the canopy present a uniform foraging surface for birds regardless of how irregular the canopy may be. However, if the lighting characteristics are equating open areas, no matter if they are high or low, there would be no way to distinguish between canopy species and "scrub" species. My observations show that only *Tyrannus melancholicus* occurred nearly as often in both canopy and low successional areas. All other open-area species were observed predominantly in either canopy or low scrub and only occasionally in the alternate area. It is obvious that lighting characteristics are not the only factor involved here.

MIXED SPECIES FEEDING FLOCKS

Mixed species feeding flocks also have a definite influence on the vertical distribution of species. Of the 46 most commonly observed species in the study area, all but 14 occurred in mixed species feeding flocks at one time or another. Table 3 lists the percentage of

times that some of the more commonly flocking species were observed in mixed species feeding flocks, the average height at which each fed while in the flock, and the average height when not in the flock.

In every case except that of *Piaya cayana*, birds were observed higher when in a mixed species feeding flock than when not. The overall average is 24.7 per cent higher for birds in mixed species feeding flocks. The Wilcoxon matched-pairs signed-ranks test shows these differences in heights of species in flocks and out of flocks to be highly significant. Willis (1960), in his study of two species of ant tanagers, also found that individuals of one of the species, *Habia rubica*, often ascended into higher levels to join mixed species feeding flocks. Perhaps most birds can forage high only when a flock is in the immediate vicinity to provide protection from predators; when not in the flock, these individuals move down into the protection of dense lower foliage. Comparison of the foliage density profile (fig. 2) with the heights of the bird species in mixed species feeding flocks (table 3), however, shows that several of these species move into the higher but denser foliage while in flocks.

FLUCTUATION OF STRATA UTILIZATION

Up to this point, I have treated vertical stratification and biomass distribution as static and have described them only as spatial phenomena. A full understanding of this important aspect of tropical ecology requires treatment of its temporal pattern.

To gain an overall picture of the vertical movements of the avian community, the total biomass distribution by hour of the day was computed for the entire study period. The per cent of that mass represented at each of four strata for each hour from 06:00 to 16:00 was then compared (fig. 4). Stratum V is omitted because the data are poor and also because most of the species are strictly terrestrial. This comparison shows definite shifts in the biomass distribution with time of day. Fluctuation is most evident in strata I and II, a fact that reflects the greater vertical range and mobility of the birds of the upper strata and perhaps the uniformity of the habitat where they forage.

This movement downward during the middle of the day may be caused by one or a combination of several of the following factors: 1) the movement of food insects to lower levels; 2) increased activity of insects making

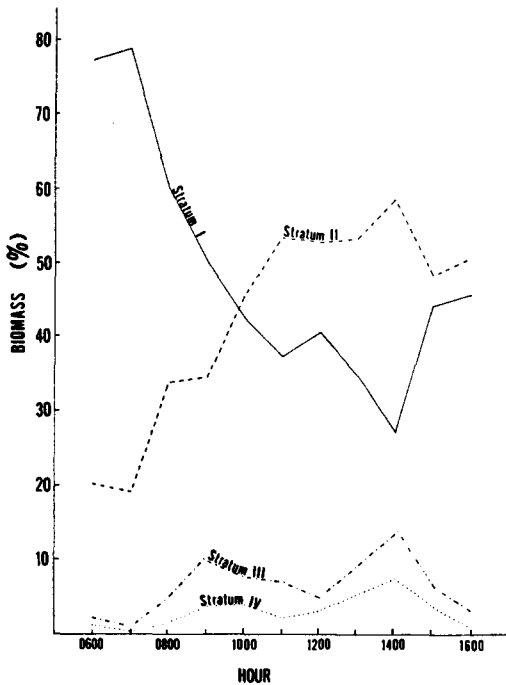


FIGURE 4. Per cent biomass distribution by hour of the day in strata I (25–40 m), II (12–25 m), III (7–12 m), and IV (0–7 m).

them more difficult to capture; 3) moisture conservation; 4) escape from mid-day heat stress; 5) escape from the high degree of solar radiation.

DISCUSSION

The inclusion of diurnal fluctuations introduces a concept that is underemphasized in hypotheses and experiments dealing with the ecology of tropical environments: cyclic change and instability. Several authors have based hypotheses on the assumption that only a narrow range of conditions is present in the tropics and that evolution there proceeds with less rigorous selection than in temperate areas (Klopfer 1959; Klopfer and MacArthur 1960). The presence of “scrub” species in the upper canopy provides a specific example of the instability of tropical areas. As was previously noted, these birds are typical of secondary growth areas. Except along rivers and other similar permanently open areas, secondary growth occurs naturally only in rapidly changing, small isolated patches brought about by windfalls, lightning, and other such forces. Because of the rapidity with which these cleared patches mature, they provide only a temporarily suitable habitat for “scrub” species. “Scrub” species, then, needed to evolve a strategy for frequently

moving over or through the less suitable primary forest in search of new successional areas. The observations from this study indicate that the ability of these second growth species to forage at canopy levels enables them to find and quickly colonize recently formed clearings that would otherwise be inaccessible. This theory was reinforced by observations in a tropical wet forest along the Urubamba River at Camisea, Departamento Cuzco. Here I found four species of “scrub” birds in a small *chaca* (ca. 0.3 ha) that had been cleared within the previous four months and which was at least a 5-hr walk from the river or any other such clearing known to the Indians. Because of the greater rainfall, the primary forest of this area was much denser than at Yarinacocha, and it offered even less habitat below canopy levels for “scrub” birds moving to other secondary growth areas. The presence of the “scrub” species in the clearing, together with the observations of “scrub” species in the canopy, is good evidence of changing conditions in the tropics that bring about selection for a distinct behavioral pattern.

Perhaps temperate zone ecologists have too often attempted to apply general temperate zone ideas and principles to tropical situations. Thus, a fluctuation in the tropics of only 4° C in the mean monthly temperature throughout the year is evidence enough for them that the tropics represent a more stable environment. Seasonal rainfall, as well as more subtle fluctuations (e.g., diurnal changes), deserve more attention in generalizations regarding the tropical environment. Wave-like fluctuations in cumulative foraging height diversity for several of the more common species (see fig. 3) provide strong indication that observation over a period of more than three months will show that birds expand and contract their vertical foraging ranges seasonally. This probable variation raises further interesting questions concerning a difference in bird species diversity between areas with a pronounced dry season and areas with cloud cover a great proportion of the day throughout the year. If direct sunlight, heat, and partial deciduousness over long periods bring about reduction and squeezing together of vertical foraging areas, as indicated in figure 4, perhaps increases in foraging height overlap are sufficient to reduce the species diversity. The cloudy areas should then have a greater species diversity with the vertical distribution of species more constant. Obviously many more factors than number of foliage layers (MacArthur et al. 1966) are in-

volved in the influence of vertical distribution on bird species diversity. Future investigations of the effects of seasonality, as well as comparisons of different tropical areas and conditions, will probably be the most profitable direction of study in bringing about a more complete understanding of the role of vertical stratification.

SUMMARY

A study of avian vertical stratification and biomass distribution was made on a 9-ha tract of tropical dry forest in central eastern Perú from June to August of 1968.

The relationship between vertical foliage density and vertical distribution of the bird community by individuals and biomass was investigated. A direct correlation between relative foliage density and utilization for foraging was evident at all levels except the top of the canopy and on the ground. The increased availability of energy apparently accounts for the inverse correlation between foliage density and feeding utilization at these latter levels.

Several factors were found to have an influence on stratification. Large body size may exclude several species from the denser foliage and smaller branches, and mixed species feeding flocks induced most species to feed higher than when they feed alone.

The vertical fluctuation of the bird community in terms of biomass was determined, and a definite vertical shift in the biomass distribution from the upper to the lower strata occurred daily between 09:00 and 14:00.

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