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THE NUMBER OF BIRD SPECIES IN SOME TROPICAL FORESTS

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Abstract. Resident birds were censused in seven plots in Costa Rica ranging from 0 to 6 months dry season and from sea level to 2,380 m in elevation. Included were one highland and two lowland sites that were dominated by one or two species of trees. All stands were tall, undisturbed forests, but some were surrounded by agricultural land. The number of species of birds recorded was not measurably affected by the tree species diversity or the length of the dry season. However, a larger proportion (about 90%) of the total forest species known to occur in the region as a whole was found in the drier areas, whereas only about 50% were recorded in the wetter areas. This suggests that "between-habitat diversity" may be greater in the areas with less severe dry seasons. The highland sites had markedly fewer species than the lowland sites, and a greater percentage of the species foraged by moving actively than was the case in the lowland sites. The large number of tropical lowland forest species that hunt by sitting and waiting for prey to move can probably be attributed to lack of wind, larger leaf size, larger biomass and higher recruitment rates of insects, more large nocturnal insects and more arboreal reptiles and amphibians. Many species of birds were limited to narrow vertical ranges in the forests, but the great increase in numbers of species in the tropics is only in small part accounted for by finer vertical subdivision of the forest. The greatest contribution is made by the addition of species with no temperate counterparts, suggesting that the greater range of resource types permanently above threshold values in tropical forests is the major cause of increased bird species diversity.

Different types of environments characteristically support different numbers of species. For example, forests have many more species of birds than adjacent grasslands, and tropical habitats usually have more species than their temperate counterparts, though there are exceptions (see Pianka 1966 for a general review of latitudinal gradients in species diversity). Studies designed to reveal the significance of this pervasive fact have developed in several directions. Some workers have examined the ecologies of the species in greater detail with the goal of measuring more precisely the methods of resource partitioning among ecologically reasonable groupings of species (Cody 1968; Orians and Horn 1969; Schoener 1968). Other investigators have attempted to measure the structural features of the environment to define more precisely their habitat selection mechanisms. This type of study in turn provides information on the nature of ecological differences among the component species, though it is not a substitute for examination of the behavior of individual species.

To date the relationship between vegetation structure and the number of species in the environment has been studied most intensively for birds. MacArthur and his associates (MacArthur and MacArthur 1961; MacArthur, MacArthur and Preer 1962; MacArthur, Recher and Cody 1966) have shown in a wide variety of environments, that the structural characteristics of the vegetation, particularly the vertical distribution of leaves,

is the best predictor of the diversity of bird species. For north temperate vegetation the best predictions were obtained if the vegetation was assumed to consist of three layers (0–2 ft, 2–25 ft, > 25 ft; or, 0–0.6 m, 0.6–7.6 m, > 7.6 m). For censuses in Panamá the foliage height profile was still a good predictor, but the diversity of bird species was greater than in temperate forests of comparable structural complexity. However, the differences were resolved if the Panamanian forests were considered to have four layers (0–2 ft, 2–10 ft, 10–50 ft, > 50 ft; or, 0–0.6 m, 0.6–3.0 m, 3.0–15.2 m, > 15.2 m) rather than three. These results suggest that birds act as though the environment is more finely subdivided, or more accurately, subdividable, in tropical forests than in temperate ones.

The present study was designed to accomplish two major objectives. First, I wished to assess the importance for bird distribution of features of the habitat other than foliage height profile. Because of the demonstrated importance of vegetation structure, this objective was best met by choosing sites in which foliage height characteristics were relatively similar but which differed strikingly in other features. Second, I wished to examine the foraging behavior of the birds to measure both the vertical distribution of the species and their general trophic positions in the communities. From these data I hoped to detect evidence that birds might be "recognizing" more layers in tropical forests than they do in temperate

ones and also to be able to compare the ecological characteristics of coexisting species.

Censuses were made at seven forest sites in Costa Rica. With the objective of testing the roles of other factors when the foliage height profiles were similar, I confined my censuses to mature forests. At the driest end of the Costa Rican moisture gradient the stature of the forests is much reduced and therefore I did not include these stands in my censuses. Ideally all census sites should have been portions of continuous forests, but in the drier parts of the country forest destruction is so complete that only isolated remnants remain. The same is true of the mountain slopes facing the Pacific except in very inaccessible areas. Therefore, several of my sites, though only lightly disturbed, were surrounded by agricultural lands.

It has been generally assumed that more species are found in tropical habitats because they are more "stable" (Klopfer 1959), thereby permitting either the coexistence of species more similar to one another ("more niche overlap"), or the use of a smaller range of environmental resources than in temperate communities ("smaller niches"). Stability is, however, a difficult thing to define or measure. Moreover, it is important not to confuse stability with predictability. For example, it is possible to have a very unstable environment which is nonetheless highly predictable, such as a temperate area with a hot summer and cold winter, both occurring without fail every year. A full understanding of the phenomena under investigation here will necessitate knowledge of both stability and predictability of environmental parameters, but Costa Rican weather records are not sufficient to permit analysis of the variance of the seasonality of climate at any of the sites I studied. Therefore my results can only be related to the average amount of seasonal change in precipitation, although the predictability of mean annual temperatures appears to be very high.

I attempted to assess the role of instability by censusing forests that differed in the length of the dry season, the most striking seasonal change in most tropical environments. In Costa Rica the dry season ranges from less than 1 month along much of the Atlantic lowlands and adjacent mountain slopes, to as long as 6 months on the Pacific lowlands in the northern part of the country. In the former region there is little or no synchronized deciduousness of trees, while in the driest areas of the Pacific coast most of the trees are deciduous except along watercourses, and upland forests may be largely leafless for 3 or 4 months. Though there are some species fruiting and flowering all year, the majority of species of trees flower and

produce fruits during the dry season (Janzen 1967) so that seasonal variations in availability of fruit should be more pronounced in areas with more severe dry seasons. The numbers of insects, particularly small ones, also decrease sharply during the dry season away from water, and almost no immature insects can be found during the dry season in areas where the drought is prolonged (Janzen and Schoener 1968).

It has also been suggested that there are more species of birds in tropical forests because of the diversity of foods provided by the large number of tree species. Most tropical forests are rich in tree species, but under certain circumstances, primarily edaphic ones, forests dominated by one or a few species of tree can be found. I censused three such sites in an attempt to assess the influence of the number of tree species upon the number of bird species.

A hypothesis relating the number of species in a system to the general level of productivity has been advanced by Connell and Orias (1964). I assessed the influence of lowered productivity by selecting sites at higher elevations with lower mean annual temperatures. Using the relationship between annual actual evapotranspiration and net annual above-ground productivity suggested by Rosenzweig (1968), I estimate that the productivity at my highland sites was only 1/3 (Barba) to 1/4 (La Chonta) as great as at the wet lowland sites. There are apparently no data available on the relative numbers of insects or fruits in lowland and montane forests in the tropics.

METHODS

The seven study sites ranged from a dry season of only a few weeks to a period of 6 months during which evaporation exceeds precipitation. They included three sites dominated by one or two species of trees and two sites in the mountains. The general characteristics of the sites are given in Table I; additional features are summarized below. Classification of the sites is according to the scheme of Holdridge (1947).

La Selva—a wet forest located at the juncture of the Atlantic coastal plain and the mountains in northeastern Costa Rica. To the south unbroken forest has extended to the tops of the mountains and for a considerable distance along the coastal plain, but it is rapidly being destroyed. The area is gently hilly, and the study area consisted of 3 acres (1.2 ha) of well-drained forest. Ravines with streams lay adjacent to the area, but no permanent water was located within the census plot. There is no well-marked dry season here, but there may be considerable leaf fall during short

TABLE 1. Characteristics of the census areas

Site	Elevation (meters above sea level)	Length of dry season (months)	Per cent decidu- ous- ness	Holdridge life zone	Area censused (hectares)	Hours censused	Census period
La Selva	<150m	0-1	<5%	Premontane wet	1.2	28.5	17-29 April
Osa- Ridgetop	"	2	5-10%	Tropical wet	1.2	28.3	7-17 March
Osa-Mora	"	2	75%	Tropical wet	0.4	19.3	11-21 March
Barranca	"	5	30-50%	Tropical moist	1.2	26	18 Apr.-19 June
Taboga- Brosimum	"	6	<5%	Tropical dry	2.0	28.5	19 Apr.-1 June
Barba	1,950m	2	<5%	Lower montane wet	1.2	21.3	4 Apr.-24 May
La Chonta	2,380m	0	<5%	Lower montane rain	1.2	20	5 Apr.-18 June

dry spells. Both palms and epiphytes are a conspicuous element in the forest.

Osa-Ridgetop—a wet forest site on a well-drained ridge on the Osa Peninsula in southwestern Costa Rica. This locality receives as much rainfall as the La Selva region, but there is a pronounced dry season during late February, March, and early April, at which time many of the smaller rivers dry up and some of the trees lose their leaves. Possibly as a result of the drying of the soil, which improves aeration of the tree roots (L. R. Holdridge pers. comm.), the forests of the Osa are the tallest and most luxuriant in all of Central America. As at La Selva, 1.2 ha with no permanent water were censused. In contrast to La Selva, both palms and epiphytes were rare.

Osa-Mora—Almost pure stands of *Mora oleifera* can be found in narrow bands between the mangrove forests (*Rhizophora* and *Avicennia*) of the tidal belt and the rich upland forests of the adjacent slopes on the Osa Peninsula. *Mora* forests are inundated only during the highest tides, but this is sufficient to produce a relatively bare forest floor. A salt-tolerant fern (*Acrostichum aureum*) formed dense stands over about 1/3 of the census site. *Mora* trees are very poor in epiphytes, and the trees in my census area were largely leafless late in the rainy season (mid-November). On this site the canopy was both lower and less dense than on any of the other sites. Owing to the narrow width of the band occupied by *Mora* forest, I was able to census a tract of only 1 acre (0.4 ha). Very different vegetation came to within 15 m of the census plot and this may have influenced the results.

Barranca—a moist forest located in the Pacific lowlands of Costa Rica just north of the town of Puntarenas. In this region there is a severe dry season lasting from mid-November to mid-April, during which time many of the trees on the census area lose their leaves. However, the large *Anacardium excelsum* trees in the valleys and the

Scheelia palms, which comprise about 32% of the leaf surface of canopy, remain green so that the forest never becomes leafless. There are few epiphytes. Sprouting of new tree leaves occurs in April, just prior to the first rains. A small stream runs through the middle of the census area, but it is dry during the dry season and did not have any water in it during the census period. The 1.2 ha censused were located inside the forest away from the edge, but the area in general is surrounded by cultivated land. One fallen tree on the census plot created an opening in which one species of bird not characteristic of closed forests was found.

Taboga-Brosimum—a floodplain forest located in the dry-forested region of northwest Costa Rica, 10 miles (16 km) SSW of Cañas. Though located in a region with a 6-month dry season (November through April) the study area of 2 ha was situated on low-lying ground where the trees had access to subsurface water. Consequently there was almost no synchronized deciduousness, though the surface of the soil became very dry toward the end of the dry season. This site was also surrounded by cultivated country, chiefly rice fields, and was dominated by *Brosimum costaricanum* and *Anacardium excelsum* which together comprised 89% of the leaf surface of canopy. The large trees supported substantial numbers of epiphytes.

Barba—a mixed lower montane forest located at 1,950 m on the southwest slope of Volcán Barba, facing the central plateau of Costa Rica. Dairying is very important in the region, but substantial areas of forest still remain. The area is characterized by almost constant strong northeast winds with considerable cloudiness and drizzle even during the dry season (December–April). Because of the high winds it was difficult to observe birds in the canopy at this site. Three acres (1.2 ha) of well-drained forest removed from the

edge were censused. The trees are nearly all evergreen and support lush growths of epiphytes.

La Chonta—a montane oak forest located at 2,380 m on the Cordillera de Talamanca, the highest mountain range in Costa Rica. This is also a region of considerable cloudiness and almost constant high winds, but the census area itself of 1.2 ha was located on the Pacific side of the crest of the mountains and was often relatively calm even when strong winds blew just above the tops of the trees. Most of the surrounding area had been cleared, chiefly by charcoal burners, and the census plot had been selectively logged at some time in the past. The forest was dominated by *Quercus seemannii* which bore immense quantities of epiphytic bromeliads on its branches. Portions of the understory were occupied by dense stands of bamboo-like grass (*Chusquea*).

Bird censuses and vegetation measurements

The bird censuses were made from March to June, depending upon the site, the peak breeding period for most Costa Rican birds (Skutch 1950). The sites were visited during the morning hours, usually in periods of about 4 hours duration beginning shortly after dawn. I slowly traversed the area listening for birds and making frequent stops. When I encountered birds, I noted their approximate foraging heights, foraging behavior, and territorial activity, if any. I made an effort to locate all unfamiliar sounds, and by the termination of the censuses there were very few sounds I was not able to recognize.

A cumulative record of the number of bird species observed at each site was maintained and censusing was terminated when continued visits yielded few new species. This point occurred earlier at the highland sites than in the lowland ones (Figure 1). Only at the La Selva site were many additional species being found at the last census interval. Therefore, the total for that site is probably low relative to the others. The bird fauna of La Selva is, however, exceedingly well known (Slud 1960).

Though most of the bird species occurring regularly on the sites were probably encountered during the census periods, there are limitations to the census data. First, I observed very little territorial behavior. Second, birds of undisturbed tropical forests sing very little as compared to birds of temperate forests or birds of disturbed habitats in the tropics. Apparently many forest birds are resident in restricted areas all year and many of them may pair permanently, perhaps accounting for the low rates of vocalizing. Third, birds are difficult to observe in tall forests.

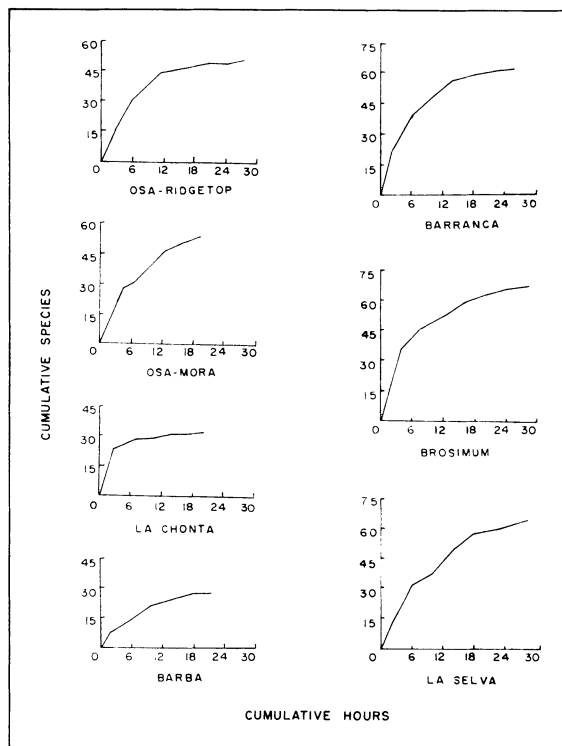


FIG. 1. Cumulative numbers of species observed at the study sites.

As a result of the low song levels and scarcity of territorial behavior, I found it difficult to distinguish birds merely passing through the study areas from those actually resident and breeding there. For example, at the Osa Ridgertop site I saw the Russet Antshrike (*Thamnistes anabatinus*) only once during the entire census period, but that instance involved a bird building a nest. I visited the nest repeatedly thereafter, but never saw the bird again. Had I not found the nest I should have been inclined to treat the bird as a vagrant.

A similar problem centers upon such birds as parrots which forage at great distances from their nests, which are often placed in very open areas. Should the bird be included in a census in an area in which it breeds but apparently does not feed or in the area where it forages even though it does not nest there, or both? What is the appropriate treatment for birds which visit a fruiting tree on the census area but leave after the fruits are gone? What about species which are seen regularly but for which one is able to obtain no evidence of breeding activity? These questions have not been dealt with sufficiently by earlier authors.

Because of my inability to devise reasonable criteria by which to handle these problems, I have arbitrarily decided to include all the species seen within the census area as "belonging." In the few

cases where I have good reason to believe that a bird was a wanderer outside its usual habitat, I will so indicate at the appropriate place in the discussion. By this procedure I am probably including a few species that do not breed at the study areas, but this seems better than attempting to make judgments about breeding on very inadequate evidence.

For the above reasons, it is extremely difficult to estimate numbers of birds in tropical forests. If a bird is seen on only half of the visits one might conclude that its territory was twice the size of the census area. Alternatively, it may simply sing less often or be less visible than a species encountered every trip. Many times I attempted to follow foraging birds and was unable to keep them in sight even when I knew they were still within the limits of my census plot. I did attempt to estimate numbers of "territories" of each bird on the census areas, taking into account the relative visibility and rates of vocalization of the species, but I have little confidence in the estimates. Moreover, my combined estimates for all census plots exceed the numbers of breeding birds reported in other tropical censuses.

Since I am uncertain about the relative abundances of the species, I am basing most of my conclusions upon the total number of species encountered on each of the sites and not upon some measure requiring an estimate of their proportional representation. This is not as serious a loss as might be supposed, however, because the information theory measure of diversity is very insensitive to the differences among censuses of the type under consideration. Rare species, which comprise a significant part of tropical forest birds, contribute very little to the diversity index. In the type of census I have made, the addition of as many as 15 new rare species would change the index little. However, they do represent 15 additional species supported by the system, and it is appropriate to attempt to account for their presence rather than to explain them by ignoring them as a weighted index would do.

The census areas were forests studied by Leslie R. Holdridge and his colleagues at the Tropical Science Center in San José. Dr. Holdridge has kindly allowed me to use these data which make available for each site, information on (i) the number of species of trees in the general area, (ii) the number of tree species on the study area itself, (iii) the total basal area in m²/ha, (iv) the height of the canopy, (v) the extent of epiphytism, (vi) the mean annual temperature, and (vii) the classification of the site according to the Holdridge system (Holdridge 1947, 1967).

In addition, I made an estimate of the foliage height profile following a method developed by R. H. MacArthur and H. Horn which is described in an appended paper. I took readings with a Pentax with a 135-mm telephoto lens mounted vertically on a tripod at a height of 1.8 m. At each study area four locations were established along each of six lines, the starting point and direction for which were determined by a spinning toss of a stick. Locations were chosen using a table of random numbers, each new reading beginning at 3-m intervals to avoid having two spots close together under the same sapling. Height measurements were accurate to within 1.5 m for leaves up to 15 m, and to within 3 m for leaves above 15 m. With the accuracy of my measurements it is possible to estimate foliage height profiles using up to as many as 17 height intervals should that be desired.

RESULTS

The general characteristics of the vegetation on the study sites are given in Table 2. It can be seen from the table that even the sites rich in tree species tend to be dominated by a relatively few species. In only one of the stands (Osa-Ridgetop) is it necessary to count more than five species before half the total basal area is accounted for. This is characteristic of most tropical forests (Richards 1952; Schulz 1960), even those supporting large numbers of species, because most of the species are very rare. Moreover, since the

TABLE 2. Features of the vegetation of the census areas

Feature	Site	La Selva	Osa-Ridgetop	Osa-Mora	Barranca	Taboga-Brosimum	Barba	La Chonta
Number of tree species in general area.....		113	128	?	111	28	80	65
Number of tree species on study area.....		57	61	5	46	18	28	20
Total basal area (m ² /ha)		50.8	40.4	35.0	35.5	48.8	57.4	40.6
Canopy height (meters).....		48	61	25	45	46	20	26
Number of species needed for 50% basal area.....		4	10	1	2	1	5	1
Tree species diversity ($-\sum p_i \log_{10} p_i$)		1.16	1.61	?	1.04	0.53	1.16	0.73
Per cent of trees with epiphytes:								
>35 m.....		100	37	—	0	100		
13-35 m.....		65	21	0	37	81		
5-13 m.....		29	0	10	4	10		

TABLE 3. Bird species and foliage characteristics of the census plots

Site	Number of bird species	Bird species diversity (rough estimate)	Avg. no. of leaves above a point	Foliage height diversity, using-		
				4 layers	7 layers	17 layers
La Selva	64	1.65	4.3	.40	.77	1.16
Osa-Ridgetop	52	1.51	5.0	.37	.75	1.13
Osa Mora	54	1.63	3.0	.47	.73	1.04
Barranca	63	1.62	3.7	.47	.77	1.22
Taboga-Brosimum	67	1.53	4.4	.36	.79	1.21
Barba	26	1.25	5.4	.49	.75	1.07
La Chonta	32	1.38	3.8	.47	.74	1.08

species-poor sites were chosen because they were nonetheless fairly tall forests, there is, in the sites I studied, no correlation between number of tree species present and the foliage height profile. Also, even though the canopies of the high altitude sites were lower than those of the lowland sites, the foliage height profiles are just as complex, no matter how many height intervals are used in the calculations.

Because the canopies at the Osa-Ridgetop and Taboga-Brosimum sites were high and dense, the understory vegetation there tended to be sparse and the foliage height diversity was lower if the four intervals used by MacArthur et al. are used. However, if more intervals, say 7 or 17 are used, the Brosimum site moves from being the site with the lowest to the site with close to the highest diversity (Table 3), because of the broad vertical width of the canopy. Thus, it is important to consider the implications of the particular intervals chosen in making a profile estimate.

The measurements taken with the camera also permit estimation of the total number of leaves above a typical point in the stand (Table 3). The number of leaves above the average point is just as great in the two high-altitude stands as in the lowland ones, and, in fact, the Mora and Barranca sites have the smallest number of leaves. A dry hillside forest in northwest Costa Rica would almost certainly have still fewer leaves above the average point even during the height of the rainy season.

Epiphytes are most abundant at the high-altitude sites, particularly on the oaks. The number of epiphytes on the trees may be of considerable significance to the birds, as there are some species which forage primarily among epiphytes and not among the leaves of the trees themselves.

In all stands the light intensity at the forest floor was very low except during the end of the dry season at Barranca and at the Mora site when the trees were temporarily leafless. Palms were absent from the high-altitude forests and were very scarce at the Osa and Brosimum sites. Only at La Selva and Barranca are they a conspicuous part

of the forest. Palms apparently support very few species of herbivorous insects even though there may be many insects resting on palm fronds. Therefore, a high proportion of palm in the canopy might be expected to have a negative influence on birds. On the other hand, palm leaves are a very different sort of substrate upon which to forage, and palm specialists might be present.

In general the shapes of leaves in tropical forests are more uniform than in temperate forests. Most leaves are ovate with entire margins. Lobed leaves such as found in oaks and maples at temperate latitudes are generally absent. Many trees have compound leaves but the leaflets also usually have a simple shape. Of potential significance to birds is the fact that leaf size decreases with increasing altitude in the tropics (L. R. Holdridge pers. comm.).

Bird census data

The complete censuses are given in Appendix A and are summarized in Table 4. The results are best discussed in the framework provided by the major questions around which the study was organized.

Is the number of tree species (i.e., tree species diversity) a good predictor of the number of bird species in a tropical forest?—In general the answer to this question appears to be "no." The Osa-Ridgetop, the site with the highest number of tree species and highest tree species diversity, had the smallest number of bird species of any of the lowland sites, while the species-poor Brosimum site had the most bird species. Similarly, at high elevations, the oak forest at La Chonta had more species than the mixed forest at Barba. Nor did I find any evidence of tree specificity among the birds I observed at any of the sites. Birds concentrated upon the fruits of a single tree species while it was available, but none seemed to be dependent upon it. All insectivorous birds moved regularly through many tree species. I encountered no species that foraged primarily or exclusively on palms.

The lack of importance of the number of tree

TABLE 4. Birds of the census areas

Feature	Site	La Selva	Osa-Ridge	Osa-Mora	Barranca	Taboga-Brosimum	Barba	La Chonta
Number of bird species.....		64	52	54	63	67	26	32
Number of bird families.....		27	24	20	27	29	18	16
Average number of species/family.....		2.4	2.2	2.7	2.3	2.3	1.4	2.0
Per cent oscines.....		20.3%	13.5%	24.1%	23.8%	18.0%	46.2%	53.1%
Per cent of total land birds of area.....		29.6%	27.5%	28.5%	39.4%	41.6%	30.2%	40.5%
Per cent of total forest birds of area.....		54.2%	54.3%	56.3%	87.5%	93.1%	48.1%	59.3%

species is also shown by preliminary observations I made in a red mangrove (*Rhizophora mangle*) stand on the Osa Peninsula. I did not have sufficient time for a complete census, but in 5¼ hours in the site I observed 40 species, many of which appeared to be breeding and many of which are largely confined to mangroves in that area (Appendix B). Also, the census carried out in mangroves in Panamá by MacArthur, Recher and Cody (1966), though it had many fewer species, had the number expected given its foliage height profile, thus showing no effects of the greatly reduced tree species diversity.

Though there are no comparable census data from African forests, the analysis of Moreau (1966a, 1966b) shows that some of the taxonomically simple African forest types, such as the *Brachystegia* woodland, are very rich in species. To my knowledge there are no data indicating a strong relationship between the number of tree species and the number of bird species in a woods with the exception that the additional presence of trees with different growth forms, e.g. conifers, (but apparently not palms) will add bird species to an otherwise broad-leaved forest.

Nevertheless, even though specific stands in the tropics may be poor in species, most regions are very rich in woody plants which provide a diversity of fruits at all seasons. Moreover, since most stands are rich in species, there may never have been selection for discrimination of sites on the basis of their plant species by birds at the time of habitat selection. If this were the case, birds would ignore species composition of the woods when settling to breed, but the diversity of species would nonetheless have played an important role in the evolution of the large number of species of birds living there. One possible test of this idea would be to compare the breeding success of birds in forests rich and poor in tree species, but this would be extremely difficult and laborious to accomplish. In Africa, the bird fauna is relatively impoverished in the northern savannahs (Moreau 1966b, p. 134), the only suggested explanation for which is the floristic poorness of that area as compared to the southern savannahs.

Is the length of the dry season (an estimate of the degree of variation in food supply) a good predictor of the number of bird species in a tropical forest?—For the sites I censused, there is no relationship between length of dry season and the number of bird species present. If I had censused a dry deciduous forest, the number of species would have been much reduced, but within tall, structurally complex forests in Costa Rica, the number of bird species on a given site does not reflect the length of the dry season. In the drier areas the number of obligate fruit eaters is reduced, but this is compensated for by an increase in the number of flycatchers and birds of prey.

There are two interesting features of the bird faunas of the drier census sites (Barranca and Taboga). First, they are the only two sites with breeding migrants, by which I refer not to North American species wintering in the area but to species which breed in Costa Rica but migrate to South America during the non-breeding season. Barranca had two such species, the Piratic Flycatcher (*Legatus leucophaius*) and the Yellow-green Vireo (*Vireo flavoviridis*). The latter also occurred at Taboga where it was estimated to be the fourth most common species. The presence of these species in regions with well-marked dry seasons may be related to the relatively greater flush of insects that characterizes these regions when the new growth of leaves occurs at the end of the dry season. When the new leaves were bursting out at Barranca there was a constant rain of caterpillar frass onto the forest floor. This occurred to a lesser extent at the Brosimum site, but I never observed a comparable event at any of the wet-forested sites. In general, the breeding ranges of migrants are restricted to the Pacific slope of Costa Rica (Slud 1964).

Second, the dry-forested sites, while containing about the same number of bird species as the wet-forested sites, held a much higher proportion of the total avifauna of the region (Table 4). Nearly all of the forest birds known to occur in the lowlands of northwest Costa Rica were found at both of the sites, whereas only about half of the poten-

tially available forest species were found at the other five sites. It is perhaps premature to speculate from such limited data, but they do suggest that in wetter areas slight changes in vegetational characteristics (profile, slope, aspect, etc.) may have much more influence on bird distributions than comparable changes in drier regions. Thus, though "within-habitat diversity" is about the same for the two areas, "between-habitat diversity" may be much greater in the wetter areas. These results provide limited support to the notion that individual species may occupy smaller ranges of environments in areas with more stable conditions (MacArthur and Levins 1967).

Is productivity a good predictor of the number of bird species in tropical forests?—Among lowland forests there are doubtless differences in both primary and secondary production, but these were not measured in this study. The amount of deciduousness on the sites I censused was not sufficient to cause a greatly lowered primary productivity, but the high altitude sites were much lower in mean annual productivity.

In the montane sites the number of bird species was only about half that found at the lowland sites. The montane sites are climatically just as stable as the lowland sites, but the wind and cold temperatures that accompany storms in the mountains may make the rainy season more adverse from the birds' perspective. Nevertheless, the most probable explanation for the correlation between reduced primary productivity and smaller number of bird species is that the lower temperatures affect the food supply. Janzen (pers. comm.) has found that the size distribution of insects obtained by sweeping does not change with increase in altitude in the tropics but that the total biomass of insects per sweep decreases. This means that there are fewer large insects per unit area in montane forests. Hence, it should be increasingly difficult for a bird dependent upon capturing large insects to find enough to maintain itself and reproduce. Not surprisingly, the first groups of birds to drop out with altitude in the American tropics are those dependent upon large insects. This point will be discussed further when the foraging behaviors of the birds of the study sites are compared.

Is foliage height profile a good predictor of the number of bird species in tropical forests?—The data of this study are not really suitable to test this question since I deliberately chose sites with similar foliage height profiles. Within the range of profiles found on my census plots one would not expect to find much of a correlation with the number of bird species. Interestingly, with the exception of the Osa-Ridgetop site, the lowland

sites give a good correlation between number of bird species and average number of leaves above a point, and this relationship should be explored further.

Even taken together, the above variables do not predict the differences in the numbers of species encountered on my census plots. Further insights can be obtained by a consideration of the foods and foraging behaviors of the species of birds.

By their foraging behavior do birds give evidence of responding to the vertical distribution of the leaves of the forest per se or do they respond to other features as well?—Based upon my observations of the foraging of the different bird species, both on the census tracts and elsewhere in Costa Rica, supplemented by the observations of D. R. Paulson and E. O. Willis, and the excellent summaries of foraging behavior given by Slud (1964), I have grouped the species according to their most prominent mode of foraging and their most important foods (Appendix C). Where more than one foraging mode and/or food are shown, they are listed in order of their importance. When two are of roughly equal importance they are joined by a dash. Subsequent analyses assume that the predominant foraging modes and foods are the ones which define the roles of the species in the forests.

The categories of foraging behavior I have found most useful are (W) gleaning on the ground, (E) dropping to the ground from an elevated perch, (D) digging in the soil or litter, (L) gleaning from trunks and branches, (P) pecking into trunks and branches, (G) gleaning from leaves, (S) sallying (both bird and prey are on the wing at the time of capture), (H) snatching or hovering (the bird is on the wing but the prey is not, at the time of capture), and (R) rummaging in dead leaves, snags and epiphytes.

Foods taken have been broken down into (A) amphibians and reptiles, (B) birds, (M) mammals, (I) insects and other arthropods, (P) mollusks, (F) fruits and berries, (S) seeds, (N) nectar, (L) leaves and buds, and (C) carrion.

Foraging heights were arbitrarily divided into (G) ground, (L) low shrubbery (0–6 ft, or 0–1.8 m), (H) high shrubbery (6–15 ft, or 1.8–4.6 m), (U) understory trees (15–40 ft, or 4.6–12 m) and (C) canopy trees (> 40 ft, or > 12 m).

Using these categories it is possible to compare the foraging modes represented in the different censuses and to demonstrate types of changes in the structure of the bird community not revealed by a simple count of species or their relative abundances. A general summary of the numbers of species in each of the different foraging cate-

TABLE 5. Foraging behavior of the birds of the census areas^a

Technique	Site	La Selva	Osa-Ridge	Osa-Mora	Barranca	Taboga-Brosim.	Barba	La Chonta
Ground gleaning		5	6	5	7	5	4	3
Drop to ground from perch		2	2	2	2	4	0	0
Gleaning on trunks and branches		5	5	3	5	4	2	3
Pecking into trunks and branches		2	3	5	2	3	0	1
Gleaning from leaves for:								
fruits		10	5	8	4	7	4	9
insects		11	8	9	14	11	3	6
fruits and insects		1	2	4	3	3	1	1
seeds		0	0	0	1	0	0	0
mollusks		0	0	0	2	1	0	0
nectar		1	1	1	1	1	0	0
Sallying for:								
insects		3	4	3	5	3	4	2
birds		1	0	0	1	0	0	0
Hovering for:								
fruit		2	2	1	1	1	1	1
insects		13	10	10	9	12	2	0
fruit and insects		3	3	1	2	3	1	1
nectar		1	0	2	4	4	3	2
vertebrates		0	0	0	0	2	0	0
Rummaging in dead leaves, snags, and epiphytes		3	1	0	0	1	1	3

^aNumbers indicate number of species foraging with each technique. Each species is entered only once on the table.

gories taken from the classifications in Appendix C is given in Table 5. Species are assigned on the basis of their most important foods and foraging modes and each species appears only once in the table.

The following general conclusions seem warranted. First, the number of ground gleaners is fairly constant at low elevations but decreases at high elevation. The missing birds at high elevations are terrestrial antbirds and tinamous.

Second, species which drop to the ground from an elevated perch are, as might be expected, better represented at the driest site, where the forest floor is more open and better illuminated during the dry season. No such species were found at either of the high-elevation sites, and very few of the species with this foraging habit range to high elevations anywhere in Costa Rica.

Third, there are few species of woodpeckers at high elevations in Costa Rica as is also true in Africa (Moreau 1966b, p. 300). The large number of species in the Mora site may have been the result of edge effects since both of the large species (*Dryocopus* and *Phloeocastes*), which are normally segregated by habitat, and both the mangrove and upland species of *Centurus*, were present on the site.

Fourth, the pattern of gleaners for fruits and insects in these censuses is very complex. Though the sample is small, the number of obligate fruit eaters probably decreases generally in dry areas, while the number of species that regularly take both fruits and insects increases. This trend will

be more striking when a dry, deciduous forest census is available. The Osa forests however, had fewer insectivorous species, the lower number of species being matched by a smaller general species list for the area. This may have a historical explanation. The number of gleaners is smaller at high elevations, but the number at La Chonta equals that at the Osa-Ridgetop site.

Tropical forest plants produce few seeds which are not enclosed in soft fruits, and most bird species which eat small, hard seeds are restricted to successional vegetation. The seed eater *Sporophila aurita* at Barranca was present only because a fallen tree created a gap into which weeds had grown. The species was not found generally within the forest. The Hook-billed Kite (*Chondrohierax uncinatus*), the only species to forage almost exclusively for arboreal mollusks, was restricted to the drier forest sites.

Fifth, the number of salliers, though slightly higher at the drier sites, was remarkably constant in all censuses and did not decrease significantly with altitude. The passerine species represented are all flycatchers (Tyrannidae), and it is significant that this is the one family of tropical Suboscines which has invaded north temperate environments in large numbers. Two to five species of salliers, mostly flycatchers, also characterize censuses in temperate deciduous forests in eastern North America as reported in *Audubon Field Notes*.

Sixth, species which snatch insect prey from the surfaces of leaves are very prominent in all low-

TABLE 6. Foraging heights of birds on census areas

Site	Major foraging heights ^a				
	Ground	Low shrubbery	High shrubbery	Understory trees	Canopy trees
La Selva	7 (11%)	6 (10%)	20 (32%)	7 (11%)	23 (37%)
Osa-Ridgetop	7 (13%)	6 (12%)	15 (29%)	7 (13%)	17 (33%)
Osa-Mora	7 (13%)	10 (19%)	11 (20%)	6 (11%)	20 (37%)
Barranca	11 (18%)	12 (19%)	13 (21%)	10 (16%)	16 (26%)
Taboga-Brosimum	10 (15%)	11 (17%)	13 (20%)	13 (20%)	19 (29%)
Barba	4 (15%)	3 (12%)	5 (19%)	6 (23%)	8 (31%)
La Chonta	3 (9%)	3 (9%)	7 (22%)	7 (22%)	12 (38%)

^aNumbers of species foraging in the given height category are shown. Figures in parentheses are percentages of the total number of species at each site.

land sites, comprising 1/5 to 1/6 of the total avifauna. If all hoverers are included, nearly 1/3 of the total number of species fall into this category. This group includes many of the classically tropical families of birds, such as trogons, motmots, and puffbirds, most of which do not occur at high latitudes.

Seventh, as might be expected, the sites poor in epiphytes (Mora and Barranca) did not have a species which foraged primarily in epiphytes, and the number of these species was highest in the epiphyte-laden forests at La Selva and La Chonta.

In general, then, many of the differences between the forest sites not explicable in terms of number of tree species, foliage height profile, or productivity, seem to be related to other aspects of the forests such as abundance of epiphytes, openness of forest floor, abundance of fruits, etc. Another factor may be the degree of vertical zone utilization by the different species on the sites. Each of the vertical zones of the forest had a number of species foraging largely, if not entirely, within it (Table 6). In general the ground and low shrubbery each contributed about the same number of species. More species were contributed by the high shrubbery and still more by the canopy as might be expected since most of the leaves and fruits are found there.

All bird species of the canopy, in my experience, forage over a wide vertical range. It is only among species of the lower zones that sharp restriction to a narrow vertical band occurs. For ground-foraging species this is, of course, inevitable. Shrubby-haunting species encounter poorer foraging as they move upward due to the general thinning of the vegetation. The wide vertical range of canopy species is probably the result of the broad vertical range of canopy itself which, to birds, appears to be a single unit. The lighting characteristics of the canopy may be the reason. No matter how irregular the top of the canopy

may be, the tops of sunlit leaves probably form a very uniform foraging surface for birds. It is noteworthy that many of the species which forage on the top of the canopy in tall forests are also found in brushy and shrubby successional vegetation where they also forage in the tops of the plants. For such a bird the height above the ground of the tops of the bushes or trees probably makes very little difference. Likewise, the canopy, as seen from below, must be similar over a broad vertical range and species foraging there also appear to have broad vertical ranges.

At intermediate levels the lower density of leaves and branches makes possible long-distance sallying owing to greater visibility and freedom of movement. A gleaning bird would have to forage in a different manner than in the zones above and below, spending more of its time moving between widely spaced leaves.

The lowest zones of the forest are characterized by very dim light even at midday, and illumination is slow to occur in the morning and rapid to disappear in the evening. Foraging here probably makes very different demands upon the sensory capabilities of the birds, many of which have large eyes. These species may be ill-suited to hunt in bright light though I know of no experimental verification of this idea. In any case, most of the species that live in the shrubbery seldom forage higher than 10 ft from the forest floor.

In his studies of birds in relation to foliage height profiles, MacArthur found that the best predictions of bird census data were obtained if the lower levels of the forest were divided more finely than the upper. The above data and arguments give further support for the reality of defining forest levels in that manner. It does leave as yet unanswered, however, the question of whether more species of birds can coexist in a tropical forest because fine vertical zonation is possible, or whether the increased number of species is due to other factors. More detailed mea-

TABLE 7. The number of species of birds in different forests that forage primarily by hovering for stationary prey

Forest type	Total number of species	Number of hoverers	Per cent of total species	Reference
Lowland tropical wet, Panamá	40	11	27.5	MacArthur, Recher and Cody 1966
Lowland tropical wet, Costa Rica	64	20	31.2	This study
Lowland tropical wet, Costa Rica	52	15	28.9	"
Lowland tropical wet, single species dominant, Costa Rica	54	14	25.9	"
Lowland tropical moist, Costa Rica	63	16	25.4	"
Lowland tropical dry, Costa Rica	67	22	32.8	"
Lowland tropical wet (disturbed), Panamá	39	9	23.1	MacArthur, Recher and Cody 1966
Premontane tropical wet, Costa Rica ^a	112	22	19.7	Davis & Aiken 1964
Lower montane tropical wet, Costa Rica	26	7	26.9	This study
Lower montane tropical wet, Costa Rica	32	4	12.5	"
Premontane subtropical wet, México	41	7	17.1	Webster & Deshayes 1965
Lower montane subtropical wet, México	38	5	13.2	Webster 1965
Temperate oak-hickory, New York	26	4	15.4	Saunders 1936
Temperate maple-beech-hemlock, New York	27	3	11.1	"
Temperate maple-beech, New York	14	0	0.0	"
Temperate aspen-red maple, New York	14	0	0.0	"

^aThis census included both undisturbed forest and edge which accounts for both the large number of species and the lower percentage of hovering species.

surements of foraging heights of birds in tropical wet and dry forests are now being gathered to test this question further.

My data indicate that birds are distributed as if there were four rather than three layers in a tropical forest, but comparable information is still not available for temperate forests. At the same time, my data do provide strong evidence that a finer division of the layers of the forest is not the only, and perhaps not the primary, factor responsible for the increased numbers of species of birds in tropical forests. For example, the tropical forests I censused contained three to five species of trunk-gleaning woodcreepers while temperate forests contain only one or two birds that forage in this manner. Most of the woodcreepers have broad vertical foraging zones so that the difference is not a result of finer vertical division of trunk space.

Similarly, there are no ecological equivalents in temperate forests to such obligate fruit eaters as parrots, toucans and manakins. These species represent an addition of a new foraging mode made possible by the variety of fruiting trees in the tropics and the continual fruiting season. Temperate forests do have some fruit eaters, such as pigeons and thrushes, but there are either similar species or ecological replacements in tropical forests. Thus, some of the fruit eaters in tropical forests represent an addition to the avian community over and above that provided by finer division of the foliage profile.

A slight increase in number of species, especially noticeable in the drier tropical forests, is provided

by the reptile-eating birds of prey. A temperate deciduous forest will be expected to have one hawk subsisting primarily upon reptiles and amphibians but, correlated with the abundance and greater size range of snakes and lizards, several may be found in a tropical forest.

Birds that follow army ant swarms form another group with no temperate-zone equivalents, and several species are included in my censuses (*Dendrocicla fuliginosa*, *D. anabatina*, *Dendrocolaptes certhia*, *Hylophylax naeviioides* and *Eucometis penicillata*). However, all of these species were also observed feeding independently, and from my observations I am unable to suggest how many of them are dependent upon the ants for their persistence on the study sites.

Finally, and very significantly, tropical forests abound in species that hunt by sitting quietly and watching for prey on the leaves and branches. The prey is then captured while the bird hovers in the air. Very few temperate-zone species of birds forage primarily in this manner but up to one-third of the species in a tropical forest do (Table 7). For the most part, these birds capture insects that are large relative to the size of the bird, and the birds are for the most part large headed. Most of these species drop out in subtropical forests in México, and among the families that do spread to higher latitudes, such as the flycatchers, it is the sallying and not the hovering species that continue northward. A dropout of similar bird species dependent upon large insects also occurs latitudinally in Africa (Moreau 1966b, p. 137).

*Why are there so many hoverers in the tropics
and so few in temperate forests?*

One possible reason is that this mode of hunting represents the culmination of selection for extreme energy conservation. Since no extra energy is expended until a prey organism is sighted, the rate of capture of organisms (number per unit time) may be lower and still meet the needs of the birds than would be the case if the bird moved around more actively. However, for a bird to forage in this manner, prey must be sighted with sufficient frequency. Search in this manner is probably greatly hindered by wind. Significantly, tropical lowland forests are usually very calm except sometimes during afternoon thunderstorms, so that such hunting should be effective most of the time. Tropical montane and temperate forests, on the other hand, are characterized by frequent winds of long duration. The Collared Trogon (*Trogon collaris*) and the Blue-crowned Motmot (*Momotus momota*), were seen foraging at Barba only below 6 m, where there is relatively less air movement, whereas they (or replacement species) regularly ranged high in the canopy at the lowland sites.

A second possibility is that insects located centrally or distally on large leaves may be difficult if not impossible for a perched bird to reach. Therefore, if a bird that foraged solely by picking up prey it could reach from branches and petioles were to move through a lowland site in the tropics, many insects that could be captured by other species that foraged by hovering, should still remain. In areas where leaves were smaller, however, a perched bird would be expected to pick up a larger fraction of the total insects present, thus leaving less for a hoverer. Since average leaf size decreases both altitudinally and latitudinally, this might be a factor contributing to the dropout of species that sit and watch for large prey.

The absolute abundance of insects might also be important. If there are fewer large insects per unit volume of forest in montane and temperate forests, then it should be correspondingly more difficult for a species to exist by sitting and looking for them. Low prey density should favor more generalized foragers that capture large insects when they are encountered but also pick up other kinds of prey. In American forests, jays appear to be the principal generalists of this sort. Jays are almost absent from lowland undisturbed forests in tropical America, but they are present in the drier areas, in successional vegetation, and at higher altitudes.

A final factor of probable importance is the presence of a large fauna of large nocturnal in-

sects in tropical forests. These species may be resting inconspicuously during the day but can be discovered by a very patient hunter. In regions with lower nighttime temperatures, there are not as many insects to be discovered.

To an important degree, then, the bird community of lowland tropical forests is augmented by species which have no ecological counterparts in temperate forests. These are not additions resulting from a finer vertical division of the foliage profile but from new ways of foraging possible in tropical forests.

Miscellaneous details

An interesting feature of the Costa Rican avifauna is the relative paucity of forest species on the Osa Peninsula, the primary reason for which may be historical. The Osa forests are the only very wet evergreen forests on the Pacific slope of Central America between southern Chiapas, México, and adjacent Guatemala to eastern Panamá. The region is isolated from the extensive lowland wet forests of the Atlantic slope by the high Cordillera de Talamanca in Costa Rica and western Panamá, and its long isolation is attested by the high degree of endemism among several of the vertebrate groups (Duellman 1966). Therefore many wet forest species capable of exploiting the Osa Forests may not have been able to invade the area. That this may be the case is also suggested by the presence of a few bird species at sea level on the Osa which do not range so low on the Atlantic slope. Examples are *Eutoxeres aquila*, *Dechonychura longicauda*, *Campylorhamphus pusillus*, *Dysithamnus mentalis*, *Myrmotherula schisticolor*, *Schiffornis turdinus*, *Tangara gyrola*, and *Lanio aurantius*.

If this is true, then it is all the more surprising that there is not more evidence of broadening of habitat tolerances among the birds in the Osa region. One might have expected that those forest birds present would have occupied a wider range of vegetation types so that the number of species present at any one site would have been as great as found on the Atlantic slope. Instead, I found about the same percentage of available forest species at the Osa-Ridgetop as I did at La Selva indicating little or no spread of habitat occupancy. For the moment, then, the structure of the bird community on the Osa remains somewhat puzzling. It is true that there are few epiphytes on the Osa, perhaps accounting for the scarcity of such birds as oropendolas, which are common in forests at slightly higher elevations in southwest Costa Rica and at sea level in all other humid parts of the country. Even so, this would explain only a very small part of the difference.

In terrestrial habitats, the number of species of nonpasserines and suboscines decreases more sharply with increasing latitude in North America than the number of species of oscines, and it has been suggested (Klopfer and MacArthur 1960) that the "more primitive" suboscines are less intelligent and flexible in their behavior and therefore less able to utilize the unpredictable environments of higher latitudes. Other workers (Mayr 1946) have even gone so far as to suggest that the suboscines are competitively inferior to the oscines in all habitats and are in the process of being replaced by the latter. My data support the view of Slud (1960) that the oscines have made only slight inroads into the bird communities of undisturbed wet lowland tropical forests. However, oscines are more conspicuous in forests in the drier areas and in early successional stages (Table 8). These data were gathered in March during two field projects of an Organization for Tropical Studies field course on the Osa Peninsula. Interestingly, suboscines also drop markedly in frequency in the montane forests despite the great stability of the latter.

TABLE 8. Taxonomic composition of bird faunas in relation to vegetation succession on the Osa Peninsula

Site	Number of bird species	Per cent oscines	Number of strictly tropical families
Early successional scrub (9 months old)	13	62	1
Early successional scrub (18 months old)	24	46	1
Selectively logged tall forest	58	21	12
Undisturbed tall forest	53	15	12

The dropout of suboscines cannot be related to the dropout of hovering species because most of them do not hunt that way and, of those that do, it is the Tyrannidae that are the most abundant in temperate latitudes. Rather, the suboscines form the dominant gleaning birds of undisturbed forest at low altitudes, but are replaced in this role by oscines at high altitudes and disturbed vegetation. The cause for this pattern is probably primarily historical. The suboscines apparently evolved in continental South America where today they are common in tropical lowlands, high altitudes and south-temperate areas. When a land bridge to Central America became available it was apparently a low-altitude one in a region of heavy precipitation. Therefore, primarily lowland-forest species were available to move into Central America, and the avifauna there represents a biased

selection from among the potential range of suboscine types in South America. Of all of the foraging methods used by these birds, it is apparently the sallying one that is most successful in open and temperate-zone habitats, and only the flycatchers have moved into temperate regions in large numbers.

CONCLUSIONS

The number of bird species in undisturbed forests in Costa Rica is not measurably affected by the number of species of trees in the forest, the tree species diversity or the length of the dry season. My study only measured proximate factors, however, and the ultimate role of tree-species diversity in tropical forests may be considerable. In areas with a longer dry season, however, a given forest will have a much greater percentage of the total avifauna of the region suggesting that "between-habitat diversity" may be greater in the wetter areas. The reasons for this difference are unknown, but the greater stability of the wetter forests may be a contributing factor.

Tropical highland forests have many fewer species than lowland forests, and the behavior of the birds is much more familiar to the temperate zone observer. Manakins, antbirds, cotingas, puffbirds and motmots are replaced by warblers, vireos and thrushes which act as the corresponding species in the United States. Moreover, in South America, the high altitude and high latitude suboscines are behaviorally convergent with their north temperate oscine counterparts. This strongly suggests that some of the same factors which influence temperate-zone bird communities are also acting in highland areas in the tropics. Such factors may include stronger wind, smaller leaf size, fewer nocturnal insects, lower absolute numbers of insects, and fewer arboreal amphibians and reptiles. If these factors are important, as suggested by this study, and if there are not greater fluctuations in insect populations than we now suspect, it may be true that the role of instability of temperate-zone areas as a factor influencing lower bird-species diversities has been overestimated. It also points to the fact that altitudinal gradients in the tropics provide an excellent system in which to study a number of community structure problems because of the possibility of selecting sites that differ primarily in one variable. Along latitudinal gradients several factors will normally be varying together.

This study must be regarded as strictly a preliminary one, representing as it does only a single season of field work at seven sites. There is a need for further altitudinal-transect studies as well as year-long work in various tropical forest sys-

tems. Only in this manner can the status of many species be determined and the generality, or lack of it, of the present conclusions be established or refuted.

Finally, it must be pointed out that though the Costa Rican avifauna is a very rich one, it is by no means as rich as that of the upper Amazon basin. In that area, perhaps twice as many species of birds can be found in a limited geographical region as can be found in a comparable area of Costa Rica (Willis pers. comm.). Not enough is known to say whether these additional species make their primary contribution to "within-habitat diversity" or "between-habitat diversity." It is sufficient for the present to note that it is dangerous to generalize too much about "the tropics."

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APPENDIX A. Bird censuses on the Costa Rican plots.^a

La Selva—Tm¹, Cau, Mr, Cn, Gv, Pha², Af¹, Pca, Cv, Psu, Fm, Tf², Cuc¹, Tma, Tru, Ep, Br, Mp¹, Mmo, Pt¹, Rs, Rsw, Pg, Df, Gs², Dc¹, Xl¹, Xe¹, Aoc¹, Xm, Tp¹, Ds¹, Mf², Ma¹, Mq, Me², Fa¹, Hn¹, Asp, Rh¹, Lu, Ts, Qp, Pm², Te¹, Mb¹, Pcr⁴, Rb, Tas¹, Mac, Po¹, Hla³, Ppl, Spu³, Ho, Hd⁶, Csp¹, Clu², Zw¹, Gmo, Cup², Eg¹, Pgr², Aau².

Osa-Ridge—Tm¹, Sp, Cau, La, St, Pp, Cn¹, Gm¹, Pha², Af², Pca, Psu, Pl, Tf², Hba¹, Tma, Tb, Tru, Mm, Mp¹, Rsw¹, Cch¹, Pg, Da¹, Dlo¹, Gs¹, Dc¹, Xg¹, Xl¹, Aoc, Xm, Tan, Msc¹, Mq, Fa¹, Lu³, Ts, Pco⁴, Pm⁸, Stu, Mt¹, Te, Mb, Pcr⁴, Po², Ho³, Hd⁴, Clu¹, Cup³, Tgy², Lau, Aau.

Osa-Mora—Ca, Cau, Ef, Bm, Ba, Cca¹, Cp², Lca¹, Am, Bj¹, Ps¹, Af¹, Gh, Tr², Psu¹, Fm², At, Aam¹, Hba¹, Rsw, Dl, Cr, Cch, Pg, Gs¹, Xg¹, Xl, Xm, Tbr, Can², Asp¹, Lu, Pci, Ts², Pco¹, Mpi, Mg², Mt, Mat, Tsu, Co¹, Tse¹, Ppl¹, Hd, Clu, Cff², Cup, El, Ei, Tl, Rp², Epe, Ccn¹, Ac.

Barranca—Cs¹, Ca, Cau, Cu, Bm, Hc, Ms, Lv¹, Gm, Bj¹, Cm, Pca¹, Tn, Ppe, Na, Pl¹, Pcu¹, He², As¹, At, Tma, Tmc¹, Tru, Es, Mp, Cho³, Pg, Sg², Gs, Dc, Xg¹, Ls², Tbr¹, Me, Asp, Ppo, Pa⁴, Ts¹, Ti, Cl⁴, Ll, Mma³, Mpi, Mt¹, Om, Tsu³, Oc⁴, Mv², Pmo, Cru¹, Tmo, Trf², Tg, Ppl, Vf², Hd⁶, Ccy, Ea, Ela², Epe¹, Sa, Aau, Ar¹.

Taboga-Brosimum—Cs, Cc, Sp, Cau, Lc, Cu, Hb, Ba, Hc, Ms, Bj, Aa², Ao, Pca¹, Ta, Lcr, Pl⁵, Pcu, He, As, At, Hl, Tma¹, Tmc³, Tru¹, Mm¹, Pt, Rs, Cho, Pg, Sg², Dc¹, Xg¹, Ls², Xm, Tbr¹, Ct², Me², Hn³, Asp², Ppo¹, Ts², Ti, Cl¹⁰, Mma², Mpi¹, Msi, Mt², Om, Pca¹⁰, Tsu⁴, Tsy, Oc¹², Mv³, Co¹, Cfo, Cru, Trf³, Tg², Rm³, Vf⁶, Hd¹², Ccy¹, Gmo, Ela¹, Epe¹, Ar².

Barba—Nb, Gc, Ch¹, Lcl², Efu, Tc, Mm, Ap, Laf², Trb, Asp, Mt, Eff⁴, Efr⁶, Pmo, Hls³, Tpl²,

^a Species are identified according to the code given in Appendix C, and listed in the same order. Superscripts refer to numbers of territories or pairs on the census area. If less than one pair was present, there is no superscript.

Cfr², Pcd, Vc¹, Vl³, Mmi², Mto, Pb¹, Cop³, Ab¹.
La Chonta—Cf, Csu, Gc, Ph, Pl¹, Lcs¹, Tc, Eb, Dv, Laf¹, Mru², Ss, Trb¹, Eff², Efr¹, To⁴, Hls², Tpl¹, Mra¹, Cg², Pcd, Vc², Mto¹, Bme², Vg², Coc, Pb, Cop³, Cpi³, Cpo, Pcp, Pti¹.

APPENDIX B. Birds observed in a red mangrove forest, Osa Peninsula, March 11–20, 1967.

Family	Species	Comments
Cathartidae	<i>Coragyps atratus</i> <i>Cathartes aura</i>	Regularly hunting over area "
Accipitridae	<i>Elanoides forficatus</i> <i>Buteo magnirostris</i> <i>Buteogallus anthracinus</i>	Commonly flying overhead Possibly transient Possibly resident
Rallidae	<i>Aramides cajaneae</i>	Definitely resident
Columbidae	<i>Columba cayennensis</i> <i>Claravis pretiosa</i>	Singing constantly "
Psittacidae	<i>Ara macao</i>	Nesting in dead mangrove stump
	<i>Brotheria jugularis</i> <i>Pionopsitta haematotis</i> <i>Pionus senilis</i> <i>Amazona farinosa</i> <i>Glauis hirsuta</i>	Nesting in stumps Only seen flying over Calling from trees Very common, nesting Hunting very low
Trochilidae	<i>Threnetes ruckeri</i> <i>Lophornis adorabilis</i> <i>Amazilia tzacatl</i>	" Feeding at <i>Tillandsia</i> "
Ramphastidae	<i>Ramphastos swainsonii</i>	Probably transient
Picidae	<i>Dryocopus lineatus</i>	Nesting in dead mangrove stump
	<i>Centurus rubricapillus</i> <i>C. chrysauhen</i>	Probably resident Excavating hole in stump
Dendrocolaptidae	<i>Xiphorhynchus guttatus</i>	Seen every visit
Cotingidae	<i>Cotinga ridgwayi</i> <i>Carpodectes antoniae</i> <i>Lipaugus unirufus</i> <i>Pachyrhamphus cinnamomeus</i>	Resting high in trees Abundant Calling in taller mangroves Regular
Tyrannidae	<i>Tityra semifasciata</i> <i>Myiozetetes similis</i> <i>Myiarchus ferox</i> <i>Camptostoma obsoletum</i> <i>Small gray flycatcher</i> <i>Poliophtila plumbea</i>	Very common Calling from tree tops Common Hunting low Common, singing Common
Sylviidae	<i>Cyanerpes lucidus</i>	Foraging high in trees
Coerebidae	<i>Coereba flaveola</i>	Foraging medium-high
Parulidae	<i>Dendroica petechia (bryanti)</i>	Abundant, many pairs with fledglings
Icteridae	<i>Cacicus uropygialis</i> <i>Cassidix mexicanus</i>	Foraging high in trees Regular
Thraupidae	<i>Tangara larvata</i> <i>Thraupis virens</i> <i>Ramphocelus passerinii</i>	Foraging medium " Foraging low-medium

APPENDIX C. Ecological characteristics of birds found on the Costa Rican census plots.

Species	Code	Habitat ^a	Foraging ^b techniques	Foraging ^c height	Foods ^d taken
Tinamidae					
<i>Tinamus major</i>	(Tm)	F,D	W	G	S,F,I
<i>Nothocercus bonapartei</i>	(Nb)	F,D	W	G	S,F,I
<i>Crypturellus soui</i>	(Cs)	D,B,F	W	G	S,F,I
<i>C. cinnamomeus</i>	(Ce)	D,B,F	W	G	S,F,I
Cathartidae					
<i>Sarcorampus papa</i>	(Sp)	F,D,S	W	G	C
<i>Coragyps atratus</i>	(Ca)	G,S,D	W	G	C,F
<i>Cathartes aura</i>	(Cau)	S,G,D,F	W	G	C
Accipitridae					
<i>Elanoides forficatus</i>	(Ef)	S,D	S,H	C	I,B,A
<i>Leptodon cayanensis</i>	(Lc)	F,D	H,E	C,U,G	A
<i>Chondrohierax uncinatus</i>	(Cu)	F,D,S	G,H	C,U	P
<i>Harpagus bidentatus</i>	(Hb)	F,D	H,S (?)	U,H	A,I
<i>Buteo magnirostris</i>	(Bm)	S,D,B	E	G	A
<i>Leucopternis albicollis</i>	(La)	F,D	E,H	H,G	A
<i>Buteogallus anthracinus</i>	(Ba)	D,S,F	E	G	I,C
<i>Spizaetus tyrannus</i>	(St)	F,D	E,S	G,U,C	M,B
Falconidae					
<i>Herpotheres cachinnans</i>	(Hc)	D,F,S	E	G	A
<i>Micrastur semitorquatus</i>	(Ms)	D,F	S,H	U,H,G	B
<i>M. ruficollis</i>	(Mr)	F,D	S,H	H,L,G	B
Cracidae					
<i>Penelope purpurascens</i>	(Pp)	F,D	G,W	C,G	F
Columbidae					
<i>Columba fasciata</i>	(Cf)	D,S,F	G	C	F
<i>C. cayennensis</i>	(Cca)	D,S	G	C,U	F
<i>C. nigristrostris</i>	(Cn)	F,D	G	C,U	F
<i>C. subrinacea</i>	(Csu)	F,D	G	C	F
<i>Claravis pretiosa</i>	(Cp)	D,B	W,G	G,L	F,S
<i>Leptotila verreauxi</i>	(Lv)	B,D,F	W	G	F,S
<i>L. cassini</i>	(Lca)	F,D	W	G	F,S
<i>Geotrygon veraguensis</i>	(Gv)	F	W	G	F,S
<i>G. costaricensis</i>	(Gc)	F	W	G	F,S
<i>G. montana</i>	(Gm)	F,D	W	G	F,S
Psittacidae					
<i>Ara macao</i>	(Am)	D,S,F	G	C	F
<i>Pyrrhura hoffmanni</i>	(Ph)	F,D	G	C,U	F
<i>Brotogeris jugularis</i>	(Bj)	D,F	G	C,U	F
<i>Pionopsitta haematotis</i>	(Pha)	F,D	G	C,U,H	F
<i>Pionus senilis</i>	(Ps)	D,S,F	G	C,U	F
<i>Amazona albifrons</i>	(Aa)	D,S,F	G	C,U	F
<i>A. ochrocephala</i>	(Ao)	S,D,F	G	C,U	F
<i>A. farinosa</i>	(Af)	F,D	G	C,U	F
Cuculidae					
<i>Coccyzus minor</i>	(Cm)	D,F	G	C,U	I
<i>Piaya cayana</i>	(Pea)	F,D,S,B	G	C,U,H	I
<i>Tapera naevia</i>	(Tn)	B,D,F	G	L,H	I
Tytonidae					
<i>Tyto alba</i>	(Ta)	S,G	E	G	M
Strigidae					
<i>Lophotrix cristata</i>	(Lcr)	F,D	?	?	?
<i>Pulsatrix perspicillata</i>	(Ppe)	F,D	?	?	?
<i>Ciccaba virgata</i>	(Cv)	F,D	?	?	?
Caprimulgidae					
<i>Nyctidromus albicollis</i>	(Na)	D,S	S	G↑	I
Trochilidae					
<i>Glaucis hirsuta</i>	(Gh)	D,B	H	L,H	I,N
<i>Threnetes ruckerti</i>	(Tr)	D,F	H	L,H	I,N
<i>Phaethornis superciliosus</i>	(Psu)	F,D	H	L,H	I,N
<i>P. longuemareus</i>	(Pl)	D,F	H	L,H	I,N

APPENDIX C.—Continued

Species	Code	Habitat ^a	Foraging ^b techniques	Foraging ^c height	Foods ^d taken
<i>Phaeochroa cuvierii</i>	(Pcu)	D,F,S	H	L,H,U	N,I
<i>Campylopterus hemileucurus</i>	(Ch)	D,F,S	H	L,H,U	N,I
<i>Florisuga mellivora</i>	(Fm)	B,D,F	H,S	L,H,U,C	I,N
<i>Thalurania furcata</i>	(Tf)	F,D	H	H,U,L	I,N
<i>Panterpe insignis</i>	(Pi)	S,D,F	H	H,L,U	N,I
<i>Hylocharis eliciae</i>	(He)	D,F	H	H,U	N,I
<i>Amazilia saucerottii</i>	(As)	D,S,F	H	L,H,U,C	N,I
<i>A. tzacail</i>	(At)	B,S,D	H	L,H,U,C	N,I
<i>A. amabilis</i>	(Aam)	D,B	H	H,U,L	N,I
<i>Chalybura urochrysa</i>	(Cuc)	F,D	H	H,U	N,I
<i>Lampornis calolaema</i>	(Lcl)	F,D	H	L,H	N,I
<i>L. castaneiventris</i>	(Lcs)	F,D	H	L,H	N,I
<i>Eugenes fulgens</i>	(Efu)	D,S,F	H	H,U	N,I
<i>Heliothryx barroti</i>	(Hba)	F,D,S	H,S	U,C	I,N
<i>Heliomaster longirostris</i>	(Hl)	D,F	H,S	U,C	I,N
Trogonidae					
<i>Trogon massena</i>	(Tma)	F,D	H	C,U	I-F
<i>T. bairdii</i>	(Tb)	F,D	H	H,U,C	I-F
<i>T. melanocephalus</i>	(Tme)	B,S,D,F	H	U,C,H	F-I
<i>T. collaris</i>	(Tc)	F,D	H	C,U	F-I
<i>T. rufus</i>	(Tru)	F,D	H	H,U	I,F
Momotidae					
<i>Electron platyrhynchum</i>	(Ep)	D,F	H	H,U	I,F
<i>Eumomota superciliosa</i>	(Es)	B,S,D,F	H	H,U	I,F
<i>Baryphthengus ruficapillus</i>	(Br)	F,D	E,H	C,U,H	I,F
<i>Momotus momota</i>	(Mm)	D,F	H,E	U,C,H	I,F
Bucconidae					
<i>Malacoptila panamensis</i>	(Mp)	D,F	H,E	U,H,G	I
<i>Monasa morphoeus</i>	(Mmo)	D,F	H	C,U	I,A
Capitonidae					
<i>Eubucco bourcierii</i>	(Eb)	F,D	G,R	U,H,C	I,F
Ramphastidae					
<i>Aulacorhynchus prasinus</i>	(Ap)	F,D	G,L	U,C,H	F,I
<i>Pteroglossus torquatus</i>	(Pt)	D,F	G	C,U,H	F
<i>Ramphastos sulfuratus</i>	(Rs)	D,F	G	C,U	F,I
<i>R. swainsonii</i>	(Rsw)	F,D	G	C,U	F
Picidae					
<i>Dryocopus lineatus</i>	(Dl)	S,D	P,L	C,U,H	I
<i>Centurus hoffmanni</i>	(Cho)	S,D,F	P,L	C,U,H	I,F
<i>C. rubricapillus</i>	(Cr)	D,S	P,L	C,U	I
<i>C. chrysauen</i>	(Ceh)	F,D	P,L	C,U	I
<i>Dendrocopos villosus</i>	(Dv)	D,S,F	P,L	U,H,C	I
<i>Phloeocastus guatemalensis</i>	(Pg)	F,D	P,L	C,U,H,L	I
Dendrocolaptidae					
<i>Dendrocinclia anabatina</i>	(Da)	F,D	S,L,E	L,H,G	I
<i>D. fuliginosa</i>	(Df)	F,D	S,L,E	L,H,G	I
<i>Deconychura longicauda</i>	(Dlo)	F,D	L	H,U	I
<i>Sittasomus griseicapillus</i>	(Sg)	F,D	L,S	H,U	I
<i>Glyphorhynchus spirurus</i>	(Gs)	F,D	L	L,H,U	I
<i>Dendrocolaptes certhia</i>	(Dc)	F,D	L,S,E	H,L,U,G	I,A
<i>Xiphorhynchus guttatus</i>	(Xg)	D,F	L,R	U,H,L	I
<i>X. lachrymosus</i>	(Xl)	F,D	L,R	C,U	I
<i>X. erythropygius</i>	(Xe)	D,F	L,R	U,C,H	I
<i>Lepidocolaptes souleyetii</i>	(Ls)	S,D,F	L	U,C,H	I
<i>L. affinis</i>	(Laf)	S,D,F	L	U,C,H	I
Furnariidae					
<i>Margarornis rubiginosus</i>	(Mru)	F,D,S	L,R	U,C	I
<i>Syndactyla subalaris</i>	(Ss)	D,F	R	H,U	I
<i>Automolus ochrolaemus</i>	(Aoc)	F,D	R	L,H	I
<i>Xenops minutus</i>	(Xm)	F,D	P,L	H,U	I
<i>Thripadectes rufobrunneus</i>	(Trb)	F,D	R,P,L	H,U	I
Formicariidae					
<i>Thamnophilus bridgesi</i>	(Tbr)	D,F	G	H,L	I
<i>T. punctatus</i>	(Tp)	F,D	G	H,U	I

APPENDIX C.—Continued

Species	Code	Habitat ^a	Foraging ^b techniques	Foraging ^c height	Foods ^d taken
<i>Thamnistes anabatinus</i>	(Tan)	F,D	G	U,H	I
<i>Dysithamnus striaticeps</i>	(Ds)	F,D	G,R	H,U	I
<i>Myromotherula fulviventris</i>	(Mf)	F,D	R	H,L	I
<i>M. azillaris</i>	(Ma)	F,D	G	H,U,L	I
<i>M. schisticolor</i>	(Msc)	F,D	G,R	H,L	I
<i>Microrhopias quizeus</i>	(Mq)	D,F	G,R	H,U	I
<i>Cercomacra tyrannina</i>	(Ct)	D,S,B	G	L,H	I
<i>Myrmeciza exsul</i>	(Me)	F,D	G,L,E	G,L	I
<i>Formicarius analis</i>	(Fa)	F,D	W,D	G	I
<i>Hylophylax naevioides</i>	(Hn)	F,D	E,H,G	G,L	I
Cotingidae					
<i>Carpodectes antoniae</i>	(Can)	D,F	G	C,U	I-F
<i>Attila spadiceus</i>	(Asp)	F,D,S	H,E	U,H,L,G	I,A
<i>Rhytipterna holerythra</i>	(Rh)	F,D,S	H	H,U,C	I-F
<i>Lipaugus unirufus</i>	(Lu)	F,D	H	C,U	I,F
<i>Pachyrhamphus polychropterus</i>	(Ppo)	D,F,S	G,H	H,U	I
<i>P. cinnamomeus</i>	(Pci)	D,B	G,H	H,U	I
<i>Platypsaris aglaiae</i>	(Pa)	D,F,B	G	H,U,C	I
<i>Tityra semifasciata</i>	(Ts)	D,F,S,B	G,H	C,U	I,F
<i>T. inquisitor</i>	(Ti)	D,F,S	G,H	C,U	I-F
<i>Querula purpurata</i>	(Qp)	F,D	H	C,U	F,I
Pipridae					
<i>Pipra coronata</i>	(Pco)	F,D	H	H,L	F,I
<i>P. mentalis</i>	(Pm)	F,D	H	H,U	F,I
<i>Chirozophia linearis</i>	(Cl)	D,F,B	H	L,H,U,C	F,I
<i>Schiffornis turdinus</i>	(Stu)	D,F	H,G,L	L,G,H	I?
Tyrannidae					
<i>Legatus leucophaius</i>	(Ll)	D,S	S,H	C	I,F
<i>Myiodynastes maculatus</i>	(Mma)	D,F,S	S,H	H,U,C	I,F
<i>Megarhynchus pitangua</i>	(Mpi)	D,F,S	H	C,U	I,F,A
<i>Myiozetetes similis</i>	(Msi)	D,S,B,F	H,S	H,U,C	F-I
<i>M. granadensis</i>	(Mg)	D,S,B	H,S	H,U	I-F
<i>Myiarchus tuberculifer</i>	(Mt)	D,F	S	U,H	I
<i>Empidonax flavescens</i>	(Efl)	F,D,S	S,H	H,U	I
<i>Terenotriccus erythrurus</i>	(Te)	F,D	S	H,U	I
<i>Myiobius barbatulus</i>	(Mb)	F,D	S	U,H	I
<i>M. atricaudatus</i>	(Mat)	D,B	S	M,U	I
<i>Onychorhynchus mexicanus</i>	(Om)	F,D	S	L,H	I
<i>Platyrinchus cancrumimus</i>	(Pca)	F,D	H	L	I
<i>P. coronatus</i>	(Pcr)	F,D	H	H,L	I
<i>Rhynchocyclus brevirostris</i>	(Rb)	F,D	H	H,U	I
<i>Tolmomyias sulphureus</i>	(Tsu)	D,F,S	H	H,U	I,F
<i>T. assimilis</i>	(Tas)	F,D	H,S	U,C,H	I,F
<i>Todirostrum sylvia</i>	(Tsy)	D,B	H	H,L	I
<i>Oncostoma cinereigulare</i>	(Oc)	D,B,F	H	H,L,U	I
<i>Myiornis atricapillus</i>	(Mac)	F,D	H	U,H,L	I
<i>Elaenia frantzii</i>	(Efr)	S,D,B,F	H	U,H,C,L	F,I
<i>Myiopagis viridicata</i>	(Mv)	D,F,B	H	U,H	I
<i>Camptostoma obsoletum</i>	(Co)	D,F	H,G	U,C	I
<i>Pipromorpha oleaginea</i>	(Po)	F,D	H,S	H,L,U	I-F
Corvidae					
<i>Calocitta formosa</i>	(Cfo)	S,D,F	G	C,L,H,U	I-F,C,B,A
<i>Psilorhynchus morio</i>	(Pmo)	S,D,F,B	G,E	C,L,H,U,G	I-F,B,C,A
Troglodytidae					
<i>Campylorhynchus rufinucha</i>	(Cru)	D,B,S,F	G,R,L	H,U,L	I
<i>Thryothorus modestus</i>	(Tmo)	B,D	G,R	L,H	I
<i>T. rufalbus</i>	(Trf)	D,F	G,R	L,H	I
<i>T. semibadius</i>	(Tse)	D,F	G,R	L,H	I
<i>Troglodytes ochraceus</i>	(To)	F,D,S	R,L	U,C,H	I
<i>Henicorhina leucosticta</i>	(Hla)	F,D	L,R,G	L,G	I
<i>H. leucophrys</i>	(Hls)	F,D	L,R,G	L,G	I
Turdidae					
<i>Turdus gra. i.</i>	(Tg)	S,D,F	G,W	U,G,L,H	F,I
<i>T. plebejus</i>	(Tpl)	F,D,S	G	C,U,H	F,I
<i>Myadestes ralloides</i>	(Mra)	D,F	G,H	H,L,U	F
<i>Catharus gracilirostris</i>	(Cg)	F,D,S,B	W,G	G,L	I,F
<i>C. frantzii</i>	(Cfr)	F,D,S,B	W,G	G,L	I,F

APPENDIX C.—Continued

Species	Code	Habitat ^a	Foraging ^b techniques	Foraging ^c height	Foods ^d taken
Sylviidae					
<i>Poliophtila plumbea</i>	(Ppl)	D,B,S,F	G,H	H,U,C	I
<i>Ramphocaenus melanurus</i>	(Rm)	D,F,B	G	L,H,U	I
Ptilonotidae					
<i>Ptilonotus caudatus</i>	(Ped)	S,D,F	G,S	C,U,H	F,I
Vireonidae					
<i>Smaragdolanus pulchellus</i>	(Spu)	D,F	G	C,U	I
Vireonidae					
<i>Vireo carmioli</i>	(Vc)	F,D	G	C,U	I
<i>V. flavoviridis</i>	(Vf)	S,D,F	G	C,U	I,F
<i>V. leucophrys</i>	(Vl)	F,D	G	C,U	I
<i>Hylophilus ochraceiceps</i>	(Ho)	F,D	G,R	H,L	I
<i>H. decurtatus</i>	(Hd)	F,D,S	G	C,U	I
Coerebidae					
<i>Chlorophanes spiza</i>	(Csp)	D,F	G	C,U	F,I
<i>Cyanerpes cyaneus</i>	(Ccy)	D,F	G,H	U,C	N,F,I
<i>C. lucidus</i>	(Clu)	D,F	G	C,U	N,F,I
<i>Coereba flaveola</i>	(Cfl)	D,S,B	G	H,U,C	I,F,N
Parulidae					
<i>Myioborus miniatus</i>	(Mmi)	D,F,B	S,G,H	H,L,U	I
<i>M. torquatus</i>	(Mto)	D,F,B	S,G,H	H,U,L	I
<i>Basileuterus melanogenys</i>	(Bme)	D,F	G	H,L	I
<i>Vermivora gutturalis</i>	(Vg)	D,F,S	G	C,U	I
Icteridae					
<i>Zarhynchus wagleri</i>	(Zw)	F,D,S	G,R	C	F,I
<i>Gymnostinops montezuma</i>	(Gmo)	D,F,S	R,G	C,U	F,A,I
<i>Cacicus uropygialis</i>	(Cup)	F,D	G,R	C,U	I,F
Thraupidae					
<i>Chlorophonia occipitalis</i>	(Coc)	D,F,S	G,H	C,U	F
<i>Euphonia affinis</i>	(Ea)	S,D,F	G	C,U,H	F
<i>E. luteicapilla</i>	(El)	S,D,F	G	C,U,H	F
<i>E. laeta</i>	(Ela)	D,F	G	C,U,H	F
<i>E. gouldi</i>	(Eg)	F,D	G	U,H,C	F
<i>E. imitans</i>	(Ei)	F,D	G	U,H,C	F
<i>Tangara larvata</i>	(Tl)	S,D	G,S	C,U	F-I
<i>T. gyrola</i>	(Tgy)	F,D	G	C,U	F-I
<i>Ramphocelus passerinii</i>	(Rp)	B,D	G	L,H	I,F
<i>Piranga bidentata</i>	(Pb)	D,F,S	G	C,U	I
<i>Lanio aurantius</i>	(Lau)	F,D	G	C,U	I
<i>Eucometis penicillata</i>	(Epe)	D,F	G,E,H	L,G,H	I,F
<i>Chlorospingus ophthalmicus</i>	(Cop)	F,D	G	C,U,H	F,I
<i>C. pileatus</i>	(Cpi)	F,D	G	U,H,C	F,I
Fringillidae					
<i>Caryothraustes poliogaster</i>	(Cpo)	F,D	G	C,U,H	I-F
<i>Pitylus grossus</i>	(Pgr)	F,D	G	C,U	F,I
<i>Cyanocopsa cyanoides</i>	(Ccn)	F,D	G	L	F-I
<i>Sporophila aurita</i>	(Sa)	B,D,G	G	L,G	S
<i>Pezopetes capitalis</i>	(Pcp)	F,D	W,R,D	G,L	S,I
<i>Pseliophorus tibialis</i>	(Pti)	F,D	G,R	L,H	I
<i>Atlapetes brunneinucha</i>	(Ab)	F,D	W,R,D	G	S,I
<i>Arremon aurantirostris</i>	(Aau)	F,D	W,R	C	S,I
<i>Arremonops rufivirgata</i>	(Ar)	B,D,F	W,R	G,L	S,I
<i>A. corirostris</i>	(Ac)	B,D	W,R	G,L	S,I

^aHabitats: closed forest (F), second growth (D), savannah and parkland (S), scrub and brush (B), grassland (G). Order indicates relative importance.

^bForaging techniques: ground gleaning (W), drop to ground from perch (E), dig in soil or litter (D), gleaning on trunks, branches, twigs (L), pecking into trunks, branches, twigs (P), gleaning from leaves (G), sallying or hawking (S), snatching or hovering (H), rummaging in dead leaves, snags, epiphytes (R).

^cForaging heights: ground (G), low shrubbery 0-6' (L), high shrubbery 6-15' (H), understory trees 15-40' (U), canopy trees > 40' (C).

^dFoods taken: amphibians and reptiles (A), birds (B), mammals (M), insects and other arthropods (I), mollusks (P), fruits and berries (F), seeds (S), nectar (N), leaves and buds (L), carrion (C). When two food categories are roughly equal in importance, the comma is replaced by a dash.