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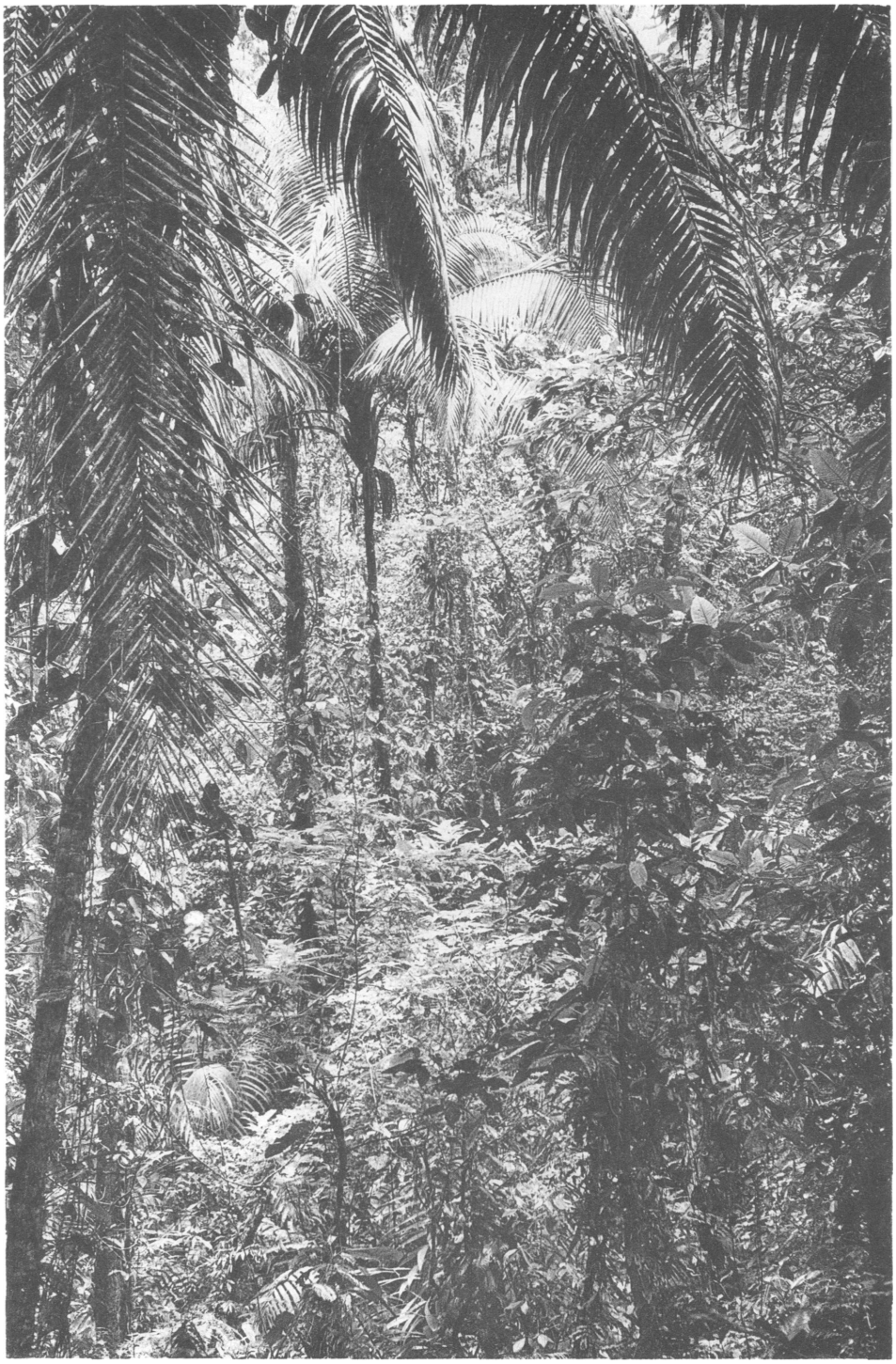

An aspect of the "La Selva" forest

THE BIRDS OF FINCA "LA SELVA," COSTA RICA: A TROPICAL WET FOREST LOCALITY

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INTRODUCTION

SCOPE AND METHODS

CENTRAL AMERICA HAS BEEN SKIMMED so effectively by collectors that very few, if any, unknown species of birds remain to be discovered. Years ago the emphasis shifted to subspecies, the rank at the present time implied in discoveries of forms that are called new to science. The ever-growing collections and the indispensable catalogues have prepared the way to the study of living birds in natural settings. For certain species some information on their environment and habits is available, but for the great majority it becomes necessary to search through annotated lists authored, usually, after but a short visit to any one place. The investigator making the collation confronts a paucity of unconnected items of little ecological significance. Even well-collected species may be virtually unknown in life.

The bird occupying many pages of print is usually the one that has been made the protagonist of a "life history." Any "life history" is, of course, of interest *per se* and of worth to comparative nesting studies, but a pair of birds undergoing reproductive stress often tells us little about the activities of the species during the rest of the year. Nevertheless, it is to be hoped that a throng of life-history enthusiasts will dedicate themselves to the tropics. The more data that are amassed, the more nicely can nesting be fitted to a bird's many-sided being.

"Such [life history] work disregards the great contribution of modern ecology, which is that taxonomically unrelated organisms form more or less closely integrated communities that react as units and should be studied as such. This important fact is recognized when the environment is classified as well as the animals living in the environment" (Allee, 1926, p. 465). To do what Allee advocates seems not to have been done for the American lowland tropics, not even at the station on Barro Colorado Island, established for decades and with a roll of the most distinguished visitors, where Allee himself worked. Nor has the intensification of ornithological activity in Mexico brought forth a study along these lines from the humid-forested lowlands. Elsewhere in the neotropics, Beebe's published work (1925; Beebe *et al.*, 1917) in British Guiana is fragmentary and regrettably discrepant. Also in British Guiana, the Oxford University Expedition of 1929 seems to have done little more than collect. T. A. W. Davis (1953), on the other hand, from long firsthand experience offers a vegetational outline that is helpful to further analyses of the lowland British Guiana avifauna. The Department of Tropical Research of the New York Zoological Society in Trinidad has not yet produced a comprehensive ornithological study of the sort recommended by Allee. As recently as 1958, "the study of the bird communities of the equatorial region of Brazil has been little investigated" (Novaes, 1958, p. 1). Rancho Grande, in Venezuela, has been treated species by species by Schäfer (Schäfer and Phelps, 1954), but this varied region of over 80,000 hectares lies largely at cool, subtropical elevations.

Costa Rica, the country of my special choice, has been host to many ornithologists, all of whom seem to have avoided a prolonged stay in the warm, wet lowlands. Carriker's (1910) collecting activities extended through five years and, as were my own, were national rather than local in scope. Ridgway (1921, p. 210), despite his nine months in the country, was least familiar with the Caribbean coastal-plain forest. It was in the spirit of ecological exploration, therefore, that I decided to spend a year in 1 square mile of wet, tropical forest in the northeastern lowlands of Caribbean Costa Rica. Having previously made country-wide observations in that republic, I wished now to make use of my broad acquaintance with the avifauna on a heterogeneous national scale by applying the experience to a concentrated investigation of a homogeneous area on a local scale; and to attempt to treat all the birds with respect to frequency, abundance, habitats, habits, sociability, and so on, in the hope of perhaps being able to derive formulations of widely applicable import. With field work as scaffolding, I sought to erect an ecological framework

wherein isolated studies might find a natural resting place. I looked forward to there becoming evident heretofore unsuspected problems the solutions of which lurk, as it were, in niches requiring illumination. But on the whole I could not anticipate quite what to expect to find while trusting to notice what the course of events might show.

The site decided upon I was already acquainted with; it was chosen for several reasons. A private tract, in effect a reserve where hunting is prohibited, Finca "La Selva" is the property of Leslie R. Holdridge and is located in a forested region that covers nearly all of northeastern Costa Rica, where the human population is one of the sparsest in the country. The property, with an area of approximately $2\frac{1}{3}$ square miles, offers the advantages of a house in which to live, the forest literally beside the door, a set of parallel cruising lines cut lengthwise through the forest, and a river, streams, small marshes, forested swamps, varied terrain, shaded plantations (semi-open country), and secondary growth. Also, it happens to lie along a migration route.

My materials and methods were simple. The materials consisted of an 8-power binocular, a 20-power binocular, a camera, a machete, mist nets, a .22-caliber pistol, maximum-minimum thermometers, a rain gauge, and two hygrothermographs. I envisioned, too, the construction of a tower for tree-top observations. Manipulation of a mist net in the forest, however, would have been wastefully time-consuming, also unscientific, for the net is a collecting device that entangles a chance assortment of species unbalanced in favor of small birds of the undergrowth. The purchase of the 20-power binocular for identifying small birds in the forest roof was a mistake. "On the floor of the forest the observer is . . . a prisoner" (Richards, 1952, p. 23). To use the glass on birds perched in open places was, however, a type of recreation. Towers would have been helpful indeed, as Nicholson (1931, p. 74) found in British Guiana, but Hingston (1932) made it clear that the rearing of the observation posts involved the entire entourage, equipment, funds, and native help. Operating alone with limited resources, for me such an undertaking was impossible; admittedly, my observations on the high canopy were haphazardly few.

I covered much territory on foot for many hours daily. The area intensively worked I reduced from the arbitrary square mile to a more realistic square kilometer. Regularly I made long excursions along any forest line which happend to strike my fancy. Periodically through the year I conducted two-week surveys, during which I recorded the species encountered, together with their relative abundance. I took such notes as past experience had shown to be worth taking. My basic materials, then, were the smaller binoculars, "the poised pencil, and the receptive notebook"; my methods, reliance on sight and sound, careful watching and patient waiting, time expended, and distance covered. The birds, it goes without saying, do not come out and perform for the observer's benefit.

This was to be a study of undisturbed living birds; hence correct identification was of crucial importance. My qualifications consisted of five full years spent in Costa Rica in selectively collecting and in observing birds. My trips, each lasting a week to six weeks or more in one locality, had taken me to all the provinces, and from both seacoasts to the summits or upper portions of all but two of the volcanoes and at or above tree line on the Talamanca Cordillera, including all the life zones (fig. 5). From 1953 to 1955 I had visited "La Selva" several times. To my knowledge I am the only person who has made formal observations on the birds of the Sarapiquí region.

I returned to Costa Rica early in June, 1957, become reacquainted with the birds, and made preparatory visits to "La Selva" before I settled there for the year lasting from September 14, 1957, to September 11, 1958. My list for the finca at the start of the study amounted to 247 species, and I supposed it to be nearly complete. By the end of the twelve-month period the number had risen to 331.

GENERAL CONSIDERATIONS

The section on Environment and the Annotated List lay the foundation for the analyses and ecological arrangements, as well as for the Discussion and Conclusions therefrom derived or proposed. The following general considerations provide a background for the kaleidoscopic variations in status of native birds and migrants.

Plate 9 shows "La Selva" as lying within a great expanse of forest penetrated by narrow avenues: the Río Sarapiquí, the Río Puerto Viejo, and a road following the left bank of the Río Sarapiquí. At their confluence the two rivers enclose a projection of land from the study area; this peninsula I call the Point (fig. 3). The Point, which has a clearing at the very tip and various stages of second growth and young tree plantations over the remainder, resembles the semi-open country across the Río Sarapiquí. Virtually all the rest of the study area is forested, with a fringe of shaded tree plantations along parts of the Río Puerto Viejo and at the east boundary near the quebrada El Sábalo. The places of occurrence in the area of certain birds enable us to decide which are forest-based inhabitants and which are not. The relative degree of independence of or dependence on forest can be inferred or demonstrated. As examples, let us look at two tanagers, *Ramphocelus passerinii* and *Mitrospingus cassinii*, and two wrens, *Thyrothorus atrogularis* and *Thyrothorus nigricapillus*. These birds are abundant outside the forest in shrubbery along riversides, second-growth thickets and overgrown edges, or bushy ground cover. *Ramphocelus* and *T. atrogularis* do not enter the forest at all; *Mitrospingus* and *T. nigricapillus* do occur in forest but only in the right habitats. My experiences in cut-over country or in altered forest in other parts of the Caribbean lowlands complement these sorts of observations at "La Selva." It appears that for certain species the habitat need only be physiognomically attractive, whether present in one life zone (formation) or more than one, that for other species the habitat must be located in a particular life zone (formation), whereas other species do well in various habitats in several life zones (formations).

Of the birds occurring typically in open or semi-open country on the west side of the Río Sarapiquí, some are found commonly over all the semi-open parts (i.e., tree plantations) of the study area, whereas others occur uncommonly. Some species are more or less confined to the Point: examples are *Capsiempis flaveola* and *Tachyphonus rufus*. Several have occurred only once at the Point, or a few times mostly at the Point: examples are *Columbigallina talpacoti* and *Elaenia flavogaster*, each seen only once; *Tyrannus melancholicus* and *Progne chalybea*, seen a few times. *Psilorhinus*, as another kind of example, seems to be pioneering the Sarapiquí region in increasing numbers; small, exploratory parties of this aggressive bird have begun to arrive occasionally on the study area, so far only at the Point. Still other species I have never seen on the "La Selva" side of the Río Sarapiquí: examples are *Troglodytes musculus* and *Sturnella magna*. On the other hand, many birds that are typically forest inhabiting at "La Selva" occur regularly in the tree plantations bordering the forest, but are uncommon to rare or absent at the Point. It appears that characteristic forest species may leave the forest for the neighboring semi-open, but typical inhabitants of open or semi-open country barely enter the forest, if at all. A third set of common birds is not restricted either to forest or to the semi-open and seems to be equally well adapted to both.

The species of hummingbirds at "La Selva" show within a single family the types of occurrences, seasonal alterations in distribution, and fluctuations in numbers that are shown by the native avifauna as a whole. Certain species are to be found exclusively or in greatest abundance at the Point; others inhabit second growth and forest but may also enter the semi-open areas. There are rarities, such as *Phaeochroa cuvierii*, which has never before been reported for the Caribbean slope, or *Amazilia cyanura*, which has been found only once before in Costa Rica. Others, such as *Popelairia conversii*, occur as

stragglers from the subtropical belt. Certain species, particularly some that prefer the Point, may be common seasonally and then may disappear for months. Others are to be found irregularly, almost accidentally, at intervals throughout the year.

Among the native avifauna, certain non-forest birds may occur as accidentals, e.g., *Aramus guarauna* and *Platypsaris aglaiae*. Some species pass over the study area, apparently seasonally, in small numbers, including such transients as *Mycteria americana* and, along the river, *Cairina moschata*. Here, too, may be included *Phalacrocorax olivaceus*, of which flocks pass high overhead from time to time, although single birds occur with fair regularity along the river. *Notharchus tectus* (previously recorded only once for the country) may appear at highly irregular intervals at any time of year.

Native birds normally resident in forested or semi-open country at higher elevations may arrive as casual visitants or accidentals. Among them, *Turdus albicollis* I have seen only once; *Trogon collaris*, several times (undoubtedly the same bird); *Procnias tricarunculata*, twice; *Myrmeciza immaculata*, once; *Tanagra anneae*, once. Several species appeared at "La Selva" for days or weeks at a time coinciding with a period of bad weather in the highlands. These include such unlooked-for species as *Leucopternis princeps* and *Pheucticus chrysopeplus*.

Some native birds remain for five or six months or more but not the entire year. For the most part they seem to be winter residents (in the North American sense); a few probably breed at "La Selva." A striking example of a non-breeding visitant is *Cephalopterus glabricollis*. Finding *Cephalopterus*, a bird I customarily associated with cool temperatures, was completely unexpected. My surprise continued as I saw it periodically for several months. The evidence for seasonal movement is provided fortuitously by Delacour (1943, p. 30): "Mr. Cordier left New York for Costa Rica on 4th March, 1942. He established a collecting base on the Cataratas River, several days' travel north of San José, the capital, and on the banks of this river at an altitude of 3,000 feet, he caught his first Umbrella Bird. The area is on the Atlantic slope of the continental divide where the rain falls constantly eleven months of the year. Although Umbrella Birds are supposed to range over all of Costa Rica, Mr. Cordier saw them nowhere except around the Cataratas River, and a journey of an hour and a half carried him out of Umbrella Bird country." Previously I had met with *Cephalopterus* during the same time of year as had Cordier, always along cool, wet-forested ridges at altitudes of about 3000 feet on the Caribbean slope and also along the continental divide in the northwest. Later in the year, in August, I had seen umbrella-birds at lower elevations in the wet foothills on the north side of Turrialba Volcano, at the time of year corresponding to their return to "La Selva."

Odd, as yet unexplained situations cropped up at "La Selva." *Micrastur semitorquatus* I had found several times during earlier visits, but in the entire year on the study area I did not find it at all. Instead, on two occasions I saw *Micrastur mirandollei*, one of the rarest birds in Costa Rica (one 85-year-old record). *Micrastur mirandollei*, here at its northern limit, is scarce through much of its geographic range. It seems to be confined to areas of heavy rainfall in the tropical belt, unlike the ecologically wide-ranging, relatively common *M. semitorquatus*. I suspect that *mirandollei* prefers virgin forest; *semitorquatus*, judging from my experience with the species, does not penetrate deeply into solid forest, but occurs along forest borders, in thinned woodland, abandoned plantations, patches of forest, and the like. Both of these birds of prey seem to be wanderers.

Another mystery concerns *Pipra mentalis*, one of the common birds at "La Selva." For a couple of weeks, despite an intensive search, I did not find a single bird; for several weeks it was actually rare. At about the same time that *Pipra* was becoming scarce, another manakin, *Corapipo leucorrhoa*, a subtropical species I did not expect at "La Selva," had already appeared and was increasing in numbers. *Corapipo* remained from December through February, then vanished; it should be added that subsequently I saw one male in July and another male (perhaps the same bird) once in August, but no other individuals from March through November. *Pipra* was (apparently) absent when *Corapipo* was most abundant. *Corapipo* was represented by

adult males, immature males, and females; it gave no sign of courtship activity. Occasionally, when the two species were feeding on the same shrub, *Pipra* behaved aggressively towards *Corapipo*. The duration of the apparent absence of *Pipra*, or at any rate of its great scarcity, was much too short to account for a migration by the species away from and back to the study area. *Pipra mentalis* is a very conspicuous bird, so I am certain of the fact of its temporary decline.

Peculiar, too, are the circumstances regarding *Rhytipterna holerythra*. This cotinga was common at "La Selva" most of the year, except for a short period from July through early September. I put forth special efforts to find it during those months, but was unsuccessful in July, observed it once in August, not at all in the first part of September, then an increasing number of times in the latter half of the month. It may perhaps be of more than passing interest that *Lipaugus unirufus*, which is confusingly similar in appearance, is present in unabated abundance the year round.

The long-distance, or intercontinental, migrants (including three neotropical species) also show a graded series of occurrences, from accidental to winter resident. Some of the transients may be present in large numbers for several weeks. The winter residents, which remain from four to usually six or maybe eight months, seem to form an integral part of the avifauna. They occupy some of the habitats and partake of the food supply for a sufficient length of time to affect, presumably, the local birds competitively. For only two and one-half months are no migrants present. For the majority of the non-resident (transient) migrants the fall migration (from North America) is far more pronounced than the spring migration (to North America), and in the fall occur a number of species not recorded at all, or perhaps only once or twice, in the spring. (See fig. 1.)

An example of an accidental migrant is *Piranga ludoviciana*, which was seen only once (on two consecutive days); it is a species seldom reported for Costa Rica, never before from the lower Caribbean slope. An example of a casual visitant is *Passerina cyanea*, which I found only in the month of February. An irregular visitant is *Dendroica coronata*, which appeared in small groups several times during the winter months. Neither *Passerina* nor *D. coronata* was noted in the spring or fall; both winter regularly in Costa Rica.

Transients are birds "passing through, en route between a summer and winter residence, both of which are outside the area concerned" (Palmer, 1949, p. 16). For the area concerned, this definition is useful if it be borne in mind that a bird that is transient at "La Selva" may pass completely beyond Costa Rica, or remain for the winter elsewhere in the country, or do both. Examples of rare transients having different patterns of occurrence are *Hylocichla minima*, seen once in the fall, of which a few individuals remain to winter elsewhere in the country; *Wilsonia pusilla*, also seen once in the fall, which winters elsewhere in the country in very large numbers; *Oporornis philadelphia*, which was seen not in the fall but once at the end of February and twice during the spring, and which winters commonly elsewhere in the country; and *Dendroica virens*, seen very few times both in the spring and fall, which winters commonly elsewhere in the country.

Then there are transients, as *Dendroica cerulea*, that are common in the fall on passage to South America, and others, such as *Dendroica fusca*, that are very abundant in the fall and remain, in part, to spend the winter elsewhere in the country; both were absent from "La Selva" during the spring migration. There are transients, such as *Setophaga ruticilla*, that are common in the fall, uncommon in the spring, and spend the winter elsewhere in the country. Others, as *Wilsonia canadensis*, are extremely abundant in the fall, present but rare in the spring, and absent from the country in winter.

The only species that I found a number of times at "La Selva" in the spring but never in the fall is *Vireo philadelphicus*. No transient that was rare in the spring was absent in the fall; rather, it was always (with the possible exception of *Dendroica virens*) more common in the fall. Another kind of transient is exemplified by *Buteo swainsoni*, which in spring and fall passes over "La Selva" in very large numbers, but alights very seldom either to roost at nightfall or to seek shelter during stormy weather.

A few normally transient species also ap-

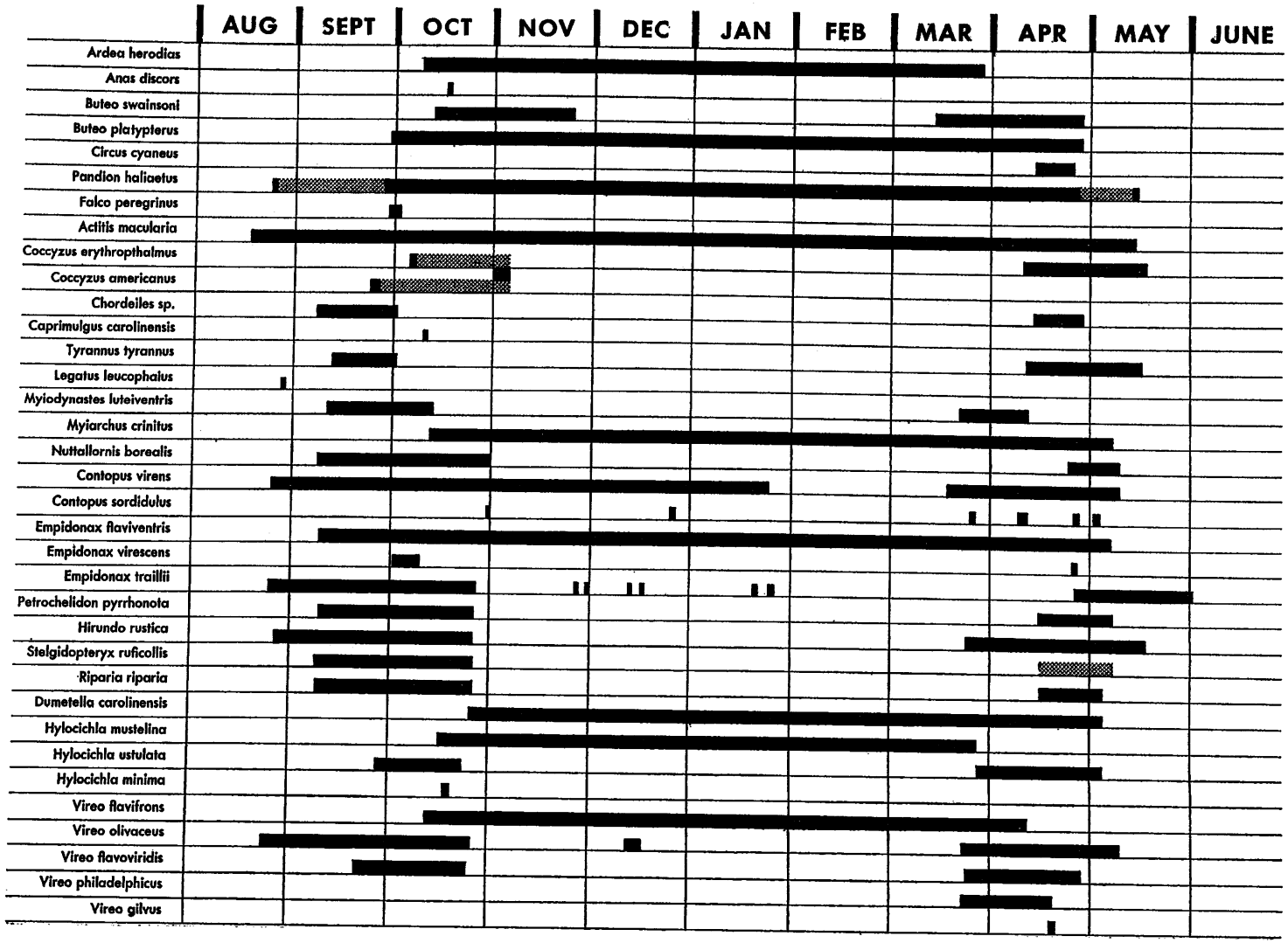

FIG. 1. (See legend below).

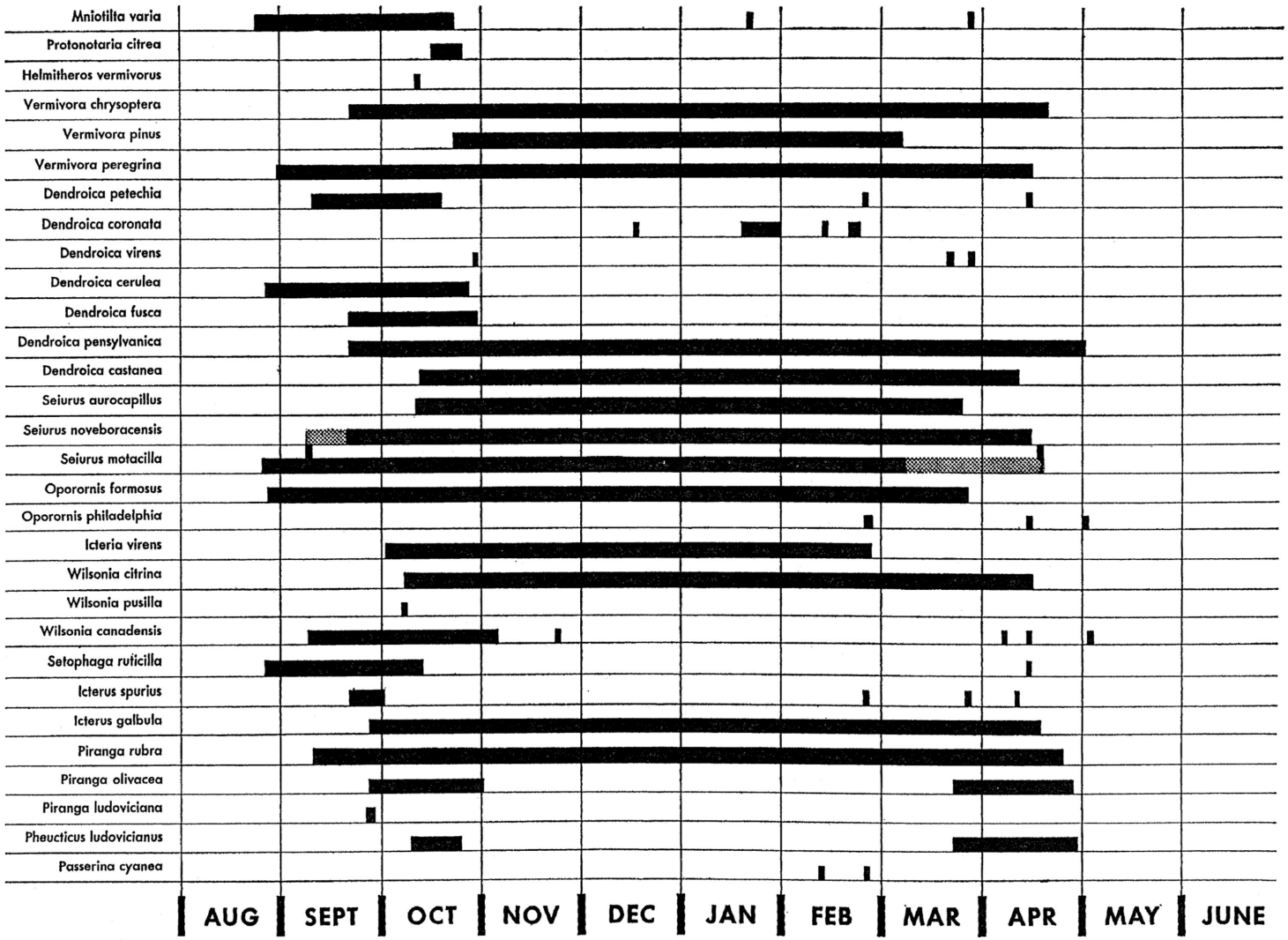

FIG. 1. List of migrant birds recorded from Finca "La Selva." Stippled portions of bars show probable occurrence.

peared occasionally as visitants during the winter months. *Vireo olivaceus*, for example, is abundant as a passage migrant in the spring and fall, not only at "La Selva" but in Costa Rica generally, yet a few individuals visited a fruiting tree for several days in mid-December during a spell of very bad weather covering the entire Caribbean side of the country. Its occurrence at "La Selva" indicates that some individuals do remain in the country, apparently as wanderers. An example of another sort is *Dendroica petechia*, a very common winter resident in much of Costa Rica, which at "La Selva" was regular but not common in the fall, was seen once during the winter, and was rare in the spring; but in spring migration it was common just across the Río Sarapiquí from the study area. *Mniotilta varia* was common during the fall, but, surprisingly, as it is essentially a woodland species, it was rare in the spring and during the winter.

Migrants that are winter residents at "La Selva" also show specific differences, as do the transients, in qualitative and quantitative aspects of occurrence. Some, as *Dendroica pensylvanica*, are common during the winter, when a number of individuals may be seen daily, and abundant during both periods of active migration. Others, as *Empidonax flaviventris*, also can be found daily, but in much smaller numbers; in the spring or fall they do not appear suddenly in flushes or waves. *Vireo flavifrons*, a species less common than the preceding, was to be found at less frequent intervals during its stay. Another type of occurrence is that shown by *Dendroica castanea*, which was a common transient in October, but which I saw relatively few times throughout the winter. *Vermivora pinus* I found once in the fall, once in the spring, and twice during the winter; its status is that of a very uncommon transient and winter resident. In addition, there are winter residents, such as *Hylocichla mustelina*, which can be met with several times daily during the first half of their winter stay, then become progressively less vocal and harder to see during the second half of their stay; I feel certain that their actual numbers do decrease drastically.

Neotropical migrants number at least three species: *Myiodynastes luteiventris*, *Legatus leucophaius*, and *Vireo flavoviridis*. At "La Selva" they were noted only as transients on their way north or south. They migrate over much of Costa Rica, where large populations remain as breeding summer residents. Of the three, *Legatus* was the least common, having been seen only in the fall on one occasion; oddly, it is the only one of the three that occurs as a summer resident in the Caribbean lowlands, including the other side of the Río Sarapiquí, not much more than a stone's throw from the tip of the study area. Figure 1 shows that both *Vireo flavoviridis* and *V. olivaceus* migrate north or south at the same time; in the spring, *olivaceus* was silent whereas *flavoviridis* sang freely.

Another group of migrants (not included in fig. 1) consists of the kites, *Elanoïdes forficatus* and *Ictinia plumbea*, and the vulture, *Cathartes aura*. *Elanoïdes* and *Ictinia* pass over "La Selva," both in spring and fall, considerably earlier than the North American hawks: *Elanoïdes* passes over from February to March and April, and from July to the first days of September; *Ictinia*, in February and from the latter part of July through August. *Cathartes* also begins to migrate very early in the spring, from the latter half of January onward through the first week in May, but its return migration coincides with that of the swarms of migrating hawks in the fall.

Having a somewhat different status are several year-round residents in Costa Rica that, as species, behave as wintering migrants at "La Selva." *Florida caerulea*, for example, was seen commonly in winter; although present in summer, it was rare. Probably many migrant individuals from the north greatly augment the presumably sparse native population in winter. *Leucophoyx thula* I saw only three times, in February and March; elsewhere in the country it is much more common in winter than in summer, when it is relatively rare. The same holds for *Casmerodius albus*, which I saw only once at "La Selva."

The number of species of birds now known from the study area is 331, a rather astonishingly high total. The list could be extended by adding those species that I personally saw in the vicinity of "La Selva" and others that were clearly described to me by people who live in the vicinity. Among the hawks migrat-

ing too high to be identified, there were undoubtedly a few unrecorded kinds. On the study area itself I suspect the presence of at least one more caprimulgid, another rail or two, one more owl, and probably other swifts. Otherwise, I feel confident that, except for accidentals, I found all the species to within 1 per cent of the total.

It is noteworthy that "La Selva," although at a low elevation above sea level, lies more than 50 kilometers inland, that the rivers are not affected by tides, and that there are no mangroves, ponds, or field habitat. No sea birds pass overhead; no terns come up the river system. There are no grebes, jaçanas, gallinules, or coots, virtually no ducks (only two rarely seen transients), and only one shore bird (a migrant). There are relatively few kinds of pigeons, hummingbirds, ovenbirds, wrens, thrushes, and finches. The following circumstances help explain the presence of the many species that have been found there. "La Selva" is situated in the Nicaraguan "break," which, to my surprise, turned out to be a flyway; both the "break" and the line of flight of the high-flying migrants (hawks, nighthawks, swallows) parallel the northwest-southeast strike of the Costa Rican mountains. Transients, therefore, help swell the list. Also, the study area is situated not very far from the slopes of the Cordillera Central, a source for native wanderers and strays. In addition, there are other neotropical species which, as might be expected, appear as rarities. A collector visiting the area almost certainly would obtain a sampling of some of these. A long stay enables the observer to evaluate occurrence, abundance, distribution, and ecological preference.

In the Annotated List the species are listed by family. Within each family the differences or similarities between related birds are indicated, especially among congeneric species which may, or may not, occur together, and which can often be segregated ecologically. For instance, *Grallaria fulviventris* and *G. perspicillata* are very similar in appearance and occur together in the same area, but they occupy distinctly different habitats and have correspondingly different habits. *Hylophilus decurtatus* and *H. ochraceiceps* both occur in forest where, however, they occupy different strata. The three species of *Tachyphonus* sort out rather neatly by habit and habitat, as do the three species of *Todirostrum*. On the other hand, the two big toucans, *Ramphastos sulfuratus* and *R. swainsonii*, seem to do exactly the same things in the same places at the same time, appear to be equally abundant, and are conspicuous, perhaps even dominant, species.

In the Ecological Classification the annotated list is broken down into various categories containing birds of similar habitat, similar habits, or similar occurrence and distribution. Thus, species associated in feeding aggregations will be seen to perform different functions in the assemblage. For other species, differences in behavior can be deduced from differences in morphology. By sifting and eliminating and by analyzing habitat, habit, and distribution, one can work out ecological arrangements cutting across taxonomic lines.

The tropical region has the world's richest floras and faunas, and its 38 life zones (formations) are missing from the rest of the globe. The biota of the temperate and cold regions, from the study of which so many ecological principles have been derived, consists perhaps of specialized appendages put forth from the great body of the tropics. Central American floras and faunas should be studied before the forests are further decimated, chopped into islands, and soon destroyed.

My work with the birds at "La Selva" is summarized in the present report. On the same property, Janis Petriceks, of the Facultad Forestal, Universidad de los Andes, Mérida, Venezuela, has conducted a forest survey, and it is he who cut the cruising lines through the forest. A sample forest plot is being maintained by the Inter-American Institute of Agricultural Sciences, Turrialba, Costa Rica. From time to time foresters of the Ministerio de Agricultura de Costa Rica visit the site. Here, too, Edith Scamman has made a comprehensive fern collection for the Harvard Herbarium. Bernice Schubert, of the United States Department of Agriculture, has visited "La Selva" in search of alkaloids. Edward H. Taylor, of the University of Kansas, has collected reptiles and amphibians. L. Irby Davis and Mrs. Davis, in collaboration with the Laboratory of Ornithology at Cornell University, have recorded bird voices.

Other foreign visitors include Milton Stelzer, entomologist from the University of Wisconsin; Robert MacArthur, of the Osborn Zoological Laboratory at Yale University, accompanied by Mrs. MacArthur; ex-King Leopold of Belgium and his party, who made natural history collections and took many photographs; Luis R. Rivas, ichthyologist, of the University of Miami; Arnold G. Kluge, Arden Brown, Jr., and Robert J. Lavenberg, herpetologists, of the University of Southern California; Paul Martin, of the Geochronology Laboratories, University of Arizona; and Joseph A. Tosi, Jr., forester and ecologist, Project 39, Lima, Peru.

ACKNOWLEDGMENTS

With pleasure I take this opportunity to express my gratitude to Dr. Leslie R. Holdridge and Mrs. Lydia Holdridge, who wholeheartedly welcomed me to spend an entire year at Finca "La Selva," to occupy their house, and to carry on my work in whatever way I pleased. I thank Dr. Holdridge additionally for his kindness in answering my many questions about the vegetation. Financial assistance enabling me to spend the year in the field was generously provided by the University of Michigan Museum of Zoology in the form of an Edwin C. Hinsdale Scholarship award. Meteorological equipment was lent to me freely by the Department of Zoology of the University of Michigan. I am grateful to Dr. J. Robert Hunter and to Prof. Elliott Coen for Costa Rican weather data which they promptly secured for me. I am indebted to Mr. Janis Petriceks for his permission to quote liberally from his silvicultural reconnaissance of Finca "La Selva" (MS). Permission to quote from "Zoogeography: the geographical distribution of animals," by Philip J. Darlington, Jr. (1957), was given by the publisher, John Wiley and Sons, Inc. The manuscript was read critically by Drs. Robert W. Storer, Rogers McVaugh, Laurence C. Stuart, and Harrison B. Tordoff, the members of my doctoral committee at the University of Michigan. This project could not have been undertaken if I had not been prepared by the several years I had spent in Costa Rica, and I wish to thank my friends, acquaintances, and even absolute strangers in Costa Rica for their courtesy and help during those years.

FIG. 2. Physical map of Costa Rica. Arrow points to site of Finca "La Selva." Reproduced from "Atlas Estadístico de Costa Rica," 1953, Dirección General de Estadística y Censos, Ministerio de Economía y Hacienda, San José, Costa Rica.

THE ENVIRONMENT

LOCATION

FINCA "LA SELVA" is located in Heredia Province in the Sarapiquí region of the northeastern Caribbean lowlands of Costa Rica. The region, named after the Río Sarapiquí which drains it, lies north of the Cordillera Central and between the Llanuras de San Carlos on the west and the Llanuras de Tortuguero and de Santa Clara on the east (fig. 2). Situated at latitude 10° 30′ N. and longitude 84° W., well inland at the junction of the Río Puerto Viejo and the Río Sarapiquí, the finca is over 50 kilometers distant from the Caribbean coast and about 30 kilometers from the Nicaraguan border. The nearest settlement, about 1 kilometer downstream from the tip of the study area, is the village of Puerto Viejo (not to be confused with Puerto Viejo [Old Harbor] on the Caribbean coast in Limón Province). The village lies on the left bank of the Río Sarapiquí and is the terminus of the only road leading into the region. Hence "La Selva," upstream on the opposite side of the river, can be reached easily only by boat.

PHYSIOGRAPHY

The material under this heading I have translated and summarized from Petriceks (MS).

The finca occupies a zone of transition between hills and level ground. The main portion is rectangular, with an average width and length of 2 and 3 kilometers, respectively. The total area is 613 hectares (approximately 1500 acres). (See pl. 9 and text fig. 3.) There are two rather level tracts: (1) north of the quebrada (stream) El Surá, except for a small elevation in the southwest, and including two small swamps in the center; (2) east of the quebrada El Salto and extending 1.2 kilometers from the Río Puerto Viejo, with the southern portion swampy. There are two lesser depressions, of 5.5 and 4 hectares each, some 600 meters to the south of the Surá. The rest of the area has broken terrain, with slopes reaching 80 per cent in extreme cases. The most broken portion is in the southwest of the property; also, along the east boundary there is a zone with steep inclines. Where a small hill separates the basins of the Surá and the Salto, the abrupt slopes reach to the Río Puerto Viejo. About 150 hectares are level, another 150 hectares have slopes greater than 30 per cent, and the remaining half of the finca has slopes of 5 to 30 per cent.

The elevation above sea level varies from 100 meters along the Río Puerto Viejo to 220 meters near the southwest boundary on the left bank of the quebrada El Salto. The mean elevation is 140 meters.

Watercourses are numerous. The finca lies east of the Río Sarapiquí and is bounded on the north (or northeast) by the Río Puerto Viejo, from its confluence with the Sarapiquí eastward to the quebrada El Sábalo. The property is drained by the quebradas El Surá and El Salto. The basin of the latter, with its tangle of tributaries, occupies 70 per cent of the entire area. The quebradas and almost all the quebraditas have running water the year round.

There are three classes of soil: (1) a zonal clay soil, deep and well drained, underlying most of the high virgin forest; (2) an interzonal soil, with a high water table and poor drainage, associated with swampy high forest; (3) an azonal soil of recent alluvial origin which is more fertile than the others, associated with riparian strips given over to plantation crops.

CLIMATE

RAINFALL

At "La Selva," from October 1, 1957, to September 30, 1958, the rainfall was 3810 mm. At the village of Puerto Viejo, 4066 mm. were recorded for the same period. La Virgen, 15 kilometers to the southwest at an elevation of about 300 meters, had a total of 4501 mm. for the year. Barra del Colorado, on the coast

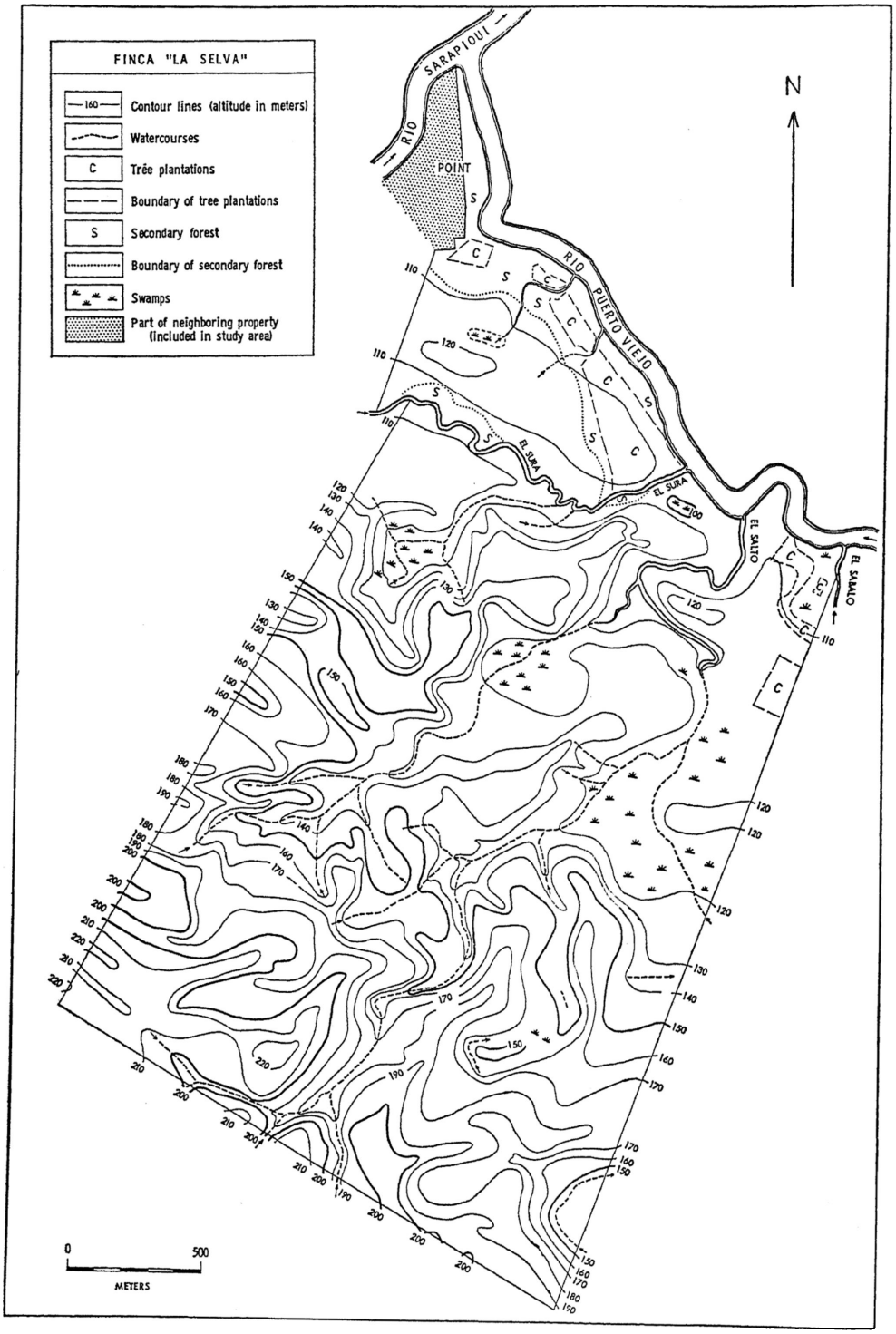

FIG. 3. Topographic map of Finca "La Selva." Redrawn from a map by J. Petriceks (MS).

57 kilometers to the northeast, reported 7184 mm. between the same dates. At Los Diamantes, 35 kilometers southeast of "La Selva" and at an elevation of about 300 meters, the figure was 4900 mm.; this station, the only one with a long-term record, has a 16-year average of 4503 mm.

TEMPERATURE

At "La Selva," from November 21, 1957, to September 1, 1958, the mean temperature, measured in the shade in the open (pl. 11, fig. 2) was 26.1° C. The maximum was 35.5° C., on March 25 and again on April 16, 1958; the minimum was 17.8° C., during the early morning of January 17, 1958. In the forest (pl. 12) the mean was 24.5° C. (Owing to circumstances beyond my control, I was unable to record temperatures from the date of my arrival in September until November 21.) At the village of Puerto Viejo, from March, 1955, to March, 1956 (December, 1955, lacking), the mean was 25.3° C. At Barra del Colorado, the mean for 1952 was 27.2° C.

REMARKS

Climatological data for the region are almost entirely lacking. Those that do exist are mostly of short-term duration, or unreliable, or both. Nevertheless, this Tropical Wet Forest Life Zone (Formation) can be characterized by the vegetation. The few weather data confirm the findings and predictions of the plant ecologist.

The northeastern lowlands are subjected to very high rainfall. The annual average exceeds 4 meters, and may surpass 6 meters at the mouth of the Río San Juan (Coen, 1953, p. 34). Mean temperatures range from a lower limit of 24° C. at the transition to the subtropical belt to nearly 28° C. at some coastal localities.

At "La Selva" the yearly rainfall undoubtedly averages well over 4000 mm. Long-term evidence is provided by the vegetation, both in physiognomy and in the presence of wet-forest species. On a short-term basis, my one-year rainfall figure of 3810 mm., although somewhat below the 4000 mm. minimum (see p. 74), is really corroborative evidence. The year 1958 was unusually, perhaps exceptionally, dry, and people native to the area commented on this fact. Even so, the nearby station at Puerto Viejo recorded a bit more than the 4000-mm. minimum. During the year, the rainfall regimen deviated little from the normal pattern for the Caribbean slope: the rains become progressively heaviest from October to December, slacken in January or late December, and decrease considerably during a "summer" season lasting from February into April; then, the rainfall mounts in May, June, and July, and this wet period is usually followed by a "little summer" during August and September. Figure 4 shows for the month of February a high total which probably would be dissipated upon incorporation into a long-term record.

Temperatures at "La Selva" appear to average between 25° and 26° C. when taken in the shade in a clearing; in the forest (at the same breast height above the ground), about 1.5°C. lower. Of interest in this regard are the almost identical minima, within half a degree of each other, in the open and in the forest. By contrast, figure 4 shows a considerable divergence between the two maxima, most pronounced on clear, sunny days. In fact, the maxima in the forest nearly approximate the mean between the maxima and minima in the open. As a mark of tropical climates, the daily range in temperature is greater than the seasonal range. Figure 4, although designed to show the averages for seven- to eight-day periods, demonstrates this clearly. In addition, figure 4 indicates a yearly march of temperature to be expected at latitude 10.5° N. The season of slightly higher average temperatures coincides in general with the longer-day months, but more particularly with the sunny days of the March-April summer.

There are direct and inverse correlations between maximum and minimum temperatures as well as between temperatures and precipitation or high humidity (fig. 4). The inverse relationship between maxima and minima is well marked during the long-day periods of little rainfall or evenly distributed rainfall. During the December-February period, however, the maxima and minima rise and fall in unison when the precipitation is unusually heavy. The low minima characterizing the short-day season also correlate with the incidence of northers, the weakened effects of which in Caribbean Costa Rica postdate the advent of a cold wave in the temperate north.

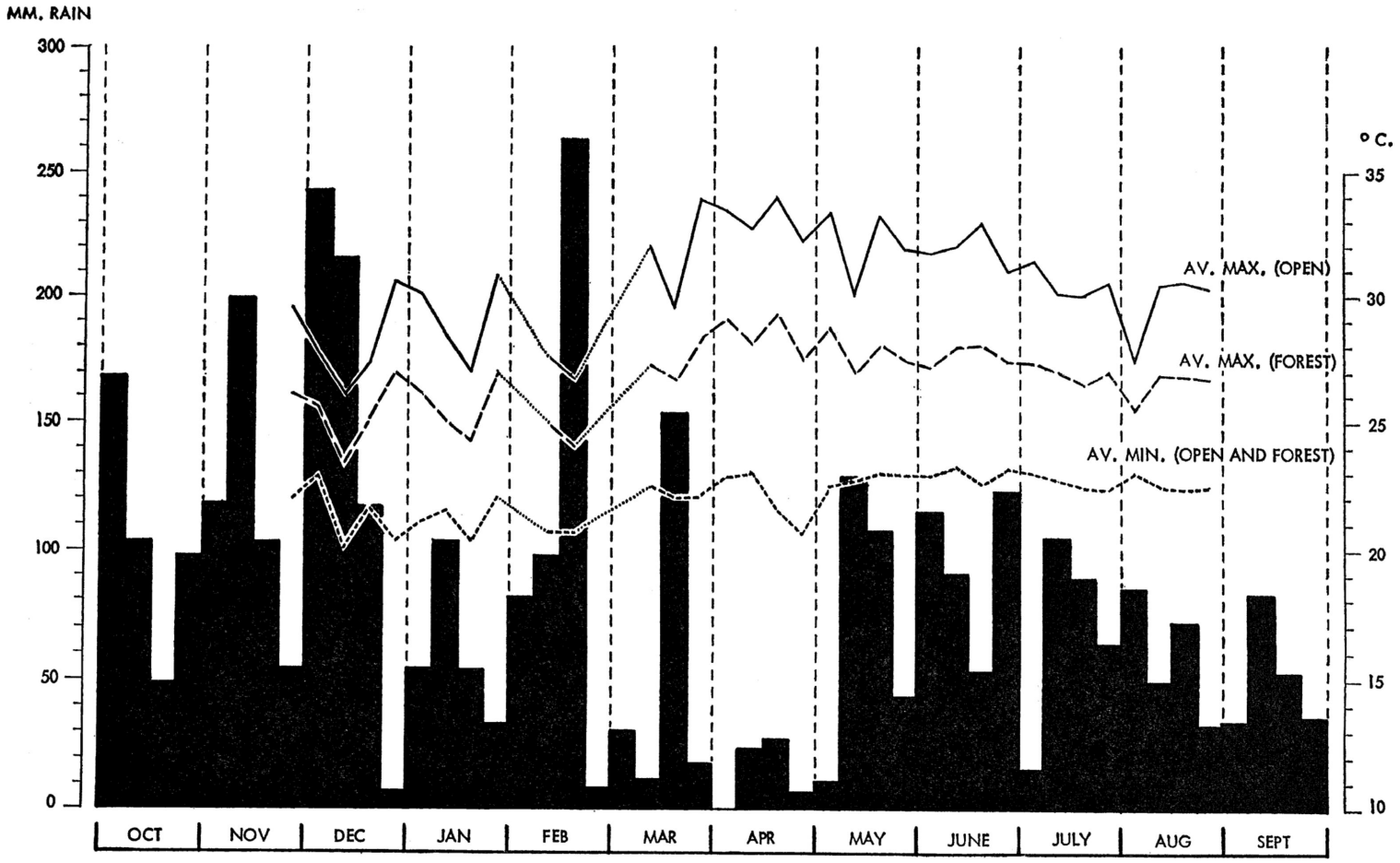

FIG. 4. Rainfall histogram and temperature graph, October, 1957, through September, 1958. Rainfall shown as quarter-monthly totals. Incomplete portions of graph represent periods when no data were obtained.

The very low minimum during the last quarter of April may have been due to a local phenomenon produced by clear weather and gravitational influx of cool air from the slopes of the Cordillera Central.

Although hurricanes seem to be unknown in Costa Rica, a factor of possible importance at "La Selva" is the occasional occurrence of strong winds of short duration, which can knock down the biggest tree. They may constitute an atmospheric factor that conceivably could modify the numerical specific composition and physiognomy of the forests of the region. These powerful winds arrive from an easterly or a westerly direction. For the most part, the region is under the almost constant influence of the trade winds coming from the northeast, east, or southeast. However, cloud movements in the upper air are complex and variable. The lack of adequate meteorological observations may be the reason why a satisfactory explanation of the high rainfall arc covering northeastern Costa Rica and southeastern Nicaragua, centered at the mouth of the Río San Juan, has not yet been advanced.

VEGETATION

The material under this heading I have translated and summarized from Petriceks (MS) and I have interpolated a number of data and observations kindly supplied by L. R. Holdridge (personal letters).

DESCRIPTION

The vegetation belongs to the life zone (formation) Tropical Wet Forest of the Holdridge classification (1947; 1957, p. 151). Within the area, five types (subdivisions) are found: (1) high virgin forest on solid ground; (2) swampy high forest; (3) swamps with few trees; (4) secondary forest; and (5) agricultural (text fig. 3; pls. 13–26).

1. The high virgin forest on solid ground occupies 521 of the 613 hectares of the finca. The tree flora, estimated at slightly more than 200 species, is over 90 per cent evergreen; approximately 25 per cent of the species have buttresses. Owing to the topographic variation, there is also a certain variation in the vegetation. Although sufficient differences have not yet been diagnosed for the categorizing of lesser divisions, additional investigation should lead to a more detailed arrangement. To this forest can be given the tentative designation: association dominated by *Pentaclethra*, the most characteristic species.

The strata are not well differentiated. The canopy, except where fallen trees have produced small openings (see pl. 26), is almost completely closed and has an average height of 30 to 36 meters, with emergents surpassing 50 meters. The species of the second stratum vary between 15 and 25 meters in height; it is likely that this stratum is composed really of two layers. The stratum of shrubs and tall herbs is relatively thin, with the exception of valley bottoms (pl. 8; pl. 24, fig. 2). About 80 per cent of the forest floor is covered by herbs and seedlings. In openings larger than 100 square meters, secondary vegetation is always formed.

The number of species of trees with a diameter of more than 20 cm. is around 140. Individual trees measuring over 20 cm. in diameter comprise one-fifth of all the individuals more than 5 cm. in diameter. Of the trees with a diameter over 20 cm., 29 per cent exceed 50 cm., and 6 per cent exceed 80 cm. The species with diameters over 100 cm. are: quebracho (*Pentaclethra macroloba*), cedro macho (*Carapa guianensis*), caoba or olla de mono (*Lecythis costaricensis*), cocora (*Guarea* sp.), manga larga (*Flacourtiaceae*), cacho venado (*Vitex cooperi*), roble (*Terminalia bucidoides*), ascá (*Hieronyma alchorneoides*), tapabotija (*Apeiba aspera*), and ceiba (*Ceiba pentandra*). The dominant species, quebracho, constitutes 37 per cent of all the trees more than 20 cm. in diameter.

The trees with stilt roots are: *Cecropia*, *Bravaisia*, and *Protium*.

Palms are common. The principal species are *Welfia Georgii*, *Socratea durissima*, *Iriartea gigantea*, *Astrocaryum alatum*, and *Cryosophila* sp., which form part of the second stratum. Smaller species include a *Euterpe* and dwarf palms of the genera *Geonoma* and *Asterogyne*. A spiny climbing palm like a rattan is *Desmoncus*.

Vines are frequent but do not have a regu-

lar distribution over the area; epiphytes are numerous and occur at all heights on the trees. There are bromeliads, orchids (mainly high up), ferns, vines such as *Philodendron* spp. and *Monstera*, shrubs such as *Clusia* and *Ficus* (young), and herbaceous plants like *Peperomia*. A big, pineapple-like, terrestrial bromeliad forming impenetrable mats is *Aechmea magdalenae*. There are three or four tree ferns, many small ferns on the tree trunks, and the little, rosette-leaved *Danaea Wendlandei* is common on the forest floor. Many of the 100 plus ferns grow along stream banks or in openings or on the trunks. The only cycad, *Zamia Skinneri*, is not common. Mistletoes are very scarce.

2. A kind of forest determined by edaphic factors, and differing from the preceding, occurs on swampy terrain, with a total extension of 35 hectares, chiefly in the southeastern part of the finca. The tree species number only about 24, and all appear to be evergreen. Trunk buttressing is present in over 50 per cent of the species. It can be called the *Carapa-Pentaclethra* association, after the two principal species (pl. 22, fig. 2; pl. 23).

The canopy is rather closed, and there are not many fallen trees. The canopy is less uniform than in the association dominated by *Pentaclethra* alone; its height varies from 32 to 45 meters, with emergents to 55 meters. The second stratum is very irregular, from 15 to 28 meters in height. The understory varies from place to place: very dense, or (especially where there is standing water) relatively thin.

All the species of trees possess individuals measuring over 20 cm. in diameter. These account for nearly 30 per cent of the trees greater than 5 cm. in diameter. The species over 100 cm. in diameter are: cedro macho (*Carapa guianensis*), quebracho (*Pentaclethra macroloba*), and caoba or olla de mono (*Lecythis costaricensis*). Of the dominant species, quebracho is represented by 37 per cent of all the trees, cedro macho by 22 per cent.

Palms are numerous, especially in the lower level. Large and small vines occur frequently, upon some trees in great abundance. The epiphytes, as in the rest of the forest, are abundant at all heights. Mistletoes were not noted.

Although quebracho is greater in number and produces seeds abundantly, reproduction is less frequent than in the forest on solid ground. Here, cedro macho dominates as much in height as in volume, yet its seedlings are scarce.

3. There are two small, swampy areas in the center of the property where the character of the forest differs notably from the one just described. The number of species diminishes still more, the heights are much reduced, and cedro macho lessens in number. A detailed description of these areas was not made.

True swamps occur near the Río Puerto Viejo over an area of 3.2 hectares. This area contains stagnant water, and the floor is softer than in the forested swamps. It is covered by grasses 30 to 50 cm. in height and includes some trees, the heights of which do not exceed 20 meters, concentrated on firmer parts of the ground.

4. The secondary forest consists of two areas: one of 7 hectares along the quebrada El Surá, and another of 17 hectares along the Río Puerto Viejo.

The part near the Surá is the older (approximately 18 years) and exhibits the typical aspect of the third stage in a secondary succession. The principal species are: guácimo blanco (*Goethalsia meiantha*), jobo (*Spondias mombin*), guava (*Inga* spp.), guarumo (*Cecropia obtusifolia*), and burío blanco (*Heliocarpus appendiculatus*). Also there are trees that have remained from the original forest, such as surá (*Terminalia lucida*). The height of the canopy varies from 20 to 25 meters, with few emergents. The low vegetation is dense, and there is little reproduction of species from the high forest.

The secondary forest along the Río Puerto Viejo has an age of about 13 years and is largely in the second stage of secondary succession, with the third stage starting in places (see pl. 13, fig. 1). The height is very irregular. The more frequent species are: balsa (*Ochroma lagopus*), laurel (*Cordia alliodora*), burío ratón (*Hampea appendiculata*), hule (*Castilla elastica*), burío blanco (*Heliocarpus appendiculatus*), and others. Also, there are residual trees of the virgin forest: quebracho (*Pentaclethra macroloba*), surá

(*Terminalia lucida*), and lagartillo blanco (*Zanthoxylum* sp.).

5. The agricultural portions are all tree plantations: cacao, rubber, and coffee. The oldest date from 1953. (See pl. 13, figs. 1 and 2; pl. 14.)

REMARKS

The characteristics of 94 per cent of the forested area are those of virgin selva. The mixture of species is uniform, that is, upon any small area are found trees of many species. The dominant tree, quebracho, almost never forms pure stands. Competition is very strong, especially in the stage between establishment of seedlings and entrance into the canopy. This is shown by the relatively small number of trees between 5 and 30 cm. in diameter (of the majority of the commercial species). The intensive struggle among the individuals for light has its repercussion in the length of the clear trunk, although this characteristic is also influenced by genetic factors.

The width of the crowns, in proportion to the height, is around 50 per cent for the dominant species. Nevertheless, there is great variation among individuals as among species.

Regeneration in some species, such as quebracho (*Pentaclethra macroloba*), cocora (*Guarea* sp.), and cotón (*Virola* sp.) is relatively frequent. Among the less frequently reproducing species are cedro macho (*Carapa guianensis*), cacho venado (*Vitex cooperi*), botaramas (*Vochysia ferruginea*), roble (*Terminalia bucidoides*), coaba or olla de mono (*Lecythis costaricensis*), surá (*Hieronyma alchorneoides*), and danto plomillo (*Sacoglottis* sp.). Information on regeneration and growth characteristics is quite scarce.

Considering the size of the trees, the root systems are superficial. In all the profiles examined the penetration of the roots did not exceed 1.25 meters. Observations on the fallen trees confirm the slight depth of the roots, in swampy areas as in well-drained ones.

On growth rhythm there are no data. Growth may be very rapid in the first year or years of life of a tree. If the opening for the young tree should not be sufficiently large, growth diminishes rapidly and is almost nil for years, until either the tree dies or an opening does appear into which its crown can penetrate. Under the latter condition there follows the stage during which the greatest growth of the tree probably takes place until physiological maturity. The dominants which persist for many years probably grow little in height and very little in diameter.

Thus the "La Selva" forest can be regarded as virgin, in a state of equilibrium with the environment, heterogeneous, and with one dominant species prevailing.

At present, it appears that some species, such as caoba (olla de mono), cacho venado, cedro macho, and others are relatively intolerant of other than highly specialized conditions; before so definite a declaration can be made, however, more information is needed. Possibly the scarcity of young individuals is due also to other factors, such as the destruction of seeds by animals, and root competition.

An interesting point is the character of the swampy high forest: the association *Carapa-Pentaclethra*. Because of the lack of aeration and the excess of water in the soil, one might expect an inferior (lower) vegetation. This is the case in such swampy areas as are generally known. Nevertheless, over its greatest extension the swampy forest at "La Selva" presents a vigorous aspect, with heights and volumes superior to the rest of the forest. Evidently this is caused by cedro macho, the prominence of which can be explained as due to an inherent suitability to the swampy conditions which are unfavorable for its competitors living in the rest of the forest. Also, it can be postulated that with improved drainage the vegetation of the small swamps would change to that existing in the large, wooded swamps.

DISCUSSION

So that the study area may not be given the false status of an isolated patch of tropical woodland, the "La Selva" forest must be related in some way to other tropical forests.

The animal ecologists have failed to devise or adhere to an unequivocal classification because of their apparent unwillingness to accept the basic patterns laid out by the plant ecologist. Instead, some of them attempt an integration of the plant and animal communities into a single biotic community. Animal and plant indicator species are used in conjunction to characterize a biotic region or province of continuous extent; this makes a comparison between geographically separated regions futile.

The concept of the biome, on the other hand, enjoys great popularity at present and has the most adherents, notably among ornithologists. The biome is said to correspond to the plant formation, but not quite, because of adjustments owing to the importance of the animals and the kinds of cover; the plant formation is said to be determined by the climax vegetation over a natural area. The biome has been elaborated almost restrictedly for temperate and cold North America, and biome types have been mapped coarsely for the world. No distinction is made, for example, between an equatorial grassland and a Siberian steppe. The placement of the coniferous forest biome, as another example, makes us wonder what should be done with the coniferous forests in Central America. "The fundamental and largest unit of plant-animal communities is the biome," concludes Pitelka (1941, p. 135). Miller (1951, pp. 531–532), analyzing the distribution of birds in California, voices his dissatisfaction. He does "not regard any one system as a master system," and proceeds "in accordance with [his] concepts of the major distributional systems, modifying them as seems required, pointing out some generalities which each reveals, and coördinating the several plans to the degree that seems permissible." This confession exposes the weaknesses of the plant-animal synthesis on the one hand, while revealing an arbitrary eclecticism to which an astute student has resorted on the other hand.

Allee and his co-authors (1949, p. 582) consider the vital point, while not professing conviction, that it "is more than ever evident in the characterization and discussion of the biomes that the animal component is in many respects secondary to the plant matrix and dependent upon it." This is the heart of the matter: the animal ecologist must (or should) follow the findings of the plant ecologist. Moreover, "no factor on a psychological plane can be admitted for plants" (Moreau, 1935, p. 188). For the Congo, Chapin's (1932, p. 209) sequence of cause and effect is of considerable interest: "Climatic factors, save perhaps the cold of the mountains, act upon birds through the vegetation," and, in general, "we may say that the principal plant associations have corresponding bird communities . . . and so the intimate connection between phytogeography and distributional ornithology is established."

"Animal communities do not ordinarily correlate with plant communities determined by the *species* of the plant dominants involved, but they do correlate with types of vegetation" (Kendeigh, 1952, p. 472). "These [physiognomic] characteristics recur throughout the Rain forest of the American and Old World tropics; in fact, they are typical of Rain forest wherever it exists and are not peculiar to any geographical region. . . . This uniformity in the aspect of the rain-forest flora contrasts sharply with its taxonomic diversity" (Richards, 1952, p. 54). The "climatic climax is the theoretical constant against which observed conditions may be compared. Thus, the degree of deviation, if any, from the theoretical climax can be measured and the factors responsible for the deviation can be more readily determined when there is a basic 'yardstick' available for comparison" (Odum, 1953, p. 197). "It therefore [becomes] necessary to devise a more natural classification of vegetation which avoids rigidity, permits world-wide comparisons, and is adapted to mapping" (Küchler, 1949, p. 201). These statements by the zoologist, botanist, general ecologist, and geographer express a convergence of ecological opinions and desiderata of which the best features are embodied in the Holdridge clas-

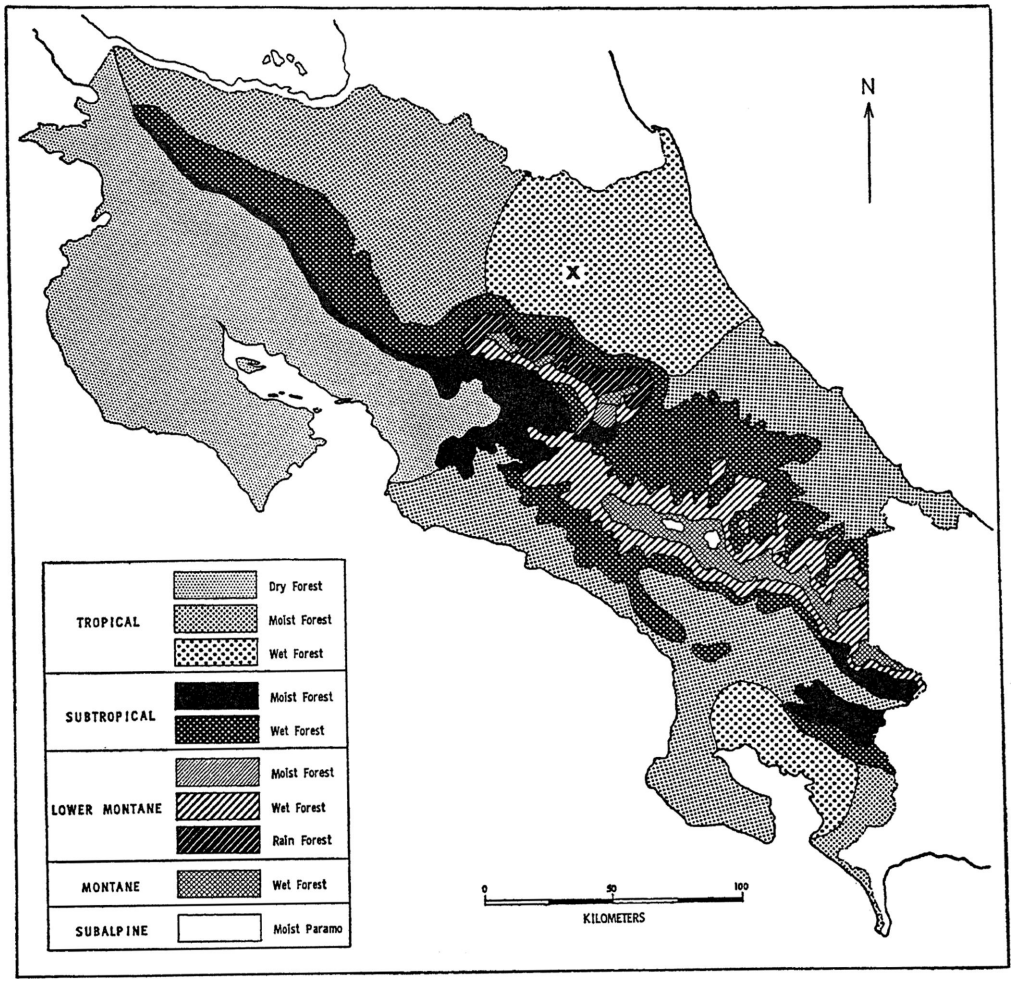

FIG. 5. Ecological map of Costa Rica. Black-and-white duplicate of "Mapa Ecológico de Costa Rica" in color by L. R. Holdridge, published by Instituto Interamericano de Ciencias Agrícolas, Proyecto 39, Programa de Cooperación Técnica, San José, Costa Rica, 1959.

sification of the world's vegetation (1947). It is a global system on a quantitative basis that includes all the life zones (formations) from the equator to the poles and from sea level to the mountain tops. By means of the Holdridge system the occurrence of an ecological counterpart of a life zone (formation) in one part of the world, given the same climatic conditions, can be predicted and its limits designated in another part of the world. The vegetation can be mapped, and upon the life zones (formations) the distribution of a particular form, or group, or community of animals can be plotted. The animal ecologist is under no compulsion to force a fit. A special virtue of the Holdridge system is that it has been elaborated exclusively for the vegetation; by extension it furnishes a basis for comparison of faunas. Vegetational form and structure respond directly to differences in climate; the plant-dependent animals are molded secondarily by the climatically controlled environment.

The Holdridge system (1947, 1957) clarifies the meaning of "tropical," "tropical forest," "tropical rain forest," and the like,

which are terms directly concerned with the present study. "Tropical" should be used when one is referring to the tropical region or the tropical belt: the tropical region is synonymous with any expanse of land bounded poleward by the mean annual sea-level isotherm of 24° C.; the tropical belt is that portion of the tropical region that is bounded altitudinally by the same isotherm. In the tropical region, the basal belt is the tropical belt, above which, where there are mountains, rise in succession other belts, such as the subtropical, lower montane, and so on, each with its upper and lower temperature limits and rainfall subdivisions. "Tropical forest" has been used so uncritically that it may include any of the forested divisions of the altitudinal belts of the tropical region: a matter of 21 possible life zones (formations). What is usually meant is "rain forest" of the tropical belt, but often the tropical belt is confounded with the subtropical and lower montane belts, while "rain forest" is itself a term begging definition. Rain forests not only occur in regions other than the tropical region, but also in various belts of several regions. The true Tropical Rain Forest, according to the Holdridge classification, is a life zone (formation) that is present only in the tropical belt, and it has a minimum annual average rainfall of 8000 mm. In the New World there seems to be but one such area, in northwestern Colombia along the foothills near the coast. Two other life zones (formations) in the tropical belt have also indiscriminately been called "rain forest": the Tropical Moist Forest and the Tropical Wet Forest, with an annual average rainfall of 2000–4000 mm. and 4000–8000 mm., respectively. In Central America, the Tropical Moist Forest is widespread along the Caribbean slope and is to be found along parts of the Pacific slope of Costa Rica and Panama. Incidentally, it is a forest of this category, with 2540 mm. of rainfall, that Beebe and Crane (1947, p. 52) cite as "an example of climax rain forest" in British Guiana. The Tropical Wet Forest, so far as is known, is present in Central America only in northeastern Costa Rica and adjacent southeastern Nicaragua, and in the Golfo Dulce region of southwestern Costa Rica.

"La Selva," then, is representative of a locality in one of the great vegetational divisions of the earth: the Tropical Wet Forest Life Zone (Formation). This term gives us to understand that the locality can be present only in the tropical belt of the tropical region; that anywhere in the world, the belt and the region are bounded by the mean annual isotherm of 24° C., and that there are no frosts; that the life zone (formation) has a mean annual rainfall of between 4000 and 8000 mm., with a normal distribution, and a maximum dry season of two months when evapotranspiration exceeds precipitation; and that the number of deciduous species of trees is small. (See Holdridge, 1947, 1956.) Climatically, geographically, and vegetationally the site is thus related to and capable of being compared with other life zones (formations) of the world, of the pantropics and neotropics, of Central America, and of Costa Rica. "La Selva" is thus assigned a definite place within a comprehensive scheme for the globe.

What is "La Selva" like? Diagnoses of environmental parts do not make the whole; photographs confine their focus to isolated frames. Even the scientist cannot disregard the psychological impact of the forest, especially when he is alone. It took me months to get the "feel" of the place, to be able to predict where to find certain birds. The sense of mystery I did not lose; such a loss is a misfortune. From the house and its small clearing one steps abruptly into the forest shadow; there is no transition. The forest is tall, and the tops of the big trees are often hidden by the crowns of the smaller ones: the forest within the forest. Thick trunks are spaced well apart; together with the more slender trunks they form a perpendicular maze of unbranched, light-colored boles. The palisade effect of the clear trunks is enhanced by the numerous lianas, some as thick as a man's arm or leg or body, hanging like weighted cables. Characteristic are the strikingly buttressed hardwoods which so attract the eye that the unbuttressed species may pass almost unnoticed. Stilt-rooted trees, particularly palms, are common. Spines or thorns may be present on trunks or roots, most often on palms. Palms differing in size and structure are numerous, especially in the swamps and on muddy or wet depressions

and valley bottoms. Their drooping fronds, like exotic trappings, weave a backdrop of tapestried detail. The general area is one of the richest for the palm collector (*fide* Harold E. Moore, Jr., verbal information). Climbers, vines, and slender aerial roots are omnipresent, interlacing trunks and limbs, knitting slender branches, looping lassoes over others, or self-tangled, forming their own coiled mass. Epiphytes are everywhere: perched, suspended, climbing, clinging; ribboned, twisted, grassy, spike-whorled. Except for new red leaves, bright colors are few.

The floor is damp and covered with a thin layer of decaying litter, mucky and treacherous on any incline. Walking may be easy or difficult, and hardly a day passed that I did not slip in the mud or trip over a root. Fallen trunks, some of tremendous size, here and there obstruct the way. Even where the undergrowth is thin or soft, it is hard to avoid entanglement by vines, many of which bear thorns. From time to time one comes to a bare area of soft soil having a rusty, overturned appearance that is nearly clear of living, low vegetation: the site of underground galleries of leaf-cutting ants, whose wavering columns are met with daily. Extensive areas of churned forest floor bear evidence of recent passage by a band of peccaries.

There are tracts of level ground, an extensive forested swamp, soft-bottomed streams, and ridges and ravines interspersed with minor watercourses. For a sojourn in the swamps it is necessary to pick one's way through the mire by stepping on clumps and roots, and poles must be cut and laid across the streamlets meandering about. Still, I sank to the hip and lost my balance at inopportune moments in awkward situations. Where fallen trunks providentially span the wider streams, they should be negotiated with suspicion because they are incredibly slippery and may be rotten.

The Sarapiquí region and heavy rainfall go together. Even during the short dry season a sudden shower between periods of sunshine is the not unreasonable expectation. With an inch or so of rainfall, or perhaps half an inch concentrated into a short space of time, the Río Puerto Viejo rises several feet, becomes discolored brownish, and the heightened current carries downstream snagging branches and entire trees. With a few inches of rainfall, the river may rise as much as 15 feet or more in a night; with heavy rains lasting several days, it may overflow banks 30 feet high. Often, when it is dry at "La Selva," the river may rise with all the signs of flood because of a local downpour somewhere in the hills, but the quebradas at "La Selva" show little change in level. During periods of heavy rains at "La Selva," the swamps become very difficult to cross, and formerly inconsequential streams back up and swell to fill grandly their now impassable valleys.

Little light reaches the forest floor, and on cloudy days the intensity is very low. Yet visibility is best and photography most satisfactory when the sky is overcast. On sunny days the strong contrast between the filtered light on the upper side of the foliage and the blackish shadows beneath, together with the dazzlingly brilliant sun flecks, make it difficult to distinguish details, whether they be the path to be followed, snakes to be watched out for, or birds to be located and observed. Morning and evening twilight, respectively, tarry and fall by at least an hour's difference from the semi-open.

Sounds in the forest can be assorted into kinds that affect the susceptible listener as portentous or benign. A storm-preceding inrush of wind tosses crowns and flexes trunks, coupled with loud, splitting cracks; twigs, branches, and tree-sized limbs crash down, and great trees topple. Normally, too, one hears at intervals the sound of falling branches as a reminder of this gratuitous hazard. On the stillest of nights it is not unusual to be wakened from afar by a prolonged stutter of rending creaks, like a succession of wedges riving the heartwood, followed by a tearing break and the devastating fall of a mature primary-forest tree. Less spectacularly, falling fruits and seeds patter or plop, and for several months ripe quebracho pods burst with an explosive crack. In season, quite without warning, a cannonball-sized monkey pot may thud into the ground after a fall of 150 feet. At times, the inoffensive investigator, discovered by a member of the troop, is then subjected to the barks, snarls, and grimaces of debris-dropping capuchin or spider monkeys. Sometimes there is to be

heard the heavy crashing and splashing of, presumably, an alarmed tapir. Ominous are the clopping, champing noises of a herd of White-lipped Peccaries; unsettling is the heavy, growling "woof" of a startled individual close at hand. Even the rustling scurry of a lizard would bring me to a sudden halt. Also serving to divert attention is the noise produced by a foraging squirrel, for it is not much different from that of a rummaging bird; its barks and chatters are bird-like also. Often cicadas make the forest whine and buzz incessantly with their vibratory drone. At night it is quiet, except, seasonally, for whooping frog choruses, tinklings and rappings, and a few very odd-sounding nocturnal birds. Tinamous and pauraques are to be heard the year round in the evening, at dawn, and sometimes at night. A howler monkey may roar at any time of day and sometimes at night.

The birds are easily the dominant vertebrates, yet there are times and places where for an hour at a stretch scarcely one will be heard or seen. Mammals, except agoutis, squirrels, tayras, and monkeys, are seldom to be observed. Of the big cats I saw only tracks. Snakes are met with daily; of obviously poisonous ones (pit vipers), excluding coral snakes, I averaged somewhat fewer than one per month. Frogs are common as are salamanders, but the latter are less noticeable. Insects, of course, are ubiquitous; ants are to be seen wherever one looks. Mosquitoes are sometimes a nuisance, or very annoying during seasonal outbreaks, but I did not find it imperative to use a headnet. Wasp and termite nests are numerous. Magnetizing one's attention are gigantic forest wasps and bumblebees, as well as exquisite butterflies and moths. Spiders and spider webs are everywhere, both inside the forest and in the semiopen. Ticks and mites are usually only a minor inconvenience.

The vegetation makes the forest; the floor itself, the supporting substrate, is but the base line of the picture. The sounds, especially some of the bird sounds, match the prevailing mood. The vegetation is always inescapably there, impressive as a mountain. By comparison, the animal component is insignificantly small in macroscopic view.

HABITATS AND HABITS

THE WAY TO CLASSIFY birds ecologically, I believe, is to place them in their habitat and describe what they do, so that habitat plus behavior add up to niche for the birds discussed in this paper. This is not quite the same as the definition by Pettingill (1956, p. 167): "The niche of a bird species is its position in the community that results from its structural, physiological, and psychological adaptations." Pettingill alludes, of course, to the ideal of the ecological niche which encompasses not only the habitat niche but everything else that has to do with the bird and the population of which it is a part. For the term to possess meaning, a complete knowledge of all phases and aspects of the life history of any species is mandatory, as well as for all other organisms in the biotic community. Because by definition no two species, nor populations of the same species, can be exactly the same in all respects, it follows that no two populations can have exactly the same ecological niche; the number or kinds of niches equal the number of genetically disparate forms. The ecological niche of the Eastern Robin, for example, would be the *Turdus migratorius migratorius* niche, for only that bird can occupy said niche, and only that niche can be occupied by said bird. In order to determine how the ecological niche of the Eastern Robin differs from that of a conspecific population, it is necessary to know all the details of one of them. Then by equating like to like, one can obtain an unequated residue of unlikenesses. An analogous instance would be the describing of a new race of robin for which need be given only the significant morphological characters whereby it differs from some other race, provided at least one race has already been described in full. An exhaustive taxonomic description is child's play compared to a complete description of an ecological niche. Certainly no animal exists about which everything is known regarding everything it does or that is done to it, nor of the immediate or ultimate consequences of its reactions and coactions. Because of the unlikelihood that all of the life history of all the organisms of a biotic community will be discovered in the near or remote future, that is, before they and their environment shall have changed into something different, a more practical working method is indicated.

With the habitats arranged into major and minor categories, behavior needs to be employed in order that one may be able to place the birds in a recognizable niche. Behavior, too, needs to be categorized sufficiently in order that one may distinguish between birds of similar habitat and habits. For some birds at "La Selva" I cannot do this. This inability is undoubtedly due to lack of sufficient information regarding situations in which two species so overlap in habitat and behavior that they seem to share the same niche. Possibly the problem can be solved at "La Selva." Possibly those portions of their ranges, where the two species occur together and where they do not, need to be compared, and perhaps in this way can be discovered the similarities and differences that permit them to live together apparently in harmony in one place and not in another. One may actually be displacing the other, but at so slow a rate that the change cannot be observed during a human lifetime. It is also conceivable that in the same amenable environment two species might indeed occupy virtually the same habitat and behavioral niche, if the limiting factors for both are other than those having to do with the food supply, whereas harsher conditions are likely to be more detrimental to one and less to the other.

HABITATS

The habitat niche, or just habitat, is where a bird lives, where it can usually be found, where it spends most of its time, regardless of what it might be doing. As birds occur at "La Selva" from ground level to high in the sky, the habitats may be said to form a continuum in which all the three-dimensional space is occupied or traversed by one or another bird at one or another time. Quite unsatisfying intellectually, this sterile statement of affairs nevertheless furnishes a starting point for a habitat analysis, if only because

it goads the investigator to a more realistic outlook. In response to the stimulus he might begin by distinguishing major categories such as forest or clearing, continue by determining the minor categories comprising each of the major categories, and eventually he might succeed in reducing the minor categories to their micro-environmental components. For the birds at "La Selva," however, micro-environments do not seem to exist. An orderly arrangement should consist of major and minor categories, of which the latter should not be subdivided below a meaningful degree. Otherwise a monotoned pointillism, similar to the one started out with, will have been ended up with.

Helpful in a general way, as pointed out by Darlington (1931, p. 356), are the terms "forest," "woodland," "semi-open," "second growth," and "field." These major habitat types may be present in more than one life zone (formation) and are useful for species occurring in more than one category. "Forest," meaning virgin forest, is the habitat of certain species, whereas "woodland" serves for others that occur both in virgin and thinned forest as well as in advanced second growth. "Second growth," in the sense of thickety growth, has a rather definite meaning, provided it is applied to the first and second stages of regeneration (see below), but not to well-advanced second growth (subforest). "Semi-open" should suggest well-thinned woodland, tree plantations, park-like pastures, mixtures of clearing and patches of forest, or fields with scattered trees. "Field" habitats are variable; what they have in common is that they are natural or cleared areas without trees or with a few isolated ones. At "La Selva," virgin forest predominates; the other terms apply to tracts worked over by man, but there is no true field habitat.

"Edge effect," "edge birds," "forest edge," and the like are terms in current use. "Edge" seems to be equivalent to ecotone; "edge effect" signifies the larger number of species living in the ecotone as compared with the community on either side; "edge birds" live mostly or only in an edge; "forest edge" is the junction of forest and open country (Odum, 1953, p. 207; Pettingill, 1956, p. 165). The ecotone seems to be a natural area of intergradation between two major communities, although Dice (1952), calling it a "tension zone" (p. 20), imparts to it an elasticity befitting a subjective impression (p. 422). The reality of the edge is a proved phenomenon in north-temperate regions where the concept arose, and where the recognizable ecotone is of some considerable extent (width).

To transfer, as has been done, the word "edge," with its ecotonal connotation, to the humid Caribbean lowlands is unwarranted in most instances. Thicket-inhabiting birds have been called edge birds; rather, they are birds that inhabit young or intermediate second growth. Nor is second-growth vegetation "edge" in the sense of being transitional between two natural communities; rather, it is a stage in succession during regeneration of the original forest. Eisenmann (1957, p. 250), for example, calls *Buteo magnirostris* an "edge" species. In Costa Rica, as no doubt in Panama, this is perhaps the commonest native hawk, yet it is absent from the "La Selva" region despite the presence of numerous "edges." I prefer to regard this hawk as one that does not occur in heavy forest. Its absence from "La Selva" (where it is surely bound to arrive) is instructive to the person undertaking a distributional or ecological analysis of a list of birds.

The very word "edge" needs to be reconsidered. A useful term, it can be employed to advantage at "La Selva" for borders of all sorts. Once put to use in this non-ecotonal manner, however, the term must also embrace forest. Wherever there is a break in the canopy or a change in density of the stand, wherever there are watercourses, ravines and valleys, stream cutoffs, and so on, edge situations have been produced which relate to habitats, affect the distribution, and increase the number and kinds of birds in the forest. Every discontinuity recognized by the birds constitutes an edge. To avoid misinterpretation, forest edge should be called instead the "forest border"; "forest edge" can be used when one is referring indiscriminately to edges inside the forest.

Some birds have more than one habitat, but if modified by appropriate qualifiers a species can often be placed in a single habitat. In Costa Rica the distribution of a particular bird might be stated in geographical terms, as, for example, the Caribbean slope. To this

statement could be added the ecological specification: tropical belt. For the species in question the ecological meaning becomes increasingly clear with the addition of supplementary information: life zone (formation)—wet forest; major habitat—forest; stratum—understory; portion of stratum—lower understory and ground cover; additional occurrence—advanced and intermediate second growth adjoining the forest.

The major habitats at "La Selva" correspond in general to the main vegetation types and to certain physiographic features already described. They are: (1) high virgin forest, (2) second growth, (3) tree plantations (semi-open), (4) watercourses, and (5) aerial.

HIGH VIRGIN FOREST

This is the dominant type. It is by far the largest in extent, and its influence affects the other types. Perhaps illogically, I make it a major habitat division while assigning the same rank to the other, subordinate types. Still, this scheme allows for commensurate treatment.

The only similar locality where attention has been directed by the avian ecologist to the structure of the forest seems to be the lowland evergreen forest in British Guiana, where Beebe and his co-authors (1917, p. 87) and T. A. W. Davis (1953, p. 457) each divided the bird population into vertical zones. Although Davis's attempt, based on the "storeys" of the vegetation, has resulted in a more natural stratification of the forest, in practice I prefer Beebe's subdivisions as being more suitable for the birds. It should be borne in mind that the locality lies in humid forest, is subjected to a lengthy dry season, and that the forest probably lacks one of the layers present at wet-forested "La Selva." Modifying somewhat Beebe's arrangement, and adding to it the aerial subdivision of Davis, I distinguish at "La Selva" (a) forest floor, (b) understory to about 5 meters from the ground, with a lower and an upper portion, (c) middle forest from about 5 meters to 15–25 meters, (d) main canopy, and (e) the air above the forest.

This arrangement sometimes leaves a gap between c and d. Owing to a variety of circumstances, the height, density, and degree of closure of the main canopy are variable both on level ground and where the topography is broken. Besides, when viewed from below, the crowns of the intermediate trees largely conceal the top story; in foreshortened view the two may merge. Usually a view in perspective is possible at openings, but here increased light encourages a profuse growth veiling the gap. Moreover, numerous vines interlace the foliage and, together with the omnipresent epiphytes, cover the branches and trunks so that even deciduous species that have shed their leaves often appear to be in leaf. In horizontal plane at ground level, the physical and botanical environment is by no means uniform. There are stretches of relatively bare or overgrown forest floor, tangles, fallen trunks, wooded swamps, grassy marshes, wooded ridges and slopes, vegetation-choked ravines, streams and gullies and their borders, thickets, and openings with seral stages of new growth (pls. 12, 16–26).

SECOND GROWTH

From this category I exclude the secondary successions inside the forest. As used here, the term stands for all the second growth in the areas cut over by man outside the forest. Secondary growth fringes the river banks, the lower courses of the quebradas where they pass through the semi-open, and wherever land that had once been cleared is no longer cultivated. Stages according to age are: (a) young, (b) intermediate, and (c) advanced second growth. Each stage has a rather distinct appearance and structure despite the fact that succession is a continuous process.

A brief description of the three stages of succession is taken from Holdridge (1953, p. 41, translated): "There is a stage, from a few months to several years, in which there is very strong competition among seedlings and sprouts of young trees, shrubs, herbaceous plants, and vines. During this period it is difficult for a man to enter without making an opening with a machete. Later, in the second stage, a closed canopy is formed higher above the ground, many of the herbaceous plants, small shrubs, and small vines are eliminated, and a man finds that he can pass without a machete, but still with some difficulty because of the lianas, through the densely shaded space beneath the moderately high canopy. In the third stage the

ground is even clearer, and the canopy becomes divided into two strata. Above are found the trees which grow well in full sunlight, as *Ochroma*, *Heliocarpus*, *Trema*, and *Cecropia*. Beneath are the species of slower growth that will constitute the dominants of the future. This period lasts several years and terminates when the species of rapid growth and relatively short life begin to succumb to the competition, growing stronger every year, by the dominant species of the original vegetation. Afterwards, the changes are slower and gradually approach the conditions of height, composition, and physiognomy of the original forest." This sketch conveniently describes the habitats, too. At "La Selva," the inclusion of large trees, left over from the original forest, in many of the second-growth areas may disguise somewhat their real nature. In short, this category consists principally of thickets of varying densities in young and intermediate stages of succession. Older stands can perhaps be called sub-forest. The very late-advanced stage is present only inside the forest (text fig. 3; pl. 11, fig. 1; pl. 13, fig. 1; pls. 15, 16).

TREE PLANTATIONS

Mentioned earlier in passing, the tree plantations deserve special consideration. The terms "partial clearing" or "semi-open" might also be applied to this category, created through human agency. Spreading with human land-use patterns, a meeting ground for birds of other main categories, the preferred environment of still other kinds of birds, the clearings at "La Selva" are avifaunally analyzable and theoretically important. They are rich in species of birds the distribution of which over the study area may or may not be uniform, the occurrence of which may be seasonal, erratic, or accidental, and the preferred habitats of which, as mentioned above, may or may not lie in the semi-open. Migrants are particularly abundant and noticeable here. (Fig. 3 should be consulted for the disposition of forest and semi-open on the study area.)

Owing to the very tall, often buttress-flanged shade trees and to rapidly growing pioneer species that colonize openings, the tree plantations have a characteristic appearance (pl. 13, fig. 2; pl. 14). Belting the study area, they are in some places park-like, with dense undergrowth which is cut periodically; in other places there are shady groves. Many of the trees are heavily foliaged, bushier and much deeper crowned than those in the forest, and they bear numerous epiphytes. The arboreal biota attracts many kinds of birds for foraging, the branches provide perches, the foliage furnishes shelter and places to roost; taken as a whole, one of these shade trees serves as a substrate for many kinds of nests. Dead and dying trees and tall stubs, as well as bare branches, are also attractive to many birds.

The pioneer plants produce a constant supply of food. An outstanding example, *Cecropia*, bears pods apparently the year round, and papaya and banana plants spring up quickly. The shaded little cacao trees, too, are frequented by many insect-eating species. By contrast, an unshaded lowland coffee plot was singularly free of bird life. The vigorous, weedy undergrowth, whether tall and thick or freshly chopped and strewn, attracts birds also. Especially at the Point (pl. 13, fig. 1) the flowering *Hamelia* shrubs evidently provide an ideal subhabitat that is exploited by a swarm of hummingbirds.

WATERCOURSES

The Río Puerto Viejo forms one of the boundaries and is the important river of the finca; only that portion of the Río Sarapiquí immediately upstream for a short distance along the Point is included in the study area (fig. 3). Although the Puerto Viejo is becoming increasingly used by traffic, and a strip of forest along each bank is being partially cleared for lumber, the virgin interior is still protected by inaccessibility and continues temporarily inviolate. The quebradas, except close to where they disembogue, are true forest streams, not small rivers. Rivers, on the other hand, can be large or small. I suppose that nowhere does a watercourse automatically become a river by conforming to a stipulated measure of length or width. The difference between a river and a stream can, however, be rather distinct, at least in forested regions. In the humid tropics a river should be defined as a watercourse the breadth of which (disregarding local con-

strictions) is not so narrow as to permit the crowns of the trees from either margin to meet, forming a bowered bridge which a wingless creature can cross. In a forested locality viewed from the air, a river resembles a canyoned highway or a jagged furrow; a stream is hidden or lost. (See pl. 10; pl. 22, fig. 1.) In contrast with the river, the habitats of the streams are occupied almost exclusively by forest-based species.

The watercourses provide habitats for a heterogeneous conglomeration of birds, comprising relatively few species in all, that are called water birds because they are associated in some intimate manner with water. Along the banks live other kinds that do not enter the water, yet do not occur away from its vicinity. The river supports two ecological groups having different sorts of environmental distributions: one is dependent on a river flowing through forest, the other is independent of forest but requires a river; in either case the presence of the river accounts for the presence of the birds. On the river occur the aquatically specialized species (only two), but these are not dependent on a heavily forested environment. Of the unspecialized water birds (those that do not possess webbed or lobed toes and do not swim), some occur at both rivers and streams, others at either but not at both. At "La Selva," very few species (none morphologically water-adapted) are confined to streams inside the forest. Some of the land birds (those that neither wade nor submerge the head or beak) are so closely associated with the borders of rivers and streams that in effect they are water birds psychologically. Some may be as dependent as kingfishers or herons on the watercourses or the periodically flooded, adjacent, muddy terrain, whereas others inhabit thickets and shrubbery lining the edges, either inside or outside the forest proper.

The question arises: Should forest rivers and streams be considered part of the virgin-forest category, or not? Unlike the birds occurring, for example, at edges, which I have not placed in a separate category, I do set apart the birds that are dependent on watercourses. The watercourse habitat obviously contains species adapted morphologically to an aquatic environment and, less obviously, a much larger number not adapted in this manner. I do exclude certain riverside birds that are really edge or thicket inhabitants rather than psychological dependents on the proximity of water. Nor do I include in the watercourse habitat the shallow marshes and wooded swamps in the forest: these are but facies reflecting local edaphic conditions. A watercourse follows where its channel leads, heedless of the environments or communities traversed.

AERIAL

The aerial habitat I reserve for birds that in pursuit of their vital activities spend all or much of the day in the air and are only secondarily dependent on other habitats (for resting, roosting, and reproducing). A flexible term, it is here restricted to a few kinds of birds that may be present over forest, river, and clearing. Ideally it should contan only the swifts. Swifts are frequent and numerous at "La Selva," where they speckle the void, as it were. A uniquely aerial group, they carry their habitat with them wherever they happen to hunt.

HABITS

Normally most birds are seen, even during the breeding season, as they perform their commonplace daily activities, such as foraging and resting, or when swept from time to time by a wave of excitement. An exception would appear to be a manakin that spends considerable time in courtship antics through much of the year, but this behavior is so absolutely characteristic of the species that it becomes the normal one to the observer. Behavior, distilled from many observations, can be described by what a bird ordinarily does, sometimes by what it does not do. It is easy to typify if narrowly specialized, but difficult to assess when broadly varied. A species at its center of abundance may exhibit boldly a wide range of actions, but where it is uncommon, as a rule, it may seem almost unrecognizably shy and inhibited. A family of only one or two species or genera

might be characterized by the habits of an individual, but one with many species and genera becomes an exercise in ingenuity to generalize collectively. Congeneric species are necessarily closely similar morphologically, and in general their ecological segregation on theoretical grounds is substantiated by the actions of the birds; yet in a few instances they occupy the same habitat and, in the absence of pertinent data, appear to have the same habits.

I am unable to devise or adapt an inclusive terminology, serving to distinguish ecological groups of birds at "La Selva," that does not suffer from ambiguity. Part of a class of terms may suit some of the orders, families, genera, or species without undue remonstrance. But in order to cut a homogeneous ecological section across unrelated phylogenetic lines, the terms must be modified and refined in so far as available information permits. For "La Selva" I consider the following sets of general terms to be of general utility. Of course, the cruder arrangements ignore the diversity of food-obtaining means used by different species, disregard differences among the habitats in which the activities are carried on, and fail to call attention to convergences and divergences in behavior.

One set of terms consists of "vegetarian," "animalivorous," "omnivorous," and the like. "Vegetarian" can be subdivided into or be substituted by "frugivorous," "granivorous," and so on; "animalivorous" includes "carnivorous," "piscivorous," "insectivorous," and so on; "omnivorous" means a mixed diet of animal and plant material. Apparently the only strictly vegetarian group is the parrots; few other families or genera are entirely frugivorous, granivorous, or, more broadly, largely vegetarian. The word "carnivorous" brings to mind raptorial birds, i.e., those with hooked beaks for tearing flesh and talons for securing living prey, as well as large-sized eaters of carrion, as the vultures. Still, a number of birds of prey may feed largely on insects and other invertebrates, some take vegetable matter, and probably many hawks eat carrion; the fish-eating osprey, if the classifier so wishes, can be put into a piscivorous category together with herons and kingfishers. A flycatcher specializing on winged insects is just as much a carnivore as a hawk, yet it would be misleading to call it other than insectivorous. On the other hand, a puffbird, which sallies for insects but also swallows scorpions and large centipedes, can be regarded either as animalivorous or insectivorous. To complicate matters somewhat, a fruit-eating cotinga may habitually include large orthopterans, frogs, and lizards in its diet, while many insectivorous flycatchers and vireos feed also on berries. Despite anomalies, it is useful to consider as carnivorous the hawks, owls, and vultures, that is, birds that feed primarily on warm- or cold-blooded land vertebrates; as piscivorous, those groups preying chiefly on fish; as insectivorous, the animalivorous groups that subsist principally on insects, as well as on other arthropods and small, cold-blooded vertebrates. Most of the birds are omnivorous, although the percentage of animal or plant food in the diet may indicate a variable tendency to, a temporary dependence upon, or perhaps a seasonal preference for, one or the other. Availability of certain food items and opportunism practiced by the birds undoubtedly help cause the percentages to fluctuate.

Another rough-and-ready scheme sets apart the terrestrial and semiterrestrial species: those that forage mostly or only on the ground. Strictly speaking, there are no truly terrestrial birds at "La Selva," because none is flightless. Perhaps the weakest flyer is the little rail *Laterallus;* the tinamous *Crypturellus* and the large rail *Aramides* escape the observer by running, although they will fly when pressed, as will the quails *Odontophorus*. All the terrestrial (and non-terrestrial) birds fly sufficiently well to suit their needs. The majority occurs in the forest; if *Laterallus* be excluded, none lives in the semi-open (although the ground dove *Columbigallina* and the meadowlark *Sturnella* will probably become regular at the Point). The birds differ in manner of progression on the ground, flying ability, size and proportions, foraging methods and diet, and in frequency and distribution. Several herons and the ibis, *Mesembrinibis*, which feed on the ground at wet or marshy places, are water birds that might be included here.

The antithesis to terrestrial and semiterrestrial is non-terrestrial. This unwieldy

category, containing most of the birds at "La Selva," is susceptible to treatment through the employment of other groups of terms. Non-terrestrial birds are aquatic, aerial, or arboreal. The common names of the water birds usually tell us something about their habits. Only two species are actually aquatic; others dive from the air, wade, or haunt the margins. The distinction between birds feeding on aquatic organisms and those that include but do not depend upon them in the diet is arbitrary. The aerial birds are few in number and consist mostly of a convergent aggregation, the fissirostral swifts and swallows. These birds hunt flying insects in the air and eat them on the wing. A kite or two and, to a limited degree, hummingbirds may do so, too.

The majority of the avifauna is arboreal. Adaptive radiation in so large a number of birds is inevitable, and different ways of "earning a living" have been developed. The interrelation between functional morphology and behavioral expression is not necessarily made apparent from the study of only one of these two aspects. The Annotated List indicates the ecological radiation among species of the same family. The outline that immediately follows consists of behavioral categories in which the assortment of species may be quite heterogeneous; however, certain taxonomic groups are so distinctive in their actions that they form a category of their own. Groups already discussed above are not remarked upon below.

Flower probing as a method of feeding is practiced universally by hummingbirds in their own special way, and to some extent by certain honeycreepers, especially *Coereba*. Sharp-billed icterids as *Icterus* spp. and even the large oropendolas may probe in flowers, as do also some warblers and tanagers.

Specialized for climbing on trunks and creeping on limbs (including the under sides) are the woodpeckers and woodhewers, whose stiff tails serve as props. The woodpeckers chisel wood; the woodhewers pry away bark (as do woodpeckers also), probe in crevices and under shingles, and they may hack or hew. The migrant warbler *Mniotilta*, which is soft-tailed, creeps upon trunks and limbs. Here, too, might be included the wren *Campylorhynchus*, which climbs on mossy, epiphyte-covered, vine-curtained trunks and limbs. The scansorial parrots climb about in the foliage of trees with the assistance of the beak, which is employed as a grappling hook if not as a hand.

A number of species habitually sally, some from a favored lookout, others from any convenient perch. The perch may be a foliaged or bare limb or twig, a stub, a leaf, or a frond, according to specific, individual, or momentary preference. Certain omnivorous or insectivorous species take winged insects in the air; others sally for stationary prey which they seize from bark or foliage; several sally for fruits or non-flying prey which they pluck during a hover. The raptorial birds are mostly still hunters, but a few sally from ambush, and one swoops for birds or insects in the semi-open. Having rather different behavior are the many species that characteristically flit or dart short distances for prey, which they snatch from leaves and immediately come to rest on any nearby perch; small berries may be plucked in the same manner. From this new stopping place the bird scans the surrounding vegetation until it spies another prey item. The two-part maneuver is performed so rapidly by tiny birds, and the stop is so sudden, that they become lost to the observer's eye, which has moved ahead. This behavior is typical of small-sized, stout-bodied, short-winged, usually stub-tailed birds, such as manakins and diminutive flycatchers. There is in addition a varied assemblage of flitting species that do not perch quietly for appreciable lengths of time, but between flits move about in the foliage, where they frequently change position: examples are the flycatchers *Tolmomyias* and *Todirostrum*.

Species that hop or leap about in the foliage and creep along branches and twigs (but do not habitually climb or flit) comprise a category not easily delimited by hard and fast lines. Primarily I refer to smaller birds such as certain antbirds, wrens, gnatwrens, and the like. They occur in undergrowth or dense vegetation, where they are usually hard to see because of the nature of the cover, and are sedentary, flying seldom, and then for short distances. One cannot exclude, however, a number of non-sedentary tanagers and honeycreepers, or a bird such as the shrike-

vireo. These birds forage in a manner similar to that of the birds mentioned above, but they generally occur higher above the ground in the foliage of trees. Similarly, toucans and oropendolas, which hop along branches and reach for food, must be admitted into this category. The cuckoo *Piaya* probably also belongs here.

A group of species that often forage by clinging to the foliage includes vireos, certain migrant warblers, antwrens, and perhaps also the pigeon *Columba nigrirostris*. This vaguely defined category possibly places undue emphasis on what to outward appearances seems to be a significant foraging mannerism. The smaller species are active, nonsedentary, often gregarious, and largely or entirely insectivorous. Except that they do not tend to cling, other nervously active, migrant warblers (mostly *Dendroica*), the native gnatcatcher, honeycreepers, and maybe some small tanagers are hardly different.

A few birds customarily rummage in dried clusters of curled-edged leaves, dead or dusty fronds, stiff-leaved air plants, hanging trash, or littered, brushy thickets. Examples are the ovenbird *Automolus* and the cacique *Amblycercus;* the wren *Campylorhynchus* operates similarly on epiphyte-laden boles and branches, usually high above the ground.

Many species still not accounted for bridge two of the above-mentioned categories or embrace several because of their unspecialized behavior. An example of a specialized bird is a woodhewer that spends the day climbing one tree and then, flying or gliding downward to the trunk of another tree, repeats the procedure. Woodpeckers, too, exhibit stereotyped behavior, although *Centurus pucherani* may fly-catch, and sometimes it even flies about in the semi-open, dodging and weaving among the trees. At the other extreme are the birds that do not behave in a predictably precise manner and that, therefore, I lump helplessly in this nameless, nebulous category. The cacique *Cacicus*, for example, seems able to do many of the things that an arboreal bird is capable of doing; it even goes to the ground occasionally. Indeed, some of these species seem to have appropriated the role of groups barely represented at "La Selva," such as corvids and thrushes and native wood warblers, or groups that are quite absent, such as tits.

Nocturnal species are very few in kinds, and their foraging habits are not remarkable. The raptorial owls are still hunters as are many hawks. The potoo apparently sallies, and the pauraque sallies and flits, in the manner of flycatchers.

An outstanding forest feature is the social aggregations of roving, mixed bird parties composed mostly of insect eaters. One type of assemblage is associated exclusively with swarming army ants. It has a faithful core of attendants consisting of three differently sized formicariids: *Gymnopithys*, *Phaenostictus*, and *Hylophylax*. Almost invariably accompanying the ants, these lively birds inhabit the understory, where they seldom rise higher than a few yards from the ground. Their whines and wild little calls announce the presence of the ants, just as the presence of the ants usually guarantees that of the birds. Only *Hylophylax* also occurs scattered about freely in the forest, independent of the ants. Although the ants do enter clearings, the birds do not follow them beyond the border of the forest. Along the forest border in thickety growth they may be joined by another regular attendant, the antbird *Gymnocichla*, which lives in dense second growth and does not penetrate the forest. The forest-dwelling *Neomorphus* was with army ants both times that I saw it at "La Selva." It seems to be a regular, perhaps a permanent, attendant, although I saw no ants during my only other observation of this rare ground cuckoo elsewhere in the country. In Brazil, Sick (1949, p. 236) has also found it with army ants, as has Howell (1957, p. 79) in Nicaragua. Nearly every time I met the woodhewer *Dendrocincla fuliginosa*, it was with army ants, both in forest and occasionally in the semi-open close to the forest, yet elsewhere in the country it is not so inveterate an ant follower. Several birds are regular attendants on a temporary basis, that is, they remain for a while but not all day. The woodhewer *Dendrocolaptes certhia*, for instance, is a part-time attendant, but this widespread species is also commonly seen where there are no ants. Many other birds are attracted to the scene of activity, either by the ants or by the

birds or on account of both. Mere mention of their names would require a long list in which would figure a number of North American migrants. Other kinds of formicariids, which ordinarily keep rather to themselves in the forest understory, become aroused and profit from the flushing drives of the ants, but their excitement dissipates as the swarm passes on. The three core species mentioned above are the ones also observed by Johnson (1954) in the Barro Colorado Island forest; however, two of the fringe attendants, *Notharchus macrorhynchos* and *Xiphorhynchus guttatum*, noted by Johnson, neither follow ants nor, to my knowledge, enter solid forest at "La Selva" or anywhere in Costa Rica.

The classic accounts by Bates (1863, pp. 334–335) and by Belt (1874, p. 123) do justice to other, more striking kinds of bird parties. The birds make use of their own endowments, rather than relying on army ants, to seek out prey. They are arboreal, and they troop about at a pace which, though steady and methodical, is confused by turbulence, and eddies of birds may range vertically through several strata. The forest turns alive at their passage, and the observer, overcome by riches, is at a loss where to feast his eyes first. One individual flitting in the foliage diverts his attention from another, and if he lists all the species he happens to see, he surely despairs at the thought of those he has missed. Chapin (1932, p. 221), in the Congo, found it "by no means easy to count or identify all of them," although D. E. Davis (1946, p. 177), in Brazil, has presented a monthly tabulation of the number of species per flock to the hundredth of an integer. At "La Selva," among the birds represented are trogons, motmots, woodhewers, ovenbirds, antbirds, manakins, cotingas, flycatchers, wrens, vireos, a honeycreeper, caciques, tanagers, finches, and others, including a variety of migrants. Some of the species may be excessively rare or seldom seen.

There is little doubt in my mind that these are primarily feeding aggregations having a diversified structure that provides niches for a complex of foraging types, the habits of which are interrelated in complementary fashion so that all the members benefit from cooperative hunting. There are several sorts of aggregations, some dominated numerically by a single species or by two species, others wihout a dominant, and one in which the species with perhaps the fewest individuals seems nevertheless to be responsible for holding the band together. The bands are variable in kinds of species, numbers of individuals per species, and total numbers. The size, composition, and complexity also vary seasonally, especially when transient migrants are incorporated.

Some bands form around a nucleus species, of which an example is the finch *Caryothraustes*. All year round, right through the breeding season, this noisy bird troops through the middle and upper stories of the forest and in the semi-open (where it may descend much lower) in groups of several or many individuals. Sometimes it travels as a pure band, but usually its rousing passage attracts many other birds belonging to a variety of families. Two other nucleus species are the tanagers *Chlorothraupis* and *Tachyphonus delatrii*. These troop about noisily in pure bands or they may join forces. Both occur only in forest, hardly ever on flat terrain, but preferably at broken, hilly portions and also at the forested swamps lying between the hilly and level parts of the study area.

Then there are aggregations in which I could detect no nucleus species predominant in numbers. Instead, perhaps no more than a pair or so of the tanager *Lanio* seems to dominate the assemblage, apparently providing leadership or lending direction by means of excited-sounding, loud cries. I never did see *Lanio* alone (at "La Selva"), but only with mixed bands in the forest, most often along ridges and valleys in the more broken parts of the finca.

Another sort of aggregation encountered as many as several times daily consists of a core of two antwrens and an antvireo (*Myrmotherula axillaris*, *Myrmotherula fulviventris*, and *Dysithamnus striaticeps*, the last-named always in fewer numbers) often joined by groups of another antwren, *Microrhopias*, and the gregarious forest vireo *Hylophilus ochraceiceps*. These birds inhabit the lower levels of the forest, and occur also in second growth bordering high forest. Other arboreal species, each represented by relatively few in-

dividuals, may attach themselves for varying lengths of time. Also taking part in the commotion, when their habitat is passed over or through, are rather sedentary birds that inhabit the lower understory: *Microbates*, *Henicorhina*, *Myrmeciza*, *Cyphorhinus*, *Hylophylax*, and others.

The paths of different parties may cross, and there may be an additional meeting with still other parties that ordinarily travel about in pure groups through the trees. The latter type (*Tanagra gouldi*, *Hylophilus decurtatus*, *Cacicus uropygialis*) often ally themselves to mixed bands, yet keep their group identity; to a slight extent they may function as minor nucleus species. Parrots and macaws, oropendolas, toucans, and others usually move about in the upper strata in their search for favorite fruiting trees, but these largely vegetarian, pure groups really bear no relation to the mixed insect-eating parties. In the same way a great variety of species may congregate upon certain flowering or food-bearing trees in the semi-open.

A common bird that travels in pure groups through undergrowth is the tanager *Mitrospingus*. It is not attracted to other groups nor are other birds attracted to it, despite its noisiness and attendant air of excitement.

THE BIRDS

ANNOTATED LIST

FOR ANY SPECIES treated in the "Checklist of North American birds" (American Ornithologists' Union, 1957), the scientific and common names used in that publication are given priority. Otherwise, the common names that are used are those that I consider the most apt or, as the case may be, the least objectionable on the understanding that a name should be a name and not a description; I have created none. The sequence of species follows Eisenmann (1955). Terms of occurrence and numbers are modeled on Trautman (1940, pp. 150–151).

FAMILY TINAMIDAE

Tinamus major (Gmelin), Great Tinamou: Resident; terrestrial; forest floor, also bordering second growth; secretive and shy; usually alone, also in twos, sometimes in threes; very common.

Crypturellus soui (Hermann), Little Tinamou: Resident; terrestrial; second growth outside forest, occasionally in similar habitat inside forest; secretive and shy; solitary, or in twos or threes; abundant.

Crypturellus boucardi (Sclater), Boucard's Tinamou: Resident; terrestrial; forest floor, also bordering second growth; secretive and shy; solitary; common.

The three tinamous are common; numerically, *C. soui* is by far the most abundant, and *Tinamus* is relatively more common than *C. boucardi*. The large *Tinamus* and the considerably smaller *C. boucardi* inhabit forest. *Tinamus* may be seen from time to time along rather open trails, and often it bursts into the air, pheasant-like, almost from underfoot; *C. boucardi* is even harder to see because it favors denser undergrowth, and it escapes on foot. The small *C. soui* is primarily a non-forest species inhabiting thick or tangled second growth; it flies seldom. Interestingly, the voices of *Tinamus* and *C. soui*, which live in different habitats, are very similar, whereas *C. boucardi* sounds completely different. All call throughout the year.

FAMILY PHALACROCORACIDAE

Phalacrocorax olivaceus (Humboldt), Olivaceous Cormorant: Resident (as a species), but turnover of individuals; aquatic, confined to river (never on streams), swims, and dives from the surface; usually seen perched low, may roost high; solitary (but occasionally flocks pass overhead); uncommon, of irregular occurrence.

This, the only cormorant in Costa Rica, is common and gregarious in suitable localities. At "La Selva," adults are seen seldom, never in breeding plumage. The flocks in the air, consisting of a dozen to perhaps 60 birds in single or double V-formation, were noted flying eastward in January and February. Elsewhere in the interior of the country it may be common along rivers with wider, more open valleys, particularly those with many boulders.

FAMILY ANHINGIDAE

Anhinga anhinga (Linnaeus), Anhinga: Seen on only one occasion at the Point in April, three birds soaring and then settling out of sight, presumably in a cove beside the Río Sarapiquí.

The Anhinga is very uncommon on the Caribbean slope, where in the past I have seen only one bird which was soaring a few kilometers inland from the coast. The above three individuals probably wandered from the coastal lagoons (which seem not to have been investigated ornithologically). At "La Selva" there is no suitable habitat.

FAMILY ARDEIDAE

Ardea herodias Linnaeus, Great Blue Heron: Migrant, winter resident (as a species); river, streams (outside forest); very wary; may stand in treetops (during migration); solitary, or groups of three or so during migration; common during fall migration, uncommon in winter, rare in spring.

Butorides virescens (Linnaeus), Green Heron: Resident (possibly migrants also); riverside mostly, occasionally at second-growth swamps outside forest, fairly regular at mouth of Río Puerto Viejo; furtive; solitary; generally uncommon.

Florida caerulea (Linnaeus), Little Blue Heron: Resident (winter visitants also?); mostly along river, also at streams (outside forest), on branches or ground; may perch in treetops; not particularly shy; alone, or in twos or threes; common in fall, fairly common in winter and spring, rare in summer.

Casmerodius albus (Linnaeus), Common Egret: Probably casual winter visitant; only one observation: a single bird passing overhead in spring (probably others in winter); transient at "La Selva" but, from second-hand reports, may appear temporarily during periods of high flood.

Leucophoyx thula (Molina), Snowy Egret: Noted only as rare visitant along river in spring; status like that of *Casmerodius*.

Agamia agami (Gmelin), Agami Heron: Resident; streams and small marshes in forest (not noted at wooded swamps or river); solitary; uncommon to rare.

Tigrisoma lineatum (Boddaert), Banded Tiger Bittern: Resident; forest streams, also river at night; solitary; uncommon to rare.

Casmerodius and *Leucophoyx* do not properly belong at "La Selva."

Agamia and *Tigrisoma* occur at forested streams and wet places in the forest, such as small marshes or depressions where water has collected, and are seldom seen. Both are short-legged and long-necked. *Agamia* has a very long, slender beak; *Tigrisoma* has a much shorter, thick beak. *Agamia* never leaves the forest (at "La Selva"); *Tigrisoma* is nocturnal as well as diurnal, and may fly to the river at night. *Agamia*, when disturbed, may rise high in the trees, visibly agitated; *Tigrisoma* flushes to a branch in the understory, where it freezes motionless. *Agamia* seems to secure prey in the water from a crouched position on the bank; *Tigrisoma* apparently moves about slowly.

Along the river and relatively open portions of the streams (outside the forest) occur *Ardea* and *Florida*, between which the great difference in size indicates differences in wading depth and kind of prey. Although seen with fair regularity, *Ardea* is present in small numbers. These two long-legged herons seldom occur together: *Ardea* is rare along the riverside, where *Florida* is relatively common; at streams, *Florida* often occurs on adjacent, muddy ground, whereas *Ardea* keeps to the stream bed. Unlike *Florida*, *Ardea* is exceedingly wary and secretive. These comparisons are, of course, artificial but serve to emphasize the distinctiveness of each.

The small, short-legged *Butorides* favors overgrown banks where it is adept at climbing about in tangled vegetation; even a little inside the forest, at apparently suitable places, it is absent or rare. The smallest of the herons at "La Selva," it occupies habitats where a larger, longer-legged bird might find it difficult to move about. When hunting along muddy banks it skulks in a rail-like manner, and steps slowly and carefully.

Family COCHLEARIIDAE

Cochlearius cochlearius (Linnaeus), Boat-billed Heron: Not present on study area proper but at a site, a few hundred meters from the east boundary, that is continuous with the "La Selva" forest. Resident; at stagnant stream a little inside forest; gregarious, three or four individuals.

This large-eyed heron differs from the others at "La Selva" in its restriction to a single site at a stagnant stream, nocturnal feeding habits, gregariousness, and noisiness when disturbed. It is relatively unwary, or "stupid," and the voice is entirely different from that of any other heron I know. Except when feeding (which I have not witnessed), it is strictly arboreal. Elsewhere in the country, too, I have seen it only in heavily shaded situations at stagnant water, including mangroves, never well inside solid forest.

Family CICONIIDAE

Mycteria americana Linnaeus, Wood Ibis: Aerial transient, never seen perched.

The Wood Ibis seems not to have been recorded from the eastern Caribbean lowlands, doubtless because the latter have not been explored for birds. Apparently this species migrates locally within the country. At "La Selva" it was noted a few times, from the end of November to mid-December and again in mid-April, passing overhead in groups of from three to six individuals. Suitable habitat is not present at "La Selva" for this gregarious species.

Family THRESKIORNITHIDAE

Mesembrinibis cayennensis (Gmelin), Green Ibis: Status uncertain, present at "La Selva" irregularly throughout the year, probably resident in region; swamps, stream banks, and small marshes inside or beside forest; feeds on the ground; usually wary, when disturbed rises high in trees, sometimes in plain sight; alone, in twos, or in groups of three or four; uncommon.

This species is restricted to the Caribbean

slope, whence it has been reported very rarely. Apparently confined to virgin-forested localities, it travels about in small groups at canopy height, undoubtedly from one feeding ground to another. It feeds by probing in mud. I know of no other mud prober at "La Selva."

Family ANATIDAE

Cairina moschata (Linnaeus), Muscovy Duck: Aerial transient, seen only twice, each time a single bird flying along the river; apparently local wanderer or migrant, rarely seen in Caribbean Costa Rica.

Anas discors Linnaeus, Blue-winged Teal: Transient migrant, seen only twice during fall migration: once a few birds in flight, once a single bird on the river.

Owing to the absence of suitable conditions, ducks, except for an occasional wanderer or transient, are absent from "La Selva."

Family CATHARTIDAE

Sarcoramphus papa (Linnaeus), King Vulture: Status uncertain, possibly resident in the Sarapiquí region; seen circling overhead, irregularly through the year; alone, or in twos or threes in the air; common.

Coragyps atratus (Bechstein), Black Vulture: Resident; in air, mostly circling over semi-open but also over forest; perches high in semi-open for long periods; solitary or in small groups; very common.

Cathartes aura (Linnaeus), Turkey Vulture: Status like that of *Coragyps*, but less common; also great migrating flocks.

Sarcoramphus seems to be a wanderer at "La Selva," where it has been seen at rest only once (by L. R. Holdridge); in the air it resembles *Coragyps* in bodily proportions. *Coragyps* and *Cathartes*, both resident, differ in their food-finding methods. In general, *Coragyps* prefers more open areas, and is abundant in the vicinity of human settlements; *Cathartes* is more common in wooded areas, even entering openings in thinned woodland during its patrols, while in more open situations it can quarter a field in a highly accomplished manner. Unlike *Coragyps*, *Cathartes* maneuvers easily in the air, flapping much less, adjusting wings and tail to the slightest deviations of air currents, and it is not so dependent on updrafts. On the ground, *Coragyps* is a much better walker than *Cathartes*. *Coragyps* is bolder, more gregarious, and, I suspect, eats more different kinds of things (including plant food). At "La Selva," however, these distinctions are obscured for the most part. Although both are present daily, they are not nearly so abundant as in other parts of the country; although they are to be seen perched, seldom if ever have I found them on the ground. *Cathartes* may circle and sail below tree height in the tree plantations beside the forest; *Coragyps* seems incapable of doing so. Although I never saw either bird inside the forest, both regularly soar over it.

Family ACCIPITRIDAE

Elanoïdes forficatus (Linnaeus), Swallow-tailed Kite: Aerial transient and occasional winter visitant, never seen perched; small or large flocks during migration, usually single birds in winter over woodland and semi-open; absent April to July.

Leptodon cayanensis (Latham), Gray-headed Kite: Resident (as a species); forest border, patches of forest (sub-forest), and tree plantations; usually high in trees, concealed in foliage; soars; alone, or in separated pairs; uncommon.

Harpagus bidentatus (Latham), Double-toothed Hawk: Resident (as a species); forest border, sometimes a little into forest; perches fairly low to fairly high; solitary, sometimes in pairs; uncommon to rare, seen at irregular intervals.

Ictinia plumbea (Gmelin), Plumbeous Kite: Status like that of *Elanoïdes* (see above), but in smaller numbers.

Accipiter bicolor (Vieillot), Bicolored Hawk: Status uncertain, probably resident at "La Selva"; woodland, generally in shade; generally perches fairly low; seldom seen.

Accipiter superciliosus (Linnaeus), Tiny Hawk: Status uncertain, probably resident in region; forest border, second growth beside forest, and slight penetration into forest; perches low to fairly low in woodland, or much higher in more open situations; rarely seen.

Buteo swainsoni Bonaparte, Swainson's Hawk: Transient migrant; great flocks passing overhead in spring and fall.

Buteo platypterus (Vieillot), Broad-winged Hawk: Transient migrant and winter resident; forest border and semi-open; great flocks passing overhead in migration; solitary resident in winter; common.

Buteo brachyurus Vieillot, Short-tailed Hawk: Status uncertain; transient migrant and rare winter visitant; only dark phase definitely iden-

tified, migrating at same time as *Ictinia* and *Elanoïdes;* uncertainly identified small flocks of white phase very high in air during spring and fall migration; single birds only in winter (never seen perched).

Leucopternis albicollis (Latham), White Snake Hawk: Casual, seen very few times; open woodland and semi-open, also once at forested swamp, but usually soaring; alone, or in twos or threes.

Leucopternis semiplumbea Lawrence, Semiplumbeous Hawk: Resident; forest and adjacent semi-open; alone or in pairs; common.

Leucopternis princeps Sclater, Prince Hawk: Wanderer or accidental; seen twice, at end of October and end of November, at forest border and a little inside forest. Hitherto unknown below subtropical and lower montane belts.

Buteogallus anthracinus (Deppe), Common Black Hawk: Status uncertain; present (as a species) irregularly throughout the year; does not enter forest (but may occur in woodland elsewhere in the country); usually alone, sometimes soars in twos or threes; uncommon to rare.

Spizastur melanoleucus (Vieillot), Black-and-white Hawk-Eagle: Status uncertain, probably resident in region; seen irregularly through the year; woodland border and semi-open; solitary; uncommon to rare.

Spizaëtus ornatus (Daudin), Ornate Hawk-Eagle: Resident; woodland; solitary; fairly common.

Spizaëtus tyrannus (Wied), Black Hawk-Eagle: Status uncertain, probably resident in region; semi-open and second growth; solitary; uncommon.

Circus cyaneus (Linnaeus), Marsh Hawk: Aerial transient migrant; seen only in spring, when uncommon.

Geranospiza nigra (Du Bus), Blackish Crane-Hawk: Status uncertain, probably resident in region; forest border, semi-open beside forest, and wet places in forest; seldom exposed; solitary; uncommon to rare. Only one other record from Caribbean slope, near Panama.

Family PANDIONIDAE

Pandion haliaetus (Linnaeus), Osprey: Migrant, winter resident (as a species), probably turnover of individuals; river; solitary; uncommon, but seen fairly often.

Family FALCONIDAE

Herpetotheres cachinnans (Linnaeus), Laughing Hawk: Resident; forest border and semi-open; alone or in separated pairs; fairly common to very common.

Micrastur semitorquatus (Vieillot), Collared Forest Falcon: Status uncertain, probably irregular visitant or wanderer; not noted during the entire year of the present study, but present during earlier visits; forest border and semi-open beside forest; usually concealed; solitary, or in twos.

Micrastur mirandollei (Schlegel), Mirandolle's Forest Falcon: Status uncertain; seen only twice during year of present study, when *M. semitorquatus* was absent; forest and forest border; solitary.

Micrastur ruficollis (Vieillot), Barred Forest Falcon: Resident; forest and forest border, including second growth beside the forest; usually concealed; solitary; uncommon.

Daptrius americanus (Boddaert), Red-throated Caracara: Resident; woodland and semi-open; seldom alone, usually in small, noisy parties; fluctuates in frequency from uncommon to very common (in dry season).

Falco peregrinus Tunstall, Peregrine Falcon: Transient migrant; seen only in fall, probably same individual, on two successive days, perched high in semi-open.

Falco albigularis Daudin, Bat Falcon: Resident at the Point; semi-open, where sometimes hunts upriver from the Point; a single pair, possibly other individuals appearing as wanderers.

The families Accipitridae, Pandionidae, and Falconidae are here treated together as "hawks." The following birds can be eliminated as of little or no significance at "La Selva": *Elanoïdes, Ictinia, Buteo swainsoni, Buteo brachyurus, Leucopternis albicollis, Leucopternis princeps, Circus, Micrastur semitorquatus, Micrastur mirandollei,* and *Falco peregrinus.*

This leaves 16 species. The maximum number encountered during any two-week survey was 11; the minimum, five. None was abundant; probably in many instances the same individuals were observed repeatedly. Some species were seen only a few times during the entire year. Few species can be assigned a particular habitat or a special kind of food. *Pandion* eats fish and is restricted to the river. *Herpetotheres* is a confirmed eater of reptiles, particularly snakes. The strange *Daptrius* feeds, among other things, on wasp pupae. *Geranospiza* specializes on the fauna found in epiphytes (at "La Selva"). *Elanoïdes* and *Ictinia* probably hunt aerially for flying insects (at "La Selva"); *Elanoïdes* also swoops at crowns of trees for prey. *Falco albigularis* keeps to the semi-open, where it makes sweeping aerial sorties.

Only four species (*Accipiter bicolor*, *Leucopternis semiplumbea*, *Spizaëtus ornatus*, and *Micrastur ruficollis*) seem to be birds of the forest, although they are not confined to it. The very large *Spizaëtus* is the only one that soars; unlike the others, which are relatively sedentary, it covers much territory. *Spizaëtus* and the small *Leucopternis* drop upon prey from a perch usually at medium heights above the ground. *Accipiter bicolor* and *Micrastur ruficollis* are both rather small in size, usually perch fairly low, have similar long-tailed, short-winged proportions, and their immatures are much alike in coloration and pattern: *M. ruficollis* favors thickety growth and dense portions of the understory in the forest, *A. bicolor* more open parts of the forest and thinned woodland; both are "bird" hawks which twist and dash through the vegetation.

Five species enter the forest not at all or only along the borders. They are: *Buteo platypterus*, *Buteogallus*, *Spizaëtus tyrannus*, *Herpetotheres*, and *Falco albigularis*. Except for *Herpetotheres*, all may soar. *Herpetotheres*, a sluggish bird, inspects the ground from a perch; as mentioned above, it feeds largely on snakes, among which it seems to have a great liking for coral snakes. *Falco albigularis* is a high-spirited, swift-flying, little falcon which captures small birds and insects on the wing. *Spizaëtus tyrannus*, very large and powerful, is uncommon; it prefers overgrown edges outside the forest, mixed stages of second growth and trees, and open woodland, where it enters into the foliage, usually not high above the ground, for varying lengths of time before flying to another grove or stand. *Buteogallus* is seen seldom, usually along the river or close to it; although quite large, it seems to search for small prey. The migrant *Buteo platypterus* is the only hawk that is common in the semi-open; rather sedentary, the wintering individuals are spaced apart, as though each occupied a territory; medium-sized, it secures small-sized prey, mostly from the ground.

Four birds (*Leptodon*, *Harpagus*, *Accipiter superciliosus*, *Spizastur*) remain to be mentioned. *Spizastur*, large and powerful, seems to be a great wanderer in forested areas. In the semi-open it generally perches very high, as *Spizaëtus tyrannus* does not, or, a little inside forest, perhaps rather low, as *Spizaëtus ornatus* sometimes does. Probably its habitat and habits overlap considerably those of the two species of *Spizaëtus;* as they do, it may soar high in the sky. *Leptodon* is rather sluggish and usually occurs high in the trees at or close to the forest border where it seeks its prey by moving about among the branches, scrutinizing the surrounding foliage at each stop; it also may soar. *Harpagus* and, especially, *Accipiter superciliosus* are small-sized "bird" hawks. *Harpagus*, favoring (at "La Selva") rather open woodland and forest borders, combines the habits of a small *Buteo* and an *Accipiter*, and it may also sweep falcon-like through the semi-open, launching itself from a perch either hidden or exposed. *Accipiter superciliosus*, which is primarily an inhabitant of thick second growth in forested areas, where, as does *Micrastur ruficollis*, it may dash at high speed through the tangled understory in forest or second growth, its small size probably enabling it to hunt in vegetation too dense for *Micrastur ruficollis*, is to be seen very seldom.

Family CRACIDAE

Crax rubra Linnaeus, Great Curassow: Status uncertain, possibly breeding resident; noted only March to June; forest; forages on ground, rises into trees when disturbed; solitary, also in twos or threes; uncommon (when present).

Penelope purpurascens Wagler, Crested Guan: Resident; forest, sometimes in semi-open; arboreal, usually in crowns of trees on thick limbs; usually two to several individuals; uncommon to common (formerly abundant).

Ortalis garrula (Humboldt), Chestnut-winged Chachalaca: Resident; mostly second growth in semi-open; arboreal, sometimes to ground; in groups of half a dozen or more individuals; common.

Crax and *Penelope* live in the forest. The turkey-sized *Crax* seems to occur seasonally in small numbers and is largely terrestrial. The pheasant-sized *Penelope* is rather common and is largely arboreal high in the trees. The much smaller *Ortalis* is strictly a bird of the semi-open, preferring thick second growth sprinkled with trees outside the forest.

Family PHASIANIDAE

Odontophorus erythrops Gould, Black-eared Wood Quail: Resident; forest and bordering second

growth; terrestrial; family-sized groups, or alone, or in twos; common.

Odontophorus guttatus (Gould), Spotted Wood Quail: Status uncertain, possibly resident; like *O. erythrops* but in much smaller numbers. Apparently no other Costa Rican report from the tropical belt.

I have no reliable observations which might tend to clarify the environmental relationships between these two species, other than those that indicate *erythrops* to be much more common at "La Selva" than *guttatus*. Possibly *guttatus* is not truly a forest species but one that prefers advanced second growth and overgrown forest borders, whereas *erythrops* occurs in this kind of habitat as well as in high forest.

Family ARAMIDAE

Aramus guarauna (Linnaeus), Limpkin: Accidental; seen once in semi-open at forest border.

Suitable habitat for this distinctive bird is not present at "La Selva," where I was startled at seeing it at all. This bird was probably a wanderer from the coastal lagoons.

Family RALLIDAE

Aramides cajanea (Müller), Cayenne Wood Rail: Resident; wet places in forest and second growth, also on drier ground; usually seen singly, but calls in chorus; common.

Laterallus albigularis (Lawrence), White-throated Crake: Resident; grassy marshes, overgrown stream banks, dense undergrowth in semi-open at wet places; terrestrial, but may flutter from one clump of vegetation to another; usually seen alone, but several in same site; uncommon to common locally.

The habitats of these two rails are mutually exclusive. The little *Laterallus* lives in very dense, low growth where it moves about like a mouse, hidden from sight; it does not enter forest or tall second growth. *Aramides* is to be seen from time to time in taller, shaded vegetation outside the forest as well as inside the forest.

Family HELIORNITHIDAE

Heliornis fulica (Boddaert), American Finfoot: Resident; watercourses; swims on river and streams wherever the latter are unshaded or follow the forest border, or a little inside forest where the surrounding vegetation is low and exposed to the sky, but not well inside forest; usually alone, also in twos; uncommon.

The finfoot exploits a niche in which grebes, even if present, would not compete. At "La Selva," or any other place where I have met it, I have not had the experience of seeing the finfoot dive. It swims along the edges of rivers and streams, plucking invertebrates from the mossy banks and from exposed portions of partially submerged trunks and limbs. This food supply is shared to some extent with *Actitis*, waterthrushes, *Phaeothlypis fulvicauda*, and possibly with *Eurypyga*. In many situations, such as vertical banks rising from the water, only the swimming *Heliornis* seems able to feed at leisure. I do not consider it a forest bird.

Family EURYPYGIDAE

Eurypyga helias (Pallas), Sun Bittern: Resident; mostly riversides and streamsides, also at forested swamp; terrestrial, sometimes flushing to branches; solitary (probably also in pairs); although met with very seldom, it is probably not uncommon.

The Sun Bittern frequents the forested river bank and was seen once at a wooded swamp inside the forest. In a stalking manner it darts the bill at prey on the ground or on moss-covered logs or overhanging branches. The riverside habitat at "La Selva" is exploited in this way by no other bird. Elsewhere in the country, at higher elevations, the Sun Bittern usually occurs at rivers and streams that have mossy boulders upon which, flying lightly from one to the other, it searches for food.

Family SCOLOPACIDAE

Actitis macularia (Linnaeus), Spotted Sandpiper: Migrant, winter resident; river, lower courses of streams and adjacent muddy terrain; solitary; common.

Practically confined to the river, the Spotted Sandpiper for the most part frequents the shore line, graveled beaches, exposed rocks, and partially submerged trunks and limbs. The habitat overlaps considerably that of the smaller-sized waterthrushes (also migrant).

Family COLUMBIDAE

Columba cayennensis Bonnaterre, Pale-vented Pigeon: Status casual or accidental at present,

will surely change to regular visitant or perhaps resident in future; only one bird seen, at the Point, but apparently resident on other side of Río Sarapiquí.

Columba nigrirostris Sclater, Short-billed Pigeon: Resident; woodland and semi-open; arboreal (rarely comes to ground in semi-open); rather sedentary; not shy; usually in small groups or at least in pairs; abundant.

Columbigallina talpacoti (Temminck), Talpacoti Dove: Status, rare visitant (seen once at the Point), but abundant on other side of Río Sarapiquí, will undoubtedly become frequent at the Point in future; feeds on ground, perches on low branches.

Claravis pretiosa (Ferrari-Perez), Blue Ground Dove: Resident; semi-open, second growth outside forest; mostly arboreal (low); alone or in pairs; uncommon to common (at the Point).

Leptotila cassinii Lawrence, Cassin's Dove: Resident; forest border, second growth, including thickety banks and ravines; rare in forest, at interior swamps, and valley breaks; terrestrial, but flushes to low branches; usually alone, sometimes in pairs; common to abundant.

Geotrygon veraguensis Lawrence, Veragua Quail-Dove: Resident; forest; terrestrial; usually in twos, occasionally alone or in threes; uncommon to common (sometimes seen daily).

Geotrygon montana (Linneaus), Ruddy Quail-Dove: Probably resident; forest; terrestrial, and perched low in understory; seen alone (but probably in pairs); rarely seen (possibly more abundant).

Columba cayennensis and *Columbigallina* play no part in the bird life of the study area at present.

Three species are largely or entirely forest birds. *Columba nigrirostris* is arboreal; it commonly enters the semi-open. *Geotrygon veraguensis* and *G. montana* are both terrestrial: *veraguensis* is fairly common, *montana* is rare; invariably *veraguensis* is to be found on the ground, whereas *montana* was perched each time I saw it (but it is a terrestrial forager).

Outside the forest occur *Leptotila* and *Claravis*. *Leptotila* forages on the ground, for the most part in thick cover in second growth; seldom occurring in forest, it there favors similar habitat. *Claravis* is typically a bird of the semi-open, where it prefers patches of second growth, and shoots by in straight, low flight in open view. At "La Selva" it does not form into groups, and seldom does it descend to the ground, as it may elsewhere in the country.

Family PSITTACIDAE

Ara ambigua (Bechstein), Buffon's Macaw: Resident (in the region); forest and bordering semi-open; high in trees, usually in crowns; social, usually groups of several pairs, sometimes in pairs or in threes, seldom alone; common.

Aratinga finschi (Salvin), Finsch's Parakeet: Fall visitant (possibly also in winter); semi-open; flocks; uncommon.

Aratinga astec (Souancé), Aztec Parakeet: Resident; semi-open; small flocks; uncommon to common.

Pionopsitta haematotis (Sclater and Salvin), Red-eared Parrot: Resident; woodland and semi-open; flocks; at all heights in trees, sometimes in understory in forest; common to very common.

Pionus senilis (Spix), White-crowned Parrot: Resident; semi-open and woodland (uncommon in interior of solid forest); flocks; abundant.

Amazona autumnalis (Linnaeus), Red-lored Amazon Parrot: Resident (in region); woodland, forest border, and semi-open; flocks; uncommon to common.

Amazona farinosa (Boddaert), Plain-colored Amazon Parrot: Status like that of *A. autumnalis*, but more abundant.

Four species seem to be dependent on heavy forest, where they frequent the high canopy, but also occur in the semi-open as commonly as non-forest birds. The very large *Ara* is capable of feeding on the toughest-shelled fruits. The two species of *Amazona* are both common and may occur together in the same tree, but I cannot separate them in regard to habitat and habits; *farinosa*, which is larger than *autumnalis*, is also considerably more abundant. The small, swift-flying *Pionopsitta* probably exploits a food supply unavailable to the heavy-bodied Amazon parrots.

Pionus, similar to *Pionopsitta* but larger and heavier, may visit the forest, but it is primarily a species of the semi-open. Occurring exclusively outside forest are the two species of *Aratinga*, long-tailed parakeets that are very swift-flying and highly maneuverable in the air. The resident *astec* is smaller than *finschi*, more agile, and is common only in the Caribbean lowlands. The center of abundance of *finschi* is in the foothill region, and it seems to be a seasonal visitor not only at "La Selva" but also elsewhere in the country; it has a much wider geographical and ecological range than *astec* (although *astec*

has a much greater geographical range in Central America).

Family CUCULIDAE

Coccyzus erythropthalmus (Wilson), Black-billed Cuckoo: Transient migrant; semi-open beside forest; arboreal, low; solitary; uncommon. Apparently unrecorded previously from Caribbean lowlands; hitherto considered very rare passage migrant in Costa Rica.

Coccyzus americanus (Linnaeus), Yellow-billed Cuckoo: Status like that of *C. erythropthalmus*, but elsewhere in Costa Rica may be common during migration, and also winters in small numbers.

Piaya cayana (Linnaeus), Squirrel Cuckoo: Resident; semi-open, second growth, and forest; arboreal at all heights (in forest, always high), sometimes to ground; usually alone; common to abundant.

Crotophaga sulcirostris Swainson, Groove-billed Ani: Casual, undoubtedly resident in region; semi-open; occasional at the Point, rare farther upstream; single individuals only. Elsewhere in Costa Rica, gregarious and common to abundant.

Neomorphus geoffroyi (Temminck), Geoffroy's Ground Cuckoo: Resident; forest; terrestrial, but rises into understory; solitary or in twos, possibly threes; seen only twice; rare.

There are only two resident cuckoos. The arboreal *Piaya* is abundant in the semi-open and also occurs high in the forest. The terrestrial *Neomorphus* is confined to the forest, seems to be a regular follower of army ants, and is rare.

Family STRIGIDAE

Otus vermiculatus (Ridgway), Vermiculated Screech Owl: Only one record, a bird dropped by a forest falcon, and secured by L. R. Holdridge; probably resident, although I never met it.

[*Lophostrix cristata* (Daudin), Crested Owl: Status uncertain, probably resident; identification tentative: one young bird with "ear tufts," whose size, coloration, and markings eliminate any other Middle American owl from consideration, seen a little inside forest, where it was observed at length.]

Pulsatrix perspicillata (Latham), Spectacled Owl: Resident; woodland, second-growth borders; solitary; not uncommon (possibly common). Elsewhere in Costa Rica, often seen in twos.

Glaucidium minutissimum (Wied), Least Pygmy Owl: Resident; woodland and semi-open; generally fairly low; nocturnal and diurnal; alone or in twos; fairly common.

Ciccaba virgata (Cassin), Mottled Wood Owl: Resident; thickety, tangled growth in forest and along forest border; solitary; fairly common.

I have little information on the owls, and the above comments on abundance are almost certainly underestimates. Apparently all the species may occur in forest and at the forest border; the tiny *Glaucidium* also occurs in the semi-open in broad daylight. *Pulsatrix* and *Lophostrix* are large species which may be met with during the day; at "La Selva," *Lophostrix* seems to be extremely rare. *Ciccaba* is medium-sized, strictly nocturnal, and is probably the most abundant species. *Otus vermiculatus* is small; I know nothing about it other than its discovery by Holdridge.

Family NYCTIBIIDAE

Nyctibius griseus (Gmelin), Common Potoo: Resident; in woodland during day, into semi-open at night; arboreal; nocturnal; seen only once, but heard from time to time; probably not uncommon.

I saw this bird during the day a little inside the forest, where it was perched crosswise on a high branch. Although it was not sitting on the end of a stub, the inanimate bird held the beak pointing stiffly upward in the usual daylight manner. That it leaves the forest at night in order to hunt in the semi-open I judged from the locations of its cries. I never saw it feeding, but it is said to sally for insects from a perch.

Family CAPRIMULGIDAE

Chordeiles sp., Nighthawk: Not identified to species, but I suspect *minor;* transient aerial migrant at dusk both in spring and fall.

Nyctidromus albicollis (Gmelin), Pauraque: Resident; woodland borders, second growth outside forest, and semi-open (at night); nocturnal; alone, or in pairs, or in small groups; abundant.

Caprimulgus carolinensis Gmelin, Chuck-will's-widow: Rare transient migrant (possibly occasional winter resident); seen once, in riverside thicket during fall migration.

The only resident nightjar is *Nyctidromus*. Active mostly at nightfall and just before dawn, it flutters after insects from the ground or from a log or stump in the semi-open, wherever there is a cleared space. In the forest

I suspect the presence of another species which I was unable to identify.

Family APODIDAE

Streptoprocne zonaris (Shaw), White-collared Swift: Daily visitant; aerial; flocks; abundant.

Chaetura cinereiventris Sclater, Gray-rumped Swift: Daily visitant, probably resident in general area; aerial; flocks; abundant.

Cypseloides sp. [probably *niger* (Gmelin), Black Swift]: Not identified to species but certainly this genus; status uncertain, probably irregular visitant; only single birds seen, together with other swifts.

Panyptila cayennensis (Gmelin), Lesser Swallow-tailed Swift: Resident (in region); aerial; singly or in twos, often mixed with *Chaetura;* uncommon but regular. Apparently no definite record for Costa Rica, although I have seen it elsewhere on the Caribbean slope.

The common swifts are the very large *Streptoprocne* and the small *Chaetura. Cypseloides* is medium-sized and seldom seen. The fork-tailed *Panyptila* is resident, but its numbers are small, possibly the same individuals being seen repeatedly.

Family TROCHILIDAE

Glaucis hirsuta (Gmelin), Hairy Hermit: Resident; second growth bordering forest, overgrown edges in vicinity of forest, and slight penetration into forest; low, at bush or shrub height; solitary; uncommon to rare.

Threnetes ruckeri (Bourcier), Rucker's Hermit: Resident; forest and bordering second growth; low above ground; solitary, or several individuals in same small area; uncommon to common.

Phaethornis superciliosus (Linnaeus), Long-tailed Hermit: Resident; woodland, bordering second growth, sometimes in semi-open; low above ground; usually solitary; abundant.

Phaethornis longuemareus (Lesson), Little Hermit: Status like that of *P. superciliosus,* but commoner in thickety second growth.

Phaeochroa cuvierii DeLattre and Bourcier, Cuvier's Hummingbird: The Caribbean race, *roberti* (specimen collected), apparently unrecorded previously from Costa Rica; status uncertain, probably irregular visitant, possibly resident in region; seen only twice, at the Point, perched at shrub height.

Florisuga mellivora (Linnaeus), Jacobin Hummingbird: Status uncertain; semi-open, second growth, and sometimes in forest; generally at shrub height or in low trees, sometimes very high; alone or in "colonies"; seasonally rare, common, or abundant (at the Point), apparently absent most of September and October.

Klais guimeti (Bourcier), Guimet's Hummingbird: Status uncertain, probably non-breeding visitant; commonest in semi-open, edges of thickety growth, not seen in forest; usually several unassociated individuals in same small area; apparently absent March to May, rare in January and February, uncommon to common during rest of year.

Paphosia helenae (DeLattre), Princess Helena's Coquette: Status uncertain, probably regular visitant, possibly resident (seen August, December, April); semi-open; bushes and shrubs to fairly high in trees; solitary; rare (but probably uncommon).

Popelairia conversii (Bourcier and Mulsant), Green Thorntail: Status uncertain, either irregular visitant or wanderer; at least two birds noted only in late August, fairly high in trees close to forest. Not recorded before from tropical belt.

Thalurania furcata (Gmelin), Common Wood Nymph: Resident; commonest in shaded, thickety second growth, less common in forest, also enters semi-open; usually low or fairly low above ground; generally alone; abundant.

Hylocharis eliciae (Bourcier and Mulsant), Elicia's Goldentail: Status uncertain; low in semi-open and in second-growth thickets, only at the Point; solitary; uncommon to rare (not seen September to March).

Amazilia amabilis (Gould), Lovely Hummingbird: Resident; semi-open and thickety second growth; usually low, sometimes high in trees; groups of unassociated individuals (not truly gregarious) in favorable habitat, sometimes alone; fairly common (in semi-open) to abundant (at the Point).

Amazilia cyanura Gould, Blue-tailed Hummingbird: Accidental; seen once, on shrub in semi-open, at the Point. Only one previous record for Costa Rica, from the central plateau.

Amazilia tzacatl (De la Llave), Rieffer's Hummingbird: Resident; semi-open and edges of second growth; usually fairly low; a number of individuals in preferred areas, sometimes alone; abundant at the Point, uncommon to fairly common elsewhere on study area.

Microchera albo-coronata (Lawrence), Snowcap: Resident; semi-open, second growth, and forest; usually low above ground; generally alone; uncommon to fairly common.

Chalybura melanorrhoa Salvin, Dusky Plumeleteer: Resident; forest, second growth, and sometimes in semi-open; mostly fairly low; usually alone; common to abundant.

Heliothryx barroti (Bourcier), Barrot's Fairy: Resident; forest border, semi-open, and occa-

sionally in forest; usually high or fairly high, occasionally low; solitary; uncommon.

Heliomaster longirostris (Audebert and Vieillot), Long-billed Starthroat: Probably resident; semi-open; medium heights to high, occasionally on shrubs; solitary; uncommon.

Phaeochroa, *Popelairia*, and *Amazilia cyanura* are accidental or casual.

None of the remaining 15 species is confined to forest. The following, however, do occur regularly inside the forest. *Heliothryx* usually keeps high above the ground and is seen most often hovering at the under sides of leaves or picking small insects out of the air. The other species overlap extensively in habits and habitat. The large *Phaethornis superciliosus*, the small *Phaethornis longuemareus*, and the medium-sized *Threnetes* have long, curved bills and feed more or less in the same way in the same sorts of places; they inhabit undergrowth, and all are common. The tiny *Microchera* is short-billed and presumably occupies a feeding niche related to its small size; it is to be seen occasionally. *Thalurania*, which is smallish and rather common, and *Chalybura*, which is rather large and quite common, occur somewhat higher in the understory than do *Phaethornis* and *Threnetes*. Of the above group, only *Chalybura* is found more consistently inside high forest than in bordering second growth. Another species that occasionally occurs in the forest is *Florisuga*, which probably enters along streams and ravines, and it may occur at all heights.

The species occurring mainly in the semi-open are the tiny, short-billed *Paphosia* and the large, long-billed *Heliomaster;* they usually perch on bare twigs. *Glaucis*, which is very similar to the largely forest-inhabiting *Threnetes*, frequents thick new second growth and dense shrubbery almost exclusively, where it and *Threnetes* overlap extensively in habits and habitat; *Glaucis* is seen seldom, *Threnetes* often.

The birds occurring with equal frequency both in the semi-open and in second growth are *Klais*, *Hylocharis*, *Amazilia amabilis*, and *Amazilia tzacatl*. All are commonest at the Point, but *Klais* and *A. amabilis* may also be common elsewhere in the semi-open beside the forest, at all heights, both in small trees and low second growth or even in tall trees, especially when the trees are in flower. At the Point, where the congeneric *Amazilia amabilis* and *A. tzacatl* are both abundant, I was unable to detect differences in habitat or behavior. *Hylocharis*, occurring in the same places as *Amazilia* at the Point, is very uncommon; it is apparently unsuccessful on the Caribbean slope when compared with its abundance on the Pacific side of the country.

Family TROGONIDAE

Trogon massena Gould, Massena Trogon: Resident; forest and semi-open; medium heights to high above the ground, occasionally low; alone, separated pairs, or a few separated individuals; common to abundant.

Trogon clathratus Salvin, Lattice-tailed Trogon: Resident; forest and forest border; medium heights to high; alone or in separated pairs; uncommon to fairly common.

Trogon collaris Vieillot, Collared Trogon: Accidental or casual; one bird (a female) noted in grove of tall trees beside river from October to January. Apparently unrecorded previously from so low an elevation.

Trogon rufus Gmelin, Graceful Trogon: Resident; forest, occasionally in bordering second growth; usually fairly low; alone, or separated pairs; common to abundant.

Trogon violaceus Gmelin, Gartered Trogon: Resident; semi-open, also second growth, occasionally in forest; medium heights to fairly high above ground; common to abundant.

Trogon collaris, a species of the subtropical belt and higher, does not properly belong at "La Selva." Practically confined to the forest are the large *T. clathratus* and the relatively small *T. rufus*, the former rather high in the trees, the latter rather low (understory). The large *T. massena*, which is very similar to *clathratus*, differs in its much broader ecological tolerance, for it occurs perhaps more commonly outside the forest than inside, is everywhere far more abundant, and has a very much wider geographical distribution. *Trogon violaceus*, which is considerably smaller than *massena*, is typically a trogon of the semi-open, hardly entering forest at all.

Family ALCEDINIDAE

Megaceryle torquata (Linnaeus), Ringed Kingfisher: Resident; river, where it perches low or at medium heights; sometimes in semi-open, on a high bare branch; alone or in twos or threes; uncommon to fairly common.

Chloroceryle amazona (Latham), Amazon King-

fisher: Resident; river, also stream mouths; perches low or at medium heights along river; usually solitary; uncommon to fairly common.

Chloroceryle americana (Gmelin), Green Kingfisher: Resident; river and streams (outside forest); low; alone or in pairs; uncommon to very common.

Chloroceryle inda (Linnaeus), Green-and-rufous Kingfisher: Resident; forest streams; perches rather low; solitary; rare. Only one previous Costa Rican record.

Chloroceryle aenea (Pallas), Pygmy Kingfisher: Resident; forest streams and small pools in shaded second growth beside forest (and probably occasionally at river); perches fairly low; alone or in pairs; uncommon.

Aside from its very large size, *Megaceryle* differs from the four species of *Chloroceryle* in coloration and proportions, in its habit of flying, sometimes very high in the air, cross-country from one part of the river to another, and in the habit of perching high on a bare branch in the tree plantations. Along the river occur *Megaceryle*, the smaller *C. amazona*, and the still smaller *C. americana;* along the streams outside the forest, *C. americana* is just about the only kingfisher; at streams inside the forest occur the rare *C. inda* and the uncommon, diminutive *C. aenea*. Even where the habitats overlap, there is always a conspicuous difference in size among the kingfishers represented; *C. americana* and *C. inda*, which are approximately the same in size, do not occur together. The four species of *Chloroceryle* fall into two color groups: all are very similar on the upper parts, but the river-inhabiting *amazona* and *americana* are mostly white on the under parts, whereas the woodland-inhabiting *inda* and *aenea* are mostly rufous.

Family MOMOTIDAE

Electron platyrhynchum (Leadbeater), Broad-billed Motmot: Resident; forest, second growth mixed with trees, occasionally in semi-open; fairly low to high above ground; alone, in twos, or in small groups; common to abundant.

Baryphthengus ruficapillus (Vieillot), Great Rufous Motmot: Resident; forest, also bordering second growth and wooded riverside; often at medium heights, or lower, above ground, occasionally high; solitary, in twos, or small groups; abundant.

The two motmots are similar in appearance and occupy more or less the same habitat, but they are of different sizes and presumably are able to secure differently sized prey.

Family GALBULIDAE

Galbula ruficauda Cuvier, Rufous-tailed Jacamar: Resident; overgrown woodland edges and second growth; low to fairly low; alone or in pairs, sometimes in threes; common to abundant.

Jacamerops aurea (Müller), Great Jacamar: Resident; forest and forest border; fairly low to fairly high; usually solitary, also in pairs; rare to uncommon.

The two jacamars are similar in appearance but differ considerably in size. The large, heavy-billed *Jacamerops* is present in small numbers and is a forest species. The smaller, slender-billed *Galbula* is common and occurs in thickety growth and overgrown edges, always outside the solid forest. *Jacamerops* is reserved and generally silent; *Galbula* is bold and noisy.

Family BUCCONIDAE

Notharchus macrorhynchos (Gmelin), White-necked Puffbird: Resident; forest border and semi-open; usually high to very high in trees, sometimes fairly low; alone or in separated pairs; uncommon.

Notharchus tectus (Boddaert), Pied Puffbird: Status uncertain; irregular visitant, possibly resident in region; usually very high, sometimes lower; usually in small, traveling groups, sometimes alone; rare (or uncommon). Only one previous record for Costa Rica.

Malacoptila panamensis Lafresnaye, White-whiskered Puffbird: Resident; forest, second growth, occasionally in semi-open; usually low or fairly low; alone, in pairs, or small, family-sized groups; common to abundant.

Monasa morphoeus (Hahn and Küster), White-fronted Nunbird: Resident; forest and semi-open; fairly low to fairly high, sometimes very high; alone, in twos or threes, or social groups up to a dozen individuals; common to abundant.

None of the puffbirds is confined to forest. *Malacoptila* and *Monasa*, however, are forest-based, but in most other respects they are completely dissimilar. Neither the large *Notharchus macrorhynchos* nor the small *N. tectus* seems to enter the forest, and, although of similar appearance, they differ very much in habits. *Notharchus tectus* seems to be unique among puffbirds (in Costa Rica) because it troops about the countryside.

Family RAMPHASTIDAE

Pteroglossus torquatus (Gmelin), Collared Araçari: Resident; semi-open, second growth, and forest; at all heights, usually not very low; in bands up to a dozen individuals or more; abundant.

Selenidera spectabilis Cassin, Cassin's Araçari: Seasonal resident (probably non-breeding); forest, semi-open, occasionally in second growth; at all heights, usually not very low; in small groups, or alone; absent mid-April to September (one bird seen in June), rare to common from October to January.

Ramphastos sulfuratus Lesson, Keel-billed Toucan: Resident; woodland and semi-open; medium heights to high above ground; two to six or more individuals together, seldom alone; abundant.

Ramphastos swainsonii Gould, Swainson's Toucan: Status like that of *R. sulfuratus*.

Although none of the toucans is confined to forest, all are forest-based. The four species fall into two size groups: the large *Ramphastos sulfuratus* and *R. swainsonii*, and the much smaller *Pteroglossus* and *Selenidera*. The two species of *Ramphastos* I cannot separate ecologically. Both are abundant and occur together and are among the dominant birds at "La Selva." Although almost identical in plumage, they differ strikingly in coloration of the beak and in voice, and bob differently when calling; also, *swainsonii* is heavier-bodied and longer-billed than *sulfuratus*. *Pteroglossus* and *Selenidera* are very similar in habitat and habits, but are totally different in plumage and voice. *Selenidera* occurs more regularly in forest, is present in much smaller numbers, and is seasonal at "La Selva," whereas *Pteroglossus* is one of the most common residents.

Family PICIDAE

Piculus simplex (Slavin), Rufous-winged Woodpecker: Status uncertain, either resident, or visitant wandering about in region; forest, occasionally in semi-open; usually at medium heights in trees; alone or in pairs; rare to uncommon.

Celeus castaneus (Wagler), Chestnut-colored Woodpecker: Status uncertain, absent from mid-April through September; woodland and semi-open; alone, also in pairs; fairly low to medium heights above ground; rare to fairly common (when present).

Celeus loricatus (Reichenbach), Cinnamon Woodpecker: Resident; forest, also semi-open; alone or in pairs; fairly low above ground to medium heights, sometimes high; common to abundant.

Dryocopus lineatus (Linnaeus), Lineated Woodpecker: Resident; semi-open and woodland; at all heights; alone or in pairs; uncommon to common.

Centurus pucherani (Malherbe), Pucheran's Woodpecker: Resident; semi-open, also forest; at all heights (high in forest); alone or in twos or threes; abundant in semi-open, rare to very uncommon in forest.

Veniliornis fumigatus (d'Orbigny), Smoky-brown Woodpecker: Resident (as a species); second growth, also semi-open; usually low; usually alone, sometimes in pairs; uncommon, seen mostly at the Point.

Phloeoceastes guatemalensis (Hartlaub), Guatemalan Ivory-billed Woodpecker: Resident; forest, also semi-open; at all heights; usually in twos, also in groups of three or four; common to abundant.

None of the woodpeckers is restricted to a single habitat. *Veniliornis* and *Centurus* are essentially non-forest species. *Veniliornis* is uncommon and occurs mostly in thickety growth and second-growth borders. *Centurus* is abundant in trees in the semi-open, and occasionally enters the forest in the canopy. Forest species are *Piculus*, the two species of *Celeus*, and *Phloeoceastes*, but they all occur regularly in the semi-open. *Piculus* is seen seldom, and I believe its center of abundance to be located at higher elevations. The two species of *Celeus* I cannot separate ecologically: *loricatus* at all times is far more abundant; *castaneus* seems to be missing from "La Selva" for part of the year. The very large *Phloeoceastes*, which is common in the forest, is also seen commonly in the semi-open. Very similar to it is *Dryocopus*, which occurs more commonly along the forest border and in the semi-open than inside the forest. Wherever *Phloeoceastes* and *Dryocopus* occur together, as in the tree plantations at "La Selva," I am unable to separate them in regard to habits and habitat: *Phloeoceastes* is the heavier, stronger bird, and it is much more abundant than *Dryocopus*.

Family DENDROCOLAPTIDAE

Dendrocincla fuliginosa (Vieillot), Brown Dendrocincla: Status uncertain: absent or extremely rare from April to latter August (one bird, seen in May), uncommon to fairly common September to March; woodland, occasionally in neigh-

boring semi-open; fairly low above ground to medium heights; usually in small groups, also alone.

Glyphorynchus spirurum (Vieillot), Wedge-billed Woodhewer: Resident; woodland, also semi-open on occasion; alone, or a few scattered individuals; usually low; common to abundant.

Dendrocolaptes certhia (Boddaert), Barred Woodhewer: Resident; woodland and semi-open; usually from medium heights to low above ground; singly or in twos or threes; common.

Xiphorhynchus guttatum (Lichtenstein), Buff-throated Woodhewer: Resident; forest border, advanced second growth, and semi-open; at all heights; usually alone; abundant.

Xiphorhynchus lachrymosum (Lawrence), Black-striped Woodhewer: Resident; forest, also semi-open; fairly low to high; often alone in forest, usually several loosely associated individuals in tree plantations; fairly common to abundant.

Xiphorhynchus erythropygium (Sclater), Spotted Woodhewer: Resident; forest, also forest border; at all heights; alone, or a few unassociated individuals; uncommon to fairly common.

Lepidocolaptes souleyetii (Des Murs), Thin-billed Woodhewer: Resident; semi-open; from low above ground to medium heights; generally alone, or in twos or perhaps threes; fairly common to abundant (at the Point).

Xiphorhynchus guttatum and the smaller, slender-billed *Lepidocolaptes* do not enter the forest. The remaining five species are forest birds, but all may be present, some of them conspicuously, in the semi-open. *Xiphorhynchus lachrymosum* occurs rather high in the forest and is common. *Xiphorhynchus erythropygium* usually occurs as an uncommon member or two of a traveling mixed band; its center of abundance lies in the subtropical belt. *Dendrocolaptes*, which occurs commonly in the semi-open, in the forest is to be seen, for the most part, together with other birds attending army-ant swarms; it is the largest, strongest-billed woodhewer on the study area. The ovenbird-like *Dendrocincla* occurs almost always in small groups accompanying army ants; it is not common, and seems to be absent seasonally. *Glyphorynchus* is very small, has a short, wedge-shaped beak, and occurs mostly in the understory.

Family FURNARIIDAE

Synallaxis brachyura Lafresnaye, Sooty Spinetail: Resident; thickety second growth and shrubbery, mostly at the Point; alone or in twos; generally uncommon.

Hyloctistes subulatus (Spix), Striped Hyloctistes: Resident; woodland mostly, also forest border, occasionally in semi-open; fairly low to medium heights; usually alone, also in twos; uncommon.

Automolus ochrolaemus (Tschudi), Buff-throated Automolus: Resident; forest and second growth; usually low or fairly low, seldom to medium heights in trees; alone or in twos or threes; abundant.

Xenops minutus (Sparrman), Plain Xenops: Resident; woodland and semi-open; at all heights, usually at medium heights to fairly low above ground; alone or in twos, also with mixed bands; uncommon to fairly common.

Sclerurus guatemalensis (Hartlaub), Scaly-throated Leafscraper: Resident; forest, also tall second growth beside forest; terrestrial, also low in understory; solitary; uncommon to fairly common.

Synallaxis occurs only in low, dense growth outside the forest. The other species are all woodland birds. *Sclerurus* is terrestrial inside the forest and contiguous woodland. The wedge-billed little *Xenops*, which occurs in various habitats, often accompanies mixed flocks and is typically arboreal. *Automolus* rummages in thickety second growth bordering forest and tangled understory inside forest; it is the most abundant ovenbird at "La Selva." *Hyloctistes*, a rummager like *Automolus*, is smaller and less robust, usually occurs upward from the upper portions of the understory, often travels about with mixed bands, is relatively uncommon, is more strictly a forest bird, yet occasionally enters the foliage of trees in the semi-open (as *Automolus* does not).

Family FORMICARIIDAE

Cymbilaimus lineatus (Leach), Fasciated Antshrike: Resident; forest border and leafy second growth, occasionally in semi-open; usually fairly low above ground; as a rule in pairs; common to abundant.

Taraba major (Vieillot), Great Antshrike: Resident; thick, low second growth, shrubbery, overgrown edges, occasionally in semi-open in small trees; usually in pairs; common to abundant.

Thamnophilus punctatus (Shaw), Slaty Antshrike: Resident; forest, shaded second growth, occasionally in small tree in semi-open; generally low or fairly low; almost always in pairs; abundant.

Thamnistes anabatinus Sclater and Salvin, Russet Antshrike: Resident; forest, tall second growth, and semi-open; generally from medium heights to high above ground, sometimes fairly low; solitary or a few loosely associated individuals; uncommon to fairly common.

Dysithamnus mentalis (Temminck), Plain Antvireo: Accidental or casual; seen once, at forested swamp with mixed band. Apparently unrecorded previously from Caribbean lowlands.

Dysithamnus striaticeps Lawrence, Streaked-crowned Antvireo: Resident; forest and advanced second growth; usually fairly low above ground to below medium heights; usually a few individuals accompanying bands of *Myrmotherula* spp., occasionally alone; common.

Myrmotherula fulviventris (Lawrence), Fulvous-bellied Antwren: Resident; forest and shaded second growth; usually low or fairly low; in twos or threes, often in larger groups; abundant.

Myrmotherula axillaris (Vieillot), White-flanked Antwren: Status like that of *M. fulviventris*, but usually in larger bands.

Microrhopias quixensis (Cornalia), Dotted-winged Antwren: Resident; second growth and forest; usually fairly low, also low above ground or at medium heights; generally in groups; abundant.

Cercomacra tyrannina (Sclater), Tyrannine Antbird: Resident; thick second growth (outside forest); low; usually in pairs; common.

Gymnocichla nudiceps (Cassin), Bare-crowned Antbird: Resident; thick second growth and overgrown forest border, where vegetation usually impenetrable; alone or in pairs; uncommon to fairly common.

Myrmeciza exsul Sclater, Sclater's Antbird: Resident; forest and shaded second growth (deep in forest, generally at wet places); semi-terrestrial; in pairs, also alone; abundant.

Myrmeciza immaculata (Lafresnaye), Immaculate Antbird: Accidental or irregular visitant; found once, together with other antbirds accompanying army ants in second growth at forest border. In Costa Rica, inhabits subtropical and lower montane belts; apparently not found before at so low an elevation.

Formicarius analis (d'Orbigny and Lafresnaye), Black-faced Antthrush: Resident; forest, also shaded second growth, terrestrial, occasionally on low branches; alone or in twos or threes; abundant.

Gymnopithys leucaspis (Sclater), Bicolored Antbird: Resident; forest and forest border; low in understory, sometimes to ground; social, in bands; regular army-ant attendant; seldom alone; common.

Hylophylax naevioïdes (Lafresnaye), Spotted Antbird: Status like that of *Gymnopithys*, but more abundant, and widespread in forest, where, alone or in pairs, it may be independent of ants.

Phaenostictus mcleannani (Lawrence), Ocellated Antthrush: Status like that of *Gymnopithys*.

Grallaria fulviventris Sclater, Fulvous-bellied Antpitta: Resident; second growth, particularly first and second stages, in forest and, more commonly, along forest border and outside forest; semi-terrestrial; solitary, occasionally in twos; uncommon to fairly common.

Grallaria perspicillata Lawrence, Spectacled Antpitta: Resident; forest, occasionally in bordering second growth; terrestrial; solitary; abundant.

Dysithamnus mentalis and *Myrmeciza immaculata* do not properly belong at "La Selva."

Eleven species are forest birds, of which several occur also in bordering second growth, and only one (*Thamnistes*) appears regularly in the semi-open. *Formicarius* and *Grallaria perspicillata* are terrestrial: the former walks like a sturdy little rail or bantam cock, the latter patters like a thrush on a lawn or a little plover on a beach. In the lower understory, occasionally descending to the ground, are the sedentary *Myrmeciza exsul* and the army-ant attendants: *Gymnopithys*, *Hylophylax*, and *Phaenostictus*. In the upper understory occurs *Thamnophilus*. In the upper understory and lower middle forest are the stout-bodied, little *Dysithamnus striaticeps* and the warbler- or vireo-like *Myrmotherula fulviventris* and *M. axillaris*. The two species of *Myrmotherula* not only do the same things but occur together in the same places, with *axillaris* seemingly somewhat more active and occurring on the average somewhat higher in the understory than *fulviventris*. Ranging from the middle forest to the canopy is *Thamnistes*.

The arboreal, social *Microrhopias* and the semi-terrestrial, sedentary *Grallaria fulviventris* occur inside forest and, more often, outside forest in second growth. In the forest *Microrhopias* acts in the same way as *Myrmotherula;* in second growth outside the forest, no other social species quite duplicates the antwren-like behavior of *Microrhopias*. *Grallaria fulviventris* in the forest is the only antbird confined to impenetrable undergrowth; outside the forest, other formicariids may occur with it, but none is terrestrial.

Four species do not enter the forest. *Cymbilaimus* occurs several yards above the ground

inside dense, leafy second growth; *Taraba*, in thick, low undergrowth that is usually exposed to the light; *Cercomacra*, a yard or two above the ground in shaded undergrowth and thickety second growth; *Gymnocichla*, low in very dense second growth, and is an inveterate army-ant attendant. All occur in pairs and are sexually dimorphic.

Family PIPRIDAE

Piprites griseiceps Salvin, Gray-headed Manakin: Resident; forest and bordering second growth; in forest, usually at borders of swamps and along breaks; fairly low above ground to medium heights; one or perhaps two individuals accompanying mixed bird parties; uncommon to fairly common. Heretofore considered extremely rare in Costa Rica.

Pipra mentalis Sclater, Yellow-thighed Manakin: Resident; forest, occasionally tall second growth, sometimes in semi-open; at all heights, but mostly fairly low above ground to below medium heights; solitary, or in groups of two to perhaps five; abundant (except January, when extremely scarce).

Corapipo leucorrhoa (Sclater), White-ruffed Manakin: Short-term visitant (end of November to March), and accidental or irregular visitant (once in July and once in August); forest, occasionally second growth and semi-open; low or fairly low; usually alone, occasionally two or three together; rare to very common (January).

Manacus candei (Parzudaki), Candé's Manakin: Resident; thickety second growth outside forest; usually very low to low; alone or in twos or threes; common to abundant.

Schiffornis turdinus (Wied), Thrush-like Manakin: Resident; forest, occasionally in adjoining second growth; low or very low; solitary; uncommon to fairly common.

Manacus lives in thickets outside the forest. The other species occur mainly inside forest. *Piprites*, a manakin of unique behavior (in Costa Rica), accompanies traveling mixed bands. *Schiffornis* wanders about alone through the lower understory. The rather sedentary *Pipra* occurs in the upper portion of the understory and lower middle forest. The non-resident *Corapipo* behaves much like *Pipra*, but generally does not rise above the understory (as it may elsewhere in the country), and shows no courtship activity, unlike *Pipra* which performs through most of the year.

Family COTINGIDAE

Carpodectes nitidus Salvin, Snowy Cotinga: Resident (as a species); forest and semi-open; usually high in trees; solitary, in pairs, or in groups of up to 10 or so (usually all males); uncommon to fairly common.

Attila spadiceus (Gmelin), Polymorphic Attila: Resident; second growth, forest, and semi-open; generally fairly low above ground to medium heights, or high (in forest); solitary; abundant (in forest, fairly common).

Laniocera rufescens (Sclater), Speckled Mourner: Status uncertain; probably breeding visitant, possibly permanent resident; not noted (perhaps merely silent) from latter June to October; forest, at wooded swamps and near streams; usually at or below medium heights, sometimes fairly low; rare to uncommon (but seen regularly, probably same calling individuals at same places). Rare in Costa Rica; in Caribbean lowlands known from one other locality.

Rhytipterna holerythra (Sclater and Salvin), Rufous Mourner: Resident; woodland (seldom noted in solid forest), second growth with emergent trees, and semi-open; fairly low above ground to, usually, medium heights or very high; solitary (in twos in dry season); extremely rare (July to September) to abundant.

Lipaugus unirufus Sclater, Rufous Piha: Resident; forest and semi-open; fairly low to high; alone, or two or three birds chasing about, or several loosely associated individuals; common to abundant.

Pachyramphus cinnamomeus Lawrence, Cinnamon Becard: Resident; semi-open, also woodland; usually at medium heights or fairly low above ground, but high in forest; alone or in twos, or a few loosely associated individuals; very common to abundant in semi-open, uncommon in forest.

Pachyramphus polychopterus (Vieillot), White-winged Becard: Resident; semi-open and advanced second growth (outside forest); fairly low to high; usually alone, also in pairs; uncommon.

Platypsaris aglaiae (Lafresnaye), Gray Becard: Accidental or casual; one bird (a female) seen twice at same site in semi-open in April.

Tityra semifasciata (Spix), Masked Tityra: Resident; mostly in semi-open, occasionally in forest canopy; usually high; usually in small groups trooping about, also in pairs, occasionally alone; common to abundant.

Erator inquisitor (Lichtenstein), Black-capped Tityra: Status like that of *Tityra*, but less frequent and in smaller groups.

Querula purpurata (Müller), Purple-throated Fruit Crow: Resident; forest border, forest, also semi-

open; medium to high; small bands, also in twos or threes; abundant.

Cephalopterus glabricollis Gould, Bare-necked Umbrella-bird: Non-breeding visitant, absent (except for one bird in April) from March to latter July (when one bird was seen in the semi-open), but reappearing in August, when a small "wave" of several individuals was noted in the semi-open beside forest; forest, on rare occasions in neighboring semi-open; fairly low to fairly high; usually alone, also in twos or threes; rare to uncommon (when present).

Procnias tricarunculata (J. and E. Verreaux), Three-wattled Bellbird: Post-breeding visitant or transient; seen only twice, once at end of August, 1957, once in latter July, 1958, a pair of adults and an immature male, respectively; the birds were calling, otherwise would have escaped notice, and were at or just behind the forest border, high in the trees.

This family is difficult to treat. Conspicuous differences in size are few, the diet is omnivorous (even in most so-called frugivorous species), and groups of related species act more or less in the same way. *Platypsaris* and *Procnias* do not properly belong at "La Selva."

Of the remaining 11 species, only *Pachyramphus polychopterus* does not enter forest. The others occur in forest, but only *Laniocera* and *Cephalopterus* do not visit regularly the neighboring semi-open. I cannot agree with published opinions that claim *Tityra*, *Erator*, and *Pachyramphus cinnamomeus* as forest species; in my experience they occur abundantly in the semi-open and uncommonly in forest. The congeneric *Pachyramphus cinnamomeus* and *P. polychopterus* differ in that the former is far more abundant, which suggests that *cinnamomeus* is better suited to a lowland, wet-forested environment. Elsewhere *polychopterus* is more common in drier or cultivated areas. *Tityra* and *Erator* are much alike, but aside from the fact that *Tityra* is much more abundant, I have been unable to detect significant differences between them. *Querula* and (the completely different) *Rhytipterna* are in an intermediate position. Although occurring only in forested regions, where they are common along the forest borders, a little way inside the forest, and in the nearby semi-open, they are seldom encountered well inside the forest. On the other hand, *Carpodectes* and (the quite different) *Lipaugus* are forest species which, respectively, visit trees in the semi-open irregularly or daily. *Attila* occurs almost anywhere.

In the forest, *Carpodectes* rarely may be glimpsed trooping over the high canopy. *Attila* keeps rather high in the trees, inside foliage, where only its voice betrays its presence. *Laniocera*, *Rhytipterna*, and *Lipaugus* are very similar in appearance. The very uncommon *Laniocera* is, however, relatively inactive, rather sedentary, and stays in the lower half of the forest, mostly in the vicinity of the forested swamps, although on two occasions I saw a single lethargic individual with a mixed band. *Rhytipterna* is very seldom met inside the forest, where an unobtrusive individual may perhaps be present high in the trees. *Lipaugus*, which is larger and considerably heavier than *Rhytipterna*, is abundant, active, noisy, and occurs at all heights above the understory. *Pachyramphus cinnamomeus* is uncommon and is almost completely hidden from sight in the trees (but is easily known by its voice); it is similar in color to the three species just mentioned but is much smaller and differently proportioned. *Tityra* and *Erator* are uncommon and troop over the canopy as though on a journey; although superficially similar to *Carpodectes*, they seem to prefer relatively bare branches and stubs, whereas *Carpodectes* forages in the protection of foliage. *Querula* is most common along the forest borders, travels in noisy groups, forages in the manner of a trogon, and is apparently largely frugivorous (as well as insectivorous). *Cephalopterus*, the largest of the cotingas at "La Selva," occurs at all heights above the understory, is sluggish, and feeds on large invertebrates as well as on fruits.

In the semi-open, *Carpodectes* forages, apparently for fruits, in leafy branches high in the trees. The flycatcher-like *Attila* usually occurs fairly low, for the most part in second-growth patches, thickets, riverside groves, and woodland edges, and seems to be almost entirely animalivorous. *Rhytipterna* occurs at medium heights to high in trees which are either semi-isolated or rise from thick second growth, and it is rather sluggish; although it has been reported as frequenting low branches and even the ground, I have seen it in such situations only during the brief dry season, when paired birds appeared to be

seeking nesting sites. *Lipaugus* behaves in the semi-open as it does in forest. *Pachyramphus cinnamomeus* occurs usually at or below medium heights and often forages off leaves in the manner of a leaping or flitting flycatcher or antshrike. *Pachyramphus polychopterus* acts in the same way as *P. cinnamomeus* but does not show itself so openly, does not occur in small groups, and does not enter the forest. *Tityra* and *Erator* occur high in the trees, often on bare branches: *Tityra* generally occurs in groups of several or many individuals, *Erator* often alone or in twos. The slow-flying *Querula* troops about, close to the forest border.

Family TYRANNIDAE

Colonia colonus (Vieillot), Long-tailed Tyrant: Resident; semi-open; at all heights, but usually at medium heights on tip of a stub; alone or in twos; abundant.

Tyrannus tyrannus (Linnaeus), Eastern Kingbird: Transient migrant; uncommon in fall, fairly common in spring; semi-open; usually high in trees; flocks or alone.

Tyrannus melancholicus Vieillot, Tropical Kingbird: Resident (in region); semi-open, almost exclusively at the Point; usually fairly high; alone; rare to very uncommon. Across the Río Sarapiquí, and elsewhere in the country, one of the most common birds, with wide latitude in habitat and behavior.

Legatus leucophaius (Vieillot), Piratic Flycatcher: Transient migrant; seen once, in fall, a group of four birds perched high in semi-open. Across the Río Sarapiquí, and elsewhere in the country, a common breeding summer resident.

Myiodynastes luteiventris Sclater, Sulphur-bellied Flycatcher: Transient migrant; semi-open and forest border; medium heights to high; alone or a few separated individuals; uncommon to fairly common. Elsewhere in country, a common breeding summer resident in subtropical belt.

Myiodynastes maculatus (Müller), Streaked Flycatcher: Accidental or casual, seen once in spring, low in semi-open. Apparently unrecorded from Caribbean lowlands; common on Pacific side of country.

Megarhynchus pitangua (Linnaeus), Boat-billed Flycatcher: Resident; semi-open, occasionally in forest; usually at medium heights or fairly low, sometimes high; alone, in twos, or a few individuals trooping about; abundant.

Conopias parva (Pelzeln), White-ringed Flycatcher: Resident; semi-open, also forest; usually high in tall trees, and tops of medium-sized trees; usually in twos, sometimes alone or in threes; abundant. Apparently unrecorded from Caribbean lowlands, where I have found it elsewhere, and heretofore considered extremely rare in Costa Rica.

Myiozetetes similis (Spix), Vermilion-crowned Flycatcher: Resident; semi-open, also second growth; usually at medium heights or fairly low; alone, in twos, or in small groups; uncommon to fairly common (mostly at the Point).

Myiozetetes granadensis Lawrence, Gray-capped Flycatcher: Resident; semi-open (including riverside); usually fairly low, also higher in trees; alone or in groups; abundant.

Pitangus sulphuratus (Linnaeus), Kiskadee Flycatcher: Resident; semi-open; usually at medium heights; alone or in twos; rare to uncommon (mostly at the Point).

Myiarchus crinitus (Linnaeus), Great Crested Flycatcher: Migrant, winter resident; forest, forest border, advanced second growth; usually high in trees; solitary; abundant October to January, becoming less common to rare during latter half of stay.

Myiarchus tuberculifer (Lafresnaye and d'Orbigny), Olivaceous Flycatcher: Resident; semi-open, occasionally a little into forest; usually fairly low to medium heights above ground; usually alone, also in twos; uncommon to fairly common.

Nuttallornis borealis (Swainson), Olive-sided Flycatcher: Transient migrant; semi-open, also openings inside forest; usually high or very high; solitary; common in fall, fairly common in spring.

Contopus virens (Linnaeus), Eastern Wood Pewee: Transient migrant, also winter resident; semi-open, also in forest; low above ground to medium heights, also high; solitary; abundant in fall and very common in spring, rare to very uncommon in winter (when mostly in forest).

Contopus sordidulus Sclater, Western Wood Pewee: Transient migrant, also winter visitant; semi-open; low above ground to medium heights, also high; solitary; rare in fall and winter, fairly common in spring. Probably more common than indicated; many individuals which I could not definitely identify were not recorded.

Contopus cinereus (Spix), Tropical Pewee: Resident; semi-open and edge of second growth; low above ground to medium heights; solitary; rare to uncommon (mostly at Point).

Empidonax flaviventris (Baird and Baird), Yellow-bellied Flycatcher: Migrant, winter visitant; second growth, semi-open, occasionally inside forest; fairly low above ground to medium heights; solitary; common to abundant.

Empidonax virescens (Vieillot), Acadian Flycatch-

er: Transient migrant; forest border and second growth; low or fairly low; solitary; rare in fall, uncommon in spring (but probably more common than indicated).

Empidonax traillii (Audubon), Traill's Flycatcher: Transient migrant and winter resident; semi-open, occasionally in forest; usually low or fairly low, also high (in forest); solitary, but many individuals during migration; abundant in fall, rare to very uncommon in winter, uncommon to fairly common in spring.

Terenotriccus erythrurus (Cabanis), Ruddy-tailed Flycatcher: Resident; forest, also adjoining second growth, occasionally in semi-open; generally low or fairly low, sometimes rather high; usually solitary; abundant.

Aphanotriccus capitalis (Salvin), Salvin's Flycatcher: Resident; second growth, edge of semi-open, overgrown forest border, overgrown riversides and streamsides (outside forest); usually fairly low; usually alone; uncommon to fairly common. Heretofore considered extremely rare in the country.

Myiobius barbatus (Gmelin), Sulphur-rumped Flycatcher: Resident; forest, also shaded second growth; usually fairly low to low, also at medium heights to, occasionally, high; generally alone, also in twos; extremely rare (February–April) to uncommon (April–September) to abundant (December–January).

Onychorhynchus coronatum (Müller), Royal Flycatcher: Status uncertain, probably resident (in region); in forest or beside forest in second growth and overgrown swampy openings; low or fairly low; non-sedentary; solitary; rare. Apparently unrecorded previously from Caribbean slope, where I have found it in three other localities in the tropical belt.

Platyrinchus coronatum Sclater, Golden-crowned Spadebill: Resident; forest; low; alone, in twos or threes, or in small groups of somewhat separated individuals; abundant.

Tolmomyias sulphurescens (Spix), Yellow-olive Flycatcher: Resident; semi-open, forest border, and second growth with emergent trees; on the average, at medium heights above ground; usually solitary; fairly common to common.

Tolmomyias assimilis (Pelzeln), Yellow-margined Flycatcher: Resident; semi-open, forest border, and forest; from below medium heights to high (especially in forest); solitary or in twos or threes; common to abundant. Heretofore considered extremely rare in Costa Rica.

Rhynchocyclus brevirostris (Cabanis), Eye-ringed Flatbill: Resident; forest, second growth; usually fairly low, sometimes very low or very high; usually alone; uncommon to common.

Todirostrum nigriceps Sclater, Black-headed Tody-Flycatcher: Resident; semi-open, woodland border; usually high to very high in trees, sometimes low; alone or in twos; abundant.

Todirostrum cinereum (Linnaeus), Common Tody-Flycatcher: Resident; leafy, low second growth, shrubs in semi-open, and hedges; low to fairly low; alone or in twos; uncommon to fairly common (mostly at the Point).

Todirostrum sylvia (Desmarest), Slate-headed Tody-Flycatcher: Resident; thickets at the Point, occasionally into semi-open; low or fairly low; alone or in twos; a single small colony of several individuals. A Pacific species, rare on Caribbean slope of Costa Rica.

Oncostoma cinereigulare (Sclater), Bent-billed Tyrant: Resident; second growth, overgrown forest border, occasionally at edge of semi-open; low or fairly low; usually alone; abundant.

Myiornis ecaudatus (d'Orbigny and Lafresnaye), Short-tailed Pygmy Tyrant: Resident; forest, second growth, semi-open; at all heights: medium to high in forest, low to fairly low in semi-open and new second growth; common to abundant. Heretofore considered extremely rare in Costa Rica.

Capsiempis flaveola (Lichtenstein), Yellow Tyrannulet: Resident; semi-open; low; small, traveling groups, or alone or in sedentary pairs; uncommon but regular, present only at the Point.

Elaenia flavogaster (Thunberg), Yellow-bellied Elaenia: Visitant; seen only once, at the Point. Common resident on other side of Río Sarapiquí, should become regular at the Point in near future.

Tyranniscus vilissimus (Sclater and Salvin), Paltry Tyrannulet: Resident; semi-open; usually tops of small or medium-sized trees; usually alone; fairly common to very common.

Ornithion semiflavum (Sclater and Salvin), Yellow-bellied Tyrannulet: Resident; forest, forest border, and second growth, occasionally in semi-open; at all heights; one to two or three individuals usually accompanying traveling mixed band; common.

Leptopogon sp. [probably *amaurocephalus* Tschudi, Brown-capped Leptopogon]: Accidental or casual; an immature-plumaged, dull brownish-capped individual, seen only twice, once in July and once in August, in same spot in shrubbery along river bank.

Mionectes olivaceus Lawrence, Olive-striped Flycatcher: Visitant, present for six weeks from mid-December to latter January; semi-open, second growth, and a little into forest; usually low; usually alone; uncommon to common when present (seen regularly). Apparently not recorded previously from Caribbean lowlands.

Pipromorpha oleaginea (Lichtenstein), Oleaginous

Pipromorpha: Resident; forest, also second growth, regularly in semi-open; usually low in forest, but may rise high when attracted to traveling mixed band, and occurs to medium heights, or higher, in semi-open; usually alone, sometimes in twos, or several individuals at same tree in semi-open; common to abundant.

The following birds (transient migrants and accidental or casual native species) do not properly belong at "La Selva": *Tyrannus tyrannus*, *Tyrannus melancholicus*, *Legatus*, *Myiodynastes luteiventris*, *Myiodynastes maculatus*, *Nuttallornis*, *Contopus sordidulus*, *Empidonax virescens*, *Elaenia*, *Leptopogon*, and *Mionectes*.

The following are forest birds. The only species that occurs regularly high in the trees is the migrant *Myiarchus crinitus;* it also stays high in tall trees outside the forest. The diminutive *Myiornis* keeps hidden in foliage in the upper understory and middle forest; outside the forest, it may appear in open view low in shrubs and small trees in the semi-open. The little *Ornithion* troops about with traveling mixed bands; it may also occur alone fairly low in the semi-open. The remaining species all inhabit the understory. The lethargic *Rhynchocyclus* behaves like one of the little flitting flycatchers; it may rise into the lower middle forest, or high in the trees when attracted to a traveling mixed band, and may enter shaded second growth outside the forest. The sedentary, tail-fanning *Myiobius* behaves much like a fly-catching redstart; it sometimes rises higher in the trees and may take up residence in second growth bordering the forest. *Onychorhynchus*, which is rare at "La Selva," seems to wander about; although it may fly-catch in the manner of a redstart, it is quite unlike *Myiobius*, besides being twice the size of the latter. The tiny *Platyrinchus* flits to snatch insects from foliage. *Pipromorpha* darts for insects, and also searches in foliage as a vireo does; it visits the semi-open regularly.

The following species occur mostly or only in the semi-open. The only typically sallying species are the abundant *Colonia*, the migrant *Contopus virens*, and the uncommon native *Contopus cinereus*. *Contopus virens* also occurs sparingly in forest, where it is the only flycatcher (excluding the transient *Nuttallornis*) which sallies from a fixed perch. There are five yellow-bellied species that superficially are very similar, falling into two size groups: the large *Megarhynchus* and *Pitangus*, and the considerably smaller *Conopias*, *Myiozetetes similis*, and *Myiozetetes granadensis*. *Megarhynchus* and *Pitangus* are very much alike in appearance and behavior: *Megarhynchus*, which is far more abundant and occurs to some extent in the forest, apparently does well in a forested environment; *Pitangus*, which avoids forest and is very uncommon at "La Selva," where it prefers the most open parts of the semi-open, is common or abundant in cultivated, cut-over areas elsewhere in the country. *Conopias*, which is common, and the almost identical *Myiozetetes similis*, which is relatively uncommon, show the same opposing tendencies as *Megarhynchus* and *Pitangus*. In addition, *Conopias*, significantly or not, nests in holes in trees high above the ground and is capable of clinging to vertical, smooth-barked trunks and limbs, quite unlike the behavior of *M. similis*. Also, for what it is worth, I have seen *Conopias* wandering about in small groups elsewhere on the Caribbean slope. *Myiozetetes granadensis* is abundant outside the forest everywhere at "La Selva," favoring especially the riverside portions of the finca, unlike the congeneric *M. similis*, which is seen most often at the Point. As *M. similis* and *M. granadensis* occur abundantly together in other parts of the country, it would appear that, at "La Selva," *M. similis* suffers from competition with *Conopias* or with *M. granadensis*, or simply does not do so well in a heavily forested environment. Of the other flycatchers in the semi-open, *Myiarchus tuberculifer* is relatively uncommon. Of retiring disposition, it both fly-catches and searches in foliage. Compared with *Myiozetetes similis*, it prefers denser tree growth in the semi-open. The congeneric *Tolmomyias sulphurescens* and *T. assimilis* repeat the *Megarhynchus-Pitangus* type of distributional situation; in actions, they both dart at leaves for insect prey. The little *Todirostrum nigriceps* and *T. cinereus* are similar, congeneric species, and neither enters the forest. The arboreal *nigriceps* forages by means of flitting dashes, and the shrub-inhabiting *cinereum* combines vireo-like searching with occasional fly-catching flutters. Elsewhere, in deforested country, *cinereum* is much more common

than *nigriceps*, the status of the two being the reverse of that at "La Selva." The migrant *Empidonax traillii* is of no community importance during its winter residence because of the great scarcity of individuals. *Capsiempis* occurs only at the Point in places which, at "La Selva," most approach field habitat in character. Bringing to mind a vireo in low shrubbery, it also makes short, almost leaping, fly-catching sallies. The little *Tyranniscus*, the appearance and actions of which are also somewhat like those of a vireo, usually occurs on the crowns of shrubs or small trees where it makes short sallies for insects or, exploring the foliage, takes animal prey and small fruits.

Largely confined to second growth are *Empidonax flaviventris*, *Aphanotriccus*, *Todirostrum sylvia*, and *Oncostoma*: all are small in size. *Aphanotriccus* and the migrant *Empidonax flaviventris* are in no way morphologically unusual, and they do just about the same things (flitting, leaping at foliage), but *E. flaviventris* is more active and seemingly more agile, more abundant, and occurs in more different sorts of situations in the second-growth habitat, as well as in forest to a slight extent. The little, tody-billed *Todirostrum sylvia* and the similar-sized, bent-billed *Oncostoma* are very much alike in appearance, voice, and habitat: *T. sylvia* occurs as a single, small colony confined to a particular site at the Point, *Oncostoma* is solitary and widespread; *T. sylvia* forages by moving about and jumping up at leaves for prey, *Oncostoma* rests quietly between sudden flits.

Family HIRUNDINIDAE

Progne chalybea (Gmelin), Gray-breasted Martin: Irregular visitant; aerial, usually very high; solitary; rare (almost exclusively at the Point). This colonial swallow is a common resident on the other side of the Río Sarapiquí.

Petrochelidon pyrrhonota (Vieillot), Cliff Swallow: Transient migrant in spring and fall; aerial, usually very high.

Hirundo rustica Linnaeus, Barn Swallow: Transient migrant, as is *Petrochelidon*, but more abundant.

Stelgidopteryx ruficollis (Vieillot), Rough-winged Swallow: Two forms: transient migrant (the status of which is like that of *Petrochelidon*), and resident; resident form, *uropygialis*, in semi-open and along river, regular in vicinity of the Point, irregular elsewhere; perches fairly low to fairly high, hunts at moderate height or fairly low in air; rather sedentary, with favorite perches; usually solitary; abundant December–April, uncommon to very uncommon rest of year.

Riparia riparia (Linnaeus), Bank Swallow: Transient migrant, as is *Petrochelidon*.

Iridoprocne albilinea (Lawrence), Mangrove Swallow: Breeding resident (permanent resident in region); river; perches very low, always on material in river; hunts very low above surface; usually in small groups, also in twos or threes; abundant December–May, absent or uncommon rest of year along Río Puerto Viejo (but a few usually present at its mouth).

The only resident swallows are *Stelgidopteryx* and *Iridoprocne*. *Stelgidopteryx* is solitary for the most part, hunts in the semi-open and over the river usually fairly low. *Iridoprocne* is confined to the river, where it becomes progressively less common upstream from the mouth, and hunts close to the surface of the water. *Progne* crosses the Río Sarapiquí to "La Selva," where, however, it is seen seldom, usually high in the air.

Family CORVIDAE

Psilorhinus morio (Wagler), Brown Jay: Irregular visitant; occasional, seen only at the Point; usually two or three individuals in semi-open.

Still uncommon in the region, this jay will undoubtedly become more common as the forest is removed, if one can judge by the coincidence of the spread of the bird with the destruction of woodland elsewhere on the Caribbean slope. These pioneering visits to "La Selva" by more than one bird at a time, together with the circumstance that in one instance nesting material was being gathered, suggest future establishment of the species on the study area.

Family TROGLODYTIDAE

Campylorhynchus zonatum (Lesson), Banded Cactus Wren: Resident; forest border and neighboring clearings; at all heights, usually fairly high to very high; in twos or small groups; abundant.

Thryothorus thoracicus Salvin, Striped-breasted Wren: Resident; forest, advanced second growth, occasionally in cover in semi-open; usually fairly low; in twos or small groups; abundant.

Thryothorus nigricapillus Sclater, Bay Wren: Resident; overgrown edges, thickety growth at

openings in forest, generally near water; low; in twos or several individuals together; abundant.

Thryothorus atrogularis Salvin, Black-throated Wren: Resident; thickety or leafy low growth in semi-open; alone or in twos; common.

Henicorhina leucosticta (Cabanis), White-breasted Wood Wren: Resident; forest and shaded second growth; semi-terrestrial; pairs or small groups; abundant.

Microcerculus marginatus (Sclater), Nightingale Wren: Resident; forest, occasionally contiguous second growth; semi-terrestrial; solitary; uncommon to relatively common.

Cyphorhinus phaeocephalus Sclater, Song Wren: Forest, also shaded second growth; semi-terrestrial; usually in small bands; abundant.

The seven species of wrens are all resident; only *Microcerculus* may not be noted daily. Two species, *Campylorhynchus* and *Thryothorus atrogularis*, do not enter the forest: *Campylorhynchus* is arboreal, *T. atrogularis* inhabits low, thick growth in the open. *Thryothorus nigricapillus* does occur in forest, but it is far more abundant outside the forest in thick undergrowth and shrubbery along watercourses; the habitat for the most part is quite distinct from that of *T. atrogularis*. *Thryothorus thoracicus* inhabits the upper portion of the understory, preferably where there are vines and tangles in which to climb about. The semi-terrestrial *Henicorhina*, which is the most common wren in the forest, occurs almost everywhere, inhabiting also shaded second growth. *Microcerculus* is probably more terrestrial than semi-terrestrial; quite unlike the social, inquisitive *Henicorhina*, it is solitary and widely scattered, walks well, and has a dashing flight. The gregarious *Cyphorhinus* forages mostly on the ground.

Family MIMIDAE

Dumetella carolinensis (Linnaeus), Common Catbird: Migrant, winter resident; thickets and shrubbery in semi-open; usually very low; uncommon to rare (few individuals, sedentary).

The possible presence of this bird, an uncommon winter resident, is determined by the availability of suitable habitat. Several years ago at "La Selva," a small-sized area entirely in shrubbery harbored at least a dozen individuals. Later, when the shrubbery was replaced by a very tall grass, catbirds were not seen at that site again.

Family TURDIDAE

Turdus albicollis Vieillot, White-throated Robin: Casual visitant or accidental; seen only once in thickety second growth beside river bank. Rare in lowlands of Caribbean Costa Rica.

Turdus grayi Bonaparte, Gray's Robin: Resident; semi-open; usually fairly low above ground to medium heights; alone or a few individuals; uncommon (mostly at the Point).

Turdus fumigatus Lichtenstein, Pale-vented Robin: Non-breeding visitant; forest border (including tall second growth), a little into forest, or occasionally deeper, also in semi-open; fairly low (in second growth) to high; alone, or, usually, in small groups; absent from latter February to latter July, rare to fairly common October to January.

Hylocichla mustelina (Gmelin), Wood Thrush: Migrant, winter resident; forest and second growth; very low to fairly low; usually a few individuals together, also alone; common to abundant during first half of stay, progressively uncommon to rare during latter half. Heretofore considered extremely rare in Costa Rica; apparently unrecorded previously from Caribbean lowlands.

Hylocichla ustulata (Nuttall), Swainson's Thrush: Transient migrant; second growth, occasionally into forest, also in semi-open, but most often (during migration) in tall thickety growth; at all heights; usually several scattered or loosely associated individuals migrating together; fairly common.

Hylocichla minima (Lafresnaye), Gray-cheeked Thrush: Transient migrant, seen only in fall; definitely identified only once, at least one other individual probably seen; low in semi-open.

Thrushes are of little importance at "La Selva." *Turdus albicollis*, *Hylocichla ustulata*, and *Hylocichla minima* do not properly belong there. *Turdus grayi*, a species of semi-open and cultivated parts of Costa Rica, where it is so well known that it could be called the national bird, is uncommon over most of the study area, apparently avoiding forest. *Turdus fumigatus*, a seasonal visitant, occurs in woodland, from the upper understory to high in the trees. *Hylocichla mustelina*, a winter resident, inhabits the understory in forest and also thick second growth outside the forest.

Family SYLVIIDAE

Polioptila plumbea (Gmelin), Tropical Gnatcatcher: Resident; semi-open, second growth,

sometimes in forest; usually fairly low in small trees or sometimes high in tall trees outside the forest; usually in pairs, also alone; uncommon to abundant (in dry season).

Ramphocaenus melanurus Vieillot, Long-billed Gnatwren: Resident; primarily inhabits second growth outside forest, also undergrowth at breaks in forest; low or fairly low; alone or in twos; uncommon to abundant.

Microbates cinereiventris (Sclater), Gray-breasted Gnatwren: Resident; forest, also bordering second growth; very low to low; usually in group of several individuals, also in twos, sometimes alone; abundant.

Polioptila is apt to occur almost anywhere in the semi-open, and occasionally high or at breaks in the canopy in forest. *Ramphocaenus* is essentially a non-forest species that inhabits shrubbery and other sorts of dense growth along woodland borders, but it also occurs sparsely scattered through the forest at second-growth breaks. *Microbates* is a true forest bird that lives close to the ground in the understory.

Family VIREOLANIIDAE

Smaragdolanius pulchellus (Sclater and Salvin), Green Shrike-Vireo: Resident; semi-open and forest; from below medium heights to high (in semi-open) or high (in forest); usually in pairs; not uncommon (forest) to very common or abundant (semi-open).

Rather sedentary and slow-moving, the branch- and foliage-searching shrike-vireo seems to occupy a niche in the semi-open which overlaps in several directions that of other birds of more or less similar habits, namely, the migrant warblers and vireos. When those birds are absent, it apparently has the niche almost to itself.

Family VIREONIDAE

Vireo flavifrons Vieillot, Yellow-throated Vireo: Migrant, winter resident; semi-open, second growth, also into forest; usually fairly low above ground to medium heights, also higher; solitary; uncommon to fairly common.

Vireo olivaceus (Linnaeus), Red-eyed Vireo: Transient migrant, casual or accidental in winter; semi-open, second growth, also in forest; usually in small "waves," also alone or a few together (in forest); rare in winter, common to abundant in migration. Apparently no previous winter record for Caribbean lowlands.

Vireo flavoviridis (Cassin), Yellow-green Vireo: Transient migrant; semi-open; usually from two to several individuals; generally at medium heights; uncommon to fairly common.

Vireo philadelphicus (Cassin), Philadelphia Vireo: Transient migrant in spring (probably also rare winter resident and fall migrant); semi-open; in shrubs or low in trees; uncommon.

Vireo gilvus (Vieillot), Warbling Vireo: Migrant, accidental; seen once in spring, fairly low in tree in semi-open, feeding together with *V. olivaceus* and *V. philadelphicus*. Apparently first report of species south of El Salvador.

Hylophilus ochraceiceps Sclater, Tawny-crowned Greenlet: Resident: forest; low or fairly low; small bands, usually with *Myrmotherula* spp.; very common to abundant.

Hylophilus decurtatus (Bonaparte), Gray-headed Greenlet: Resident: forest, second growth, semi-open; high in forest, at all heights outside of forest; in bands; abundant.

The only vireos properly belonging at "La Selva" are the migrant *Vireo flavifrons* and the native *Hylophilus ochraceiceps* and *Hylophilus decurtatus*. The relatively sedentary, solitary *V. flavifrons* occurs mostly outside forest. *Hylophilus ochraceiceps* is a forest species that travels about in groups through the understory. *Hylophilus decurtatus* travels about in bands high in the forest, and at all heights above shrubbery outside the forest; it is as active as an arboreal warbler.

Family COEREBIDAE

(Although this family may well be, as claimed, an artificial aggregation consisting of convergent wood warblers and tanagers, the plumages, proportions, bill shapes, general appearance, and general habits of the Costa Rican species are embodied by a distinctive group of birds, none of the members of which in life I would call without reluctance either a warbler or a tanager. But, if the diphyletic nature of the family be granted, do Beecher's (1951) findings command sufficient authority by which to draw an undisputed line of demarcation? Skutch's objection (1954, p. 438) based on regurgitative feeding is so at variance with Beecher's "clean separation" (*ibid.*, p. 286) that it seems preferable to keep the group under continuing surveillance than to dismember it with a hasty stroke. It is quite possible that the ethological character noted by Skutch is more deep-seated than the particular aspect of adaptive morphology de-

scribed and interpreted by Beecher. The unavoidable inference is that if one author is right the other must be wrong. If it be supposed that neither is wholly correct, it may be that the Coerebidae, if not monophyletic or diphyletic, are polyphyletic.)

Chlorophanes spiza (Linnaeus), Green Honeycreeper: Resident; semi-open, forest border, and forest at streams and ravines; at all heights; solitary, in twos, and in small groups; uncommon (February–March) to abundant (August–September).

Cyanerpes caeruleus (Linnaeus), Shining Honeycreeper: Resident; semi-open and forest border, also a little into forest on canopy; medium heights to high or very high; generally in small groups, also in larger bands (August–September), occasionally alone; uncommon (January–April) to abundant (May–September).

Dacnis cayana (Linnaeus), Blue Dacnis: Resident; semi-open and forest border; at all heights; alone or in small groups; very uncommon (January–July) to common (October–December).

Dacnis venusta Lawrence, Scarlet-thighed Dacnis: Probably non-breeding visitant; semi-open; at all heights; a few individuals together or larger bands; rare to uncommon (latter July and early August), common (late August and September), rare to uncommon (October–December), absent (January–July).

Coereba flaveola (Linnaeus), Bananaquit: Resident; semi-open; usually fairly low, also fairly high; alone or in twos or threes; uncommon to abundant.

At "La Selva," all the honeycreepers are primarily inhabitants of the forest border and semi-open. Only *Coereba* and *Chlorophanes* are to be seen regularly throughout the year, but all the species fluctuate cyclically in numbers. During the first six months of the year, both species of *Dacnis* are rare or absent, and *Cyanerpes* is distinctly uncommon.

Coereba moves about in the foliage of shrubs and trees, feeding largely on the contents of flowers to which it clings. *Chlorophanes*, the only genus met inside the forest below the canopy, behaves variously; it differs from *Cyanerpes* and *Dacnis* in being less nervously quick acting, is rather sedentary, and is obviously resident in the sense that it does not usually troop about. *Cyanerpes* and the two species of *Dacnis* behave in much the same manner. They may move about actively in the foliage as warblers do, fly-catch, or search and scan the branches as do certain tanagers. Only *Cyanerpes* is apt to perch in an exposed position high on a bare limb or stub or on the tops of trees.

Family PARULIDAE

Mniotilta varia (Linnaeus), Black-and-white Warbler: Transient migrant common in fall but rare in spring, and rare winter resident; in winter, seen only once, high at break in forest; in fall, in semi-open, usually below medium heights, also high in forest; solitary or sometimes in twos; in forest, always seen with mixed band; outside forest, generally independent of other birds.

Protonotaria citrea (Boddaert), Prothonotary Warbler: Transient migrant, seen only in fall; in semi-open at medium heights to high in trees 25–50 yards from river, and also low in trees lining river bank.

Helmitheros vermivorus (Gmelin), Worm-eating Warbler: Transient migrant, seen only in fall on one occasion; two individuals low in semi-open at overgrown stream bed.

Vermivora chrysoptera (Linnaeus), Golden-winged Warbler: Migrant, winter resident; semi-open and forest edge, sometimes into forest with mixed band; usually fairly low, may go to ground, or high (in forest); generally alone; common in fall, uncommon to fairly common in winter, relatively uncommon in spring.

Vermivora pinus (Linnaeus), Blue-winged Warbler: Migrant, winter resident; semi-open; fairly low to medium heights; alone or in twos; very uncommon. Not recorded previously from Caribbean lowlands, where I have found it in two other localities.

Vermivora peregrina (Wilson), Tennessee Warbler: Migrant, winter resident (as a species); semi-open; generally low above ground to medium heights, also to ground; usually in small to fairly large bands, also alone; in fall becomes abundant first week in October, fluctuates in winter between fairly common and very uncommon, uncommon in spring.

Dendroica petechia (Linnaeus), Yellow Warbler: Transient migrant; semi-open; low; solitary; fairly common in fall, uncommon to rare in spring. Common in spring on other side of Río Sarapiquí, probably uncommon winter resident in region.

Dendroica coronata (Linnaeus), Myrtle Warbler: Irregular winter visitant, seen several times December–February; semi-open; low; usually in small band, uncommonly alone.

Dendroica virens (Gmelin), Black-throated Green Warbler: Transient migrant; semi-open; fairly

low to fairly high; alone; rare in fall, very uncommon in spring.

Dendroica cerulea (Wilson), Cerulean Warbler: Transient migrant; semi-open; fairly low to high; in small "waves," sometimes alone; common to very common in fall, absent in spring. Heretofore considered a very rare migrant.

Dendroica fusca (Müller), Blackburnian Warbler: Transient migrant; medium heights to high, sometimes low; in "waves"; abundant in fall, absent in spring.

Dendroica pensylvanica (Linnaeus), Chestnut-sided Warbler: Migrant, winter resident; semi-open, also second growth, occasionally in forest; usually low to fairly low; solitary; abundant.

Dendroica castanea (Wilson), Bay-breasted Warbler: Transient migrant, winter resident; semi-open; medium heights to high, sometimes fairly low; usually alone, but in "waves" during migration; common in fall, uncommon in winter and spring. Heretofore considered only a rare fall migrant in Costa Rica; apparently not previously recorded in winter.

Seiurus aurocapillus (Linnaeus), North American Ovenbird: Migrant, winter resident; forest and wet or muddy places in second growth; on ground and in undergrowth; solitary; common in fall, uncommon in winter, rare in spring.

Seiurus noveboracensis (Gmelin), Northern Waterthrush: Migrant, winter resident; river, streams outside forest, uncommonly in semi-open; terrestrial, also low in vegetation; solitary; abundant in fall, common in winter and spring.

Seiurus motacilla (Vieillot), Louisiana Waterthrush: Status like that of *S. noveboracensis*, but fewer individuals, and occasionally in forest.

Oporornis formosus (Wilson), Kentucky Warbler: Migrant, winter resident; forest and second growth, occasionally in semi-open at forest border; low, often on ground; solitary; very common in fall, uncommon in winter, rare in spring.

Oporornis philadelphia (Wilson), Mourning Warbler: Migrant, seen once in late winter and twice in spring; undergrowth in semi-open; solitary.

Geothlypis semiflava Sclater, Olive-crowned Yellowthroat: Resident; undergrowth in semi-open, usually at edges; generally alone; uncommon to rare, mostly in vicinity of the Point.

Icteria virens (Linnaeus), Yellow-breasted Chat: Migrant, present in fall and winter, absent in spring; shrubbery and overgrown edges in semi-open; solitary; uncommon to rare (probably same sedentary individual or two seen several times).

Wilsonia citrina (Boddaert), Hooded Warbler: Migrant, winter resident; undergrowth in second growth and forest border, also low in semi-open; solitary; very uncommon to rare. Heretofore considered extremely rare; no previous winter record.

Wilsonia pusilla (Wilson), Wilson's Warbler: Transient migrant, seen once in fall, low in semi-open.

Wilsonia canadensis (Linnaeus), Canada Warbler: Transient migrant; semi-open, second growth, and forest; at all heights, generally low outside forest, fairly high to high inside forest; solitary but may join mixed bands in forest; extremely abundant in fall, uncommon in spring.

Setophaga ruticilla (Linnaeus), American Redstart: Transient migrant; semi-open, second growth, also in forest; solitary; common in fall, rare in spring.

Phaeothlypis fulvicauda (Spix), Buff-rumped Warbler: Resident; watercourses, including forest at breaks, also away from water; less terrestrial than waterthrushes; in twos, or threes; very common to abundant.

The following passage migrants need not be considered: *Protonotaria*, *Helmitheros*, *Dendroica petechia*, *Dendroica virens*, *Dendroica cerulea*, *Dendroica fusca*, *Oporornis philadelphia*, *Wilsonia pusilla*, *Wilsonia canadensis*, and *Setophaga*.

Of the remaining 15 species, only two are native to Costa Rica, and one of them is seldom seen. No species is confined to or even occurs mostly in forest. The species that do occur consistently in the forest are the migrants *Oporornis formosus*, *Mniotilta varia* (rare in winter), *Seiurus aurocapillus*, and the native *Phaeothlypis*. *Oporornis* is semi-terrestrial in the lower understory; *Seiurus* walks about on the ground; *Phaeothlypis* frequents streams; *Mniotilta* is arboreal.

Outside the forest, *Seiurus noveboracensis*, *Seiurus motacilla*, and *Phaeothlypis* are closely associated with watercourses. The two species of *Seiurus* are largely terrestrial, and I am unable to separate them ecologically, the only differences noted being the greater abundance of *noveboracensis* and the occasional occurrence inside forest of *motacilla*. *Phaeothlypis* flits about.

Elsewhere outside the forest, the rare *Icteria* usually keeps concealed low in thickets, shrubbery, or hedges. The rare *Wilsonia citrina*, which may forage on the ground, prefers somewhat more open undergrowth along edges of second growth, tree-covered, sloping

river banks, and low shrubs or small trees in the semi-open. The uncommon *Geothlypis* occurs in semi-open (or semi-closed) situations, where it seems to prefer leafy, bushy growth, but not dense thickets. The wandering *Dendroica coronata* troops about in groups low above the ground in the manner of open-country sparrows. Somewhat similar is the more abundant *Vermivora peregrina*, which often rises into the trees and behaves as an active, flitting, clinging warbler; unlike other arboreal warblers, it wanders about in groups. More strictly arboreal are *Mniotilta*, which explores the bark of trunks and limbs; *Dendroica pensylvanica*, active in the foliage in small trees or fairly low in bigger trees; the uncommon *Dendroica castanea*, which generally keeps higher in the trees than the abundant *D. pensylvanica;* the fairly common *Vermivora chrysoptera* and the seldom seen *Vermivora pinus*, both of which habitually cling to foliage (unlike the species of *Dendroica*).

Family ICTERIDAE

Zarhynchus wagleri (Gray and Mitchell), Wagler's Oropendola: Breeding at "La Selva," probably resident in region; semi-open and forest; at all heights, usually above medium heights to high; bands; common to abundant December–July, irregular occurrence in tight flocks August-November.

Gymnostinops montezuma (Lesson), Montezuma Oropendola: Resident; semi-open, also into forest and tall second growth; usually medium to high, often fairly low, sometimes very low; loose or tight groups or flocks; abundant.

Cacicus uropygialis (Lafresnaye), Scarlet-rumped Cacique: Resident; semi-open, second growth, and forest; at all heights; usually high in forest (also commonly in mid-forest), fairly high to high in semi-open, and fairly low in second growth; bands; abundant.

Amblycercus holosericeus (W. Deppe), Prévost's Cacique: Resident; thickety second growth and shrubbery in semi-open and woodland border and edges; fairly low to low; alone or in twos, sometimes in threes or fours; abundant.

Psomocolax oryzivorus (Gmelin), Giant Cowbird: Status uncertain, probably irregular visitant or wanderer; semi-open; usually high; usually alone, also seen in small groups (January); uncommon.

Icterus spurius (Linnaeus), Orchard Oriole: Transient migrant (possibly erratic winter visitant); semi-open; fairly low to low; traveling in small groups; uncommon.

Icterus prosthemelas (Strickland), Black-cowled Oriole: Resident; semi-open and woodland borders; generally at medium heights; seldom alone, usually in twos or threes; fairly common to common, especially in vicinity of the Point.

Icterus mesomelas (Wagler), Yellow-tailed Oriole: Resident; riverside thickety growth, canebrakes, and clumps of banana plants, also in semi-open; alone or in twos; generally uncommon, but regular at the Point.

Icterus galbula (Linnaeus), Baltimore Oriole: Migrant, winter resident; semi-open; usually fairly high to high, occasionally low; sometimes alone, generally in groups of a few to over a dozen individuals; abundant from mid-October onward, but less numerous in spring.

No species is confined to forest. However, three genera (the very large *Gymnostinops*, the smaller *Zarhynchus*, and the still smaller *Cacicus*) may occur in the forest daily, although they do not nest or spend the night there. All are social: *Zarhynchus* and *Gymnostinops* each nests in colonies; *Cacicus* is a solitary nester but travels about and roosts in groups. *Zarhynchus* forages inside the forest more than outside, is swifter flying and more agile than *Gymnostinops*, and covers more territory. *Gymnostinops* forages outside the forest more often than inside and, unlike *Zarhynchus*, may often do so at lesser heights, even close to the ground. The very abundant *Cacicus* spends the day in the forest or beside it. The range of behavior is very wide, for it climbs, clings, rummages, creeps, and probes, feeding on a wide variety of animal and plant food in many sorts of situations.

Outside the forest, *Amblycercus* moves about in concealment low in dense thickets and shrubbery. *Psomocolax* is an infrequent visitor and generally stays high in the trees. The migrant *Icterus spurius* (not noted in winter) wanders about at shrub height in the semi-open, seldom straying from the vicinity of the Point. The migrant *Icterus galbula* generally stays high in the trees; its behavior and diet are quite varied, and its geographical and altitudinal range is much greater than that of any native *Icterus*. *Icterus mesomelas* occurs mostly at the Point in the vicinity of impenetrable canebrakes and wild banana thickets. *Icterus prosthemelas* occurs

generally in the semi-open and along the forest border, unlike the larger, relatively sedentary *mesomelas*.

Family THRAUPIDAE

Tanagra anneae (Cassin), Tawny-capped Euphonia: Accidental; seen once, in December, with mixed band at forested swamp.

Tanagra minuta (Cabanis), White-vented Euphonia: Resident; semi-open and slightly into forest; usually high; travels about in bands; fairly common but irregular.

Tanagra luteicapilla (Cabanis), Yellow-crowned Euphonia: Resident (as a species); semi-open, occasionally a little into forest; usually high; traveling in small-sized groups; fairly common but irregular. Common and regular on other side of Río Sarapiquí.

Tanagra gouldi (Sclater), Gould's Euphonia: Resident; forest, forest border, and semi-open; at all heights; generally in small groups, also alone and in apparently sedentary pairs; abundant.

Tangara icterocephala (Bonaparte), Silver-throated Calliste: Visitant, seen several times November–December; semi-open; usually at medium heights.

Tangara larvata (Du Bus), Golden-masked Calliste: Resident; semi-open; usually medium heights to high; generally in small groups; common to abundant.

Tangara inornata (Gould), Plain-colored Calliste: Resident; semi-open; medium heights to high; usually several individuals together, sometimes in threes. Unrecorded in literature for Costa Rica, where I have seen it elsewhere in the Caribbean lowlands.

Thraupis virens (Linnaeus), Blue Tanager: Resident; semi-open; fairly low to, usually, medium or high; generally in pairs; common only in vicinity of the Point. Common on other side of Río Sarapiquí.

Thraupis palmarum (Wied), Palm Tanager: Resident; semi-open and forest border; usually above medium heights; generally in small groups, also in twos; common.

Ramphocelus passerinii Bonaparte, Passerini's Tanager: Resident; semi-open and overgrown edges outside forest; low to fairly low; generally several individuals together; abundant.

Phlogothraupis sanguinolenta (Lesson), Crimson-collared Tanager: Resident; semi-open and overgrown edges outside forest; usually below medium heights, often rather low; generally in twos; uncommon to relatively abundant.

Piranga rubra (Linnaeus), Summer Tanager: Migrant, winter resident; semi-open, seldom in forest (at wooded swamp); fairly low to high; solitary; very common, especially after first week in October.

Piranga olivacea (Gmelin), Scarlet Tanager: Transient migrant, common in spring and fall; semi-open; medium heights to high; alone, or several individuals. In Costa Rica, apparently no published records from Caribbean lowlands, where I have seen it regularly in migration.

Piranga ludoviciana (Wilson), Western Tanager: Migrant, probably accidental; at least two individuals (females) seen on two successive days in fall in medium-sized trees outside forest. Not recorded previously from eastern lowlands.

Chlorothraupis carmioli (Lawrence), Carmiol's Tanager: Resident; forest; low to fairly low; in bands, pure or mixed with other species; common to abundant.

Habia gutturalis (Sclater), Red-throated Ant Tanager: Resident; dense, thickety second growth (shaded), and slight penetration of forest in similar habitat; fairly low to low; generally several individuals together; very uncommon to fairly common.

Lanio aurantius Lafresnaye, Great Shrike-Tanager: Resident (as a species); forest; generally two or three individuals in traveling mixed band; few individuals, but met regularly.

Tachyphonus rufus (Boddaert), Boddaert's Tanager: Resident; semi-open; low or fairly low, sometimes to medium heights; usually in pairs; uncommon, irregularly met with, probably the same one or two pairs, only at the Point.

Tachyphonus luctuosus Lafresnaye and d'Orbigny, White-shouldered Tanager: Resident; mostly woodland border, including second-growth edges, also forest; fairly low to above medium heights, also high; often in groups of several individuals traveling together, or with mixed band, occasionally a single bird; uncommon to rare January–September, uncommon to common September–December.

Tachyphonus delatrii Lafresnaye, Tawny-crested Tanager: Resident; forest; usually low to fairly low, also to medium heights; traveling bands, pure or mixed, and also occasionally in pairs; common to abundant.

Mitrospingus cassinii (Lawrence), Cassin's Tanager: Resident; edges of all kinds, overgrown or undergrown with shrubbery or tangled thickets, inside or, mostly, outside the high forest; low; traveling bands; abundant.

The following species do not properly belong at "La Selva": *Tanagra anneae*, *Tangara icterocephala*, *Piranga olivacea*, and *Piranga ludoviciana*.

Three species are confined to forest. The

tooth-billed *Lanio* occurs as a noisy member or two of traveling mixed bands that follow forest breaks. *Chlorothraupis* and *Tachyphonus delatrii* each troops about in pure bands which may join each other and to which other birds may be attracted; both are noisy and occur at low levels.

Occurring mostly in the forest, but also in the adjacent semi-open, is the abundant little *Tanagra gouldi*. The very common *Mitrospingus* follows forest breaks but is most common along the forest border. The relatively uncommon *Tachyphonus luctuosus* keeps higher in the trees in forest than the congeneric *T. delatrii*, and it occurs in much smaller numbers, at most a few individuals attaching themselves to mixed bands; but in general it prefers lighter woodland to heavy forest.

Largely restricted to thick second growth outside the forest are *Ramphocelus*, *Phlogothraupis*, and *Habia*. *Habia* occurs only in the shade of rather tall, dense, second growth, where it travels about. *Ramphocelus* and *Phlogothraupis* are similar in that they occur in low, second-growth situations where they are regularly exposed to open view. Although *Phlogothraupis* tends to frequent more heavily wooded borders, at "La Selva" there is complete overlap in habitat. *Ramphocelus* is social, abundant, and relatively sedentary, whereas *Phlogothraupis* occurs alone or in twos, is present in much smaller numbers which fluctuate seasonally, is a stronger flyer, and seems to wander about.

The remaining eight species occur typically in the semi-open. The euphonias *Tanagra minuta* and *T. luteicapilla* travel about, mostly high in the trees, usually in search of mistletoe berries: *minuta* is generally found in forested regions, and it roosts (at least during part of the year) close to the forest at "La Selva"; *luteicapilla* prefers partially deforested country, and at "La Selva" seems to be a visitor from nearby areas which have been cut over. The callistes *Tangara larvata* and *T. inornata* are typically arboreal birds of the semi-open, such as country of plantation type. Although they act more or less the same way, *inornata* carefully scrutinizes leafless branches and twigs (many other kinds of birds also do this) and, in general, frequents bare branches with greater regularity than does *larvata*. *Thraupis virens* and *T. palmarum* are another pair of congeneric species that behave similarly: *palmarum* is much more abundant close to the forest, occurs in groups, generally keeps higher in the trees, is swifter flying and wider ranging, and is much harder to observe closely than *virens*. In many other places in the country, where virgin forest is not dominant, *virens* is more abundant than *palmarum*. The migrant *Piranga rubra* is common, may enter forest occasionally, is sedentary, but is difficult to characterize. It generally keeps inside foliage in the more wooded portions of the semi-open, often moves in sudden bursts, fly-catches, flutters off leaves for insects, and also eats vegetable matter. *Tachyphonus rufus*, quite unlike its two congeneric relatives, both of which are social and travel about, is restricted to the more open parts of the semi-open at the Point, where it is sedentary in pairs.

Family FRINGILLIDAE

Saltator atriceps (Lesson), Black-headed Saltator: Resident; second growth, woodland border, and semi-open; usually fairly low above ground to medium heights; often several individuals together; common to abundant.

Saltator maximus (Müller), Buff-throated Saltator: Status like that of *S. atriceps*, but more abundant and widespread.

Caryothraustes poliogaster (Du Bus), Bishop Grosbeak: Resident; forest, second growth, semi-open; at all heights (mostly high in forest); traveling bands, up to three dozen individuals, sometimes in twos; abundant.

Pitylus grossus (Linnaeus), Slate-colored Grosbeak: Resident; forest, also into semi-open; high in forest, fairly low to fairly high in semi-open, seldom to ground; alone or in pairs; abundant.

Pheucticus chrysopeplus (Vigors), Yellow Grosbeak: Visitant, mid-December through most of January; seen regularly in semi-open beside forest, also (once) a little inside forest; usually at medium heights; several individuals in all. Apparently never recorded before from the tropical belt in Costa Rica.

Pheucticus ludovicianus (Linnaeus), Rose-breasted Grosbeak: Transient migrant, fairly common both in spring and fall; semi-open; medium to high; usually several individuals at a time.

Cyanocompsa cyanoides (Lafresnaye), Blue-black Grosbeak: Resident; forest, second growth,

semi-open; usually low; almost always in pairs; abundant.

Passerina cyanea (Linnaeus), Indigo Bunting: Migrant, irregular winter visitant; a single bird seen on two occasions, in February, very low in semi-open at the Point, not at all in spring or fall.

Tiaris olivacea (Linnaeus), Yellow-faced Grassquit: Status uncertain, resident in region; seen seldom, single birds only, in shrubbery in or beside semi-open, almost exclusively at the Point. Elsewhere in Costa Rica, common in most cleared areas; will undoubtedly become more frequent at "La Selva."

Sporophila (aurita) corvina (Sclater), Black Seed-eater: Resident; semi-open; usually in undergrowth, also to medium heights in trees; gregarious, also alone or in pairs; abundant at the Point, fluctuating numbers elsewhere on study area.

Oryzoborus funereus Sclater, Thick-billed Seed Finch: Status uncertain; resident in region; seen very seldom; undergrowth and shrubbery in semi-open and along edges. Not uncommon on other side of Río Sarapiquí.

Volatinia jacarina (Linnaeus), Blue-black Grassquit: Status like that of *Oryzoborus*, but almost exclusively at the Point.

Arremon aurantiirostris Lafresnaye, Orange-billed Finch: Resident; forest, forest border, second growth; semi-terrestrial, or low in undergrowth; alone or in twos; abundant.

Arremonops conirostris (Bonaparte), Green-backed Finch: Resident; semi-open; semi-terrestrial, or low in undergrowth; usually alone; uncommon to fairly common, mostly at the Point.

Pheucticus chrysopeplus, *Pheucticus ludovicianus*, and *Passerina* do not properly belong at "La Selva."

The following are primarily forest birds. The arboreal *Caryothraustes* troops about in bands. The arboreal *Pitylus* is sedentary and non-gregarious. *Cyanocompsa* and *Arremon* occur in the understory: *Cyanocompsa* moves about actively above the ground, whereas *Arremon* is relatively sedentary and semi-terrestrial.

The remaining species are non-forest birds. Arboreal and second-growth inhabiting are *Saltator atriceps* and *S. maximus*. Although the overlap in habitat is almost complete, *atriceps* seems to prefer thick second growth (at "La Selva"), whereas *maximus* occurs in mixed growth halfway in character between semi-open and woodland; *maximus* is smaller and considerably lighter in weight than *atriceps*, and has a wider range of activity, as it may flutter, sally, dart, creep, search bark and crevices, and attend army ants.

Occurring in those portions of the semi-open that approach field habitat are *Tiaris*, *Sporophila*, *Oryzoborus*, *Volatinia*, and *Arremonops*. *Tiaris*, *Oryzoborus*, and *Volatinia* are seen very seldom at "La Selva," but they are common on the other side of the Río Sarapiquí. *Tiaris* and *Volatinia* are very small in size, are small-billed, and feed primarily on tiny seeds, such as grass or weed seeds; the very thick-billed *Oryzoborus* presumably feeds on larger, tougher seeds, but its scarcity may perhaps be due to competition by *Sporophila*. *Sporophila* is the only common field finch, occurring anywhere in the semi-open on the study area, and it seems to have a varied diet, possibly in keeping with its intermediate-sized beak. *Arremonops*, considerably larger than the other field finches, lives in dense shrubbery and is omnivorous.

HYPOTHETICAL LIST

Bubulcus ibis Linnaeus, Cattle Egret: Seen twice by L. R. Holdridge in March, 1959, at mouth of Río Puerto Viejo on opposite side from "La Selva."

Eudocimus albus (Linnaeus), White Ibis: Ibises of which the description more or less matches the immature of this species have been reported from the finca. These would undoubtedly be transient individuals.

Ara macao (Linnaeus), Scarlet Macaw: This unmistakable bird is well known to people living in the neighborhood. It seems to have been relatively common on the Caribbean slope until recent years.

Amazona ochrocephala auropalliata (Lesson), Yellow-naped Amazon Parrot: A large, green parrot with a yellow nape, said to be an irregular visitant by people living in the region, can be only this bird.

Chaetura pelagica (Linnaeus), Chimney Swift: Lone swifts traveling together with swallows during the fall migration may perhaps be this species.

Chaetura vauxi (Townsend), Vaux's Swift: Flocks

of small swifts with no discernible identifying marks may be this species. It is probably the most common swift in the country.

Phaethornis guy (Lesson), Green Hermit: I glimpsed what was almost certainly an individual of this subtropical species at the end of August.

Xenops rutilans Temminck, Streaked Xenops: I strongly suspect it was this species I saw accompanying a traveling band very high in the forest. It can be confused only with *X. minutus*, which is not streaked.

Empidonax minimus (Baird and Baird), Least Flycatcher: Several times during the fall migration I saw what were almost positively individuals of this species.

OTHER BIRDS TO BE EXPECTED

Hydranassa tricolor (Müller), Louisiana Heron
Nycticorax nycticorax (Linnaeus), Black-crowned Night Heron
Nyctanassa violacea (Linnaeus), Yellow-crowned Night Heron
Tigrisoma salmoni Sclater and Salvin, Salmon's Tiger Bittern
Buteo magnirostris (Gmelin), Roadside Hawk
Hypomorphnus urubitinga (Gmelin), Great Black Hawk
Harpia harpyja (Linnaeus), Harpy Eagle
Falco sparverius Linnaeus, American Sparrow Hawk
Rhynchortyx cinctus (Salvin), Long-legged Colin
Amaurolimnas concolor (Gosse), Uniform Crake
Aramides axillaris Lawrence, Rufous-necked Wood Rail
Tringa solitaria Wilson, Solitary Sandpiper
Erolia melanotos (Vieillot), Pectoral Sandpiper
Pionus menstruus (Linnaeus), Blue-headed Parrot
Tyto alba (Scopoli), Barn Owl
Ciccaba nigrolineata Sclater, Black-and-white Owl
Caprimulgus cayennensis Gmelin, White-tailed Nightjar
Cypseloides spp.
Cotinga amabilis Gould, Lovely Cotinga
Thryothorus modestus zeledoni (Ridgway), Zeledon's Plain Wren
Troglodytes musculus Naumann, Tropical House Wren
Cyanerpes cyaneus (Linnaeus), Blue Honeycreeper
Dendroica magnolia (Wilson), Magnolia Warbler
Tangavius aeneus (Wagler), Red-eyed Cowbird
Sturnella magna (Linnaeus), Common Meadowlark
Tangara lavinia (Cassin), Lavinia's Calliste
Sporophila torqueola (Bonaparte), White-collared Seedeater

ECOLOGICAL CLASSIFICATION

AN ASTERISK (*) placed before the name of a bird indicates in the listings that follow that the species is characteristic of or confined to the habitat division in which it is placed. Some birds occur in more than one category. For other details, see the Annotated List.

FOREST

FOREST FLOOR

TERRESTRIAL SPECIES

These are the species that forage mostly or entirely on the ground; a number of them may rise into the understory or even high into the trees in order to escape danger, build nests, or rest. The number of species is small; few are abundant. Ground-dwelling birds are usually very difficult to see. If not for their calls, several common species might mistakenly be considered rare.

The following birds walk, run, or hop on the forest floor:

Tinamous: **Tinamus major*, **Crypturellus boucardi*
Cracids: **Crax rubra*
Wood quails: **Odontophorus erythrops*, *Odontophorus guttatus*
Ground doves: **Geotrygon veraguensis*, **Geotrygon montana*
Ground cuckoos: **Neomorphus geoffroyi*
Ovenbirds: **Sclerurus guatemalensis*
Antbirds: **Formicarius analis*, **Grallaria perspicillata*
Wrens: **Microcerculus marginatus*, **Cyphorhinus phaeocephalus*
Warblers: *Seiurus aurocapillus*

Rare, seasonal, or both, are *Crax*, *Odontophorus guttatus*, *Geotrygon montana*, *Neomorphus*, and *Seiurus aurocapillus*. Few in numbers, widely separated, or erratically met with are *Microcerculus*, which is solitary; *Odontophorus erythrops*, occurring usually in coveys; *Geotrygon veraguensis*, seen in pairs, as a rule. Common (encountered daily or almost daily) are *Tinamus* and *Crypturellus boucardi;* relatively abundant are *Formicarius*, *Grallaria perspicillata*, and *Cyphorhinus*.

Obviously specialized foragers are *Neomorphus*, which accompanies army ants; *Sclerurus*, which flicks earth and trash aside with its beak; and *Cyphorhinus*, which pries up the edges of fallen leaves and peers underneath.

The two tinamous seem to be similar in their foraging habits, but differ considerably in size. The two wood quails are similar in size and proportions, but one is common, and the other is uncommon or rare. The two antbirds are, respectively, fowl- or rail-like (*Formicarius*) and thrush- or plover-like (*Grallaria*). *Microcerculus* and *Seiurus aurocapillus* are small, and both teeter their hindquarters, but differ in proportions and habits: *Microcerculus* is rail-like, *Seiurus* is rather thrush-like.

The following species, all of which are more common outside the forest, keep concealed in dense undergrowth at forest breaks:

Tinamous: *Crypturellus soui*
Ground doves: *Leptotila cassinii*
Antbirds: *Grallaria fulviventris*

Practically confined to their habitat, they live apart from the species of the more open forest floor.

At wet places occur water birds or marsh birds. Most are rare or seldom seen and, because of the nature of the habitat, highly localized in occurrence. They are:

Herons and bitterns: **Agamia agami*, **Tigrisoma lineatum*
Boat-billed herons: *Cochlearius cochlearius*
Ibises: **Mesembrinibis cayennensis*
Rails: **Aramides cajanea*
Sun bitterns: *Eurypyga helias*
Waterthrushes: *Seiurus motacilla*

Agamia and *Tigrisoma* are solitary. Both are long-necked and short-legged, but the gaudy *Agamia* is extremely long-billed, and the dull-colored *Tigrisoma* has a much shorter, thicker beak. The scoop-billed *Cochlearius* is social, completely sedentary, and nocturnal. *Mesembrinibis* probes in mud. *Aramides* skulks in wet, generally impenetrable undergrowth. *Eurypyga*, which I saw only once at a rela-

tively open, muddy portion of the forested swamps, walks about freely and stalks its prey or gleans. The migrant *Seiurus motacilla* is rare in the forest, where I have seen it only on exposed mud at the interior swamps. Of the birds listed above, *Aramides* is the only common species.

Semi-terrestrial Species

These are medium- to small-sized birds that inhabit the lower undergrowth and regularly drop to the ground in order to forage. Some are more consistently terrestrial than others, so differ only in degree from those terrestrial species that regularly rise into the undergrowth. Mostly common or abundant, but few in kinds, they are:

Antbirds: **Myrmeciza exsul*
Wrens: **Henicorhina leucosticta*, **Cyphorhinus phaeocephalus*
Thrushes: *Hylocichla mustelina*
Warblers: *Oporornis formosus*, **Phaeothlypis fulvicauda*

Myrmeciza is a typically stout-bodied, short-tailed, tail-jetting, semi-terrestrial antbird. In the undergrowth it moves about deliberately; on the ground, where it occurs less often, it may flick aside leaves with its beak. *Cyphorhinus* is antbird-like in appearance, exhibits wren-like behavior in the undergrowth, and moves finch-like on the ground. The stout, little *Henicorhina* creeps and flits in undergrowth or hops on the ground, generally protected by cover. The migrant *Oporornis* is a sprightly warbler: in the understory it flits about; on the ground it hops, pokes its head under dead leaves, and leaps up at overhanging foliage. *Phaeothlypis* occurs at or near watercourses and behaves both as a tail-jetting waterthrush and an acrobatic flycatcher or redstart. The migrant *Hylocichla mustelina* usually prefers patches of dense undergrowth, where it is relatively inactive, or hops robin-like on the ground, where it rather resembles a long-tailed *Grallaria*. The thick-billed *Arremon* occurs in tangled parts of the understory where it moves actively among the twigs and vines; on the ground it hops, but exhibits no noticeably specialized behavior (unlike some other ground-foraging forest finches elsewhere in the country).

UNDERSTORY

Low (to 1 or 2 Meters Above the Ground, or to About Eye Level)

Some of the semi-terrestrial species could be fitted equally well into this transitional category. Delimited somewhat arbitrarily, it is nevertheless a stratum in which a number of birds characteristic of forest undergrowth are to be seen most often.

Hummingbirds: **Threnetes ruckeri*, **Phaethornis superciliosus*, **Phaethornis longuemareus*, *Microchera albo-coronata*
Ovenbirds: **Automolus ochrolaemus*
Antbirds: **Myrmeciza exsul*, **Gymnopithys leucaspis*, **Hylophylax naevioïdes*, **Phaenostictus mcleannani*
Manakins: **Schiffornis turdinus*
Wrens: *Thryothorus nigricapillus*, **Henicorhina leucosticta*, **Cyphorhinus phaeocephalus*
Gnatwrens: *Ramphocaenus melanurus*, **Microbates cinereiventris*
Tanagers: *Mitrospingus cassinii*
Finches: **Cyanocompsa cyanoides*, **Arremon aurantiirostris*

The hummingbirds, three of the antbirds, and the tanager exhibit obviously specialized behavior. The hummingbirds feed while hovering, and they are of different sizes or shapes. *Gymnopithys*, *Hylophylax*, and *Phaenostictus* habitually follow army ants and constantly drop to the ground for prey; in size they are medium, small, and large, respectively. *Mitrospingus* troops about in bands beside the wooded swamps or along forest breaks. *Myrmeciza*, which in appearance and actions resembles the army-ant attendant antbirds, is sedentary and forages in a deliberate manner low above the ground or upon it. *Automolus* prefers tangled portions of the understory where it creeps, clings, climbs, and habitually rummages. *Schiffornis*, a cotinga-sized manakin, wanders about low in the dark understory, makes sudden flits, but otherwise is lethargic in the manner of a trogon or becard. The social *Cyphorhinus*, an antbird-like wren, occurs commonly in the low undergrowth but forages mainly on the ground. The stocky *Henicorhina* is wren-like; although it occurs low in the undergrowth, it does not specialize in ground foraging. *Thryothorus nigricapillus* is confined to dense growth at the swamps or along streams where they are open to the sky. The little *Micro-*

bates is rather antbird-like in appearance and wren-like in behavior; light-bodied and long-billed, it occurs in the same places, i.e., almost anywhere, as *Henicorhina*. The very long-billed *Ramphocaenus* (which is much more common outside the forest) occurs mostly in thickety tangles at forest breaks; in behavior it is rather wren-like. The thick-billed *Arremon* and *Cyanocompsa* occur together in this stratum: the bright *Arremon* may descend to the ground, whereas the dull-colored, non-terrestrial *Cyanocompsa* often rises higher into the understory.

High (From About Eye Level to 5 Meters or so Above the Ground, i.e., Top of Understory)

Here the species and the families represented increase in number, and the range of behavior broadens accordingly. This stratum, too, is transitional at its upper and lower limits. Traveling mixed bands may intersect, join temporarily, and attract sedentary birds from several levels. Birds from the upper levels are apt to descend to the lower understory; birds inhabiting the undergrowth ordinarily do not rise into the middle forest. Several species are characteristic of this stratum, notably small arboreal formicariids and small flycatchers.

Hawks: *Accipiter bicolor, Micrastur mirandollei, *Micrastur ruficollis*
Owls: *Pulsatrix perspicillata, Glaucidium minutissimum, *Ciccaba virgata*
Hummingbirds: **Threnetes ruckeri, Phaethornis superciliosus, Phaethornis longuemareus, Florisuga mellivora, *Thalurania furcata, Microchera albo-coronata, *Chalybura melanorrhoa*
Trogons: **Trogon rufus*
Kingfishers: **Chloroceryle inda, Chloroceryle aenea*
Motmots: *Electron platyrhynchum, Baryphthengus ruficapillus*
Puffbirds: **Malacoptila panamensis, Monasa morphoeus*
Woodpeckers: *Dryocopus lineatus, Phloeoceastes guatemalensis*
Woodhewers: *Dendrocincla fuliginosa, *Glyphorynchus spirurum, Dendrocolaptes certhia, Xiphorhynchus erythropygium*
Ovenbirds: **Hyloctistes subulatus, *Automolus ochrolaemus, Xenops minutus*
Antbirds: **Thamnophilus punctatus, *Dysithamnus striaticeps, *Myrmotherula fulviventris, *Myrmotherula axillaris, Microrhopias quixensis*
Manakins: **Piprites griseiceps, *Pipra mentalis, *Corapipo leucorrhoa*
Cotingas: *Laniocera rufescens*
Flycatchers: *Empidonax flaviventris, *Terenotriccus erythrurus, *Myiobius barbatus, *Onychorhynchus coronatum, *Platyrinchus coronatum, Rhynchocyclus brevirostris, Myiornis ecaudatus, Ornithion semiflavum, *Pipromorpha oleaginea*
Wrens: **Thryothorus thoracicus, Thryothorus nigricapillus*
Gnatwrens: *Ramphocaenus melanurus*
Vireos: *Vireo flavifrons, *Hylophilus ochraceiceps*
Honeycreepers: *Chlorophanes spiza*
Tanagers: *Tanagra gouldi, *Chlorothraupis carmioli, Lanio aurantius, *Tachyphonus delatrii, Mitrospingus cassinii*
Finches: **Cyanocompsa cyanoides*

Birds of prey are seen seldom. Of the hawks, only *Micrastur ruficollis* is met from time to time; of the owls, only the tiny *Glaucidium*, and perhaps *Ciccaba*. Hummingbirds, excepting the tiny *Microchera* and the seasonal *Florisuga*, are fairly common. *Threnetes* and the two species of *Phaethornis* are usually hidden by foliage as they perch in the lower half of the understory, whereas *Thalurania* and *Chalybura* perch and feed higher, and generally rest on exposed, bare twigs. The two kingfishers are rare or uncommon and are restricted to watercourses, including shallow little pools in the case of the pygmy *C. aenea*. On trunks and limbs occur the two large woodpeckers: *Dryocopus* (uncommon in forest) and the common *Phloeoceastes*, and several woodhewers. Only the little *Glyphorynchus* is common; *Dendrocolaptes* and *Dendrocincla* commonly join birds accompanying army ants, and *Xiphorhynchus erythropygium* usually travels about with mixed bands.

Species that normally creep about in the vegetation and/or rummage are ovenbirds and wren-like birds. The thrush-sized *Automolus* prefers tangled portions of the understory; the similar *Hyloctistes* frequents the upper understory and lower middle forest, occurring higher and in more open situations than *Automolus*. Perhaps to be included here is the little *Xenops*, which clings like a tit and pecks like a piculet. The wren *Thryothorus thoracicus* climbs and creeps where slender vines, lianas, and tangled arcades are mixed with leafy vegetation. *Thryothorus nigricapillus* may rise occasionally from the lower

understory into this stratum. The wren-like *Ramphocaenus* is sedentary in dense thickety growth at forest breaks where it forages in concealment.

Birds that rest quietly but suddenly sally for prey are the two motmots, differing greatly in size of body and serration of beak; the two puffbirds, of which the larger, *Monasa*, generally keeps above the understory, whereas the much smaller *Malacoptila* frequents the understory; and the short- and thick-billed *Trogon rufus*, which plucks living prey or fruits during a spectacular hover.

Birds that alternate stationary perching with lightning-like flits are exemplified by the small flycatchers and manakins: the flycatchers *Platyrinchus* and *Terenotriccus*, the somewhat larger *Empidonax flaviventris*, and the diminutive *Ornithion* and *Myiornis;* the manakins *Pipra*, *Corapipo*, and *Piprites;* and the stocky little antvireo *Dysithamnus*. Larger in size, but similar in behavior, is the flat-billed *Rhynchocyclus*. More varied, or less distinctive, in behavior are the slender-billed *Pipromorpha*, which also searches like a vireo; *Myiobius*, which flits acrobatically like a redstart; *Onychorhynchus*, which sallies, but also moves about through the forest. Except for the rare *Onychorhynchus*, the migrant *Empidonax flaviventris*, and the seasonal *Corapipo*, all are common residents.

Several species habitually travel about in bands, primarily tanagers and antwrens. I cannot describe the behavior of the tanagers as other than varied. The lively little antwrens cling to foliage, vines, and hanging trash, search like vireos, and flit like warblers. The tanagers *Chlorothraupis*, *Tachyphonus delatrii*, and *Lanio* are each a nucleus species; *Mitrospingus* is not. The finch-like *Chlorothraupis* is mostly confined to the understory; *T. delatrii*, about the same length as, but one-half of the weight of, *Chlorothraupis*, and much thinner-billed, rises into the middle forest; *Lanio* generally follows forest breaks, such as valleys and ridges; *Mitrospingus*, which is much more common outside the forest than inside, troops about in dense undergrowth along forest breaks. Nucleus antwrens are the two species of *Myrmotherula:* both occur commonly in forest, but *M. fulviventris* also frequents contiguous second growth. Often associating with them are small bands of *Hylophilus ochraceiceps*, a forest vireo that apparently behaves in just the same way as the antwrens; it does not rise above the understory. The antwren *Microrhopias*, which is much more common outside the forest, often joins the other two antwrens. The sharp-billed little ovenbird *Xenops* generally accompanies mixed bands, as does also the euphonia *Tanagra gouldi.* Occurring almost exclusively as members of traveling mixed bands are *Xiphorhynchus erythropygium*, *Dysithamnus*, *Piprites*, and *Ornithion*, as well as some passage migrants.

Other species of the upper understory are the sedentary antshrike *Thamnophilus*, which, with heavy-bodied, deliberate little leaps, gleans its prey from the foliage; the cotinga *Laniocera*, which is relatively inactive in the foliage and is becard-like in behavior; the grosbeak *Cyanocompsa*, of varied, lively actions, which prefers tangled parts of the lower understory; the long-billed, warbler-like *Chlorophanes;* and the migrant *Vireo flavifrons*. Of these birds, *Thamnophilus* and *Cyanocompsa* are common; *Laniocera* is very uncommon, and possibly seasonal; *Chlorophanes* is uncommon; *Vireo flavifrons* is very uncommon.

MIDDLE FOREST

The intensity of light is much stronger than at lower levels, and there are fewer obstacles to hinder flight. Here occur several species of the upper understory and many species of the canopy. Birds of the undergrowth and thickets are mostly absent. Several larger birds are present, whereas small birds are the rule in the understory. Largely or partly frugivorous species, such as parrots and toucans and oropendolas, descend from the higher levels. Bright colors in the plumage become more frequent. This broad stratum is the one favored by woodpeckers and woodhewers, large trogons, the large jacamar, a large puffbird, and the only arboreal pigeon in the forest. Antbirds, ovenbirds, and flycatchers are uncommon; hummingbirds are rarely seen; wrens are absent.

Hawks: *Harpagus bidentatus*, *Accipiter bicolor*, *Accipiter superciliosus*, **Leucopternis semiplumbea*, *Spizaëtus ornatus*, *Geranospiza nigra*,

Micrastur mirandollei, Micrastur ruficollis, Daptrius americanus
Pigeons: **Columba nigrirostris*
Parrots: *Pionopsitta haematotis*
Owls: [*Lophostrix cristata*], *Pulsatrix perspicillata*
Trogons: **Trogon massena*, **Trogon clathratus*, *Trogon rufus*
Motmots: **Electron platyrhynchum*, **Baryphthengus ruficapillus*
Jacamars: **Jacamerops aurea*
Puffbirds: **Monasa morphoeus*
Toucans: *Pteroglossus torquatus, Selenidera spectabilis, Ramphastos sulfuratus, Ramphastos swainsonii*
Woodpeckers: *Piculus simplex*, **Celeus castaneus*, **Celeus loricatus, Dryocopus lineatus, Phloeoceastes guatemalensis*
Woodhewers: *Dendrocincla fuliginosa, Glyphorynchus spirurum, Dendrocolaptes certhia*, **Xiphorhynchus lachrymosum, Xiphorhynchus erythropygium*
Ovenbirds: *Hyloctistes subulatus, Xenops minutus*
Antbirds: *Thamnistes anabatinus, Dysithamnus striaticeps, Myrmotherula axillaris, Microrhopias quixensis*
Manakins: *Piprites griseiceps, Pipra mentalis*
Cotingas: *Laniocera rufescens*, **Lipaugus unirufus*, **Cephalopterus glabricollis*
Flycatchers: *Terenotriccus erythrurus, Myiobius barbatus, Rhynchocyclus brevirostris*, **Myiornis ecaudatus, Ornithion semiflavum, Pipromorpha oleaginea*
Thrushes: *Turdus fumigatus*
Vireos: *Hylophilus decurtatus*
Honeycreepers: *Chlorophanes spiza*
Caciques: *Zarhynchus wagleri, Gymnostinops montezuma*, **Cacicus uropygialis*
Tanagers: **Tanagra gouldi, Piranga rubra, Lanio aurantius, Tachyphonus luctuosus, Tachyphonus delatrii*
Finches: *Caryothraustes poliogaster, Pitylus grossus*

Raptorial birds are seldom met, excepting *Leucopternis semiplumbea* and, occasionally, the un-hawk-like *Daptrius*. Vegetarian species are the dove *Columba nigrirostris*, the small parrot *Pionopsitta*, all four toucans (two large and two small species), and the euphonia *Tanagra gouldi*. All are common except the toucan *Selenidera*. Of tree-trunk birds, only the woodpeckers *Celeus loricatus* and *Phloeoceastes*, and the woodhewer *Xiphorhynchus lachrymosum*, are common. The sallying birds are the trogons, motmots, and the puffbird *Monasa*, which are common, and the very uncommon jacamar *Jacamerops;* the cotinga *Cephalopterus* might be included here.

The species that flit off the foliage are the antvireo *Dysithamnus*, the two manakins, and all the flycatchers. All are encountered regularly, but none is abundant. *Dysithamnus*, *Piprites*, and *Ornithion* are to be found only as members of traveling mixed bands. Birds of warbler- or vireo-like behavior are the active antwrens *Myrmotherula* spp. and *Microrhopias*, the antshrike *Thamnistes*, the vireo *Hylophilus decurtatus*, the honeycreeper *Chlorophanes*, and the tanagers *Tanagra gouldi, Tachyphonus delatrii*, and *Tachyphonus luctuosus;* of these, only *Hylophilus*, *Tanagra*, and *Tachyphonus delatrii* are common. The active little *Xenops* usually travels about with mixed bands.

Because of their varied behavior there are several species I cannot aptly characterize. The cotingas *Laniocera* (very uncommon) and *Lipaugus* (very common), and the thrush *Turdus fumigatus* (uncommon), all have a varied diet and alternate bursts of activity, such as flitting, leaping at or clinging to foliage, hopping along branches, hovering, and so on, with intervals of waiting. The behavior of *Cephalopterus* (mentioned in the preceding paragraph) is cotinga-like also, but reaches an extreme of lethargic deliberateness. The migrant tanager *Piranga rubra* (rarely seen in the forest) hovers, flutters, and fly-catches. *Tanagra gouldi*, the only forest-adapted euphonia at "La Selva," is one of the most common birds. Probably largely frugivorous, it may occur at all levels except the lower understory, often in groups. The grosbeak *Pitylus* is common but sedentary and hard to see; I surmise that it subsists to a considerable extent on small, hard fruits.

Birds that troop about in small groups or large bands also act in many different ways. The brightly plumaged grosbeak *Caryothraustes* is a nucleus species that generally keeps to the upper middle forest and high canopy. The lively tanager *Tachyphonus delatrii*, also a nucleus species, is most common in the understory and lower middle forest. The two oropendolas and the cacique *Cacicus* occur mostly in the upper middle forest and canopy; the oropendolas hop along branches, examine the encrusted bark of limbs, and probe in flowers and epiphytes; the highly animated *Cacicus*, in addition,

clings and rummages, may behave acrobatically, and seems to be omnivorous to the point of eating almost anything.

CANOPY

Ibises: *Mesembrinibis cayennensis*
Hawks: *Leucopternis semiplumbea, Spizaëtus ornatus, Geranospiza nigra, Daptrius americanus*
Cracids: **Penelope purpurascens*
Pigeons: *Columba nigrirostris*
Parrots: **Ara ambigua, *Pionopsitta haematotis, Pionus senilis, *Amazona autumnalis, *Amazona farinosa*
Cuckoos: *Piaya cayana*
Hummingbirds: *Heliothryx barroti*
Trogons: *Trogon massena, Trogon clathratus, Trogon violaceus*
Toucans: **Pteroglossus torquatus, *Selenidera spectabilis, *Ramphastos sulfuratus, *Ramphastos swainsonii*
Woodpeckers: *Celeus loricatus, Dryocopus lineatus, Centurus pucherani, Phloeoceastes guatemalensis*
Woodhewers: *Xiphorhynchus lachrymosum, Xiphorhynchus erythropygium*
Ovenbirds: *Xenops minutus*
Antbirds: **Thamnistes anabatinus*
Cotingas: **Carpodectes nitidus, Attila spadiceus, Rhytipterna holerythra, Lipaugus unirufus, Pachyramphus cinnamomeus, Tityra semifasciata, Erator inquisitor, Querula purpurata, Cephalopterus glabricollis*
Flycatchers: *Megarhynchus pitangua, Conopias parva, *Myiarchus crinitus, Contopus virens, Empidonax traillii, Myiobius barbatus, Tolmomyias assimilis, Rhynchocyclus brevirostris, *Ornithion semiflavum, Pipromorpha oleaginea*
Gnatcatchers: *Polioptila plumbea*
Shrike-vireos: **Smaragdolanius pulchellus*
Vireos: *Vireo flavifrons, Vireo olivaceus, *Hylophilus decurtatus*
Honeycreepers: *Chlorophanes spiza, Cyanerpes caeruleus*
Warblers: *Mniotilta varia, Vermivora chrysoptera, Dendroica pensylvanica, Wilsonia canadensis, Setophaga ruticilla*
Caciques: **Zarhynchus wagleri, *Gymnostinops montezuma, Cacicus uropygialis*
Tanagers: *Tanagra minuta, Tanagra gouldi, Lanio aurantius, Tachyphonus luctuosus*
Finches: **Caryothraustes poliogaster, *Pitylus grossus*

Probably the outstanding feature of bird life in the canopy is the large number of species that travel about in groups or bands. Wholly or partly frugivorous birds are common, especially parrots, toucans, cotingas, and cacique-like icterids (the only kind in the forest). Antbirds and ovenbirds are each represented by only one species. Hummingbirds are undoubtedly represented by more than the single species I have listed; a hundred or more feet in the air they are mostly unidentifiable. Wrens and wren-like birds are absent. Flycatchers of several kinds occur in the canopy, but none is a permanent resident or even typical of the stratum. Several species that are common in the semi-open occur in the forest only here, and they are generally met in the company of mixed parties. Some of the migrants, most of which I do not associate with heavy forest, do occur in the canopy during transience in the fall and spring; they are to be seen where the canopy dips low, or in openings, and as a rule they occur as members of mixed bands. There are only two permanent nucleus species, and both are brightly plumaged: the finch *Caryothraustes*, which dominates its band numerically, and the shrike-billed tanager *Lanio*, of which a few individuals seem to dominate the band vocally. Temporary nuclei of attraction are bands of the cacique *Cacicus* and the forest vireo *Hylophilus decurtatus*. Traveling about in pure groups are the frugivorous parrots and toucans; oropendolas and *Cacicus;* the cotingas *Tityra*, *Erator*, *Carpodectes*, *Cephalopterus* (occasionally), and *Querula;* the vireo *Hylophilus decurtatus;* the euphonias *Tanagra minuta* (hardly penetrating the forest), and the ubiquitous *T. gouldi*. Other species occurring in small groups are the ibis *Mesembrinibis* (which forages on the ground), the peculiar hawk *Daptrius*, and the guan *Penelope*.

The following species are usually found as members of mixed bands, seldom or never alone. Typical woodland birds are the woodhewer *Xiphorhynchus erythropygium*, the ovenbird *Xenops* (also in the semi-open), the antshrike *Thamnistes*, and the flycatchers *Rhynchocyclus*, *Ornithion*, and *Pipromorpha*. Species that also occur regularly outside the forest are the honeycreeper *Chlorophanes* and the tanagers *Tanagra gouldi* and *Tachyphonus luctuosus*. Species characteristic of the semi-open are the flycatchers *Megarhynchus*, *Conopias*, and *Tolmomyias assimilis*, and the gnatcatcher *Polioptila;* these are uncommon and confined to the canopy. During the peri-

ods of active migration the following species occur together with mixed bands, especially at breaks in the forest or where the canopy lies well below the level of the high roof: the flycatcher *Empidonax traillii*, the thrush *Hylocichla ustulata*, the vireos *Vireo olivaceus* and *V. flavifrons*, and the warblers *Mniotilta*, *Vermivora chrysoptera*, *Dendroica pensylvanica*, *Wilsonia canadensis*, and *Setophaga*.

Birds occurring independent of traveling bands are of several sorts. The raptorial species are the large and powerful *Spizaëtus ornatus*, the small *Leucopternis semiplumbea*, the long-legged, weakly built *Geranospiza*, and the peculiar, rather fowl-like *Daptrius;* of these, only *Leucopternis* is encountered regularly. The tree-trunk birds are the woodpeckers and woodhewers. The woodpeckers comprise two forest species: the very different *Phloeoceastes* and *Celeus loricatus;* also *Dryocopus*, which is occasional in virgin forest, and *Centurus pucherani*, a typical species of the semi-open, which sometimes occurs in the forest, only in the canopy. The only woodhewer belonging to this category is *Xiphorhynchus lachrymosum; X. erythropygium*, as mentioned above, accompanies traveling bands.

Sallying birds are the large trogons *Trogon massena* and *T. clathratus*, and the much smaller *T. violaceus*, the last-named being very uncommon in forest where its occasional presence in the canopy is revealed by its voice; the heavy-bodied, lethargic cotinga *Cephalopterus;* the migrant flycatchers *Nuttallornis* (transient) and *Contopus virens*, both of which are much more common outside the forest. Perhaps the hummingbird *Heliothryx* should also be placed here.

As might be expected, there are several species the behavior of which is difficult to characterize. The dove *Columba nigrirostris*, which is vegetarian, is very common throughout the forest. The cuckoo *Piaya*, which is more common outside the forest, is confined to the canopy. The cotinga *Attila*, although fairly common in the forest, seems to be confined to the canopy, where it sits like a puffbird and forages like a flycatcher or a becard. The lively *Lipaugus*, one of the common birds of the forest above the understory, behaves like a combination of flycatcher, becard, and thrush. *Rhytipterna* is uncommon behind the forest border, and is sedentary in the canopy. Among flycatchers, the migrant *Myiarchus crinitus* is fairly common, and keeps inside the canopy, where it moves about in the foliage and may flit off leaves; *Myiobius*, which acts much like a redstart, is rare in the canopy. The robin *Turdus fumigatus*, alternating statuesque posing with flurries of activity, behaves much like the cotinga *Lipaugus*, but in a restrained manner, and it is uncommon and seasonal. The shrike-vireo *Smaragdolanius*, one of the common birds of the semi-open, occurs in the forest only in the canopy, where it searches deliberately in the manner of a slow-paced vireo, and is extremely difficult to observe. The honeycreeper *Cyanerpes* can be seen occasionally on top of the canopy; it is much more common outside the forest. The grosbeak *Pitylus* is a forest species that usually occurs high above the ground; a common bird, it is rather sedentary, keeping hidden in the foliage.

ABOVE THE FOREST

Vultures: *Sarcoramphus papa*, **Coragyps atratus*, **Cathartes aura*

Hawks: *Elanoïdes forficatus*, *Leptodon cayanensis*, *Ictinia plumbea*, *Buteo brachyurus*, *Leucopternis albicollis*, *Spizastur melanoleucus*, **Spizaëtus ornatus*, *Spizaëtus tyrannus*

Parrots: **Ara ambigua*, **Pionopsitta haematotis*, *Pionus senilis*, **Amazona autumnalis*, **Amazona farinosa*

Swifts: **Steptoprocne zonaris*, **Chaetura cinereiventris*, *Cypseloides* sp., *Panyptila cayennensis*

Vultures, a few hawks, parrots, and swifts are commonly seen in the air above the forest. The vultures soar high in the air, but I have never seen them inside the forest. The hawks soar, apparently moving from one locality to another; some may feed on the wing (*Ictinia* and *Elanoïdes*, seldom seen outside migration), or display (*Spizaëtus ornatus*), or call repeatedly (*Spizaëtus ornatus* and *S. tyrannus*). Parrots fly above the canopy to a feeding ground, or to discover a fruiting tree, or to and from roosts located apparently outside the forest. Swifts are the most abundant in number of individuals and

feed only on the wing. In addition, white-plumaged cotingas (*Carpodectes*, *Tityra*, *Erator*) may troop about on the upper side of the canopy as may also toucans, the honeycreeper *Cyanerpes*, oropendolas, and several flycatchers.

SECOND GROWTH (OUTSIDE THE FOREST)

TERRESTRIAL

Tinamous: *Tinamus major*, **Crypturellus soui*, *Crypturellus boucardi*
Wood quails: *Odontophorus erythrops*, *Odontophorus guttatus*
Rails: *Aramides cajanea*, **Laterallus albigularis*
Ground doves: **Leptotila cassinii*
Goatsuckers: *Nyctidromus albicollis*
Ovenbirds: *Sclerurus guatemalensis*
Antbirds: *Formicarius analis*, **Grallaria fulviventris*, *Grallaria perspicillata*

The small tinamou *Crypturellus soui*, walking about in concealment, is one of the characteristic thicket inhabitants; the other two tinamous are primarily forest birds. The wood quails occur in more advanced second growth having an admixture of trees (sub-forest). The large wood rail *Aramides*, a woodland bird, may be present in vegetation-choked ravines, heavily overgrown, shaded, marshy edges, and similar places; the little *Laterallus*, which does not enter woodland, inhabits open places covered with dense, low vegetation, such as muddy stream beds and grassy ditches—arbitrarily it might also be classed as an open-country bird. The ground dove *Leptotila* is much like the little tinamou in size, habitat preference, and foraging habits, but it is differently formed, relatively easy to observe, flies lightly and well, occurs inside leafy shrubbery as well as in reed-like thickets, and probably feeds mostly on small seeds. The whip-poor-will-like *Nyctidromus* is crepuscular or nocturnal; it passes the day resting on the ground in all sorts of shaded growth, including the forest border. The leaf-scraper *Sclerurus*, a forest species, may enter tall second growth merging with the forest. The antthrush *Formicarius* and the antpitta *Grallaria perspicillata* are forest species which also walk about in shaded, tall second growth connected with the forest. *Grallaria fulviventris* is a sedentary inhabitant of the most impenetrable parts of leafy or thickety second growth.

SEMI-TERRESTRIAL

Antbirds: **Myrmeciza exsul*
Wrens: **Henicorhina leucosticta*, *Cyphorhinus phaeocephalus*
Thrushes: *Hylocichla mustelina*
Warblers: *Seiurus aurocapillus*, *Oporornis formosus*
Finches: **Arremon aurantiirostris*, *Arremonops conirostris*

The antbird *Myrmeciza*, the wren *Henicorhina*, and the finch *Arremon* are very common woodland species that also dwell in the later stages of second growth, where the undergrowth is shaded and tangled, but not in dense, wild plantain thickets. The forest wren *Cyphorhinus* may be encountered in the same sorts of places, but less commonly. The migrant warblers *Seiurus aurocapillus* and *Oporornis formosus* are often present in tangled undergrowth, the former generally in tall thickets, the latter often at muddy or wet places. The migrant thrush *Hylocichla mustelina* occurs in tall thickets, dense shrubbery at wet places, and heavily overgrown edges. The finch *Arremonops* inhabits patches of wild shrubbery or overgrown borders in the semi-open, mostly at the Point; unlike all the above species, it is absent from forest.

NON-TERRESTRIAL

Hawks: *Micrastur ruficollis*
Owls: *Pulsatrix perspicillata*, *Glaucidium minutissimum*, *Ciccaba virgata*
Hummingbirds: **Glaucis hirsuta*, **Threnetes ruckeri*, **Phaethornis superciliosus*, **Phaethornis longuemareus*, *Klais guimeti*, **Thalurania furcata*, *Hylocharis eliciae*, **Amazilia amabilis*, *Amazilia tzacatl*, *Microchera albo-coronata*, *Chalybura melanorrhoa*
Kingfishers: *Chloroceryle aenea*
Motmots: **Electron platyrhynchum*, **Baryphthengus ruficapillus*
Jacamars: **Galbula ruficauda*
Puffbirds: **Malacoptila panamensis*
Woodpeckers: **Veniliornis fumigatus*
Ovenbirds: **Synallaxis brachyura*, **Automolus ochrolaemus*

Antbirds: **Cymbilaimus lineatus*, **Taraba major*, *Thamnophilus punctatus*, *Myrmotherula fulviventris*, *Myrmotherula axillaris*, **Microrhopias quixensis*, **Cercomacra tyrannina*, **Gymnocichla nudiceps*
Manakins: *Piprites griseiceps*, **Manacus candei*
Cotingas: *Attila spadiceus*
Flycatchers: **Empidonax flaviventris*, **Aphanotriccus capitalis*, *Rhynchocyclus brevirostris*, **Todirostrum sylvia*, **Oncostoma cinereigulare*
Wrens: *Thryothorus thoracicus*, **Thryothorus nigricapillus*, **Thryothorus atrogularis*
Catbirds: **Dumetella carolinensis*
Gnatwrens: **Ramphocaenus melanurus*
Warblers: **Icteria virens*
Caciques: **Amblycercus holosericeus*
Tanagers: **Ramphocelus passerinii*, **Phlogothraupis sanguinolenta*, **Habia gutturalis*, **Mitrospingus cassinii*
Finches: **Cyanocompsa cyanoides*

Birds of prey are seen seldom but may occur occasionally in dense thickety growth mixed with a considerable number of trees. The accipiter-like *Micrastur ruficollis* is sometimes met fairly low in viny tangles. The owls *Pulsatrix* and *Ciccaba* are largely or entirely nocturnal, hiding in dense growth during the day but hunting in the semi-open or along woodland borders at night; the tiny *Glaucidium* is diurnal as well as nocturnal and seems to rest in thickets but to hunt in more open situations.

Hummingbirds are common; the abundant heliconias attract species both from woodland and the semi-open. The two species of *Phaethornis*, *Threnetes*, *Thalurania*, and *Chalybura* seldom occur away from shade. *Glaucis*, which is much like *Threnetes*, often forages in exposed situations, such as low shrubbery or thickety growth along borders beside woodland or streams. The other species are common in the semi-open.

The only woodpecker to be seen in dense growth is the little *Veniliornis*, which travels about, is uncommon, but is to be expected at the Point in particular; it does not enter the forest. There are no thicket-inhabiting woodhewers.

Birds that sally (broadly interpreted) are the seldom-seen pygmy kingfisher *Chloroceryle aenea*, sometimes found at water-filled depressions in well-shaded, luxuriantly tangled second growth (sub-forest); the two motmots, both of which are common, in intermediate and more advanced second growth wherever trees remain from the original forest; the jacamar *Galbula*, commonly seen at openings in intermediate or later stages of second growth and along overgrown borders of woodland and streams, where it is often fully exposed to view; and the small puffbird *Malacoptila*, common in tall thickets and advanced second growth, always in shade.

The species that dart suddenly in order to flit off leaves are few in number. The manakin *Piprites* may be seen occasionally with traveling bands in advanced second growth beside the forest; the sedentary *Manacus* usually keeps low in dense or closely tangled portions of intermediate or later-stage second growth, always outside the forest; *Corapipo*, at the height of its seasonal abundance, may occur almost anywhere. The flycatcher-like cotinga *Attila* may occur in shaded thickets and older growth; it often takes rather large-sized prey. Among the flycatchers, the flat-billed *Rhynchocyclus* may be present, uncommonly, in most kinds of shaded second growth but is primarily a woodland species; *Aphanotriccus*, with its rather deliberate behavior, is sedentary in tall thickets and overgrown borders, but occasionally enters into the foliage of trees nearby in the semi-open; the migrant *Empidonax flaviventris* acts much like *Aphanotriccus*, but is more animated and more abundant; and the little, bent-billed *Oncostoma* is sedentary, usually occurring fairly low in all sorts of second growth and borders overgrown with shrubbery.

There are several species, exemplified by the antshrikes, that unhurriedly hop, leap, and search with heavy-bodied movements in the foliage. They are highly sedentary and, for the most part, very hard to see, but they are curious and react to squeaking. The antshrike *Taraba* dwells in low, dense shrubbery and thickets, impenetrable borders, tangled grass, and scrubby growth, generally in places unshaded by trees. *Cymbilaimus* is to be found in low, bushy trees mixed with heavy undergrowth which together form borders of one sort or another. *Thamnophilus* is a forest bird which may, however, enter shaded second growth adjoining the forest. The antbird *Gymnocichla* is almost exclusively an inhabitant of dense thickets in or beside the semi-open; it is a regular army-ant attendant.

Rather different are the migrant chat *Icteria* and the catbird *Dumetella*, which are more active than the above birds, and occur mostly at the Point in hedges, low thickets, or wild shrubbery; both are very uncommon, and under certain circumstances could perhaps be considered birds of the semi-open. The little, tody-billed flycatcher *Todirostrum sylvia* might be included here; it inhabits young and intermediate-stage thickets where, circumspectly, it hops about in the vegetation and makes little leaps for prey; it is extremely local.

Birds of wren-like behavior, i.e., those that creep about and search more or less constantly inside cover, are well adapted to dense vegetation. They are mostly sedentary, and all are resident. There are three congeneric wrens: *Thryothorus atrogularis*, which is antbird-like in appearance, is extremely sedentary, keeping well hidden in very dense, wild shrubbery and low thickety growth that is often unshaded; *T. nigricapillus* moves about actively in overgrown borders, especially along watercourses, and may venture a little way into the semi-open (inside cover); and *T. thoracicus* occurs well above the ground in tall thickets and advanced second growth (sub-forest), as well as in forest. The little, long-billed gnatwren *Ramphocaenus* is sedentary in all kinds of thickets and behaves like a wren that happens to have the slender proportions of a gnatcatcher. The spinetail *Synallaxis* moves about in low shrubbery, hedgerows, overgrown borders, edges of thickets, and the like, and it is fairly common only at the Point; it might also be considered an inhabitant of undergrowth in the semi-open. The antbird *Cercomacra* is sedentary, keeping fairly low in dense thickety growth; although somewhat wren-like, it is slow-moving. Two other species are rather large and quite un-wren-like morphologically: the ovenbird *Automolus* and the cacique *Amblycercus* rummage noisily in clusters of dry leaves or banana fronds, clamber on vines and stems, where the thickets are very dense; *Amblycercus*, in addition, pries apart decaying stems.

There remain several species of active birds, mostly antwrens and tanagers, which occur often, or only, or sometimes outside the forest. Of the antwrens, *Microrhopias* is common almost anywhere in thickety growth of tall or medium height; *Myrmotherula axillaris* and *M. fulviventris* are forest species that enter shaded thickets adjoining forest, but *axillaris* is to be seen seldom whereas *fulviventris* is fairly common. Of the tanagers, *Mitrospingus* travels in bands low in leafy or thickety growth along riversides and streamsides, ravines, and forest borders, where it can be expected to make its rounds at least once daily. *Habia* moves about in small parties, almost exclusively in tall, shaded thickets or older second growth. *Ramphocelus* inhabits shrubbery, scrubby growth, and edges of thickets, generally in unshaded situations, and often occurs in family-sized groups; it is perhaps a species of the semi-open rather than of thickets. *Phlogothraupis* is much like *Ramphocelus*, but occurs alone or in twos and is far less abundant. The finch *Cyanocompsa*, for the most part, occurs rather low in the tangled undergrowth of tall thickets and advanced second growth.

TREE PLANTATIONS (SEMI-OPEN)

Vultures: **Coragyps atratus*, **Cathartes aura*
Hawks: *Leptodon cayanensis*, *Harpagus bidentatus*, *Accipiter superciliosus*, **Buteo platypterus*, *Leucopternis semiplumbea*, *Buteogallus anthracinus*, *Spizastur melanoleucus*, **Spizaëtus tyrannus*, *Geranospiza nigra*, **Herpetotheres cachinnans*, *Daptrius americanus*, **Falco albigularis*
Cracids: *Penelope purpurascens*, **Ortalis garrula*
Doves: *Columba cayennensis*, *Columba nigrirostris*, *Columbigallina talpacoti*, **Claravis pretiosa*
Parrots: *Ara ambigua*, **Aratinga finschi*, **Aratinga astec*, *Pionopsitta haematotis*, **Pionus senilis*, *Amazona autumnalis*, *Amazona farinosa*
Cuckoos: **Piaya cayana*, **Crotophaga sulcirostris*
Owls: *Glaucidium minutissimum*
Potoos: **Nyctibius griseus*
Goatsuckers: **Nyctidromus albicollis*
Hummingbirds: *Phaeochroa cuvierii*, **Florisuga mellivora*, *Klais guimeti*, **Paphosia helenae*, *Hylocharis eliciae*, **Amazilia amabilis*, **Amazilia tzacatl*, *Microchera albo-coronata*, *Heliothryx barroti*, **Heliomaster longirostris*
Trogons: *Trogon massena*, **Trogon violaceus*
Jacamars: **Galbula ruficauda*
Puffbirds: **Notharchus macrorhynchos*, **Notharchus tectus*, *Malacoptila panamensis*, **Monasa morphoeus*

Toucans: *Pteroglossus torquatus, Selenidera spectabilis, Ramphastos sulfuratus, Ramphastos swainsonii*

Woodpeckers: *Piculus simplex, Celeus castaneus, Celeus loricatus, *Dryocopus lineatus, *Centurus pucherani, *Veniliornis fumigatus, Phloeoceastes guatemalensis*

Woodhewers: *Dendrocincla fuliginosa, Glyphorynchus spirurum, Dendrocolaptes certhia, *Xiphorhynchus guttatum, Xiphorhynchus lachrymosum, *Lepidocolaptes souleyetii*

Ovenbirds: *Hyloctistes subulatus, Xenops minutus*

Antbirds: *Thamnistes anabatinus*

Cotingas: *Carpodectes nitidus, Attila spadiceus, Rhytipterna holerythra, Lipaugus unirufus, *Pachyramphus cinnamomeus, *Pachyramphus polychopterus, *Tityra semifasciata, *Erator inquisitor, Querula purpurata*

Flycatchers: **Colonia colonus, *Tyrannus melancholicus, *Megarhynchus pitangua, *Conopias parva, *Myiozetetes similis, *Myiozetetes granadensis, *Pitangus sulphuratus, Myiarchus crinitus, *Myiarchus tuberculifer, *Contopus virens, *Contopus sordidulus, *Contopus cinereus, Empidonax flaviventris, *Empidonax traillii, Terenotriccus erythrurus, Aphanotriccus capitalis, *Tolmomyias sulphurescens, *Tolmomyias assimilis, *Todirostrum nigriceps, *Todirostrum cinereum, Myiornis ecaudatus, *Capsiempis flaveola, *Elaenia flavogaster, *Tyranniscus vilissimus, Ornithion semiflavum, Mionectes olivaceus, Piprомorpha oleaginea*

Swallows: **Stelgidopteryx ruficollis*

Jays: **Psilorhinus morio*

Wrens: **Campylorhynchus zonatum, Thryothorus nigricapillus*

Catbirds: **Dumetella carolinensis*

Thrushes: **Turdus grayi, Turdus fumigatus*

Gnatcatchers: **Polioptila plumbea*

Shrike-vireos: **Smaragdolanius pulchellus*

Vireos: **Vireo flavifrons, *Vireo olivaceus, Hylophilus decurtatus*

Honeycreepers: **Chlorophanes spiza, *Cyanerpes caeruleus, *Dacnis cayana, *Dacnis venusta, *Coereba flaveola ,*

Warblers: **Mniotilta varia, *Vermivora chrysoptera, *Vermivora pinus, *Vermivora peregrina, *Dendroica coronata, *Dendroica pensylvanica, *Dendroica castanea, *Oporornis philadelphia, Icteria virens, *Geothlypis semiflava, Wilsonia citrina*

Icterids: *Zarhynchus wagleri, *Gymnostinops montezuma, Cacicus uropygialis, *Psomocolax oryzivorus, *Icterus prosthemelas, *Icterus mesomelas, *Icterus galbula*

Tanagers: **Tanagra minuta, *Tanagra luteicapilla, Tanagra gouldi, *Tangara larvata, *Tangara inornata, *Thraupis virens, *Thraupis palmarum, *Ramphocelus passerinii, *Phlogothraupis sanguinolenta, *Piranga rubra, *Tachyphonus rufus, Tachyphonus luctuosus*

Finches: **Saltator atriceps, *Saltator maximus, Caryothraustes poliogaster, Pitylus grossus, Cyanocompsa cyanoides, *Passerina cyanea, *Tiaris olivacea, *Sporophila corvina, *Oryzoborus funereus, *Volatinia jacarina, *Arremonops conirostris*

Obviously very many birds occur in the semi-open. The increase over forest is most noticeable among hawks, hummingbirds, puffbirds, woodpeckers, woodhewers, cotingas, flycatchers, honeycreepers, warblers, icterids, tanagers, and finches. Many other species, including most passage migrants, casual visitors, accidentals, aerial birds such as swifts, and the like, are to be seen most often or only here. There are no terrestrial species and few thicket inhabitants. Scarce or absent are motmots, ovenbirds, antbirds, and manakins. Typical forest species may appear so regularly in the tree plantations that as a matter of course they might mistakenly be called birds of the semi-open. Conversely, some birds which have been called forest species in the literature are, according to my experience, rare in the "La Selva" forest, or absent.

The vultures *Coragyps* and *Cathartes* are always present, either perched or in the air; *Sarcoramphus* (not listed above) occurs occasionally in the air. Among the raptorial birds, the hawks typical of the semi-open, i.e., those that do not enter forest, are only two: the migrant *Buteo platypterus*, which is common, and the native *Falco albigularis*, which is not common. Fairly common are the woodland-inhabiting *Leucopternis semiplumbea*, the lethargic, snake-eating *Herpetotheres*, and the peculiar, gregarious *Daptrius*. The remaining hawks are seen seldom and at highly irregular intervals, and are few in individuals. Of the owls, the little *Glaucidium* is met from time to time.

Among the hummingbirds, *Amazilia amabilis* and the rather similar *A. tzacatl* are common residents, especially at the Point; the larger *Florisuga* and the smaller *Klais* are common seasonally; the other species are uncommon or rare. (See Annotated List.)

Birds that are scansorial on trunks and limbs are, of course, the woodpeckers and

woodhewers. Easily the most abundant woodpecker is the medium-sized *Centurus*. The very large *Phloeoceastes*, a forest species, is to be seen often; the very similar *Dryocopus*, of thinned woodland and park-like areas, is only fairly common. The two species of *Celeus* are both forest birds: *loricatus*, which is much more common than *castaneus* in the forest, is also much more common in the semi-open. *Piculus*, a very uncommon forest species at "La Selva," occasionally enters the neighboring tree plantations. The small *Veniliornis*, which does not penetrate the forest, is uncommon, roaming about in thickety growth and sometimes in trees in the semi-open. Among the woodhewers, *Xiphorhynchus guttatum* and the smaller *Lepidocolaptes* are resident in the semi-open, the former being abundant in well-shaded parts of the tree plantations, the latter common in the more open parts. *Xiphorhynchus lachrymosum*, a forest species, is present daily in the well-shaded portions of the tree plantations. The large *Dendrocolaptes* seems to be equally well adapted to woodland and the tree plantations. The ovenbird-like *Dendrocincla* is quite uncommon in the semi-open, which it may enter occasionally close to the forest border. The little, wedge-billed *Glyphorynchus*, an abundant species in the forest, is occasional in the semi-open (where it may even nest). Here, too, might be included the wren *Campylorhynchus*, which climbs on mossy trunks and limbs, vines and lianas, high on tall trees close to the forest. The migrant warbler *Mniotilta* is an accomplished bark-creeper.

There are several frugivorous species. The largely arboreal chachalaca *Ortalis* occurs only outside the forest; the large guan *Penelope* is a forest species which passes through the semi-open rarely. The pigeon *Columba nigrirostris* is perhaps even more common in the semi-open than in the forest. *Columba cayennensis*, seen only once, is a species of partially wooded areas; it should become more frequent at "La Selva." The same should be true for the little ground dove *Columbigallina*, an open-country bird that enters clearings in formerly solidly wooded localities. The rather small *Claravis* is seen from time to time, usually low in bushy trees, or sometimes on the ground at the Point; typically it is an inhabitant of country of plantation type. All the parrots listed are (with one exception) common; *Pionus* and the two species of *Aratinga* are non-forest species, whereas the others are dependent on forest. The toucans, excluding the seasonal *Selenidera*, occur commonly in the semi-open as well as in the forest. *Selenidera*, when present, is not nearly so abundant as the others, but is met regularly. Of the euphonias, *Tanagra minuta* and *T. luteicapilla* are non-forest species that travel about in groups, usually high in the trees; *T. gouldi* is present almost everywhere, both in forest and the semi-open.

About a score of species sally in various ways. The large trogon *Trogon massena*, a woodland species, and the smaller *T. violaceus*, a non-forest species, pluck fruit or living prey during a hover. The jacamar *Galbula*, which hardly rises into the trees, makes typically flycatcher-like sallies for winged insects. The puffbirds consist of the forest-based *Monasa*, which is common and very noisy in the semi-open; the much smaller *Malacoptila*, which is relatively uncommon and retiring; the non-forest *Notharchus macrorhynchos*, which is sedentary and silent, and the much smaller, seldom-seen *N. tectus*, which travels about noisily in small parties that make sporadic incursions into the study area. All the puffbirds sally mostly for non-flying prey, both vertebrate and invertebrate. The cotinga *Querula* travels about in trios or small parties and plucks its food as does a trogon; *Cephalopterus* (not listed above) occasionally may enter the semi-open. The following flycatchers habitually sally for winged insects: the abundant *Colonia*, the rare *Tyrannus melancholicus*, the migrant *Contopus virens* and *C. sordidulus*, and the uncommon, native *C. cinereus*. *Myiozetetes granadensis* sallies often but by no means always. *Capsiempis*, occurring at the Point in places that approximate field habitat, keeps low in the undergrowth where it searches in shrubs and makes short sallies. The migrant *Empidonax traillii* may occur fairly high above the ground in arboreal situations or low on shrubs or fallen branches, where it either flits or fly-catches in short sallies. In this category might be included the small falcon *Falco albigularis*, which secures its prey during sweeping sallies; and the potoo *Nyctibius*,

which apparently sallies from branches at night.

Birds that flit instead of sallying, or at least do so more often, are cotingas and, especially, flycatchers; most of the species eat berries as well as animal prey. The cotinga *Attila* is flycatcher-billed, lethargic, usually keeps hidden in foliage, and often takes rather large-sized prey. The spirited *Lipaugus*, a bird of highly varied behavior, is a forest species that is common in the tree plantations. *Rhytipterna* is practically indistinguishable from *Lipaugus* in appearance (but not in voice), and is secretive, rather inactive, and occurs beside the woodland border rather than in the semi-open. The becards *Pachyramphus cinnamomeus* and *P. polychopterus*, birds of deliberate behavior, are, respectively, very common and uncommon at "La Selva." *Tityra* and *Erator* troop about in groups, generally high in the trees. Among the flycatchers, the large-sized *Megarhynchus* and *Pitangus*, closely resembling each other, are, respectively, common and uncommon. *Megarhynchus* may occur in forest in the canopy; *Pitangus* does not enter forest, and occurs mostly at the Point. The medium-sized *Conopias*, *Myiozetetes similis*, and *M. granadensis* are superficially very similar. *Conopias* and *M. similis* are almost identical in appearance (but sound very different), yet the former is common and generally keeps rather high in the trees, whereas the latter is uncommon and occurs mostly at the Point. *Myiozetetes granadensis*, unlike the congeneric *similis*, is very common, and fly-catches with much greater frequency; unlike *Conopias* and *M. similis*, it is partial to riversides and streamsides. The medium-sized, migrant *Myiarchus crinitus* and the smaller, native *M. tuberculifer* are congeneric species that differ in behavior (at "La Selva"): *crinitus* generally keeps concealed fairly high or very high in the trees (and is the only arboreal migrant occurring in good numbers inside the forest); *tuberculifer* does not enter forest, but is a typical species of cultivated or cut-over areas, where it seldom rises above medium heights from the ground. The energetic *Elaenia*, seen only once at the Point, will probably be seen there more often in the future. The remaining flycatchers are small in size. The following species do not properly belong in the semi-open: *Terenotriccus*, a forest species (which may nest in the semi-open); *Capsiempis* (whose short sallies might be called flits), a species of brushy or bushy field habitat, occurring only at the Point; *Pipromorpha*, a forest species that visits berry-bearing trees in the semi-open; *Mionectes*, which replaces *Pipromorpha* at higher elevations in the country, a short-term visitant from the subtropical belt; *Aphanotriccus*, primarily an inhabitant of second growth and sub-forest; the migrant *Empidonax flaviventris*, which occurs mostly in second growth and sub-forest rather than in the semi-open; and the diminutive *Myiornis*, in forest evidently a replacement for *Todirostrum*, regularly occurring low in the semi-open in shrubs and on fallen limbs. Flycatchers (among the flitting species) characteristic of the semi-open are: the very similar, congeneric flatbills *Tolmomyias sulphurescens* and *T. assimilis*, of which the latter is the more common, more active, and apparently better adapted to wet-forested regions, where it also enters forest in the canopy; the tody-billed, congeneric *Todirostrum nigriceps* and *T. cinereum*, neither of which enters forest, *nigriceps* being arboreal in the semi-open and abundant, while *cinereum* inhabits shrubbery and hedges, and is uncommon and largely restricted to the Point; the migrant *Empidonax traillii*, occurring almost exclusively in the semi-open, either in leafy branches of trees or low on shrubs, brush, or along borders; the little *Tyranniscus*, occurring typically on the crowns of small trees; and the tiny *Ornithion*, which ordinarily accompanies traveling mixed bands, occasionally making its appearance alone or in twos in low trees in the semi-open. Perhaps to be included in this category is the very common goatsucker *Nyctidromus*, which is active nocturnally at ground level in the semi-open, where it flits rather than sallies for winged insects.

A type of behavior not always clearly distinguishable from that of some of the birds mentioned above is warbler- or vireo-like, and it is exhibited by vireos, honeycreepers, and warblers. Except for *Hylophilus decurtatus*, all are characteristic birds of the semi-open. The genus *Vireo* is represented only by migrants. Only *flavifrons* is a winter resident; *olivaceus* is common as a transient but rare or accidental in winter. *Hylophilus decurtatus*, a forest vireo that travels about in pure groups,

is nervously active, as are many warblers, and is to be seen almost daily in the semi-open. The shrike-vireo *Smaragdolanius*, which occurs high in the forest, is much more common in the tree plantations. Acting in the manner of a slow-paced vireo, it does more creeping and less clinging. The warblers are all migrants (except *Geothlypis semiflava*); only *Dendroica pensylvanica* is at all times common. Among the honeycreepers, *Cyanerpes* and *Dacnis cayana* may be as active as the arboreal warblers, but combine a taste for insect food with one for nectar. Unlike warblers, they sit quietly for long periods on exposed perches, usually very high above the ground. *Dacnis venusta* shows up at irregular intervals, when it appears in waves; it forages actively, often high in the trees. *Chlorophanes* is resident, rather less active, but at times it may also troop about in groups, and it may be met inside the forest. *Coereba* is more typically a "honeycreeper." It is most abundant at blossoming hedges, shrubbery, and small trees, where it creeps, clings, and probes flowers. The gnatcatcher *Polioptila* also belongs in this general category. Nervously active, it flits, hovers, and makes short sallies, but lacks the swift flight of warblers and honeycreepers.

At this point, the matter of distribution in the semi-open can perhaps be approached better by our following another tack. Below are listed the species that occur in undergrowth, that is, birds that ordinarily seldom or never rise well up into the trees in the semi-open. Several of the species have already been discussed.

Doves: *Columbigallina talpacoti, Claravis pretiosa*
Cuckoos: *Crotophaga sulcirostris*
Goatsuckers: *Nyctidromus albicollis*
Hummingbirds: *Phaeochroa cuvierii,* [*Florisuga mellivora*], *Klais guimeti, Hylocharis eliciae,* [*Amazilia amabilis*], *Amazilia tzacatl, Microchera albo-coronata*
Flycatchers: *Empidonax traillii, Todirostrum cinereum, Myiornis ecaudatus, Capsiempis flaveola*
Wrens: *Thryothorus nigricapillus*
Catbirds: *Dumetella carolinensis*
Honeycreepers: *Coereba flaveola*
Warblers: *Vermivora peregrina, Dendroica coronata, Dendroica pensylvanica, Oporornis philadelphia, Geothlypis semiflava, Icteria virens, Wilsonia citrina*
Tanagers: *Ramphocelus passerinii, Phlogothraupis sanguinolenta, Tachyphonus rufus*
Finches: *Passerina cyanea, Tiaris olivacea, Sporophila corvina, Oryzoborus funereus, Volatinia jacarina, Arremonops conirostris*

Few of the species listed above are common. The little ground dove *Columbigallina* has been seen only once; *Claravis*, although noted with fair regularity, is generally seen as it dashes low through the semi-open to disappear from sight into the protection of thickets. The ani *Crotophaga* is as yet accidental or erratic, only single individuals having been seen occasionally. The goatsucker *Nyctidromus* comes into the semi-open at dusk, usually on or beside cleared patches of ground. The majority of the hummingbirds occurs mostly or only at the Point. The flycatchers have already been commented upon. The wren *Thryothorus nigricapillus* barely enters into the edge of the semi-open. The migrant catbird *Dumetella* is included here, only because it may occur in low growth that is open to the sky. The honeycreeper *Coereba*, numerous in flowering, low vegetation at the Point, is far less common either higher in the trees or elsewhere in the tree plantations. The migrant *Dendroica pensylvanica* is one of the few warblers characterizing this stratum; the native *Geothlypis*, an inhabitant of shrubbery in cultivated areas, is very uncommon at "La Selva." (See the Annotated List for the other warblers.) Among the tanagers, *Ramphocelus* and *Phlogothraupis* have already been mentioned above; *Tachyphonus rufus* is barely represented, only at the Point. Of the seed-eating finches, *Sporophila* is the only common species, occurring almost anywhere in the semi-open but especially at the Point; *Tiaris*, *Oryzoborus*, and *Volatinia* are seldom-seen visitants that occur mostly at the Point. *Arremonops* inhabits shrubbery and patches of second growth; it is fairly common at the Point, uncommon or rare elsewhere on the study area.

If we continue with this approach, the birds, all arboreal, still not accounted for are:

Cuckoos: *Piaya cayana*
Ovenbirds: *Hyloctistes subulatus*
Antbirds: *Thamnistes anabatinus*
Cotingas: *Carpodectes nitidus*
Swallows: *Stelgidopteryx ruficollis*
Jays: *Psilorhinus morio*
Thrushes: *Turdus grayi, Turdus fumigatus*
Icterids: *Zarhynchus wagleri, Gymnostinops monte-*

zuma, Cacicus uropygialis, Psomocolax oryzivorus, Icterus prosthemelas, Icterus mesomelas, Icterus galbula

Tanagers: *Tangara larvata, Tangara inornata, Thraupis virens, Thraupis palmarum, Piranga rubra, Tachyphonus luctuosus*

Finches: *Saltator atriceps, Saltator maximus, Caryothraustes poliogaster, Pitylus grossus, Cyanocompsa cyanoides*

Icterids, tanagers, and finches predominate. Many are among the most characteristic birds of the semi-open. The behavior of the majority is quite varied and hard to generalize.

The cuckoo *Piaya* is very common; it creeps and runs along branches and searches in the foliage. The ovenbird *Hyloctistes* sometimes leaves the forest for the semi-open, where it remains quietly in a tree; *Xenops* appears occasionally, and clings, flits, and searches actively. The antshrike *Thamnistes*, with behavior much like that of a large antwren, enters the semi-open from time to time, usually when accompanying a band of *Caryothraustes*. The cotinga *Carpodectes* appears erratically; usually it sits quietly on a high branch, slowly turning its head, and is apt to fly off suddenly in an unexpected direction, or forages in active spurts. The swallow *Stelgidopteryx* is an aerial feeder; it is not common, its numbers fluctuate, and it is to be met regularly only in the vicinity of the Point. The jay *Psilorhinus* appears once in a while at the Point, where it has yet to become established. The robin *Turdus grayi*, elsewhere a common and well-known semi-arboreal species of open and semi-open country, is present on the study area in small numbers and is regular only at the Point; the arboreal *T. fumigatus* is a seasonal, woodland species that may visit fruiting trees in the semi-open, usually close to the forest. The gregarious icterids *Zarhynchus* and, especially, *Gymnostinops* and *Cacicus* are always to be seen in the tree plantations, as are, for example, the toucans. Often roaming about in pure groups or bands, hopping along limbs, climbing, probing, and searching, they also act quite at home in the forest. The cowbird *Psomocolax* apparently visits "La Selva" in order to parasitize nests of the oropendolas and *Cacicus;* I have not seen it on the ground. The native orioles *Icterus prosthemelas* and *I. mesomelas* do not enter the forest; *prosthemelas* roams about, usually in twos, anywhere in the semi-open, whereas *mesomelas* occurs mostly at the Point in the neighborhood of canebrakes and banana plots. The migrant *I. galbula* is common during most of its stay, often flies high and rapidly, unlike the native species of the genus, and in general seems to be better adapted to and occurs in more diverse environmental situations, including the canopy of the forest near the periphery. The callistes *Tangara larvata* and *T. inornata* behave in the same way, roving about in small groups, feeding omnivorously, searching limbs for insect prey, and so on: *larvata* is wide ranging and abundant, while *inornata* is very local and seems to consist of a small colony of few individuals at "La Selva." *Thraupis virens* and *T. palmarum* are much alike in behavior, feeding omnivorously, roaming about, searching bare limbs meticulously: *virens* is fairly common or regular only at the Point, whereas *palmarum* is much commoner, occurring beside the forest as well as in more open situations. The migrant *Piranga rubra* is common throughout the semi-open, solitary, and exhibits very varied behavior. *Tachyphonus luctuosus*, a bird of open woodland, may occur along edges of the tree plantations beside forest or in stands of advanced second growth, where, often in small parties, it behaves in a varied, active, almost warbler-like manner, but it may also rest quietly for a while. The two species of *Saltator*, each an indicator of semi-open country, are very much alike in appearance and actions and often occur in small groups: *maximus* is common where there are many trees in the semi-open, whereas (at "La Selva") the larger *atriceps* is much less abundant and rather restricted to more open country and less advanced second growth. Of the grosbeaks, *Caryothraustes* regularly troops through the tree plantations; the non-gregarious *Pitylus* may leave the forest for the semi-open in order to feed on nuts and fruits; and *Cyanocompsa*, which inhabits woodland and second growth, from time to time enters the semi-open, where it may nest.

WATERCOURSES

Cormorants: **Phalacrocorax olivaceus*
Anhingas: [*Anhinga anhinga*]
Herons: **Ardea herodias*, **Butorides virescens*, **Florida caerulea*, [*Casmerodius albus*], [*Leucophoyx thula*], **Agamia agami*, **Tigrisoma lineatum*
Boat-billed herons: **Cochlearius cochlearius*
Storks: [*Mycteria americana*]
Ibises: *Mesembrinibis cayennensis*
Ducks: [*Cairina moschata*], [*Anas discors*]
Ospreys: **Pandion haliaetus*
Limpkins: [*Aramus guarauna*]
Rails: *Aramides cajanea*
Finfoots: **Heliornis fulica*
Sun bitterns: **Eurypyga helias*
Sandpipers: **Actitis macularia*
Kingfishers: **Megaceryle torquata*, **Chloroceryle amazona*, **Chloroceryle americana*, **Chloroceryle inda*, **Chloroceryle aenea*
Swallows: **Iridoprocne albilinea*
Wrens: *Thryothorus nigricapillus*
Warblers: [*Protonotaria citrea*], **Seiurus noveboracensis*, **Seiurus motacilla*, **Phaeothlypis fulvicauda*

The species in brackets do not properly belong at "La Selva." Anhingas, storks, ducks, and limpkins are transient or accidental. Under special circumstances, such as flooding, the herons *Casmerodius* and *Leucophoyx*, and possibly other species not yet recorded, might appear as temporary visitants. Entirely absent are grebes, gallinules, coots, jaçanas, shore birds (except *Actitis*), river flycatchers, and dippers, all of which occur elsewhere in the country.

The only aquatic species are the cormorant *Phalacrocorax* and the finfoot *Heliornis*: both obtain their prey by swimming, *Phalacrocoras* under water in the river, *Heliornis* on the surface of the river and streams. Species that dive into the water from the air are the kingfishers and the osprey (a migrant). The kingfishers segregate ecologically into habitat groups in which the species are graded by size (see Annotated List).

The wading birds (in the absence of storks and long-legged shore birds) are the herons: *Agamia* and *Tigrisoma* occur in the forest at streams and marshy openings, and *Cochlearius* has a fixed abode at a stagnant stream a little way inside forest. The sun bittern *Eurypyga* patrols riversides and streamsides at "La Selva," where it may also occur at the interior swamps; it may wade occasionally. Much more common than the preceding species, all of which are rare or seldom seen, are *Ardea*, *Butorides*, and *Florida*. They differ in size, coloration, proportions, and habitats, but none enters the forest.

The migrant sandpiper *Actitis*, the migrant warblers *Seiurus noveboracensis* and *S. motacilla*, and the native *Phaeothlypis* occur commonly along watercourses outside the forest. All teeter their hindquarters or jet their tails or do both. *Seiurus motacilla* occasionally, and *Phaeothlypis* commonly, occur in suitable habitat inside the forest.

Other species associated with wet places are the mud-probing ibis *Mesembrinibis*, which frequents muddy stream banks, marshes, and swamps in woodland; the rail *Aramides*, which skulks in dense vegetation (and seldom wades); and the wren *Thryothorus nigricapillus*, which seldom occurs away from overgrown banks or their immediate vicinity. The flycatcher *Myiozetetes granadensis* (not listed above) shows only a tendency to congregate at streamsides or riversides and to frequent small islands in the river. The swallow *Iridoprocne*, a true river inhabitant, hunts in the air and is referred to the next category.

AERIAL

Here are included those birds that spend much time in the air, often covering great distances, and obtain their prey directly from the air. It is difficult to limit the category. Swifts spend the entire day on the wing and may occur almost anywhere. Swallows hunt and feed on the wing but perch frequently and do not occur everywhere. Certain hawks, too, secure aerial prey and may feed during flight. Sallying flycatchers are not very different. However, they obtain only a single item at each sally and perch between sallies; even a lengthy sally is but a prolonged flit. Frugivorous birds, as the parrots and macaws, fly

about in order to locate a fruiting tree. In a similar manner, the soaring vultures locate their food chiefly from the air. Hummingbirds feed almost entirely on the wing, but they cover short distances and perch frequently. Perhaps arbitrarily I limit the category to two hawks, the swifts, and the resident swallows:

Hawks: *Elanoïdes forficatus, Ictinia plumbea*
Swifts: **Streptoprocne zonaris*, **Chaetura cinereiventris*, **Cypseloides* sp., **Panyptila cayennensis*
Swallows: *Progne chalybea, Stelgidopteryx ruficollis, Iridoprocne albilinea*

The swifts are the only truly aerial birds. The very large *Streptoprocne* and the small *Chaetura* occur daily in flocks, and apparently cover great distances. The medium-sized *Cypseloides* is very uncommon. The small *Panyptila* occurs alone or in twos and is almost surely a resident at "La Selva" or in the neighborhood.

Of the swallows, *Stelgidopteryx*, as a species, is resident at "La Selva," where it hunts only in the more open portions of the semi-open, and it may sweep over the river, usually well above the surface. *Iridoprocne* is strictly a river swallow which hunts close to the surface of the water. *Progne* is seen seldom, mostly at the Point, where it generally keeps higher in the air than *Stelgidopteryx*.

The hawks are the two kites listed above. Except during migration they are rare at "La Selva," where I have never seen them perched. They occur over forest as well as over the semi-open. The falcon *Falco albigularis* (not listed) also secures winged prey in the air, it may feed on the wing, and it may even soar, yet in a sense it is tied to a perch and it does not stay aloft for very long periods. The sorties are rather like those of the long-sallying flycatcher *Nuttallornis*, but are far more spectacular.

DISCUSSION AND CONCLUSIONS

IN THIS PAPER I have been speaking of tropical "rain"-forest birds in a locality in southern Central America. The composition of the avifauna at "La Selva" has raised to conviction my belief that the suboscines are both a successful group and one that thrives in the neotropics, especially in the humid-forested lowlands. This belief has been controverted in the literature. The term "neotropical" has even been dispensed with by certain eminent authors. Moreover, the tropics are regarded by many as a peripheral area of survival for forms driven by competition from the north-temperate region. Prevalent is the notion that temperate-region birds are more vigorous and adaptable than birds belonging to tropical groups; openly expressed has been a presumption of suboscine inferiority in particular.

Regarding the tropics in general, Wallace (1891, pp. 309–310) wrote: "Animal life is, on the whole, far more abundant and more varied within the tropics than in any other part of the globe, and a great number of peculiar groups are found there which never extend into temperate regions. . . . The equatorial regions are then, as regards their past and present life-history, a more ancient world than that represented by the temperate zones, a world in which the laws which have governed the progressive development of life have operated with comparatively little check for countless ages." On the other hand, it is the opinion of Mayr (1946, p. 37) that the tropics today are a "refuge" for species having a preference for an equable humid climate. But Griscom (1945, p. 114) said: "Climatically, 85 per cent of the species and subspecies of birds in the world occur only in tropical regions, leaving only 15 per cent in temperate or cold climes. Moreover, two-thirds of all the birds in the tropics live in humid climates rather than in the arid ones." Mayr (*ibid.*, p. 26) suggested that perhaps "a temperate zone family can more easily become adapted to the tropics than a tropical family to a temperate climate." Darlington (1957, p. 562), however, regarded the tropics as "being the great reservoir and apparent main dispersal center of vertebrates," and disagreed (p. 556) with that portion of the Matthew hypothesis that postulated the north-temperate region, because of its variable climate, as the principal center of evolution and dispersal of land and fresh-water vertebrates. A continental land mass located in the tropics should provide the greatest number of evolutionary opportunities, and this thesis Darlington has propounded for the Old World tropics.

Of more immediate concern is the neotropics. Certain authors deducing ancestral homes for modern faunas call "neotropical" misleading. Darlington (1957, p. 446) reaffirmed the classical conception of Sclater and Wallace: "The Neotropical Region . . . is South and Central America and the tropical lowlands of Mexico with Trinidad and, if one wishes, the West Indies proper." In the Neotropical Region, added Darlington (p. 449), "Wallace distinguished 'Brazilian' (main South American), 'Mexican' (Central American), and 'Chilean' (south-temperate) subregions." Details regarding the subregional avifaunas were furnished long ago by Newton (1896, pp. 321–328). By contrast, Griscom (1950, p. 377) defined the region as equatorial South America, extending north to southern Mexico in the rain-forested lowlands, and Andean South America, consisting of the subtropical and temperate zones (as expounded by Chapman) from Costa Rica to Bolivia, but excluding warm North America (the equivalent of the Sonoran subregion) and temperate or austral South America (including the Paramo zone of the Andes). This is very complicated, because he is really listing subregions.

Mayr (1946), following Dunn and Simpson who avoided the use of "neotropical," also eschewed "this error" (p. 11) as he analyzed the American bird fauna by origins. He based his paper on the self-styled speculations by Lönnberg, who believed that "present Middle America and Mexico were integrating parts of North America" before the formation of the isthmus of Panama (1927, p. 5). Hence, Mayr lumped Central America with North America. This seems curious in view of his statement (1946, p. 5) that "instead of thinking of fixed regions, it is necessary to think of fluid faunas." Mayr conceded that the only major

faunal break in the warmer parts of North America occurs along the northern edge of the tropical rain-forest belt in southern Mexico (p. 32). This is the border set by Wallace, in 1876, between his Neotropical and Nearctic regions. Mayr, however, preferred to call the region north of the tropical forest the North American region, and was silent on what to call the region to the south. Mayr, therefore, seemed to accept tacitly Wallace's Neotropical Region, at least in regard to present-day distributions. He did not suggest how to apply his zoogeography of origins to the distribution of modern birds, probably because he considered this approach a wrong method employed for "the older, static, regional zoogeography" (p. 5). But he did use modern distributions to determine sites of origin.

Mayr listed (p. 27), among other families, the Momotidae as a member of his North American element. Here he followed Lönnberg who followed Chapman (1923). Nevertheless, Darlington (1957, p. 280) disputed the supposedly North American origin of the family: "In discussing Tertiary zoogeography a clear distinction should be made between North America proper and Central America, which may have been an island or archipelago during the Tertiary . . . and which may have had a separate fauna. Ornithologists discussing 'tropical North America' have sometimes not made this distinction. For example, motmots have been called tropical North American birds, but they are really Central American." Both Mayr and Darlington presented clearly drawn maps that depicted a Tertiary water gap across the Isthmus of Tehuantepec. Both authors utilized the gap to emphasize the isolation of Central America from southern North America during part of the Tertiary. Mayr (1946, p. 9) went so far as to say that the oceanic gaps shown on his map (p. 8) not only seemed to be well-established rather than controversial facts but must also have been of considerable width, perhaps even wider than shown. A Cenozoic seaway crossing the Isthmus of Tehuantepec is, however, a myth (see Durham and his co-authors, 1955), which Mayr has helped to disseminate (Durham and co-authors, 1952). It would appear, therefore, that a physiographic barrier must be sought much closer to South America, and a South American origin for the Momotidae now becomes the more likely choice. In any event, the Momotidae emerge again as an American family of neotropical birds occurring at present and undoubtedly in the past in tropical latitudes.

The historical analysts, on the one hand, redivide the Neotropical Region into the well-known subregions, while on the other hand they unite fluid paleofaunas with modern climates and geography. Families the purported origins of which were extra-tropical (as judged by present climate and geography) they apparently regard as extra-tropical today, even though the birds now occur exclusively or preponderantly in the tropics. If the majority of the present-day species of a family breeds in north-temperate latitudes, even though these are abandoned for the tropics during the rest of the year, the fact is apparently interpreted to signify the place of origin of the family. The following remarks by Darlington (1957, p. 22) are pertinent: "Recently there have been two not entirely justified tendencies among zoogeographers. One is to make zoogeography a subdivision of ecology. To bring ecology into zoogeography is a very good thing, but zoogeography is not ecology. The other tendency is to glorify historical zoogeography—the past evolutions and movements of animals—and almost to despise the study of present 'static' distributions. This seems to me to be a great mistake. It is true that present distributions cannot be understood without reference to the past, but it is equally true that the past cannot be understood without reference to the present. It is present patterns which show how animal distributions really are related to climates and barriers, etc. Unless we know this, how can we understand what past distributions tell us of past climates and barriers? It seems to me that, in zoogeography, the present and past are equally important and dependent on each other."

For the motmots, discussed above, there are no fossils to support the perhaps semantic North American claims. Cracids, or procracids, however, have been found as fossils in the United States as far back as the Eocene. Because of this tangible evidence the family was said to be probably of North American origin by Mayr (1946, pp. 7, 27) and by Tordoff and Macdonald (1957, p. 179).

Darlington (1957, p. 281), presenting an opposing view, said: "The present distribution of genera makes it almost certain that cracids were in South America long before the late Pliocene connection with Central and North America. The distribution of cracids seems to reflect multiple dispersal and differentiation during a long period in the Americas as a whole (excepting the West Indies), not radiation from southern North America." In fact, Darlington (p. 283), evaluating conjectures as to the presumed southern North American origin of a number of kinds of birds, found them good for only one group of family rank, the turkeys, and perhaps for a few of less than family rank, as the American quails.

Let us take the Cracidae as a case in point. Tordoff and Macdonald (1957, p. 179) said that the family "seems to have originated in North America and undergone a substantial adaptive radiation there before its retreat southward, which may have been hastened or brought about by competition with contemporaneous species of the Tetraonidae and, perhaps, Odontophorinae." From what is known of the cracids in life today, I must agree that they have withdrawn southward. Competition may have been a contributory or concomitant factor, not the cause. Today the cracids are neotropical in distribution, occurring in the lowlands and in the mountains, although one form reaches the Rio Grande Valley in Texas (but belongs to a species ranging to Costa Rica), and they consist of arboreal and semi-arboreal kinds. The middle Eocene *Gallinuloides* occurred in Wyoming, which at that time was presumably subtropical; in eastern Oregon, at any rate, remains have been unearthed of an Eocene "lush, subtropical forest" composed of "forms typical of a forest dominated by large, smooth-margined dicot leaves whose nearest living equivalents are found in the lowlands of Central America" [which are tropical] (Dorf, 1959, p. 186). The lower Oligocene cracid-like *Procrax* was discovered in South Dakota, where the climate was then subtropical (p. 187). Other Tertiary cracids lived under subtropical (possibly tropical) conditions which may have been transitional in an instance or two to warm temperate. Apparently, neotropical floras and neotropical cracids occurred together in the United States just as they do in the Neotropical Region today. Because Tordoff and Macdonald assume a North American origin for the cracids, are we to assume, too, that the flora with which they were associated also had a North American origin? The point has already been made by Chapin (1932, p. 209): "It seems certain that the equatorial forest of Africa has been in the past one of the most stable environments. . . . If there were periods, such as the Miocene is assumed to have been, of more uniform mild climate over the earth's crust, then it is likely that the width of the forest girdle was greatly enlarged. . . . And even though the climate of Africa is, as some claim, now growing progressively drier . . . it will apparently only result in a diminution of the size of the equatorial forest, without any further effect upon the forest fauna than a limitation in its numbers, or the isolation of certain parts in disconnected portions of forest."

The fundamental cause of the withdrawal of the Cracidae into Central and South America seems to have been the withdrawal of the habitat. Just as there are no cracids in temperate North America today, so are there none in austral South America for the same climato-vegetational reasons. The limpkins present an analogous situation, but are supposed to be harder to analyze because there is only one living species. Knowing something of the habits and habitat of the limpkin, however, one finds that the discontinuous distribution correlates with the geographical discontinuity of the habitat. If we look in the right places we find the bird widespread, abundant, and apparently successful, rather than a relict clinging to an outmoded way of life. Today it is neotropical. Fossil genera of limpkins probably lived in a habitat similar to that of today but covering a relatively enormous area in Tertiary times in the United States, where the right climate and habitat have mostly disappeared.

The above digression serves to direct attention to the neotropics as a distinct zoogeographic region at present and in the past, and to the evolution in the New World of the great majority of American birds, especially pronounced in the Neotropical Region. But, forgetting the Neotropical Region as a zoo-

geographic division, and extrapolating the neotropics as an ecological concept backward in time or forward in our imaginations, we will be dealing with fluid faunas, as recommended by Mayr; yet at any of our projected temporal stopping places we will have in our mind's eye the picture of a fixed region. Casting back to one of the warmer Tertiary epochs, with the aid of fossil plant assemblages as indicators, we can visualize an altitudinal and poleward movement as having taken place by the belts and regions, upward and outward from the tropics. The tropical region is centric, whereas the other regions form a succession of hemispherically paired latitudinal bands. As the tropics have expanded, so have the bands pressed successively poleward as well as up the mountainsides. The Neotropical Region has taken on a new dimension, with altered climatic boundaries, and is characterized by the floras and faunas that have been carried along. Geographically and historically, therefore, much of North America would have become part of the Neotropical Region, and the animals and plants would be tropical American. Conversely, during the Pleistocene epoch at maximum refrigeration, the neotropics would have been withdrawn equatorward, but with a complication in a mountainous isthmus such as Central America, where a lowering of the altitudinal belts may have displaced much of the tropical belt. Under these circumstances the Neotropical Region would have become more or less equivalent to geographical South America. During an interglacial period, such as we experience now, tropical conditions have been returning to Central America, and neotropical faunas and floras have returned in fair abundance. In short, the dependent faunas and the supporting vegetation, which in turn is determined by climate, are fluid over a period of time, yet fixed at any point in the time sequence.

Among the non-passerines the present neotropical elements which have entered probably from the north are the families Phasianidae (the strictly American Odontophorinae, with distinctive neotropical genera), the Meleagrididae (southern North American and northern Central American), the Alcedinidae (represented mostly by the neotropical genus *Chloroceryle*). Hawks, owls, most water birds, rails, pigeons, cuckoos, parrots, goatsuckers, swifts, trogons, barbets, and woodpeckers have a world-wide or pantropical distribution.

The American character of the neotropical avifauna is best marked in the passerines. Families thought to be of Old World origin are, for the most part, poorly represented. They include the Alaudidae, Sylviidae, Regulidae, Motacillidae, Certhiidae, Paridae, Cinclidae (probably Old World or North American, possibly South American), and the subfamily Carduelinae. Several of the species occur only in the mountains of northern Central America, just as certain Canadian species occur in the Appalachians in eastern United States. Well represented are the jays (Corvidae), thrushes (Turdidae), and the genus *Spinus* (Carduelinae). Including all the odds and ends, the total number of species amounts to perhaps 5 per cent of the neotropical passerines. Considering the motility of birds, the relative narrowness of the transisthmian seaways and their varying times of closure, the lowering of temperatures during the second half of the Cenozoic, and the completed connection between North America and South America dating from the late Pliocene, one is struck by the nearly total exclusion of Old World and North American passerines from the neotropics. The only fairly recent invaders, that is, the ones that, for all we know to the contrary, are the only forms to have survived, are a localized subspecies of horned lark, and the successful genera *Anthus*, with several species, and *Turdus* and *Spinus*, with many species. *Zonotrichia* (*Brachyspiza*) *capensis*, a sparrow belonging or closely related to the North American genus *Zonotrichia*, is, however, an example of a single species that has spread over most of the Neotropical Region. Despite its northern affinities (which are those of New World nine-primaried stock), it is today an endemic species of the neotropics, or perhaps an endemic genus.

Whether wrens, mimids, warblers, vireos, and emberizine finches had a tropical North American, Middle American, or South American primary or secondary center of evolution, their status as neotropical groups remains unchanged. The gnatcatchers (*Polioptila*) and

the gnatwrens (*Microbates* and *Ramphocaenus*), irrespective of their taxonomic relationships, are today and have been for a long time completely American and characteristically neotropical. The swallows (Hirundinidae) occur the world over. It is not known when any of the above birds evolved, but whether in the Cretaceous or in the first half of the Tertiary, available evidence indicates a continuity of geographically widespread tropical conditions.

The neotropical passerines consist of suboscines (Suborder Tyranni), including, among the better represented families, the woodhewers, ovenbirds, antbirds, manakins, cotingas, and tyrant flycatchers; and oscines, or true song birds (Suborder Passeres [= Oscines]), including primarily the great New World nine-primaried assemblage (vireos, honeycreepers, warblers, icterids, tanagers, richmondenine and emberizine finches), and also such commonly represented families as the wrens, mimids, thrushes, jays, and swallows. All these groups, incidentally, have been recorded at "La Selva."

The case against the suboscines was stated by Mayr and Amadon (1951, pp. 12–13): "The various suboscine perching birds give every appearance of being in the process of replacement by the Oscines. Many of the families of the former group have a relict distribution in Madagascar, New Zealand, Australia, or South America. The last continent was of course isolated for a long time. It has few well-differentiated families of indigenous song birds, although the subfamilies of the tanager-pyrrhuloxine finch assemblage are richly developed. An adaptive radiation of the wrens, mimids, and other song birds of South America might reduce the Suboscines of that continent to the subordinate position they occupy in the Old World." It appears that what may have been a decline, an ecological replacement, or an arrested development of the suboscines in the Old World is taken as indicative of a corresponding inability of suboscines to withstand an oscine invasion in the New World. Just why this should have happened in the Old World has somehow been associated with the lower standing of the suboscines in a linear classification. It is as though they were encumbered with an inherent incapacity linked genetically to certain morphological characters: "The Oscines, or songbirds, are regarded as more highly evolved than the sub-oscines in all recent classifications. This is based largely on the greater refinements in the muscles of the syrinx. . . . Such a criterion is not, of course, infallible. The Oscines, although more advanced as regards this character, might be more primitive than the sub-oscines in several others and hence, on the whole, less highly evolved. As a matter of fact, the presence of an aftershaft in many Oscines and its absence, for the most part, in the other group do provide a character in which the sub-oscines seem to represent a later step in evolution. On the whole, however, morphological characters support the general consensus that the Oscines represent the apex of avian evolution. Zoogeographical considerations also lead to the same conclusion" (Amadon, 1957, p. 260). Amadon added (p. 266): "The appearance of the Oscines apparently led to the displacement of the sub-oscines in many areas, even though we can scarcely believe the refinements in the syrinx to have been the critical factor." Darlington (1957, p. 276) calls the process of replacement gradual and complex and points out that it still has not forced a general retreat in South America.

Because of zoogeographical considerations, by imputation an Old World effeteness is ascribed to 1100 species of suboscines in the New World. Without actually saying so, the above quotations seem to draw a parallel between the replacement of suboscines by oscines and that of marsupials by placentals. South America is thus considered a zoogeographical outpost providing a temporary refuge for remnants and a haven for relicts. But if the suboscines are primitive passerines with a former world-wide distribution, it seems odd that they should have been so thoroughly replaced in Australia, which placental mammals have had difficulty in reaching, but so successful in South America, into which the placentals have swarmed. If the comparison in South America be limited to placentals versus placentals, the later ones, earthbound as they are, seem to have immigrated often with a great measure of success.

According to Amadon (1957, p. 267), correlated with the evolution of primitive and more advanced oscines was a decline in the

TABLE 1

PER CENT OF PASSERINES AND SUBOSCINES IN THE NEOTROPICAL AVIFAUNA

Locality	Total Avifauna		Passerines	
	Total Birds	Resident Birds	Total Passerines	Resident Passerines
	Per Cent Passerines	Per Cent Passerines	Per Cent Suboscines	Per Cent Suboscines
Mexico (Friedmann *et al.*, 1950; Miller *et al.*, 1957)	51	53	21	22
Guatemala (Eisenmann, 1955)	51	51	30	35
Honduras (Eisenmann, 1955)	51	50	35	40
Nicaragua (Eisenmann, 1955)	51	50	37	42
Southeast Nicaragua, "El Recreo" (Howell, 1957)	61	61	47	47
Costa Rica (Slud, MS)	52	53	41	46
Finca "La Selva"	59	54	46	55
Panama (Eisenmann, 1955)	53	55	45	49
Barro Colorado I. (Eisenmann, 1952, and *in litt.*)	53	49	47	56
Colombia (de Schauensee, 1948–1952)	55	56	53	55
Venezuela (Phelps and Phelps, 1950, 1958)	55	56	54	56
Rancho Grande (Schäfer and Phelps, 1954)	53	53	45	49
British Guiana (Chubb, 1916–1921)	51	52	55	57
Bartica District (Beebe *et al.*, 1917; Beebe, 1925; Davis, 1953)	51	51	59	61
Surinam (Haverschmidt, 1955)	48	50	58	60
Brazil (Pinto, 1938, 1944)	55	57	64	65
Northeast Brazil (Hellmayr, 1929)	53	55	63	63
Amazon region (Snethlage, 1914)	53	54	65	67
Mato Grosso (Naumburg, 1930)	54	55	55	57
Western Brazil (Gyldenstolpe, 1945, 1951)	58	58	70	70
Ecuador (Chapman, 1926)	56	58	55	56
Bolivia (Bond and de Schauensee, 1942, 1943)	60	61	57	57
Paraguay (Laubmann, 1939–1940)	52	53	56	57
Argentina (Sociedad Ornitológica del Plata, 1935–1942)	50	52	57	58
Chile (Goodall *et al.*, 1946–1951)	36	42	55	56

status of the suboscines, "except in South America where comparatively few of the competing Oscines are present, even to this day." Here I think the key word is "competing," because the number of oscines in the neotropics is actually high.

I invite the reader's attention to table 1. In the last column is listed by country the percentage of suboscine species, which, subtracted from 100, gives the percentage of resident oscines in the resident passerine avifauna. In order to obtain the data in table 1, I consulted the regional works given in the same table. It will be seen that in South America the ratio of suboscines to oscines is remarkably uniform, approximately 57:43 (with the exception of Brazil and Surinam discussed below), all the way from northern South America to southern South America. It is noteworthy that Chile, an austral country of which the total avifauna (mainland and coastal) is a fraction of that of Colombia or Venezuela or Ecuador, and in which the proportion of passerines is greatly reduced, nevertheless maintains the same ratio between suboscines and oscines. On the other hand, it will be noticed that in Central America the proportion of suboscines becomes pro-

gressively smaller from Panama to Mexico, while the oscines decrease progressively in the opposite direction. Somewhere between central Panama and the Colombian frontier the ratio equalizes at 1:1. (If the proportions are plotted as a percentage of the resident avifauna, which in turn has been treated as a percentage of the total avifauna, the resident suboscines and oscines cross one another in Costa Rica.) In all of South America the suboscines are dominant, and the ratio between them and the oscines remains constant. To me this suggests that a balance has been struck between suboscines and oscines, that the two groups exist, in a manner of speaking, side by side, and that the reason is to be sought in their complementary ways of life instead of in a struggle between taxonomic group and taxonomic group. Moreover, the number of oscines is very large and consists mostly of the vast nine-primaried array.

Were Old World oscines to be presented with the hypothetical opportunity to enter the New World in force, presumably by a northern route in an age of warmer world temperatures, they would have to contend first with the resident North American oscines, which themselves hardly seem to have been able to colonize the neotropics. Then, having surmounted or filtered through this biotic barrier, they would face the swarm of neotropical nine-primaried oscines and the suboscines. In order to overcome the American oscines, the invaders must be credited with potentialities already so keen as to cut at once a displacing swath. Should the neotropical oscines remain adamant, the suboscines, so goes the assumption, should prove less refractory. As the neotropical oscines do not seem to be replacing the suboscines or exhibiting a divinable prophetic trend in this direction, to expect Old World oscines to perform the feat seems a doubly groundless speculation.

It is immaterial whether ancestral American suboscines originated in the tropics of the New World or the Old World. The main evolution and radiation have taken place in the neotropics, possibly since the early Tertiary or perhaps the Cretaceous. Their center of abundance is located today, as it undoubtedly was in the past, in equatorial South America. That they are commonest in the humid portions of the tropical belt, table 1 confirms as a fact. No matter what proportion of the avifauna the passerines comprise, the suboscines make up the majority of the passerine species. An exception to the uniform ratio, mentioned above, which proves the rule is in Brazil, where the suboscines dominate in a 65:35 ratio. But it is in Brazil that the Amazon region, with the largest continuous area of tropical "rain" forest in the world, straddles the equator and is bounded by the northern and southern limits of the transequatorial migration of the intertropical front (James, 1959, pp. 390–391, maps). Is the compatibility of Amazonian lowland forest with suboscine dominance a mere coincidence? Northeastern Brazil, with a relatively dry climate, has a lower proportion of suboscines than does Brazil as a whole; the largely forested Amazon region, a higher proportion; Mato Grosso, with its great stretches of open country, a much lower proportion; and the wet western part of the Amazon basin, with its high rainfall and solid forest, the highest proportion in the neotropics.

Elsewhere in South America, Venezuela has a slightly higher ratio than Colombia, lying to the west, and a slightly lower ratio than British Guiana to the east (table 1). These slight degrees of difference I attribute to the influence of mountains and lowlands, respectively: only spurs of the Andes enter Venezuela from Colombia; high mountains are absent from British Guiana. The Rancho Grande area of Venezuela, however, has a markedly lower proportion of suboscines than the country as a whole; most of Rancho Grande lies above the tropical belt, with cool temperatures and cloud-forest conditions. The Bartica District of British Guiana, on the contrary, has a noticeably higher proportion of suboscines than the colony as a whole; the district lies in lowland "rain" forest. Troublesome to explain is the sudden rise in the percentage of suboscines in neighboring Surinam (where the proportion of suboscines is, nevertheless, slightly lower than in the Bartica District). This could be due to the circumstance that Surinam has comparatively more humid-forested lowland than British Guiana (where there is also a savanna element), and because it is smaller in area, with a lesser variety of physical features and climate; the hills

are quite isolated and low. The number of species in Surinam is substantially fewer than that of British Guiana, thus reflecting either a lack of vertical differentiation and consequently a decrease in the kinds of open-country species, or a smaller amount of ornithological attention paid to the higher parts of the country in the interior than to the coastal lowlands. Ecuador, situated on the equator, has about the same proportion of suboscines as Colombia and Venezuela; this I attribute to the effects of altitude (much of the country is taken up by the Andes) and perhaps to incomplete exploration of the Amazonian lowlands.

In Central America there are two small-sized, lowland areas with quite complete bird lists: Finca "La Selva" in Costa Rica and Barro Colorado Island in Panama. Table 1 shows that the proportion of suboscines at each locality jumps above that in the country as a whole. A second-growth, "rain"-forest locality in southeastern Nicaragua likewise shows an increase in suboscines as compared with the country as a whole.

In Costa Rica, with the entire country and "La Selva" serving as "yardsticks," the suboscines show a comparable progression horizontally or vertically. The greatest proportion of suboscines is found in lowland, "rain"-forested localities. In partially cleared areas in the humid portions of the tropical belt, just as in the dry-forested portions, the proportion of suboscines drops. Vertically, the proportion falls with each successive rise through the altitudinal belts; the decrease is greater in deforested localities. These observations bear out the generalizations made above for South America.

The suboscines seem to have evolved primarily in the tropical belt in intimate association with the continuing development of preëxisting "rain" forest. From this equatorial wellspring the tyrannids and furnariids have streamed into austral South America, where they have radiated as ecological counterparts of Old World types; they may or may not be better adapted to a temperate-region environment than their Old World homologues. But the truly tropical groups in a real sense have grown up with the forest, which, for the world, "reaches its largest continuous extent in South America, where half of the continent is covered by a tropical rain-forest, approximately 4000×3000 km. in extent" (Hesse *et al.*, 1951, p. 515). Just as the rise and proliferation of the insects seem to have marched hand in hand with the development and spread of the angiosperms, so, as Amadon remarks (1957, p. 263), "the entire evolution and dominance of the Passeriformes are often regarded as accompanying or complementing the adaptive radiation of the true flowering plants during the Tertiary period."

"The Tropical Rain forest is the home *par excellence* of the broad-leaved evergreen tree, the plant form from which all or most other forms of flowering plants seem to have been derived. Converging evidence of many kinds indicates that our temperate floras have directly or indirectly a tropical origin, of which many temperate species still bear evident traces either in their phenology . . . or in their structure. Bews . . . has found strong evidence that the moist tropical flora of Africa is older than that of the drier and cooler regions; his statistical comparison of fossil and modern floras suggests that from the beginning of the Cretaceous period until the end of the Tertiary a large part of the world had a 'phanerophyte climate,' and that its vegetation was, at least in physiognomy, like the modern Tropical Rain forest. It may well be . . . that the earliest angiosperms were similar ecologically and in their life-forms to the existing rain-forest flora, which may be regarded as an ancient type of vegetation from which the flora of the drier tropical and temperate regions has arisen relatively recently. The immense floristic richness of the Tropical Rain forest is no doubt largely due to its great antiquity; it has been a focus of plant evolution for an extremely long time" (Richards, 1952, p. 16). It even "appears that the deciduous habit may have evolved in the tropics, and have permitted such trees to spread from the equatorial belt to more seasonal regions. Hitherto it has been thought probable that deciduous trees in the equatorial regions are invaders from seasonal climates" (Holttum, 1953, p. 165).

But what about the suboscines and oscines in Central America, which is faunally transitional between North and South America? I trust it has been made clear that the Neotropical Region should not be regarded merely as

a zoogeographical contrivance fashioned to simulate the pattern of distribution of suboscines. Central America and southern Mexico are avifaunally neotropical because most of the birds, particularly the Passeriformes, have neotropical origins, affinities, and distributions. Although the percentage of suboscines shows a progressive decrease northward from South America, even in the humid Mexican lowlands the species are practically identical with those in Costa Rica. As a group, the suboscines do suffer depletion in number of species, and Griscom (1932, p. 44) adduces the example of the "rain"-forest family Formicariidae, the representation of which diminishes from 23 genera and 36 species in eastern Panama to seven genera and seven species in Mexico. The essential clue is provided by two circumstances: subtraction in number of species of suboscines, and generic representation equivalent to specific representation.

On the face of it, the northward decrease might be explained as the result of a filtering process through a narrow corridor leading out from South America. Consequently, one would expect the South American suboscines that have been dropping out along the way to be replaced by species of oscines. But such is not the case, because there seems to be no replacement. Two conclusions can be drawn: niches remain unoccupied in northern Central America and southern Mexico, or else there are no unoccupied niches. Despite the overall physiognomic similarity of the Tropical Moist Forest Life Zone (Formation), the composition of the forests grows less complex northward. First, with latitudinal distance from the equator, the upper limit of the tropical belt dips lower and lower until finally, at the northern edge of the tropical region, the upper limit of the belt has been depressed to sea level. Second, the plant associations become fewer in number. Among the more obvious associations, "the Orey forests, the cativo forest, the *Raphia* palm swamps are not known by the time you get to Honduras, Guatemala and Mexico" (Holdridge, personal letter). Reduction in the number and kinds of niches cannot be divorced from reduction in complexity of the vegetation: a reduced number of niches can be filled only by a reduced number of bird species. The fact that the species of forest-based suboscines are, in effect, equivalent to the number of genera indicates generic selection as opposed to specific differentiation into a plethora of congeneric types. In northern Central America there are fewer variations on fewer themes.

In southern Central America the suboscine difficulty is less acute. Indeed, the proportion of suboscines at "La Selva" and at Barro Colorado Island matches the general situation in South America. Still, Costa Rica and Panama, taken together, comprise a neotropical area the suboscine element of which is appreciably smaller than that in South America. It should be remembered, however, that a relatively short time ago Central America was subjected to cooler climatic conditions (including mountain glaciation in Costa Rica), accompanied by incursions of extratropical faunas. A continued advance by the present interglacial into a period of warmer world temperatures would be coupled with a geographical expansion of neotropical conditions: the tropical belt in Central America would rise vertically and spread latitudinally. We know that this has happened in the past. Amazonian genera or families of trees have been found at "La Selva" (Holdridge, personal letter) and in the Golfo Dulce region (Allen, 1956) of Costa Rica, both wet-forested localities, and nowhere else in Central America. Wetmore (1957) has discovered on Isla Coiba, Panama, an isolated South American spinetail belonging to a species heretofore unknown north of the Orinoco Valley in southern Venezuela and southeastern Colombia. Tropical America has expanded and shrunk repeatedly. Even at maximum shrinkage the equatorial base remains unimpaired, a great heartland where uniform climatic conditions have endured through eras of geologic time.

In the forest at "La Selva," the passerines consist primarily of suboscines, with a contingent of nine-primaried oscines, and a small element made up of wrens and an abundant gnatwren. The more prominent suboscine families are the antbirds, cotingas, and flycatchers. Woodhewers, ovenbirds, and manakins are represented by relatively few species, but individuals are met all the time. Of the nine-primaried oscines, the resident vireos belong to a South American genus (*Hylophilus*),

with two common species; the tanagers are represented by several species, which almost without exception travel about in social groups; the finches have very few species; no icterid is truly resident inside the forest; and warblers and honeycreepers are almost entirely missing. The only other oscine families are the thrushes, with no resident species; the wrens, with three abundant members belonging to South American genera (*Henicorhina*, *Cyphorhinus*, *Microcerculus*), a South American species (*Thryothorus nigricapillus*) which is commoner outside the forest, and a southern Central American species (*Thryothorus thoracicus*); and the gnatwrens, with two South American genera (*Microbates* and *Ramphocaenus*), only one of which is common in the forest.

The wrens in general and the gnatwrens in particular remind me of antbirds, or atypical wrens; they may have as long a history in the New World as the suboscines. As far as I can see, they have taken on an antbird-like character while becoming adapted in size and habits in such a way as not to compete with forest antbirds or ovenbirds. The wrens *Cyphorhinus* and *Microcerculus* could well be termed "peculiar." *Henicorhina* could pass for a diminutive, slender-billed *Myrmeciza*. The little gnatwren *Microbates*, I speculate, has kept or assumed wren-like habits in conjunction with an extreme development in length and slenderness of bill (as has the second-growth-inhabiting *Ramphocaenus*), which is even hooked as is that of a small antbird. In this manner it has survived and flourished; the alternative was to perish. Possibly it preëmpted a niche that no antbird was able to fill. It seems to have undergone an evolution complementary to that of the antbirds.

It may be of interest to compare Barro Colorado Island with "La Selva," even though Panama has a larger avifauna and a larger percentage of suboscines than Costa Rica. Besides, there seems to be no other well-worked area of comparable size with which to make a meaningful comparison. Barro Colorado Island is located 325 miles closer to South America than is "La Selva," and its bird list has been accumulating over a period of 35 years. It is nearly three times the size of "La Selva," or many times larger than the area I worked intensively. Barro Colorado also has several acres of clearing and, as is "La Selva," is almost entirely wooded, half with mature forest and half with various stages of second growth (Eisenmann, 1952, p. 3). In addition, "well-marked trails crisscross the forest, and at various points on the periphery small houses are strategically located, so that the night may be spent in the more remote portions of the island" (Eisenmann, 1952, p. 2). Moreover, the avifauna includes water birds and a number of species of the Pacific slope ("birds of the arid or semi-arid tropics" [Chapman, 1929, p. 9]), elements largely or entirely missing from "La Selva." On the other hand, "La Selva" has a longer list of migrants and is situated not very far from mountains. The numbers in the following tabulation are numbers of species; species living in the country the year round are considered residents. (See also table 1.)

	"La Selva"	Barro Colorado
Total avifauna	331	314
Resident avifauna	269	259
Total passerines	195	167
Resident passerines	144	127
Resident oscines	65	56
Resident suboscines	79 (68 genera)	71 (57 genera)

Another measure is provided by comparative surveys. Eisenmann (1952, p. 3, footnote) ordinarily noted between 120 and 125 species during a two-week period in June and July, when there are no migrants, while covering the laboratory clearing and perhaps a third of the trails on Barro Colorado Island. At "La Selva," during a two-week survey in June, I met 189 species; during a two-week survey in July, 193 species. Possibly another sort of measure is that at "La Selva" the bird list amounts to 44 per cent of the total avifauna of Costa Rica; at Barro Colorado, 38 per cent, of Panama. At "La Selva," the suboscines amount to 56 per cent of all the spe-

cies of suboscines in Costa Rica; at Barro Colorado, 41 per cent of those in Panama.

The principal difference between the two sites, I believe, is that "La Selva" is located in the Tropical Wet Forest Life Zone (Formation), Barro Colorado in the Tropical Moist Forest Life Zone (Formation). There seems to be no recourse other than to correlate the above statistics with the more complex structure of the forest at "La Selva" than that at at Barro Colorado; the suboscines alone are excellent indicators of this state of affairs. Yet, in spite of the longer list of birds and of the larger number of species of suboscines at "La Selva", the suboscine proportion of the resident passerines is very slightly lower at "La Selva"; the number of suboscine genera in relation to the number of species at "La Selva" is, however, proportionately higher than at Barro Colorado. Thus, apart from the greater richness of the avifauna at "La Selva," the percentages still show the northward subtraction discussed earlier. I venture to predict that if a wet-forested life zone (formation) were to be worked out in lowland Panama, and if a site comparable in size to "La Selva" were to be chosen in which to study the birds, it would be found to have a larger avifauna and a higher suboscine ratio than either "La Selva" or Barro Colorado. I would expect, too, that a lowland moist-forested area in Costa Rica, if well investigated, would have a smaller avifauna and a substantially smaller proportion of suboscines than either moist-forested Barro Colorado or wet-forested "La Selva."

The composition of the avifauna in alliance with the wet-forested environment at "La Selva" provides a basis for another kind of comparison dealing with individual species. For example, Howell (1957) has reported on "El Recreo," a locality in southeastern Nicaragua, which is situated 120 miles north of "La Selva" on the other side of the Nicaraguan "break," and which, in the absence of details, one is led to assume to be wet lowland. But, although Howell called it a second-growth rain forest area, the size and composition of the avifauna, compared with that of "La Selva," make one suspicious that it has moist-forested conditions, perhaps even transitional to dry-forested. Over a period of 44 days, Howell with the aid of assistants listed 158 species, of which all but four are year-round Nicaraguan residents. This is very much lower than the number to be found at wet-forested "La Selva," or considerably lower than that to be found during a shorter period in comparable second-growth areas in the moist-forested Caribbean lowlands of Costa Rica. Incidentally, it is likely that the high percentage (61%) of resident passerines at "El Recreo" (see table 1) would be reduced if the avifauna were more completely known; at "La Selva," the list of 247 species compiled during my earlier, short visits also showed a higher percentage (58%), which subsequently was reduced by 4 per cent. Also, the avifauna at "El Recreo" obviously contains a drier, Pacific element, including commonly seen species, which is missing from eastern Costa Rica.

Howell's annotations bring out several interesting similarities and dissimilarities. *Buteo magnirostris* is common at "El Recreo"; it is absent from "La Selva," but is fairly common in cultivated parts of the Caribbean lowlands of Costa Rica. *Columba speciosa* is frequent at "El Recreo"; in Costa Rica it is absent not only from "La Selva" but from the entire Caribbean slope. Provocatively, Eisenmann (1957) reported this pigeon from Caribbean Panama only a few miles from the Sixaola region of Costa Rica, where I once spent a full month without ever finding the bird. The species is common in Costa Rica in the southwestern (Pacific) part. Howell listed *Piculus rubiginosus*, a species not known below the forested subtropical belt in Costa Rica; the species at "La Selva" is *P. simplex*. At "El Recreo," the antbird *Gymnocichla* occurs in mature forest; at "La Selva," and along both slopes in Costa Rica, the habitat is dense, thickety second growth outside or adjoining the forest. According to Howell, the antpitta *Grallaria fulviventris* calls like the congeneric *G. perspicillata* (not recorded at "El Recreo"); at "La Selva," as elsewhere in Costa Rica, the calls of the two species bear not the slightest resemblance to each other. Also reported from "El Recreo" is the second Nicaraguan specimen of *Aphanotriccus capitalis*, a species known only from Caribbean Costa Rica and Nicaragua. In Costa Rica it occurs fairly commonly at "La Selva" and has been found occasionally in other wet-forested local-

ities in the tropical and subtropical belts, where the environment appears to be rather different from that at "El Recreo." To complicate matters, Griscom (1945, pp. 129–130) claimed that this flycatcher inhabits only "special palm jungles of a peculiar species." At "El Recreo," *Todirostrum sylvia* is common; along all of the Caribbean slope of Costa Rica it is extremely scarce. Howell (1957, p. 107) reported the song of *Arremon aurantiirostris* as agreeing in all details with Skutch's description in a life history of the species (1954, p. 94). What is of particular interest here is that the subspecies at "El Recreo," as at "La Selva" and over all of eastern Nicaragua and eastern Costa Rica, is the Caribbean form, whereas Skutch wrote about the Pacific subspecies, which ranges from Panama into southwestern Costa Rica. Solely Skutch's description of the song makes this unmistakable, because the two races in Costa Rica have extremely different songs. Howell's observation, therefore, underscores a problem worthy of further investigation.

Virgin-forested "La Selva" provides the opportunity for making a distinction between semi-open and thicket-inhabiting birds which either do or do not occur also in the forest, and this sort of distinction may perhaps be applied in another direction. Wetmore (1957), reporting on Isla Coiba, Panama, mentioned several species (e.g., *Centurus rubricapillus*, *Thamnophilus doliatus*, *Hylophilus flavipes*) that are typically non-forest inhabitants on the mainland but that occur in the high crown of the inland forests on the island. Wetmore interpreted this to mean that the forest crown may have been the normal home on the mainland, but that when the forests were cut, the birds descended to pasture and semi-open country, second-growth thickets, and similar ground cover. I wish to offer the alternative view that, under the special conditions that characterize islands, such as the absence of many mainland ecological types, the birds referred to by Wetmore are freed through lack of competition to exploit unoccupied niches. The almost unbroken forests of the island are like those on the mainland, but entire families and many genera of birds are quite absent from the island, and the high amount of endemism seems to prove the island inaccessible to many mainland birds. The relict spinetail, *Cranioleuca vulpina*, for example, is common. It is, on the one hand, the only furnariid found on the island; on the other hand, it is absent from the Central American mainland where there are competing species. The three species mentioned above, forms of which I have seen in the field, do not occur in heavy forest, where presumably all the niches, suitable to the various adaptive levels attained by the full complement of birds, are occupied.

The North American migrants, of which the warblers make up the largest and most conspicuous group at "La Selva," are difficult to evaluate as a community constituent. The species that remain as winter residents are apparently as well adapted to "La Selva" as to their temperate-region environment during summer, filling niches unused by the resident avifauna in the tropics as in the north. As there are no native arboreal warblers at "La Selva," the visiting warblers either compete or do not compete with the native birds. The only native birds at all warbler-like in morphology and habits are the forest vireo *Hylophilus decurtatus*, the various woodland antwrens, the gnatcatcher *Polioptila plumbea*, and several honeycreepers. The wintering warblers, therefore, have their preferred semi-open habitat in effect to themselves. From this circumstance I draw the conclusion that the abundance of warblers in the north during summer may be dependent upon the enlargement of the winter habitat caused by the removal of the forests in Latin America, and that before the explosive increase of the human population in Latin America the warblers were much less numerous in North America. Continuing with the assumption that the semi-open in the past in Central America was a fraction of that existing in recent years, I wish to suggest that native passerines in forested tropical America had but a limited semi-open "field" to exploit, that there was insufficient selective pressure for evolution of the warbler types we know so well in temperate North America, and that the natural openings that did exist were visited by small passerines with somewhat warbler-like adaptations fitted primarily to a forested environment. According to this view, migrant warblers should be better suited in their specialized morphology and habits than the native birds

at "La Selva" to the semi-open habitat. The presence of the migrants during half or more of the year has closed to the native birds incipient avenues of warbler-like evolutionary development that might be advantageous to such birds in recent times. As a corollary, migrants have by no means replaced native birds but complement them ecologically.

Just as natural selection may be responsible for having determined in large part the most favorable areas to which the birds resort in order to breed or to spend the winter, so might migration routes be regarded as having been determined in the same manner. I have already called attention to the differences between the fall and spring migrations at "La Selva," which hold for Central America in general. Unlike the migratory habits of large birds such as hawks, those of small passerines seem to be determined by the availability of a daily food supply. I conjecture, therefore, that in Central America migration routes, through a process of selective trial and error, follow shifting lines of least resistance to successful foraging by the birds en route. I assume a seasonal variation in food supply correlating with periodic or seasonal outbreaks of insects. An entomologist working in a cacao plantation elsewhere in the Caribbean lowlands of Costa Rica told me, in reply to my question, that it was his impression that insects in the spring were far less numerous than in the late summer and fall (Milton Stelzer, verbal information). Such was my impression, too, in the tree plantations at "La Selva," and it was fortified in the fall by the appearance of spider webs strung almost everywhere, presumably as a response to an outbreak of winged insects. This sort of evidence, if it can be called that, is at least suggestive of the kind of information an ecologically minded entomologist might uncover for the surmising ornithologist.

The tropical mixed forests are remarkable if only because many dominant species of trees are represented by very few or, in places, by apparently no young individuals. Floristically the composition of a forest association in places separated by only a short distance and seemingly with identical environmental conditions may vary as though different associations were involved. Whether the forests actually do or do not undergo a cyclical or mosaic regeneration whereby one constellation of dominant trees periodically replaces another, or whether the tree floras are still struggling to attain rather than maintain a stable climax (Richards, 1952, pp. 49–50), the floristic diversity the world over nevertheless exhibits a physiognomic uniformity. In the same way the taxonomic diversity of birds may be overlain by similar life forms. In the neotropical forests, of which "La Selva" is an example, the prominent passerine element is a taxonomically definable group, the suboscines. It is this group that I have been using to describe the character of the forest avifauna. It consists of avian life forms which are repeated in the oscines, particularly in the forest understory. Among both passerines and non-passerines terrestrial forms show similar adaptations, as do, for example, climbing or creeping types. Ecological counterparts of the forest types, both in adaptive morphology and in kinds of social aggregations, exist in the Eastern and Western Hemispheres in the several separated areas of pantropical "rain" forest. One level of ornithological investigation may concern itself with the life history of a particular species, or with a quantitative analysis of variables that can be measured. Another sort of investigation requires qualitative insight into the natural laws to which a fauna conforms, and these laws are to be derived from repeatedly observed correlations between the fauna or its parts and the environment. For "La Selva" I have tried to convey a rudimentary conception of the ecological groups of birds. I hope it can be used for a firsthand comparison with the avifauna of an analogous locality in the Old World.

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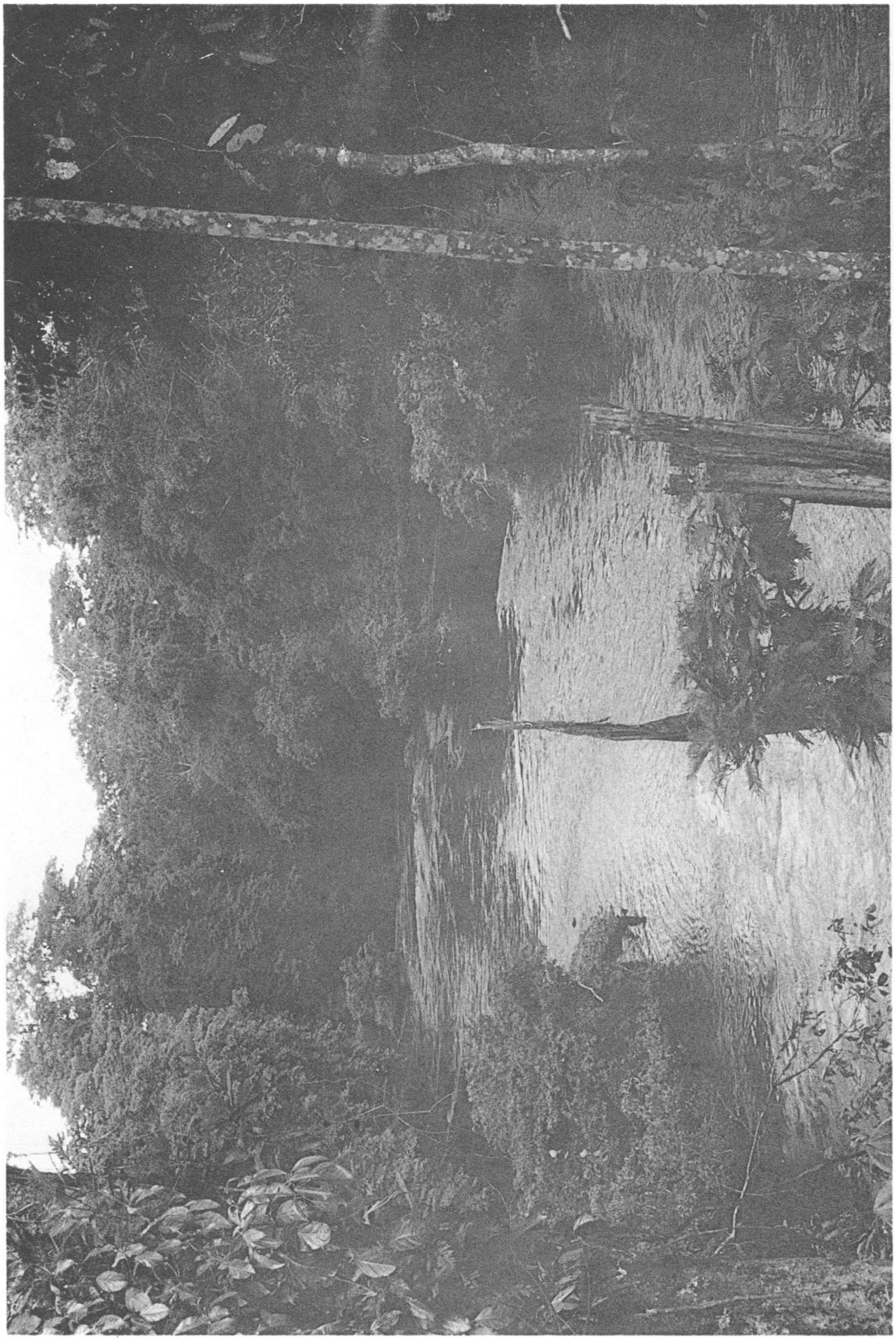
PLATES 9–26

Aerial view of small part of Sarapiquí region. Finca "La Selva" outlined in white on three sides; the fourth side is bounded by the Río Puerto Viejo. Original photographs are the property of the Union Oil Company; copies supplied through the courtesy of the Sección de Ingeniería, Universidad de Costa Rica



View of Río Puerto Viejo

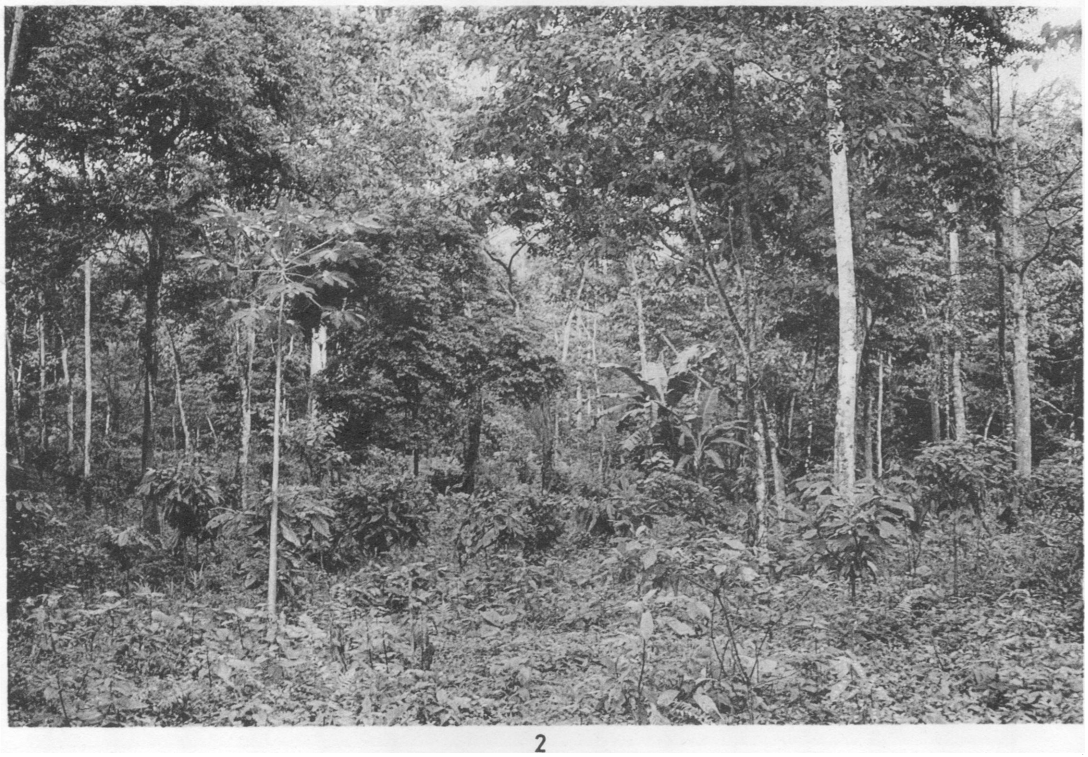
1

2

1. Partially cut-over river bank covered with secondary growth
2. Weather station in small clearing

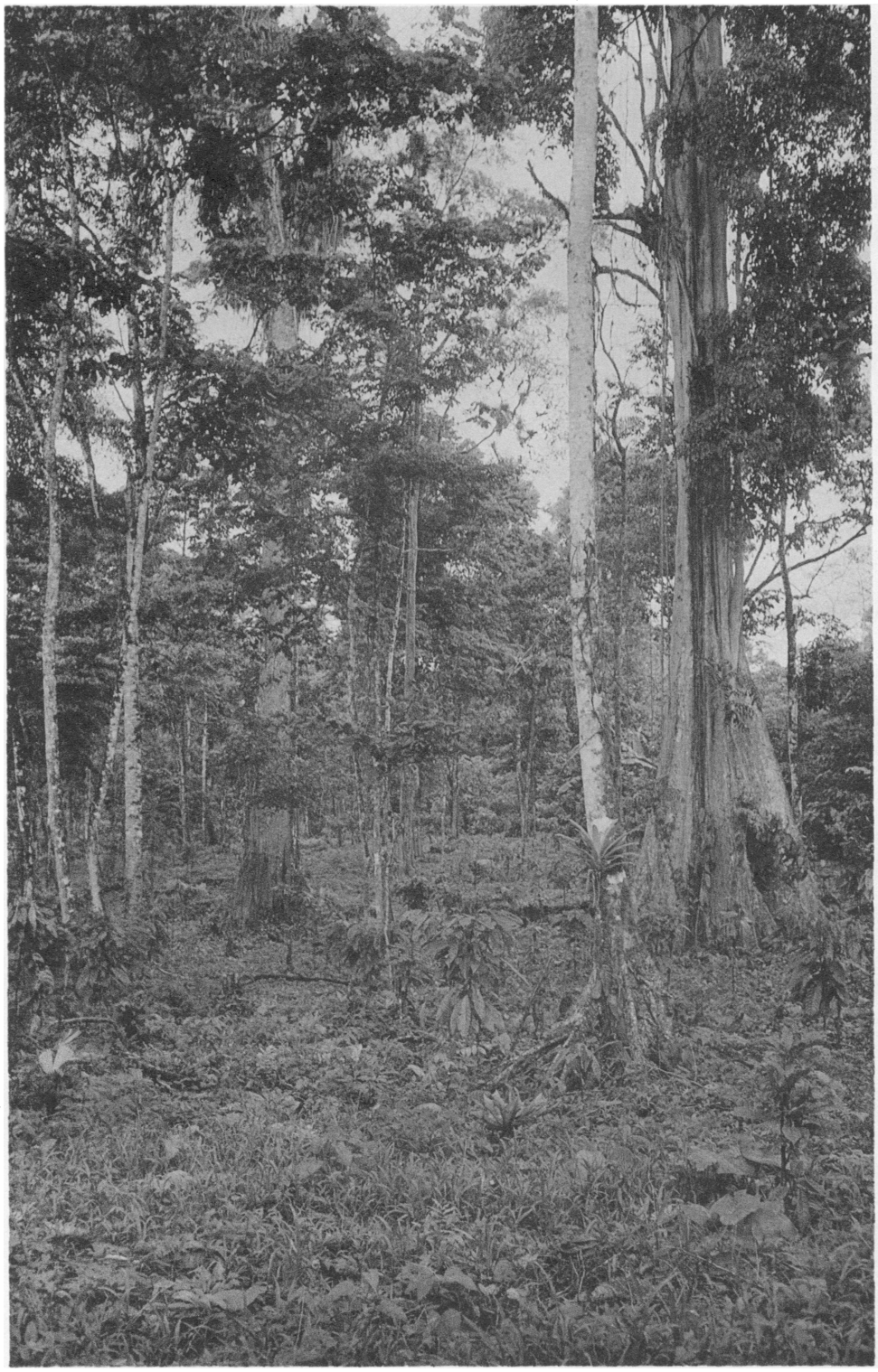
Weather station in the forest

1



2

1. View at the Point. At left, intermediate-stage second growth with emergent trees; at right, young cacao trees and *Hamelia* shrubs
2. View of shaded tree plantation



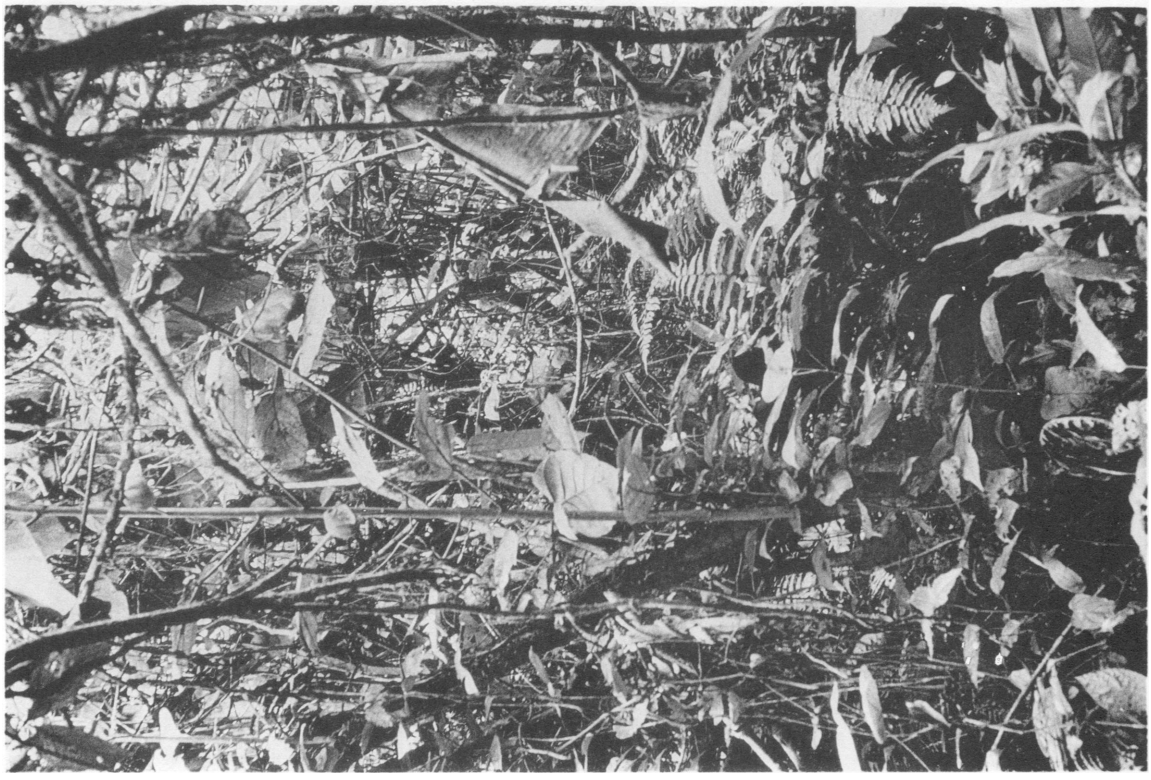
View of shaded tree plantation

1

2

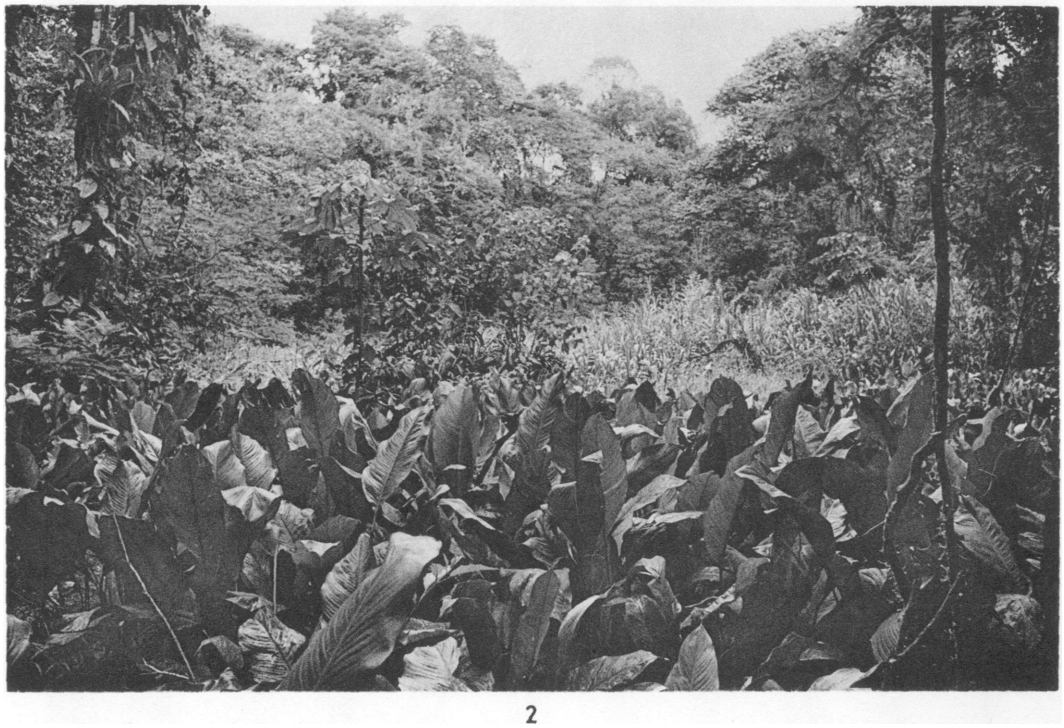
1. Dense second-growth thicket with emergent trees
2. Wild plantain thicket

2



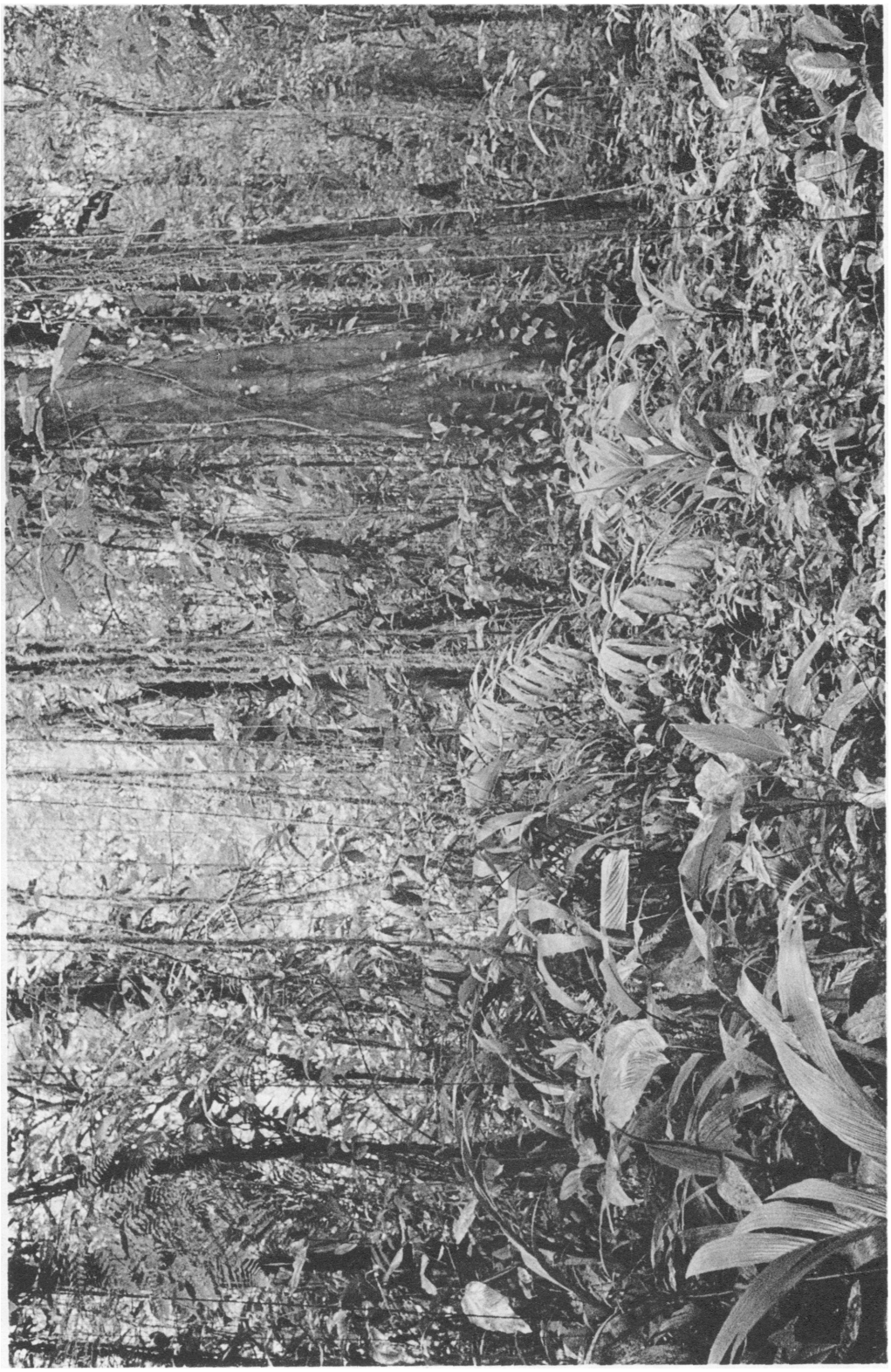
1. Thicket in intermediate stage of succession
2. Heavily overgrown forest border

1



2

1. Streamside thicket in third-stage secondary forest
2. Small marsh behind forest border



View in forest

1

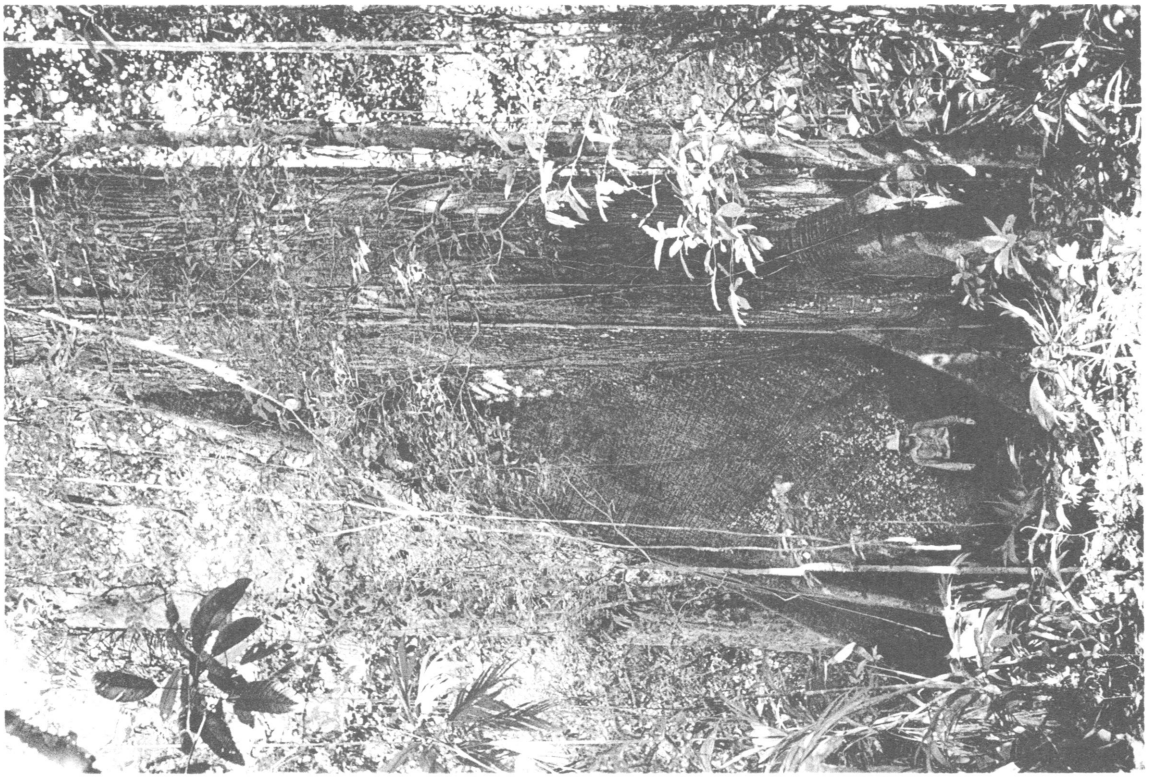
2

1. Vines and fallen lianas
2. Close-up view in forest

1

2

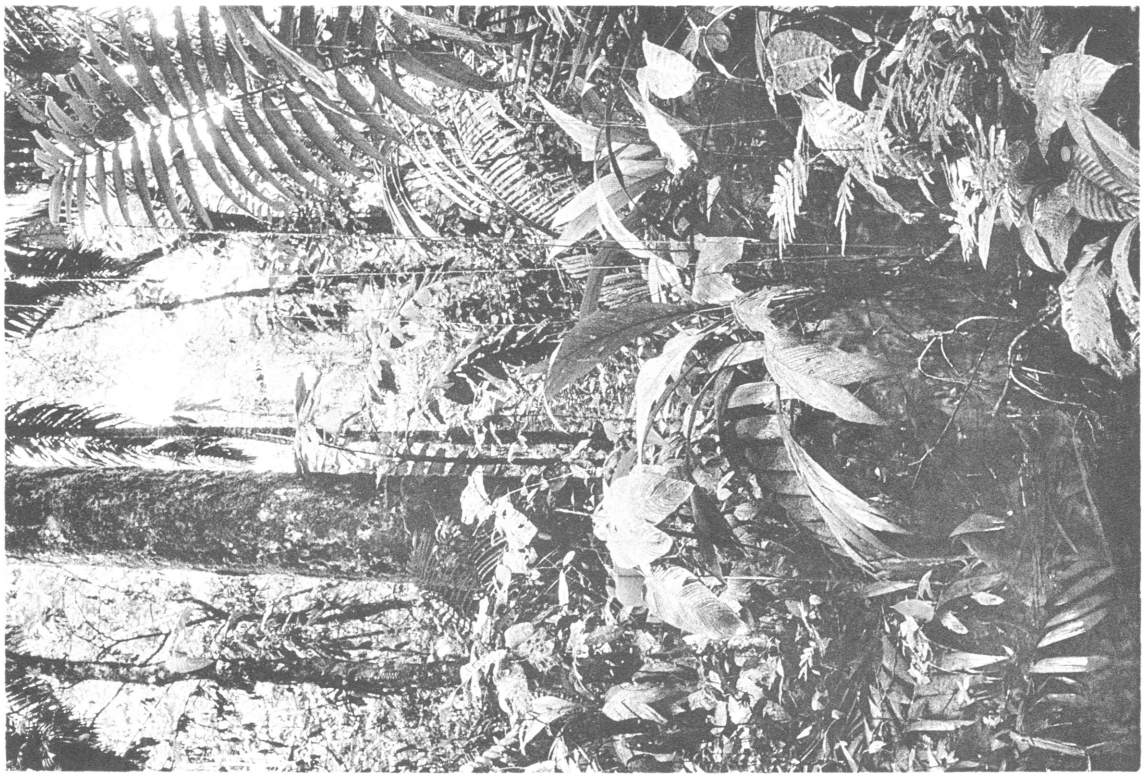
1. Open forest floor
2. Tangled forest undergrowth; fallen vines in foreground



2

1

1. Example of stilt roots
2. Example of tree buttresses



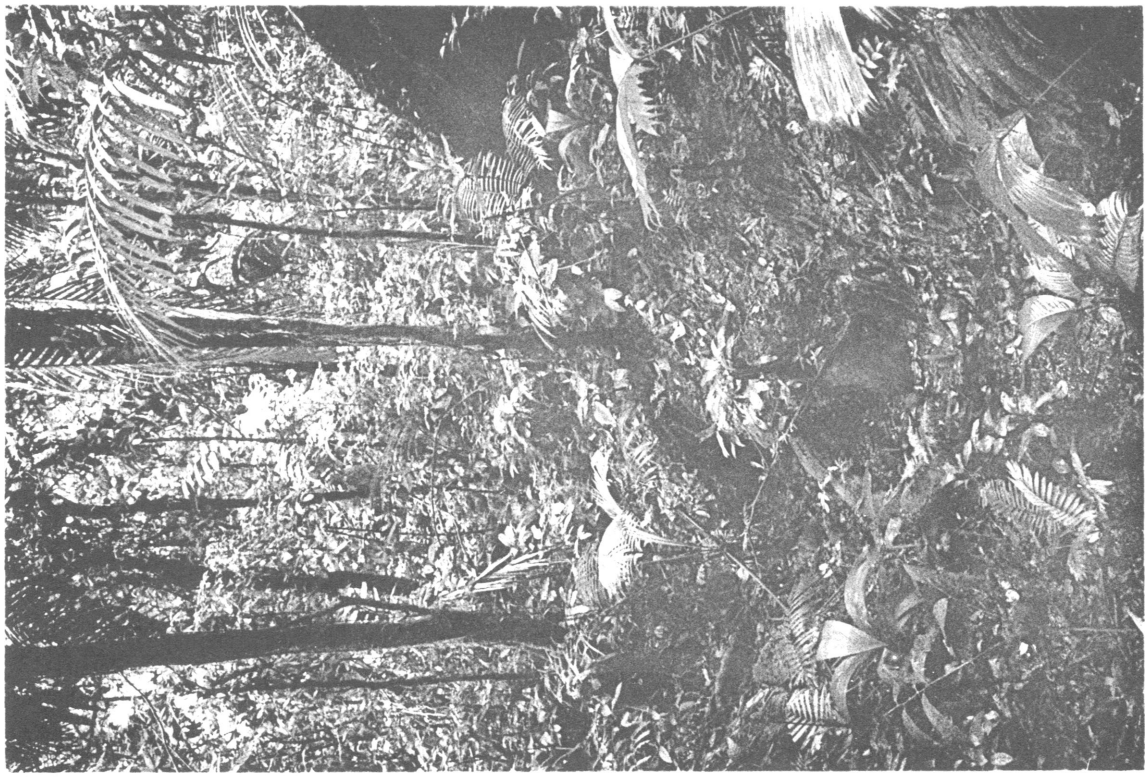
2

1

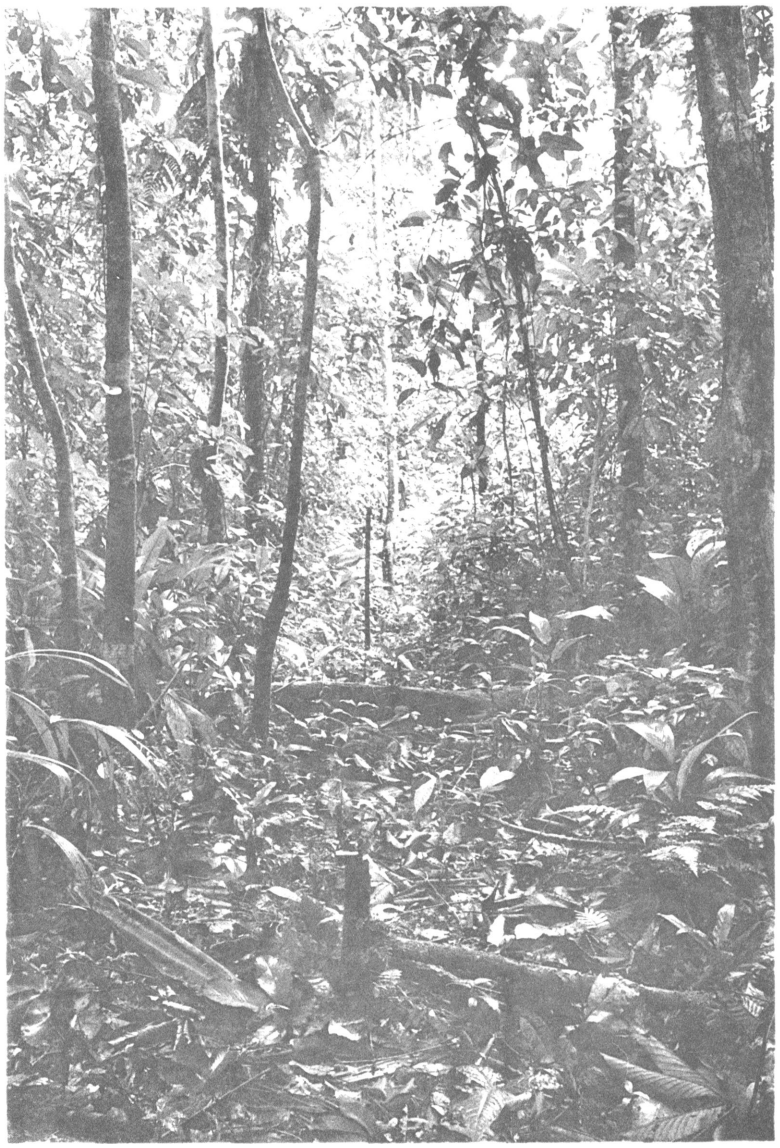
1. A forest stream
2. View in forested swamp

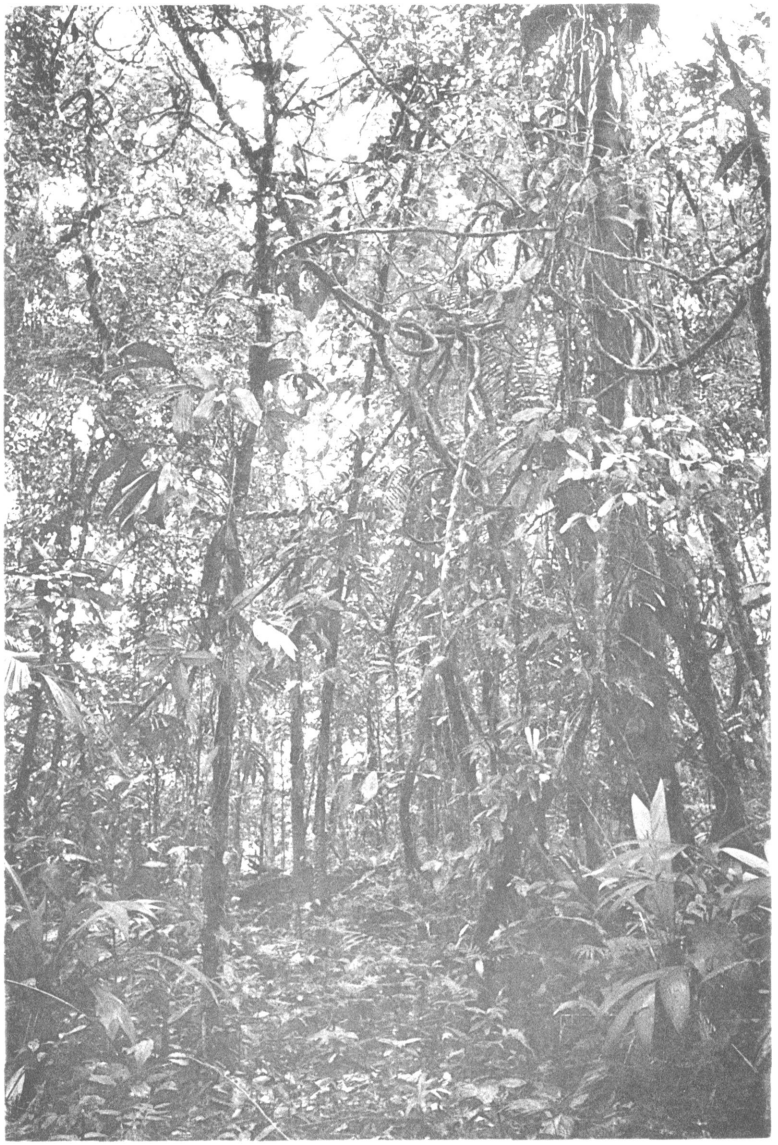
View in forested swamp

2



1. Eroded gully in forest
2. Vegetation-choked gully at break in forest





1. *Cruising line along ridge in forest.* Note the change in ground cover from shaded foreground to light background
2. Top of ridge in forest; fewer big trees, foliage less dense

An opening in the forest