Geographic and Climatic Relationships of Avifaunas with Special Reference to Comparative Distribution in the Neotropics

PAUL SLUD

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 212

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ABSTRACT

Slud, Paul. Geographic and Climatic Relationships of Avifaunas with Special Reference to Comparative Distribution in the Neotropics. *Smithsonian Contributions to Zoology,* number 212, 149 pages, 37 figures, 11 tables, 1976.—A simple species list of birds contains within itself environmental information which is analogous to that obtained from a weather station. In both instances the numerical data do not become meaningful until used comparatively.

The Class Aves is divisible into passerines, comprising two-thirds of the world's land birds, and nonpasserines, comprising the remaining third. The passerines in turn are divisible into oscines and suboscines. The suboscines are numerous only in the Neotropical region, where they outnumber the oscines. Utilization of these major taxonomic components as though they were ecological assemblages is substantiated on objective grounds for the mainland but is not justifiable for islands.

In the neotropics, the relative proportions of the major taxonomic components correlate with the major climatovegetational parameters of rainfall and temperature to provide a comparative measure of faunal and environmental similarity or dissimilarity and of biotic complexity. The suboscine proportion is highest in the rain-forested Amazonian lowlands, thence decreases radially and altitudinally. The oscine proportion fluctuates to varying degree in the opposite direction from that of the suboscine proportion. The nonpasserine proportion decreases with increasing elevation to tree line and with increasing rainfall altitudinally and latitudinally.

Crossplotted, the passerine-nonpasserine and suboscine-oscine relationships produce a two-dimensional "map" on which to visualize the comparative distribution of neotropical avifaunas. Avifaunas having similar proportions of passerines (or nonpasserines) and of suboscines (or oscines) form into discrete climatic clusters. Any faunal level can be accommodated from the zoogeographic region down to the habitats at a study site, provided the comparisons are restricted to units of similar size.

The smaller the size of the unit, the more precise is the avifaunal or environmental information it furnishes. Whether for purposes of comparison or prediction, equivalent samples from equivalent points at equivalent times of year are not only necessary but also feasible to obtain, and a simple methodology by which to accomplish this is presented. The proposition that site-oriented comparisons in which the loci each approach a bioclimatic standard are fundamental to the choice, study, and preservation of representative natural areas is supported on theoretical grounds and by examples.

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Geographic and Climatic Relationships of Avifaunas with Special Reference to Comparative Distribution in the Neotropics

Paul Slud

Introduction

There are about 8650 living species of birds in the world (based on Austin, 1971). This total, differing little from that of other recent authors or even from one compiled a generation ago by Mayr (1946), can be accepted as virtually complete. Including extinctions in the last few centuries (based on Austin, 1971) the number rises to 8717. This is the figure used here, inasmuch as recently defunct species formed part of existing natural assemblages and often appear in faunal works.

Faunal works, or compilations, are for the most part freely available in the printed literature (but not, in my experience, when unpublished or private). The boundaries can be regional, geographic, political, or ecological, the scope supracontinental to local. Ranging from a set of volumes on a shelf to a pocket pamphlet or card, a compilation may or may not inventory an area completely. The ones which do are the source of species lists that can be put to comparative use.

On the basis of simple species lists, this paper attempts to point out elementary sets of avifaunal relations and to utilize these relations to compare avifaunas and to link them to their surroundings. One set of relations is that between passerines and nonpasserines. This is a global relationship making it possible to compare the whole with its parts and the parts with one another. Eliminating the water birds serves to place the passerines (all of them land birds) and the nonpasserines (one-quarter of them aquatic) on the same terrestrial footing. A second set of relations is that between oscines and suboscines. This is primarily a neotropical relationship, which is here further strengthened and substantiated. The two sets of relations are considered separately, then together. Cross-plotted, they produce a two-dimensional distribution of neotropical avifaunas. As an imitation of nature, the picture can be appreciated on its own merits or in relation to vegetation, climate, and topography. The paper concludes with a rationale in which avifaunal sampling and choice of locale are considered interdependent, provided the objective is the acquisition of comparative data.

ACKNOWLEDGMENTS.—The American Museum of Natural History and the Carnegie Museum permitted me to examine the extensive Amazonian ornithological materials in their care. At the Smithsonian Institution, H. Daniel Roth, formerly, and Lee Ann Hayek, at present, in the Information Systems Division were instrumental in calculating correlation coefficients and regressions; Robert G. Tuck, Jr., formerly in the Department of Vertebrate Zoology, supplied species counts of reptiles and amphibians in the eastern Caribbean area;

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Robert H. Gibbs, Jr., Chairman of the Department of Vertebrate Zoology, made many valuable comments aimed at improving the manuscript.

Species Lists

Categories

A species list may consist of (1) the entire avifauna or (2) the resident, or native, avifauna, (3) all the land birds or (4) the resident, or native, land birds. Categories (1) and (3) contain species whose status is for the most part self-evident. Categories (2) and (4) include species whose status is variable, questionable, or unascertainable not only in poorly known tropical regions but even in the well-worked temperate north; consistency of treatment is always a problem. Residents, or natives, are nonintroduced species that occur year-round, the others are nonresidents. (A compromise between native land birds and total land birds is presented in columns 4 and 7 of Table 1, where a resident has a value of one, a nonresident has a value of one-half.) Breeding species offer a poor alternative. Their status is often presumptive and therefore the most difficult to determine. Some occur, or have been recorded, irregularly or in very small numbers, others lack pertinent data. Nonbreeding species may inhabit an area for as long a period of year as the breeding species, yet they are often ignored.

Need to Compare Equal Areas

The thoroughgoing compiler generally strives to assemble as complete a faunal list as he can. Particularly in the tropics he is apt to emphasize the "richness" of his area by contrasting it with one that is larger or less complex or lies outside the tropics: e.g., Mayr, 1941a (New Guinea), Meyer de Schauensee, 1948, 1964 (Colombia), Phelps and Phelps, 1950, 1963 (Venezuela), Friedmann and Williams, 1971 (Bwamba, Uganda), Wetmore, 1972b (Panama), Mayr and Serventy, 1944, and Keast, 1972 (Australia). The favored area is thus represented as possessing proportionately or absolutely as many taxa as, if not more than, the moderately to enormously larger area. Obviously, unequal-size units having similar-size lists are not acceptable for unit-area comparison (see below).

As Table 1 demonstrates, species densities increase as the area being considered decreases. Therefore, in order to compare avifaunal size (species density) it is necessary to compare units of similar area. It is equally necessary that the lists be both accurate and comprehensive. Suitable data for similar-size units, whether they differ by belonging to different biogeographical regions or are similar if only in being located somewhere in the global tropics, occur infrequently in the literature. How infrequently is made evident by the mélange of entries in Table 1. Indeed, some of the entries are really a synthesis of two or more geographically contiguous units, specially created to serve as areal mates for otherwise unpaired units. The units are almost all political; few ecological reports treat an entire avifauna or mention the size of the area. Even so, species densities diverge among entries of comparable size when these differ in overall environmental complexity and converge when they are similar.

Elimination of Water Birds

Water birds are the Sphenisciidae, Gaviidae, Podicipedidae, Procellariiformes, Pelecaniformes, Ciconiiformes, Anseriformes, Gruidae, Aramidae, Rallidae, Heliornithidae, Eurypygidae, and the Charadriiformes minus Burhinidae, Glareolidae, and Thinocoridae. Arbitrary determination of individual species as land birds or water birds (viz. Rallidae and Alcedinidae) is avoided by not going below the family level (see Moreau, 1966).

Certain generalizations are made apparent by Table 1 and Figure 1. The relative size of the water bird component, whether on a unit-area basis or as a percentage of the avifauna, is obtainable from the difference in species density between Total Avifauna and Total Land Avifauna in a global survey of checklists (Table 1). A visualized sampling of these, based on actual numbers of species (Figure 1), shows that the ratio of water birds to land birds broadly correlates with climate. The ratio decreases drastically with decreasing latitude from very high in the boreal region (also on isolated oceanic islands) and well marked in the cool-temperate region to moderate in the warm-temperate region, low in the subtropical region, and extremely low in the tropical region; paradoxically, the water bird ratio is usually smaller in the humid tropics than in the dry tropics. Among

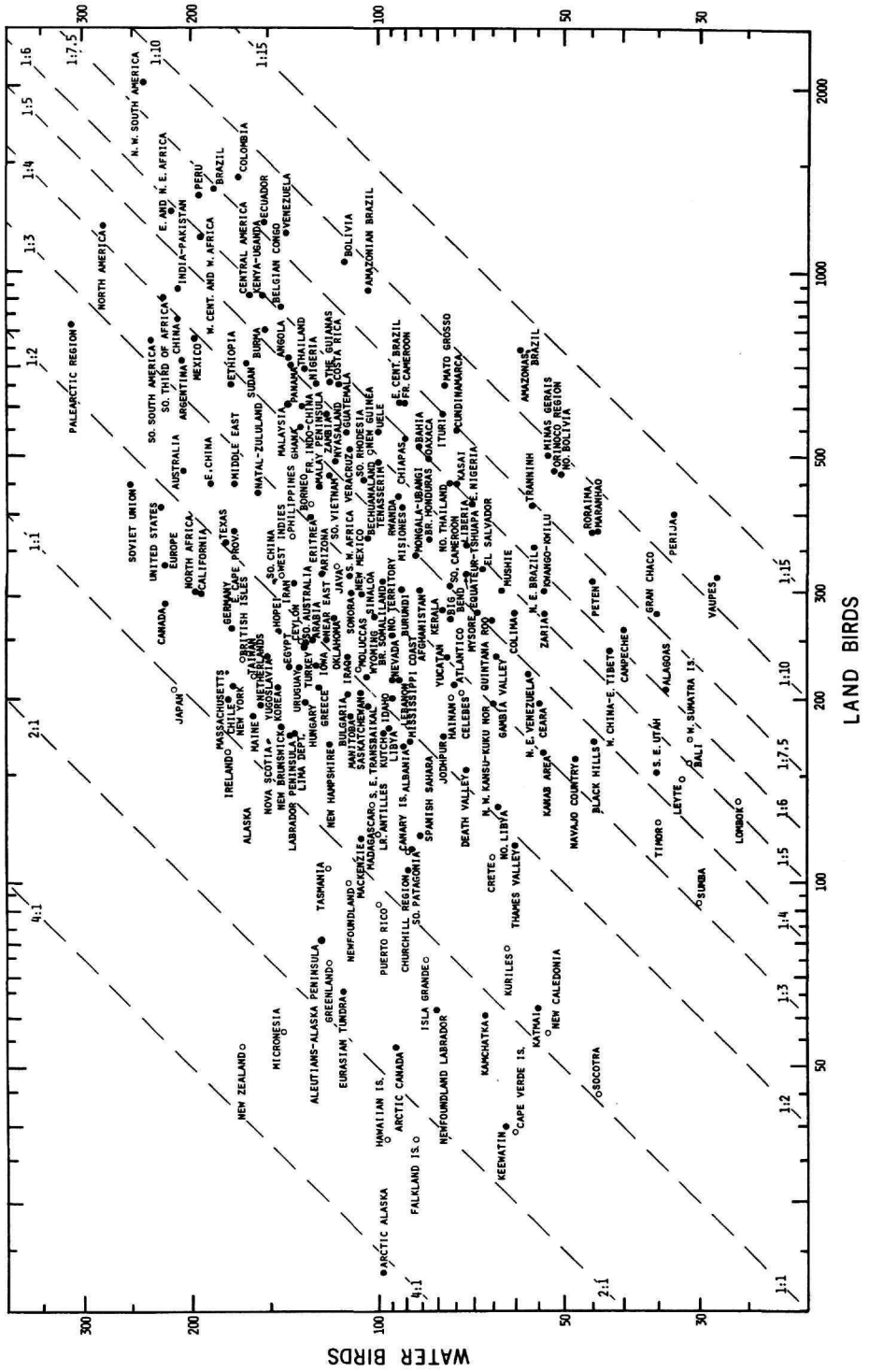


FIGURE 1.—Global survey of species of water birds versus species of land birds. (Dashed diagonals = ratios; solid circles = mainland units; open circles = islands.)

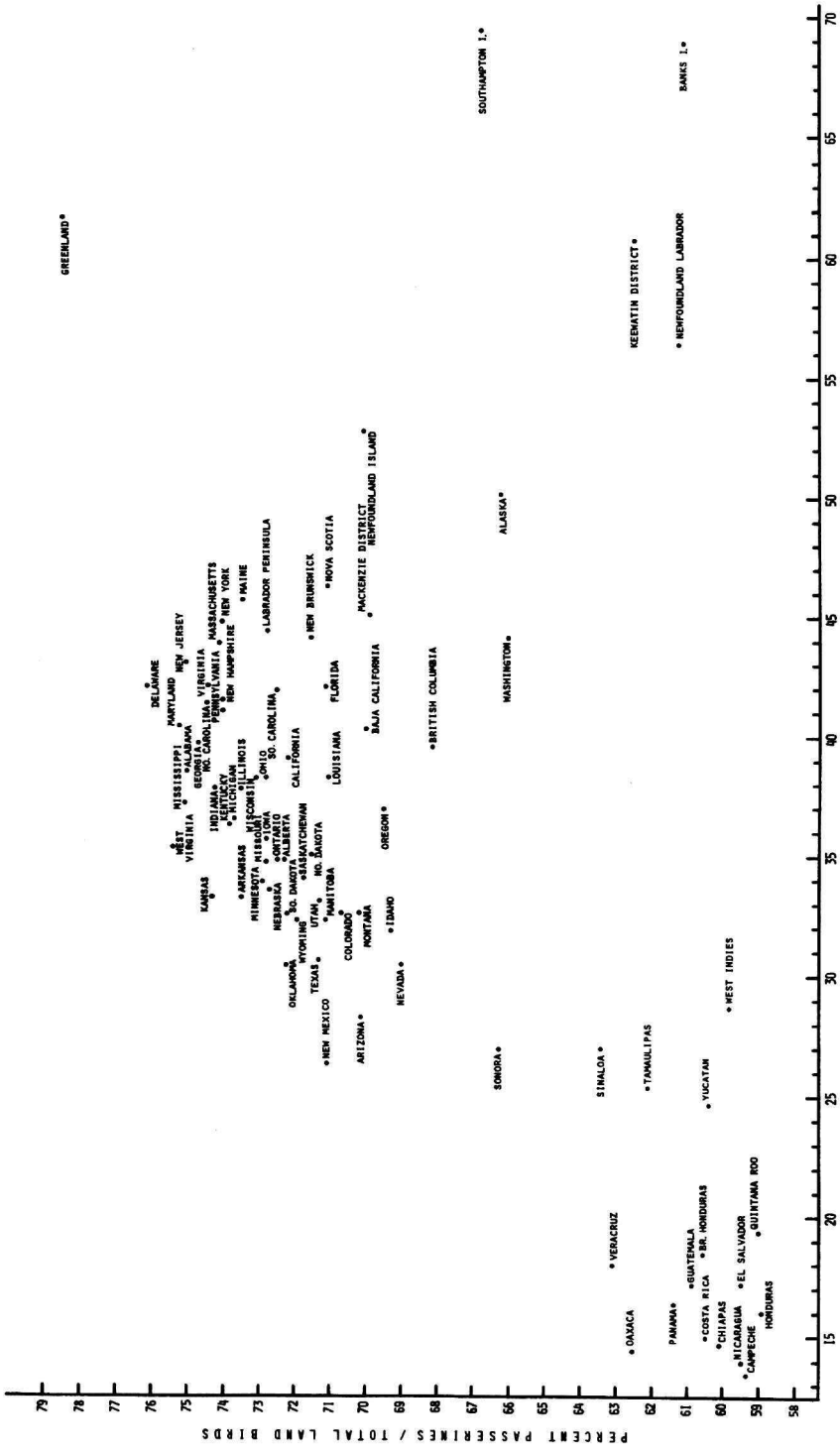


FIGURE 2.—Scattergram of North and Middle American political divisions: percent water bird species in total avifauna versus percent species of passerines in total land birds.

mainland units of approximately the same size, inclusion or exclusion of water birds has little effect on the total avifauna relative to the total land avifauna: species densities rise or fall equivalent amounts, provided tropical units are compared with tropical units and extratropical units with extratropical units.

On a subregional to regional scale, water bird percentages parallel each other in the Old World and in the New World, not only in size but also in latitudinal sequence. The Congo and Brazil, on opposite sides of the Atlantic, have respective percentages of 14 and 12; southern Africa and southern South America, 26 and 23. Nearctic North America (United States and Canada) and the Palearctic Soviet Union each have a percentage of 37.

A survey of water bird percentages in North America shows that they fall into a distributive pattern (Figure 2). In the temperate part of the continent, the lowest percentages are found in arid southwestern United States and adjacent Mexico. The percentages increase northward and eastward into the Great Basin, the Rocky Mountains, the Great Plains, and the area between the Mississippi-Missouri rivers and the Appalachian Mountains. The eastern seaboard and to some extent the Pacific sector are distinct from the interior. Much the highest values occur peripherally at boreal latitudes. The neotropical units, southward from Veracruz and Oaxaca, have the lowest values and lie apart as a cluster of their own.

In view of the fact that aquatic areas are inhabited by a specialized water bird fauna, it follows that water birds should, as a matter of normal procedure, be excluded from consideration when comparing the land birds: terrestrial environments are best represented by terra firma faunas.

For example, Hall (*in* Voous, 1972:585) compared the breeding land bird proportion of the avifauna in Africa with that in the Palearctic region without eliminating the water birds. Hall concluded that Africa is richer in "younger" elements, that is, the passerines and the nonpredatory arboreal nonpasserines (pigeons through woodpeckers), where they comprise 62 percent and 18 percent, respectively, of the avifauna than is the Palearctic, where the corresponding percentages are 55 and 9.5. If, however, the water birds are removed, Hall's own figures show that Africa becomes poorer than the Palearctic in percent passerines (67 versus 69) and less rich in percent nonpredatory arboreal nonpasserines (19 versus 11). The combined percentage of "younger" elements is 80 in Africa and 64.5 in the Palearctic when water birds are included, 86 in Africa and 80 in the Palearctic when water birds are excluded.

The need to remove the water birds becomes increasingly apparent as the units to be compared become smaller or as their overall environments increasingly differ. Examples are an oceanic rock frequented by sea birds and, say, a wood lot supporting a community of land birds; a place that teems with water birds in the wet season and the same place when the water has evaporated in the dry season; an inland area that lacks wetlands and a coastal area possessing estuaries, marshes, and swamps. The problem also arises when comparing places at very different altitudes. In contrast to the lowlands, aquatic birds are rare to absent at montane elevations, except very locally: Sikkim, in the Himalaya, has a water bird percentage of only 2.6 (based on Ali, 1962); at San Antonio, in the Colombian Andes, it was 1.2 (based on Miller, 1963).

Total Land Birds

Eliminating the water birds depresses species densities markedly, sometimes enormously, in the temperate zone and on oceanic islands, moderately or insignificantly on the tropical mainland. When nontropical mainland units are now compared with tropical ones, the latter appear overwhelmingly rich. Darlington (1957:265) put it this way: "The land bird faunas of temperate Eurasia and North America are little more than depauperate fringes of adjacent tropical faunas." Even those of luxuriant tropical islands, such as New Guinea, Borneo, or Java, rate poorly when set against analogous areas on the tropical mainland. (See Table 1.)

A total land bird figure can be viewed as a comparative measure of faunal "richness" or environmental complexity, whether the unit is a Colombia or an oceanic islet. Nevertheless, multiple factors complicate the interpretation of a single figure. The figure is uninformative as to the relative "richness" or "poorness" of subdivisions within the unit. It does not distinguish between common or regular, rare or irregular, evenly distributed or disjunct taxa. Equal-size areas having unequal

diversities may have similar totals for different reasons: an area, owing to its position, may be visited by more species of migrants than it has residents; an island normally accessible only to aquatic species may have a list that includes a number of mainland strays. Many lists are incomplete, and better knowledge of the migrants and of the natives could increase the species numbers and densities appreciably. Lack of standards permits one author to list taxa the occurrence of which another author does not accept as proved.

Migrants

A world count does not distinguish between total avifauna and native avifauna, residents and migrants, breeders and nonbreeders. A reproducing resident in one part of the world may be a transient, a visitant, or an accidental in other parts. A taxon restricted to a remote bit of land in the ocean has the same value in a count as one which is cosmopolitan and abundant. The zoogeographic regions, apart from the Holarctic, have such large land avifaunas that the presence or absence of migrants is hardly noticeable percentagewise. Migratory effects are nevertheless present and can affect the comparability of geographic units on opposite sides of the equator.

A global survey of migrant percentages (Figure 3) shows that these follow parallel courses in the eastern and western hemispheres. Old World and New World counterparts, insofar as these can be approximately determined latitudinally, climatically, and areally, have migrant percentages which, if not quite equivalent, occupy similar relative positions within the progression for their respective regions. An inverse geometric correlation, in which the native land avifauna more than doubles in size each time the migrant percentage is halved, extends through most of the progression. At either extremity, i.e., the high latitude-low species density units and the low latitude-high species density units, the percentages tend to curve from the alignment. In the north, this begins to take place when the number of species has declined to 60 or so; in the tropics, when the migrant proportion has declined to less than 5 percent. If, however, the migrants were each assigned a value of one-half and added to the number of residents (as in Table 1), the extremities would follow the alignment. High-latitude units, having the largest numbers of migrants, would be shifted the most, units in the subtropics and outer tropics very much less, and units in the inner tropics hardly at all. The avifauna would increase an average of 1.8 times in size each time the migrant percentage is halved.

Figure 3 shows further that islands and satellites of islands lie varying distances "at sea," so to speak, generally to the left of the mainland units but never to the right. The distances correspond roughly to the size of the islands and to their latitudinal position or degree of isolation. A north-south sequence, or set of sequences, is also discernible. Islands, in part because of their small size compared to the mainland units, tend to have relatively high migrant percentages.

Latitude.—*Western Hemisphere:* Temperate North America and tropical to subtropical Middle America alternate semiannually in gaining and losing an enormous avian mass. South America has a much smaller flux of species and individuals, this principally in the northwest, especially the Caribbean versant. Large areas, virtually amounting to subregions, show a progressive reduction southward in percentage and number of migrants.

	Land bird migrants	*% Migrants / total land species*
Texas	170	51.3
Mexico	125	16.1
Central America	112	12.2
Northwestern South America (Colombia, Ecuador, Peru)	78	4.2
Central South America (Brazil)	40	2.9
Southern South America (Uruguay, Paraguay, Argentina, Chile)	14	1.8

The states and countries that succeed one another geographically from northwestern Mexico through Central America to equatorial South America substantiate and refine the progression. In the tabulation that follows, the figures for Nicaragua have been compiled largely from Eisenmann (1955) and for Ecuador and Peru from Meyer de Schauensee (1970). Those for all the other entries come from their own published checklists. It need be emphasized perhaps that the figures are unadorned counts of the species listed in standard works. No assumptions or guesses have been made or values assigned or formulas devised to modify the totals or to give added weight to regularity,

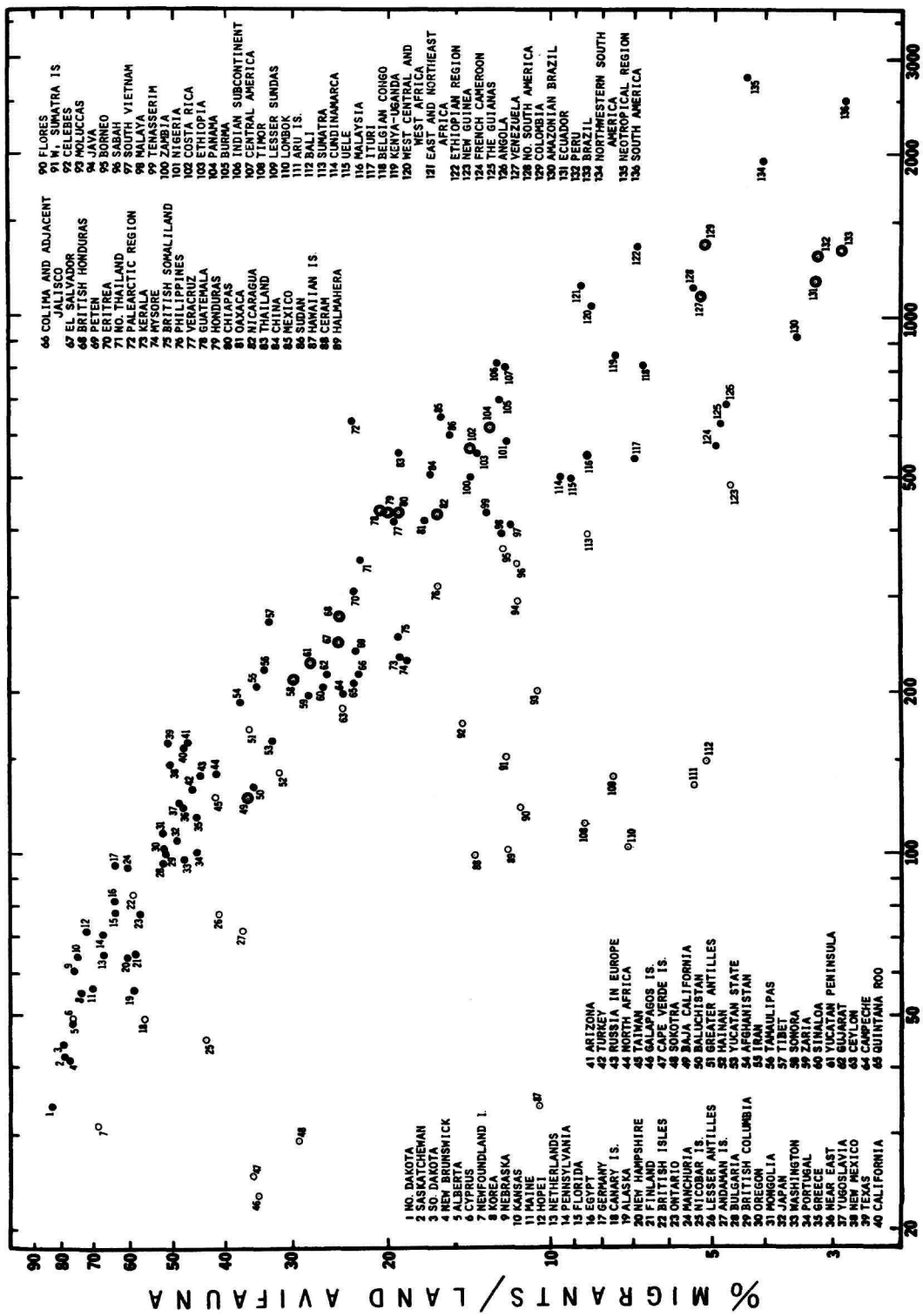


FIGURE 3.—Influence of migrants relative to numbers of species and location of land avifaunas: global survey of percent migrants versus size of resident avifaunas. (Large solid circles with enclosed stars = the units tabulated in the text on page 8; small solid circles = mainland units; small open circles = islands.)

abundance, frequency, environmental impact, "importance," or whatever.

	Area (1000 mi²)	*Land bird migrants*	*Native land species*	*% Migrants/ total land species*
Baja California	56	73	127	36.5
Sonora	70	90	210	30.0
Yucatan Peninsula	63	93	227	28.0
British Honduras	9	91	277	24.8
Chiapas	29	103	431	19.3
Guatemala	42	114	433	20.8
El Salvador	13	82	247	24.9
Honduras	59	109	432	20.2
Nicaragua	57	84	428	16.4
Costa Rica	19	94	568	14.2
Panama	29	94	622	13.1
Colombia	440	74	1351	5.2
Venezuela	352	61	1090	5.3
Ecuador	101	39	1161	3.25
Peru	482	43	1291	3.2
Brazil	3286	40	1323	2.9

The migrant percentages are not directly related to area. They do show an inverse correlation with size of avifauna: the regression has a correlation coefficient of 0.99. Even if the sequence were extended northward into the border states of Texas, New Mexico, and Arizona, the coefficient would be 0.94. A decrease of 10 (where feasible) in percent migrants tends to be accompanied by a twofold increase in size of avifauna.

Notwithstanding the extraordinarily high coefficient, the sequence is not quite right in two places. Chiapas probably ought to have a somewhat higher migrant percentage than Guatemala (with which it is physiographically linked) instead of one that is barely lower; Nicaragua should perhaps have more species than neighboring Honduras. The progression can be almost idealized if Chiapas is replaced by a unit that completely crosses southern Mexico and if British Honduras, on the Caribbean versant, and El Salvador, on the Pacific versant, are merged, respectively, with Guatemala and with Honduras so as to cross-section the Middle American isthmus, as do the countries to the south. The sequence of percentages now becomes 21.0 for southern Mexico, 21.2 for Guatemala-British Honduras, 19.8 for Honduras-El Salvador, 16.4 for Nicaragua, 14.2 for Costa Rica, and 13.1 for Panama.

Units represented in the literature by two or more checklists as a rule have the shorter, or earlier, list with a lower migrant land bird percentage (and passerine percentage) than the later, or longer, list (Table 2); successively earlier lists fit less and less well, if at all, into the geographic sequence; largest numbers of migrants occur in the block of mountainous units comprising southern Mexico and northern Central America. With these things in mind, we can evaluate the relative status of Nicaragua, the only Middle American country without its own checklist, from the numbers in the above tabulation.

Nicaragua has a resident land avifauna nearly the same size as in Honduras, Guatemala, and Chiapas to the north but a migrant percentage closer to that of Costa Rica and Panama to the south. Also, Nicaragua has 25 fewer migrants than Honduras and 10 fewer migrants, instead of more, than Costa Rica. If the Nicaraguan list were increased only by the 10 required to match the number in Costa Rica, the migrant percentage would rise to 18.0; if increased by 25 to the number in Honduras, the migrant percentage would nearly equal that of Honduras. Additional native species that might come to light in a country as sufficiently well known as Nicaragua would be too few to appreciably alter the percentage compared to the number of migrants yet to be expected. The present figures suggest that Nicaragua is transitional between northern and southern Central America. An up-to-date checklist should place it with northern Central America both in size of avifauna and in migrant percentage.

Before leaving the above tabulation, one might add that migrant species of passerines, outnumbering migrant nonpasserines by as much as four to one (Table 2), correlate almost as well with total passerines as do total migrants with total land avifauna and much better than do the relatively few migrant nonpasserines with total nonpasserines.

Eastern Hemisphere: Moreau (1966: chapt. 8) compared two groups of African and extra-Ethiopian units to illustrate "the difference between the land-bird fauna of a tropical area and a temperate-zone fauna." In the accompanying tabulation, I have combined Moreau's groups, used his numbers, and listed his units in order of decreasing latitude.

	Area (1000 mi²)	Land bird migrants	Native land species	% Migrants/ total land species
Thames Valley	–	49	67	42.3
Arizona	114	78	146	34.8
Morocco	170	44	132	25.0
Gambia "Valley"	–	42	194	17.8
"British" Somaliland	68	24	214	10.1

The progressive reduction in percent migrants correlates roughly with decreasing latitude and, if Arizona is omitted, directly with number of migrants and inversely with size of avifauna.

Figures compiled by me from a larger number and variety of checklists substantiate the above progression and follow it into southern Africa, where the migrant percentage rises again. On the west, the percentages range from 60 or more in the north (Finland 59, Great Britain 59, Germany 64, Netherlands 67) to 45 in Portugal and 42 in North Africa; in sub-Saharan Africa, from 12 in Nigeria down to 9 in Liberia, 7 in the Congo, and 5 in French Cameroon and in Angola, then up to 11 in Bechuanaland, 11.5 in West Cape Province, and 19 in South-West Africa. On the east, the percentages range from about 50 in the Balkans (Yugoslavia 48.5, Bulgaria 53, Greece 46.5), 46 in Asia Minor (Turkey), 49 in the Near East, and 45 in Arabia to 64 in Egypt and 60 in Libya; in sub-Saharan Africa, from 23 in Eritrea, 19 in British Somaliland, 15.5 in the Sudan, and 14 in Ethiopia down to about 7.5 in Central Africa (Kenya-Uganda 8, Rwanda 7, Burundi 8), then up to 13 or so farther south (Nyasaland 12, Zambia 14, Rhodesia 13, Natal-Zululand 14, East Cape Province 13).

A similar progression extends southward to the equator in eastern Asia. The migrant percentages drop from 50 or more in the north (Mongolia 52, Manchuria 60, Hopei 72, Korea 70, Japan 49) to 19 in southern China (Fukien) and in Thailand, 16 in the Philippines, 12.5 in Burma, 12 in Malaya and in South Vietnam, about 11 in the Greater Sundas (Sumatra 9, Java 12, Borneo 12), 8 in the Lesser Sundas, and 5 in New Guinea.

Areal Size.—Areal size also affects the size of the migrant percentage on the mainland, hence a small area and a large area are not really comparable with respect to migrants. In the wintering range, small areas have a smaller number but a higher proportion of migrants than the larger area of which they are part. The proportional disparity increases as the difference in area increases: e.g., Guatemala versus Petén versus Tikal, Costa Rica versus Finca La Selva, Panama versus the Canal Zone versus Barro Colorado Island (Table 2). The disparity becomes more pronounced when the large area is elongated latitudinally, so that a taxon which occurs seasonally in a part of the country remains a resident of the entire country, as in Mexico or Argentina. Apparent exceptions are the Yucatan Peninsula and the Guianas (Table 2). Both are subdivided into thirds, and the difference in size between the whole and its parts is evidently not overwhelmingly great.

Nature of Compilation.—Number or percentage of migrants is coupled to the date or size of the compilation, whether the unit is a country, such as Honduras or Costa Rica, or a site, such as Finca La Selva or Barro Colorado Island (Table 2). Accumulating data are accompanied by (a) the number and percentage of migrants growing faster than those of residents, (b) passerine migrants increasingly outnumbering the nonpasserine up to several times or more, and (c) the percentage of nonpasserine migrants rising faster than that of passerine migrants.

Role of Migrants.—Whether migrants benefit the economy of a natural environment or detract from it depends upon whether an author is inclined to believe they complement the residents or compete with them (Slud, 1960:144–145, 1964b). The species counts and percentages (Table 2) suggest it is the former, the increasing complexity of the resident biota which has evolved under increasingly amenable climatic conditions, rather than distance, that is responsible for a decreasing number of ecological opportunities left open to a diminishing migrant proportion. Both in Africa and South America it is the richest biotope, the equatorial rain belt, that acts as a barrier which many migrants do not cross, very few enter, and the remaining ones skirt or pass over in order to winter in the southern third of the continent.

In the Neotropical region, the passerine percentages of the total land avifaunas of the sovereign states and territories, thanks to the inclusion of the migrants, all fit into a narrow range (Figure 4). The influence of the migrants declines most markedly in South America, where the total land percentages and native land percentages are nearly

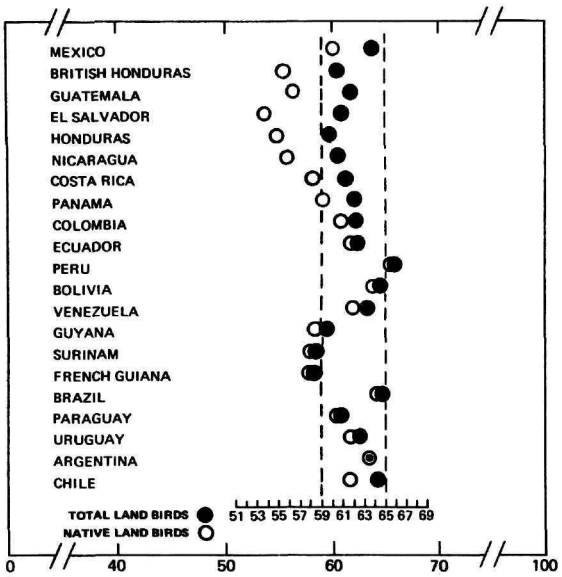


FIGURE 4.—Neotropical land birds: percent passerines per country.

identical. Northward from Panama, the native land percentages, owing to the increasing size of the migrant proportion, veer away from the total land percentages. Figure 4 can be interpreted as supporting the view that migrants complement residents and play a constructive ecological role.

The Passerine-Nonpasserine Relationship

RECOGNITION OF THE RELATIONSHIP

Division of the Class Aves into two taxonomic entities, the order Passeriformes, or passerines, versus all the other orders, collectively termed the nonpasserines, permeates the ornithological literature. Many faunal works are organized into approximately equal halves, one of nonpasserines, the other of passerines. The 15-volume checklist of birds of the world, for example, was planned to consist of nonpasserines in the first seven volumes and passerines in the remaining eight (Mayr and Greenway, 1962). One reason is undoubtedly practical convenience. A second motivation could lie in the fact that authors generally agree on the sequence and content of the nonpasserine higher categories but disagree on family limits and arrangements in the passerines.

Because of the fossil record and certain features of their anatomy, it is assumed that the passerines were the last order to appear, that they are in the midst of a radiation complementing that of the true flowering plants, whereas many nonpasserines seem to have passed their peak, and that they have been evolving mostly as small arboreal perching birds which, having added seeds and nectar to the diet, have become dominant on land both in species and individuals (Amadon, 1957; Darlington, 1957; Storer, *in* Marshall, 1960). If reliance be placed on the estimates by Brodkorb (*in* Farner and King, 1971) of species numbers in the past, the passerine percentage of all birds has risen from 54.8 in the Pleistocene to 59.6 today.

"Passerine" and "nonpasserine" carry the connotation of ecological opposites. To some the terms imply an aggressive rivalry between adversaries, to others they perhaps bring to mind a dynamic balance in which the expanding passerines exert the greater counterpressure, and possibly to others they suggest a communal sharing of the environment under long-term or climax conditions. The following examples show how authors have seen fit to employ the passerine-nonpasserine relationship toward various ends.

Moreau (1966:94) divided the African avifauna into five "broadly ecological as well as taxonomic" groups: one of passerines, three of land nonpasserines, and one of water birds. This enabled him to point out that the nonforest fauna south of the Sahara contains more species of passerines than any other group and to conclude that passerines have on the average much smaller geographic ranges than nonpasserines. Winterbottom (1959: 40) found that in South Africa "a much higher percentage (61 as against 29) of the Non-passerines have a distribution all over the Ethiopian Region or beyond and therefore the Passerines are much more useful as indicating the faunal affinities of our birds." Not dissimilarly, Moreau (1966:112) compared African and South American families, genera, and species with the result that the degree of taxonomic affinity between the two regions was shown to be much greater in the nonpasserines than in the passerines.

Moreau (1966:10), noting "the fact that with . . . different techniques the number of families

recognized in the non-passerines remains almost unchanged, while the number of passerine families varies greatly, shows how much more imperfectly differentiated the passerines are," suggested "one possible interpretation . . . is that the passerine species . . . average much younger than those of other birds." Enlarging upon this premise, Moreau (1966:96) thought that "the passerines, as apparently the youngest and most rapidly evolving group of birds, would be the quickest to speciate in response to the vicissitudes of African ecology. Indeed, the proportion of passerine species which belong to superspecies, nearly two-thirds . . . probably greatly exceeds the proportion in other groups."

Lack (1968:11), in the style of Moreau, divided the Class Aves taxonomically into six ecological groups of subfamilies: one of passerines (93 subfamilies), two of land nonpasserines (94 subfamilies), and three of aquatic birds (49 subfamilies). Assuming the order Passeriformes to be the last to appear and the one which probably "did not start its adaptive radiation until the mid-Tertiary," Lack found, "fitting with this view, the distribution of passerine subfamilies is more circumscribed than that of many other nidicolous land birds, presumably in part because they have not had so long in which to spread."

Darlington (1957:254), on the other hand, wrote:

> That most species and genera (and families) of passerines are relatively limited in distribution is apparently not (or not entirely) owing to any peculiarities of classification or rate of evolution or geological age. Passerines are probably relatively recent birds, but many have been in existence long enough to spread over the world if they had the power to do so rapidly, as have the swallows. Apparently most do not have the power to do so, perhaps partly because they are mostly small birds.

Klopfer and MacArthur (1960) tried to equate passerines and nonpasserines with niche size and faunal diversity. On the basis of selected breeding-bird censuses, the authors obtained mean-abundance ratios of passerine individuals to nonpasserine individuals, indicating that "at all latitudes . . . non-passerines are less abundant than passerines." Their assumption that "the phylogenetically younger passerines . . . have a less limited central nervous capacity than the non-passerines and thus . . . [are] more capable of modifying their behavior to fit changing environmental stimuli" they interpreted "as support for the notion that the phylogenetically older non-passerine species are insufficiently plastic in their niche requirements to colonize temperate areas, tropical niches being smaller and less subject to change."

Regional Diversity and Climate

Globally the passerines comprise 66 percent of all the species of recent land birds (based on Austin, 1971), a ratio of two passerines to every nonpasserine. As to the zoogeographic regions, "modern comparative statistical details of their bird faunas are not readily available owing to the absence of good regional surveys" (Serventy, *in* Marshall, 1960:106). The statement largely still holds true, especially in the case of the Oriental region. The passerine percentages that can be derived from available regional and subregional faunal works, despite the great differences in area and faunal magnitude, closely approximate the global percentage (Figure 5). Malaysia and possible New Guinea appear to be somewhat out of alignment. Only these two of all the subregional entries are insular, and both lie in the direction of lower passerine percentage.

The largest continuous tropical areas and the largest avifaunas occur in the Neotropical and Ethiopian regions. Yet the former has twice as many species of land birds as the latter. Moreau (1966:145) was "inclined to find the basis for the present difference in the Pleistocene history," when the vicissitudes of climate affected wide areas of Africa in particular and caused the extinction of many species "so recently that there would have been only limited opportunities for subsequent evolution of new ones."

Keast (*in* Dobzhansky et al., 1972:269) contrasted the evolution in isolation enjoyed by most South American groups with the situation in Africa, where nearly all the avian families are shared with one or more of the other zoogeographic regions. Africa, in his view, has continually been receiving colonists that presumably were already highly efficient and competitive, and the avifauna has been built up as a stratified series of families occurring together, each of which "tended to become restricted, or confined, to the narrow zone where it was optimally efficient." Keast concluded (*in* Dob-

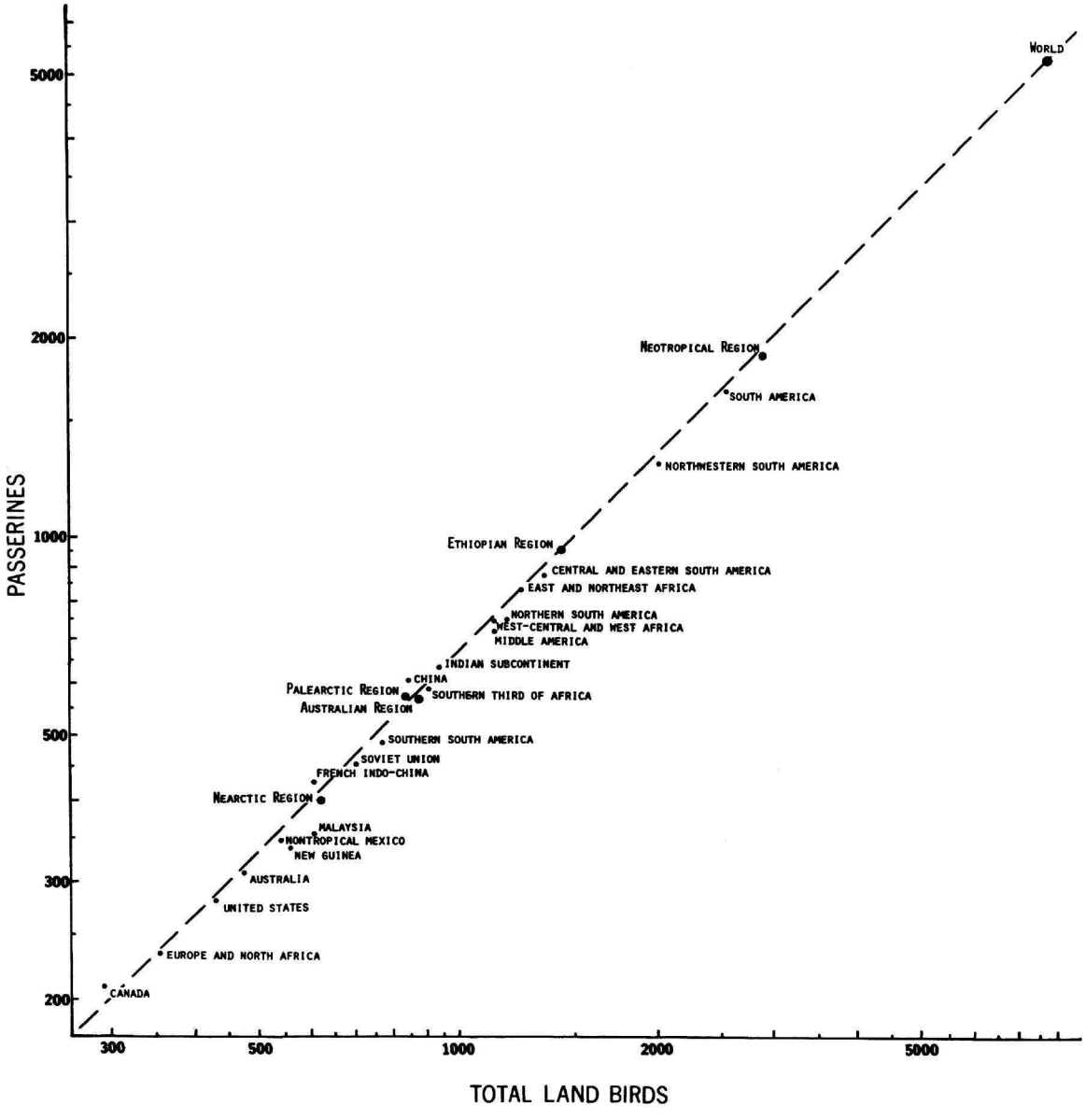


FIGURE 5.—Regional and subregional survey of the passerine percentages of the numbers of total land birds. (Dashed line = passerine-nonpasserine ratio of 2:1.)

zhansky et al., 1972:274): "It is apparent that all available ecological opportunities, and ways of life, are taken up on each continent."

Fittkau (*in* Fittkau et al., 1969:631), agreeing that humid-forest conditions remained relatively stable in South America, emphasized the drier climate in Africa: "The evolution of steppe, savannah and desert faunas has always had sufficient areas of appropriate environment at its disposal, whereas over wide areas the rain forest fauna that

was also formerly present has probably yielded because of increasing aridity." This was seconded by Keast (*in* Dobzhansky et al., 1972:272), who pointed to the "tremendous range of savannah-adapted animal groups in Africa where that vegetation type is particularly prominent."

On the other hand, "abundant evidence from many fields of research has recently begun to show that the Quaternary in both South America and Africa was a time of drastic climatic change" and that the inclination "to ascribe the discrepancy [in species numbers] to a supposed stabler climatic history in South America . . . we now know to be improbable" (Vanzolini, *in* Meggers et al., 1973: 255–257). Sufficient time has elapsed for speciation to have probably taken place both in Africa and South America from as recently as the late Pleistocene and post-Pleistocene (Haffer, 1969; Keast, *in* Dobzhansky et al., 1972; Moreau, 1966:10–11; Vanzolini, *in* Meggers et al., 1973).

Accepting neither climate nor gross ecology as affording any prominent clues, Vanzolini (*in* Meggers et al., 1973:255–257) attributed the discrepancy in species numbers to the increased opportunities for speciation made possible by a ring of humid-forested refuges around the Amazonian lowlands during dry climatic cycles compared to only two diametrically opposed humid refuges during dry cycles in the Congo. Evidently duplication and reduplication of species have occurred primarily under humid-forest conditions in the neotropics but less often under drier conditions in Africa. Moreover, biotic complexity may in itself be capable of generating further biotic complexity: "Interbiotic relationships apparently had increasingly profound effects on the evolution of floras in the Cretaceous and later. With more kinds of organisms involved in a variety of climatological, topographical, and biological combinations, conditions became ripe for the proliferation of evolutionary series culminating in the diversity manifested in the world today" (Delevoryas, *in* Meggers et al., 1973:19).

Nevertheless present-day climatovegetational factors can indeed be invoked to explain much of the present difference in faunal size. Wallace (*in* Thomson, 1964:516) long ago distinguished the Neotropical region "from all the other great Zoological divisions of the globe by the small proportion of its surface occupied by deserts, by the large proportion of its lowlands, and by the altogether unequalled extent and luxuriance of its tropical forests." Moreau (1966:145) thought the decisive element in the South American predominance, the abundance of evergreen forest birds (mainly suboscine), reflected the botanical situation: the African forest is poor and uniform relative to the tropical American forest, South America is some two and a half times richer floristically than Africa.

Africa, compared to South America, is a higher, drier continent. Much of eastern, central, and southern Africa lies above 1500 meters; frost is registered at least 100 nights a year, in some places at least 150, over much of the South African plateau, and occasionally damages nursery plants at 3000 feet in the Zambezi Valley only 18° from the equator; except for a few isolated spots, the equatorial rain belt receives only 2000–2500 mm of rain a year, much less than in parts of Amazonia or the East Indies; the greater part of Africa on both sides of the equator is dominated by extremely well-marked dry periods extending unbrokenly from five to nine months according to the area, deciduous vegetation (wooded savanna and steppe of various kinds) covers most of the region, and the seasonal contrast in appearance is very great (Moreau, 1966, chapt. 2). While "over most of its vast surface the influence of man on the vegetation has been great, both directly and indirectly, and overwhelmingly towards impoverishment," there have probably been few large-scale changes in geographical range as a result of the use or even the misuse of land in Africa, although that stage is beginning (Moreau, 1966:34, 36).

Habitat destruction may not yet have led to the extinction of species of birds on the African continent, but it has made comparisons of natural environments or analogous localities within Africa, or between Africa and other biogeographic regions, enormously difficult if not impossible. The Upper Guinea Forest in West Africa, formerly some 150,000 square miles in size, has probably less than half the area in "actual forest" and much of that in various stages of secondary growth following agricultural occupation; the Nigerian forest block, mapped as occupying nearly 50,000 square miles, appears to have hardly any primary forest left, while fully grown, tall secondary occurs only in patches; in the Congo, Chapin, 40 years ago, stated "the virgin forest has been devastated over wide areas"; only vestiges of Congo-type forest remain

in Angola and the East African lake region; vestigial forests along the East African coast "have suffered greatly in the last hundred years of 'development,' so that several species of birds discovered in them in the 1880's have not been found there since" (Moreau, 1966:102, 159–160). "Man, as a fire-raiser and especially as a cattle-keeper in modern times, has tended to push upwards the lower edges of the montane forests and greatly to change the nature of the other montane vegetation" (Moreau, 1966: 49).

In contrast to the discrepancy in numbers of species, the Neotropical and Ethiopian regions, respectively, have passerine percentages of 64.8 and 66.3 or, more usefully for comparative purposes, passerine-nonpasserine ratios of 1.84 and 1.96. Their tropical analogs, Brazil and the Congo, have corresponding ratios of 1.80 and 1.71. The rainforest avifaunas in the Amazon basin (compiled by me from Meyer de Schauensee, 1970) and in the Congo basin (compiled by Amadon, *in* Meggers et al., 1973) have respective ratios of 1.40 and 1.44. This parallel example of passerine-nonpasserine environmental convergence on either side of the Atlantic lends numerical support to a statement of belief such as the following: "The real value of comparative ecological studies covering different continents" is that "observations and data collected from one continent may be important and relevant to another, notwithstanding the fact that the faunas may be distinct taxonomically and their ecological similarities due to parallelism and convergence" (Brenan, *in* Meggers et al., 1973:4).

In the New World, Figures 2 and 6 trace the passerine proportion of the total land avifauna through North America from the Arctic Circle to Panama. If we exclude Greenland, the passerine percentages (Figure 2) are highest in the temperate zone, that is, continuously through the southern tier of Canadian provinces and virtually all of coterminous United States, except the Pacific Northwest (Washington, British Columbia, and Alaska); they are lowest south of the Isthmus of Tehuantepec at one extreme and also, apparently, in boreal to arctic Canada at the other extreme. Constructed from actual numbers of passerines and nonpasserines, Figure 6 illustrates how the passerine-nonpasserine ratio decreases from between 2:1 to 3:1 in temperate and boreal North America to around 1.5:1 in tropical Middle America; makes apparent the relatively large size of the avifauna in southwestern United States, particularly the large states bordering Mexico; and sets apart the small but avifaunally rich Central American states, especially the two southernmost, Costa Rica and Panama.

Mainland Environmental Correlations

Area and Complexity.—Figure 7 illustrates how continued subdivision of an area increasingly accentuates differences in the passerine-nonpasserine ratios of the smaller units which have been averaged out in the ratios of the larger units. Brazil was chosen because of its very large size, central position, few mountains, paucity of migrants, and fair to good species compilations for a number of states and territories. Subdivided into states and territories, Brazil has a ratio range between 1.3 and 2.0 (Figure 7*a*). When the states and territories are consolidated into the country's major geographic sectors, the ratio range becomes extremely narrow, between 1.5 and 1.7 (Figure 7*b*).

Colombia, in contrast to Brazil, is physiographically and environmentally a highly varied and complex Andean country. In the accompanying tabulation, the principal faunal sectors are ecological, hence have neither marked boundaries nor stipulated areas; passerine-nonpasserine ratios are followed by numbers of species in parentheses (compiled from Meyer de Schauensee, 1964).

Sector	*Total land birds*	*Native land birds*
Pacific	1.27 (419)	1.15 (384)
Caribbean	1.16 (332)	1.03 (305)
Central Mountain	1.84 (896)	1.77 (843)
Orinocan	1.34 (544)	1.22 (509)
Amazonian	1.64 (551)	1.52 (523)

Species allocations and counts are almost certainly inaccurate in a number of instances, owing to insufficient distributional information, whereas the ratios are less subject to error.

The "Central Mountain" ratios of 1.84 and 1.77, respectively, are probably representative of the sector: Cundinamarca (based on Olivares, 1969), a department in the heart of the massif, has corresponding ratios of 1.79 and 1.72. The 1.16 and 1.03 of the dry Caribbean sector agree with the 1.14 and 1.04 of the department of Atlántico (based on Dugand, 1947). The Amazonian sector, with ratios of 1.64 and 1.52, is paralleled by the 1.52 and

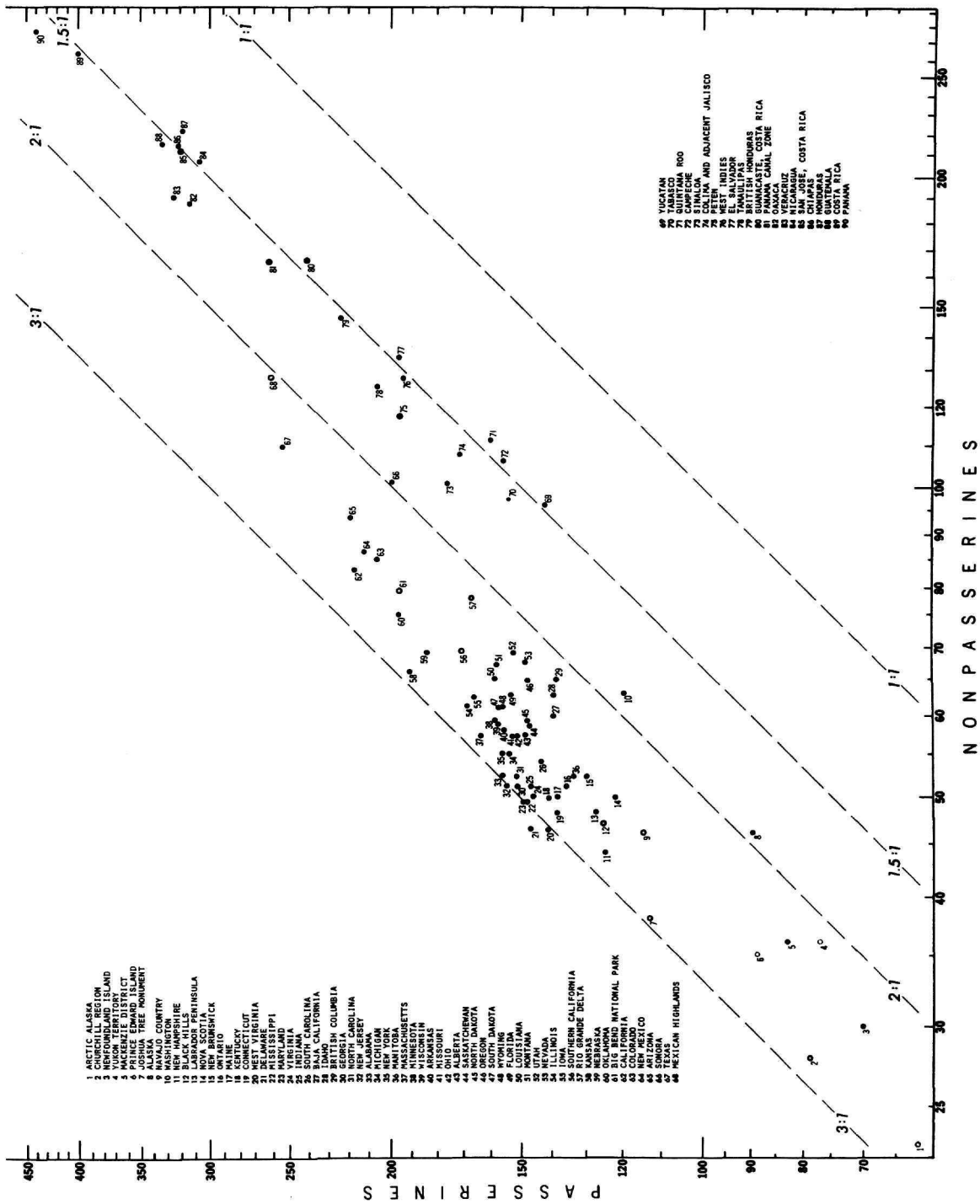


FIGURE 6.—Numbers of species of land birds in North and Middle America: passerines versus nonpasserines. (Dashed diagonals = passerine-nonpasserine ratios; solid circles = same political units (and islands) as in Figure 2; open circles = political units (and islands) additional to those in Figure 2; enclosed solid circles = political units contained within larger political units; enclosed open circles = nonpolitical units contained within larger units.)

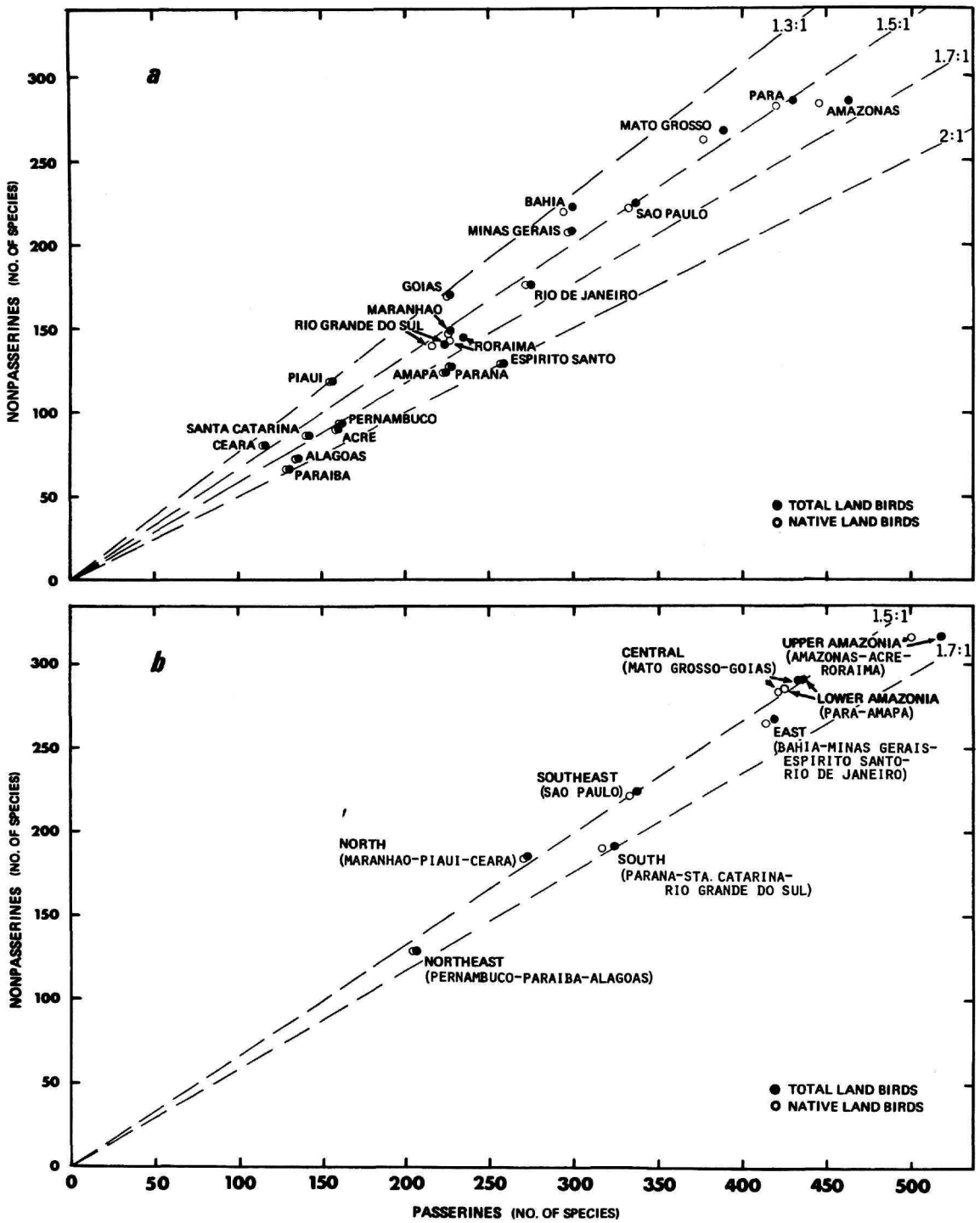


FIGURE 7.—Numbers of passerine and nonpasserine land birds in Brazil: *a*, per state or territory; *b*, per sector. (Dashed diagonals = passerine-nonpasserine ratios.)

1.41 of the commissary of Caquetá (based on Meyer de Schauensee, 1964) and the 1.54 and 1.51 of Amazonian Brazil (based on compiled sources). The 1.34 and 1.22 of the Orinocan sector are not so closely matched by the 1.51 and 1.39 of the intendancy of Meta (based on Meyer de Schauensee, 1964). I have no adequate comparative information for the Pacific sector.

ELEVATION.—Colombia (Meyer de Schauensee, 1964) and Venezuela (Phelps and Phelps, 1958, 1963), as well as isolated Santa Marta (Todd and Carriker, 1922), have their avifaunas distributed by their authors according to the altitudinal zonation of Chapman (1917); passerine-nonpasserine ratios are followed by numbers of species in parentheses. (See below.)

Ratio and elevation rise jointly from the tropical lowlands to the temperate highlands (excluding paramo). The midpoint between the two follows the 1500-meter mark, an altitudinal line of division that is paralleled in the mountains of southeast Asia, New Guinea, and east-central Africa. In the Congo basin (based on Schouteden, 1961–1966b), total land and native land ratios together range between approximately 1.15 and 1.45 in the lowlands. The easternmost province, Ituri, rises into humid-forested highlands, and both its ratios rise to 1.76.

Chapin (1932–1954, 65:98) saw similarities between the highland zone in the Congo and in Colombia, where Chapman's subtropical zone "is dependent upon abundant precipitation, whereas decreasing rainfall and increasing cold are responsible for the changes marking the temperate and Paramo zones" and, one might add, the same factors could be responsible for the fall in ratios. On Mt. Ruwenzori, between the Congo and Uganda, the native land ratio works out to 3.46 above 5000 feet (based on Chapin, 1932–1954, 65:252–256) or to 3.42 above 8000 feet (based on Weekes, 1949). In Uganda, the Bwamba "lowlands," at an elevation of 2200–3500 feet, have a ratio of 1.35 (based on Friedmann and Williams, 1971); the Impenetrable Forest area has a ratio of 1.69 at 3500–4000 feet, 2.75 at 8000 feet, and 3.79 when restricted to typically montane species (based on Keith et al., 1969). In Kenya, the coastal Sokoke Forest has a ratio of 1.17, the Kakamega Forest area at 5000 feet has a ratio of 1.85 (based on Ripley and Bond, 1971). The ratio for strictly montane species at Kakamega is 3.25 (based on Zimmerman, 1972).

Another sort of example comes from three "island" mountains in Portuguese East Africa (Vincent, 1934). These have species numbers of 48, 68, and 65 and ratios of 3.00, 2.24, and 2.61. Taken together, the number of species rises to 104 and the ratio falls to 1.89. Isolated Santa Marta (tabulated above) bears a similar relation to the Colombian or Venezuelan highlands taken as a whole. It appears that a list of the species actually recorded from a locality reflects the environment more faithfully than does a combined, compiled, much less an assumed, list from a large area.

ARIDITY.—If the entire North American continent be taken as an example, the distribution of passerine-nonpasserine ratios of the native land avifaunas shows a gross correlation with general environment (Figure 8). The plains states and provinces of the United States and Canada are conspicuous in having the lowest ratios, ranging from around unity (1:1) to well below unity. The highest ratios, as well as highest species numbers (Figure 6), are concentrated in mountainous southwestern United States and adjoining northwestern Mexico. South of the Isthmus of Tehuantepec, the ratios are lowest in the dry Pacific lowlands, in the Yucatan Peninsula, and in the arid interior of Caribbean Guatemala.

The few comparative data that are available for dry areas in South America also have low ratios, that is, they approach unity and are much lower than in humid areas. These are the department of Atlántico in Caribbean Colombia (Dugand, 1947), with a ratio of 1.04; the interior of northeastern Venezuela (Friedmann and Smith, 1950, 1955), with a ratio of 1.06; Santa Elena peninsula in

	Total land birds		*Native land birds*		
	Columbia	*Venezuela*	*Colombia*	*Santa Marta*	*Venezuela*
Tropical (0–1500 m.)	1.56 (1149)	1.58 (868)	1.48 (1082)	1.34 (311)	1.51 (822)
Subtropical (1500–2600 m.)	1.79 (570)	1.82 (583)	1.72 (532)	1.67 (193)	1.75 (552)
Temperate (2600–3400 m.)	1.81 (253)	1.77 (130)	1.65 (230)	3.22 (39)	1.64 (124)
Paramo (3400 m. to snow line)	1.22 (40)	2.00 (27)	1.31 (37)	2.33 (10)	1.67 (24)

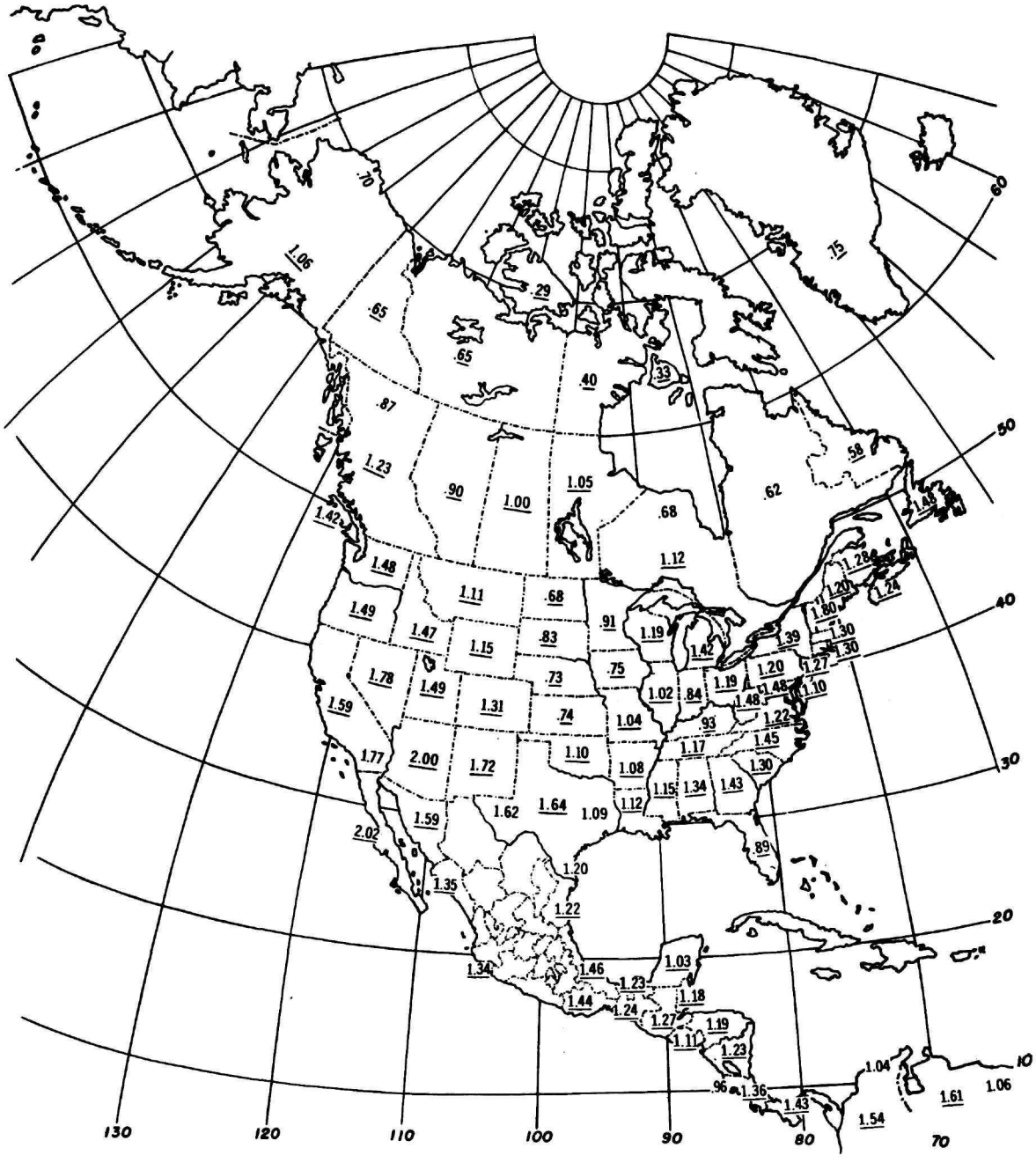


FIGURE 8.—Passerine-nonpasserine ratios of resident land avifaunas in North and Middle America and adjacent South America. (Numbers not underlined = nonpolitical areas.)

southwestern Ecuador (Marchant, 1958), with a ratio of 1.05; Mollendo District in southwestern Peru (Hughes, 1970), with a ratio of 1.04.

A "peninsular" effect, identified by Simpson (1964: 74) with reduced species densities of North American mammals on large peninsulas, would appear to belong in this section. The resident birds likewise drop markedly, not only in species density, as do the mammals, but also in passerine-nonpasserine ratio in Florida and the Yucatan Peninsula (Figure 8). Florida and the Yucatan Peninsula mostly consist of physiographically undramatic lowland and the vegetations display a monotonously simple physiognomy. This is reason enough to make them predictably poor in variety of habitats and numbers of species. The very low ratio in Florida could correspond to that in the featureless plains states, in the Yucatan Peninsula to that in other dry neotropical lowlands.

Two possibly "peninsular" areas are brought to conjectural light solely on account of their ratios. One is the mountainous Honduran "hump," jutting into the Caribbean Sea between the Yucatan Peninsula and the Nicaraguan lowland "break" (Figure 8), with a relatively low ratio compared to neighboring units. The other is low-lying northeastern Pará, opposite the Amazon delta, with a relatively very low ratio of 1.14 (based on compiled data). Both, however, have species densities at least as high as if not higher than those in adjoining areas.

Costa Rica.—*Altitude and Climate:* Smaller, better-known units are preferable to larger, less well-known units if the object is to make faunal and environmental comparisons. Costa Rica may be more useful in this respect than any other neotropical country. I have species lists for a number of altitudinally representative "areas" or localities (Table 3), few of which have been delimited or described. They differ from one another in size, topography, climate, exposure, diversity, and thoroughness of inventory. I chose them because they appear to have at least minimally adequate species totals per Holdridge life zone (formation). (See Slud, 1964a, map.) Preference was given when possible to places reported upon more than once as more likely to have balanced lists than those known from a single visit.

The localities in the relatively dry northwest Pacific lowlands (TD) have the nonpasserine proportion (50 percent or more) of the native land avifauna so much larger than in the other life zones (formations) that they form a distinct group.

All the rest of the country, comprising some 85 percent of the national territory, is humid, and the species of passerines outnumber the nonpasserines. The localities in the tropical, or basal, belt (TM, TW) have the lowest ratios, averaging 1.50 for native land birds and 1.75 for total land birds (Tables 3 and 4). A rise to 1.60 or more roughly corresponds to an actual rise in elevation from the coastal plain onto foothills or ridges and reflects the inclusion of some subtropical species.

The subtropical tier of localities (SW) is characterized by a rather abruptly higher set of ratios, particularly along the Caribbean slope. A corroborative exception is the Turrialba-Angostura area, located just inside the subtropical belt on the Holdridge ecological map of 1959 (see Slud, 1964a), which has since been found to occupy a Tropical Moist (TM) transitional enclave in a revised version (Tosi, 1969). Compared to the Caribbean side, a lowering in subtropical ratios at analogous altitudes and topographies on the Pacific slope is probably related to the difference in climatic regime.

The lower-montane belt (LMW, LMR) succeeds the subtropical belt altitudinally and complements it faunally. The two belts have species that are characteristic of, but not exclusive to, one or the other as well as species that normally range upward or downward from either. Unfortunately, the lower-montane entries are few in number and have poor data. It is upon this unsatisfactory basis that these appear to have somewhat higher average ratios than do the subtropical entries.

The lower-montane belt is even more closely allied to the montane belt (MR), to the extent that a faunal resemblance formula favoring similarity would find them virtually identical. Together these two belts comprise a homogeneous unit in that they completely share a species complex undergoing depletion with increasing altitude: no bird in the montane belt has not also been reported from the lower-montane belt. This does not mean that typically montane species are not more common, even ubiquitous, at montane-belt elevations, where they form a distinctive assemblage. The montane-belt entries (Table 3), of which there are only two, fall so sharply in value that, in a manner of speaking, they counterbalance the lowest ratios in the basal

belt. The decreasing size of the passerine proportion would appear to correspond to the decreasing complexity of the montane forest with increasing altitude and to the inclusion, at Cerro de la Muerte, of treeless paramo.

FOREST: The countrywide effect of forest on the passerine-nonpasserine ratios of the native avifauna at localities in Costa Rica is not readily apparent. In general, forest-bird ratios do tend to increase with increasing rainfall horizontally in the lowlands and with decreasing temperature vertically into the highlands. My information is limited to a small number of unreplicated samples in which I indicated at the time of my visit the species that in my opinion were primarily forest birds within the context of the local conditions (Table 5). On the Pacific slope, from the subhumid north to the humid south, passerine-nonpasserine ratios are consistently lower for nonforest birds than for forest birds or for the entire local avifauna. These Pacific localities have in common as a possible causative factor a monsoon-type seasonal climate.

On the Caribbean slope, localities in the tropical and subtropical belts often have a higher ratio for nonforest birds than for forest birds or for the entire local avifauna. The large proportion of these instances on the heavily wooded Caribbean side might appear to be the opposite of what would be expected, namely, higher passerine-nonpasserine ratios in forest than in nonforest. Here, however, the extremely humid climate, lacking an effective dry season, is responsible for an aboriginal "rain"-forest cover that even when disturbed has not until recently begun to be penerated to appreciable extent by species from open-country biotopes. Indeed, tree plantations, regenerating clearings, and shrubby secondary and and broken primary growth are richer in opportunities for arboreal, predominantly passerine birds than is closed lowland forest. The apparent exceptions are the very places it could be rewarding to investigate comparatively.

In the Old World, by way of comparison, I have only two forest versus nonforest examples, both of them areal compilations rather than local samples, from Africa. There, as elsewhere, the authors have their own interpretations of the terms forest and nonforest. The Impenetrable Forest area in Uganda (Keith et al., 1969), occuping about 150 square miles, has a native land passerine-nonpasserine ratio of 2.52 for forest species and 2.22 for forest species plus nonforest species in forest, 1.73 for nonforest species and 1.50 for nonforest species plus forest species in nonforest. The entire African breeding land avifauna south of the Sahara (Moreau, 1966) has a lowland forest ratio of 1.75 and a lowland nonforest ratio of 1.70, a montane forest ratio of 4.00 and a montane nonforest ratio of 2.48.

Recency of Compilation: A later or more complete compilation tends to have a lower passerine-nonpasserine ratio than does an earlier or less complete compilation, irrespective of the size of the unit. Put another way, the larger the number of contributing samples the smaller will be the passerine proportion, especially among the residents. This is exemplified by the Central American units that have more than one published checklist: Guatemala, Honduras, Costa Rica, Panama Canal Zone, and Barro Colorado Island (Table 4). The disparity is usually greater still between a compilation and a sample, as exemplified by the Costa Rican localities in the same table.

In the case of Costa Rica and Honduras, the early checklists were far from complete, yet were already sufficiently representative to be in passerine-nonpasserine equilibrium. The two field stations, Barro Colorado Island and Finca La Selva, are also well enough known for their ratios to be in equilibrium, at least for the resident avifauna, and neither is likely to change without extensive alteration of the environment. At Barro Colorado, the recent slight increase in total land bird ratio reflects a mounting record of scarce passerine migrants, which the addition of a nonpasserine or two would reverse.

Among native land birds, the one clear instance of a locality in which the compilation has a higher ratio than the sample is the Villa Mills-Cerro de la Muerte entry, but only in one of six monthly samples (Table 4). Among total land birds, there are fewer than a handful of such instances: the General Valley and Monteverde when migrants were absent, Taboga during the "mid-winter" lull, and Villa Mills-Cerro de la Muerte during the same monthly visit mentioned above.

Limitations of Knowledge: Species distributions in general works are incomplete or inexact, overly broad and insufficiently detailed. Belts vary in width and elevation and are apt to be disjunct. The composition of the corresponding avifaunas varies accordingly, and many species are included on assump-

tion. A species found once or at one place can enter into a count as though it were a commonly known, widespread inhabitant. If recorded from separated points, its political or ecological occurrence either horizontally or vertically anywhere between may or may not be taken for granted. So many decisions if not guesses must be made by the person trying to compile distributional categories from a faunal work, intended merely as a digest or guide by its author, that a second set of totals taken from the same material will seldom turn out the same as the first. The ratios, manifestly so precise, have been derived from the species totals, which have been synthesized from sources that in turn often depend upon other sources.

In Costa Rica, a word should be said about the two Tropical Wet localities, Rincón de Osa on the Pacific side and Finca La Selva on the Caribbean side (Table 4). Rincón de Osa has a larger area, more complex topography, more seasonal climate, taller and "richer" forest, and more habitats, yet its bird list is considerably shorter, not for want of observers, than at Finca La Selva. On the other hand, a survey I made at Rincón de Osa, where I was unacquainted, resulted in a list that was not much shorter than ones I had obtained in surveys of comparable length at Finca La Selva, which I knew quite well. It is conceivable from this, the only evidence at hand, that the number of occupied niches may be approximately the same at any moment in both places.

The little information that is available for the damp and chilly Costa Rican highlands is neither comprehensive nor precise, and it rapidly decreases in quantity with increasing elevation. Probably the lower-montane and especially the montane ratios are too low. I may have unwittingly excluded quite a few subtropical passerines from both these belts, as in Table 8, simply because so little is known of their distributional limits, and included as residents certain nonpasserines that are actually visitors. A number of species, particularly among the nonpasserines, are scarce, scattered, secretive, or otherwise hard to find, while wind, rain, and mist often severely hinder observation. Species recorded during different trips usually differ from one another more in the highlands than at lower, warmer elevations. Native birds that rise seasonally to higher altitudes, even if no more abundant in species than those moving downward, produce a proportionately greater numerical impact on the highland counts than do the latter on the lowland counts. Whether compiled, sampled, or made the objects of special study, the status of a number of kinds as temporary or permanent inhabitants of the belt, let alone the site, is not known. Local horizontal movements by some, either alone or mixed with others and casually or opportunistically noted, can further affect already imbalanced results. Only when proper attention is paid to representative points will suitable comparative data be forthcoming.

Islands

Insular avifaunas tend to correlate in size with the area of the island, but only in a general way. Equal-area islands that appear to be similar to each other ecologically and are similarly situated with respect to the mainland are richer in native land birds in equable warm climates than in seasonally inhospitable climates. Tropical islands are largely populated opportunistically by colonizer species arriving from areas with climates and, inferentially, ecologies that are like their own. Land migrants in the tropics originate almost entirely from outside the tropics, colonizers from inside the tropics. Invasion of the mainland by insular taxa is at best local or coastal and seldom successful.

Islands are the preferred source of area-species formulations, if only because of their clearly bounded insularity and the apparent lack of success with mainland situations. Islands come closest to constituting discrete, independent ecosystems or natural laboratories: this makes islands desirable for the study of geographic variation. Insular biotas, however, conform to no universal standard and their compositions are each the unique result of interplay among many factors that are differentially peculiar to islands: this makes islands synecologically nonintercomparable. Moreau (1966:309), for example, stated he would not follow uniform lines when discussing the islands around Africa, "since the circumstances of each African island or archipelago differ a good deal."

If it be assumed that islands do not differ environmentally from comparable mainland under similar conditions, the impoverishment of insular avifaunas becomes a reflection of unfilled niches owing to difficulties of overwater colonization. But if it be assumed, as by Lack (1970), "that the primaeval

habitats on islands are 'ecologically full' so far as birds are concerned, and that the reduced numbers of bird species are due to ecological impoverishment, as exemplified by the reduced numbers of plant species (with which the numbers of bird species are correlated)," an impoverished avifauna is the sign of an impoverished biota.

Vegetations in different biogeographical regions have evolved similar physiognomies in response to correspondingly similar climatic conditions on the mainland. Modifying the physiognomy is the number or variety of species in the association or community. Islands, on the other hand, can be similar to one another in size, age, physiography, and climate, but, owing to the degree to which they are inaccessible to potential colonizers, can have widely divergent numbers and constellations of species. Some islands are relatively more impoverished than others. Compared to the mainland, they are all impoverished botanically and altered physiognomically. Only the mainland is in full flower, so to speak, and it is there that environmental standards must be formulated and established.

Area, Species, and Ratio

AREA-SPECIES.—Figure 9 is the usual double-log representation of area-species distributions which has become current in the literature. Here it is restricted to single islands, whether alone or a member of an island group, in tropical and subtropical waters around the globe, including the southwestern Pacific Ocean. Not included are the myriad islets for which information is lacking, also islands at high northern latitudes where species of native land birds are few and their resident status is often unknown or hard to decide. The few entries that, for islands, have high counts are situated on continental shelves and, except Trinidad, are mostly large. Islands with very low counts are mostly small. Both kinds follow a weakly rising gradient. Viewed in toto, the entries combine a decelerating increase in number of species with an accelerating increase in area.

The same array acquires a different appearance on semilog paper (Figure 10). Most of the islands under 1000, and all under 100, square miles have fewer than 50 species of land birds. The proportion of islands with more than 50 species suddenly rises near the 1000-square-mile mark; even so, few islands of less than 1000 square miles have as many as 100 species and none reaches 150. The acceleration and the abruptness of the increase are both contrary to what happens on the mainland. (Intra-island comparisons, however, may duplicate if not exaggerate the mainland situation: Borneo has 367 land species and a ratio of 1.30; Sabah [North Borneo], one-tenth as large, has 95 percent of the species and the same ratio.) More than one-fifth of the islands from approximately 1000 to over 50,000 square miles in area continue to have fewer than 50 species; against this background, Trinidad (number 122), a tropical continental island, is outstandingly rich. Upward from about the 7000-square-mile mark (an area smaller than Israel), the number of entries decreases drastically with increasing area. The large, luxuriant, tropical continental islands (Ceylon, the individual Greater Sundas, and New Guinea) follow a gradient of increasing species numbers; the others, barely excepting perhaps Mindanao and Luzon and possibly Celebes, do not.

Figure 11 is a semilog survey of tropical, subtropical, and southern-hemisphere island groups containing at least two islands. In overall appearance it differs little from that of the single islands. The majority of the entries fit between the 100 and 10,000 square-mile marks: those under 500 square miles have less than 50 species; those between 500 and 10,000 square miles in size include fewer than a handful with 100 or more species, and only one of these, just barely, exceeds 150 species. The 10,000 square-mile mark represents a dividing line between island groups with small avifaunas and those with large avifaunas. Large-size island groups are few, and they follow a steep species-number slope.

AREA-RATIO.—Area-ratio distributions of the single islands (Figure 10) are for the most part rather evenly dispersed within a horizontal band spreading across the survey from the smallest to the largest island; those of the island groups slant very slightly upward (Figure 11). Insular passerine-nonpasserine ratio thus appears to be largely independent of island size or number of species. Rather, it is related to or modified by the type of island, its age, its position with respect to faunal sources and interchange with other islands, secondary differentiation of its avifauna, and the local environment.

Islands having generally similar topographic and biotic conditions are often, though not always,

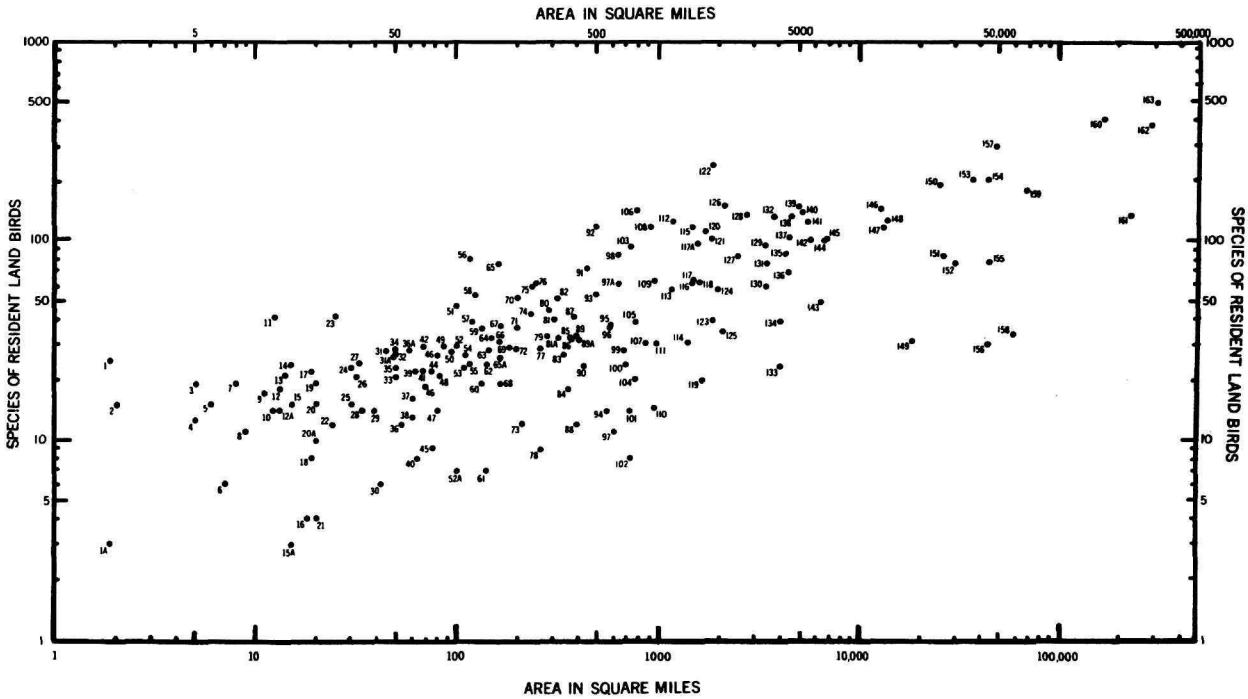
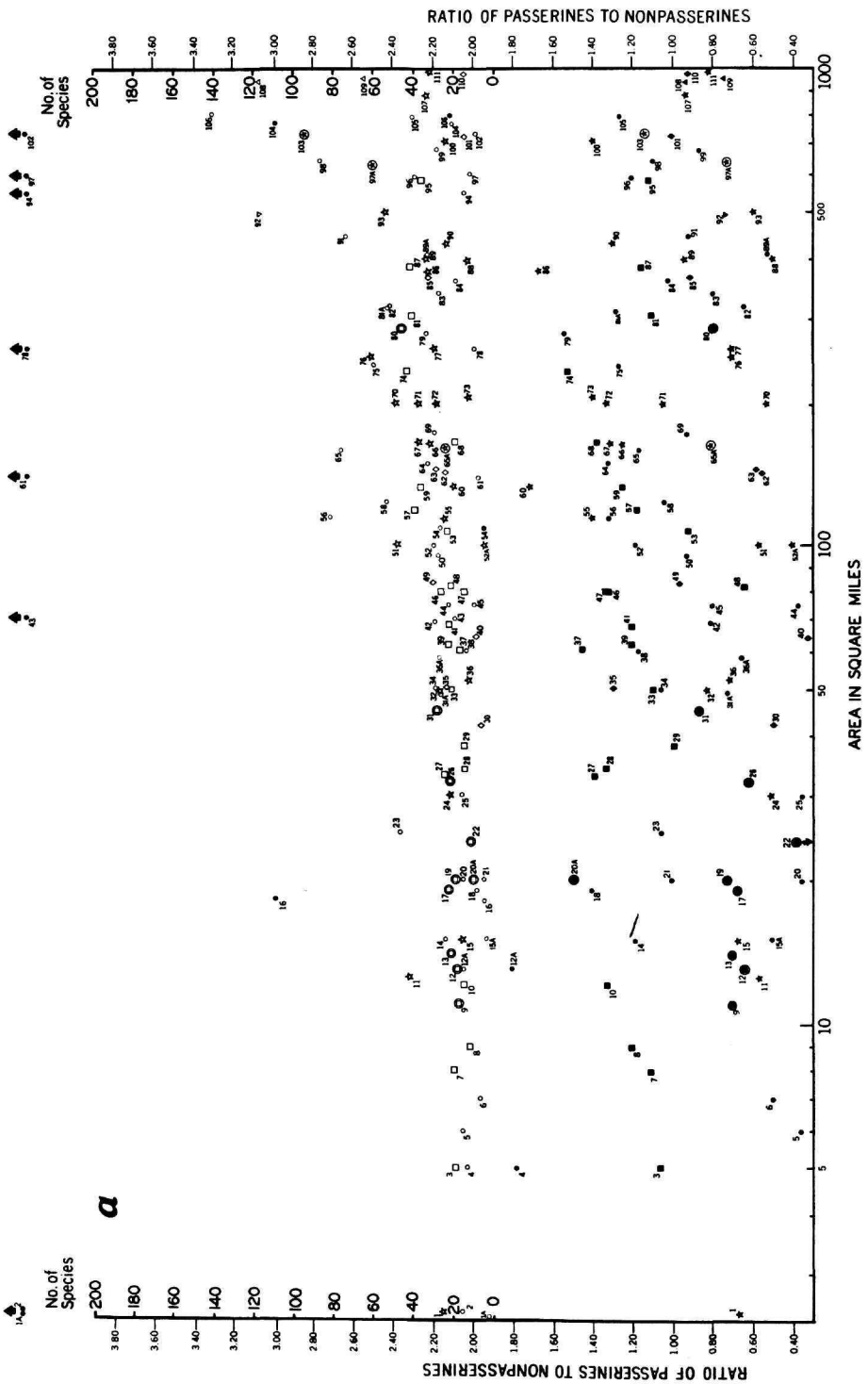


FIGURE 9.—Area-species distribution of single islands (including New Zealand and Tasmania) in the warmer oceans. (1, Santa Ana (Solomons); 1A, Laysan; 2, Jervis (Galapagos); 3, Saba; 4, Lord Howe; 5, Barbareta; 6, Annobon; 7, St. Eustatius; 8, Old Providence; 9, Anegada; 10, St. Andrew; 11, Gizo; 12, Virgin Gorda; 12A, Norfolk; 13, Culebra; 14, María Cleofas; 15, Mono; 15A, Henderson; 16, Cocos (E. Pacific); 17, St. John; 18, Bermuda; 19, Tortola; 20, Utila; 20A, Cayo Largo; 21, Clarion; 22, Mona; 23, San José (Pearl Is.); 24, Nissan; 25, Guanaja; 26, St. Thomas; 27, Montserrat; 28, Anguilla; 29, St. Martin; 30, Rodriguez; 31, Vieques; 31A, Car Nicobar; 32, Aneiteum; 33, Nevis; 34, María Magdalena; 35, Principe; 36, Tutuila; 36A, Camorta; 37, Marie Galante; 38, Aldabra; 39, Barbuda; 40, Christmas (Indian Ocean); 41, St. Kitts; 42, Aruba; 43, Charles; 44, Roatan; 45, Socorro; 46, Grand Cayman; 47, Guadalupe; 48, St. Croix; 49, Moheli; 50, Bonaire; 51, Rendova; 52, María Madre; 52A, Niue; 53, Antigua; 54, Hierro; 55, Aurora; 56, Tobago; 57, Grenada; 58, Cozumel; 59, St. Vincent; 60, Ponape; 61, Lanai; 62, Mayotte; 63, Anjouan; 64, Gomera; 65, Coiba; 65A, Enggano; 66, Kandavu; 67, Taveuni; 68, Barbados; 69, Curaçao; 70, Vella Lavella; 71, Efate; 72, Pentecost; 73, Guam; 74, St. Lucia; 75, Mafia; 76, Kolombangara; 77, Tanna; 78, Molokai; 79, Palma; 80, Gonave; 81, Dominica; 81A, São Tomé; 82, Pemba; 83, Lanzarote; 84, São Tiago; 85, Gran Comoro; 86, Ambrym; 87, Martinique; 88, Tahiti; 89, Rennell; 89A, Great Nicobar; 90, Upolu; 91, Margarita; 92, Basilan; 93, New Georgia; 94, Kauai; 95, Guadeloupe; 96, Gran Canaria; 97, Oahu; 97A, Simalur; 98, Zanzibar; 99, Fuerteventura; 100, Savaii; 101, Mauritius; 102, Maui; 103, Bunguran; 104, Indefatigable; 105, Tenerife; 106, Fernando Po; 107, Erromanga; 108, Japen; 109, Biak; 110, Reunion; 111, Malekula; 112, Waigeu; 113, Isle of Pines; 114, Socotra; 115, Bohol; 116, Choiseul; 117, Santa Isabel (Solomons); 117A, Nias; 118, San Cristobal (Solomons); 119, Albemarle; 120, Cebu; 121, Lombok; 122, Trinidad; 123, Espíritu Santo; 124, Malaita; 125, Vanua Levu; 126, Bali; 127, Guadalcanal; 128, Leyte; 129, Buru; 130, Puerto Rico; 131, Bougainville; 132, Mindoro; 133, Hawaii; 134, Vitu Levu; 135, Sumba; 136, Jamaica; 137, Panay; 138, Palawan; 139, Negros; 140, Samar; 141, Flores; 142, Sumbawa; 143, New Caledonia; 144, Ceram; 145, Halmahera; 146, Hainan; 147, Timor; 148, Taiwan; 149, Isla Grande (Tierra del Fuego); 150, Ceylon; 151, Tasmania; 152, Hispaniola; 153, Mindanao; 154, Luzon; 155, Cuba; 156, North Island (New Zealand); 157, Java; 158, South Island (New Zealand); 159, Celebes; 160, Sumatra; 161, Madagascar; 162, Borneo; 163, New Guinea.)

members of chains or archipelagos and tend to follow the same area-ratio tier (Figure 10): Lesser Antilles, Greater Antilles, Sundas (the larger islands on a higher level, the smaller islands on a lower level), Philippines, Solomons, French Polynesia; far above lie islands of the Hawaiian and Galapagos groups, all with very high ratios; the few higher northern-latitude islands which have


RATIO OF PASSERINES TO NONPASSERINES
No. of Species
AREA IN SQUARE MILES
a

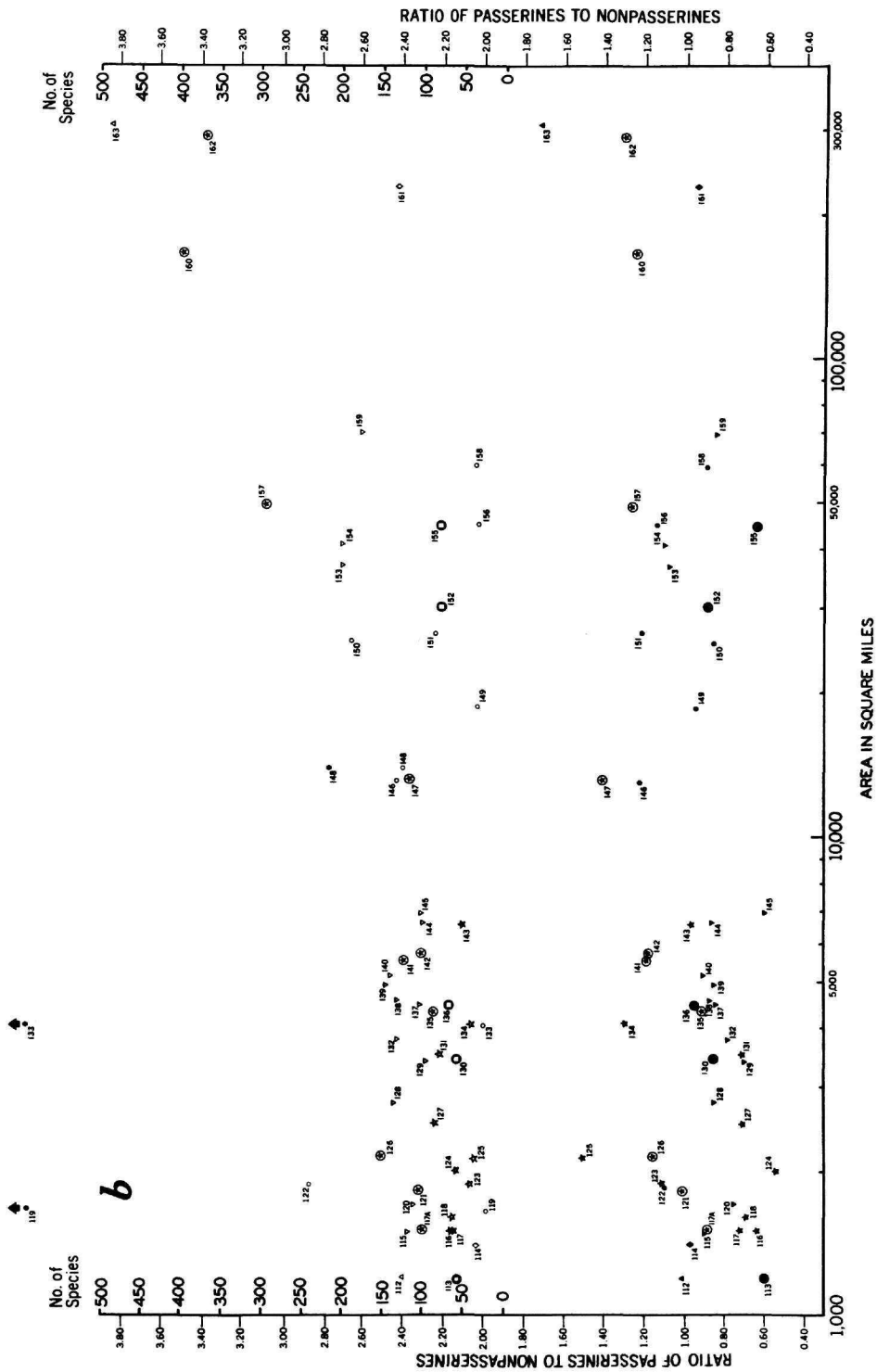


FIGURE 10.—Area-species and area-ratio semilog distribution of single islands: *a*, species numbers scaled in twenties; *b*, species numbers scaled in fifties. (Entries the same as in Figure 9; open symbols = numbers of native land species, solid symbols = passerine-nonpasserine ratios. Symbols are: star in circle = Sunda Islands; triangle pointing downward = Moluccas-Celebes-Philippines; triangle pointing upward = New Guinea area; star = southwest Pacific; square in circle = Greater Antilles and Virgins; square = Lesser Antilles and western Caribbean; diamond = Indian Ocean; small circles = all others.)

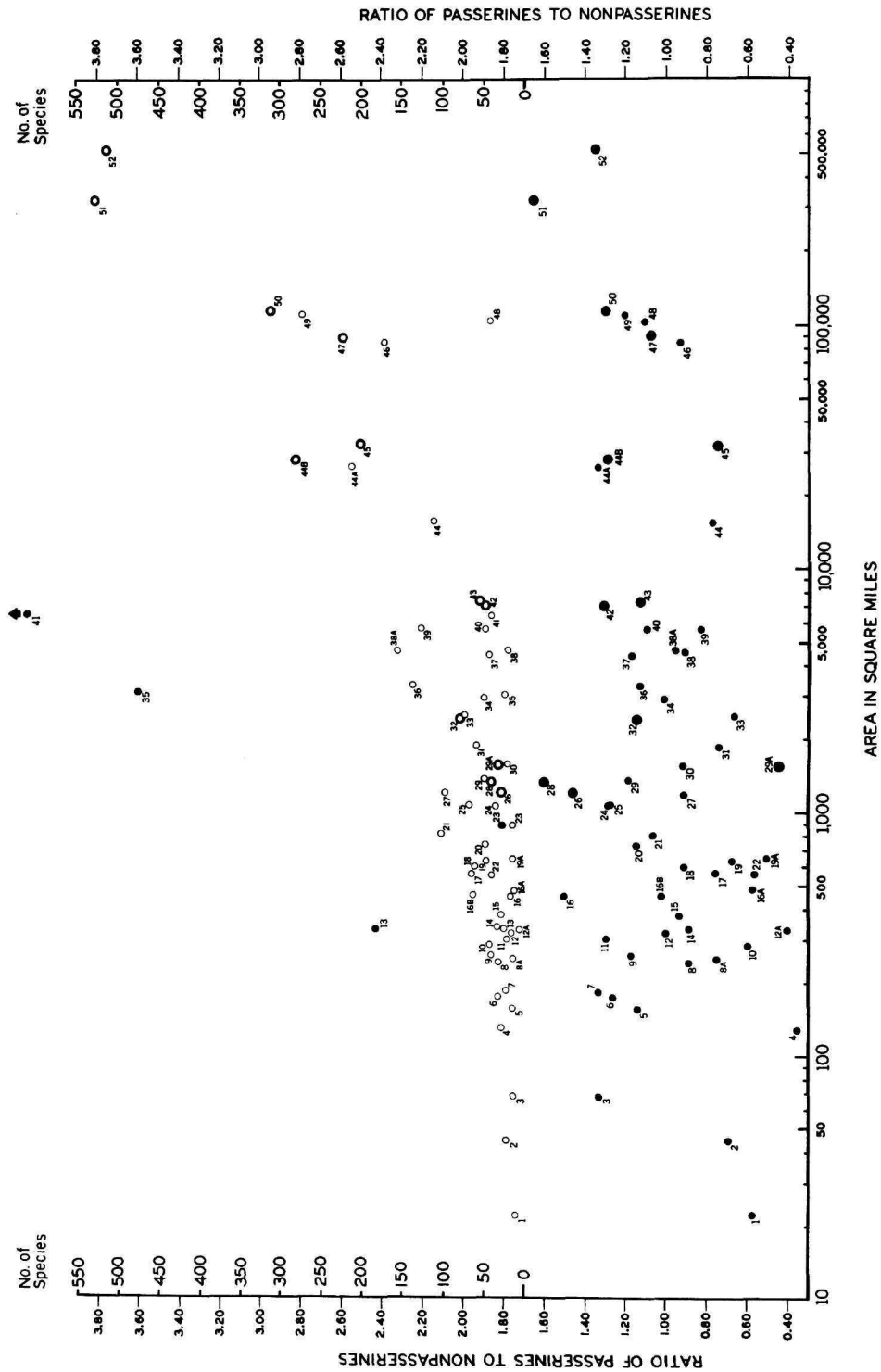

RATIO OF PASSERINES TO NONPASSERINES
No. of Species
AREA IN SQUARE MILES
10
50
100
500
1,000
5,000
10,000
50,000
100,000
500,000

FIGURE 11.—Area-species and area-ratio semilog distribution of island groups (including New Zealand) in the warmer oceans. (Open circles = numbers of native land species; solid circles = passerine-nonpasserine ratios; double circles = a smaller group and larger group to which it belongs. 1, Manua; 2, Lau; 3, Aldabra; 4, Bay Is. of Honduras; 5, Seychelles; 6, Tres Marías; 7, Palau; 8, Virgin; 8A, Tonga; 9, Anamba; 10, Kangean; 11, Madeira; 12, Revilla Gigedos; 12A, Tuamotu; 13, Caroline; 14, Dutch Leeward; 15, Santa Cruz (southwest Pacific); 16, Mariana; 16A, Marquesas (South Pacific); 16B, Pearl; 17, Kei; 18, Louisiade; 19, Nicobar; 19A, Society; 20, Comoro; 21, Natuna; 22, Admiralty; 23, Azores; 24, Loyalty; 25, Windward (Lesser Antilles); 26, Samoa; 27, D'Entrecasteaux; 28, Micronesia; 29, Leeward (Lesser Antilles); 29A, French Polynesia; 30, Cape Verde; 31, Sula; 32, Lesser Antilles; 33, Andaman; 34, Canary; 35, Galapagos; 36, Aru; 37, Bahamas; 38, Falkland; 38A, West Sumatra; 39, Palawan; 40, New Hebrides; 41, Hawaii; 42, Fiji; 43, New Caledonia; 44, Solomon; 44A, Lesser Sunda (excluding Bali and Kangean Is.); 44B, Lesser Sunda (including Bali and Kangean Is.); 45, Moluccas; 46, Greater Antilles; 47, West Indies; 48, New Zealand; 49, Philippine (excluding Palawan); 50, Philippine; 51, New Guinea; 52, Greater Sunda.)

been included also tend toward higher ratios, as do mainland areas. Passerine-nonpasserine ratios of island groups likewise tend to remain stable rather than rise with island size or species numbers (Figure 11).

RATIO.—An attempt was made to formalize the relation of the passerines to the nonpasserines on single islands and on island groups by plotting the logarithms of the numbers of passerines against the logarithms of the numbers of nonpasserines and subjecting them to regression analysis.

For single islands, the complete set of entries that appears in Figure 10 produced these values: for the regression of Y (passerines) on X (nonpasserines), 0.33 for the Y-intercept, 0.85 for the regression slope, and 0.05 for the variance of estimate of Y on X; the correlation coefficient was 0.84. Thus, for a given number of nonpasserines, say, 100, the predicted mean number of passerines rounds to 75. Seventy percent of the known variation in the number of passerines is explainable by the number of nonpasserines.

Deleting the very small entries, i.e., those with less than a minimum of ten species of passerines or nonpasserines, and those lying outside the tropics, the remaining 116 entries produced these values: for the regression of Y (passerines) on X (nonpasserines), 0.075 for the Y-intercept, 0.94 for the regression slope, and 0.016 for the variance of estimate of Y on X; the correlation coefficient was 0.92. For a given number of nonpasserines, say, 100, the number of passerines rounds to 94. Eighty-five percent of the known variation in the number of passerines is explainable by the number of nonpasserines.

For island groups (Figure 11), excluding those with fewer than ten species of passerines or nonpasserines, the values were these: for the regression of Y (passerines) on X (nonpasserines), 0.005 for the Y-intercept, 0.996 for the regression slope, and 0.015 for the variance of estimate of Y on X; the correlation coefficient was 0.95. In other words, the regression line, bisecting the graph into almost exactly equal halves, represents a near-perfect 1:1 ratio of passerines to nonpasserines. For a given number of nonpasserines, say, 100, the predicted mean number of passerines rounds to 100. Ninety percent of the known variation in the number of passerines is explainable by the number of nonpasserines.

Several of the above entries, however, form part of larger entries or incorporate smaller ones—for example, the Lesser Antilles and its two components, the Windward Islands and the Leeward Islands, were entered as separate entities—while another, New Zealand, lies well outside the tropics. But even when the list is purged of these elements (numbers 11, 18, 25, 27, 29, 36, 47, 48 in Figure 11), the 34 island groups that remain yield virtually the same values as before: -0.02 for the Y-intercept, 1.009 for the regression slope, 0.017 for the variance of estimate of Y on X, and 0.94 for the correlation coefficient. If the given number of nonpasserines is 100, the predicted mean number of passerines rounds to 100. Eighty-nine percent of the known variation in the number of passerines is explainable by the number of nonpasserines.

The above results, ultimately derived from simple species lists, make it appear that the predictable ratio of native land passerines to nonpasserines is almost exactly 1:1 on island groups in the warmer oceans and seas around the globe, irrespective of such contributory factors as area, distance, origin, ecology, number and variety of islands, or size of avifauna. Island groups are preferred to single islands for regression analysis on the assumption that an island group, taken as a whole, is populated by a more or less representative spectrum of species. Apart from the fact that groups with many entries would "swamp" groups with very few, the member islands may be so diverse or so small areally or avifaunally as to bear little relation to the whole. The assumption receives support from the following example, that of the Pearl Archipelago in the Bay of Panama (based on MacArthur et al., 1972, 1973; A. Wetmore, oral communication).

The Pearl Archipelago is arbitrarily divisible into (a) a northern sector that consists entirely of a scattering of islets and (b) a southern sector that consists principally of the three "large" Pearl Islands but also includes (c) islets ringing the periphery of the largest island (Rey). For the northern sector (a), such data as are available for eight of the islets show a species-number range from 1 to 24 and passerine-nonpasserine ratios from 0 to 3.50. The three "large" main islands (b), in order of decreasing area, have species numbers of 44, 42, and 35 and ratios of 1.45, 1.10, and 0.95. For (c) the islets around Rey, such data as are

available for six of them show a species-number range from 4 to 25 and passerine-nonpasserine ratios from 0 to 3.67.

When the islets of the northern sector (a) are considered as a group, they have a total of 34 species of resident land birds and a passerine-nonpasserine ratio of 1.43. In the southern sector (b), the largest island (Rey) has 44 species and a ratio of 1.45 (or, if as is probable it also has at least one of the two vultures found on the other smaller islands, a ratio of 1.37). The peripheral islets (c), when taken together, have 34 species, or three-quarters as many as on the source island (Rey) and exactly the same number as on the islets in (a); their ratio of 1.43 is virtually identical to that of (a) and (b). The other two main islands, San José and Pedro González (ca. 20 and 8 square miles, respectively), are a fraction the size of Rey (ca. 100 square miles). As their progressively reduced ratios suggest, San José and Pedro González act as satellites of Rey, though they include a few species not recorded from the latter. Combined, the three islands have 52 species and a ratio of 1.00 compared to 54 species and a ratio of 1.00 for the Pearl Archipelago as a whole. Thus the three main islands as a group are equivalent avifaunally to the entire archipelago, but each is apparently too small to be reliably considered so by itself.

Turnover

TURNOVER RATES.—"Modern biogeographic theory states that the number of species in a class or other large taxonomic unit that inhabits an island is maintained within narrow bounds by a dynamic steady state between colonization and extinction (MacArthur and Wilson 1967)" (Terborgh and Faaborg, 1973). Terborgh and Faaborg, reporting on the changes in the birdlife of Mona Island, Puerto Rico, cited only two previous studies of avifaunal turnover on islands that had come to their attention, one involving the California Channel Islands, the other, the island of Karkar off the north coast of New Guinea.

The Channel Islands, a temperate-zone archipelago of nine islands or island groups off southern California, with areas of 1 to 96 square miles and distances of 8 to 61 miles from the mainland, were compared for avifaunal turnover between 1917 and 1968, by Diamond (1969). Minimum turnover rates per island ranged from 17 to 62 percent of the breeding land and freshwater species over the intervening 51 years, or 0.33 percent to 1.2 percent per year. The number of species per island remained about the same, provided the habitat conditions had also remained about the same and the two surveys were equally thorough.

Diamond did not include species lists in his analysis. Data from the earlier survey (A. B. Howell, 1917) show that the Channel Islands had at that time a resident land avifauna of approximately 35 species with a passerine-nonpasserine ratio of 1.92 and a breeding land avifauna of approximately 41 species with a passerine-nonpasserine ratio of 1.73. The only comparative information to have come to my attention is contained in a statement by N. K. Johnson (1972:313) that approximately 41 species of land birds breed in the Channel Islands. Evidently the size of the breeding land avifauna has not changed since 1917. Whether or not the passerine and nonpasserine proportions have changed cannnot be determined in the absence of comparative species lists.

If one were to sum into an aggregate total the numbers of species tabulated by Diamond for each of the nine islands in 1917 and 1968, the minimum turnover rate for the archipelago would be 29 percent for the 51-year period or 0.57 percent per year; the aggregate species totals would be 166 in 1917 and 177 in 1968. The increase in species totals of about six percent seems to be largely due to the fact that the island (Santa Rosa) with the largest increase (from 14 species to 25) had been incompletely censused in 1917. Omitting Santa Rosa, the archipelago shows an identical aggregate total of 152 species in 1917 and again, a half-century later, in 1968; the turnover rate remains the same at 29 percent.

Karker, a volcanic island lying 10 miles off the nearest point on New Guinea, has an area of 142 square miles, a maximum elevation of 6100 feet, and 88 percent of its area below 2500 feet; the fauna has been derived entirely by overwater colonization, mainly from New Guinea but with seven additional species from New Britain; recent volcanic activity has not affected bird distribution significantly; the original vegetation was principally rain forest, but habitat conditions were apparently similar at the two times the island was

surveyed, in 1914 and in 1969 (Diamond, 1971: 2742).

Diamond (1971) compared Karkar with Santa Cruz, the Channel Island most nearly similar to it in size and position, for extinction rates and immigration rates. Qualifying the actual figures, Diamond concluded that "the figures suggest that an adequately surveyed tropical island and a temperate island of identical size and isolation would have similar avifaunal extinction rates" and that, expressed as percentage of the source pool, "an adequately surveyed tropical island would have an avifaunal immigration rate at least twofold lower than that of a temperate island of identical size and isolation."

The actual figures show that the turnover rate in the breeding land avifauna on Karkar was 15 percent (including sight records) or 13 percent (excluding sight records) in 55 years, or 0.27 percent per year (including sight records) and 0.24 percent per year (excluding sight records); on Santa Cruz, the turnover rate was 17 percent in 51 years, or 0.33 percent per year. Thus the actual figures suggest that the yearly turnover rate is moderately to appreciably lower on Karkar than on Santa Cruz.

The extinction rate for the breeding land avifauna on Karkar works out to 0.13 percent per year with or without sight records; on Santa Cruz, 0.32 percent per year. Thus the extinction rate on tropical Karkar, far from being similar to that on temperate Santa Cruz, is more than twofold lower. Apart from Diamond's immigration rates, which are calculated in relation to the size of the presumed source pool whose precise composition is largely based on surmise, it might be added that on Karkar, over the 55-year period, and on Santa Cruz, over the 51-year period, the number of land species involved in the turnover, 12, was the same on either island.

In 1914, the number of resident land species collected on Karkar was 40, with a passerine-nonpasserine ratio of 0.48. Between 1914 and 1969, three of the land birds may have become extinct (all nonpasserines), while ten, presumably breeding, land birds (eight nonpasserines and two passerines) apparently colonized the island. In 1969, within the same elevational limits as in 1914, the number of species (including sight records) was 47, with a virtually unchanged passerine-nonpasserine ratio of 0.47. On the basis of the two surveys, the total number of resident land species known from Karkar is 54, with a passerine-nonpasserine ratio of 0.46.

Mona Island, with an area of 24 square miles, "lies nearly midway between Puerto Rico and Hispaniola, being 42 miles from the former and 36 miles from the latter. . . . About 90% of the island's surface is contained in a nearly featureless plateau covered by a thick, mostly evergreen, sclerophyll scrub. Over most of the plateau the tree stratum reaches a height of 15–20 feet. . . . A dense layer of 2–3 foot shrubs forms the understory, . . ." (Terborgh and Faaborg, 1973:760).

In the first comprehensive survey, in 1901, and again in the last, in 1972, on Mona (see Terborgh and Faaborg, 1973:761), the nonintroduced resident land avifauna remained at three passerines and five nonpasserines, despite two extinctions and two natural colonizations (all nonpasserines); the breeding land avifauna consisted of three passerines and seven nonpasserines in 1901, three passerines and eight nonpasserines in 1972. If a parrakeet not recorded since 1892 be included, the number of extinctions is increased by one in either category; the passerine-nonpasserine ratio for the native residents was presumably 3:6 in 1892 compared to 3:5 in 1972 and, for the breeding species, 3:8 in 1892 and 3:8 in 1972. Or, based on the annotated complete list of the birds of Mona by Raffaele (1973), the resident land avifauna presumably consisted of three passerines and eight nonpasserines in 1892 compared to three passerines and eight nonpasserines in 1972; the breeding land avifauna consisted of three passerines and eight nonpasserines in 1892 compared to three passerines and nine nonpasserines in 1972.

Between 1901 and 1972, Mona had a yearly turnover rate of about 0.34 percent both among the nonintroduced resident land birds and the breeding land birds, whether based on Terborgh and Faaborg (1973) or on Raffaele (1973). This yearly turnover rate, coincidentally or not, closely matches the 0.33 percent on Santa Cruz but not the 0.27 percent with, or 0.24 percent without, sight records on Karkar.

The yearly extinction rate on Mona works out to 0.35 percent (based on Terborgh and Faaborg) or 0.27 percent (based on Raffaele) for the resident land avifauna, 0.27 percent (based on

Terborgh and Faaborg) or 0.26 percent (based on Raffaele) for the breeding land avifauna. If the extinct parrakeet is included, the yearly extinction rate since 1892 is either 0.44 percent (based on Terborgh and Faaborg) or 0.34 percent (based on Raffaele) for the resident land avifauna, and either 0.34 percent (based on Terborgh and Faaborg) or 0.33 percent (based on Raffaele) for the breeding land avifauna. It appears, therefore, that the yearly extinction rate of either 0.26 or 0.34 percent (based on Terborgh and Faaborg) for the breeding land avifauna on tropical Mona is roughly similar to the 0.32 percent on temperate Santa Cruz, whereas the 0.13 percent of tropical Karkar is more than twofold lower than on Santa Cruz or Mona. The prediction that small, far islands, such as Mona, and large, near islands, such as Karkar, should have similar extinction rates "is gratifyingly upheld by these two tropical islands on opposite sides of the globe" (Terborgh and Faaborg, 1973:762) is not supported by the above data.

COLONIZATION RATES.—On Santa Cruz, Karkar, and Mona, the islands for which some documentation of turnover exists, the resident land avifauna shows a colonization rate of 0.34, 0.34, and 0.35 percent per year, respectively, whereas the corresponding extinction rates are 0.32, 0.13, and either 0.35 or 0.27 percent per year. If it be assumed that these islands are in dynamic balance between colonization and extinction, the imbalance in the case of Karkar is due either to a real difference between the two rates or, more likely, to the earlier survey having been less thorough than the later one. In the latter instance, the larger number of colonizations than extinctions becomes an artifact, and the colonization rate is probably as low as the extinction rate.

Diamond (1971) calculated immigration rates, not on the basis of newly established species relative to the number of species known to have bred on Santa Cruz or on Karkar, but as a percentage of a pool of presumed colonizer species on the mainland adjacent to either island. Moderately isolated Mona and well-isolated Cocos, however, provide examples of the difficulties to be encountered when attempting to estimate the size, contents, or even the location of a source pool.

Mona Island was compared with the Guánica Reserve in southwestern Puerto Rico by Terborgh and Faaborg (1973:765), who considered the two very similar ecologically and avifaunally, to the extent that all the land birds currently resident on Mona are to be found among those nesting at Guánica and constitute a subset of the latter. Guánica thus harbors a species pool of some 43 prospective colonizers (based on Kepler and Kepler, 1970; Cameron B. Kepler, in litt.). Yet four (all nonpasserines) of the 14 species of land birds known to have bred on Mona (see Terborgh and Faaborg, 1973:761) are not included in the Guánica list, two species (both of them Antillean nonpasserines) that have occurred but have not bred on Mona are not known from Guánica, while another six species (all Antillean passerines) that breed at Guánica have reached Mona, where Terborgh and Faaborg (1973) and Raffaele (1973) regarded them as accidentals, vagrants, or otherwise unestablished visitants rather than propagules emanating from a pool of potential colonizers.

Cocos Island has no record at all of immigrants that could qualify as potential colonizers. Not including the Galapagos Archipelago, the species pool from which to draw extends through southern Central America and northern South America and is enormous. Though the distance from the mainland is not great compared to interisland distances in the tropical western Pacific and has not prevented the arrival of numbers of North American land bird migrants, I would hesitate to nominate a single species on the tropical American mainland as a candidate to successfully colonize Cocos. "One cannot predict on the basis of morphological, ecological or physiological characteristics whether or not a given species will be a successful colonizer" (Mayr, quoted by Moreau, 1966:368).

The chances that islands will be colonized by species that breed at warmer or cooler latitudes distant from those in which the islands lie are close to zero. A way to estimate the probability that certain islands or island groups are apt to have higher or lower colonization rates than others is furnished simply by counting the numbers of residents and of nonresidents in a species list. With few exceptions, lists in which the ratio of residents to nonresidents is less than 1:1 pertain to islands or island groups outside the tropics, lists in which the ratio of residents to nonresidents is more than 1:1 pertain to islands or island groups inside the tropics. Though sufficient examples are hard to

find, the ratios of islands that are at least roughly comparable to one another in position and area or size of avifauna also tend to follow a latitudinal progression, as in the accompanying tabulation of single islands lying off the coast of eastern and southeastern Asia.

	Area (mi²)	*Latitude*	*No. of land birds*	*No. of residents*	*Residents: non-residents*
Hokkaido	30,300	42–45°	155	52	0.51
Honshu	87,000	34–40°	184	84	0.84
Taiwan	13,800	22–25°	219	127	1.38
Hainan	13,000	19°	205	140	2.15
Singapore	217	2°	219	156	2.48

Ratios of island groups increase even more markedly than do those of the single islands from the Japanese Empire in the north to the Papuan subregion at the equator: Japan, 1.4; Philippines, 5.1; Sula Islands, 5.9; Moluccas, 8.3; Lesser Sundas, 13.2 (average of six islands); New Guinea and satellites, 17.6.

Checklist data that are at hand point to only three nontropical islands or island groups on which the residents outnumber the nonresidents. All three are located peripherally in the Southern Hemisphere, where they face open, cold oceans and have land avifaunas consisting largely to almost entirely of nonmigratory populations: the Falklands (with a borderline ratio of 1:1), east of the southern tip of South America; Tasmania, off southeastern Australia; and oceanic New Zealand.

In the tropics, the few islands on which nonresidents outnumber residents occur mostly in the Western Hemisphere. Cuba, Cozumel, and the Swan Islands are easily explainable as steppingstones utilized by transients crossing the Gulf of Mexico and the Caribbean Sea; depauperate Barbados has an "abnormally" small number of residents compared to the cumulative number of migrants and strays it has been receiving over the years; the Virgin Islands, as a political entity, have a ratio of 0.65, but if St. Croix, which lies isolated off the Puerto Rican shelf, be excluded, the ratio rises to a "normal" 1.21 (compared to the 1.31 of Puerto Rico). Elsewhere, the Aldabra archipelago in the Malagasy area, with a below-unity ratio based on 12 resident and 15 nonresident land birds, apparently is in position to intercept transients and strays to or from East Africa and Madagascar (Benson and Penny, 1971:512). In the same area, the Comoros, which lie closer to East Africa and Madagascar, and the Seychelles and the Mascarene Islands, which lie farther out in the Indian Ocean, have more recorded residents than nonresidents.

Mona in the Caribbean area and Cocos in the eastern Pacific, with resident:nonresident ratios of 0.35 and 0.17, respectively, run counter to expectation. The situation on Mona may be similar to that on Barbados, where the number of residents is small on an island that is accessible to a mounting number of irregular and accidental visitors. Cocos appears to be too small, too distant, too isolated, and conceivably too inhospitable for neotropical species of land birds to reach it or to colonize it. Evidently it is not too distant for strays and, probably, a number of regular transients and visitors whose migratory urge causes them to strike out over open ocean.

Turnover and Endemism.—A relationship between island size and percent endemism among the species of land birds was postulated by Mayr (1965): "The percentage of endemic birds on islands increases with island area at a double logarithmic rate. This relation is apparently due to extinction, which is more rapid the smaller the island." This view was seconded by MacArthur and Wilson (1967:173–174), who wrote that "the percentage of non-endemic species is probably a measure of the turnover rate," that "we know on both theoretical and empirical grounds that the turnover rate of species varies inversely with island area," and that the data in the above-cited note by Mayr are consistent with the prediction that percentage endemicity should increase with island area.

Predicated upon the four islands he selected for plotting on a double-log graph, Mayr (1965) made the statement that solitary, well-isolated islands show only small deviations from expectancy. Read from his graph, the expectancy is that the endemic species of land birds range from about seven percent on an island of 10 square miles to about 75 percent on an island of 300,000 square miles.

It happens that the one island on which I published a report, Cocos, in the tropical eastern Pacific, I selected precisely because it is a solitary, well-isolated island (Slud, 1967). Its four species of resident land birds, made known to science in the nineteenth century, are the same four species found there today. No other species of resident land

bird has ever been reliably reported by any of the many visitors to the island.

Thus, Cocos Island, surveyed from 1891 to 1963, may not have come to the attention of Terborgh and Faaborg (1973) as an example of avifaunal turnover on islands, because it hasn't had any. The statement by Mayr (1965) that, the smaller the island, the turnover "appears to be far more rapid than hitherto suspected" or the one by Diamond (1969:57), based upon the Channel Islands, that "percentage turnover rates vary inversely as insular species diversities, with no effect of distance apparent" cannot begin to apply to Cocos, with four species of resident land birds, an area of 10 square miles, and surveys the extremes of which are spaced 72 years apart. Nor does the statement by Terborgh and Faaborg (1973:762) that "the equilibrium theory qualitatively anticipates similar extinction rates on small far islands and large near islands" apply to Cocos, since it has neither an extinction rate nor an immigration rate that can be used to uphold theoretical expectancies.

In regard to the predictably low percentage of endemic species of land birds on small islands claimed by Mayr (1965) and by MacArthur and Wilson (1967), little Cocos Island, instead of an expected endemicity of seven percent, has an actual endemicity either of 50 percent (if one excludes the Cocos Island cuckoo), a higher rate than on any island or island group, save Madagascar, in any of the insular categories graphed by Mayr (1965), or of 75 percent (if one includes the Cocos Island cuckoo), a rate as high as that of 22,000 times larger Madagascar.

"A further consequence," wrote Mayr (1965), "is that the smaller the island the lower the percentage of endemic species should be, because most of the populations become extinct before they reach species level, or soon thereafter. MacArthur and Wilson. . . , on the basis of slightly different considerations, arrived at a similar conclusion." Again Cocos stands apart. The first land bird to be discovered there, around 1840, was the Cocos Island cuckoo. A well-marked Pacific isolate immediately distinguishable from the Middle American and Caribbean Mangrove cuckoo (*Coccyzus minor*), it is either an endemic race of the latter or an endemic species confined to Cocos. The least common of the land birds, though by no means rare, it seems not to have decreased but perhaps even to have increased in numbers. The Cocos Island flycatcher is the sole representative of an endemic genus (*Nesotriccus*) restricted to Cocos. Previously deemed rare to infrequent, it was common and widespread in 1963 (Slud, 1967:286). The third endemic is the abundant Cocos Island finch (*Pinaroloxias*), the sole representative of the genus and found only on Cocos. The fourth species of land bird on Cocos is a mangrove-type warbler (*Dendroica petechia*). Belonging to the race *aureola,* it is endemic to the Galapagos Archipelago and Cocos Island, on both of which it is without doubt a relatively recent arrival. Unlike the other three species on Cocos, the unknown geographical origin of which could have been West Indian rather than continental, *aureola* is weakly differentiated from the population on the opposite coast of South America.

" 'There is little doubt that . . . well isolated islands are evolutionary traps, which in due time kill one species after another that settles on them' " (Mayr, 1965). On Cocos, however, sufficient time has evidently elapsed for two of the land birds to have evolved, presumably in situ (if not marooned there as relicts), to the generic level and a third, almost if not quite to the specific level. Moreover, the two that are least common are not rare and, instead of disappearing, have apparently been increasing in numbers. Cocos Island is either an actual or a potential death trap for all its land bird arrivals, every one of which, so far as known, is a northern migrant that has not become established or even lingered there unseasonably.

Island Types

CONTINENTAL ISLANDS.—*"Recent" Continental Islands:* Darlington (1957:480) loosely categorized obviously recent continental islands as those with more or less reduced continental faunas, such as Sumatra, Java, Borneo, New Guinea, Ceylon, and Trinidad in the tropics, Formosa (Taiwan) on the edge of the tropics, and the British Isles, Japan, Newfoundland, Greenland, Tasmania, Tierra del Fuego, and the Falklands outside the tropics. Moreau (1966:302–303) gave as typical examples the small islands of Fernando Po, Zanzibar, and Mafia on the continental shelf of Africa, which, cut off from the mainland in the Late Pleistocene as a result of the postglacial rise of ocean level, are too

young for evolution to have proceeded far, are located sufficiently close inshore for gene-flow from the continent to hamper the divergence of the insular populations, and at the start of their independent existence had a full complement of species.

Recent tropical continental islands have native land avifaunas with passerine-nonpasserine ratios that are generally about the same as or somewhat reduced from the ratio on the opposite mainland (Figures 13 and 15). The proportional representations of passerines and nonpasserines on the island may thus tell us something of the relative age of the island or the recency of its avifauna.

Tropical American examples are Isla Coiba, with a ratio of 1.17, compared to the facing slope of the Azuero Peninsula, 1.29, and the Pearl Archipelago, with a ratio of 1.00 (ranging from 0.95 to 1.44 for the three main islands), compared to the Canal Zone, 1.46, or all of Panama, 1.43; Margarita and Trinidad, with respective ratios of 0.93 and 1.09, compared to northeastern Venezuela, with a ratio of 1.06, while all of Venezuela has a ratio of 1.61. Another probable example of islands on the continental shelf is the offshore Tres Marías, with a ratio of 1.26, compared (in lieu of Nayarit, which lacks a checklist) to Colima and the immediately adjacent portion of Jalisco, with a ratio of 1.34. Possibly another example is Isla Cozumel, with a ratio of 1.00, compared to nearby Quintana Roo, with a ratio of 1.06, and the Yucatan Peninsula, with a ratio of 1.03; the adjoining, more humid Petén and British Honduras have respective ratios of 1.21 and 1.18. In the Old World tropics I have even fewer examples for which matching data are available: Ceylon, 0.85, compared to Kerala, at the tip of peninsular India, 0.89; Sumatra, 1.24, compared to the Malay Peninsula, 1.28, and Singapore, 1.21, compared to Malaya, 1.20.

In the temperate zone, at least at northern latitudes, passerine-nonpasserine ratios on continental islands exceed those on the neighboring mainland, but again available matching data are hard to come by. Examples are Taiwan (Formosa), at the edge of the tropics, with a ratio of 2.23, and Fukien, 1.92; Vancouver Island, 1.42, and southern British Columbia, 1.19; Prince Edward Island, 1.50, and New Brunswick, 1.28, or Nova Scotia, 1.24; Great Britain, 2.00 and Ireland, 2.54 compared to the Netherlands, 1.83, or France (including Belgium and Switzerland), 1.66; Newfoundland Island, 1.48, and Newfoundland Labrador, 0.58, or the entire Labrador Peninsula, 0.62. At southern latitudes, my only examples have the ratio smaller on the continental island: Tasmania, 1.59 and Victoria, on the north side of Bass Strait, 1.71; Isla Grande (Tierra del Fuego) and the Falklands (300 miles out in the ocean and with only 19 species of land birds), respectively, 0.94 and 0.90 compared to southern Argentina, 1.77. In respect to Tasmania, it could perhaps be a case of one island, Tasmania, being satellic to a very much larger island, Australia (see below). On the other hand, Tasmania, Isla Grande, and the Falklands, lying at the southern edge of the terrestrial world (they can expect no land birds from Antarctica) would appear to correspond in their situation to islands at far northern latitudes, where the ratios are all extremely reduced (Greenland, 0.75; Southampton Island, 0.33; Banks Island, 0.29).

Intraisland comparisons are extremely hard to find. Only altitudinal data are at hand and solely for Java (based on Hoogerwerf, 1948): 229 species and a ratio of 1.01 between sea level and 1500 meters, 111 species and a ratio of 1.52 between 1000 and over 3000 meters. These figures, i.e., relative numbers of species and passerine-nonpasserine ratios, correspond to those on the nearest comparable mainland, the Malay Peninsula: 342 species and a ratio of 1.02 in the lowlands (based on Chasen, 1939), 257 species and a ratio of 1.67 in the hill country (based on Robinson, 1928).

"Old" Continental Islands: The east African trio of Zanzibar, Mafia, and Pemba, with respective areas of 640, 240, and 320 square miles, are low, generally similar islands, none more than 30 miles distant from the Tanzania mainland (for which I have no list). The most striking difference, the fact that Zanzibar and Mafia lie on the continental shelf and Pemba does not, is not obvious to the eye (Moreau, 1966:350–351), but it is certainly suggested by the passerine-nonpasserine ratios: Zanzibar, 1.10; Mafia, less effectively isolated than Zanzibar, 1.27; old-continental Pemba, 0.65. "The passerine bird fauna of Pemba . . . looks almost like that of an oceanic island, and it is extremely difficult to imagine why this should be so" (Moreau, 1966:352). Evidently great distance is not necessarily required to produce an oceanic effect, particularly in tropical latitudes.

Socotra, like Pemba, is probably "an 'old' conti-

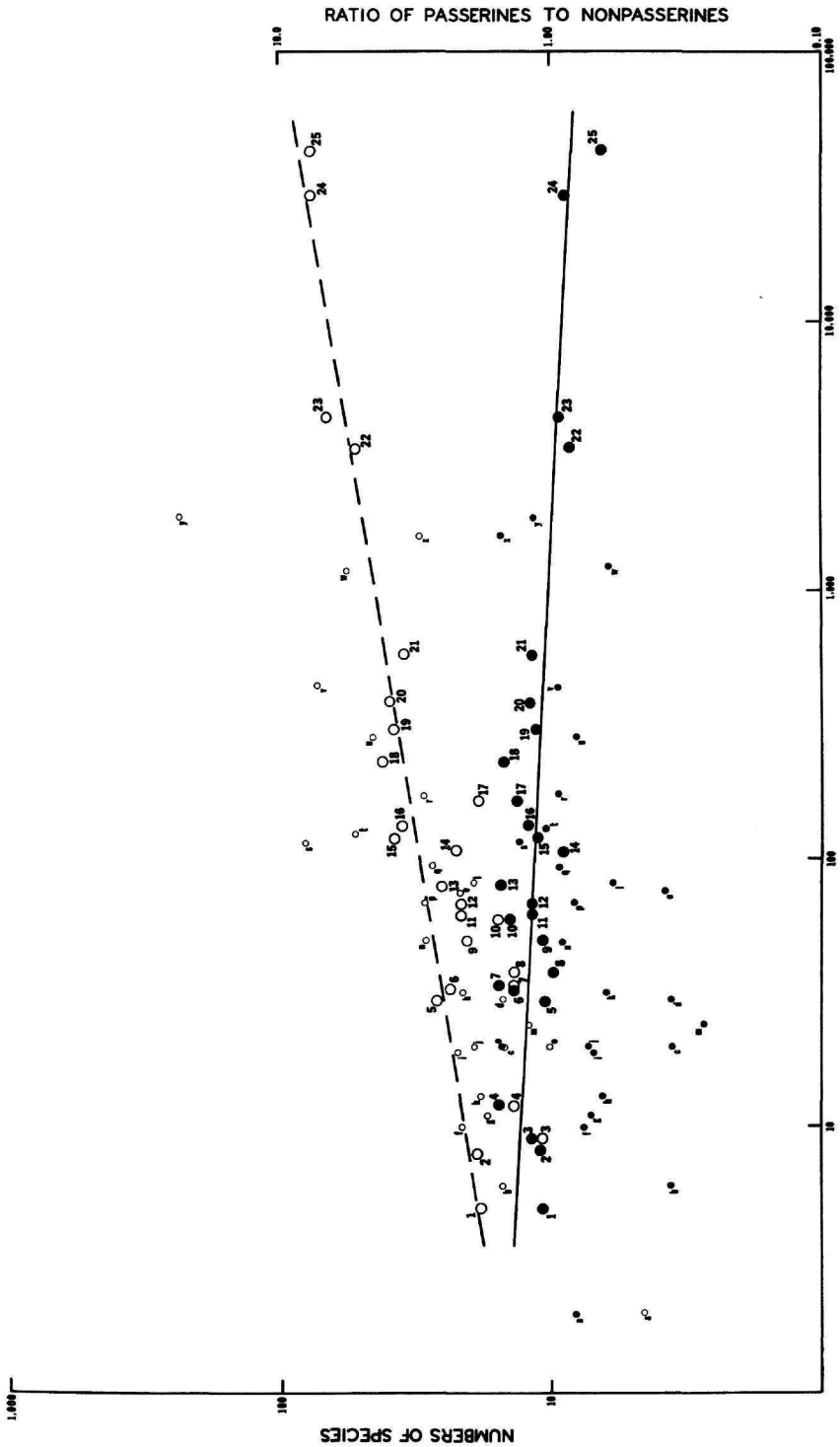


FIGURE 12.—West Indian native land avifaunas: correlation between area and numbers of species (numbered large open circles and dashed regression line) and between area and passerine-nonpasserine ratios (numbered large solid circles and solid regression line). (Numbered entries include islands of the Greater and Lesser Antilles and in the open Caribbean Sea: 1, Saba; 2, St. Eustatius; 3, Old Providence; 4, St. Andrew; 5, Grenadines; 6, Montserrat; 7, Anguilla; 8, St. Martin; 9, Nevis; 10, Marie Galante; 11, Barbuda; 12, St. Kitts; 13, Grand Cayman; 14, Antigua; 15, Grenada; 16, St. Vincent; 17, Barbados; 18, St. Lucia; 19, Dominica; 20, Martinique; 21, Guadeloupe; 22, Puerto Rico; 23, Jamaica; 24, Hispaniola; 25, Cuba. Lettered entries (small circles) stand for satellite islands (including the Virgins) and islands fringing the mainland: a, Swan Islands; b, Barbareta; c, Utila; d, Guanaja; e, Roatan; f, Culebra; g, Anegada; h, Virgin Gorda; i, St. John; j, Tortola; k, St. Thomas; l, St. Croix; m, Mona; n, Vieques; o, Cayo Largo; p, Aruba; q, Bonaire; r, Curaçao; s, Tobago; t, Cozumel; u, Gonave; v, Margarita; w, Isle of Pines; x, Andros; y, Trinidad.)

nental island dating from Plio-Pleistocene times, so that opportunity for evolution on its surface has been considerable" (Moreau, 1966:303). Situated 130 miles off the Somali coast, it has a resident land avifauna of 15 passerines and 14 nonpasserines and a close-to-unity ratio of 1.07. This ratio is virtually equivalent to the 1.04 of former British Somaliland, with which Socotra presumably was once connected. The approximately equal proportion of passerines to nonpasserines also characterizes many isolated islands, particularly in the Indian Ocean (see below).

FRINGING ARCHIPELAGOS.—Under this heading, Darlington (1957, Chapter 8) enumerated the Philippines, the islands of the western Pacific, and the West Indies as the principal archipelagos of the world (all tropical),

> which, though not simply recent continental, lie close to continents and receive the fringes of continental faunas and are extensive enough, with enough comparable islands, to show informative patterns of distribution. The archipelago of Wallacea [Celebes, Lesser Sundas, Moluccas] . . . might be added to this list. It lies between the continental shelves of Asia and Australia and receives the fringes of the faunas of both continents.

West Indies: Main Islands: Recent attempts at area-species formulations for islands have come to be associated most prominently with MacArthur and Wilson (1963, 1967). The double-log area-species curve of the West Indian herpetofauna presented by these authors (1967:8) is a virtually perfect model, though it only includes the four major Greater Antillean islands at one end of the scale of magnitude and three of the smallest and northernmost Lesser Antillean islets at the other end.

Using the same coordinates, I plotted the area-species distribution of the land birds, as well as their corresponding passerine-nonpasserine ratios, for the islands of the entire Caribbean area (Figure 12). As have other authors, I excluded migrants. My reason is that islands range in status from migrant-free in parts of the tropics to migrant-dominated outside the tropics, particularly in the northern hemisphere. Hence the only common basis upon which to make intercomparisons is the resident avifauna. Islands 1, 6, 22, 23, 24, and 25 are the same as in the above model, only omitting the smallest, Redonda (area 1 square mile), for which I have no list. Remarkably, these islands align themselves as ideally for the birds as for the reptiles and amphibians. The neatness of the picture is spoiled, however, when the other islands are included.

The two regressions in Figure 12 are constructed upon the islands numbered from 1 to 25, comprising the Greater and Lesser Antilles and a scattered few in the western Caribbean Sea (excluding satellites, e.g., Isle of Pines, Gonave, islets on the Puerto Rican shelf). These satisfy two requirements: all are single islands, except the Grenadines, and all are zoogeographically West Indian (in the sense of Bond, 1948). Increasing numbers of species show a very high, positive correlation with increasing area. Islands 1 through 14, ranging in size from 5 to 100 square miles and in number of species from 11 to 24, lie along approximately the same level. Their small avifaunas could as well be explained by their geographic position out at sea as by their small areas. A step higher lie islands 15 through 21, comprising the principal members of the Lesser Antilles, that is, Guadeloupe through Grenada. These range in size from 100 to some 500 square miles and have a compiled species-number range from 36 to 43 (except for outlying, overpopulated, impoverished island 17, Barbados).

The passerine-nonpasserine ratios correlate negatively with increasing area along a slightly falling slope. I do not attribute this correlation, though highly significant statistically, to the geometric increase in area which the West Indies are, so to speak, preadapted to show on a graph (Figure 12). Rather, the four main Greater Antillean islands (22–25) are sufficiently large and old to have a faunal evolutionary history of their own. Singly or collectively they have below-unity ratios, as do other comparable tropical noncontinental islands. Cuba (25), the largest of the four, has the lowest ratio, but it also has the simplest physiography. The other numbered islands (1–21) are very much smaller, and all but one have ratios rising above unity. The exception, Antigua, a low, dry island converted to sugar production, would reach unity with the addition of one passerine. Small and isolated Grand Cayman (13) is structurally Greater Antillean but Lesser Antillean in size and ratio.

Offshore Islands and Satellites: Islands that lie off the Caribbean shores of Middle America and northern South America or are satellic to the main West Indian islands are symbolized by letter in

Figure 12. Islands that pertain to the same complex tend to align themselves along a slope which lies parallel to that of either regression, particularly the one of area-ratio, and at a different level from that of another island complex. (An attempt to cluster all the Caribbean islands two-dimensionally into natural groupings based on passerine-nonpasserine and suboscine-oscine ratios is presented in Figure 30.)

Margarita and Trinidad, off northeastern Venezuela, were included above with continental islands, as was also Isla Cozumel, off the Yucatan Peninsula. Cozumel, strictly speaking, appears to be somewhat separated from the continental shelf proper, hence could belong in the offshore category, together with the Bay Islands, off Honduras, and the Dutch Leewards, off northwestern Venezuela.

The Bay Islands of Honduras "are evidently the tops of a submerged mountain range, which, through isolation from the mainland, have retained a number of Central American species, which have entirely or mostly disappeared from Central America proper and which appear as relicts, not only on the Bay Islands, but also on islands off the coast of Yucatan" (Bond, 1936:354). Of the main islands, "Utila is situated on the Continental Shelf, separated from the mainland by waters not exceeding 10 meters in depth, while Roatán, Guanaja, and associated smaller islands are surrounded by waters at least 275 meters deep" (Monroe, 1968: 11). Utila, however, is the smallest of the major islands. It reaches an elevation of only 90 meters and, unlike the others, is otherwise flat. The major islands are all small, the fauna is very limited, and the passerine-nonpasserine ratios are extremely low.

The low-lying, dry Dutch Leewards (Aruba, Curaçao, Bonaire) are situated only 20 to 40 miles off Venezuela. Despite the short distance, the islands, particularly Curaçao and Bonaire, are separated from the mainland by deep water (Figure 13). Both geologically and zoogeographically, all three islands seem never to have been part of the South American mainland (Voous, 1957:32). All have below-unity passerine-nonpasserine ratios, including Aruba, which is closest to shore but is also the most barren. Possibly the low ratios of the islands are a reflection of the composition of the avifauna on the arid opposite coast; endemism on the islands is extremely low, it is confined to the subspecific level, and it affects only four of the land birds. The only figure I have for the arid opposite coast, 1.14, is based solely on the 24 passerines and 21 nonpasserines reported in the lowlands of the Paraguaná Peninsula, opposite Aruba, by Barnés (1940). On the other hand, the islands conceivably show an oceanic effect, manifested by marked reduction in ratio compared to the mainland, as do the following: Guadalupe Island, 180 miles out at sea and with a ratio of 1.33, compared to Baja California, with a ratio of 2.02; the Revilla Gigedos Islands, over 400 miles at sea and with a ratio of 1.00, compared to Colima (and adjacent Jalisco), with a ratio of 1.34.

Satellites are relatively small to extremely small islands which have native land avifaunas that range in passerine-nonpasserine ratio from about the same as, to very much lower than, that of the very much larger island to which they pertain. Examples are the Isle of Pines, with a ratio of 0.60, compared to the 0.64 of Cuba; Gonave, 0.80, Beata, 0.84, and Ile à Vache, 0.85, compared to Hispaniola, 0.88; Vieques, 0.87, compared to Puerto Rico, 0.86.

The islets, primarily including the Virgin Islands, that are situated on the Puerto Rican shelf (Figure 12*f–l*) or, in the case of St. Croix, associated with it are satellic to Puerto Rico. Though often considered Lesser Antillean in atlases and dictionaries, the Virgins have a mixed avifauna that is predominantly Puerto Rican, while their low passerine-nonpasserine ratios ally them to the geologically similar Greater Antilles and separate them from the Lesser Antilles as surely as does the Anegada Passage (Figure 13). The islets of the Puerto Rican shelf follow a pattern typical of insular satellites in which diminution in area goes hand in hand with reduction in number of species of land birds accompanied by falling passerine-nonpasserine ratios, probably in response to a broadening in the size and a reduction in the number of occupied niches.

Supplemental data for the Old World are few, but these tend to corroborate the situation in the New World tropics. In the Philippines (Figure 16), Mindoro, with a ratio of 0.78, is satellic to Luzon, with a ratio of 1.09; Basilan, 0.74, is satellic to Mindanao, 1.07. In Indonesia (Figure 15), the West Sumatra Islands have a combined ratio of

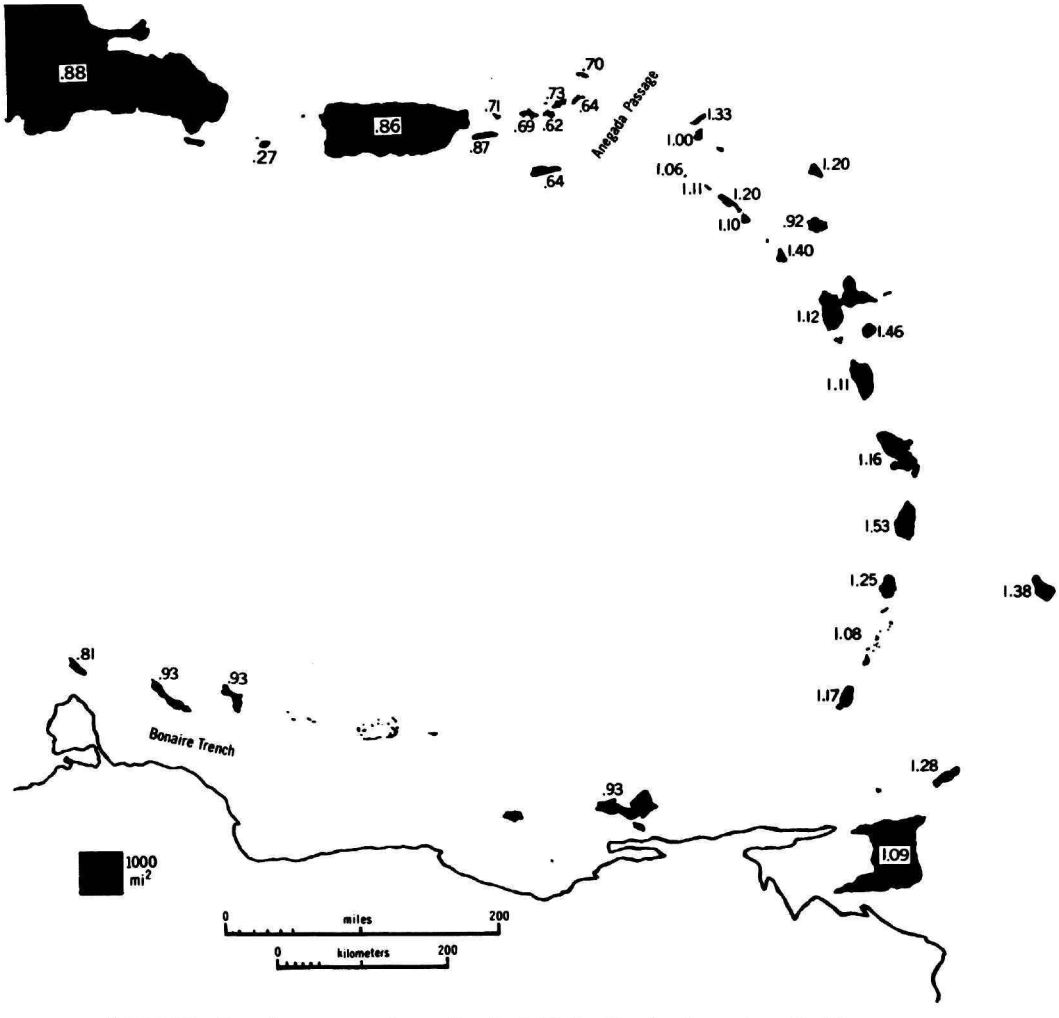


FIGURE 13.—Passerine-nonpasserine native land bird ratios in the eastern Caribbean area.

0.95 (the Mentawei Group, 0.89; Nias, 0.89; Simalur, 0.73; Enggano, 0.80) compared to Sumatra, 1.24; Bali has a ratio of 1.15 compared to that of Java, 1.26. In the Papuan subregion, New Guinea has a ratio of 1.71, whereas the coastal islands range from 1.13 to 0.65. The pattern recurs among island groups in the western Pacific.

Apparently the trend to smaller ratios may be reversed when the areal difference is of a lesser magnitude or when the larger island is under a certain minimum size: Tobago, with a ratio of 1.28, compared to Trinidad, 1.09; Marie Galante, 1.46, compared to Guadeloupe, 1.12.

Distance and Ecology: MacArthur and Wilson (1967:20) reproduced a diagram of the number of bats on islands off Venezuela to demonstrate that area and ecology are the critical factors affecting species numbers rather than degree of geographic isolation when distance can be minimized as an influence. I have converted the diagram into the following table in which the herpetofauna and the avifauna (including passerine-nonpasserine ratios) have been incorporated.

	Area (mi²)	Species of bats	Species of amphibians, lizards, snakes	Species of resident land birds	Passerines: nonpasserines
Xerophytic					
Aruba	69	3	13	29	0.81
Curaçao	173	6	11	29	0.93
Bonaire	95	3	9	27	0.93
Traces of rain forest					
Margarita	444	7	17	77	0.93
Rain forest					
Trinidad	1864	53	85	239	1.09
Tobago	116	16	42	82	1.28
Grenada	120	11	17	39	1.17

With respect to the bats, the above authors pointed out that "Grenada, which is both small and isolated, still has four more species than the large, near island of Margarita, and many times more species than the small, near islands of Aruba and Bonaire." The statement holds poorly for the herpetofauna and not at all for the avifauna. Grenada, instead of more species of birds, has half as many species as Margarita and only one-third more than the xerophytic Dutch Leewards.

Distance and faunal origin could be responsible for the different numbers, whether of bats, of amphibians, lizards, and snakes, or of birds, on Tobago and Grenada. Both are rain-forested, high islands of equal size and with similar passerine-nonpasserine ratios: Tobago lies close to and is fed by its parent, Trinidad; Grenada sits apart as the terminal link in the Antillean chain. In the case of Margarita, the island may have traces of rain forest, but these are severely restricted to tiny areas of high ground; the island is otherwise as arid as the Araya Peninsula on the opposite mainland (see Ewel et al., 1968, map). Margarita, apart from its much larger size and closer distance to shore, is a continental island, and it has more than twice as many species of land birds than noncontinental Aruba, Curaçao, or Bonaire, individually or as a group. In the accompanying table, it appears that the passerine-nonpasserine ratios tend to correlate with the climato-vegetational conditions of the islands, whereas species numbers, unless individually qualified, do not.

Southeastern Asia, New Guinea, and the Western Pacific: MacArthur and Wilson (1967:23) presented an area-species curve of the land and freshwater birds based on a selection of continental and noncontinental islands and archipelagos that included the Sundas, Philippines, and New Guinea (but not the Moluccas), as well as tiny, isolated Christmas Island in the Indian Ocean. I was able to compile lists of resident land birds for 17 of MacArthur's and Wilson's 23 entries, substituting the Anamba, Natuna, and Palawan islands for the omissions. These are represented by the 20 numbered entries upon which the regressions are constructed in Figure 14. (Also see Figure 15.)

The steepness of the area-species slope is caused by the very low values of the very small entries and the high values of the very large entries. If the extremes were removed, the slope would be depressed toward that of the West Indies; the middle entries are scattered more or less horizontally, as in the West Indies (Figure 12). The inclusion of tiny Christmas Island contributes to the weakly positive correlation between area and ratio. Without Christmas Island, the area-ratio slope would show a closer approach to the horizontal.

Supplementing the numbered entries are the lettered entries. These include individual islands in the Moluccas, in the Philippines, and on the western New Guinea, or Sahul, shelf. Most of the lettered entries fall amid the numbered entries and strengthen the correlations, especially that of area-ratio. (In the West Indies the lettered entries weakened the correlations, especially that of area-ratio.)

The East and West Indies appear to differ mainly in the steepness of their area-species slopes and in positive versus negative correlation between area and ratio. These differences may be directly attributable to their contrasting magnitudes, due to the paucity of small islands in the East Indies. For example, Dominica, one of the principal islands in the Lesser Antilles, is only the size of New York City. It occurs about midway in Figure 12, but would be one of the smallest if entered into Figure 14. Thresholds of insular size in relation to stepwise increase in faunal, and presumably environmental, complexity could be involved, as well as faunal origin and history and the distances and directions the islands lie from one another and from faunal reservoirs.

Philippine Islands: The Philippines are incompletely separated from the Sunda shelf. The passerine-nonpasserine ratio of 1.30 for the archipelago as a whole, including Palawan, or 1.20

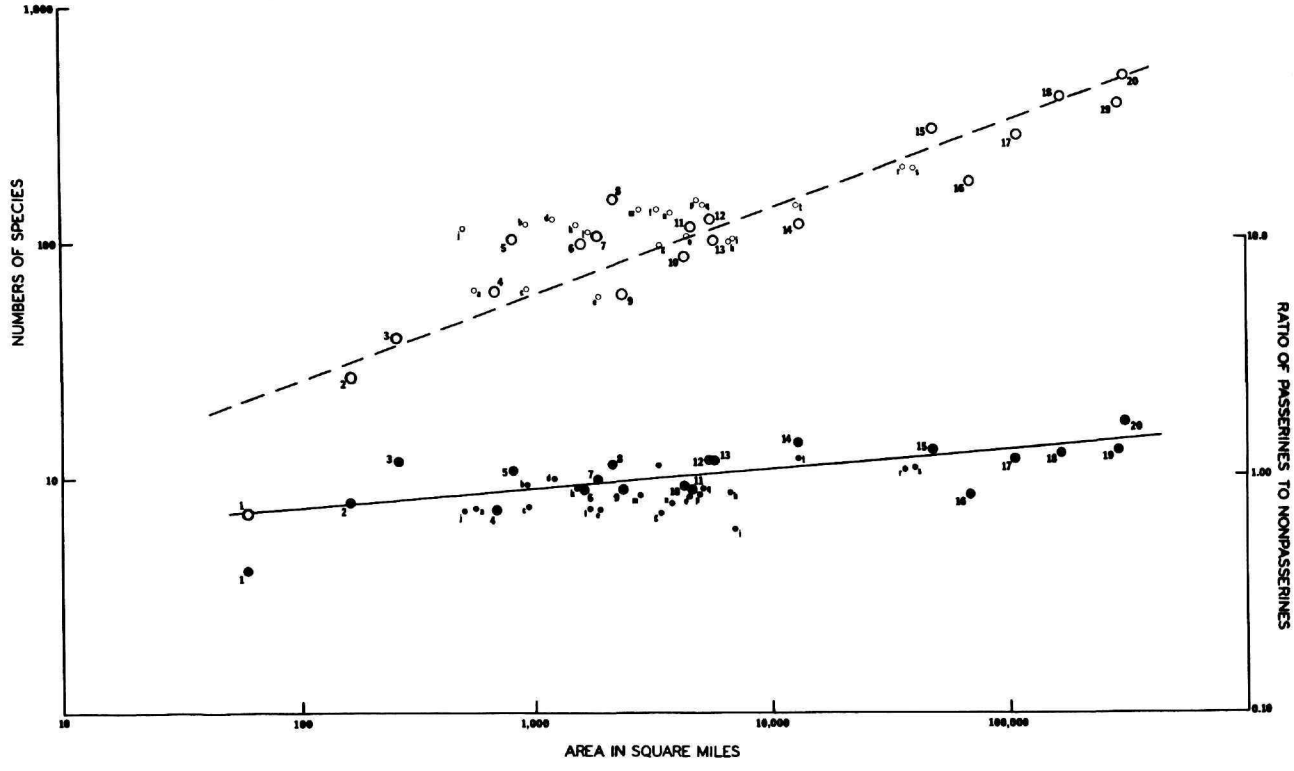


FIGURE 14.—Malayo-Papuan insular native land avifaunas: correlation between area and numbers of species (numbered large open circles and dashed regression line) and between area and passerine-nonpasserine ratios (numbered large solid circles and solid regression line). (1, Christmas; 2, Enggano; 3, Anambas; 4, Simalur; 5, Natunas; 6, Nias; 7, Lombok; 8, Bali; 9, Mentawai; 10, Sumba; 11, Palawan; 12, Flores; 13, Sumbawa; 14, Timor; 15, Java; 16, Celebes; 17, Philippines (minus Palawan); 18, Sumatra; 19, Borneo; 20, New Guinea. Lettered entries (small circles) include islands in the New Guinea, Moluccan, and Philippine areas: a, Kei Is.; b, Japan; c, Biak; d, Waigeu; e, Sula Is.; f, Aru Is.; g, Buru; h, Ceram; i, Halmahera; j, Basilan; k, Bohol; l, Cebu; m, Leyte; n, Mindoro; o, Panay; p, Negros; q, Samar; r, Mindanao; s, Luzon; t, Hainan.)

without Palawan, is slightly less than the average for the Greater and Lesser Sundas (Figure 15). The two largest islands, Luzon and Mindanao, have about the same area and virtually identical species totals and somewhat above-unity ratios (Figure 16). Either island features a long, peninsular extension which, if lists were available, would no doubt prove to have a distinctly lower ratio than the entire island, just as in mainland situations. The principal smaller islands have the reduced ratios that characterize satellites and species numbers that correspond more or less to individual island size and position. Only Panay, compared to the other islands, is impoverished, not, as has been stated (Delacour and Mayr, 1946:12), the entire central province. Palawan, lying between Borneo and the Philippines, is closer to Borneo zoogeographically but more like similar-size islands of the Philippines in number of species and below-unity ratio. In both these respects, however, it also acts as a satellite of Borneo.

The same variables apply of course to the numerous other small islands lying between southeast Asia and Australia (Figure 15). These occur as

loose or tight, linear or clumped configurations situated beside or between larger masses of land, compared to which they have markedly lower ratios. Distance and position, type of island, and history contribute to and help cause this effect. Examples are the Andaman, Nicobar, West Sumatra, and Kangean islands, also to some extent the Anambas and Natunas, in the Malaysian area, and the Aru, Admiralty, D'Entrecasteaux, and Louisiade groups, as well as peripheral, or satellic, Waigeu, Japen, and Biak, in the New Guinea area.

Wallacea: The Lesser Sundas are situated upon a projection of the Sunda shelf extending eastward from Java, a disposition that brings to mind the Antillean volcanic arc stretching north of Venezuela. They have above-unity ratios, except Lombok and Sumba.

Lombok is narrowly separated from similar-size Bali yet has a markedly lower ratio and a one-third smaller avifauna. The smaller size of the avifauna could be due to the zoogeographic effectiveness of Lombok Strait, between Bali and Lombok, which apparently persisted through the Pleistocene while the strait between Bali and Java dried up at the height of the glaciation (Mayr, 1944b:7). The low ratio on Lombok is perhaps explained by the "heavy Pleistocene eruptions of Mount Rindjani [which] seem to have destroyed much of the mountain fauna" (Mayr, 1944b:9). The predominantly montane passerines would thus have been affected far more adversely than the nonpasserines. The implication that the number of species on Lombok ought to be higher is difficult to prove. Lombok, in fact, has a few more species than thrice-larger Sumbawa, an even closer neighbor than Bali, with which it was presumably connected at the height of the Pleistocene glaciation (Mayr, 1944b:9).

Sumba, twice as big as Bali and more like Flores and Sumbawa in size, has fewer species than any of the Lesser Sundas figured and only two-thirds the number on Flores 25 miles away. The fact that Sumba is a low and arid island without a mountain fauna (Mayr, 1944a:176) could in itself account for the low species total and low ratio. According to Mayr (1944a:181), "lack of pronounced endemism indicates either that Sumba is a young island, or that it has had a continued active faunal exchange with neighboring islands, or both." Applied to Sumba in relation to its similar-size neighbors, this reasoning would seem to demand a higher immigration rate and species number instead of a smaller. If greater endemism and fewer species are a function of increasing distance or inaccessibility, expressed as a low immigration rate (MacArthur and Wilson, 1967), the more distant island ought to have a larger proportion of endemics and a smaller number of species. The converse is true of Sumba with respect to endemism but not to number of species, hence other variables need be brought into play.

Celebes and the Moluccas (and to lesser extent the Philippines) occupy a zone of complicated large-scale and violent tectonic movement between the Indo-Malayan and Australo-Papuan continental shelves (Mayr, 1944b). Celebes and the Moluccas, even Waigeu off the western tip of New Guinea, have distinctly smaller avifaunas and sharply lower ratios than do the shelf islands. This could be a reflection of a derived fauna on the one hand and of reduced competitive success of passerines as overseas colonists compared to nonpasserines on the other hand.

A selective brake may at the same time be applying counterpressure against immigration. To quote Mayr (1941c:198):

> . . . of the 265 species of land birds which are known from that part of New Guinea which is opposite New Britain, only about 80 species have a representative on New Britain. In other words, the 45-mile-wide stretch of water which separates the two islands has prevented the crossing over of 70 per cent of the New Guinea species . . . . Literally hundreds of similar instances could be listed from the distribution of birds in the Indo-Australian archipelagos, all of them indicating the sedentary habits of their avian inhabitants.

In the American tropical Pacific, eight families of land birds regularly occurring on the Panamanian mainland have not been found nearby on Isla Coiba (Wetmore, 1957:12). Tiny, oceanic Cocos Island has not yielded an additional species of native land bird since the original four were discovered, yet many migrants arrive alone or in groups (Slud, 1967). Obviously a distinction must be made between potential colonizers and visitors, especially in the tropics.

Tropical Western Pacific: Darlington (1957: 506–507) observed that

> considered together, as one fringing archipelago, all the islands of the tropical western Pacific east of Australia and New Guinea, and as far out into the ocean as terrestrial vertebrates go . . . . None of these islands is connected with

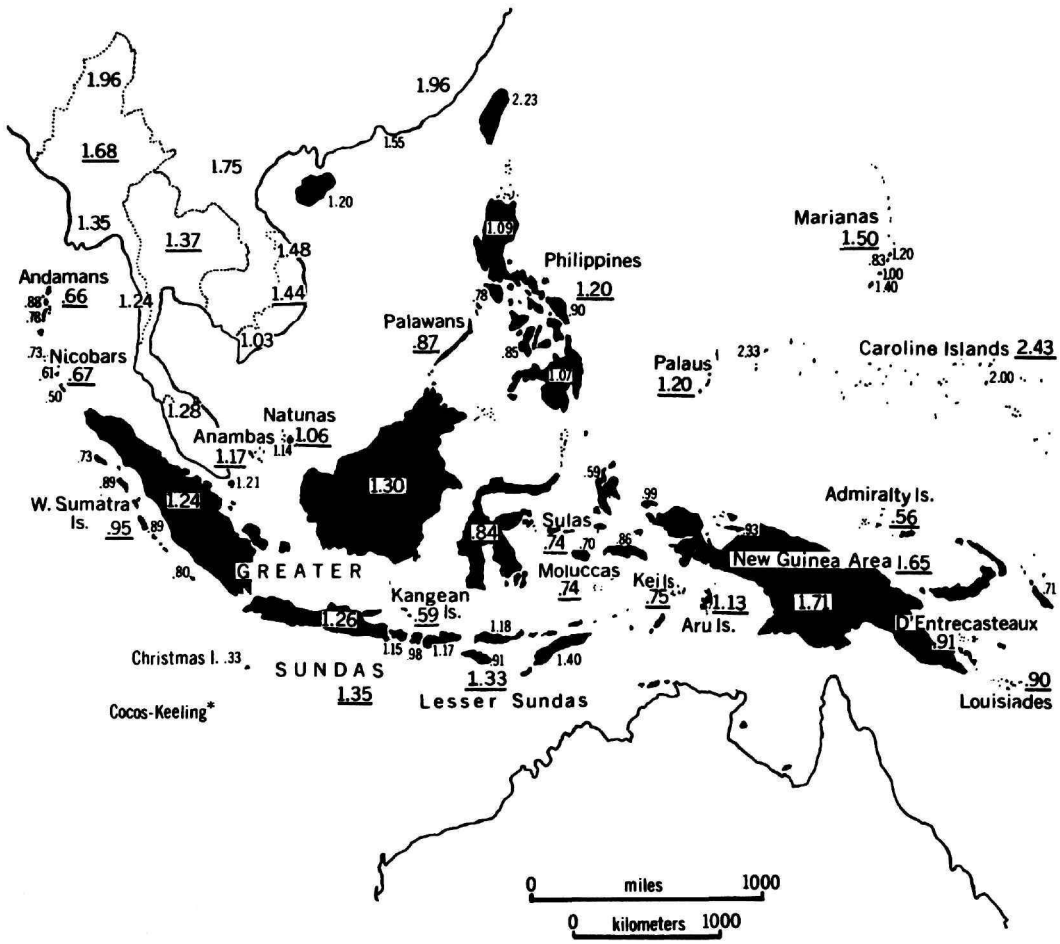
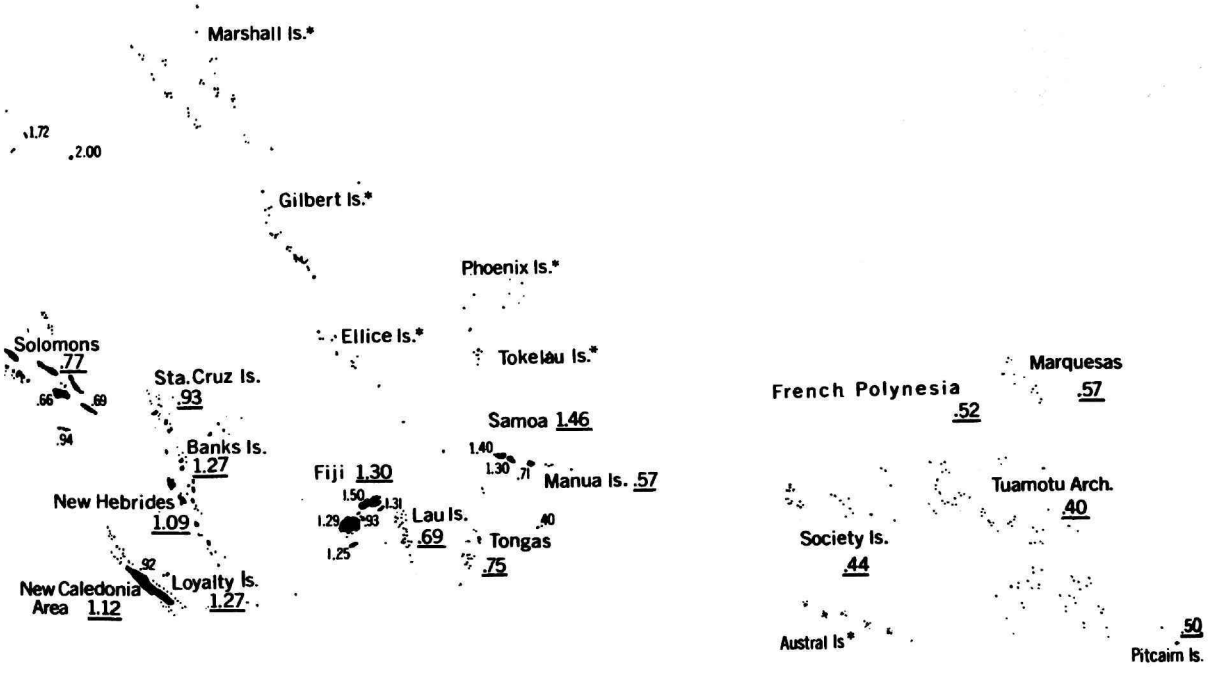


Figure 15.—Southeast Asia to tropical central Pacific: passerine-nonpasserine ratios of native land birds.

the continental shelf. Even the Bismarcks and Solomons are narrowly separated from it and from each other. Zoogeographically, all these islands should be treated as of unknown geological history, and their faunas should be allowed to speak for themselves.

The New Guinea area is the primary center for the evolution, radiation, and dispersion of birds over the tropical western Pacific. Two sorts of passerine decrease, relative to the nonpasserines, become apparent (Figure 15). One takes place, as already mentioned for New Guinea, on peripheral shelf islands, the other on groups of oceanic islets, usually low ones, with depauperate avifaunas derived from much larger and richer, high islands.

Area, avifaunal size, and ratio, relative to increasing distance from Australia and New Guinea (see Figure 15), are summarized in the following tabulation.



	Area (mi²)	Resident land species	Passerines: nonpasserines
Solomon Is. (excluding Rennell)	15,700	111	0.77
Rennell	400	33	0.94
New Caledonia Area	7,325	55	1.12
New Caledonia	6,530	50	0.92
Loyalty Is.	1,059	34	1.27
Santa Cruz Is.	380	27	0.93
New Hebrides Group	6,000	46	1.09
New Hebrides	5,700	46	1.09
Banks Is.	300	34	1.27
Fiji	7,069	46	1.30
Samoa	1,209	27	1.46
French Polynesia	1,575	32	0.52
Society Is.	650	13	0.44
Marquesas	480	11	0.57
Tuamotu Archipelago	330	7	0.40
Austral Is.	115	3	–
Pitcairn Is.	18	3	0.50
Easter Island	50	0	0.00

Northeast from New Guinea, the Admiralties (and probably New Britain, for which I lack a compilation) have a very low ratio. The effect spreads eastward through the Solomon group, which, as New Britain, has "strictly an impoverished Papuan fauna, except for a few endemics of

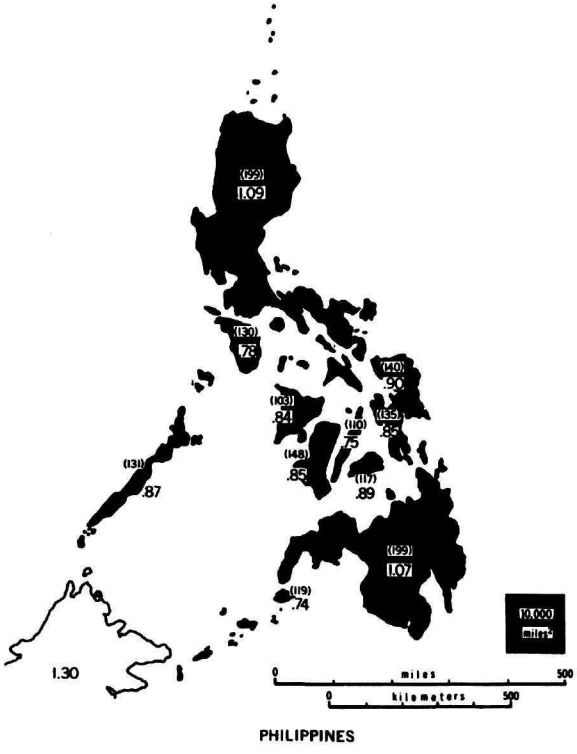


FIGURE 16.—Philippine Islands: passerine-nonpasserine ratios of native land birds (numbers of species in parentheses).

uncertain relationship" (Mayr, 1944a:189). The Solomons also have the low ratios of a faunal satellite (Figures 15, 17). On an equal-area basis, individual Solomon islands have very much lower species totals and ratios than do the Philippines far to the northwest but not much lower than the Moluccas on the opposite side of New Guinea. The Solomons have even lower ratios individually than as a group, indicating that here, as in other archipelagos, forested mountain conditions are more conducive to passerine than to nonpasserine differentiation. The larger islands generally have larger avifaunas, but some smaller ones, such as Rendova and especially tiny Gizo, have many more species than their sizes might warrant. A similar example is to be found in the Galapagos, where minute Jervis has nine species of permanently resident Darwin's Finches while islands hundreds of times larger have at most ten (Bowman, 1961:20). Other such instances, once brought to view (Figure 10), might then be explained from the vantage of hindsight.

Rennell Island, though separated by deep water, appears to belong with the Solomons on a map (Figures 15, 17). Unlike the Solomons, it has been populated from several directions, more or less in agreement with the prevailing winds (Mayr, 1931). It is similar to the Santa Cruz Islands not only ecologically but also in area, species number, and ratio.

East of the Solomons, low ratio is still evident in the Santa Cruz Islands, with avifaunal elements from the New Hebrides, Fijis, and Solomons (Mayr, 1945:201). Species and ratio keep approximate pace with decreasing area, at least until the numbers become very small.

	Area (mi²)	*Resident land species*	*Passerines: nonpasserines*
Santa Cruz Is.	380	27	0.93
Ndemi	215	16	1.29
Vanikoro	100	18	0.80
Utupua	50	15	0.67
Reef Is.	?	12	0.50
Duff Is.	?	8	0.33
Swallow Group	?	6	0.50
Tikopia	?	4	1.00

Fiji, Samoa, New Caledonia, and the New Hebrides contain the principal large islands east of the Solomons. Fiji and Samoa constitute the avifaunal core of Oceania and (in view of the distance from the nearest continent) have a comparatively rich, typically Polynesian bird life; both consist of several old, big, mountainous islands and many small, mostly coralline, impoverished islands lacking distinctive endemic elements (Mayr, 1941c: 205). The accompanying tabulation contrasts avifaunal size and passerine differentiation in the high islands and in the small or low islands (see Figure 15).

	Area (mi²)	*Resident land species*	*Passerines: nonpasserines*
Fiji Islands	7069	46	1.30
Viti Levu	4053	39	1.29
Vanua Levu	2128	35	1.50
Taveuni	166	37	1.31
Kandavu	165	32	1.25
Ovalau	43	29	0.93
Lau Archipelago	45	22	0.69
Tonga Archipelago	250	14	0.75
Samoa	1209	27	1.46
Savaii	703	24	1.40
Upolu	430	23	1.30
Tutuila	52	12	0.71
Manua Is.	22	11	0.57

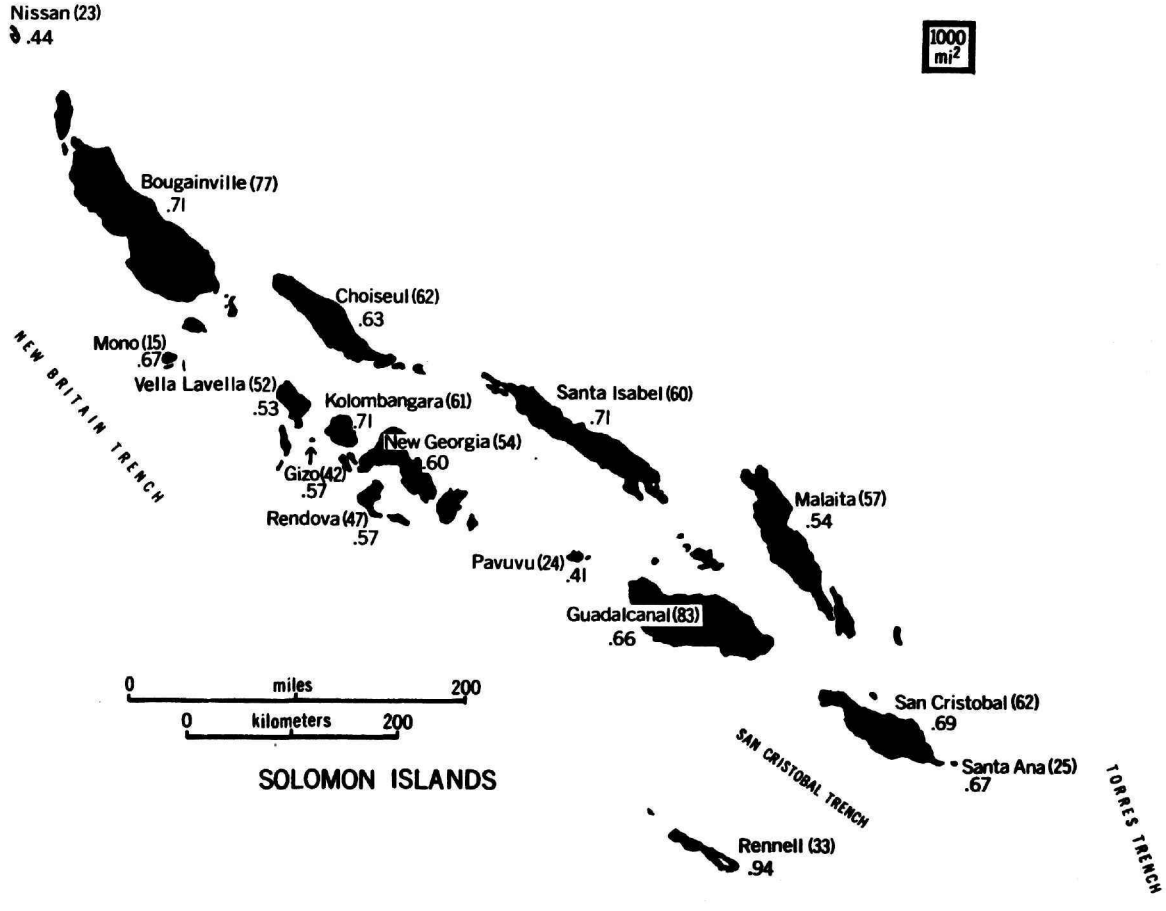


FIGURE 17.—Solomon Islands: passerine-nonpasserine ratios of native land birds (numbers of species in parentheses).

High, oceanic New Caledonia (Figure 18), the largest island east of New Guinea and the richest east of the Solomons, has a relatively high species count that may be due to the comparative vicinity of Australia and to an equally strong Papuan influence; long isolation is indicated by the high endemism, about one species in three, but "the number of endemic genera of birds is amazingly small" (Mayr, 1941c:209; 1945:149). The below-unity ratio of New Caledonia is "normal" for an isolated oceanic island.

The Loyalty Islands ought to have at least as low a ratio as New Caledonia, provided they are indeed satellites (Figure 18). They are located, however, on a different, probably younger island arc, have a weakened Australian element and show a stronger Papuo-Melanesian influence, share only four of the New Caledonian endemics, and have received a number of New Hebridean strays that might otherwise have reached New Caledonia (Mayr, 1941c:210). In relation to area, environmental complexity, and species number, the three Loyalties seem to vary unpredictably, as do the Banks Islands at the opposite end of the New Hebrides. In both these groups, sharp reductions in area are accompanied by equally sharp drops in ratio.

The New Hebrides as a whole have a close-to-unity ratio of 1.09 based on 22 nonpasserines and 24 passerines. Individually the islands have an

ostensibly perplexing range of values. Ratios in particular but also species numbers present a distributional pattern of sorts (Figure 18). Excluding the two largest islands (Espíritu Santo and Malekula), avifaunas become impoverished with increasing distance from the center of the arc, ratios decrease most markedly through the islands trailing southward into completely open ocean.

	Approximate area (mi²)	*Resident land species*	*Passerines: nonpasserines*
Torres Islands	?	10	0.67
Banks Islands			
Valua (Saddle)	10	21	0.91
Bligh	?	22	1.20
Vanua Lava	100	29	1.23
Gaua (Santa María)	125	31	1.39
New Hebrides (excluding Espíritu Santo and Malekula)			
Aurora (Maewo)	115	24	1.40
Oba	100	31	1.21
Pentecost	200	28	1.33
Ambrym	375	32	1.67
Epi	150	34	1.13
Efate	350	37	1.06
Erromanga	315	33	0.94
Tanna	250	29	0.71
Aneiteum	50	27	0.83

The three southernmost islands lack most of the New Hebridean endemic species and have a distribution indicating accidental dispersal owing to age (considerably younger than New Caledonia and Espíritu Santo); also "on Tanna (and perhaps on Erromanga and Aneityum) volcanic eruptions have exterminated part of the indigenous fauna . . . [while] destructive hurricanes are another factor that should not be ruled out altogether, particularly for smaller islands" (Mayr, 1941c:211). One might add that the destructive effects would probably be greater on the passerines than on the larger, more robust nonpasserines. The two large islands of Espíritu Santo and Malekula are situated off to one side from the others. Espíritu Santo has the richest avifauna, the most endemics, and a relatively low ratio (21 passerines and 19 nonpasserines). Malekula has, for its size, a low species total and a much lower ratio than any nearby island, as if it stood apart from the mainstream of interisland colonization.

French Polynesia: French Polynesia (based on Bruner, 1972) has in toto 32 resident land species; its principal components have the following totals:

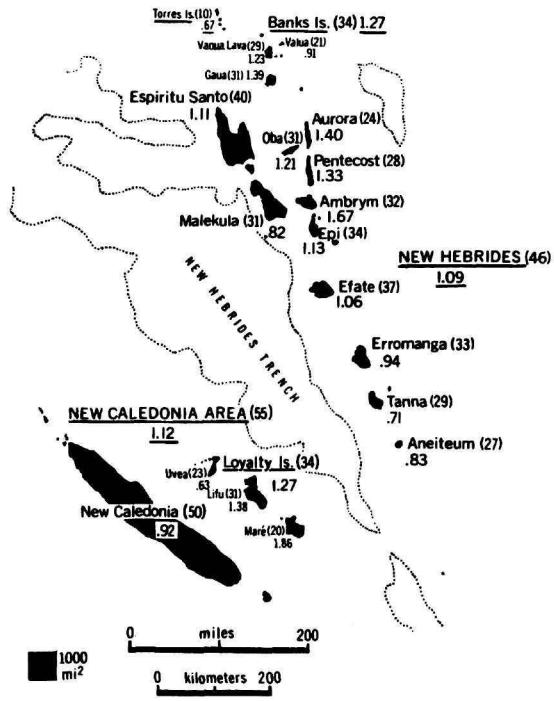


FIGURE 18.—New Hebrides and New Caledonia: passerine-nonpasserine ratios of native land birds (numbers of species in parentheses).

Society Islands, 13; Marquesas, 11; Tuamotu Archipelago, 7; the Austral Islands, 3. Compared to island groups less distant from Australo-Papua, French Polynesia, judged by the foregoing figures, has a somewhat larger avifauna than expected, whereas its four component groups each have a smaller avifauna than expected, at least on the high islands. Visual inspection of the figures gives rise to the suspicion that representative forms may have been raised to specific rank. In other insular groups, the aggregate number of species obtained by summing the components' totals is very much larger than the number in a checklist of the insular group as a whole. Here, in contrast, the aggregate total of the four components is hardly larger than that of French Polynesia as a whole. The suspicion is bolstered by Mayr (1941c:209), who regarded the avifauna of eastern Polynesia as exceedingly poor, with a high degree of slight, and a very low

degree of strong, endemism, and with little difference between the component groups.

Micronesia: Micronesia has few resident land birds and generally high passerine-nonpasserine ratios. The Palaus, on the near side of the Carolines least distant from a faunal source, have the most species (10 nonpasserines and 12 passerines) and a birdlife and ratio similar to the Philippines' (Figure 15). Ponape, on the far side of the Carolines, with three fewer nonpasserines and the same number of passerines, has a much higher ratio (1.72). The three remaining Caroline entries (Yap, Truk, Kusaie) and four in the southern Marianas (Saipan, Tinian, Rota, Guam) are very small and support only 9 to 12 species each. All the above-named are high islands.

The Carolines are strongly dominated by passerines, the Marianas less strongly. Individually the islands have avifaunas that are perhaps too small for their ratios to be meaningful. Nevertheless the high ratios of Micronesia as a whole and of each of its component groups suggest that a suitable set of explanatory circumstances probably does exist and waits to be found.

Other Islands and Archipelagos.—Following Darlington (1957:480), this category consists of "single islands or isolated archipelagos not falling into either of the preceding categories, but diverse otherwise, from large islands like Madagascar to the smallest oceanic ones": Celebes (previously included under fringing archipelagos); Madagascar, Mascarenes, Seychelles; New Caledonia (previously included under fringing archipelagos), Lord Howe, Norfolk; New Zealand; Hawaiian Islands; Galapagos; Atlantic islands; Antarctica (lacking land birds). Their existing faunas have all been derived overseas.

Indian Ocean: The islands in the Malagasy region—Madagascar, the Comoros, and the outlying Aldabras, Seychelles, and Mascarenes—and Christmas Island, near Indonesia, for the most part have native land avifaunas with approximately equal numbers of passerines and nonpasserines. All have the total land bird ratio lower than the native land bird ratio, suggesting that in this part of the world the islands are reached more easily or more often by more kinds of nonpasserines than of passerines, despite the larger species pools and greater numbers of individuals of the latter.

Madagascar, one of the world's great islands, dating from the Secondary and possessing a variety of climates, altitudes, and environments, has a smaller avifauna than on mainland areas or even on continental islands a tiny fraction of its size, while passerines comprise a much smaller proportion than on the mainland and include hardly any nonendemics (Moreau, 1966, chapt. 17). That Madagascar is sufficiently old and distant to have an "impoverished" avifauna and a reduced number of passerines is in keeping with its below-unity ratio of 0.94, which is considerably smaller than on comparable mainland but typical of oceanic islands in general. "The most likely explanation," according to Moreau, "is that there have been widespread extinctions, not only of the sub-oscines . . . but also of the 'modern' birds, especially the passerines," the cause of which must have been climatic.

Moreau pointed to three features of the Madagascan bird fauna. "The first is its poverty and unbalance compared to African areas." But these are the very characteristics one associates with chance dispersal from the mainland. Further, Moreau noted that over one-third of the passerines belong to two families and all but one to endemic genera. Elsewhere, however, this would be a certain sign of local radiation in an insular environment. "The second is the low average number of species per genus, which, compared with the African figures, suggests that in Madagascar more than twice as many species as now exist there may have recently been lost." An alternative explanation, relating reduction in number of species per genus to reduction in number of niches (Slud, 1960:141), could also apply here. "Thirdly, the bird species in Madagascar are so imperfectly segregated into each of the main habitats . . . that a considerable proportion of them occupy both forest and also one or both of the drier zones . . . a degree of adaptability extremely rare in Africa . . . and it is difficult to imagine how it can have come about in Madagascar except by such casualties in the bird fauna of one or other of the habitats that numerous niches became vacant." Yet Moreau's reference to the "obvious broadening of niche . . . occupied by the same species in Madagascar or in Africa" can be interpreted to mean that there are fewer niches on the island than on the mainland.

The remaining islands are the Comoros, with 46

species and a ratio of 1.19 for the group (or 0.97 and 1.04 for forested Gran Comoro and Moheli, 0.62 and 0.59 for deforested Anjouan and Mayotte); the Aldabras, with only eight passerines and six nonpasserines; the Seychelles, with eight passerines and seven nonpasserines; the Mascarenes, with seven species each of passerines and nonpasserines on Reunion and on Mauritius, two passerines and four nonpasserines on Rodriguez; and Christmas Island, with two passerines and six nonpasserines.

Lord Howe Island and Norfolk Island: "Lord Howe is a small volcanic island about 300 miles east of Australia and about twice as far south (and a little west) of New Caledonia, 5 square miles in area and nearly 3000 feet in greatest altitude" (Darlington, 1957:525). It has a native land bird total of eight passerines and four nonpasserines or, excluding recent extinctions, three passerines and two nonpasserines. Of the land and fresh-water species, "two or three seem to have come from Australia, three from New Caledonia, and one from New Zealand, and the geographical origin of the rest is doubtful" (Darlington, 1957:525).

"Norfolk Island is a small volcanic island about 800 miles east of Australia and midway between New Caledonia and New Zealand, about 13 square miles in area, and 1000 feet high" (Darlington, 1957:526). It has a list of nine passerines and five nonpasserines, though two of the latter are now extinct.

It would appear that Lord Howe and Norfolk, both of them high nontropical islands and with lists of almost equal length, are in position to receive colonists from at least three directions. That they are dominated by passerines is due in part to the sympatric presence on Lord Howe and Norfolk, respectively, of two and three species of *Zosterops*, almost certainly the result of separate colonizations (Lack, 1947:150). With respect to total land birds, at least on Lord Howe, where some data are available (Hindwood, 1940), the ratio is close to unity (11 passerines and 12 nonpasserines), as in the Indian Ocean.

New Zealand: New Zealand is located about 1000 miles east-southeast of Australia; the two main islands have a combined area of more than 100,000 square miles; the islands are old, with high mountains, and are ecologically diverse within the limits of their temperate climate; the existing vertebrate fauna appears to have accumulated gradually across wide water gaps (Darlington, 1957:526–527).

The two main islands have a combined list of only 20 passerines and 16 nonpasserines (based on Fleming et al., 1953). The number of nonpasserines, however, considerably exceeds that of the passerines if recent species of moas are included: "The living birds were well known to the Maoris; and extinction became complete only within the last few centuries" (Thomson, 1964:477). As on little Lord Howe and Norfolk islands to the west, the total land bird ratio on New Zealand, excluding moas, is much lower than the resident land bird ratio: nonresident nonpasserines outnumber nonresident passerines by about two to one.

Cool New Zealand and warm Madagascar, with the oldest vertebrate island faunas (Darlington, 1957:536), both have avifaunas and passerine-nonpasserine ratios that are greatly reduced from those on comparable mainland; they receive extremely few potential colonizers; and both have given rise, especially on more isolated New Zealand, to a variety of flightless birds, including spectacularly gigantic ones.

Hawaiian Islands and Galapagos: Adaptive radiation from a single ancestor into a number of related species on oceanic archipelagos has taken place most dramatically in these two groups, probably because newer, more efficient colonists have been arriving too infrequently to eliminate the earlier inhabitants; similar considerations probably account for the absence of local adaptive radiations among the land birds of archipelagos off Europe, Africa, America, or even in Polynesia (Lack, 1947: 150–151).

On the forested Hawaiian Islands, at least 2000 miles away from North America, 28 of 35 native birds (80 percent) have evolved from three propagules (a drepanid, a meliphagid, and a turdid), all passerines and presumably the first successful land birds to have arrived (see Darlington, 1957: 528); only two species are nonpasserines. On the dry Galapagos, two-thirds the area of the Hawaiians and one-third their closest distance from the American mainland, some 13 of 24 native land species (54 percent) have evolved in this manner, again from an ancestral passerine (a fringillid) that presumably was the first land bird to successfully colonize the islands; only five of the land

	Area (mi²)	Latitude	Closest distance to coast	Resident land birds	Passerines: nonpasserines	Residents: migrants
Azores (Portugal)	888	38°	800 mi.	14	1.80 (1.61)	0.42
Madeira Is. (Morocco)	302	33°	400	23	1.30 (1.46)	0.32
Canary Is. (Spanish Sahara)	2807	28°	60	49	0.96 (1.26)	0.77
Cape Verde Is. (Gambia "Valley")	1557	16°	350	25	0.92 (1.06)	1.79

birds are nonpasserines.

If one could hypothesize a geographical situation which prohibited specific radiation on these islands, the Hawaiians would have five passerines and two nonpasserines, the Galapagos seven passerines and five nonpasserines. As to total land birds, the Hawaiians as a whole would have either ten passerines and eight nonpasserines or, excluding the westernmost atolls, five passerines and eight nonpasserines (based on Berger, 1972); the Galapagos would have 11 passerines and eight nonpasserines. It is paradoxical, also difficult to explain, why six nonresident nonpasserines and no nonresident passerines have been recorded from the main Hawaiian chain (the State of Hawaii) when the residents are so heavily passerine.

Atlantic Islands: The North Atlantic groups—Azores, Madeiras, Canaries, and Cape Verdes—lie at different distances off southern Europe and western Africa. (See above.)

Their passerine-nonpasserine ratios, as on the mainland, decrease with latitude from well above unity on the Azores and Madeira Islands in cooler waters to below-unity on the Canary and Cape Verde islands in warmer waters. The ratio of residents to nonresidents, increasing equatorward (as on the island groups off eastern Asia), remains low on the Azores and Madeiras, mounts on the subtropical Canaries, and rises high above unity on the tropical Cape Verdes. The Canaries have two to over three times the number of species on the other groups, but they are also the closest to shore. The two innermost Canary Islands are dry and have passerine-nonpasserine ratios under 0.90, the five other main islands are much higher, more humid, and have ratios ranging upwards of 1.20 (based on Moreau, 1966:360).

The four tropical Gulf of Guinea islands "lie on a straight line, diverging somewhat from the main north-and-south direction of the African coast" (Moreau, 1966:318). In the following tabulation, the numbers of resident land species and passerine-nonpasserine ratios are based on Moreau, 1966; the other entries are based on Amadon, 1953.

	Fernando Po	Principe	São Tomé	Annobon
Area (mi²)	800	50	400	7
Distance from mainland (mi)	20	140	175	210
Distance from preceding island (mi)	–	140	90	115
Number of species	140	23	32	6
Percent endemic species	1	20	38	33
Passerine-nonpasserine ratio	2.11	1.30	1.29	0.50
Percent passerines on Fernando Po	100	33	23	25
Percent nonpasserines on Fernando Po	100	76	48	50

Fernando Po is the largest, highest, and by far the wettest of the four. Situated on the coastal shelf and of recent continental origin, it has a well-balanced avifauna, three-quarters of which are typically forest birds; it bears a very close faunistic resemblance to Cameroon Mountain and its immediately surrounding lowlands only 20 miles away; though it has only one endemic species, fully one-quarter of the species show some divergence from the mainland populations, a proportion close to that shown by montane species on Cameroon Mountain compared to other montane populations in the Cameroons (Moreau, 1966:320). The high passerine-nonpasserine ratio unquestionably is a reflection of and is probably reduced from that on Cameroon Mountain as a whole (for which I have no list).

The other three islands stretch some 300 miles southward of Fernando Po and cross the equator. Of oceanic origin, they have been populated overseas, probably in larger part from the mainland than from one another. Taking into account their different sizes and positions, they follow a trailing sequence of greatly reduced species numbers and sharply decreasing passerine-nonpasserine ratios. The extent to which the species that reached these islands are the same as those on Fernando Po, particularly among the nonpasserines (see accom-

panying tabulation), is suggestive of the degree to which these are good colonizers in general or have successfully occupied similar habitats on these islands in particular. Principe and São Tomé (based on the island lists of Amadon, 1953) today share only 12 out of a total of 50 species of resident land birds, yet have similar passerine-nonpasserine ratios.

In the tropical South Atlantic, Ascension and St. Helena have no known members of strictly land bird families.

The three islands of the south-temperate Tristan da Cunha group, with an area of 52 square miles and nearly 2000 miles distant from the tip of Africa and farther from South America, have four resident passerines and no nonpasserines. With respect to adaptive radiation and passerine predominance, "Tristan da Cunha is Galapagos in miniature. At the other extreme . . . the Hawaiian Islands are as remote in the Pacific as is Tristan da Cunha in the Atlantic, and only five passerine forms have succeeded in reaching them" (Lack, 1947:152), compared to the original two or perhaps three that reached Tristan da Cunha.

Summary

Division of the Class Aves into two elements, the passerines and the nonpasserines, has enabled various authors to utilize the reciprocal relation of one to the other toward distributional, environmental, or evolutionary ends. The interrelationship is here justified on objective grounds.

Over the terrestrial globe, the species of passerines outnumber those of nonpasserines two to one. The ratio remains about the same for the zoogeographic regions: slightly lower in the tropics, slightly higher outside the tropics. Continued subdivision into smaller and increasingly homogeneous units expands the ratio range from very high above to far below unity (1:1). The passerines and the nonpasserines both have species densities that are considerably higher in the total land avifaunas and very much higher in the native land avifaunas of tropical units than of comparable extratropical units. Climatovegetational factors can explain much of the difference in faunal size that occurs latitudinally and biogeographically.

Migrants of course account for the difference in size between the total land bird and native land bird categories. Their percentage of the avifauna shows a parallel decrease equatorward along either side of the Atlantic and Pacific oceans in inverse proportion to the size of the avifauna. Wintering migrants hardly add to the residents in tropical "rain" forest but occur in greatest abundance under brokenly forested and disturbed conditions.

In the tropics, the passerine-nonpasserine ratio rises jointly with altitude from the lowlands to the temperate highlands. An avifauna under forested conditions has a higher proportion of passerines than one under nonforested or mixed conditions in the lowlands or in the highlands. A highland avifauna under forested conditions has a higher passerine proportion than a neighboring lowland avifauna under forested conditions. For purposes of faunal or environmental comparison, well-known small units are preferable to necessarily less well-known large units. A list of species actually recorded at a locality reflects the environment more faithfully than does an amalgamated list from a large area.

Islands are each unique and conform to no universal standard. Two islands the same in size, age, physiography, and climate will have different constellations of taxa, numbers of species, and vegetational physiognomies to the degree that they are inaccessible to potential colonizers; an impoverished avifauna is surely the sign of an impoverished biota. Comparative judgments must relate ultimately to standards set on the mainland.

The Suboscine-Oscine Relationship

The Passeriformes, also known as the passerines or perching birds, contains 5168 species or two-thirds of the world's recent land birds (based on Austin, 1971). Almost four-fifths belong to a single suborder, the oscines or true songbirds. The several remaining suborders comprise the antithetically designated suboscines and contain approximately 1100 species. About 50 species of suboscines are known from the Old World, the rest are American and are mostly confined to the Neotropical region. The complementary nature of the neotropical suboscine-oscine relationship had been suggested by Slud (1960), largely on the comparative basis of compilations from the distributional literature. Since then new faunal works have appeared which treat several major units for the first time and bring several others up to date.

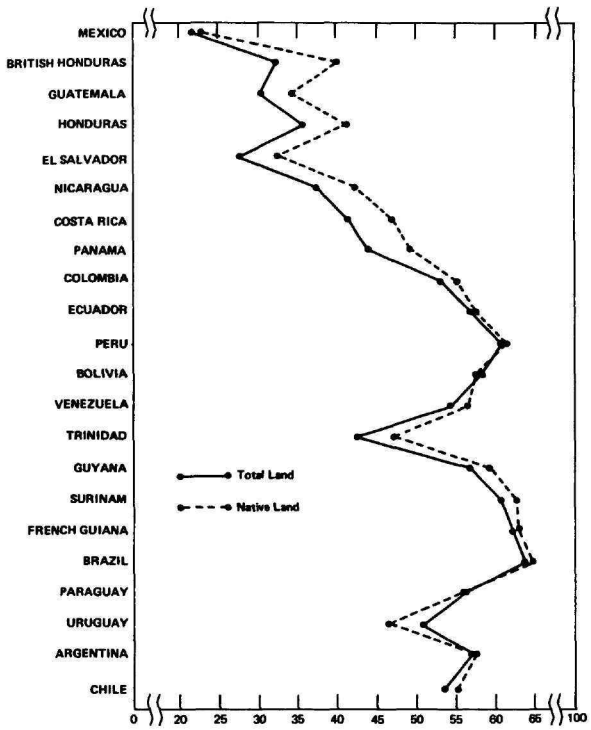


FIGURE 19.—Neotropical suboscines: percent of the species of passerines per country.

NEOTROPICAL DISTRIBUTION

GENERAL.—The nearly 1050 New World suboscines are equally divided between the strictly neotropical Furnarii, including woodhewers, ovenbirds, antbirds, and tapaculos, and the more widespread Tyranni, principally cotingas, manakins, and tyrant-flycatchers. Suboscines amount to more than half the species of native passerines or total passerines on the neotropical mainland (i.e., south of the Isthmus of Tehuantepec), three-fifths of the species in South America, two-fifths of the species in Central America, and between one-quarter and one-fifth of the species in Mexico.

The suboscine proportion of the passerines among the individual Latin American countries, both with and without extralimital migrants, is shown in Figure 19. Suboscines are dominant over oscines throughout mainland South America, except perhaps in deforested Uruguay, and keep approximately the same proportion in Colombia in the north as in Chile in the south, despite the sevenfold difference in number of species. Percentagewise the suboscines decline linearly from northern South America northward through Middle America, except for displacement toward lower percentage in "dry" El Salvador on the Pacific side and toward higher percentage in the British Honduran lowland on the Caribbean side. If El Salvador were united with adjoining Honduras, and British Honduras with adjoining Guatemala, so as to cross-section the Central American isthmus and thus embrace a wider range of environments, as do Panama, Costa Rica, and Nicaragua, there would be no displacement. Mexico's suboscine percentages would not fall nearly so low if the country were represented only by its neotropical portion, that lying south of the Isthmus of Tehuantepec.

Figure 20 compares absolute numbers of suboscines and oscines, shows their relative magnitudes, and relates them to suboscine-oscine ratios. Further, it illustrates the relative effect of the presence or absence of migrants on numbers of species and on suboscine-oscine ratios. Southwestern United States and adjoining Mexico have been included to emphasize the suboscine decline northward into North America. The Middle American units and the South American units are separated by, and face one another across, the suboscine-oscine line of unity (1:1).

BRAZIL.—Brazil, the country with the largest extent of lowland "rain" forest, has the largest number of suboscines and the highest ratio of suboscines to oscines. As with passerines and nonpasserines, the individual states and territories, excluding those in Amazonia (Figure 21*a*), have a wider range of suboscine-oscine ratios than do the country's principal geographic sectors, excluding Amazonia (Figure 21*b*). Whether plotted by individual state and territory or divided into halves, Amazonia lies in a suboscine direction well away from the other units. Throughout the "rain"-forested Amazon drainage, suboscines outnumber oscines up to two to one, locally up to three to one (Table 6), in species and comprise two-fifths or more of the entire land avifauna.

The suboscine-oscine relationship within the Amazonian sector of Brazil is presented in Table 6. Only those "areas" and places are included that have a minimum of 150 recorded species of passerines. All have suboscine-oscine ratios which

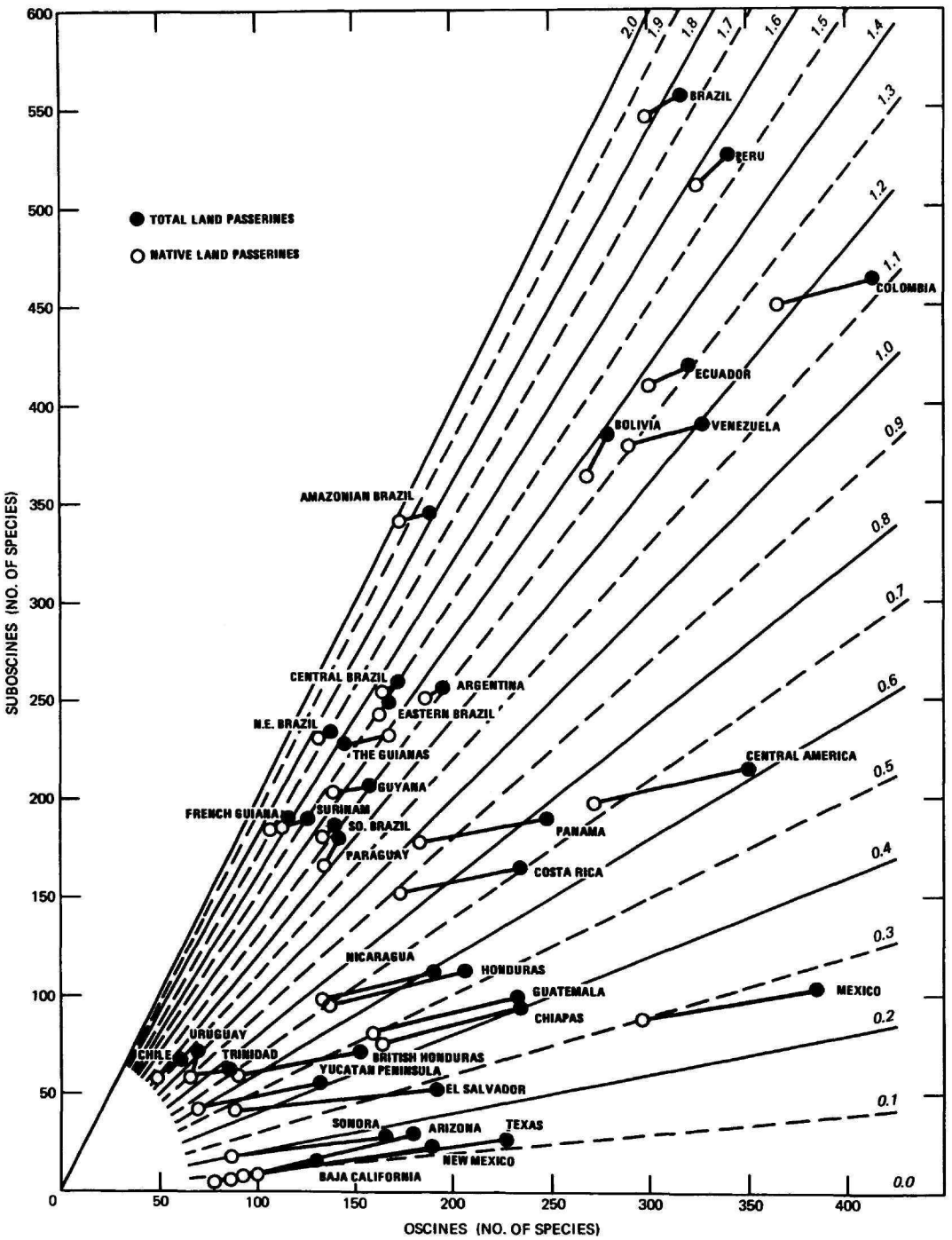


FIGURE 20.—Neotropical passerines (including southwestern United States): number of species of suboscines and oscines. (Radiating lines = suboscine-oscine ratios.)

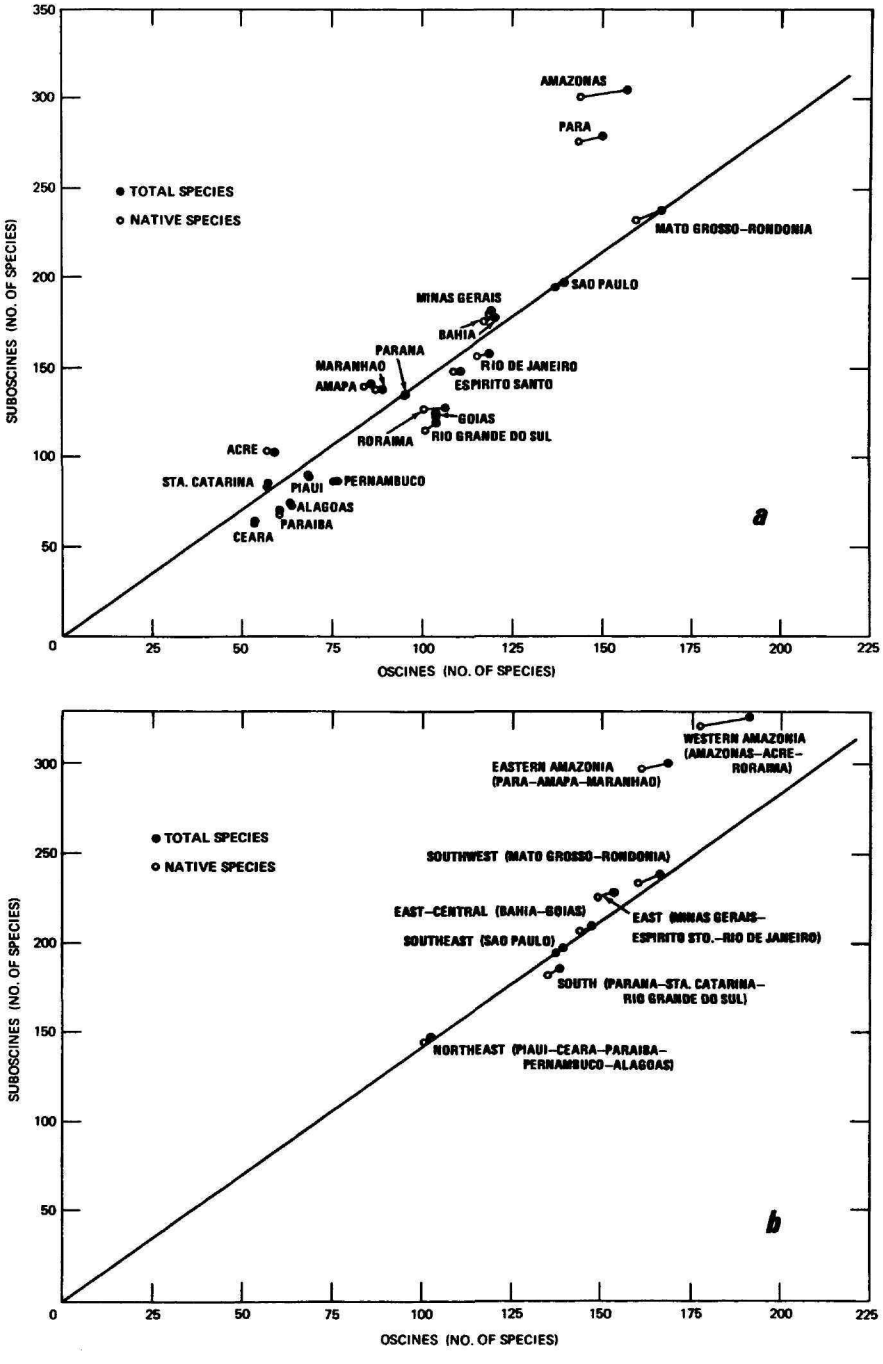


FIGURE 21.—Numbers of species of suboscines and oscines in Brazil: *a*, per state and territory; *b*, per sector. (Diagonal = suboscine-oscine ratio of 1.4.)

exceed that of the sector as a whole (1.85), except northeastern Pará (1.49), at the mouth of the Amazon, and the Manaus-Itacoatiara area (1.46, 1.70), along the juncture of the Rio Negro and the Rio Madeira with the Amazon. In northeastern Pará, where there is an admixture of species from the dry northeast of Brazil and the climate and vegetation appear to be broadly transitional (see Weber, *in* Fittkau et al., 1969:476–479, maps), the reduced suboscine proportion forms part of an eastward-spreading decrease that seems to originate in the neighborhood of the right bank of the lower Tapajos (2.12) or possibly nearer the Xingú (2.15). At Manaus-Itacoatiara the drop in ratio is abrupt, as though the area were isolated from the surrounding high levels. The great width of the Rio Negro at its confluence with the Amazon cannot be invoked here as a distributional barrier to birds. Igarapé Cacau Pereira (not included in Table 6), situated on the opposite side of the Rio Negro from Manaus, has total and native ratios of 1.42 and 1.43 (based on 133 passerines, including two migrants) that are virtually identical to the 1.46 and 1.48 of Manaus. The area around Manaus, it appears, is one of bleached sandy soil associated with a distinctive type of rain forest (Richards, *in* Meggers et al., 1973:21).

Colombia.—More diverse environments should show greater avifaunal differences than those discernible in the relatively uniform Amazon basin. In the accompanying tabulation, the principal faunal sectors are the same ones previously employed for passerines and nonpasserines in Colombia; suboscine-oscine ratios are followed by numbers of species of passerines in parentheses (compiled from Meyer de Schauensee, 1964).

	Total passerines		*Native passerines*	
Pacific	1.11	(234)	1.31	(204)
Caribbean	0.79	(178)	0.94	(155)
Central Mountain	0.91	(578)	0.96	(537)
Orinocan	1.38	(311)	1.59	(280)
Amazonian	1.80	(342)	1.97	(315)

Suboscines predominate in the humid lowlands of Colombia, whether Amazonian, Orinocan, or Pacific, but fall below unity on the dry Caribbean versant and in the mountains. As was the case with passerine-nonpasserine ratios, the total and native suboscine-oscine ratios of 0.91 and 0.96, respectively, for the "Central Mountain" sector appear to be a good representative average: the corresponding figures for Cundinamarca are 0.88 and 0.94. The 0.79 and 0.94 of the Caribbean sector agree with the 0.82 and 0.98 of Atlántico. The ratios of 1.80 and 1.97 of the Amazonian sector are virtually duplicated by the 1.80 and 1.92 of Caquetá and the 1.85 and 1.97 of Amazonian Brazil. The 1.38 and 1.59 of the Orinocan sector are approached by the 1.33 and 1.49 of Meta. The 1.11 and 1.31 of the declivitous Pacific sector compare, respectively, less well with the 1.29 for total passerines but extremely well with the 1.38 for native passerines of a collection from Guapi, on the coast, reported by Olivares (1957–1958).

Other Areas.—The few adequate data available indicate that as a general rule the suboscine proportion decreases with increasing elevation (Table 7). Exceptions, i.e., lowland areas with low suboscine proportions, are the interior valleys of eastern Guatemala, Caribbean Colombia, northeastern Venezuela, southwestern Ecuador, the department of Lima in coastal Peru, and southwestern Peru. These units are doubly distinguishable, on the one hand by the fact that they are climatically dry, on the other hand by their small avifaunas, which, together with low ratio, produce a combination found elsewhere only at high altitudes.

The relatively high suboscine proportion for Peru, a typically Andean country, is explainable by the fact that it possesses extensive Amazonian lowland teeming with suboscines. The relatively low ratio for the Apurímac valley in eastern Peru is in itself sufficient reason to suspect a subtropical influence, the actual presence of which is borne out by the valley's description as "a broad finger of Amazonian lowland that penetrates 150 miles into the Andes between two high ranges" (Terborgh and Weske, 1969:765). Also in Peru, the Urubamba valley passes through tropical Amazonia and would be expected to have higher ratios than shown (Table 7), but the low ones are in accord with its having been collected most heavily at its middle and upper reaches (Chapman, 1921:11).

Costa Rica.—*Altitude:* Whether or not a climatic pattern emerges from the distribution of the suboscine-oscine ratios of the same "areas" and localities in Costa Rica previously compared for their passerine-nonpasserine ratios can be determined from Table 3. Strictures to be kept in mind are that some places have been visited more often or at more different times of year than others, that

for many places the avifaunal representation has passed little beyond the stage of a sample, and that the major components of the native avifauna are far less affected proportionally by local movements of native species than are those of the total avifauna by the occurrence of extralimital migrants.

Native ratios indicate in the main that the suboscine proportion does decrease from one set of localities with rise to another set in the next higher belt. The humid tropical entries all have ratios above unity, except Los Chiles and La Lola, both of which have been extensively deforested. Two other areas, Boruca-Paso Real on the Pacific slope and Sixaola on the Caribbean slope, each have a close-to-unity ratio of 1.03. (The two also have identical passerine-nonpasserine ratios.) The Boruca-Paso Real area is located in edaphically poor, cutover savanna-type country; the Sixaola area has been heavily deforested by commercial interests and includes old records that probably apply to the subtropical belt. Their low ratios would appear to ally the above-mentioned localities to those in the Tropical Dry Life Zone, but they are immediately separable from the latter by their considerably longer species lists and high passerine-nonpasserine ratios.

The subtropical entries (Table 3) fall below unity, with two exceptions: Juan Viñas-Tucurriqui on the Caribbean slope and Las Mellizas-Cotón on the Pacific slope. I combined lists for Juan Viñas and Tucurriqui, which I had compiled from the literature (primarily Carriker, 1910), in hope of achieving a better representation than separate treatment would furnish. Either the combined list continues to be unrepresentative or the Reventazón valley, in which the two localities lie, affords suboscine-dominated birds from the tropical belt unimpeded access to the interior. In the case of Las Mellizas-Cotón, the data appear to reflect the climatic regime governing the humid Pacific southwest, "where the suboscine proportion remains at approximately the same level from the Osa Site [Rincón de Osa] upward to the Río Cotón Site. On the Caribbean side the suboscines suffer approximately a 40 percent drop in relative proportions between the lowlands and the equivalent altitude of the Río Cotón Site" (Slud, 1965: 117). Still, I place little confidence in this list, which consists of a wet-season sample from Las Mellizas combined with a dry-season sample from Cotón. Cotón, judged by its physiognomy, assortment of birds, and climate, has no Caribbean counterpart. At higher elevations, the suboscine-oscine ratios in the lower-montane and montane belts plunge to half their value or less in the subtropical belt.

Forest versus Nonforest: How the suboscine-oscine relationship fares at a site under forested and under unforested conditions cannot be determined reliably, comprehensively, or comparatively from the literature. Some information is available for Costa Rica, based almost entirely on what I considered to be a forest bird at the time and place of my visits (Table 5). The impression that the suboscine proportion increases inside woods is amply substantiated, with three apparent exceptions. One, the Bagaces site, is perhaps an "abnormal" example as it was very small, very disturbed, and depauperate (Slud, 1965:6). Second, the Río Suab locality, with only four nonforest passerines and 56 forest-inhabiting passerines, was poorly censused, as was the third, the San José de la Montaña site; neither would remain an exception if it had one more suboscine.

Forest-inhabiting avifaunas have suboscine-oscine ratios that tend to increase with increasing elevation (Table 5). Whether for climatic or edaphic reasons, as the case may be, humid-forested tropical-belt localities have above-unity forest ratios (except La Lola and Los Chiles, both extensively deforested and poorly represented by forest species). Subtropical localities with a Caribbean climate, viz. trade-wind influenced and a very short effective dry season, have forest ratios ranging downward from unity. Apparent exceptions are Hacienda Santa María and Silencio de Tilarán, both of which, however, occupy low gaps in the continental divide and thus are subject to faunal overlap from the Caribbean and the Pacific lowlands on either side. In the subtropical belt in the Pacific southwest, unlike the situation at analogous elevations along the Caribbean slope, humid-forest ratios tend to remain at least as high as in the lowlands, apparently in correlation with the more marked seasonality of the Pacific slope in general. At still higher altitudes, localities for which data are available are few. These are virtually restricted to the Caribbean slope and the Caribbean-influenced central mountains, and their ratios are distinctly low. An exception, La Hon-

dura, situated on a long, steep slope, would surely have its ratio fall below unity if its list did not include species more properly known from lower, warmer elevations.

Sample versus Compilation

Table 4 compares suboscine-oscine ratios of compilations with those of samples for countries and localities. Countries, such as Honduras and Costa Rica, but also the Canal Zone territory, apparently have a large enough area and a sufficiently well-known birdlife for the relative proportions of the avifaunal components to have become fixed some time ago. The localities have suboscine-oscine ratios that, unlike their passerine-nonpasserine ratios, vary little between compilation and sample or, more often, differ increasingly as the difference in size between the compilation and the sample increases. The only group of related localities in which the ratio decreases from sample to compilation is confined to, and apparently characterizes, the Tropical Dry sector.

Barro Colorado Island and Finca La Selva, the best known of the localities, still have not reached suboscine-oscine stability (Table 4). Barro Colorado, in particular, shows a progressive decrease in ratio that correlates roughly with increase in number of passerines. The decrease is due in part to foreign and native visitants, the majority of which are oscine. As a result, the growth of the oscine proportion has increasingly outstripped that of the suboscine proportion:

	Total suboscines / *Native suboscines*	*Total oscines* / *Native oscines*	*Total passerines* / *Native passerines*
1970	84/73 = 1.15	101/60 = 1.68	185/133 = 1.39
1952	78/70 = 1.11	85/54 = 1.57	163/124 = 1.31
1938	67/64 = 1.05	71/46 = 1.54	138/110 = 1.25
1929	61/58 = 1.05	58/40 = 1.45	119/98 = 1.21

Finca La Selva, with a much shorter history, has suboscine-oscine ratios that have changed little (Table 4). However, the sequence of periodic increase in numbers of suboscines, oscines, and passerines is similar at Barro Colorado Island (above) and Finca La Selva (below) and the sequence of ratios of total to native suboscines, oscines, and passerines, respectively, is practically identical:

	Total suboscines / *Native suboscines*	*Total oscines* / *Native oscines*	*Total passerines* / *Native passerines*
1970	89/80 = 1.11	110/68 = 1.62	199/148 = 1.35
1960	88/79 = 1.11	105/64 = 1.64	193/143 = 1.35
1957	69/66 = 1.05	84/57 = 1.47	153/123 = 1.24

Summary

The suboscines decline from three-fifths of the native passerines in South America to one-fifth in Mexico. Brazil, more than any other country, and Amazonia, more than any other area, have the most species of suboscines and the highest suboscine-oscine ratios. Suboscines not only outnumber oscines or nonpasserines in the "rain"-forested Amazon basin, but they are also very successful under analogous climatovegetational conditions in other tropical American lowlands, from Central America to western Ecuador and southeastern Brazil.

Broadly viewed, suboscine-oscine ratios in the neotropics are lower in the dry than in the humid life zones of the tropical belt on the one hand, and higher in the lowlands than in the highlands on the other hand. Two further types of ecologically based ratio are obtainable. One type is derived from the sum of reports for an entire belt or life zone. Altitudinally to tree line, the compiled data become progressively poorer in quantity and quality, yielding ratios that decrease irregularly or may even level out in the highlands. Thus qualified, suboscine-oscine ratios correlate inversely with rising elevation upon mountain slopes facing the lowlands, not upon isolated hills or ridges. The ratio tends to be higher than expected in intermontane situations, as in the central highlands of Colombia or Costa Rica, where the climatic and topographic conditions are complex and the available data imprecise. The other type of ratio is derived from a sample or from a sum of samples for a particular locality or "area." Individual localities in Costa Rica have suboscine-oscine ratios that vary inversely with rise from one altitudinal, or

thermal, belt to the next, at least on the Caribbean versant. On the Pacific versant, the pattern is only weakly distinguishable, perhaps as a consequence of the markedly seasonal climate, not only here but possibly in monsoonal climatic regimes in general. Other ratios which are lower than expected pertain to places that at present are extensively unforested when climatically they ought to be forested.

Countries or other sizeable units with large avifaunas that are represented by lists compiled a generation apart show little change in suboscine-oscine ratio from one to the other. Few localities or sites possess information, adequate or not, that permits their being compared against themselves chronologically. The well-worked ones are well along the road to suboscine-oscine stability, and the way from sample to checklist is marked by decreasing ratio, at least in humid localities. At all magnitudes of faunal or areal size, suboscines increase at the expense of the oscines in the forested portion of an environment compared to the unforested portions. The increase becomes relatively greater as the climate becomes warmer and wetter. Possibly the suboscines will yet be found to show a decrease under conditions that are warm but increasingly dry.

The Passerine-Nonpasserine Suboscine-Oscine Relationship

Comparative Categories

Just as passerines and nonpasserines comprise an avifauna, suboscines and oscines complement each other to comprise the neotropical passerines. Converted into percentages or ratios and cross-plotted, the two relationships produce a graph or scattergram permitting measurement and visual appreciation of the degrees of similarity or dissimilarity among avifaunas. An intraregional comparison might involve such major areas as Middle America, northwestern South America, eastern South America (Brazil), and southern South America (Figure 22). At a lesser scale of magnitude, a strictly political comparison would involve all the neotropical countries, regardless of size (Figure 23). Similarly, political comparisons within a major area, such as Brazil, would involve all the states and territories, again regardless of size.

The treatment becomes increasingly effective ecologically, rather than geographically, when applied locally to points on the map, whether these are scattered over different political units (Figure 27) or confined to a single political unit (Figures 28 and 29). Potentially the most useful subdivision is that created by parceling a locality into homogeneous environments. Comparisons could then be made of similar habitats at different places or dissimilar habitats at the same place. The factors limiting further refinement are those which so reduce a list of names that upon replication a small change in the number of species causes disproportionately large changes in the percentages or ratios.

Subregional Sectors.—Four sorts of lists for each of the major areas—Middle America, northwestern South America, Brazil, southern South America—are plotted in Figure 21. The lists separate into two sets, one with total avifauna and resident avifauna closely paired, the other set with total land avifauna and native land avifauna closely paired. Taking into account the prominent waterbird element in southern South America, the lists bear an overall similarity to one another despite their considerable neotropical spread. The straightness of the vertical alignment is due to the very small difference in passerine percentages (1.2 percent in the case of total passerines).

Countries.—In Figure 23, the unit of comparison is the individual Latin American countries (exclusive of the Antilles, Figure 30). The units are represented by their total land avifaunas in part *a* and by their native land avifaunas in part *b*. Changes in position of the units in the two parts of the figure are an indication of the relative size of their migrant proportions. In the Central American units, the distribution of the native land avifaunas, compared to that of the total land avifaunas, shows an equatorward shift toward the high suboscine proportions of the South American units, which remain stationary (except temperate-zone Chile and Uruguay), and a shift toward higher nonpasserine proportions in a direction away from those of the South American units, which again remain nearly stationary (except Chile).

Brazil lies closer to the Andean countries than to the Guianas (Figure 23). If, however, Brazil were sectioned geographically, its principal sectors would help fill the gap between Ecuador, Peru,

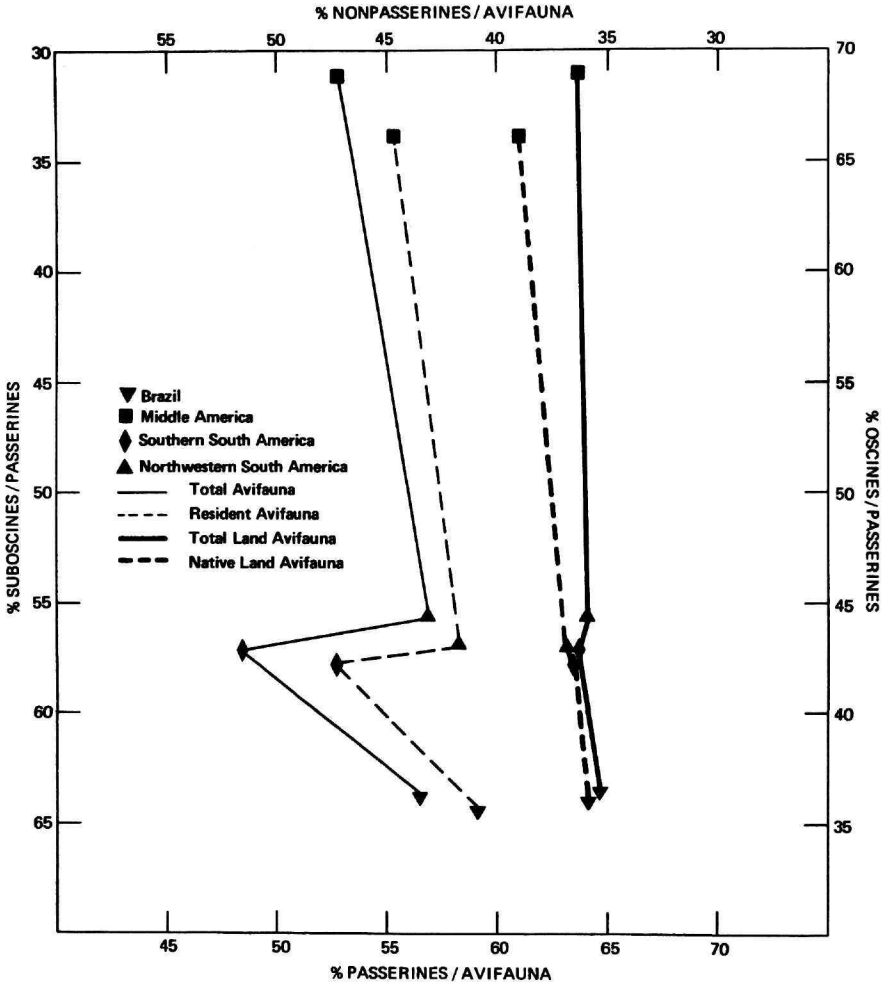


FIGURE 22.—Relative positions of four neotropical subregions: passerine (or nonpasserine) percentage of avifauna versus suboscine (or oscine) percentage of passerines.

Bolivia, and Paraguay on one side and the Guianas on the other side. The individual states and territories, especially the drier ones or those with little forest, would be dispersed more widely than the sectors, because a smaller unit is less heterogeneous than the larger unit to which it belongs. In principle, further subdivision into a countrywide array of small units would cause them to more fully occupy a still wider expanse. Graphed, a small unit tends to lie to one side of the larger unit of which it is part; the less it is known and the more unrepresentative is its list, the farther the small unit should lie from the large unit.

Figure 23 bears a distorted likeness to Middle America and to a condensed South America, the outline of which would be more complete if Brazil were divided into its country-size sectors. The similarity may not be entirely accidental, provided one is impressed by the correct alignment of Middle American units, including the pairing of southern Mexico with Guatemala, Honduras with Nicaragua, and Costa Rica with Panama; the location of the Yucatan Peninsula "offshore" from the neighboring mainland; the sequence of Andean

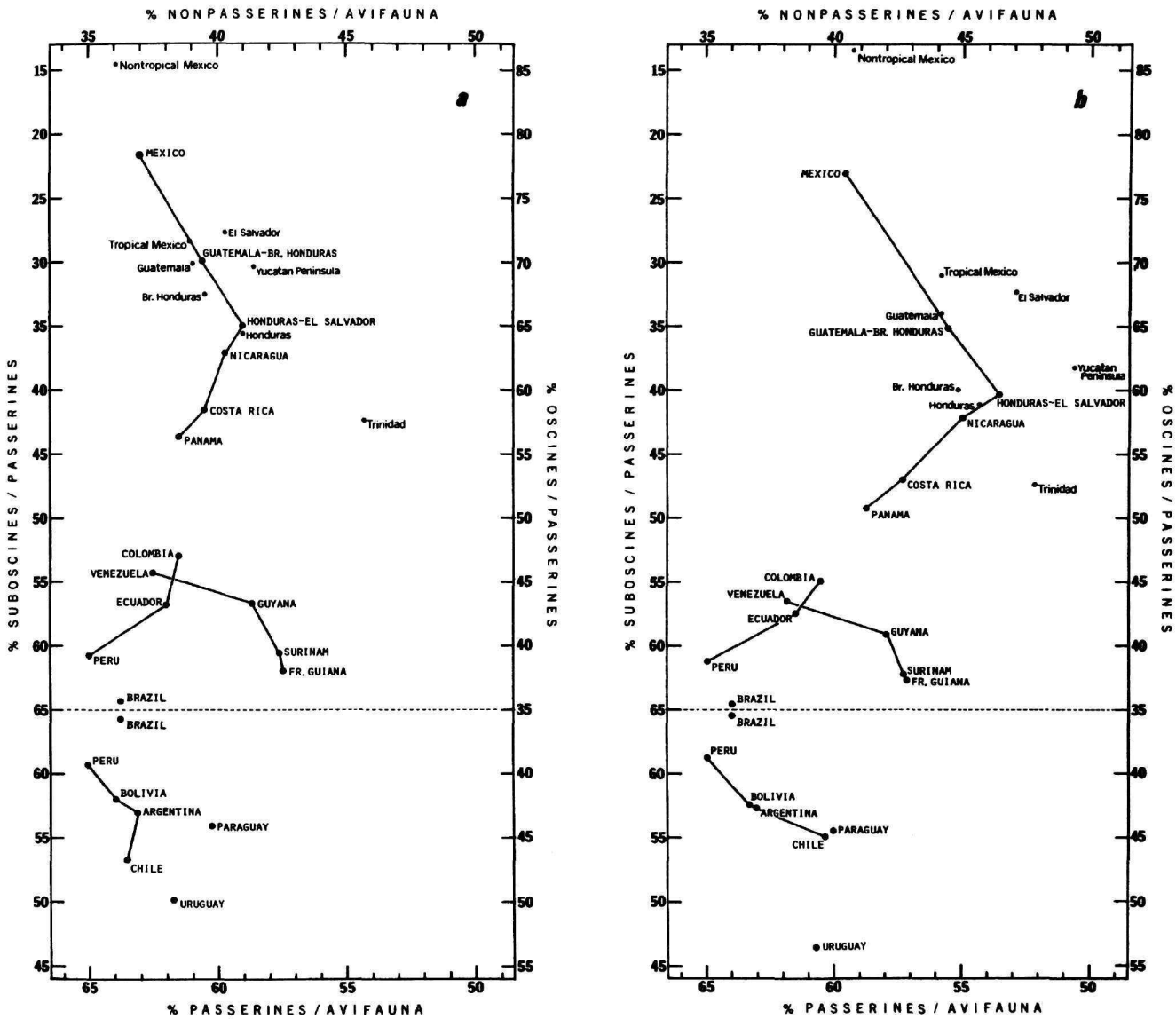


FIGURE 23.—Scattergram of neotropical countries based on avifaunal components (suboscine or oscine percentage of passerines versus passerine or nonpasserine percentage of avifauna; horizontal dashed line = equatorial transition between northern and southern South America): *a*, total land birds; *b*, native land birds.

countries on the west; the location of the Guianas on the opposite side of the continent, with Guyana followed at a distance by Surinam and French Guiana, closely paired and in proper order; the placement of Brazil closer to its Andean neighbors, with which it shares the Amazonian watershed, than to the Guianas, which occupy a different versant.

The suboscine-oscine ratio of 65:35 (approximately 2:1) was chosen arbitrarily to represent the line of division between the northern and southern hemispheres in Figure 23. A strict latitudinal accounting would, of course, require that southeastern Colombia, most of Ecuador, all of Peru, and the greater part of Brazil, including most of the Amazon and Rio Negro drainages, be transposed equivalent distances south of the equator. A way to circumvent the difficulty is to devise some sort of representative single figure and place it directly on a map (Figures 24–26).

Single-Figure Values

The components contributing to the land bird passerine-nonpasserine ratio, designated (a), and to the suboscine-oscine ratio, designated (b), can be interrelated directly and reciprocally in several ways. In my opinion, the simple (a): (b) relationship furnishes a single-figure value that is not only the best representative average of a unit, whatever its magnitude, but is also the most usefully comprehensible for comparative purposes (Table 8 and Figure 24; also Tables 3–5). At low elevations, the lowest (a): (b) values to be found anywhere in the neotropics occur in the Amazon valley (except the Manaus-Itacoatiara area) and the next lowest in the Guianas and along the "rain"-forested coastal strip of eastern Brazil. The highest (a): (b) values occur in arid areas—northeastern Venezuela, southwestern Ecuador, coastal Peru—and also in Uruguay (which is largely unforested and where the resident status of a number of species is not clear). The (a): (b) value increases with increasing elevation, reaching an extreme in the high cordilleras, and with increasing latitude, particularly in Middle America.

A list which one has reason to suspect is deficient usually yields an (a): (b) value that looks exaggerated or "wrong." A value that looks "wrong" should make one wonder about the representativeness of a list which had not previously come under suspicion. (Incidentally, "wrong" (a): (b) values can be intensified to stand out all the more when (a) and (b) are multiplied.) If, in place of ratios, the passerine (or nonpasserine) percentage of the land avifauna is termed (a) and the suboscine (or oscine) percentage of the passerines is termed (b), the (a): (b) values now tend to emphasize the similarities instead of the dissimilarities among units. Either way, one is provided with a measure of humid tropicality that relates to units of known area and to quantifiable climatic parameters.

The (a): (b) interaction apparently has the potential of bringing a degree of order into the distribution of similar avifaunas. For example, Vuilleumier (1970) analyzed 15 paramo "islands" in northwestern South America. An unpublished appendix supplied by the author enabled me to total 56 land species for one "island," 25 to 32 species (average 28.8) for each of five "islands," and 11 to 17 species (average 13.6) for each remaining "island" (disregarding one "island" with only four species): a virtually perfect geometric progression. Table 9 lists the "islands" individually, followed by five discrete physiographic groupings into which the "islands" separate according to the contours on the author's map. The groupings reveal an exponential (a): (b) increase from central Ecuador to central Colombia, thence to eastern Colombia, then to western Venezuela and to Santa Marta in northern Colombia. This pattern would not have come to light if reliance had been placed solely on correlation coefficients. Ratios for high Andean Ecuador, Colombia, and Venezuela are presented in the following tabulation.

	Passerines: nonpasserines (a)	*Suboscines: oscines* (b)	(a) : (b)
Ecuador	1.00	1.55	0.65
Colombia	1.28	1.29	1.00
Venezuela	2.00	1.00	2.00

The discrepancy, noted earlier, between the paramo zones of Colombia and Venezuela might now be regarded instead as support for an "island" sequence in the high mountains of northwestern South America.

Table 9 goes on to contrast the correlation coefficients of the 15 "islands" with those of the five groups. The coefficients of the 15 "islands" are fair to good for species and distance and for species

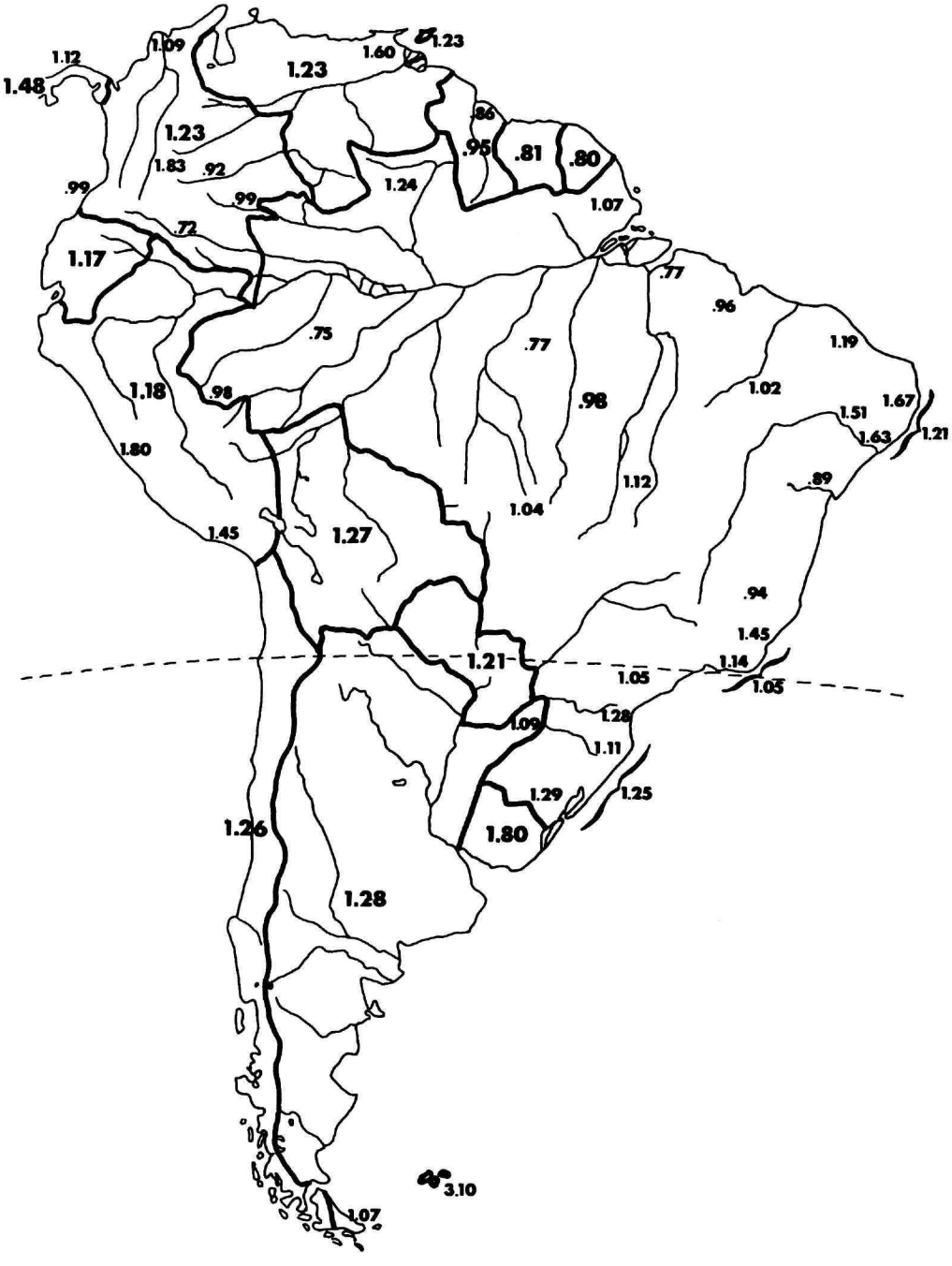


FIGURE 24.—South American native land birds: ratio of passerines-nonpasserines to suboscines-oscines. (Numbers in large type = countries; numbers in smaller type = political subdivisions.)

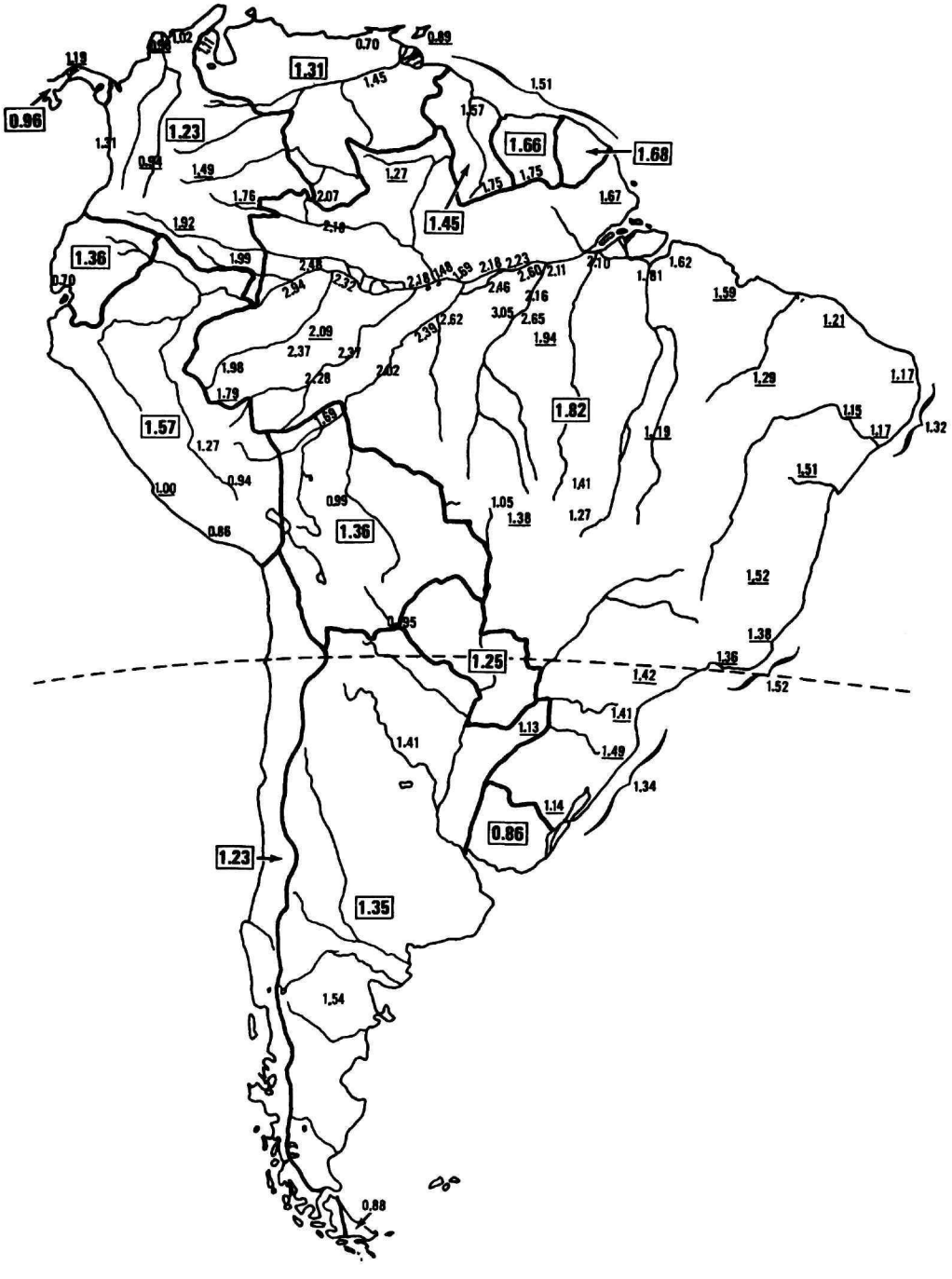


FIGURE 25.—Native suboscine-oscine ratios in South America. (Numbers in boxes = countries; underlined numbers = political subdivisions; unmarked numbers = smaller areas or general localities.)

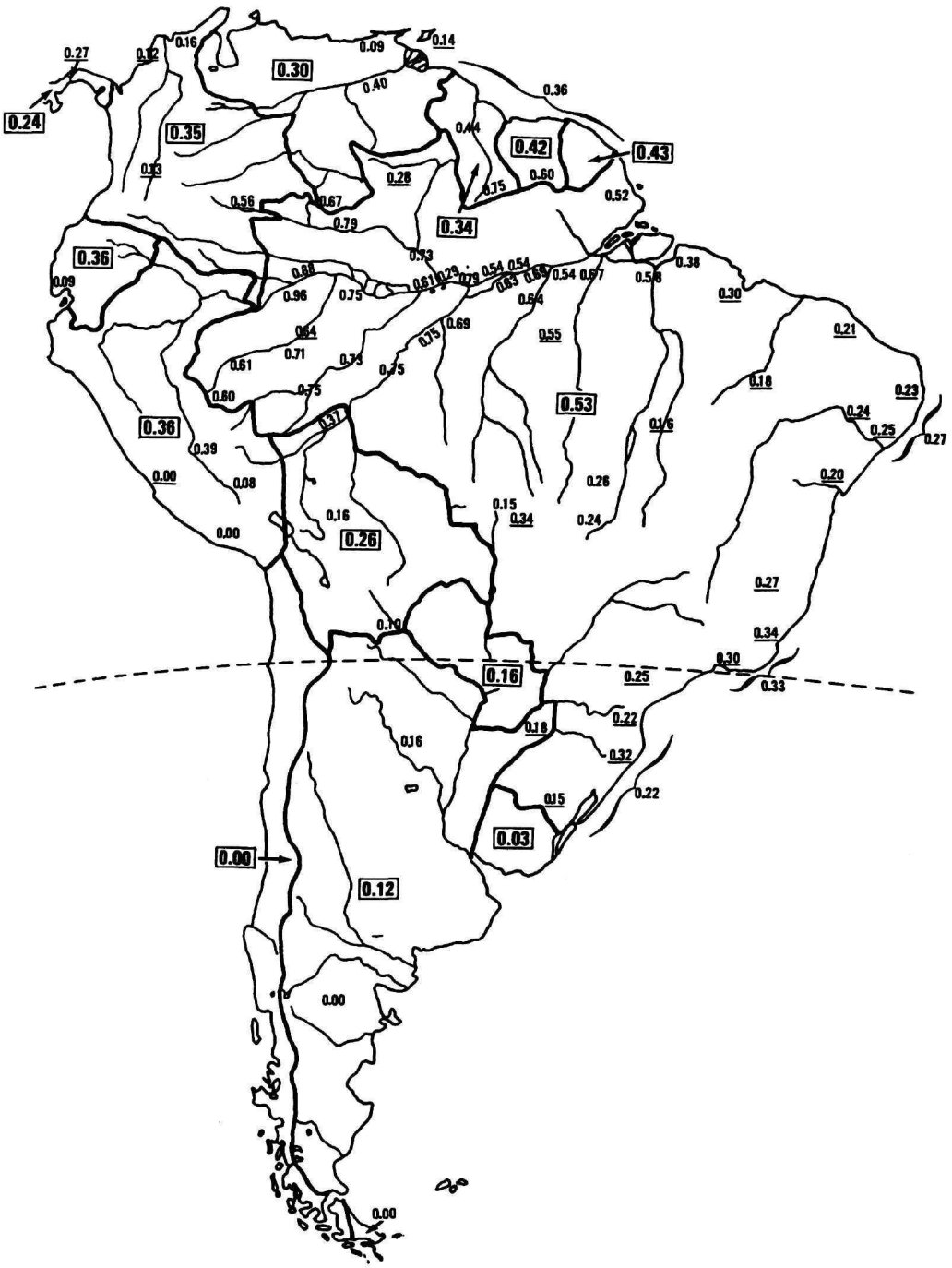


FIGURE 26.—Ratios of species of Formicariidae to those of native oscines in South America. (Numbers in boxes = countries; underlined numbers = political subdivisions; unmarked numbers = smaller areas or general localities.)

and area. The coefficients of the five groups are extraordinarily high in these respects. In addition, they range from significantly high to very high in categories where those of the 15 "islands" correlate poorly or not at all. Provided it is statistically permissible to do so, a reduction from five to four groups, owing to the removal of isolated, non-Andean Santa Marta, would result in even higher correlations, most strikingly with passerine-nonpasserine ratios and suboscine-oscine ratios.

The (a): (b) single-figure value would appear to have advantages that are best suited to site-oriented situations. Unfortunately, it is often the local list that engenders doubts as to its reliability and comprehensiveness. A telltale sign is the presence of few birds of prey, a deficiency which indicates in turn that the entire nonpasserine component may be too small. Yet the same lists can have good representations of suboscines and oscines. Elimination of the nonpasserines, therefore, actually increases their accuracy and usefulness. Indeed, suboscine-oscine ratios (Figure 25) provide single-figure comparative values that may be only little less representative of the distribution and affinities of South American land avifaunas than are the (a): (b) values. Perhaps this should have been expected from a "bird continent" that is also a suboscine stronghold.

A single-figure example of more restricted utility is furnished by the Formicariidae, or antbirds. The distribution of this large suboscine family, from southern Mexico to northern Argentina (Figure 26; Table 10), coincides with that of frost-free broadleaf woodland. Centered in Upper Amazonia, where the species of antbirds per locality number three-fifths to nine-tenths those of all the oscines, the family acts as a comparative climatovegetational indicator of biotic richness in the New World tropics, exclusive of the Antilles (all of which lack this sedentary family). Since the mainland distribution of the Formicariidae, or of any other selected group of "rain"-forest families, is ecological rather than political, comparisons between localities should be based upon environmental data, but few are available. In any event, one ought to be wary of relying on a single group, whether a large family or several "characteristic" small families, as representative of an avifauna. For instance, Costa Rica and Nicaragua approach each other in species of antbirds but are separated by a gap between their total numbers of suboscines.

Environmental Clusters

Altitudinal and latitudinal relations that result from cross-plotting passerine-nonpasserine and suboscine-oscine ratios are visualized in Figure 27. Avifaunas having similar relative proportions form a cluster, irrespective of shared or unshared taxa and of geographical proximity or distance. The assortment of entries, even though based on what was available rather than on true areal, faunal, or climatic comparability, is poor. Notwithstanding, the entries separate into two sets of environmental clusters, one set for the highlands, the other for the lowlands, in both of which the member groups succeed one another latitudinally. The dry lowlands in South America for which data are available—Caribbean Colombia, northeastern Venezuela, southwestern Ecuador, and coastal Peru—would, if entered in Figure 27, form an "out-of-place" cluster of their own in the area already occupied by the humid Central American lowlands, hence were omitted for the sake of clarity. But even if they had been included, the drastic reduction in numbers of species in the dry climates could be invoked as a third dimension that would keep them spatially distinct. An analogous concept is the "complexity index" of Holdridge (Holdridge et al., 1971:545–546) in which the climatic plant associations can have the same numerical value in different life zones lying along different temperature belts or in different humidity provinces.

"Areas" and localities within a single political unit are compared in Figures 28 and 29. Costa Rica was selected, because it is the unit for which I have the most information. The entries differ in size, complexity, range of elevation and climate, degree of disturbance, and extent to which they are known. A few consist of neighboring localities with inadequate lists, which I combined in hope of obtaining a more representative list of the local avifauna. Sometimes this procedure produces the opposite effect, but the alternative was to utilize lists that are too skimpy or not use them at all. In any event, the entries that are close to one another geographically but not climatically lie separated to the extent that differences in climate are reflected by changes in proportions of the avifaunal components.

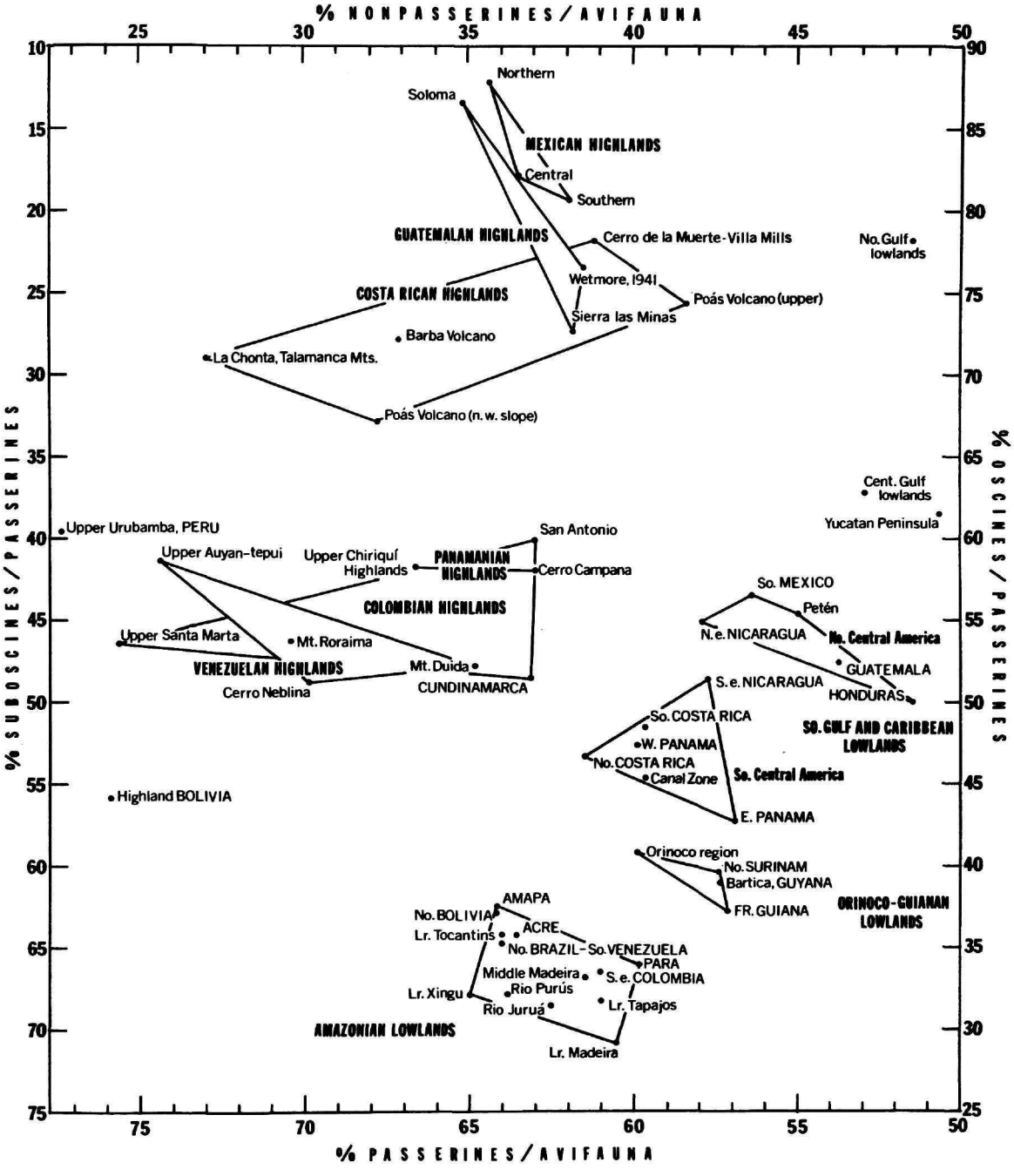


FIGURE 27.—Latitudinal and altitudinal distribution of Central American and northern South American areas and localities based on percentages of major avifaunal components.

Figure 28 is restricted to Costa Rican localities with a typically Caribbean, almost constantly humid, climatic regime. These form into groups the placement of which corresponds to the altitudinal zonation of the temperature belts. Not to be passed over is the apparently misplaced trio of entries consisting of Angostura (at an elevation of 600 m) and Los Chiles and La Lola (in the lowlands). These agree in having little primary woodland coupled with a reduced proportion of suboscines from that normally present at tropical-belt elevations. Another entry, Hacienda Altamira, situated in the northern lowlands, also ought to occur lower in the tropical belt. It is only known, however, from a one-week sample. Further work would almost surely bring its suboscine proportion up to expectation, provided the remaining forest has not been destroyed in the meantime.

Figure 29 plots localities on the more seasonal, partially monsoonal, Pacific slope of Costa Rica. These form into clusters that are disposed more or less horizontally, unlike the vertical arrangement on the Caribbean side. This pattern on the Pacific side suggests that the avifauna may be affected more by rainfall than by temperature. In the northern, seasonally arid sector of the slope, two entries, Miravalles and Rincón de la Vieja, lie above the others. Actually, both these "areas" range from the climatically dry lowlands upward into the Caribbean-influenced humid subtropical belt along the facing continental divide. In the southern, humid sector of the slope, the transition from tropical to subtropical is rapid and short in terms of suboscine or oscine percentage. Intermediately placed entries occupy an area the nature of which may not be so much transitional as confused, owing to seasonal effects having been blended into an annual average in some instances, while the majority are represented each by a single sample.

The fact that environmentally similar units form discrete clusters can be utilized to evaluate the degree to which a list may or may not be representative of an avifauna. For example, reports on general collections, such as those of Dearborn in Guatemala and of Sassi or Ferry in Costa Rica (Table 4), yield ratios that favor the climatovegetational zones and altered countrysides in which the authors spent most of their time. If plotted, these reports would lie outside the cluster of native land bird ratios formed by the checklists that are available for either country, whether in the direction of higher passerine percentages or of lower suboscine percentages. The (a): (b) values further emphasize the extent of the gap between the checklists and these reports, especially the one by Ferry, who did not work in the lowlands. Another example has recently come to hand (Table 4), thanks to Burt L. Monroe, Jr., who sent me the results of a midwinter tour he led in Costa Rica. The itinerary allowed little time in the humid tropical belt compared to that spent in the higher or drier parts of the country. This is reflected in the increased passerine proportion, the decreased suboscine proportion, and the very high (a): (b) value.

In like manner, it is conceivable that a measure of the environmental changes caused by man can be obtained from the numerical changes in the avifaunal values, especially in small units such as localities or sites, through a chronological sequence of checklists or of representative samples.

Summary

Cross-plotted, the passerine-nonpasserine and suboscine-oscine relationships produce a geographical or ecological "map" showing the comparative distribution of neotropical avifaunas. Any faunal level can be accommodated, from the subregional down to the parceling of habitats in a study site. At the scale of magnitude represented by the individual Latin American countries, the avifaunal "map" takes on the appearance of a political map of the region, with the line of division between the northern and southern hemispheres corresponding to a suboscine-oscine ratio that peaks at about 2:1 in the Amazon basin. At a lesser scale of magnitude, local avifaunas having similar proportions of passerines (or nonpasserines) and of suboscines (or oscines), irrespective of faunal resemblance or geographical distance, form into discrete ecological or climatic assemblages or clusters.

When the passerine-nonpasserine ratio (a) is combined with the suboscine-oscine ratio (b) into a simple (a): (b) relationship, the result is a single-figure value that can be put to comparative use. Placed directly on a map, it permits one to see whether the unit it represents follows certain trends or fits into a general pattern. From a low in the humid equatorial lowlands, the (a): (b)

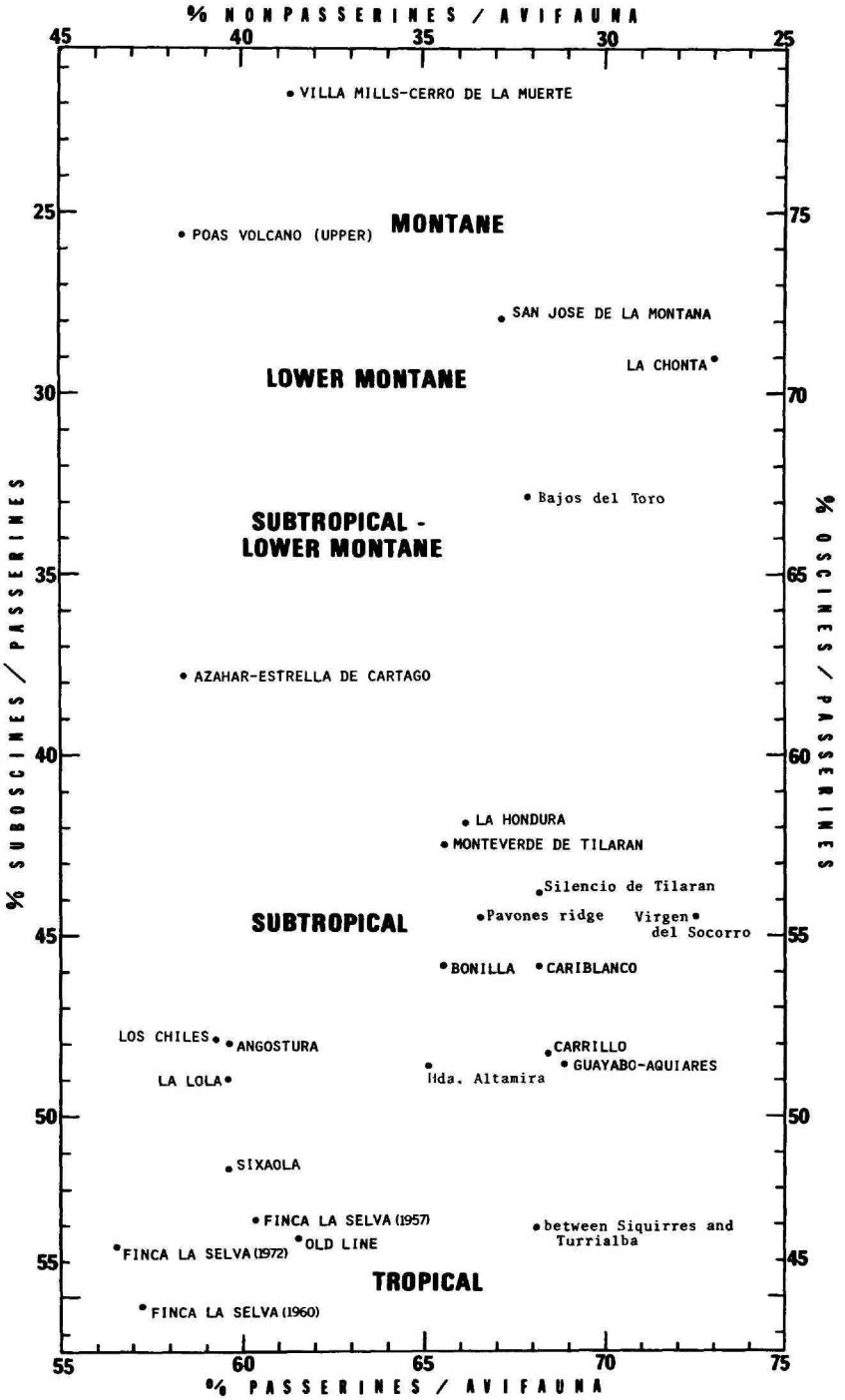


FIGURE 28.—Altitudinal disposition of areas and localities on the Caribbean slope of Costa Rica based on percentages of major avifaunal components.

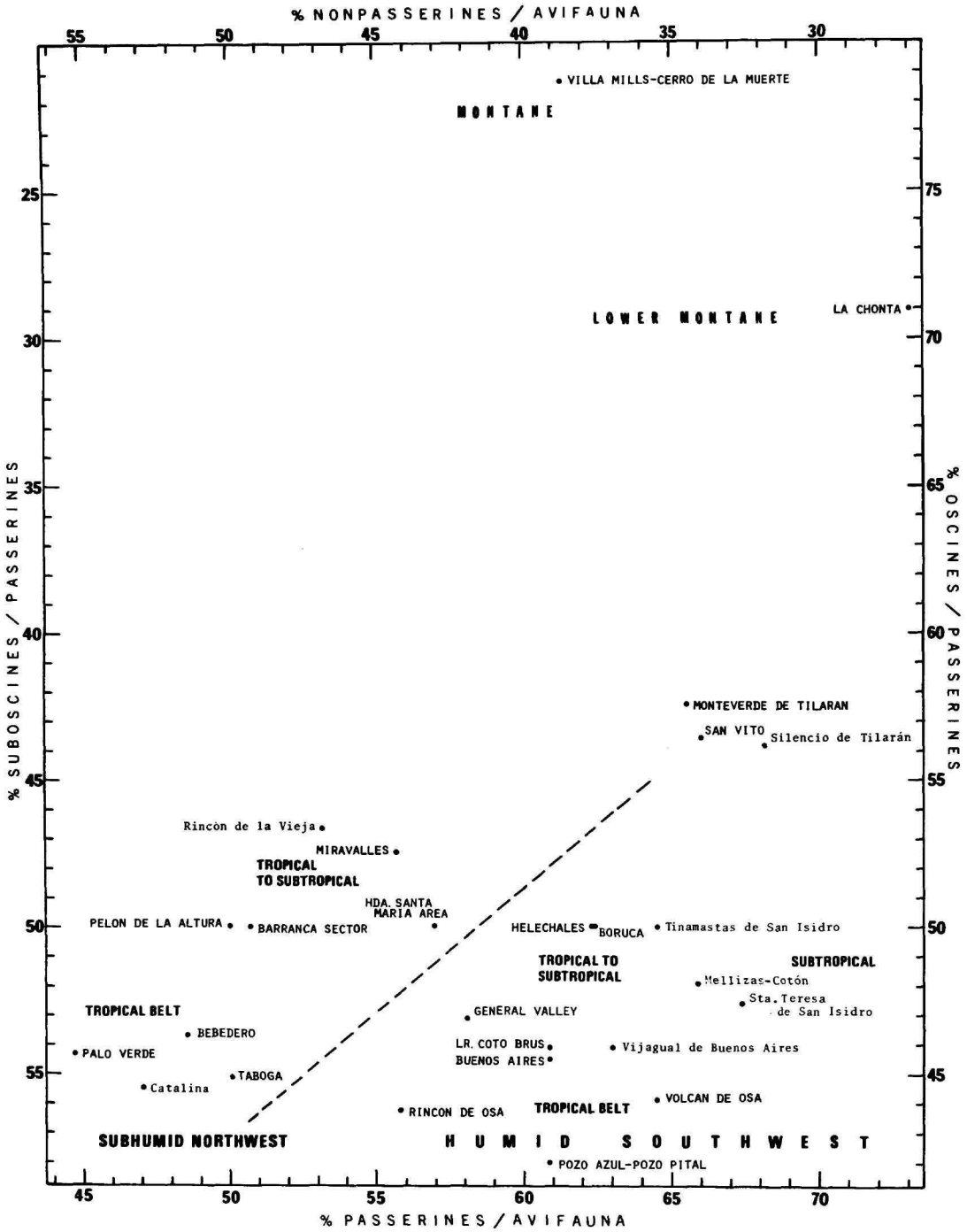


FIGURE 29.—Latitudinal and altitudinal disposition of areas and localities on the Pacific slope of Costa Rica based on percentages of major avifaunal components.

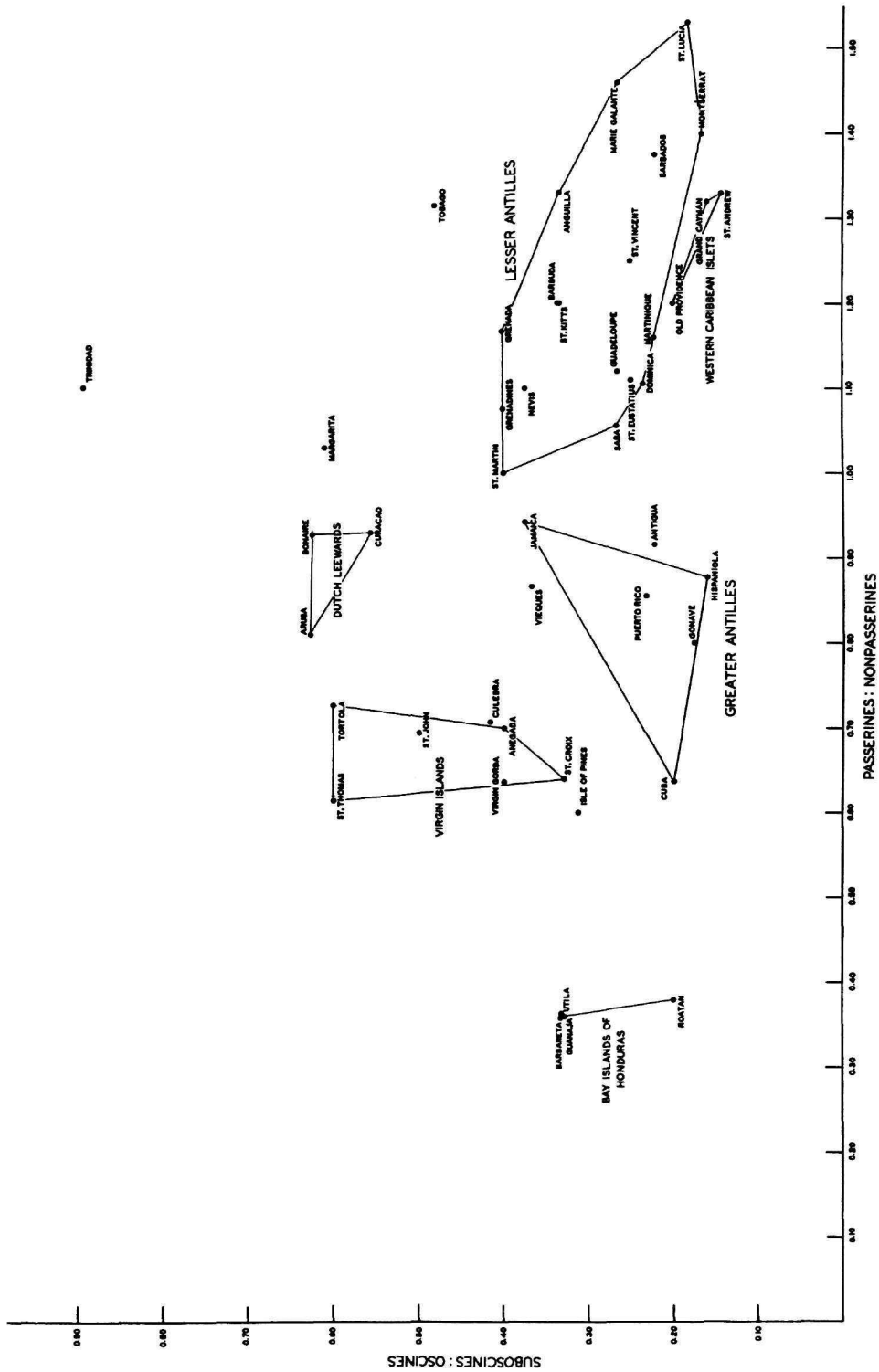


FIGURE 30.—Scattergram of islands in the Caribbean area: passerine-nonpasserine ratios versus suboscine-oscine ratios.

value increases altitudinally, latitudinally, and, at least in South America, horizontally in the dry tropics. The (a): (b) value can be used to best advantage in site-oriented situations.

Requirements for Further Research

Sampling

Checklists versus Samples

The lists employed in this report have proven useful in providing a basis upon which to made bioclimatic generalizations, but they also point to the need of something better. Long-term compilations, or checklists, no matter how comprehensive, cannot tell us the species composition of a unit at any given time past or present. A checklist for a large unit incorporates seasonal and nonregular taxa scattered over a wide range of conditions; one for a small unit has fewer nonresident taxa and a limited environmental range that can be defined by the local microclimate or by the dominant vegetation.

A checklist for a small unit, that is, a point on the map, such as a locality or a study site, occurs in the literature rarely compared to one for a large unit, such as a country. The few localities that do occur have been so unequally investigated that their lists range in status from that of a single collection to that of a long-term compilation. Particularly in the neotropics, few places are known to have a reliably comprehensive list, even fewer have been delimited areally and altitudinally or are truly representative of a natural life area or habitat type on the mainland. To help determine the status of a local list on a comparative basis, another list from the same place is needed. Rarely if ever is a replication available for the place in question or even for its general vicinity. Indeed, no tropical American field station to my knowledge ever inventories its biotic stock.

On the other hand, a sample from a small area, such as a locality or site, is considerably more restrictive as it tends to include few nonregular taxa and to group them seasonally. Moreover, a short-term survey not only yields a sample of what is actually present but it can only census a small area adequately. Further, the small area, i.e., the locality or site, is manageable in the sense that it can be worked at will to provide samples at different times in the same year or at the same time in different years. Sample can be compared against sample from the same place or from different places.

Thus the elaboration of a bioclimatic scheme by which to plot the comparative distribution of neotropical avifaunas comes to depend upon a supply of representative points in much the same manner as a climatic map is constructed upon the data supplied by a network of weather stations. The fundamental requirement, therefore, is a site-oriented method that produces equivalent samples and can easily be put into effect, whether apart from or in conjunction with general or special field studies.

Analytical Methods

Prime considerations in making a survey, besides deciding where to do it, are how to go about it and knowing when to stop. Ideally, a group of competent persons employing a variety of data-gathering means would work cooperatively regardless of cost. In practice an investigator usually works alone and has limited resources. As to the size of his area, it ought to have a radius about as long as a half day's bird-seeking amble, while the pace at which he proceeds continually adjusts to the nature of his surroundings, whether closed or open, broken or level. The unit should not be so small or unbuffered as to be exposed to internal contamination, so to speak, by the dissimilar biota of a neighboring unit.

Length of Survey.—The rate at which additional species continue to be met, rather than an arbitrary allocation of time, determines the length of the survey. One way to do this is to plot the daily cumulative species totals. The result is a steeply rising arc which soon declines toward the horizontal (Figures 31, 32). The straightening of the curve signifies the onset of unprofitable yield relative to time invested. Or one can decide to wait until it takes a few days to record another species. Instead of continuing this survey it is better to start a new one and obtain a second sample.

The point of diminishing returns is reached first with the native land avifauna, last with the total avifauna (Figure 32). The native land avifauna has the fewest species; nevertheless, it is the least variable of the four categories of list. A rapidly

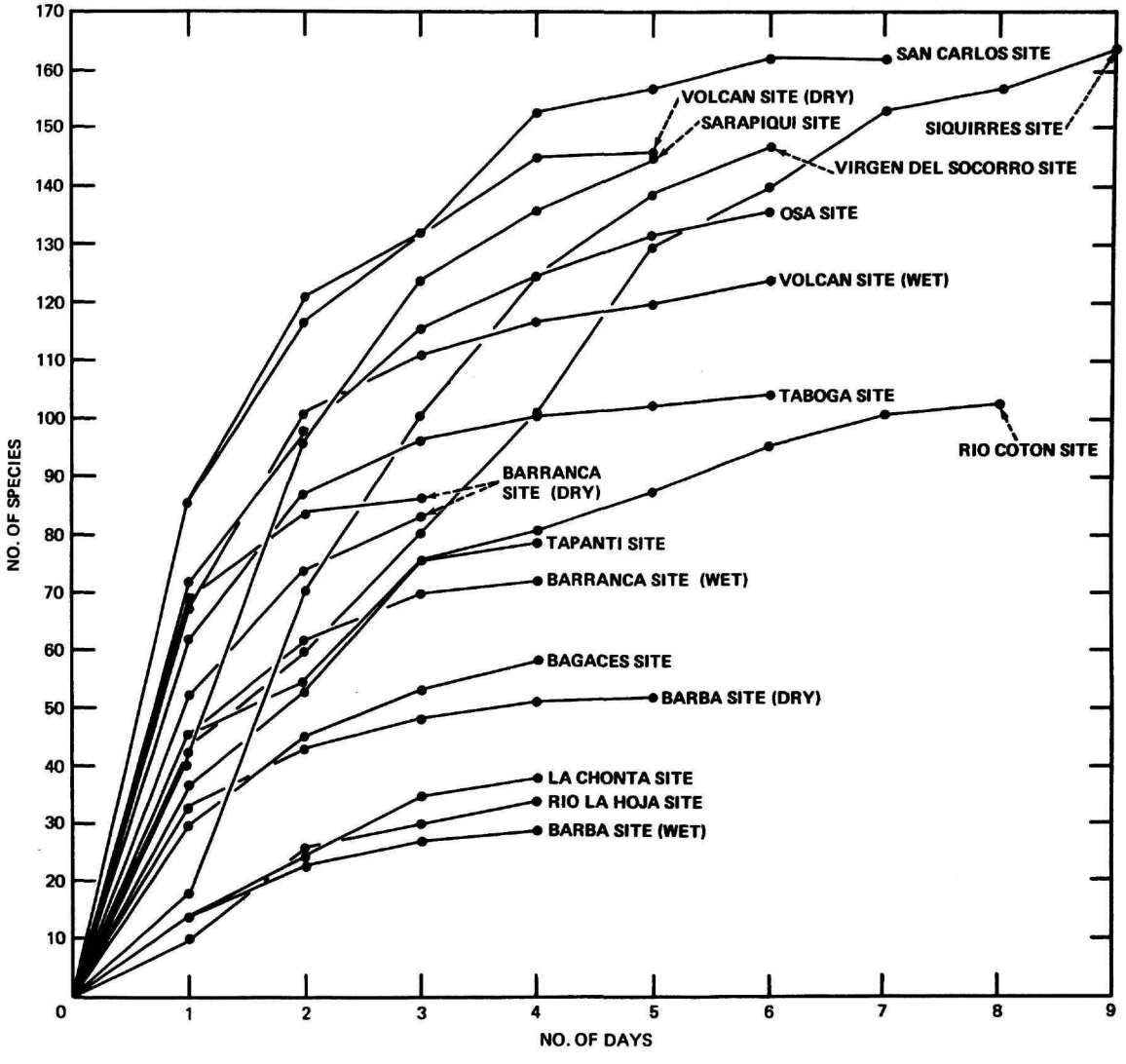


FIGURE 31.—Cumulative native land birds recorded at Costa Rican localities by P. Slud in 1964–1965.

acquired sample is preferable to a slowly acquired one, because of the reduced chances of incorporating seasonal effects. The better the investigator's acquaintance with the birds of an area the sooner the curves approach the asymptote.

Figures 32 and 33 illustrate what should have been done but was not during a trip I made to Barro Colorado Island in the Panama Canal Zone. It was my first visit, yet I had preset a departure date on the assumption that the time allotted would be ample. During the penultimate two days I found only one more species, and the curve appeared well on its way toward apogee. The upturn produced by four additional species the final day makes it clear I should have stayed longer. The same conclusion can be drawn from some of the Costa Rican localities in Figure 31.

Another way to determine the length of a survey

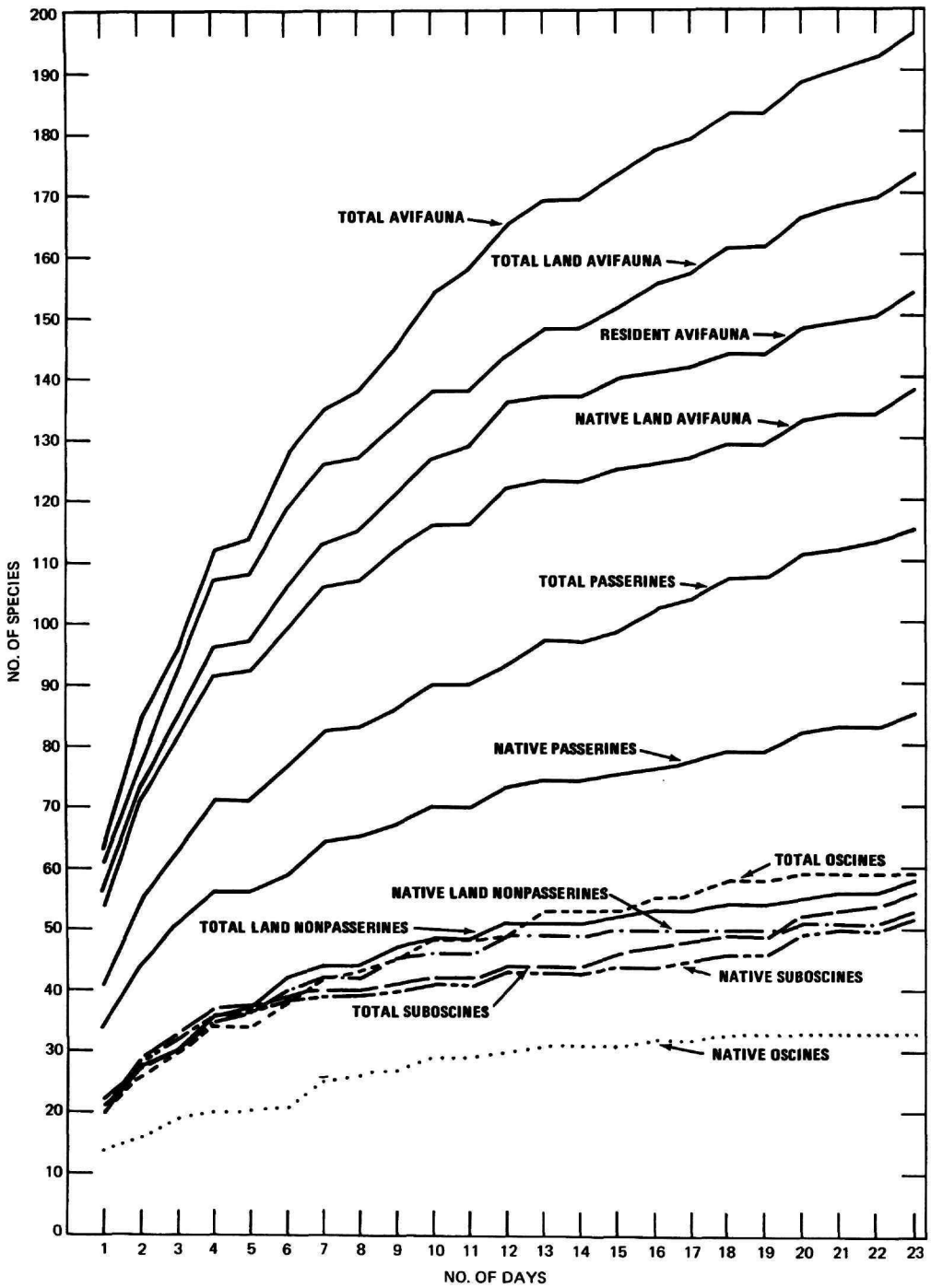


FIGURE 32.—Cumulative native land birds recorded at Barro Colorado Island, Panama Canal Zone, by P. Slud, 16 March to 8 April 1966.

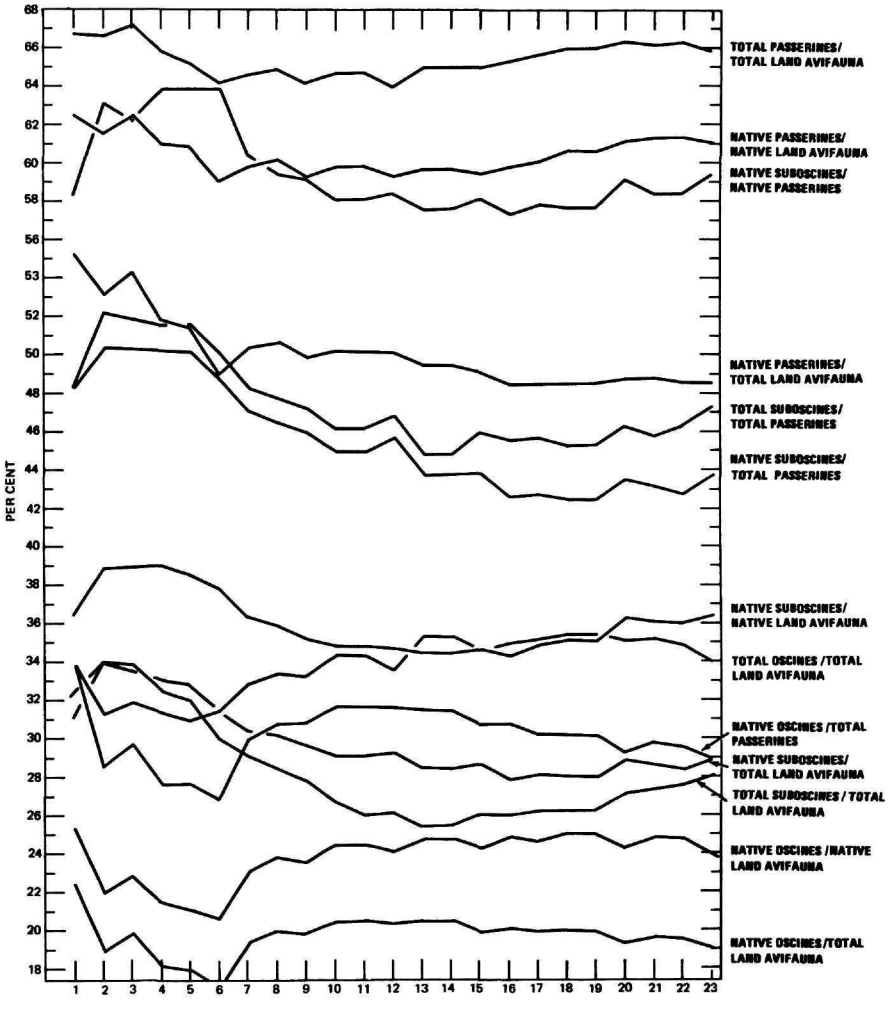


FIGURE 33.—Cumulative daily percentages of avifaunal components recorded at Barro Colorado Island, Panama Canal Zone, by P. Slud, 16 March to 8 April 1966.

is to convert the daily cumulative totals into their component percentages of oscines, suboscines, passerines, and nonpasserines. The percentages mostly level out while the numbers of species are still climbing (Figures 32, 33). It is a rapid method which usually becomes effective as soon as a majority of the sample has been gathered. For the experienced person this happens as a rule early in the survey. Whether obtained this way or the other, the sample should be as representative of the composition and relative size of the avifauna at the time and place of the survey as is any other similarly acquired sample at any other time or place.

In Figures 34 to 37, the abscissa stands for number of species instead of number of days. Figure 34 cumulatively plots the proportions of the major components. It also shows the exponential increase in the number of days that are needed to record in the field each additional equal-size increment in number of species. The appearance of the components plotted by percentage (lower

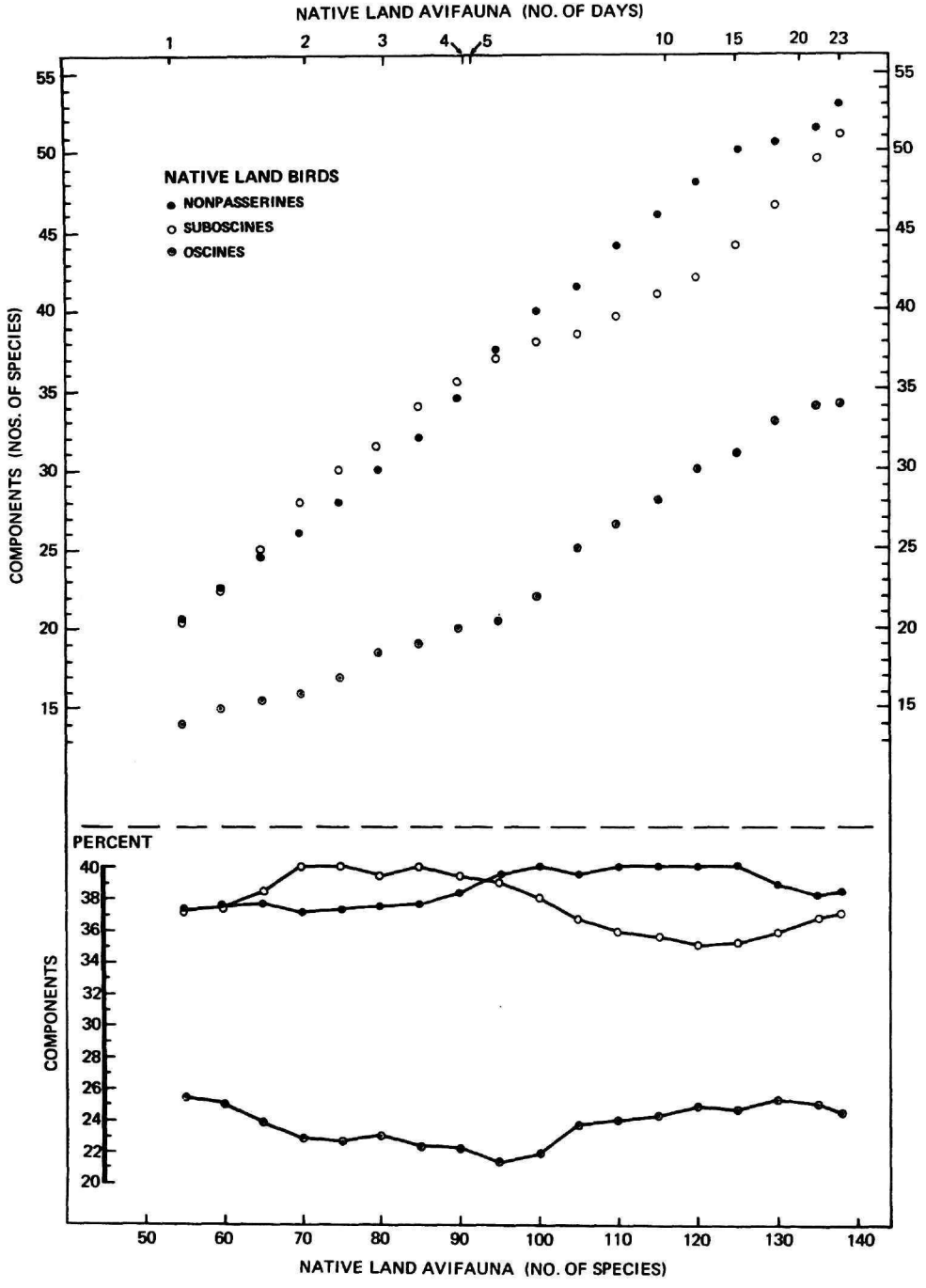


FIGURE 34.—Cumulative number of species (upper) and cumulative percentages (lower) of avifaunal components per day and per cumulative number of species in total avifauna during visit to Barro Colorado Island, Panama Canal Zone, by P. Slud, 16 March to 8 April 1966.

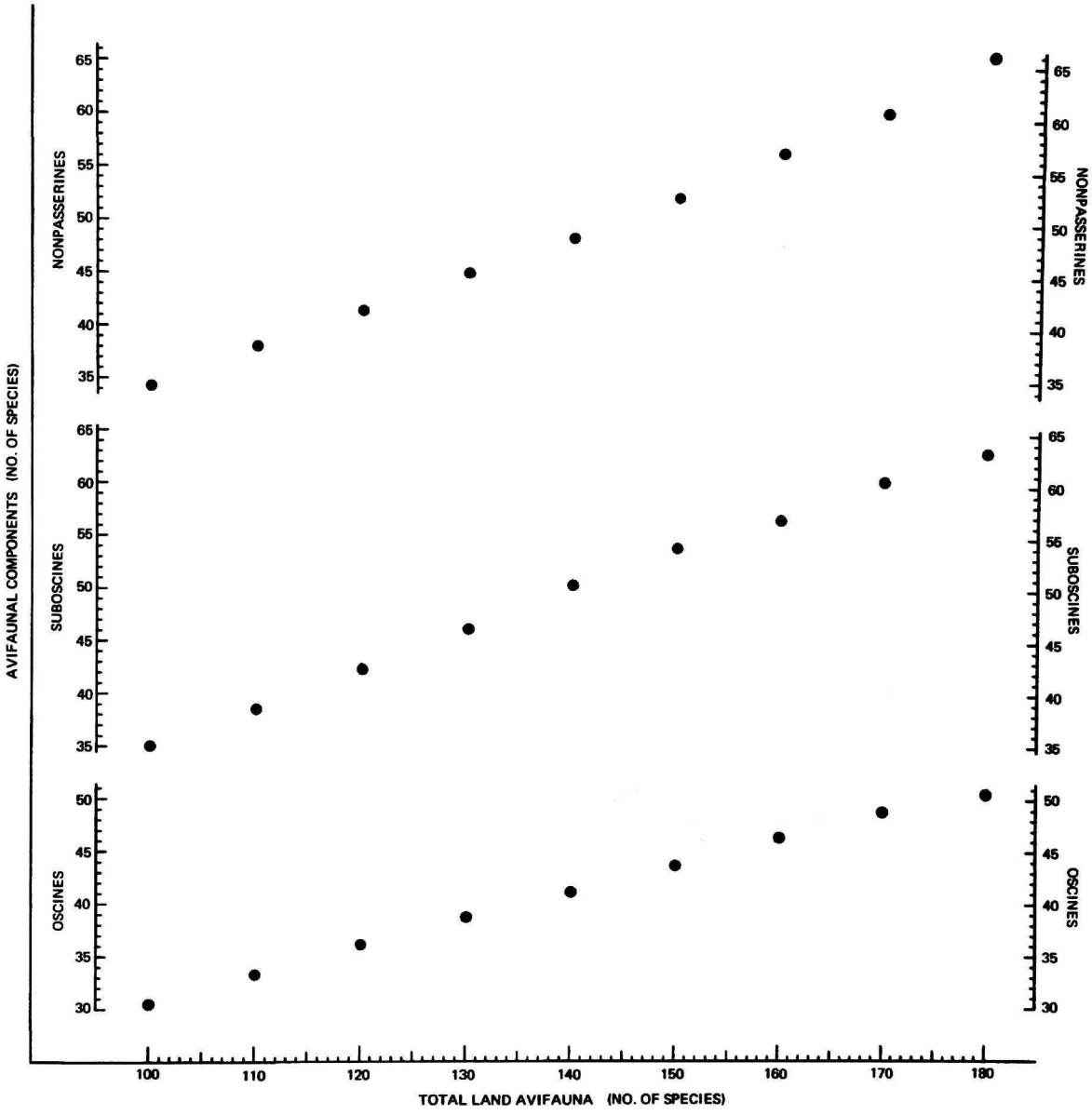


FIGURE 35.—Average of nine 2-week surveys at Finca La Selva, Costa Rica, made by P. Slud in 1957–1958: cumulative number of species of avifaunal components per cumulative number of species in total avifauna.

part of Figure 34) complements their appearance when plotted by days (Figure 32). Taken together they enable the investigator to view a survey in progress and to estimate its stage of completion. That the components were perhaps being encountered at an approximately constant rate during the above-mentioned reconnaissance I was making at Barro Colorado Island, Panama, as suggested by their appearance in Figure 34, is substantiated by the rigid alignment of the totals

when averaged for a number of surveys I had made at Finca La Selva, Costa Rica (Figure 35).

As a rule the nonpasserine proportion of the land birds is considerably smaller than the passerine proportion in compilations or checklists generally, even more so in samples from the humid tropics. In full-term samples (those with a flattened cumulative-species curve) the nonpasserines, after a retarded start, tend to increase faster than do the other two components, and the rate accelerates once the majority of the sample has been obtained (Figures 34, 35). This is the logical pattern to expect since the nonpasserine component, owing to the larger size and smaller numbers of its members, consists principally of low-frequency species and includes hard-to-find terrestrial and nocturnal groups as well as wide-ranging elements and those most heavily persecuted by man. The nonpasserine upturn at the end of a graph, when the total avifauna has been leveling out, indicates that for practical purposes the survey has come to a close.

It can happen that the cumulative-total curve which has been gradually approaching the horizontal suddenly shoots upward. An example comes from the Carnegie Museum catalog of collections made by Samuel L. Klages and party on 81 days between 22 December 1920 and 4 May 1921 at Obidos on the north side of the Amazon River in western Pará (Table 11). The insurgence began abruptly the 68th day of collecting. During the ensuing 13-day period, that is, until the next to last day in the field, the increment amounted to 66 species (including two migrants). During the preceding 13-day period it had been only eight species (none migrant). Obviously the increase was not caused by an influx of migrants. It is possible that the skipping of only one collecting day between the two 13-day periods was enough to permit dismantling and reestablishing camp at a new site not noted on the labels or to exploit a habitat not previously visited in 68 days of collecting. (The Obidos data do not include the Obidos Islands, treated separately in Figure 36.)

Usually a renewed rise in the cumulative species total is a sign of incomplete sampling. The percentages of the components comprising the Obidos native land sample are, however, affected slightly if at all (Table 11): fluctuations exceeding 1.5 percent above or below the average of the remainder of the survey do not occur after the 22nd day, when 55 percent of the sample had been obtained, for the nonpasserines; after the 32nd day, when 62.5 percent of the sample had been obtained, for the suboscines; and after the 33rd day, when 63 percent of the sample had been obtained, for the oscines. The suboscine proportion of the passerines does not level out until the final 13 days of collecting, after most of the sample had been obtained. This leveling out is apparent on a daily basis, not from the 10-day averages in Table 11. The Obidos sample of 281 native land species yields higher ratios than does the compiled Obidos total of 354 (Table 8), as is usual when a sample is compared to a compilation: 2.16 versus 1.70 in the passerine-nonpasserine ratio (a), 2.49 versus 2.23 in the suboscine-oscine ratio (b), and 0.87 versus 0.76 in the (a): (b) value. The degree of difference between the sample and the compilation can be magnified by multiplying (a) and (b), the product of which is 5.38 in the sample and 3.80 in the compilation.

The Obidos sample calls for further remark. For one thing, competent observers probably could have obtained a list in a fraction of the time needed by the collectors, and the cumulative species curve would have started out steeper and higher and become flattened much sooner. Whether the observers might have ultimately amassed a higher total than the collectors is problematical. Most likely the proportional representation would have been similar since either method records the components at a regular rate (Figures 34–36). For another thing, the Obidos data follow a pattern that is common to comprehensive samplings. The dominant component, here the suboscines, is met most frequently at the beginning of the survey. Afterwards its proportion of the total either levels out or undergoes a barely perceptible decline within a percent or two of the horizontal. Encounters with the other two components tend to be relatively infrequent at the start of the survey, then increase more rapidly at the expense of the dominant component. The minority components, here the nonpasserines and the oscines, follow this trend at Obidos, except when interrupted temporarily by the late surge already discussed. Graphed, the nonpasserine and oscine percentages more or less mirror each other as long as the suboscine proportion remains fairly constant.

The suboscine-oscine ratio can be particularly

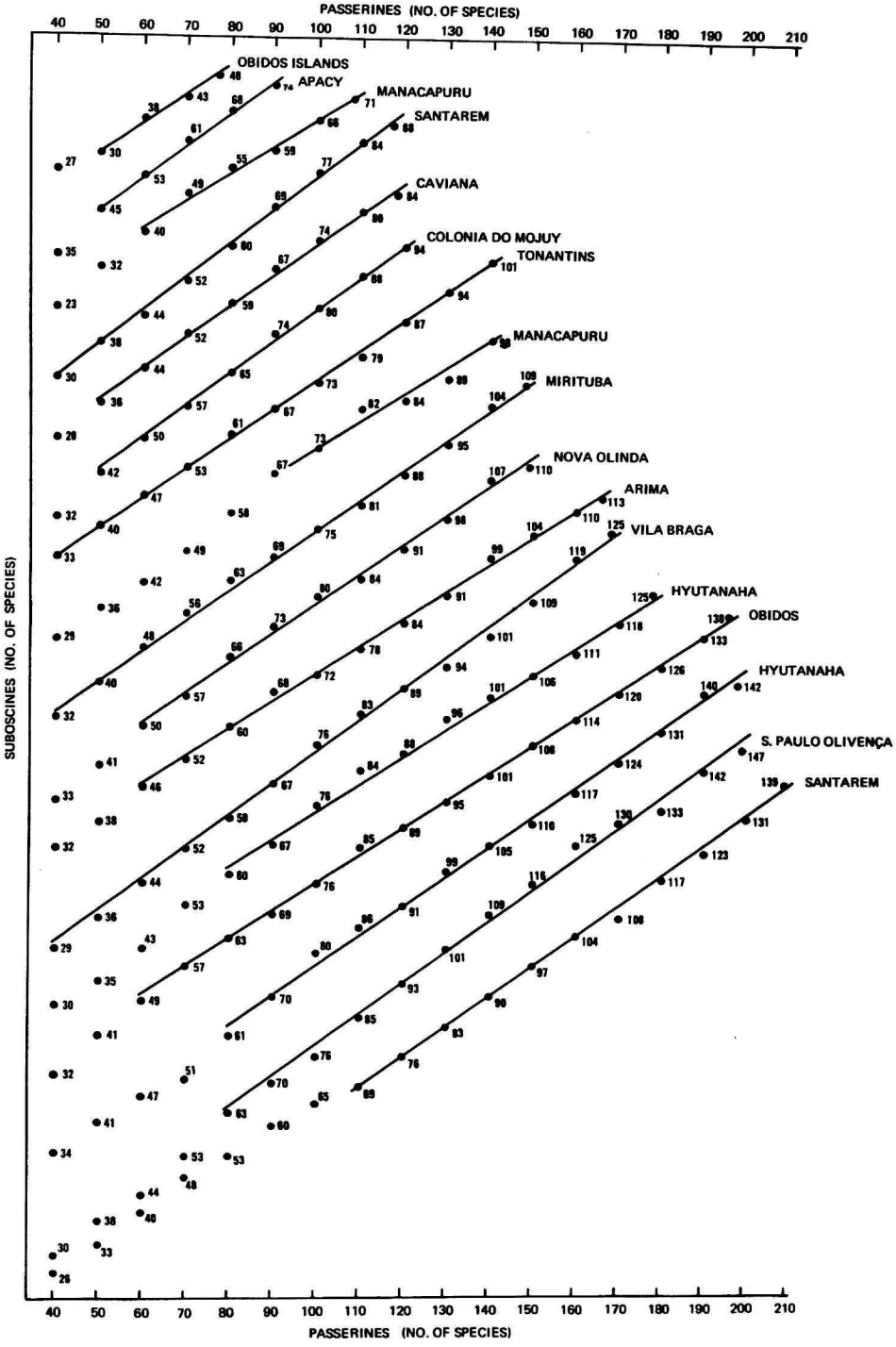


FIGURE 36.—Collecting localities of S. M. Klages in Amazonian Brazil: cumulative number of suboscines per cumulative number of passerines. (Slopes determined visually to emphasize constant rate of increase in number of suboscines. Diameter of dots equivalent to two species on abscissa.)

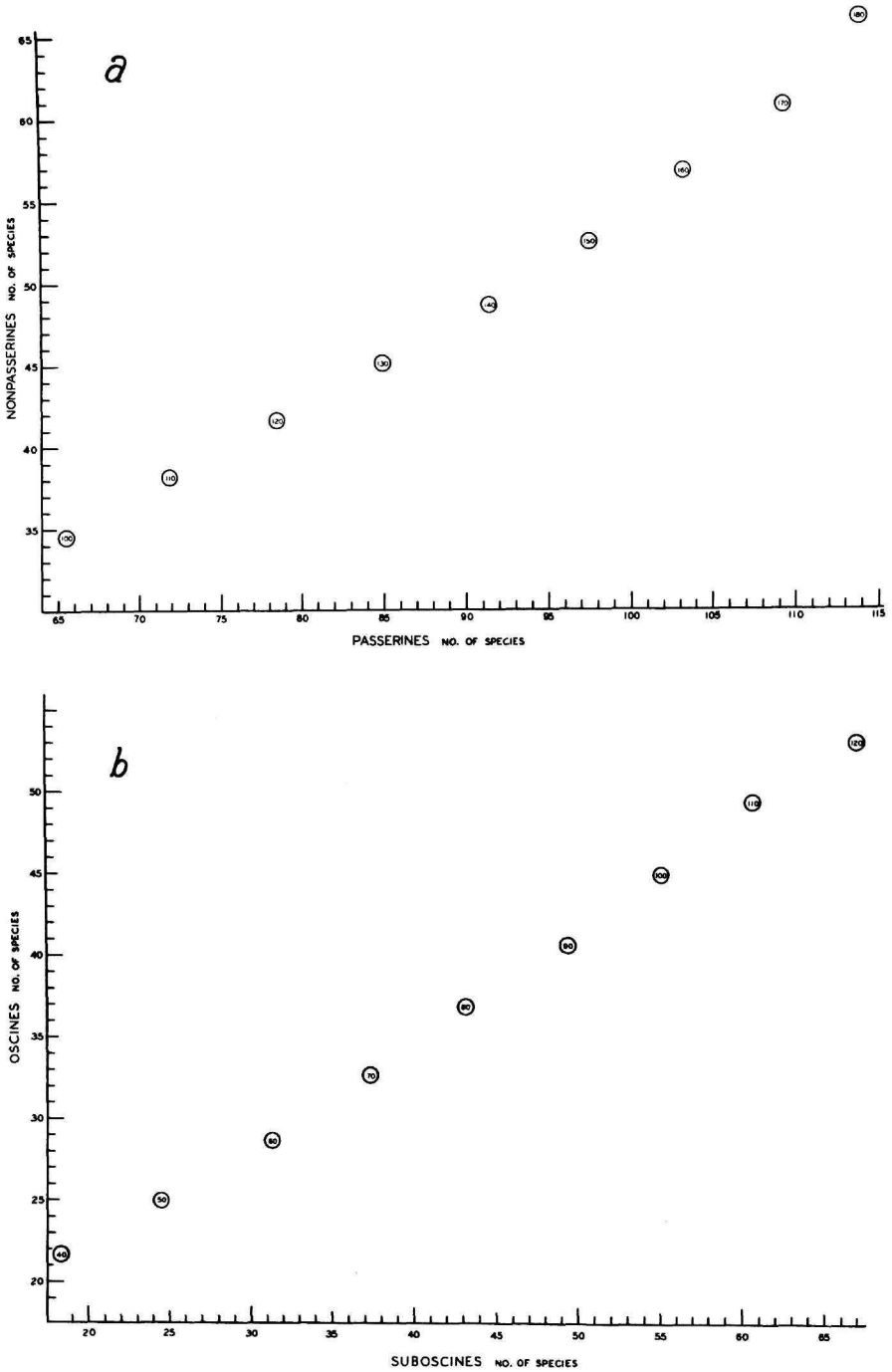


FIGURE 37.—Average of nine 2-week surveys at Finca La Selva, Costa Rica, made by P. Slud in 1957–1958 (cumulative numbers of species per major component): *a*, passerines versus nonpasserines (numbers in circles = avifaunal totals); *b*, suboscines versus oscines (numbers in circles = passerine totals). (Diameter of circles equivalent to one species on either coordinate.)

useful distributionally when the representativeness of the nonpasserine component is in doubt, if only because of its unusually small size. This is the common situation at Amazonian localities, many of which are known mostly from a single collection. Whether actually or only apparently "poor" in nonpasserines, these localities are evidently "rich" in passerines. The passerines, more abundant and more easily found and presumably better sampled than the nonpasserines, are in turn "rich" in suboscines (or "poor" in oscines). There is little reason to doubt that this is the true state of affairs. Indeed, many species of suboscines can be harder to find than many of the oscines. It follows that suboscine-oscine ratios in Amazonia vary much less than do the passerine-nonpasserine ratios.

Figure 36 cumulatively plots the number of suboscine species versus that of total passerines at localities in Amazonian Brazil. The localities are each represented by samples obtained during a single continuous stay, though not necessarily on consecutive days. When total passerines reach the 150-species mark, the proportion of suboscines and oscines is as follows: 97 and 53 at Santarém, 116 and 34 at São Paulo de Olivença, 110 and 40 at Hyutanahã, 108 and 42 at Obidos, 109 and 41 at Vila Braga, 104 and 46 at Arimã, and approximately 110 and 40 at Nova Olinda and at Mirituba. These "rich" samples almost all attain a constant rate of suboscine increase long before the number of passerines reaches 100; the smaller, or "poor," samples mostly do so before the number of passerines reaches 50. One ought not, however, suppose a survey has been completed simply because the suboscines have settled into a regular rate of increase.

Figure 37*a* and *b* plots the passerine-nonpasserine and suboscine-oscine species averages of a number of surveys at a locality, Finca La Selva, in Costa Rica. Ratios are preferred, because they have a greater range of variation, hence show a finer regard for departures from the norm than do percentages (Figure 35). The passerine-nonpasserine ratio stabilizes by the time approximately two-thirds of the sample has been obtained, usually well within a week; the nonpasserine upturn at the end of the graph signifies the effective end of a survey. The suboscine-oscine ratio stabilizes even earlier, when one-half of the sample has been obtained. Thereafter the rate of increase remains constant for the suboscines and for the oscines.

Faunal Resemblance

A more conventional analysis of comparative distribution with ecological overtones is that of taxonomic faunal resemblance as determined by formula (see Hagmeier and Stults, 1964; Peters, 1968). Individually the formulas tend to emphasize similarities, to emphasize dissimilarities, or to strike a balance between the two tendencies, though they all produce a similar pattern when graphed and none eliminates the effects caused by the different sizes of the faunas being compared. Whereas a proportional relationship among its major components is an innate property of a list which the passerine-nonpasserine suboscine-oscine interrelationship brings to light, faunal resemblance tells us nothing about an individual list but can only compare it with other lists. From the faunal-resemblance point of view, comparison is based on the number of shared taxa relative to total taxa; two lists can be dissimilar if only because one has more entries than the other; the fact that the internal proportions may be similar is immaterial.

Faunal resemblance formulas and the passerine-nonpasserine suboscine-oscine interrelationship both treat the same raw material, i.e., lists of taxa. Either method can be applied from the level of the continent or faunal realm down to the habitats at a site. When the avifaunas to be compared are taxonomically similar, the two reinforce each other as they perform much the same function. When the two avifaunas are taxonomically dissimilar, the methods interact. Faunal resemblance now becomes a measure of degree of difference, the passerine-nonpasserine suboscine-ocine interrelationship continues to be concerned with relative proportions of the major components. Now if two lists that are similar in proportions of components but dissimilar in taxonomic content should be matched against each other, a residue of unshared taxa would be left over in one list that conceivably is equivalent ecologically to the residue in the other list.

Further, interplay between the two methods names the taxa and the units, the study of which could develop insight into such matters as replacement and displacement or convergence and divergence. The result would be constant improvement

in the making of quantitative comparisons between geographically changing faunas. The ability to discern taxonomic derivatives and ecological counterparts could be used qualitatively in helping to plan a numerical framework for the housing of niches in the neotropics. Superimposed upon the Old World tropics, the framework would serve to compartmentalize environmental equivalence for unrelated taxa around the globe.

Accuracy of Counts

A twofold difficulty involving taxonomic status arises, due to the occurrence of migrants and to the size and location of the faunal unit. With regard to the former, two or more closely related forms considered conspecies by one author and separate species by another author can be present in the same list. How to treat them is an avoidable issue in short-term samples, few of which ever include more than one. In long-term compilations the chances are that all will have been recorded, if only once. The rule that the smaller area will have fewer kinds of North American migrants than the larger area becomes virtually absolute at points in Amazonia, where few migrants occur in compilations and none in most of the samples. In general, a summation of samples from one or more sites or a checklist for a large unit overemphasizes the proportion of nonregular taxa. The number of nonregular taxa is minimized in a sample.

For another thing, an increase in area or in number of distributional barriers fosters geographic variation and results in subspecies tending increasingly to outnumber species. For instance, Costa Rica, oversimplified, consists of Caribbean and Pacific halves. Widespread taxon A, deemed a monotypic species, would be counted once in a species list for the Caribbean side, once in a species list for the Pacific side, and once in a species list for the entire country. Taxon B, deemed a polytypic species with a Caribbean race and a Pacific race, would be counted once in each of the three species lists and twice in a subspecies list for the entire country. Taxon, C, deemed a superspecies with one Caribbean species and one Pacific species, would be counted once in a species list for either slope and twice in a species list for the country. Species confined to one slope would be counted once for the slope and once for the country, thus increasing the disparity between the country and either slope. Actually, the disparity between the country and either slope or between the two slopes is even greater, because some species are represented by two races on one slope and by one or none on the opposite slope.

The disparities dissipate, especially on the subspecific level, as the units diminish in size down to a point on the map. If Costa Rica happened to occupy only one slope, the lists of species and of subspecies for the country would be the same as for the slope. A sector of the slope would be expected to have fewer species and relatively still fewer subspecies than the slope. A subdivision of the sector would have both lists further reduced, and so on, down to the locality or site, at which point the two lists become identical. Incidentally, the degree of difference between the corresponding proportions of any two of the above lists would be less than that suggested by faunal resemblance formulas.

Counts are further affected by differences in the taxonomic outlook of catalogers, particularly when treating large or complex units inhabited by polytypic species. Counts would become more truly comparable if ecological equivalence were better understood and if superspecies were no longer determined intuitively and could be assigned a binomial for comparative purposes.

Since by definition there can be no allopatry at a site, at least during the reproductive period, one need not rely upon intuition to decide the specificity of closely related birds. Put another way, the site is the testing ground for the belief that sympatric populations do not interbreed and are specifically distinct in the area of geographic overlap irrespective of their ecological requirements. The site is also the place at which to evaluate notions concerning character displacement and to look for traits that distinguish sibling species in life. Implicit is the assumption that in birds the species is the basic, the only biologically definable, taxonomic unit. It follows that the number of forms, i.e., species and subspecies, at a site is tantamount to the number of species. The statement, for example, that "Chapman records 1508 species and subspecies of birds from Ecuador, while I record 736 from Guatemala" (Griscom, 1932a:3) is the sort that has appeared commonly in faunal works, yet it tells nothing about the number of species in either

country and would be meaningless for a site. Again the conclusion is reached that only site-oriented studies can be truly intercomparable and provide suitable material for environmental constructs.

Choice of Locale

Amazonia

Equatorial Amazonia approaches the theoretic ideal of a locale in which to begin to compare avifaunas. The very vastness virtually guarantees it will be a heartland of evolutionary dynamism and ecological radiation, the proliferation of species that it can supply good-size samples. These two properties, promising variety and quantity, are indispensable to the investigation of a "rain"-forest lowland in which the only physical barriers appear to be the great waterways. A dual objective would be to determine the extent to which the faunas, represented by samples, differ taxonomically and in proportions of major components on opposite sides of rivers. Another objective would be to evaluate the extent to which the differences may have evolved disjunctly in similar environments or in climatically or vegetationally dissimilar environments. Evidence that can be interrelated should be forthcoming from the vegetation, the birds, and the weather records.

Biologically complex Amazonia seems to be macroclimatically simple over much of its basin. The basic parameters are average annual precipitation, which varies geographically in quantity and seasonal distribution, and average temperature, which seems to be fairly uniform annually and seasonally. Variation in one of the parameters provides the simplest condition for making environmental and faunal comparisons. Responses to significantly different ranges of rainfall should be recognizable in the physiognomies of the mature natural vegetation (perhaps the intermediate stages, too).

> The evolutionary goal of undisturbed vegetation seems to be the attainment of the most complete utilization of the qualities of the site as possible. Each association is, in effect, a natural mechanism endeavoring to sustain the greatest possible amount of living matter per unit area. To do this, the vegetation adjusts to the given total set of environmental factors, i.e., both to the general climatic pattern and also to special conditions existing in the local area. The natural vegetation anywhere in the world is, in a metaphorical sense, an organic computer that evaluates all the controlling environmental conditions in an association, assigns proper weights to each, and produces an answer in terms of a vegetative cover. (Holdridge et al., 1971:16.)

Responses of the vegetation-dependent birds are secondary or indirect.

The investigator will be confronted by bioclimatic alternatives in Amazonia. Should average rainfall prove insufficiently variable geographically to produce measureable differential effects on the biota, the entire region could be regarded as a single unit. Should it prove to be sufficiently variable the responses of the biota might then be agglomerated into life-zone type units. Should it be clinal the problem arises whether a climatic continuum is paralleled by a continuum in the vegetation and in the composition of the avifauna. Should it take the form of a step-gradient the opportunity arises to test the efficacy of the passerine-nonpasserine suboscine-oscine method within narrow climatic limits.

The primary unit to investigate, the standard against which to make comparisons, is the "climatic association" of Holdridge (1947) or the at-times analogous "climatic climax" of other authors. Theoretically only one climatic association can exist anywhere in a natural division of climate, i.e., the life zone (plant formation) of Holdridge, from which the mature vegetations of all the other associations can deviate almost infinitely in kind and degree. The climatic association should in principle be the same wherever found, that is, in predictable conjunction with quantitative climatic parameters and be recognizable physiognomically and by the presence of shared taxa or ecological counterparts.

A phytoecological reconnaissance of Thailand by personnel with neotropical experience elicited the following observations (Holdridge et al., 1971:684):

> The life form, as a morphological expression of the plant's physiological adaptation to a given habitat, tends to be similar (but not identical) wherever the same habitat conditions prevail anywhere in the world. This ecological-evolutionary principle proved true to a remarkable degree for these widely separated and floristically unique regions. Uncounted cases arose in which trees, taxonomically unknown to the observers, possessed such a striking morphological resemblance to tropical American species with which they were familiar that they independently recorded their life

form in terms of the same American species name. Moreover, these taxonomic prototypes were observed to occupy equivalent ecological niches, by Life Zone and association, in both hemispheres.

The Holdridge life-zone system provides equally weighted natural areas among and within which to select representative points, not only for taxonomic, faunal, and comparative ecological study but also, ever more urgently, for preservation. Selections are thus made from a theoretical global perspective rather than randomly and opportunistically.

Amazonia need be treated no differently for comparative purposes than an area with strong climatic contrast. By concentrating on representative points one should be able to reassemble thermopluvial divisions of the earth's surface on the basis of the avian samples as well as from the weather data. The opposite course, which is the one we are usually compelled to follow, is to obtain the average of a single master list for a large block of terrain and try to gauge microclimates from generalizations about the macroclimate. For the Amazonian hylea, a comparison of the proportional representations of the major components over a network of points should indicate the location of centers of avian speciation and ecological radiation. This approach also serves to associate recurrent migrants with clearly defined environments, whereas coverage of a large unit records even a lone migrant as inhabiting the entire area.

There are several reasons that make it preferable to institute a comparative survey in monotonously immense Amazonia than, say, in complex little Costa Rica, the other area figuring prominently in this report.

Costa Rica

Costa Rica in an area less than one percent that of Amazonia possesses a number of altitudinal and latitudinal life zones (plant formations) so closely juxtaposed that an observer can quickly accumulate a long list of birds. The country would appear, therefore, to be eminently desirable for comparative life-zone treatment on theoretical or practical grounds. Yet the intermixture of biotic richness, telescoped physiography, and rapid changes in climate can produce a perplexing jumble. The transitional zones, some of relatively great breadth for such a rugged little country, are so numerous (see Tosi, 1969) that attempting to preselect a site as a climatic standard often becomes guesswork. But even if a representative set of climatic points were reliably determined, distances remain so short that a brief flight can carry a bird into a different environmental context. Vertically a difference of a few hundred meters in the occurrence of a species could be interpreted as a dislocation of the altitudinal belts or an example of avian distribution not in accord with vegetation or climate. The difficulty in knowing precisely which species are resident and which are irregular or seasonal may not be inconsiderable at such climatic extremes as the lowlands and the mountain tops. It is very considerable throughout the intermediate elevations, where environmental influences are multidirectional and knowledge of faunal movements is rudimentary. By contrast, the Amazonian lowland is essentially free of altitudinal complexities, and it apparently contains huge, climatically similar blocks of vegetation: "In regard to the large-area vegetation types it is possible to define a series of zoogeographic provinces. Within the vast, climatically very homogeneous, tropical rain-forest area several faunal areas can be observed to respond to the degree of the fertility of the soil and to the geological structure of the region" (Fittkau, *in* Fittkau et al., 1972:652). Large size alone should protect them from other than marginal infiltration by external biotic elements, unlike the usual situation in Costa Rica.

Costa Rica, at ten degrees above the equator, has an avifauna whose reproductive period generally coincides with that in the temperate north. "It seems . . . that the majority of the birds in Central America breed during the second quarter of the year" and "the peak . . . is March to June or July, inclusive, with a reduced but still important amount of nesting activity in August and September, whereas only a small proportion of the birds have nests from October to February" (Skutch, 1950). Amazonia, on the other hand, straddles the equator and is analogous to the Congo. "In no part of the Congo is there any approach to a universal breeding season, or even a time of year when the great majority of birds are nesting. The region of least seasonal change in this respect is unquestionably the equatorial belt of heavy forest, though

conditions may be equally stable in the mountain forests" (Chapin, 1932–1954, 65:320). In those areas, therefore, where breeding activity is spread over the year, no survey should on this account be affected more than any other.

In Amazonia, long-distance migrants are few in kinds and numbers: a list of the total avifauna hardly differs in length from a list of the native avifauna. In Costa Rica, the two lists match each other closely during the approximately three migrant-free months of the year and fluctuate from little different to considerably different the other nine months. Percent total migrants, including water birds, in the two areas are as follows:

	Costa Rica	*Amazonia*
Total Avifauna	20	5
Nonpasserines	23	8
Suboscines	8	1
Oscines	25	7

Restricted to land birds, migrants make up 14 percent of the avifauna in Costa Rica and 2.5 percent in Amazonia, 8 percent of the nonpasserines in Costa Rica and 1 percent in Amazonia; suboscines and oscines remain the same.

At a Costa Rican locality, Finca La Selva, in the wet Caribbean lowlands, the migrant percentages over a 12-month period (Slud, unpublished) are as follows:

	12 months	*Sept.-Oct.*	*Jan.-Feb.*	*Mar.-Apr.*	*June-July*
Total Avifauna	20	17	10	14	0
Nonpasserines	9	8	4	6	0
Suboscines	11	10	4	8	0
Oscines	41	32	21	29	0

Incidentally, I know of no comparable seasonal information that is available for any other locality in the neotropics. It can be obtained only through site-oriented studies.

Finally, transitions between life zones (formations) should be amenable to analysis, provided these have not been unduly disturbed. Findings having to do with the bird-life, even if obtained as here proposed, would be secondary to, dependent upon, and variously intermediate between the adjacent climatic standard of the life zone, or ecosystem, on either side. Transects made horizontally, say, in Amazonia or vertically in Costa Rica should, if properly planned, pass through a natural sequence of life zones (see Holdridge, 1947; Holdridge et al., 1971). The transitions ought then be made recognizable by the occurrence of a small contingent of indicator species associated with the next succeeding humidity province or thermal belt, by the sympatric occurrence of congeneric or closely related counterparts normally restricted to opposite sides of the transition, and perhaps, as the case may be, by a larger number or by a smaller number of species forming a hump or a trough in the smooth curve expected from a climatic continuum.

Appendix 1

Bibliographic Key to Geographic Units in the Tables and Figures

Acre, Brazil (Pinto, 1938, 1944, 1954; Novaes, 1957; Meyer de Schauensee, 1970)
Admiralty Islands, New Guinea region (Rothschild and Hartert, 1914; Ripley, 1947)
Alabama (Imhof, 1962)
Alagoas, Brazil (Pinto, 1954; Meyer de Schauensee, 1970)
Alajuela Province, Costa Rica (Carriker, 1910; Slud, 1964a; compiled sources)
Alaska (Gabrielson and Lincoln, 1959)
Albania (Ticehurst and Whistler, 1932)
Albemarle, Galapagos Islands (Swarth, 1931)
Alberta, Canada (Salt and Wilk, 1961)
Aldabra Islands, Indian Ocean (Benson and Penny, 1971)
Amapá, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970; compiled sources)
Amazonas, Brazil (compiled sources)
Amazonian Brazil (compiled sources)
Ambrym, New Hebrides (Mayr, 1945)
Anamba Islands, South China Sea (Oberholser, 1917)
Andaman Islands, Bay of Bengal (Abdulali, 1965, 1968)
Andros, Bahamas (Bond, 1971)
Anegada, Virgin Islands (Bond, 1971)
Aneiteum, New Hebrides (Mayr, 1945)
Anglo-Egyptian Sudan (Cave and Macdonald, 1955)
Angola (Traylor, 1963; Ripley and Heinrich, 1966)
Anguilla, West Indies (Peters, J. L., 1927; Bond, 1971)
Anjouan, Comoro Islands (Benson, C. W., 1960)
Annobon, Gulf of Guinea (Moreau, 1966)
Antigua, West Indies (Danforth, 1934; Bond, 1971)
Arabia (Meinertzhagen, 1954)
Arctic Canada (Snyder, L. L., 1957)
Arctic slope of Alaska (Bailey, 1948)
Argentina (Olrog, 1963; Meyer de Schauensee, 1970)
Arizona (Phillips et al., 1964)
Arkansas (Baerg, 1951)
Aru Islands, New Guinea (Rand and Gilliard, 1967)
Aruba, Netherlands Antilles (Voous, 1957)
Atlántico, Colombia (Dugand, 1947)
Aurora (Maewo), New Hebrides (Mayr, 1945)
Austral Islands, French Polynesia (Bruner, 1972)
Australia (Slater, 1971)
Australian Region (Mayr, 1941a; Rand and Gilliard, 1967; Slater, 1971)
Azores (Bannerman and Bannerman, 1965–1968)
Azuero Peninsula (Aldrich and Bole, 1937)

Bahamas (Bond, 1971)
Bahía, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Baja California, Mexico (Grinnell, 1928; Edwards, 1972)
Bali, East Indies (Kuroda, 1936)
Baluchistan (Vaurie, 1959–1965)
Banks Island, Canada (Manning et al., 1956)
Banks Islands, New Hebrides (Mayr, 1945)
Barbados, West Indies (Bond, 1971)
Barbareta, Bay Islands of Honduras (Bond, 1936; Monroe, 1968)
Barbuda, West Indies (Bond, 1971)
Barro Colorado Island (Eisenmann, 1952; compiled sources)
Bartica, Guyana (Beebe, 1925; Beebe et al., 1917)
Basilan, Philippines (duPont, 1971)
Bay Islands, Honduras (Bond, 1936; Monroe, 1968)
Bechuanaland (Smithers, 1964)
Belém, Brazil (Novaes [MS.]; compiled sources)
Belgian Congo (Chapin, 1932–1954; White, 1960-1965)
Bermuda (Wingate, 1959)
Biak Island, New Guinea (Mayr and Meyer de Schauensee, 1939; Rand and Gilliard, 1967)
Big Bend National Park, Texas (Wauer, 1973)
Black Hills, So. Dakota-Wyoming (Pettingill and Whitney, 1965)
Bohol, Philippines (duPont, 1971)
Bolivia (Meyer de Schauensee, 1966, 1970)
Bonaire, Netherlands Antilles (Voous, 1957)
Borneo (Smythies, 1968)
Bougainville, Solomon Islands (Mayr, 1945)
Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
British Columbia, Canada (Munroe and Cowan, 1947)
British Honduras (Russell, 1964)
British Isles (British Ornithologists' Union, 1952)
British Somaliland (Archer and Godman, 1937–1961)
Bulgaria (Pateff, 1950)
Bunguran, Natuna Islands (Oberholser, 1932)
Burma (Smythies, 1953)
Buru, Moluccas (van Bemmel, 1948)
Burundi (Schouteden, 1966b)
Bwamba County, W. Uganda (van Someren and van Someren, 1949; Friedmann and Williams, 1971)

California (McCaskie et al., 1970)
Camorta, Nicobar Islands (Abdulali, 1968)
Campeche, Mexico (Paynter, 1955; Storer, 1961)
Canada (Godfrey, 1966)
Canary Islands (Bannerman, 1963)
Cape Verde Islands (Bannerman and Bannerman, 1965–1968)
Car Nicobar, Nicobar Islands (Abdulali, 1968)
Caroline Islands, Micronesia (Baker, 1951)
Cartago Province, Costa Rica (Carriker, 1910; Slud, 1964a; compiled sources)
Cayo Largo, Cuba (Bond, 1950)
Ceará, Brazil (Hellmayr, 1929; Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Cebu, Philippines (duPont, 1971)

Celebes (Stresemann, 1939–1941)
Central America (Eisenmann, 1955)
Central and eastern South America (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Central Brazil (Pinto, 1938, 1940, 1944; Meyer de Schauensee, 1970)
Ceram, Moluccas (van Bemmel, 1948)
Ceylon (Henry, 1955)
Charles, Galapagos Archipelago (Swarth, 1931)
Chiapas, Mexico (Alvarez del Toro, 1964; Edwards, 1972)
Chile (Johnson, 1965–1967)
China (Chêng, 1955–1958)
Choiseul, Solomon Islands (Mayr, 1945)
Christmas Island, Indian Ocean (Pearson, 1966)
Churchill region, Manitoba (Jehl and Smith, 1970)
Clarion, Revilla Gigedos Islands, Mexico (Brattstrom and Howell, 1956)
Cocos Island, E. Pacific (Slud, 1967)
Cocos-Keeling Islands, Indian Ocean (Watson et al., 1963)
Coiba Island, Panama (Wetmore, 1957)
Colima and adjacent Jalisco, Mexico (Schaldach, 1963)
Colombia (Meyer de Schauensee, 1964)
Colorado (Bailey and Niedrach, 1965)
Comoro Islands, Indian Ocean (Benson, C. W., 1960)
Costa Rica (Slud, 1964a)
Cozumel Island, Mexico (Paynter, 1955)
Crete (Stresemann, 1956)
Cuba (Bond, 1971)
Culebra Island, Puerto Rico (Leopold, 1963; Bond, 1971)
Cundinamarca, Colombia (Olivares, 1969)
Curaçao, Netherlands Antilles (Voous, 1957)
Cyprus (Cyprus Ornithological Society, 1972)

Darjeeling area, India (Matthews and Edwards, 1944)
Death Valley, California (Wauer, 1962)
Delaware (Barnhill, 1972)
D'Entrecasteaux Archipelago, New Guinea (Rand and Gilliard, 1967)
Dominica, West Indies (Bond, 1971)

East and northeast Africa (Mackworth-Praed and Grant, 1952–1955)
East Cape Province, South Africa (Skead, 1967)
East-central Brazil (Meyer de Schauensee, 1970; compiled sources)
Eastern China (La Touche, 1925–1934)
Eastern Nigeria (Serle, 1957)
Ecuador (Meyer de Schauensee, 1970)
Efate, New Hebrides (Mayr, 1945)
Egypt (Etchécopar and Hüe, 1967)
Ellice Islands, W. Pacific (Child, 1960)
El Salvador (Rand and Traylor, 1954)
Enggano, W. Sumatra Islands (Ripley, 1944)
Epi, New Hebrides (Mayr, 1945)
Equateur-Tshuapa, Congo (Schouteden, 1961)
Eritrea (Smith, K. D., 1957)
Erromanga, New Hebrides (Mayr, 1945)
Espírito Santo, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Espíritu Santo, New Hebrides (Mayr, 1945)
Ethiopia (Urban and Brown, 1971)
Ethiopian Region (White, 1960–1965)
Eurasian tundra (Pleske, 1928)
Europe (Bruun, 1970)
Europe and North Africa (Heinzel et al., 1972)

Falkland Islands (Cawkell and Hamilton, 1961)
Fernando Po, Gulf of Guinea (Moreau, 1966)
Fiji Islands (Mayr, 1945)
Finca La Selva, Costa Rica (Slud, 1960)
Finland (Bruun, 1970)
Flores, East Indies (Kuroda, 1936)
Florida (Sprunt, 1954)
France-Belgium-Switzerland (Barruel, 1949)
French Cameroon (Good, 1952)
French Guiana (Berlepsch, 1908; Meyer de Schauensee, 1970; compiled sources)
French Indo-China (Delacour and Jabouille, 1931)
Fuerteventura, Canary Islands (Moreau, 1966)
Fukien, China (Chêng, 1955–1958)

Galapagos Islands (Swarth, 1931; Lévêque et al., 1966)
Gambia Valley (Moreau, 1966)
Gaua (Sta. Maria), Banks Islands (Mayr, 1945)
Georgia (Burleigh, 1958)
Germany (Niethammer et al., 1964)
Ghana (Karr, [MS.])
Gilbert Islands, W. Pacific (Amerson, 1969)
Gizo, Solomon Islands (Mayr, 1945)
Goiás, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Gomera, Canary Islands (Moreau, 1966)
Gonave, Hispaniola (Wetmore and Swales, 1931; Bond, 1971)
Gran Canaria, Canary Islands (Moreau, 1966)
Gran Chaco (Laubmann, 1930)
Gran Comoro, Comoro Islands (Benson, C. W., 1960)
Grand Cayman, West Indies (Cory, 1886; Bangs, 1916; Bond, 1971)
Great Britain (British Ornithologists' Union, 1952)
Great Nicobar, Nicobar Islands (Abdulali, 1968)
Greater Antilles (Bond, 1971)
Greater Sundas (Delacour, 1947)
Greece (Lambert, 1957)
Greenland (Salomonsen, 1950)
Grenada, West Indies (Wells, 1887; Bond, 1971)
Grenadines, West Indies (Bond, 1971)
Guadalcanal, Solomon Islands (Mayr, 1945; Cain and Galbraith, 1956)
Guadalupe Island, Mexico (Howell and Cade, 1954)
Guadeloupe, West Indies (Danforth, 1939a; Bond, 1971)
Guam, Marianas (Baker, 1951)
Guanacaste Province, Costa Rica (Carriker, 1910; Slud, 1964a; compiled sources)
Guanaja, Bay Islands of Honduras (Bond, 1936; Monroe, 1968)
Guatemala (Land, 1970)
Gujarat, India (Ali, 1954–1955)
Guyana (Snyder, D. E., 1966; Meyer de Schauensee, 1970)

Hainan, China (Hachisuka, 1939)
Halmahera, Moluccas (van Bemmel, 1948)
Hawaii (Peterson, 1961)
Hawaiian Islands (Peterson, 1961)
Henderson Island, Central Pacific (Williams, 1960)
Heredia Province, Costa Rica (Carriker, 1910; Slud, 1960, 1964a; compiled sources)
Hierro, Canary Islands (Moreau, 1966)
Hispaniola (Wetmore and Swales, 1931; Bond, 1971)
Hokkaido, Japan (Ornithological Society of Japan, 1958)
Honduras (Monroe, 1968)
Hong Kong Colony (Macfarlane and Macdonald, 1966)
Honshu, Japan (Ornithological Society of Japan, 1958)
Hopei, China (Shaw, 1936)
Hungary (Keve, 1960)

Ibadan, Nigeria (Elgood and Sibley, 1964)
Iberian Peninsula (Bruun, 1970)
Idaho (Burleigh, 1972)
Illinois (Smith and Parmalee, 1955)
Impenetrable Forest, Uganda (Keith et al., 1969; Friedmann and Williams, 1970)
Indefatigable, Galapagos Islands (Swarth, 1931)
Indian subcontinent (Ripley, 1961)
Indiana (Mumford, [MS.])
Iowa (Grant, 1963)
Iran (Hüe and Etchécopar, 1970)
Iraq (Hüe and Etchécopar, 1970)
Ireland (Kennedy, 1961)
Isla Grande, Tierra del Fuego (Humphrey et al., 1970)
Isla Margarita, Venezuela (Fernández and Benedetti, 1940; Yépez, 1957)
Isle of Pines, Cuba (Bangs and Zappey, 1905; Bond, 1971)
Ituri, Congo (Schouteden, 1963b)

Jamaica (Bond, 1971)
Japan (Austin and Kuroda, 1953; Ornithological Society of Japan, 1958)
Japen Island, New Guinea (Rand and Gilliard, 1967)
Java (Kuroda, 1936; Delacour, 1947)
Jervis, Galapagos Archipelago (Swarth, 1931)
Jodhpur, India (Whistler, 1938)
Joshua Tree Monument, California (Miller and Stebbins, 1964)

Kamchatka, Siberia (Bergman, 1935)
Kanab area, Utah (Behle et al., 1958)
Kandavu, Fiji Islands (Mayr, 1945)
Kansas (Johnston, 1960)
Kasai, Congo (Schouteden, 1964)
Katmai, Alaska (Cahalane, 1959)
Kauai, Hawaiian Islands (Peterson, 1961)
Keewatin District, Canada (Godfrey, 1966)
Kei Islands, Moluccas (van Bemmel, 1948)
Kentucky (Mengel, 1965)
Kenya-Uganda (Jackson, 1938)
Kerala (Ali, 1969)
Kolombangara, Solomon Islands (Mayr, 1945)
Korea (Austin, 1948; Gore and Won, 1971)
Kurile Islands (Bergman, 1935)
Kusaie, Caroline Islands (Baker, 1951)
Kutch, India (Ali, 1945)
Kwango-Kwilu, Congo (Schouteden, 1965)

Labrador Peninsula, Canada (Todd, 1963)
Lanai, Hawaiian Islands (Peterson, 1961)
Lanzarote, Canary Islands (Moreau, 1966)
Lau Islands, Southwest Pacific (Mayr, 1945)
Lebanon (Benson, S. V., 1970)
Laysan, Hawaiian Islands (Peterson, 1961)
Leeward Islands, Lesser Antilles (Bond, 1971)
Lesser Antilles, West Indies (Clark, 1905; Bond, 1971)
Lesser Sundas, East Indies (Kuroda, 1936)
Leyte, Philippines (duPont, 1971; Parkes, 1973)
Liberia (Forbes-Watson, [1970])
Libya (Toschi, 1969)
Lifu, Loyalty Islands (Mayr, 1945; Delacour, 1966)
Lima Department, Peru (Koepcke, 1964)
Lombok, East Indies (Kuroda, 1936)
Lord Howe Island, So. Pacific (Hindwood, 1940; Darlington, 1957)
Louisiade Archipelago, New Guinea (Rand and Gilliard, 1967)
Louisiana (Lowery, 1955)
Lower Amazonia (Snethlage, 1914; Griscom and Greenway, 1941; Pinto, 1938, 1944; Meyer de Schauensee, 1970; compiled sources)
Loyalty Islands, New Caledonia (Mayr, 1945; Delacour, 1966)
Luzon, Philippines (duPont, 1971)

Mackenzie District, Canada (Godfrey, 1966)
Madagascar (Rand, 1936)
Mafia Island, Tanzania (Moreau, 1966)
Maine (Palmer, 1949)
Malaita, Solomon Islands (Mayr, 1945)
Malay Peninsula (Glenister, 1951)
Malaya (Delacour, 1947)
Malaysia (Delacour, 1947)
Malekula, New Hebrides (Mayr, 1945)
Manchuria (Vaurie, 1959–1965)
Manitoba, Canada (Godfrey, 1966)
Manua Islands, Samoa (Mayr, 1945)
Maranhão, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Maré, Loyalty Islands (Mayr, 1945; Delacour, 1966)
Margarita I., Venezuela (Fernández and Benedetti, 1940; Yépez, 1957)
María Cleofas, Tres Marías Islands, Mexico (Stager, 1957)
María Madre, Tres Marías Islands, Mexico (Stager, 1957)
María Magdalena, Tres Marías Islands, Mexico (Stager, 1957)
Mariana Islands, Micronesia (Baker, 1951)
Marie Galante, West Indies (Danforth, 1939a; Bond, 1971)
Marquesas, French Polynesia (Bruner, 1972)
Marshall Islands, Micronesia (Baker, 1951)
Martinique, West Indies (Bond, 1971)
Maryland (Stewart and Robbins, 1958)

Massachusetts (Griscom and Snyder, 1955)
Mato Grosso, Brazil (Pinto, 1938, 1940, 1944; Sick, 1955; Meyer de Schauensee, 1970; Fry, 1970)
Maui, Hawaiian Islands (Peterson, 1961)
Mauritius, Indian Ocean (Watson et al., 1963)
Mayotte, Comoro Islands (Benson, C. W., 1960)
Mentawai group, W. Sumatra Islands (Ripley, 1944)
Meta, Colombia (Meyer de Schauensee, 1964)
Mexico (Edwards, 1972)
Michigan (Zimmerman and Van Tyne, 1959)
Micronesia (Baker, 1951)
Middle America (Eisenmann, 1955; Edwards, 1972)
Middle East (Hüe and Etchécopar, 1970)
Minas Gerais, Brazil (Pinto, 1952; Meyer de Schauensee, 1970)
Mindanao, Philippines (duPont, 1971)
Mindoro, Philippines (duDont, 1971)
Minnesota (Roberts, T. S., 1949)
Misiones, Argentina (Olrog, 1963; Meyer de Schauensee, 1970)
Mississippi (Mississippi Ornithological Society, 1962)
Mississippi Coast (Burleigh, 1944)
Missouri (Widmann, 1907)
Moheli, Comoro Islands (Benson, C. W., 1960)
Mollendo, Peru (Hughes, 1970)
Molokai, Hawaiian Islands (Peterson, 1961)
Moluccas (van Bemmel, 1948)
Mona Island, Puerto Rico (Raffaele, 1973)
Mongala-Ubangi, Congo (Schouteden, 1962b)
Mongolia (Vaurie, 1959–1965, 1964)
Mono, Solomon Islands (Mayr, 1945)
Montana (Skaar et al., 1971)
Montserrat, West Indies (Danforth, 1939b; Bond, 1971)
Morocco (Etchécopar and Hüe, 1967)
Mushie, Congo (Schouteden, 1962a)
Mysore, India (Ali, 1943–1944)

Natal-Zululand, South Africa (Clancey, 1964)
Natuna Islands, South China Sea (Oberholser, 1932)
Navajo country, Utah-Arizona (Woodbury and Russell, 1945)
Near East (Hüe and Etchécopar, 1970)
Nearctic Region (American Ornithologists' Union, 1957; Edwards, 1972)
Nebraska (Rapp et al., 1958)
Negros, Philippines (duPont, 1971)
Neotropical Region (Edwards, 1972; Eisenmann, 1955; Meyer de Schauensee, 1970)
Netherlands (Commissie Nederlandse Avifauna, 1962)
Nevada (Linsdale, 1936)
Nevis, West Indies (Danforth, 1936; Bond, 1971)
New Brunswick, Canada (Squires, 1952)
New Caledonia, Indian Ocean (Delacour, 1966)
New Georgia, Solomon Islands (Mayr, 1945)
New Guinea (Rand and Gilliard, 1967)
New Hampshire (Richards, 1964)
New Hebrides, Southwest Pacific (Mayr, 1945)
New Jersey (Fables, 1955)
New Mexico (Hubbard, 1970)
New York (Reilly and Parkes, 1959)
New Zealand (Fleming et al., 1953)
Newfoundland Island, Canada (Peters and Burleigh, 1951)
Newfoundland Labrador, Canada (Austin, 1932)
Nias, W. Sumatra Islands (Ripley, 1944)
Nicaragua (Eisenmann, 1955)
Nicobar Islands, Bay of Bengal (Abdulali, 1968)
Nissan, Solomon Islands (Mayr, 1945; Ripley, 1947)
Niue, South Pacific (Wodzicki, 1971)
Nontropical Mexico (Edwards, 1972)
Norfolk Island, South Pacific (Darlington, 1957)
North Africa (Etchécopar and Hüe, 1967)
North America (Robbins et al., 1966; Eisenmann, 1955)
North America (A.O.U.) (American Ornithologists' Union, 1957)
North Carolina (Pearson et al., 1959)
North Dakota (Stewart, [MS.])
North Island, New Zealand (Fleming et al., 1953)
Northeastern Brazil (Pinto, 1938, 1944, 1954; Pinto and Camargo, 1961; Meyer de Schauensee, 1970)
Northeastern Pará (compiled sources)
Northeastern Venezuela (Friedmann and Smith, 1950, 1955)
Northern Bolivia (Gyldenstolpe, 1945b)
Northern Brazil-Southern Venezuela (Friedmann, 1948)
Northern Libya (Stanford, 1954)
Northern South America (Phelps and Phelps, 1958, 1963; Meyer de Schauensee, 1970)
Northern Territory, Australia (Condon, 1944–1945)
Northern Thailand (Deignan, 1945)
Northwest Kansu and Kuku Nor (Stresemann et al., 1937–1938)
Northwest South America (Meyer de Schauensee, 1970)
Nova Scotia, Canada (Tufts, 1961)
Nyasaland (Benson, C. W., 1953)

Oahu, Hawaiian Islands (Peterson, 1961)
Oaxaca, Mexico (Friedmann et al., 1950; Miller et al., 1957; Edwards, 1972; Peterson and Chalif, 1973)
Oba, New Hebrides (Mayr, 1945)
Obidos, Brazil (compiled sources)
Ohio (Trautman and Trautman, 1968)
Oklahoma (Sutton, 1967)
Old Providence, West Indies (Bond, 1950, 1971)
Ontario, Canada (Snyder, L. L., 1951)
Oregon (Bertrand and Scott, 1971)
Orinoco region, Venezuela (Cherrie, 1916)
Ovalau, Fiji Islands (Mayr, 1945)

Palau Islands, Micronesia (Baker, 1951)
Palawan, Philippines (Delacour and Mayr, 1946; duPont, 1971)
Palearctic Region (Vaurie, 1959–1965)
Palma, Canary Islands (Moreau, 1966)
Panama (Griscom, 1935; Eisenmann, 1955; Wetmore, 1965–1972a)
Panama Canal Zone (Eisenmann and Loftin, 1968)
Panay, Philippines (duPont, 1971)
Pará, Brazil (Pinto, 1938, 1944; compiled sources)

Paraguana Peninsula (Barnés, 1940)
Paraguay (Laubmann, 1939–1940; Meyer de Schauensee, 1970)
Paraiba, Brazil (Pinto and Camargo, 1961; Meyer de Schauensee, 1970)
Paraná, Brazil (Pinto, 1938, 1944; Pinto and Camargo, 1955; Meyer de Schauensee, 1970)
Patagonia, Argentina (Olrog, 1959)
Pavuvu, Solomon Islands (Mayr, 1945)
Pearl Archipelago (MacArthur et al., 1972; Wetmore, 1965–1972a)
Pemba Island, Tanzania (Moreau, 1966)
Pennsylvania (Poole, 1964)
Pentecost, New Hebrides (Mayr, 1945)
Perijá, Venezuela (Phelps, 1943; Gines et al., 1953)
Pernambuco, Brazil (Pinto, 1938, 1944; Berla, 1946; Meyer de Schauensee, 1970)
Peru (Meyer de Schauensee, 1970)
Petén, Guatemala (Smithe, 1966; Land, 1970)
Philippines (duPont, 1971)
Phoenix Islands, Central Pacific (Roger Clapp, pers. comm.)
Piauí, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Pitcairn Islands, Central Pacific (Williams, 1960)
Ponape, Caroline Islands (Baker, 1951)
Portugal (Themido, 1952)
Prince Edward Island, Canada (Godfrey, 1954)
Principe, Gulf of Guinea (Moreau, 1966)
Puerto Rico (Wetmore, 1927; Leopold, 1963; Bond, 1971)
Puntarenas Province, Costa Rica (Carriker, 1910; Slud, 1964a; compiled sources)

Quintana Roo, Mexico (Paynter, 1955)

Rancho Grande, Venezuela (Schäfer and Phelps, 1954)
Rendova, Solomon Islands (Mayr, 1945)
Rennell, Solomon Islands (Mayr, 1931, 1945)
Reunion (Watson et al., 1963)
Revilla Gigedos Islands, Mexico (Brattstrom and Howell, 1956)
Rio de Janeiro, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Rio Grande do Sul, Brazil (Pinto, 1938, 1944; Camargo, 1962; Meyer de Schauensee, 1970)
Roatán, Bay Islands of Honduras (Bond, 1936; Monroe, 1968)
Rodriguez, Indian Ocean (Watson et al., 1963)
Roraima, Brazil (Pinto, 1966)
Rota, Marianas (Baker, 1951)
Rwanda (Schouteden, 1966a)

Saba, West Indies (Voous and Koelers, 1967)
Saipan, Marianas (Baker, 1951)
Samar, Philippines (duPont, 1971)
Samoa (Ashmole, 1963)
San Cristobal, Solomon Islands (Mayr, 1945; Cain and Galbraith, 1956)
San José, Pearl Islands, Panama (Wetmore, 1946)
San José Province, Costa Rica (Carriker, 1910; Slud, 1964a; compiled sources)
Santa Ana, Solomon Islands (Mayr, 1945)
Santa Catarina, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Santa Cruz Islands, Southwest Pacific (Mayr, 1945)
Santa Elena Peninsula, Ecuador (Marchant, 1958)
Santa Isabel, Solomon Islands (Mayr, 1945)
Santa Marta area, Colombia (Todd and Carriker, 1922; Darlington, 1931)
Santarem, Brazil (Riker, 1890–1891; Griscom and Greenway, 1941; Pinto, 1938, 1944; Meyer de Schauensee, 1970; compiled sources)
São Paulo, Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
São Tiago, Cape Verde Islands (Moreau, 1966)
São Tomé, Gulf of Guinea (Moreau, 1966)
Saskatchewan, Canada (Houston et al., 1958)
Savaii, Samoa (Mayr, 1945)
Scandinavian Peninsula (Bruun, 1970)
Seychelles (Gaymer et al., 1969; Watson et al., 1963)
Sierra Macarena, Colombia (Blake, 1962)
Simalur, W. Sumatra Islands (Ripley, 1944)
Sinaloa, Mexico (Friedmann et al., 1950; Miller et al., 1957; Edwards, 1972; Peterson and Chalif, 1973)
Singapore (Gibson-Hill, 1950a, 1950b)
Society Islands, French Polynesia (Bruner, 1972)
Socorro, Revilla Gigedos Islands, Mexico (Brattstrom and Howell, 1956)
Socotra, Indian Ocean (Ripley and Bond, 1966)
Solomon Islands, S. W. Pacific (Mayr, 1945; Cain and Galbraith, 1956)
Sonora, Mexico (van Rossem, 1945; Edwards, 1972)
South America (Meyer de Schauensee, 1966, 1970)
South Australia (Condon, 1962)
South Carolina (Sprunt and Chamberlain, 1949)
South China (Caldwell and Caldwell, 1931)
South Dakota (Over and Thoms, 1946)
South Island, New Zealand (Fleming et al., 1953)
South Vietnam (Wildash, 1968)
Southampton Island, Canada (Sutton, 1932)
Southeastern Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Southeastern Transbaikal (Gagina, 1960)
Southeastern Utah (Behle, 1960)
Southern Africa (Roberts, A., 1970)
Southern Brazil (Pinto, 1938, 1944; Meyer de Schauensee, 1970)
Southern Burma (Smythies, 1953)
Southern California (Pyle, 1953)
Southern Cameroon (Germain et al., 1973)
Southern Illinois (George, 1968)
Southern Patagonia, Argentina (Olrog, 1959)
Southern Rhodesia (Smithers et al., 1957)
Southern South America (Meyer de Schauensee, 1970)
Southern third of Africa (Mackworth-Praed and Grant, 1962–1963)
South-West Africa (Hoesch and Niethammer, 1940)
Southwestern Ohio (Kemsies and Randle, 1953)
Soviet Union (Dementiev and Gladkov, 1951–1954)
Spanish Sahara (Valverde, 1957)

St. Andrew, West Indies (Bond, 1950, 1971)
St. Croix, Virgin Islands (Wetmore, 1918; Beatty, 1930; Leopold, 1963)
St. Eustatius, West Indies (Voous and Koelers, 1967)
St. John, Virgin Islands (Nichols, 1943; Robertson, 1962; Bond, 1971)
St. Kitts, West Indies (Danforth, 1936; Bond, 1971)
St. Lucia, West Indies (Danforth, 1935; Bond, 1971)
St. Martin, West Indies (Voous and Koelers, 1967)
St. Thomas, Virgin Islands (Wetmore, 1918; Nichols, 1943; Leopold, 1963)
St. Vincent, West Indies (Bond, 1971)
Sudan (Cave and Macdonald, 1955)
Sula Islands, Moluccas (van Bemmel, 1948)
Sumatra (Delacour, 1947)
Sumba, East Indies (Mayr, 1944a)
Sumbawa, East Indies (Kuroda, 1936)
Sunda Islands, East Indies (Kuroda, 1936; Mayr, 1944a; Delacour, 1947)
Surinam (Haverschmidt, 1968)
Swan Islands, West Indies (Paynter, 1956)

Tabasco, Mexico (Friedmann et al., 1950; Miller et al., 1957; Peterson and Chalif, 1973)
Tahiti, French Polynesia (Bruner, 1972)
Taiwan (Hachisuka and Udagwa, 1950–1951; Severinghaus et al., 1970)
Tamaulipas, Mexico (Friedmann et al., 1950; Miller et al., 1957; Edwards, 1972; Peterson and Chalif, 1973)
Tanna, New Hebrides (Mayr, 1945)
Tasmania (Sharland, 1945)
Taveuni, Fiji Islands (Mayr, 1945)
Tenasserim, Burma (Smythies, 1953)
Tenerife, Canary Islands (Moreau, 1966)
Texas (Peterson, 1963)
Thailand (Lekagul, 1968)
Thames Valley, England (Moreau, 1966)
The Guianas (Meyer de Schauensee, 1966, 1970)
Tibet (Vaurie, 1972)
Tikal, Guatemala (Smithe, 1966)
Timor, East Indies (Mayr, 1944a)
Tinian, Marianas (Baker, 1951)
Tobago, West Indies (Herklots, 1961; ffrench and ffrench, 1966)
Tonga Islands, Southwest Pacific (Mayr, 1945)
Torres Islands, New Hebrides (Mayr, 1945)
Tortola, Virgin Islands (Bond, 1971)
Tranninh, Laos (David-Beaulieu, 1944)
Tres Marías Islands, Mexico (Stager, 1957)
Trinidad, West Indies (Herklots, 1961; ffrench and ffrench, 1966)
Truk, Caroline Islands (Baker, 1951)
Tuamotu Archipelago, French Polynesia (Bruner, 1972)
Tunisia (Etchécopar and Hüe, 1967)
Turkey (Hüe and Etchécopar, 1970)
Tutuila, Samoa (Mayr, 1945)

Uele, Congo (Schouteden, 1963a)
United States (American Ornithologists' Union, 1957)
Upolu, Samoa (Mayr, 1945)
Upper Amazonia (Pinto, 1938, 1944; Gyldenstolpe, 1945a, 1951; Meyer de Schauensee, 1970; compiled sources)
Uruguay (Cuello and Gerzenstein, 1962; Meyer de Schauensee, 1970)
Utah (Woodbury et al., 1969)
Utila, Bay Islands of Honduras (Bond, 1936; Monroe, 1968)
Uvea, Loyalty Islands (Mayr, 1945; Delacour, 1966)

Valua (Saddle I.), Banks Islands (Mayr, 1945)
Vanua Lava, Banks Islands (Mayr, 1945)
Vanua Levu, Fiji Islands (Mayr, 1945)
Vaupés, Colombia (Olivares, 1955, 1964a, 1964b; Olivares and Hernández, 1962)
Vella Lavella, Solomon Islands (Mayr, 1945)
Venezuela (Phelps and Phelps, 1958, 1963)
Veracruz, Mexico (Friedmann et al., 1950; Miller et al., 1957; Edwards, 1972; Peterson and Chalif, 1973)
Victoria, Australia (Wheeler, 1967)
Vieques, Puerto Rico (Wetmore, 1927; Danforth, 1937; Leopold, 1963)
Virgin Gorda, Virgin Islands (Bond, 1971)
Virgin Islands (Wetmore, 1927; Leopold, 1963; Bond, 1971)
Virginia (Murray, 1952)
Vitu Levu, Fiji Islands (Mayr, 1945)

Waigeu Island, New Guinea (Rand and Gilliard, 1967)
Washington (Alcorn, 1971)
West Chiriquí Highlands (Eisenmann and Loftin, 1967a)
West Indies (Bond, 1971)
West Sumatra Islands (Ripley, 1944)
West Virginia (Hall, 1971)
West-central and west Africa (Mackworth-Praed and Grant, 1970–1973)
Western Australia (Serventy and Whittell, 1951)
Western China-eastern Tibet (Schäfer, 1938)
Windward Islands, Lesser Antilles (Bond, 1971)
Wisconsin (Gromme, 1963)
World (Austin, 1971)
Wyoming (McCreary, 1939)

Yap, Caroline Islands (Baker, 1951)
Yucatan, Mexico (Paynter, 1955)
Yucatan Peninsula, Mexico (Paynter, 1955)
Yugoslavia (Matvejev and Vasic, 1973)
Yukon Territory, Canada (Godfrey, 1966)

Zambia (Benson et al., 1971)
Zanzibar Island, Tanzania (Moreau, 1966)
Zaria, Northern Nigeria (Fry, 1966)

Appendix 2

Tables

TABLE 1.—*World survey of species densities and passerine-nonpasserine ratios* (TL = total land species, NL = native land species)

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	$NL+\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	$NL+\frac{(TL-NL)}{2}$	Native (NL)
World (living and recently extinct)	52,410,000	0.0165	0.015	0.015	0.015	1.94	1.94	1.94
Soviet Union	8,354,200	0.0084	0.0053	0.0040	0.0026	2.05	1.88	1.60
North America (mainland)	8,150,000	0.018	0.015	0.014	0.014	1.71	1.70	1.68
Ethiopian Region (mainland)	8,000,000	0.021	0.018	0.018	0.017	1.96	1.96	1.95
Neotropical Region (mainland south of Isthmus of Tehuantepec)	7,280,000	0.045	0.040	0.039	0.038	1.84	1.80	1.77
Temperate North America (excluding Middle America and Greenland)	7,156,000	0.0093	0.0059	0.0052	0.0044	2.08	2.00	1.79
China (mainland)	3,878,150	0.027	0.022	0.017	0.013	2.51	2.62	2.75
Europe	3,800,000	0.015	0.0087	0.0067	0.0046	1.97	1.70	1.39
Canada	3,610,000	0.014	0.0079	0.0057	0.0035	2.52	2.06	1.35
Brazil	3,286,000	0.047	0.041	0.041	0.040	1.80	1.79	1.78
Australia	2,974,500	0.023	0.016	0.016	0.016	1.87	1.90	1.93
United States (coterminous)	2,959,500	0.022	0.014	0.012	0.010	2.08	1.96	1.82
Indian Subcontinent (mainland)	1,730,650	0.067	0.054	0.051	0.047	2.06	2.00	1.93
Russia in Europe	1,595,500	——	0.016	0.013	0.0090	1.78	1.63	1.39
Southern South America (Paraguay, Uruguay, Argentina, Chile)	1,588,300	0.063	0.049	0.048	0.048	1.71	1.72	1.73
Northwestern South America (Colombia, Ecuador, Peru, Bolivia)	1,536,650	0.15	0.13	0.13	0.13	1.76	1.73	1.70
Southern South America (Argentina, Chile)	1,359,150	0.073	0.055	0.054	0.053	1.73	1.73	1.74
Southern Africa	1,312,000	0.061	0.046	0.044	0.042	1.55	1.59	1.64
Northwest Africa (Morocco, Algeria, Tunisia)	1,141,600	0.034	0.020	0.016	0.012	1.72	1.60	1.43
Amazonian Brazil (Amazonas, Pará, Amapá)	1,121,700	0.088	0.079	0.078	0.077	1.54	1.53	1.51
Bolivia-Mato Grosso (including Rondonia)	1,095,400	0.12	0.11	0.11	0.10	1.75	1.72	1.70
Argentina	1,072,750	0.086	0.067	0.066	0.065	1.71	1.71	1.71
Northwest South America (Colombia, Ecuador, Peru)	1,023,500	0.20	0.18	0.18	0.17	1.75	1.72	1.69
Mongolia	1,016,100	——	0.022	0.016	0.010	1.76	1.57	1.25
Arabia	1,000,000	0.038	0.025	0.020	0.014	1.41	1.33	1.19

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	$NL+(\frac{TL-NL}{2})$	Native (NL)	Total (TL)	$NL+(\frac{TL-NL}{2})$	Native (NL)
Middle America (mainland)	992,952	0.14	0.11	0.11	0.10	1.71	1.63	1.54
Anglo-Egyptian Sudan	950,950	0.092	0.074	0.069	0.063	1.61	1.58	1.55
Belgian Congo	895,348	0.11	0.098	0.095	0.091	1.71	1.71	1.72
Greenland	839,800	0.023	0.0088	0.0050	0.00083	3.63	3.05	0.75
Tibet	835,660	0.060	0.048	0.040	0.032	3.14	3.24	3.41
Western Australia (minus Kimberley Division)	831,920	0.042	0.024	0.024	0.024	1.54	1.58	1.62
Mexico	763,944	0.13	0.10	0.093	0.085	1.72	1.59	1.47
Libya	679,358	0.041	0.027	0.018	0.0093	1.76	1.66	1.47
Iran	628,000	0.071	0.049	0.041	0.032	1.81	1.74	1.64
Malaysia	617,924	0.12	0.098	0.094	0.090	1.39	1.38	1.37
Amazonas, Brazil	595,474	0.14	0.13	0.12	0.12	1.62	1.59	1.57
Alaska (mainland)	586,400	0.047	0.023	0.016	0.0095	1.96	1.62	1.06
Ecuador-Peru	583,738	0.30	0.27	0.26	0.26	1.80	1.79	1.78
Mato Grosso (including Rondonia)	582,391	0.13	0.11	0.11	0.11	1.45	1.44	1.43
Venezuela-The Guianas	531,504	0.25	0.23	0.22	0.21	1.68	1.65	1.61
Labrador Peninsula	530,000	0.059	0.033	0.020	0.0064	2.67	2.04	0.62
Pará-Amapá, Brazil	526,241	0.16	0.14	0.14	0.14	1.49	1.48	1.48
Mackenzie District, Canada	525,000	0.041	0.023	0.014	0.0053	2.30	1.77	0.65
Northern Territory, Australia	523,620	0.067	0.049	0.049	0.049	1.45	1.45	1.45
Bolivia	513,086	0.23	0.20	0.20	0.20	1.78	1.76	1.73
Peru	482,257	0.32	0.28	0.27	0.27	1.87	1.86	1.85
Angola	481,226	0.18	0.15	0.15	0.14	1.53	1.54	1.56
Pará, Brazil	470,752	0.17	0.15	0.15	0.15	1.51	1.50	1.49
East-central Brazil (Bahía-Goiás)	459,659	0.15	0.13	0.13	0.13	1.41	1.41	1.41
Colombia	439,825	0.36	0.32	0.32	0.31	1.61	1.58	1.54
Manchuria	408,162	—	0.059	0.041	0.023	1.79	1.69	1.47
Egypt	386,200	0.095	0.058	0.040	0.021	1.63	1.43	1.01
South Australia	380,070	0.10	0.065	0.063	0.060	1.55	1.57	1.60

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)
Ontario	363,282	0.078	0.051	0.036	0.021	2.62	2.00	1.12
British Columbia	359,279	0.094	0.057	0.042	0.027	2.14	1.77	1.23
Nigeria	356,667	0.22	0.18	0.17	0.16	1.54	1.55	1.55
Venezuela	352,141	0.37	0.33	0.32	0.31	1.68	1.64	1.61
New Guinea (including coastal islands)	322,044	0.21	0.17	0.17	0.16	1.54	1.59	1.65
Southeastern Brazil (São Paulo through Rio Grande do Sul)	319,468	0.24	0.19	0.19	0.19	1.61	1.60	1.59
New Guinea (mainland)	306,600	0.20	0.17	0.16	0.16	1.65	1.68	1.71
Kenya-Uganda	306,000	0.35	0.30	0.29	0.28	1.78	1.77	1.77
Ethiopia	305,731	0.27	0.21	0.20	0.18	1.49	1.44	1.38
South-West Africa (excluding Caprivi Strip and Okavango)	296,887	0.15	0.11	0.10	0.091	1.25	1.32	1.40
Zambia	290,320	0.24	0.20	0.19	0.17	1.55	1.63	1.72
Borneo	289,993	0.19	0.14	0.14	0.13	1.30	1.30	1.30
Chile	286,396	0.13	0.070	0.066	0.061	1.74	1.64	1.55
Turkey (Asia Minor)	285,162	0.13	0.086	0.066	0.046	1.78	1.76	1.71
Scandinavian Peninsula	277,480	——	0.064	0.047	0.030	1.45	1.37	1.22
Texas	262,398	0.18	0.13	0.11	0.06	2.48	2.16	1.64
Burma	261,610	0.37	0.31	0.29	0.27	1.86	1.78	1.68
Afghanistan	250,965	0.16	0.12	0.099	0.076	2.30	2.32	2.34
Alberta	248,800	0.13	0.082	0.051	0.020	2.62	2.08	0.90
Goiás, Brazil	244,330	0.18	0.16	0.16	0.16	1.33	1.33	1.32
France-Belgium-Switzerland	240,369	0.14	0.082	0.066	0.050	1.65	1.65	1.66
Saskatchewan	237,975	0.13	0.086	0.052	0.018	2.53	2.13	1.00
Central America	228,578	0.47	0.40	0.37	0.35	1.60	1.51	1.42
Keewatin District, Canada	228,000	0.045	0.018	0.012	0.0061	1.67	1.16	0.40
Madagascar	227,678	0.10	0.059	0.058	0.056	0.93	0.93	0.94
Iberian Peninsula	227,384	——	0.083	0.067	0.051	1.84	1.88	1.93
Minas Gerais, Brazil	226,179	0.25	0.22	0.22	0.22	1.43	1.43	1.43
Southern Brazil (Paraná, Sta. Catarina, Rio Grande do Sul)	224,009	0.28	0.23	0.23	0.23	1.70	1.69	1.67
Bechuanaland	222,000	0.21	0.17	0.16	0.15	1.30	1.33	1.37

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)
Manitoba	219,723	0.14	0.085	0.053	0.020	2.48	2.07	1.05
Bahía, Brazil	215,329	0.28	0.24	0.24	0.24	1.35	1.35	1.34
Yukon Territory, Canada	205,346	—	0.055	0.034	0.014	2.14	1.66	0.65
Thailand	198,247	0.42	0.35	0.32	0.28	1.50	1.43	1.36
Germany	182,426	0.24	0.14	0.098	0.051	1.94	1.77	1.37
Patagonia (Santa Cruz, Chubut)	180,398	—	0.063	0.061	0.060	1.72	1.74	1.77
The Guianas	179,363	0.44	0.37	0.36	0.35	1.48	1.47	1.45
Morocco	173,700	0.20	0.12	0.10	0.076	1.64	1.57	1.46
East Cape Province, South Africa	167,000	0.33	0.23	0.21	0.20	1.31	1.36	1.41
Sumatra	166,789	—	0.25	0.25	0.24	1.28	1.26	1.24
French Cameroon	166,489	0.42	0.36	0.36	0.35	1.60	1.61	1.61
California	158,693	0.31	0.19	0.14	0.097	2.60	2.18	1.59
Paraguay	157,006	0.41	0.34	0.33	0.32	1.51	1.51	1.50
Northeastern Brazil (Ceará through Sergipe)	156,865	0.26	0.22	0.22	0.22	1.49	1.49	1.48
Piauí-Ceará, Brazil	152,190	0.25	0.21	0.21	0.21	1.33	1.32	1.31
Southern Rhodesia	150,333	0.38	0.30	0.28	0.26	1.45	1.50	1.57
Montana	147,138	0.23	0.15	0.095	0.039	2.36	1.98	1.11
Guyana-Surinam	144,623	0.53	0.45	0.44	0.43	1.48	1.47	1.45
Japan	141,086	0.30	0.15	0.11	0.075	1.90	1.72	1.43
Kasai, Congo	136,222	0.39	0.33	0.32	0.31	1.36	1.36	1.35
Baluchistan	134,638	—	0.15	0.13	0.097	1.54	1.49	1.41
Maranhão, Brazil	133,674	0.32	0.28	0.28	0.28	1.52	1.53	1.53
Finland	130,165	—	0.12	0.085	0.049	1.68	1.54	1.24
Near East (Syria, Lebanon, Israel, Transjordan)	122,905	0.30	0.20	0.15	0.10	1.74	1.71	1.65
New Mexico	121,266	0.32	0.24	0.18	0.12	2.46	2.18	1.72
British Isles	120,459	0.33	0.19	0.13	0.070	2.20	2.15	2.00
Iraq	116,600	0.30	0.20	0.14	0.076	1.66	1.51	1.19
Philippines	114,830	0.44	0.32	0.30	0.27	1.42	1.36	1.30
Northern Central America (Guatemala, Honduras, El Salvador)	114,380	0.63	0.52	0.47	0.43	1.53	1.39	1.23

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)
Algeria (minus Saharan Departments)	113,912	0.30	0.19	0.15	0.11	1.78	1.69	1.54
Arizona	113,909	0.38	0.27	0.21	0.14	2.36	2.23	2.00
Newfoundland Labrador, Canada	112,630	0.13	0.055	0.036	0.017	1.58	1.25	0.58
Nevada	110,540	0.28	0.20	0.14	0.080	2.22	2.08	1.78
Rio Grande do Sul, Brazil	110,150	0.47	0.39	0.37	0.36	1.70	1.69	1.68
West Cape Province, South Africa	110,000	0.38	0.28	0.26	0.25	1.24	1.29	1.35
Spanish Sahara	105,409	0.20	0.11	0.076	0.041	1.37	1.34	1.26
Colorado	104,247	0.41	0.28	0.19	0.099	2.41	2.03	1.31
New Zealand	103,410	0.21	0.052	0.046	0.039	0.93	1.00	1.11
Ecuador	101,481	1.34	1.18	1.16	1.14	1.62	1.61	1.59
Wyoming	97,914	0.33	0.22	0.15	0.072	2.56	2.07	1.15
Roraima, Brazil	97,438	0.44	0.39	0.39	0.38	1.61	1.60	1.58
Oregon	96,981	0.35	0.22	0.16	0.11	2.28	1.97	1.49
Yugoslavia	96,201	0.40	0.25	0.19	0.13	1.60	1.60	1.60
São Paulo, Brazil	95,459	0.71	0.58	0.58	0.58	1.51	1.51	1.50
Piauí, Brazil	94,819	0.35	0.29	0.29	0.29	1.32	1.32	1.31
Uele, Congo	91,897	0.71	0.60	0.57	0.54	1.37	1.37	1.38
Surinam-French Guiana	89,883	0.76	0.64	0.62	0.61	1.39	1.38	1.37
Guyana	89,480	0.83	0.70	0.68	0.66	1.42	1.40	1.37
Great Britain	88,619	—	0.26	0.18	0.091	2.20	2.15	2.00
Victoria, Australia	87,884	0.48	0.30	0.28	0.25	1.54	1.60	1.68
Honshu, Japan	87,000	0.44	0.21	0.15	0.096	1.69	1.94	2.07
Korea	85,225	0.44	0.26	0.17	0.078	1.85	1.59	0.99
Utah	84,916	0.38	0.25	0.18	0.12	2.20	1.94	1.49
Greater Antilles	84,750	0.48	0.33	0.26	0.20	1.60	1.29	0.93
Minnesota	84,068	0.39	0.26	0.16	0.062	2.70	2.08	0.91
Idaho	83,557	0.36	0.24	0.17	0.095	2.26	1.99	1.47
Paraná, Brazil	82,741	0.48	0.43	0.43	0.43	1.79	1.80	1.80
Kansas	82,276	0.47	0.31	0.19	0.078	2.90	2.12	0.74
Southern Burma	80,874	0.71	0.56	0.52	0.47	1.57	1.46	1.35
Nebraska	77,227	0.49	0.33	0.20	0.078	2.66	2.02	0.73

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)
South Dakota	77,047	0.42	0.28	0.17	0.057	2.58	2.09	0.83
Southern Central America (Nicaragua, Costa Rica)	76,381	1.09	0.93	0.87	0.80	1.55	1.47	1.39
Mysore, India	74,326	0.47	0.38	0.34	0.31	1.33	1.23	1.12
Uruguay	72,172	0.50	0.31	0.29	0.27	1.60	1.58	1.55
Northeastern Brazil (Pernambuco, Paraiba, Alagoas)	70,937	0.54	0.47	0.47	0.47	1.60	1.59	1.58
North Dakota	70,665	0.45	0.29	0.17	0.048	2.51	2.04	0.68
Sonora, Mexico	70,477	0.58	0.43	0.36	0.30	1.97	1.80	1.59
Malay Peninsula	70,000	0.82	0.64	0.60	0.56	1.23	1.22	1.20
Oklahoma	69,919	0.56	0.39	0.25	0.12	2.62	2.08	1.10
Missouri	69,674	0.46	0.30	0.19	0.077	2.68	2.16	1.04
Celebes	69,255	0.40	0.29	0.27	0.25	0.90	0.87	0.84
Washington State	68,192	0.49	0.28	0.21	0.14	1.76	1.66	1.48
British Somaliland	67,936	0.61	0.46	0.42	0.37	1.26	1.16	1.04
Honduras-El Salvador	67,420	0.99	0.83	0.74	0.66	1.44	1.30	1.16
Kwango-Kwilu, Congo	65,400	0.55	0.46	0.45	0.45	1.12	1.14	1.16
South Vietnam	65,000	0.90	0.72	0.68	0.63	1.49	1.47	1.44
Gujarat, India	64,000	——	0.45	0.39	0.34	1.27	1.17	1.04
Yucatan Peninsula, Mexico	63,034	0.65	0.51	0.43	0.36	1.42	1.24	1.03
Fukien, China	61,259	——	0.48	0.36	0.24	2.10	2.03	1.92
Hopei, China	59,341	0.68	0.44	0.28	0.12	1.92	1.79	1.40
Honduras	59,160	1.09	0.91	0.82	0.73	1.44	1.32	1.19
Georgia	58,876	0.57	0.34	0.24	0.13	2.96	2.38	1.43
Florida	58,560	0.64	0.37	0.26	0.15	2.47	1.84	0.89
Michigan	58,216	0.58	0.37	0.25	0.13	2.80	2.32	1.42
Vaupés, Colombia	57,857	0.60	0.55	0.54	0.54	1.79	1.76	1.73
Ceará, Brazil	57,371	0.44	0.35	0.35	0.35	1.44	1.44	1.44
Nicaragua	57,143	1.04	0.90	0.82	0.75	1.47	1.36	1.23
Illinois	56,400	0.66	0.41	0.26	0.10	2.75	2.20	1.02
Iowa	56,290	0.57	0.36	0.22	0.080	2.69	2.07	0.75
Wisconsin	56,154	0.62	0.38	0.26	0.13	2.72	2.16	1.19
Baja California, Mexico	55,629	0.60	0.36	0.29	0.23	2.33	2.21	2.02

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)
Surinam	55,143	1.19	0.99	0.97	0.95	1.36	1.35	1.34
Arkansas	53,104	0.61	0.41	0.26	0.12	2.78	2.19	1.08
North Carolina	52,712	0.67	0.38	0.31	0.14	2.90	2.35	1.45
Alabama	51,609	0.66	0.40	0.27	0.14	3.00	2.37	1.34
Guatemala-British Honduras	50,732	1.34	1.08	0.98	0.87	1.54	1.40	1.25
New York State	49,576	0.77	0.42	0.29	0.15	2.84	2.31	1.39
Java	48,830	0.92	0.68	0.64	0.60	1.25	1.25	1.26
Louisiana	48,523	0.75	0.46	0.30	0.13	2.44	2.03	1.12
Southern Central America (Costa Rica, Panama)	48,462	1.93	1.63	1.53	1.42	1.56	1.48	1.40
Tunisia	48,300	0.68	0.42	0.33	0.23	1.64	1.63	1.59
Mississippi	47,716	0.66	0.41	0.27	0.14	3.02	2.31	1.15
Greece	46,948	0.72	0.45	0.35	0.24	1.65	1.63	1.61
Eritrea	45,754	1.15	0.87	0.77	0.67	1.26	1.22	1.16
Pennsylvania	45,333	0.79	0.47	0.32	0.16	2.86	2.25	1.20
Cuba	44,164	—	0.39	0.28	0.17	1.81	1.30	0.64
Liberia	43,000	1.00	0.84	0.80	0.76	1.36	1.35	1.33
Bulgaria	42,796	0.72	0.47	0.35	0.22	1.58	1.50	1.33
Newfoundland Island	42,734	0.50	0.23	0.15	0.073	2.33	2.08	1.48
Guatemala	42,044	1.57	1.28	1.15	1.02	1.56	1.42	1.27
Ohio	41,222	0.82	0.51	0.32	0.14	2.67	2.20	1.19
Virginia	40,815	0.82	0.48	0.33	0.17	2.92	2.26	1.22
Kentucky	40,395	0.74	0.48	0.31	0.15	2.82	2.12	0.93
Pernambuco, Brazil	38,315	0.75	0.67	0.66	0.66	1.74	1.74	1.73
Tenasserim, Burma	37,614	1.57	1.31	1.23	1.15	1.38	1.32	1.24
Nyasaland	37,374	1.63	1.31	1.24	1.16	1.46	1.47	1.50
Oaxaca, Mexico	36,371	1.60	1.37	1.26	1.15	1.67	1.56	1.44
Indiana	36,291	0.88	0.55	0.36	0.15	2.88	2.11	0.84
Hungary	35,918	0.92	0.55	0.39	0.22	1.52	1.51	1.45
Natal-Zululand, South Africa	35,284	1.68	1.24	1.15	1.06	1.30	1.33	1.37
Zaria, Nigeria	35,000	0.95	0.79	0.68	0.56	1.25	1.36	1.52
French Guiana	34,740	1.79	1.52	1.50	1.48	1.35	1.35	1.34

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)
Portugal	34,240	0.93	0.54	0.42	0.30	1.71	1.67	1.61
Maine	33,215	1.04	0.56	0.36	0.17	2.76	2.23	1.20
Rio de Janeiro-Espírito Santo, Brazil	32,915	1.86	1.56	1.55	1.54	1.60	1.60	1.61
Meta, Colombia	32,903	—	1.44	1.40	1.36	1.50	1.44	1.37
Moluccas	32,300	1.02	0.69	0.66	0.62	0.75	0.75	0.74
Ireland	31,840	1.07	0.55	0.37	0.19	2.12	2.23	2.54
Santa Catarina, Brazil	31,118	0.86	0.73	0.73	0.73	1.65	1.65	1.65
South Carolina	31,055	1.09	0.64	0.45	0.26	2.64	2.12	1.30
Tamaulipas, Mexico	30,731	1.44	1.08	0.89	0.71	1.64	1.46	1.22
Hokkaido, Japan	30,300	1.04	0.51	0.34	0.17	1.82	1.67	1.31
Hispaniola	29,979	—	0.37	0.32	0.26	1.15	1.03	0.88
Sabah (North Borneo)	29,388	1.69	1.34	1.26	1.19	1.36	1.33	1.29
Panama	29,224	2.92	2.45	2.29	2.13	1.59	1.52	1.43
Chiapas, Mexico	28,729	2.18	1.87	1.69	1.51	1.51	1.38	1.24
Veracruz, Mexico	27,736	2.26	1.85	1.67	1.49	1.70	1.59	1.46
New Brunswick, Canada	27,473	1.19	0.66	0.41	0.15	2.50	2.18	1.28
Banks Island, Canada	26,400	0.22	0.068	0.043	0.017	1.57	1.14	0.29
Tasmania	26,304	0.80	0.40	0.33	0.26	1.12	1.29	1.59
Ceylon	25,332	1.50	0.98	0.86	0.74	0.98	0.92	0.85
Northern Thailand	25,000	2.12	1.81	1.61	1.40	1.72	1.61	1.48
Ituri, Congo	24,840	2.68	2.36	2.28	2.20	1.76	1.76	1.76
West Virginia	24,181	1.19	0.77	0.52	0.27	3.06	2.50	1.48
Yucatan State, Mexico	23,926	1.30	0.98	0.83	0.67	1.53	1.32	1.06
Sinaloa, Mexico	22,580	1.68	1.22	1.06	0.90	1.74	1.56	1.35
Paraiba, Brazil	21,251	0.97	0.91	0.91	0.90	1.97	1.97	1.96
Nova Scotia, Canada	20,743	1.55	0.83	0.52	0.21	2.44	2.11	1.24
Campeche, Mexico	19,670	1.53	1.33	1.17	1.01	1.46	1.28	1.08
Quintana Roo, Mexico	19,438	1.73	1.39	1.23	1.07	1.44	1.26	1.06
Costa Rica	19,238	4.05	3.44	3.20	2.95	1.53	1.45	1.36
Southampton Island, Canada	19,100	0.31	0.094	0.058	0.021	2.00	1.44	0.33
Isla Grande (Tierra del Fuego)	18,530	0.86	0.41	0.29	0.17	1.34	1.21	0.94
Espírito Santo, Brazil	16,543	2.56	2.32	2.32	2.32	2.01	2.00	1.99

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)
Southern Illinois	16,515	1.79	1.16	0.72	0.29	2.98	2.32	1.00
Rio de Janeiro, Brazil	16,372	3.28	2.74	2.72	2.70	1.56	1.56	1.55
Lima Department, Peru	15,052	2.08	1.17	1.15	1.14	1.71	1.76	1.80
Kerala, India	15,035	2.53	1.88	1.71	1.54	1.04	0.97	0.89
Petén, Guatemala	13,843	2.59	2.26	2.00	1.74	1.68	1.45	1.21
Taiwan	13,808	2.72	1.60	1.25	0.91	2.17	2.21	2.23
Netherlands	13,433	2.61	1.46	0.97	0.48	1.88	1.87	1.83
Timor, East Indies	13,094	—	0.96	0.92	0.88	1.29	1.34	1.40
Hainan Island, China	13,000	—	1.58	1.33	1.08	1.45	1.35	1.20
Mushie Territory, Congo	12,500	2.92	2.42	2.36	2.30	1.34	1.33	1.31
Misiones, Argentina	11,506	4.39	3.57	3.22	3.13	1.36	1.30	1.23
Alagoas, Brazil	11,031	2.20	1.89	1.89	1.89	1.90	1.90	1.90
Burundi	10,747	3.68	2.83	2.71	2.59	1.34	1.38	1.43
Maryland (including District of Columbia)	10,646	3.13	1.86	1.33	0.80	3.08	2.40	1.48
Rwanda	10,166	5.15	4.24	4.10	3.96	1.27	1.28	1.28
Tabasco, Mexico	9,782	—	2.56	2.28	2.00	1.59	1.42	1.23
New Hampshire	9,304	3.10	1.82	1.27	0.70	2.83	2.48	1.80
Cundinamarca, Colombia	9,108	6.88	6.06	5.81	5.57	1.79	1.75	1.72
British Honduras	8,688	5.41	4.24	3.71	3.19	1.54	1.37	1.18
Kutch, India	8,461	3.25	2.09	1.71	1.34	1.24	1.11	0.94
El Salvador	8,268	4.80	3.98	3.48	2.99	1.47	1.30	1.11
Massachusetts	8,257	4.76	2.66	1.70	0.74	2.86	2.36	1.30
New Jersey	7,836	4.61	2.62	1.72	0.82	3.02	2.40	1.27
Tranninh, Laos	7,500	6.35	5.60	5.03	4.45	1.90	1.83	1.75
Halmahera, Moluccas	6,928	—	1.67	1.57	1.47	0.68	0.64	0.59
Ceram, Moluccas	6,621	—	1.60	1.56	1.51	0.91	0.89	0.86
New Caledonia	6,531	1.69	0.87	0.82	0.77	0.87	0.89	0.92
Hawaiian Islands	6,435	2.10	0.59	0.56	0.53	5.33	8.00	16.0
Black Hills, South Dakota-Wyoming	6,000	3.62	2.86	1.81	0.75	2.66	2.24	1.25
Sumbawa, East Indies	5,693	—	1.87	1.81	1.76	1.10	1.15	1.17
Palawan Group, Philippines	5,690	—	2.76	2.49	2.22	0.92	0.87	0.83

TABLE 1.—Continued

	Area (mi^2)	Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
		Total Avifauna	Total (TL)	$NL+\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	$NL+\frac{(TL-NL)}{2}$	Native (NL)
Flores, East Indies	5,509	—	2.48	2.35	2.22	1.11	1.14	1.18
Connecticut	5,009	6.24	3.72	2.48	1.24	2.87	2.30	1.30
Falkland Islands	4,618	2.71	0.82	0.62	0.41	1.24	1.11	0.90
West Sumatra Islands	4,600	4.41	3.74	3.51	3.28	1.05	1.02	0.99
Jamaica	4,450	—	2.65	2.10	1.55	1.68	1.36	0.94
Bahama Islands	4,400	6.44	3.66	2.34	1.02	3.35	2.55	1.13
Sumba, East Indies	4,305	—	2.16	2.08	2.00	0.98	0.95	0.91
San Diego County, California	4,258	9.61	5.70	4.19	2.68	2.80	2.40	1.78
Puntarenas Province, Costa Rica	4,210	—	11.9	11.1	10.2	1.59	1.53	1.46
Guanacaste Province, Costa Rica	4,020	—	10.1	9.29	8.46	1.45	1.37	1.27
Alajuela Province, Costa Rica	3,670	—	13.3	12.4	11.5	1.64	1.55	1.46
Cyprus	3,572	9.41	5.85	3.61	1.37	1.82	1.80	1.72
Puerto Rico	3,423	5.61	2.69	2.20	1.72	1.57	1.24	0.86
Buru, Moluccas	3,400	—	3.18	2.99	2.80	0.74	0.72	0.70
Aru Islands, New Guinea	3,305	—	4.35	4.25	4.15	1.08	1.11	1.13
Galapagos Archipelago	3,029	—	1.02	0.89	0.77	2.88	3.16	3.60
Death Valley, California	2,892	7.81	5.32	2.82	0.31	3.28	2.97	0.80
Canary Islands	2,807	7.19	4.02	2.88	1.75	1.51	1.32	0.96
Leyte, Philippines	2,785	6.45	5.31	5.08	4.84	1.00	0.93	0.85
Sikkim	2,745	15.2	14.7	14.1	13.5	2.82	2.84	2.86
Gambia Valley	2,500	12.0	9.44	8.60	7.75	1.09	1.08	1.06
Andaman Islands, Bay of Bengal	2,500	6.88	4.56	3.71	2.86	0.97	0.84	0.66
Lesser Antilles	2,420	—	4.84	4.05	3.26	1.60	1.40	1.14
Prince Edward Island, Canada	2,184	9.56	5.62	3.38	1.14	2.51	2.29	1.50
Bali, East Indies	2,146	8.80	7.36	7.17	6.98	1.16	1.16	1.15
Delaware	2,057	16.2	9.39	6.01	2.62	3.20	2.45	1.10
San José Province, Costa Rica	2,010	—	26.4	24.4	22.5	1.52	1.46	1.39
Sula Islands, Molucca Sea	1,872	—	3.68	3.42	3.15	0.77	0.74	0.70
Trinidad, West Indies	1,864	20.7	14.7	13.8	12.9	1.20	1.14	1.09
Lombok, East Indies	1,825	7.56	6.08	5.86	5.65	0.98	0.98	0.98
Cape Verde Islands	1,557	6.36	2.50	2.06	1.61	0.86	0.88	0.92

TABLE 1.—Continued

		Species/100 mi^2				Passerines:Nonpasserines		
			Land Avifauna			Land Avifauna		
	Area (mi^2)	Total Avifauna	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)	Total (TL)	NL+$\frac{(TL-NL)}{2}$	Native (NL)
Socotra, Indian Ocean	1,400	6.36	2.93	2.50	2.07	1.16	1.11	1.07
Southwestern Ohio	1,400	20.9	13.5	8.33	3.18	2.94	2.31	0.98
Atlántico, Colombia	1,340	21.4	15.8	15.2	14.5	1.14	1.09	1.04
Micronesia	1,335	14.9	4.27	3.63	3.07	1.60	1.38	1.49
Heredia Province, Costa Rica	1,120	—	42.2	39.1	36.0	1.64	1.56	1.48
Big Bend National Park, Texas	1,107	31.7	24.8	15.3	6.15	2.48	2.30	1.72
Joshua Tree Monument, California	1,025	16.2	14.7	9.5	4.20	2.98	2.50	1.46
Cartago Province, Costa Rica	1,020	—	48.3	44.8	41.3	1.75	1.67	1.59
Reunion, Indian Ocean	970	4.85	1.96	1.76	1.55	0.61	0.74	0.93
Biak Island, New Guinea	948	—	6.96	6.85	6.75	0.61	0.63	0.65
Japen Island, New Guinea	936	—	12.8	12.7	12.6	0.97	0.95	0.93
Azores	888	19.5	5.29	3.43	1.58	0.96	1.10	1.80
Natuna Islands, South China Sea	815	15.1	12.8	12.6	12.4	1.12	1.09	1.06
Comoro Islands, Indian Ocean	740	10.4	6.75	6.55	6.35	1.00	1.06	1.14
Mauritius, Indian Ocean	720	8.05	2.64	2.29	1.94	0.58	0.74	1.00
Nicobar Islands, Bay of Bengal	635	19.5	12.6	9.85	7.08	0.82	0.76	0.67
Santa Elena Peninsula, Ecuador	475	29.3	16.2	14.5	12.8	1.19	1.12	1.05
Isla Margarita, Venezuela	444	—	18.7	18.0	17.4	0.89	0.91	0.93
Bwamba County, W. Uganda	400	106.	95.0	92.1	89.3	1.66	1.65	1.64
Hong Kong Colony	391	89.0	56.2	35.7	15.1	2.01	1.89	1.51
Panama Canal Zone (land area)	372	114.	94.6	86.7	78.8	1.71	1.59	1.46
Rancho Grande, Venezuela	325	156.	134.	129.	123.	1.62	1.56	1.49
Dominica, Lesser Antilles	305	34.1	20.0	16.7	13.4	1.54	1.37	1.16
Madeira Islands	302	67.5	31.8	19.7	7.61	1.91	1.77	1.30
Ibadan, Nigeria	300	94.3	81.6	74.4	67.3	1.40	1.45	1.51
Darjeeling area, India	275	163.	152.	130.	108.	2.16	2.20	2.28
Curaçao, Netherlands Antilles	173	68.8	34.1	25.4	16.8	1.36	1.20	0.93
Seychelles, Indian Ocean	156	35.3	13.5	11.5	9.61	0.91	1.00	1.14
Impenetrable Forest area, Uganda	150	189.	183.	181.	179.	2.20	2.20	2.20
Cozumel Island, Mexico	125	—	80.6	61.9	43.2	2.11	1.72	1.00

TABLE 2.—*Numbers and percentages of land bird migrants in Middle America (and adjacent southwestern United States) and in South America*

	Total Land Spp.			Migrant Land Spp.			% Migrants/Total Land Spp.		
	Non-passerines	Passerines	Total	Non-passerines	Passerines	Total	Non-passerines	Passerines	Total
California	83	216	299	23	120	143	27.7	55.6	47.8
Texas	95	236	331	34	136	170	35.8	57.6	51.3
New Mexico	86	212	298	32	119	151	37.2	56.1	50.6
Arizona	93	219	312	41	115	156	44.1	52.5	50.0
Mexico	286	490	776	22	103	125	7.7	21.0	16.1
Baja California	60	140	200	18	55	73	30.0	39.3	36.5
Tamaulipas	125	205	330	27	85	112	21.6	41.5	34.0
Sonora	101	199	300	20	70	90	19.8	35.2	30.0
Sinaloa	101	175	276	15	58	73	14.9	33.2	26.4
Oaxaca	187	312	499	18	68	86	9.6	21.8	17.2
Veracruz	190	324	514	22	79	101	11.6	24.4	19.7
Chiapas	213	321	534	21	82	103	9.9	25.6	19.3
Tabasco	97	154	251	9	46	55	9.3	29.9	21.9
Yucatan Peninsula	132	188	320	20	73	93	15.1	38.8	29.1
Yucatan State	93	142	235	15	59	74	16.1	41.5	31.5
Campeche	106	155	261	11	52	63	10.4	33.6	24.2
Quintana Roo	111	160	271	10	53	63	9.1	33.1	23.3
Cozumel Island	34	76	110	8	49	57	23.6	64.5	51.8
Central America	353	566	919	19	93	112	5.4	16.4	12.2
British Honduras	145	223	368	18	73	91	12.4	32.8	24.8
Guatemala	214	333	547	23	91	114	10.7	27.3	20.8
Petén	117	196	313	8	64	72	6.8	32.6	23.0
Tikal	89	159	248	10	61	71	11.2	38.4	28.6
Honduras (1968)	222	319	541	25	84	109	11.3	26.4	20.2
" (1955)	192	287	479	15	73	88	7.8	25.4	18.4
" (1932)	138	209	347	8	44	52	5.8	21.0	15.0
El Salvador	133	196	329	16	66	82	12.0	33.7	24.9
Nicaragua	207	305	512	15	69	84	7.3	22.6	16.4
Costa Rica (1970)	262	400	662	22	72	94	8.4	18.0	14.2
" (1964)	259	393	652	21	69	90	8.1	17.6	13.8
" (1910)	235	372	607	16	56	72	6.8	15.1	11.9
Finca La Selva (1970)	125	199	324	14	51	65	11.2	25.6	20.1
" (1960)	116	195	311	9	52	61	7.8	26.7	19.6
" (1957)	83	153	236	3	32	35	3.6	20.9	14.8

TABLE 2.—Continued

	Total Land Spp.			Migrant Land Spp.			% Migrants/Total Land Spp.		
	Non-passerines	Passerines	Total	Non-passerines	Passerines	Total	Non-passerines	Passerines	Total
Panama (1970)	276	440	716	20	74	94	7.3	16.8	13.1
" (1935)	261	423	684	17	60	76	6.5	14.2	11.1
Canal Zone (1970)	130	222	352	11	48	59	8.5	21.6	16.8
" (1928)	126	209	335	8	42	50	6.4	20.1	14.9
Barro Colorado I. (1970)	122	185	307	10	52	62	8.2	28.1	20.2
" (1952)	110	163	273	5	39	44	4.5	24.0	16.1
" (1938)	90	138	228	5	28	33	5.6	20.3	14.5
" (1929)	73	119	192	4	21	25	5.5	17.7	13.0
Colombia	546	879	1425	14	60	74	2.6	6.8	5.2
Santa Marta area	170	286	456	5	42	47	2.9	14.7	10.3
Atlántico	99	113	212	4	14	18	4.0	12.4	8.5
Cundinamarca	198	354	552	11	33	44	5.6	9.3	8.0
Venezuela	430	721	1151	12	49	61	2.8	6.8	5.3
Rancho Grande	167	271	438	5	29	34	3.0	10.7	7.8
Perijá	160	245	405	3	28	31	1.9	11.4	7.7
Trinidad	125	149	274	10	24	34	8.0	16.1	12.4
The Guianas	269	399	668	10	23	33	3.7	5.8	4.9
Guyana	257	365	622	7	22	29	2.7	6.0	4.7
Surinam	233	316	549	9	16	25	3.9	5.1	4.6
French Guiana	224	302	526	4	7	11	1.8	2.3	2.1
Ecuador	458	742	1200	10	29	39	2.2	3.9	3.25
Peru	465	869	1334	11	32	43	2.4	3.7	3.2
Bolivia	375	667	1042	7	31	38	1.9	4.7	3.6
Brazil	487	876	1363	11	29	40	2.3	3.3	2.9
Southern South America	283	487	770	6	8	14	2.1	1.6	1.8
Paraguay	213	322	535	11	19	30	5.2	5.9	5.6
Uruguay	88	139	227	11	20	31	12.5	14.4	13.7
Argentina	265	452	717	8	12	20	3.0	2.7	2.8
Misiones	175	238	413	13	38	51	7.4	16.0	12.4
Chile	74	127	201	5	20	25	6.8	15.7	12.4
Isla Grande (Tierra del Fuego)	32	43	75	16	28	44	50.0	65.1	58.6
Falkland Islands	17	21	38	7	12	19	41.2	57.2	50.0

TABLE 3.—*Passerine-nonpasserine and suboscine-oscine ratios in Costa Rica* (P = passerines; N = nonpasserines; S = suboscines; O = oscines; (a):(b) = passerine-nonpasserine ratio/suboscine-oscine ratio; life zones (formations): TD = Tropical Dry, TM = Tropical Moist, TW = Tropical Wet, SW = Subtropical Wet, LMW = Lower Montane Wet, LMR = Lower Montane Rain, MR = Montane Rain)

	Land Avifauna				Passerines				
	Total		Native		Total		Native		(a):(b)
	P:NP	(No. of Species)	P:NP	(No. of Species)	S:O	(No. of Species)	S:O	(No. of Species)	
Lower Tempisque valley (TD Pacific)	1.19	(204)	0.88	(156)	0.76	(111)	1.09	(73)	0.81
Barranca area (TD Pacific)	1.30	(186)	0.96	(143)	0.72	(105)	1.00	(70)	0.96
El Pelón de la Altura (TD Pacific)	1.12	(108)	1.00	(100)	1.11	(57)	1.00	(50)	1.00
Miravalles (TD-SW Pacific)	1.55	(263)	1.26	(212)	0.70	(160)	0.90	(118)	1.40
Los Chiles-Río Frío (TM Carib.)	1.70	(200)	1.46	(162)	0.68	(126)	0.92	(96)	1.59
La Lola (TM Carib.)	1.93	(214)	1.48	(171)	0.72	(141)	0.96	(102)	1.54
Rincón de Osa (TW Pacific)	1.48	(238)	1.19	(203)	1.00	(142)	1.29	(110)	0.92
Finca La Selva (TW Carib.)	1.59	(324)	1.33	(259)	0.81	(199)	1.18	(148)	1.13
Pozo Azul-Pozo Pital (TM Pacific)	1.67	(184)	1.55	(176)	1.30	(115)	1.38	(107)	1.12
Buenos Aires area (TM Pacific)	1.69	(258)	1.45	(213)	0.86	(162)	1.17	(126)	1.24
Boruca-Paso Real area (TM Pacific)	1.81	(233)	1.56	(197)	0.81	(150)	1.03	(120)	1.51
Sixaola area (TM-TW Carib.)	1.88	(276)	1.56	(220)	0.75	(180)	1.03	(134)	1.51
Old Line area (TW Carib.)	1.83	(280)	1.60	(244)	0.91	(181)	1.14	(150)	1.40
El General valley (TM-SW Pacific)	1.81	(286)	1.45	(230)	0.79	(184)	1.19	(136)	1.22
Turrialba-Angostura area (TM-SW Carib.)	1.78	(308)	1.48	(245)	0.67	(197)	0.92	(146)	1.61
Juan Viñas-Tucurriqui (SW Carib.)	2.18	(191)	1.90	(168)	0.93	(131)	1.12	(110)	1.71
Las Mellizas-Cotón (SW Pacific)	2.26	(188)	1.93	(161)	0.88	(130)	1.08	(106)	1.79
San Vito (SW Pacific)	2.19	(236)	1.94	(212)	0.71	(162)	0.77	(140)	2.52
Bonilla (SW Carib.)	2.36	(265)	1.90	(220)	0.81	(186)	0.85	(144)	2.24
Guayabo (SW Carib.)	2.34	(214)	2.07	(187)	0.79	(150)	0.94	(126)	2.21
Matrículas de Pavones-Silencio de Sitio Mata (SW Carib.)	2.32	(206)	1.98	(176)	0.64	(144)	0.80	(117)	2.47
Cariblanco (SW Carib.)	2.28	(213)	2.14	(195)	0.81	(148)	0.85	(133)	2.53
Carrillo (SW Carib.)	2.41	(225)	2.17	(206)	0.85	(159)	0.93	(141)	2.34
Monteverde (SW Pacific)	2.16	(161)	1.90	(145)	0.62	(110)	0.73	(95)	2.60
Silencio de Tilarán (SW Pacific-Carib.)	2.42	(130)	2.33	(120)	0.77	(92)	0.83	(84)	2.82
La Hondura (SW-LMR Central Mountains)	2.11	(146)	1.96	(130)	0.62	(99)	0.72	(86)	2.72
Bajos del Toro (SW-LMR Central Mountains)	2.20	(99)	2.10	(90)	0.45	(68)	0.49	(61)	4.30

TABLE 3.—Continued

	Land Avifauna				Passerines				(a):(b)
	Total		Native		Total		Native		
	P:NP	(No. of Species)	P:NP	(No. of Species)	S:O	(No. of Species)	S:O	(No. of Species)	
San José de la Montaña (LMR Central Mountains)	2.22	(71)	2.04	(64)	0.36	(49)	0.39	(43)	5.27
La Chonta (LMR Central Mountains)	3.14	(58)	2.72	(52)	0.42	(44)	0.41	(38)	6.68
Río La Hoja (LMW Central Mountains)	2.81	(61)	2.07	(43)	0.22	(45)	0.26	(29)	7.95
Poás Volcano (LMW-MR Central Mountains)	1.60	(65)	1.40	(60)	0.33	(40)	0.35	(35)	4.05
Villa Mills-Cerro de la Muerte (MR Central Mountains)	1.74	(85)	1.59	(75)	0.29	(54)	0.28	(46)	5.70

TABLE 4.—*Passerine-nonpasserine and suboscine-oscine ratios in Central America and in Costa Rica: checklists versus earlier lists or samples* (P = passerines; N = nonpasserines; S = suboscines; O = oscines; (a):(b) = passerine-nonpasserine ratio/suboscine-oscine ratio; life zones (formation): TD = Tropical Dry, TM = Tropical Moist, TW = Tropical Wet, SW = Subtropical Wet, LMR = Lower Montane Rain, MR = Montane Rain)

	Land Avifauna				Passerines				(a):(b)
	Total		Native		Total		Native		
	P:NP	(No. of Species)	P:NP	(No. of Species)	S:O	(No. of Species)	S:O	(No. of Species)	
Guatemala									
1970 (Land)	1.56	(547)	1.27	(433)	0.43	(333)	0.51	(242)	2.45
1932a (Griscom)	1.62	(528)	1.31	(409)	0.44	(326)	0.53	(232)	2.34
1879-1904 (Salvin and Godman)	1.50	(502)	1.23	(403)	0.41	(301)	0.47	(221)	2.60
Dearborn (1907)	1.76	(281)	1.40	(226)	0.42	(179)	0.47	(132)	2.98
Honduras (mainland)									
1968 (Monroe)	1.44	(541)	1.19	(432)	0.55	(319)	0.69	(235)	1.72
1955 (Eisenmann)	1.50	(479)	1.21	(391)	0.55	(287)	0.69	(214)	1.77
1932 (Stone)	1.52	(347)	1.23	(299)	0.56	(209)	0.68	(165)	1.80
Panama									
1972 (compiled)	1.59	(716)	1.42	(622)	0.78	(440)	0.96	(366)	1.48
1935 (Griscom)	1.62	(684)	1.47	(608)	0.83	(423)	0.99	(363)	1.48
1879-1904 (Salvin and Godman)	1.49	(564)	1.39	(513)	0.80	(337)	0.86	(298)	1.61

TABLE 4.—Continued

	Land Avifauna				Passerines				
	Total		Native		Total		Native		(a):(b)
	P:NP	(No. of Species)	P:NP	(No. of Species)	S:O	(No. of Species)	S:C	(No. of Species)	
Panama Canal Zone									
1968 (Eisenmann and Loftin): including doubtful and unusual records.	1.59	(427)	1.34	(348)	0.86	(262)	1.19	(199)	1.12
1968 (Eisenmann and Loftin): definitely known and modern presence.	1.71	(352)	1.46	(293)	0.87	(222)	1.20	(174)	1.22
1928 (Sturgis)	1.66	(335)	1.42	(285)	0.94	(209)	1.23	(167)	1.15
Barro Colorado Island									
Total	1.52	(307)	1.19	(245)	0.83	(185)	1.22	(133)	0.97
1952 (Eisenmann)	1.48	(273)	1.18	(229)	0.92	(163)	1.30	(124)	0.91
1938 (Chapman)	1.53	(228)	1.29	(195)	0.94	(138)	1.39	(110)	0.93
1929 (Chapman)	1.63	(192)	1.42	(167)	1.05	(119)	1.45	(98)	0.98
P. Slud, March 16-April 7, 1966	1.81	(180)	1.51	(143)	0.90	(116)	1.46	(86)	1.03
Costa Rica (mainland)									
Total	1.53	(662)	1.37	(568)	0.71	(400)	0.88	(328)	1.55
1964 (Slud)	1.52	(652)	1.36	(562)	0.76	(393)	0.88	(324)	1.54
1910 (Carriker)	1.58	(607)	1.44	(535)	0.74	(372)	0.88	(316)	1.63
1879-1904 (Salvin and Godman)	1.54	(539)	1.40	(474)	0.74	(327)	0.86	(277)	1.61
1887 (Zeledón)	1.51	(568)	1.35	(494)	0.72	(343)	0.86	(285)	1.57
1869 (Frantzius)	1.56	(440)	1.39	(384)	0.68	(268)	0.81	(224)	1.74
Sassi (1938-1939)	1.48	(226)	1.40	(214)	0.65	(135)	0.64	(125)	2.20
Ferry (1910)	2.80	(171)	2.52	(148)	0.60	(126)	0.74	(106)	3.42
Monroe, Burt L., Jr. (pers. comm.)	1.93	(296)	1.69	(256)	0.52	(195)	0.58	(161)	2.92
Taboga, Brosimum woodland area (TD Pacific)									
Total	1.51	(153)	1.07	(122)	0.92	(92)	1.25	(63)	0.86
P. Slud, Jan. 24-28, 30, 1965	1.39	(136)	1.06	(109)	0.88	(79)	1.44	(56)	0.74
El Pelón de la Altura (TD Pacific)									
Total	1.12	(108)	1.00	(100)	1.11	(57)	1.00	(50)	1.00
P. Slud, May 26-30, 1961	1.21	(93)	1.05	(86)	1.32	(51)	1.20	(44)	0.87
Scheelia woodland site, northwest from Barranca (TD Pacific)									
Total	1.39	(141)	0.93	(108)	0.86	(82)	1.36	(52)	0.68

TABLE 4.—Continued

	Land Avifauna				Passerines				
	Total		Native		Total		Native		(a):(b)
	P:NP	(No. of Species)	P:NP	(No. of Species)	S:O	(No. of Species)	S:O	(No. of Species)	
P. Slud, Aug. 30-Sept. 2, 1964; Jan. 18-20, Apr. 20-22, 1965	1.49	(137)	0.96	(102)	0.86	(82)	1.50	(50)	0.64
Miravalles (TD-SW Pacific)									
Total	1.55	(263)	1.26	(212)	0.70	(160)	0.90	(118)	1.40
P. Slud, Apr. 20-May 5, 1955	1.70	(193)	1.34	(159)	0.70	(122)	0.78	(91)	1.72
Underwood (1896)	1.72	(152)	1.42	(126)	0.66	(96)	0.90	(74)	1.58
Hacienda Santa María (TD-SW, Pacific)									
Total	1.58	(152)	1.36	(132)	0.86	(93)	1.11	(76)	1.22
Wetmore (1944) plus P. Slud, Nov. 20-24, 1954	1.76	(124)	1.60	(109)	0.88	(79)	1.09	(67)	1.47
Rincón de Osa (TW Pacific)									
Total	1.48	(238)	1.19	(203)	1.00	(142)	1.29	(110)	0.92
P. Slud, Mar. 12-27, 1962; Oct. 26-31, 1964	1.45	(202)	1.23	(174)	1.05	(120)	1.23	(96)	1.00
Finca La Selva (TW Carib.)									
Total to 1970	1.59	(324)	1.33	(259)	0.81	(199)	1.18	(148)	1.13
Total to 1960 (Slud)	1.63	(311)	1.34	(250)	0.83	(193)	1.24	(143)	1.07
Total to 1957, P. Slud	1.80	(238)	1.52	(204)	0.82	(153)	1.12	(123)	1.36
4 40-day totals, 1957-58									
Sept.-Oct. 1957	1.90	(249)	1.55	(199)	0.81	(163)	1.16	(121)	1.32
Jan.-Feb. 1958	1.87	(235)	1.61	(209)	1.01	(153)	1.30	(129)	1.24
Mar.-May 1958	1.86	(249)	1.56	(210)	0.95	(162)	1.27	(128)	1.23
July-Sept. 1958	1.68	(217)	1.57	(203)	1.23	(136)	1.30	(124)	1.21
Average	----	----	1.57	(205)	----	----	1.26	(126)	1.25
9 2-week totals, 1957-58									
Sept. 20-Oct. 4, 1957	2.17	(206)	1.85	(171)	0.91	(141)	1.18	(111)	1.58
Jan. 13-27, 1958	1.92	(219)	1.65	(196)	1.03	(144)	1.30	(122)	1.27
Feb. 11-25, 1958	2.05	(198)	1.86	(180)	0.99	(133)	1.21	(117)	1.54
Mar. 17-29, Apr. 3-4, 1958	1.90	(209)	1.64	(182)	0.93	(137)	1.22	(113)	1.35
Apr. 6-20, 1958	1.76	(221)	1.57	(193)	1.02	(141)	1.27	(118)	1.24
Apr. 24-May 9, 1958	1.71	(217)	1.63	(192)	1.11	(137)	1.25	(119)	1.31

TABLE 4.—Continued

	Land Avifauna				Passerines				
	Total		Native		Total		Native		(a):(b)
	P:NP	(No. of Species)	P:NP	(No. of Species)	S:O	(No. of Species)	S:O	(No. of Species)	
May 31-June 14, 1958	1.55	(186)	1.53	(185)	1.31	(113)	1.29	(112)	1.20
July 13-26, 1958	1.61	(188)	1.61	(188)	1.32	(116)	1.32	(116)	1.22
Aug. 3-9, 13-17, 23-25, 1958	1.78	(186)	1.70	(181)	1.25	(119)	1.28	(114)	1.33
Average	----	----	1.67	(185)	----	----	1.26	(116)	1.34
Buenos Aires area (TM Pacific)									
Total	1.69	(258)	1.45	(213)	0.86	(162)	1.17	(126)	1.24
P. Slud, Jan. 7-25, 1955	1.90	(217)	1.72	(183)	0.88	(143)	1.17	(117)	1.47
Boruca (TM Pacific)									
Total	1.96	(219)	1.66	(186)	0.79	(145)	1.00	(116)	1.68
P. Slud, Feb. 2-6, 1955	2.04	(164)	1.76	(138)	0.75	(110)	1.00	(88)	1.76
Los Chiles-Río Frío area (TM Carib.)									
Total	1.70	(200)	1.46	(162)	0.68	(126)	0.92	(96)	1.59
P. Slud, April 2-8, 1962	1.84	(156)	1.65	(130)	0.63	(101)	0.84	(81)	1.96
La Lola area (TM Carib.)	1.89	(234)	1.48	(191)	0.74	(153)	0.97	(114)	1.53
La Lola, Total	1.93	(214)	1.48	(171)	0.72	(141)	0.96	(102)	1.54
" P. Slud, Sept. 14-24, 1953	2.26	(176)	1.79	(148)	0.72	(122)	0.86	(95)	2.08
Sixaola area (TM Carib.)									
Total	1.88	(276)	1.56	(220)	0.75	(180)	1.03	(134)	1.51
P. Slud, October 1954	2.22	(248)	1.91	(195)	0.71	(171)	0.94	(128)	2.03
El General valley (TM-SW Pacific)									
Total	1.81	(286)	1.45	(230)	0.79	(184)	1.19	(136)	1.22
P. Slud, June 23-July 9, 1954	1.73	(164)	1.70	(162)	1.21	(104)	1.22	(102)	1.39
Monteverde (SW Pacific)									
Total	2.16	(161)	1.90	(145)	0.62	(110)	0.73	(95)	2.60
P. Slud, June 17-July 1, 1961	2.02	(139)	1.96	(136)	0.69	(93)	0.67	(90)	2.93
Cariblanco (SW Carib.)									
Total	2.28	(213)	2.14	(195)	0.81	(148)	0.85	(133)	2.53
P. Slud, March 23-30, 1955	2.72	(160)	2.49	(143)	0.67	(117)	0.70	(102)	3.56
La Hondura (SW-LMR Central Mountains)									

TABLE 4.—Continued

	Land Avifauna				Passerines				(a):(b)
	Total		Native		Total		Native		
	P:NP	(No. of Species)	P:NP	(No. of Species)	S:O	(No. of Species)	S:O	(No. of Species)	
Total	2.11	(146)	1.96	(130)	0.62	(99)	0.72	(86)	2.72
P. Slud, July 9-17, 1955	2.48	(94)	2.44	(93)	0.81	(67)	0.78	(66)	3.11
La Chonta (LMR Central Mountains)									
Total	3.14	(58)	2.72	(52)	0.42	(44)	0.41	(38)	6.68
P. Slud, Sept. 9-12, 1964	4.00	(45)	3.33	(39)	0.39	(36)	0.37	(30)	9.15
Villa Mills-Cerro de la Muerte (MR Central Mountains)									
Total	1.74	(85)	1.59	(75)	0.29	(54)	0.28	(46)	5.70
P. Slud, Apr. 26-30, 1951; Oct. 13-14, 1964	2.36	(47)	1.93	(41)	0.38	(33)	0.29	(27)	6.75
L. L. Wolf, part of Jan. 1967	1.87	(43)	1.79	(39)	0.27	(28)	0.32	(25)	5.67
" " Feb. "	1.83	(34)	1.75	(33)	0.10	(22)	0.11	(21)	16.8
" " Mar. "	1.05	(45)	1.17	(39)	0.21	(23)	0.23	(21)	4.98
" " Apr. "	2.12	(50)	1.93	(44)	0.31	(34)	0.32	(29)	6.06
" " May "	2.12	(53)	1.88	(49)	0.29	(36)	0.23	(32)	8.14
" " June "	2.00	(45)	2.00	(45)	0.30	(30)	0.30	(30)	6.58
" Average Jan.-June 1967	1.78	(45)	1.73	(41.5)	0.25	(28.8)	0.25	(26.3)	6.81
" Total " "	1.61	(73)	1.54	(61)	0.29	(45)	0.28	(37)	5.58

TABLE 5.—*Passerine-nonpasserine and suboscine-oscine ratios of Costa Rican localities: forest versus non-forest* ((a):(b) = passerine-nonpasserine ratio/ suboscine-oscine ratio; life zones (formations): TD = Tropical Dry, TM = Tropical Moist, TW = Tropical Wet, SW = Subtropical Wet, SR = Subtropical Rain, LMR = Lower Montane Rain, MR = Montane Rain)

	(a) Native Land Avifauna		(b) Native Passerines		
	Passerines: Nonpasserines	(No. of Species)	Suboscines: Oscines	(No. of Species)	(a):(b)
Bagaces site (TD Pacific): Slud (1965)	0.93	(58)	1.16	(28)	0.81
Forest	1.57	(18)	0.83	(11)	1.88
Non-forest	0.74	(40)	1.43	(17)	0.52
Taboga, Brosimum site (TD Pacific): Slud (1965)	1.06	(105)	1.46	(54)	0.73
Forest	1.21	(42)	1.88	(23)	0.64
Non-forest	0.97	(63)	1.21	(31)	0.80
G. H. Orians and D. R. Paulson (pers. comm.)	1.09	(94)	1.58	(49)	0.68
Forest (Orians, 1969)	1.17	(66)	2.27	(36)	0.52
Barranca, Scheelia site (TD [= TM (Tosi, 1969)] Pacific): Slud (1965)	0.96	(102)	1.50	(50)	0.64
Forest	1.17	(39)	2.50	(21)	0.47
Non-forest	0.85	(63)	1.07	(29)	0.80
Aug. 30-Sept. 2, 1964	1.06	(72)	1.29	(37)	0.82
Forest	1.29	(32)	2.60	(18)	0.50
Non-forest	0.91	(40)	0.73	(19)	1.24
Jan. 18-20, 1965	1.07	(85)	1.44	(44)	0.74
Forest	1.43	(34)	2.33	(20)	0.61
Non-forest	0.89	(51)	0.85	(24)	1.05
Apr. 20-22, 1965	1.26	(86)	1.29	(48)	0.98
Forest	1.43	(34)	1.50	(20)	0.95
Non-forest	1.17	(52)	1.15	(28)	1.02
Orians (1969): Forest	1.26	(61)	1.43	(34)	0.88
Rincón de la Vieja-Guachipilín (TD-SW Pacific): P. Slud, May 13-20, 1955	1.13	(113)	0.88	(60)	1.29
Forest	1.32	(58)	1.06	(33)	1.25
Non-forest	0.96	(55)	0.69	(27)	1.40
Miravalles (TD-SW Pacific): P. Slud, Apr. 20-May 5, 1955	1.34	(159)	0.78	(91)	1.72
Forest	1.58	(67)	1.16	(41)	1.36
Non-forest	1.19	(92)	0.56	(50)	2.12

TABLE 5.—Continued

	(a) Native Land Avifauna		(b) Native Passerines		
	Passerines: Nonpasserines	(No. of Species)	Suboscines: Oscines	(No. of Species)	(a):(b)
Hacienda Sta. María (TD-SW Pacific): P. Slud, Nov. 20-24, 1954	1.79	(92)	1.03	(59)	1.74
Forest	2.75	(60)	1.20	(44)	2.29
Non-forest	0.88	(32)	0.67	(15)	1.32
La Lola (TM Carib.): P. Slud, Sept. 14-24, 1953	1.81	(149)	0.86	(96)	2.08
Forest	1.32	(79)	0.96	(45)	1.38
Non-forest	2.68	(70)	0.76	(51)	3.54
Los Chiles-Río Frío area (TM Carib.): P. Slud, Apr. 2-8, 1962	1.69	(129)	0.84	(81)	2.01
Forest	1.47	(42)	0.92	(25)	1.60
Non-forest	1.80	(87)	0.81	(56)	2.23
Sixaola area (TM Carib.): P. Slud, October 1954	1.90	(194)	0.94	(127)	2.03
Forest	1.82	(110)	1.22	(71)	1.49
Non-forest	2.00	(84)	0.75	(56)	2.67
Chase: Oct. 7-9	2.06	(104)	1.19	(70)	1.73
Forest	1.28	(41)	2.28	(23)	0.56
Non-forest	2.94	(63)	0.88	(47)	3.34
Río Suab (TM-SW): Oct. 10-16	1.47	(101)	1.31	(60)	1.12
Forest	1.87	(86)	1.24	(56)	1.51
Non-forest	3.63	(15)	3.00	(4)	1.21
Volio: Oct. 18-24	1.72	(125)	1.19	(79)	1.44
Forest	1.36	(59)	1.62	(34)	0.84
Non-forest	2.14	(66)	0.96	(45)	2.24
Cahuita: Oct. 25-31	1.98	(137)	0.90	(91)	2.20
Forest	1.68	(75)	1.14	(47)	1.48
Non-forest	2.44	(62)	0.69	(44)	3.52
Hacienda Altamira, San Carlos (TM Carib.): Slud (1965)	1.86	(163)	1.08	(106)	1.72
Forest	1.66	(93)	1.64	(58)	1.01
Non-forest	2.18	(70)	0.66	(48)	3.33
Siquirres site (TM [= TW (Tosi, 1969)] Carib.): Slud (1965)	2.16	(164)	1.13	(112)	1.86
Forest	1.83	(116)	1.27	(75)	1.44
Non-forest	3.36	(48)	0.85	(37)	3.95

TABLE 5.—Continued

	(a) Native Land Avifauna		(b) Native Passerines		
	Passerines: Nonpasserines	(No. of Species)	Suboscines: Oscines	(No. of Species)	(a):(b)
Finca La Selva (TW [= SW (Tosi, 1969)] Carib.)					
Average of 9 2-week surveys 1957-58, P. Slud	1.67	(185)	1.26	(116)	1.34
Forest	1.63	(118)	1.50	(73)	1.09
Non-forest	1.79	(67)	0.91	(43)	1.97
Slud (1965)	1.75	(150)	1.29	(95)	1.36
Forest	1.72	(95)	1.61	(60)	1.07
Non-forest	1.75	(55)	0.95	(35)	1.85
Orians (1969): Forest	1.79	(64)	2.16	(41)	0.83
Rincón de Osa (TW Pacific)					
P. Slud, Mar. 12-27, 1962	1.25	(169)	1.19	(94)	1.05
Forest	1.34	(96)	1.62	(55)	0.83
Non-forest	1.15	(73)	0.77	(39)	1.49
Slud (1965)	1.32	(139)	1.39	(79)	0.95
Forest	1.43	(85)	1.94	(50)	0.74
Non-forest	1.16	(54)	0.81	(29)	1.43
Gromaco, Río Coto Brus (TM Pacific): P. Slud, Feb. 15-23, 1962	1.40	(156)	1.12	(91)	1.26
Forest	1.54	(84)	1.55	(51)	0.99
Non-forest	1.25	(72)	0.74	(40)	1.69
La Granja, Tilarán (SW [= TM (Tosi, 1969)] Pacific-Carib.): P. Slud, Jan. 21-29, 1954	2.35	(114)	1.00	(80)	2.35
Forest	1.91	(64)	1.33	(42)	1.44
Non-forest	3.17	(50)	0.73	(38)	4.35
Volcán site (TM [= SW (Tosi, 1969)] Pacific): Slud (1965)	1.81	(157)	1.27	(101)	1.43
Forest	1.84	(88)	1.72	(57)	1.07
Non-forest	1.76	(69)	0.83	(44)	2.11
Oct. 7-12, 1964	2.47	(125)	1.17	(89)	2.11
Forest	2.65	(73)	1.65	(53)	1.61
Non-forest	2.25	(52)	0.72	(36)	3.14
Mar. 9-13, 1965	1.79	(148)	1.32	(95)	1.35
Forest	1.79	(81)	1.74	(52)	1.03
Non-forest	1.79	(67)	0.96	(43)	1.87

TABLE 5.—Continued

	(a) Native Land Avifauna		(b) Native Passerines		
	Passerines: Nonpasserines	(No. of Species)	Suboscines: Oscines	(No. of Species)	(a):(b)
Matrículas de Pavones (SW Carib.): P. Slud, Oct. 2-15, 1953	2.02	(145)	0.73	(97)	2.76
Forest	2.06	(104)	1.00	(70)	2.06
Non-forest	1.93	(41)	0.29	(27)	6.75
Silencio de Sitio Mata (SW Carib.): P. Slud, July 29-Aug. 1, 1955	2.80	(118)	0.74	(87)	3.78
Forest	2.67	(77)	0.81	(56)	3.30
Non-forest	3.10	(41)	0.63	(31)	4.90
Cariblanco (SW Carib.): P. Slud, Mar. 23-30, 1955	2.49	(143)	0.70	(102)	3.56
Forest	2.03	(92)	0.85	(61)	2.31
Non-forest	4.10	(51)	0.52	(41)	7.88
Virgen del Socorro (SW [= SR (Tosi, 1969)] Carib.): Slud (1965)	2.61	(148)	0.81	(107)	3.21
Forest	2.38	(104)	0.87	(73)	2.74
Non-forest	3.40	(44)	0.70	(34)	4.86
Silencio de Tilarán (SW Pacific-Carib.): P. Slud, Feb. 2-8, 1954	2.12	(106)	0.80	(72)	2.65
Forest	1.80	(70)	1.14	(45)	1.58
Non-forest	3.00	(36)	0.42	(27)	7.12
Monteverde (SW Pacific): P. Slud, June 17-July 1, 1961	1.96	(136)	0.67	(90)	2.93
Forest	1.86	(80)	0.93	(52)	2.00
Non-forest	2.11	(56)	0.41	(38)	5.18
Helechales de Potrero Grande (TM-SW Pacific): P. Slud, July 14-29, 1961	1.66	(157)	1.08	(98)	1.53
Forest	2.06	(95)	1.67	(64)	1.23
Non-forest	1.21	(62)	0.48	(34)	2.53
Río Cotón (SW Pacific): Slud (1965)	2.00	(102)	1.34	(68)	1.49
Forest	2.08	(77)	1.74	(52)	1.20
Non-forest	1.78	(25)	0.60	(16)	2.97
La Hondura (SW-LMR Central Mountains): P. Slud, July 9-17, 1955	2.44	(93)	0.78	(66)	3.11
Forest	2.56	(64)	1.09	(46)	2.35
Non-forest	2.22	(29)	0.33	(20)	6.67

TABLE 5.—Continued

	(a) Native Land Avifauna		(b) Native Passerines		
	Passerines: Nonpasserines	(No. of Species)	Suboscines: Oscines	(No. of Species)	(a):(b)
Bajos del Toro (LMR Central Mountains): P. Slud, Mar. 10-21, 1955	2.10	(90)	0.49	(61)	4.30
Forest	2.00	(57)	0.65	(38)	3.08
Non-forest	2.30	(33)	0.35	(23)	6.52
San José de la Montaña (LMR Central Mountains): Slud (1965)	2.00	(57)	0.36	(38)	5.60
Forest	2.78	(34)	0.32	(25)	8.70
Non-forest	1.30	(23)	0.44	(13)	2.93
La Chonta (LMR Central Mountains): Slud (1965)	3.33	(39)	0.37	(30)	9.15
Forest	10.0	(22)	0.43	(20)	23.3
Non-forest	1.43	(17)	0.25	(10)	5.73
Villa Mills - Cerro de la Muerte (MR Central Mountains): P. Slud, Apr. 26-30, 1951; Oct. 13-14, 1964	1.93	(41)	0.29	(27)	6.75
Forest	2.00	(21)	0.17	(14)	11.9
Non-forest	1.86	(20)	0.44	(13)	4.19

TABLE 6.—*Suboscine-oscine ratios in Amazonian Brazil*

	Total Passerines		Native Passerines	
	Suboscines: Oscines	(No. of Species)	Suboscines: Oscines	(No. of Species)
Amazonian Brazil (Amazonas-Pará)	1.85	(535)	1.97	(516)
Lower Amazonia (Pará)	1.87	(430)	1.94	(420)
Northeastern Pará (excluding Belém area)	1.49	(182)	1.51	(181)
Belém area	1.59	(236)	1.62	(231)
Instituto Agronómico do Norte	1.90	(168)	1.90	(168)
Lower Rio Tocantins	1.82	(217)	1.81	(216)
Baião area	1.90	(180)	1.89	(179)
Lower Rio Xingu	2.15	(151)	2.10	(149)
Lower Rio Tapajos	2.12	(350)	2.16	(341)
Right bank	2.10	(313)	2.11	(305)
Santarém area	2.00	(276)	2.01	(271)
Mirituba area	2.82	(153)	2.80	(152)
Left bank	2.58	(268)	2.60	(263)
Itaituba area	2.51	(200)	2.65	(197)
Vila Braga	2.91	(168)	3.05	(166)
Obidos area	2.15	(227)	2.23	(223)
Faro area	2.08	(231)	2.18	(226)
Upper Amazonia (Amazonas)	1.94	(462)	2.09	(445)
Lower Rio Madeira				
Parintins area	2.41	(198)	2.46	(197)
Rosarinho-Borba areas	2.45	(262)	2.44	(258)
Rosarinho	2.67	(165)	2.62	(163)
Borba	2.37	(192)	2.39	(190)
Middle Rio Madeira	1.99	(209)	2.02	(205)
Calamá area	2.10	(158)	2.06	(156)
Itacoatiara area	1.70	(194)	1.69	(188)
Manaus	1.46	(160)	1.48	(156)
Manacapuru area	2.17	(184)	2.18	(181)
Rio Negro	2.06	(260)	2.20	(250)
Tatú-S. Gabriel area	2.18	(165)	2.18	(165)
Tefé	2.35	(164)	2.32	(159)
Tonantins	2.49	(150)	2.48	(146)
S. Paulo de Olivença	2.79	(197)	2.94	(193)

TABLE 6.—Continued

	Total Passerines		Native Passerines	
	Suboscines: Oscines	(No. of Species)	Suboscines: Oscines	(No. of Species)
Western Amazonas (Rio Juruá plus Rio Purús)	2.30	(304)	2.37	(300)
Rio Purús	2.09	(287)	2.11	(283)
Lower Purús (Jaburu-Nova Olinda-Arimã)	2.33	(213)	2.37	(209)
Arimã	2.15	(167)	2.22	(164)
Middle Purús				
Canutama-Oco do Mundo	2.33	(223)	2.28	(220)
Hyutanahã	2.38	(210)	2.35	(208)
Upper Rio Juruá	2.07	(267)	2.08	(259)
João Pessoa area	1.99	(248)	1.98	(241)

TABLE 7.—*Suboscine-oscine ratios in Central America and northern South America*

	Total Passerines		Native Passerines	
	Ratio	(No. of spp.)	Ratio	(No. of spp.)
Guatemala (Land, 1970)	0.43	(333)	0.51	(242)
Lowlands:				
Petén (Smithe, 1966)	0.59	(187)	0.78	(123)
Northern Petén (Van Tyne, 1935)	0.55	(130)	0.69	(103)
Eastern lowlands (Land, 1963)	0.64	(177)	0.91	(122)
Arid interior to 1000 m. (Land, 1962a)	0.41	(62)	0.36	(34)
Highlands:				
1500-3000 m. (Land, 1970)	0.32	(174)	0.37	(122)
Above 1000 m. (Wetmore, 1941)	0.26	(92)	0.31	(63)
Sierra de las Minas (Land, 1962b)	0.30	(105)	0.38	(73)
Restricted to highlands (ibid.)	--	--	0.26	(49)
Soloma region, Huehuetenango (Baepler, 1962)	0.20	(73)	0.15	(45)
Honduras (mainland) (Monroe, 1968)	0.55	(319)	0.69	(235)
Caribbean lowlands (Peters, 1929)	0.70	(102)	1.12	(72)
Nicaragua (based on Eisenmann, 1955)	0.59	(305)	0.73	(236)

TABLE 7.—Continued

	Total Passerines Ratio	(No. of spp.)	Native Passerines Ratio	(No. of spp.)
Northeastern lowlands (Huber, 1932)	0.75	(103)	0.82	(89)
Southeastern lowlands (Nutting, 1884; Richmond, 1893; Howell, 1957)	0.72	(165)	0.94	(126)
Panama (1970, compiled)	0.78	(440)	0.96	(366)
Lowlands:				
Almirante-Changuinola area (compiled sources)	0.71	(169)	1.03	(122)
Canal Zone, total (Eisenmann and Loftin, 1968)	0.86	(262)	1.19	(199)
Canal Zone, definitely known and modern presence (ibid.)	0.87	(222)	1.20	(174)
Extreme eastern Caribbean (Griscom, 1932b)	1.04	(151)	1.34	(124)
Cana, Darien (Griscom, 1929)	1.55	(130)	1.67	(123)
Highlands:				
W. Chiriquí, below 5000 ft. (Eisenmann and Loftin, 1967a)	0.66	(179)	0.90	(135)
W. Chiriquí, above 4000 ft. (ibid.)	0.53	(144)	0.69	(108)
Chiriquí Volcano, above 5000 ft. (Blake, 1958)	0.57	(152)	0.72	(124)
Cerro Campana (Eisenmann and Loftin, 1967b)	0.55	(121)	0.72	(93)
Colombia (Meyer de Schauensee, 1964)	1.11	(868)	1.19	(814)
Lowlands:				
Pacific coast, Guapi (Olivares, 1957-1958)	1.29	(87)	1.38	(81)
Southeast (Meyer de Schauensee, 1964)	1.86	(334)	1.99	(284)
Meta (ibid.)	1.33	(284)	1.49	(259)
Sierra Macarena area (Blake, 1962)	1.43	(182)	1.70	(167)
Caquetá (Meyer de Schauensee, 1964)	1.80	(224)	1.92	(207)
Putumayo (ibid.)	1.62	(144)	1.66	(141)
Vaupés (compiled sources)	1.69	(204)	1.76	(196)
Caribbean slope (Meyer de Schauensee, 1964)	0.79	(178)	0.94	(155)
Depto. Atlántico (Dugand, 1947)	0.82	(113)	0.98	(99)
Rio Frio, Magdalena (Darlington, 1931)	0.73	(107)	0.91	(86)

TABLE 7.—Continued

	Total Passerines Ratio	(No. of spp.)	Native Passerines Ratio	(No. of spp.)
Arid upper Magdalena valley (Miller, 1947, 1952)	0.76	(102)	0.89	(85)
Highlands (Meyer de Schauensee, 1964)	0.91	(578)	0.96	(537)
Cundinamarca (Olivares, 1969)	0.88	(354)	0.94	(321)
Santa Marta area (Todd and Carriker, 1922)	0.85	(286)	1.02	(244)
San Antonio, altitude 2000 m. (Miller, 1963)	0.65	(107)	0.62	(95)
Venezuela (Phelps and Phelps, 1958, 1963)	1.20	(718)	1.32	(672)
Lowlands:				
Orinoco region (Cherrie, 1916)	1.34	(288)	1.45	(277)
Northeast (Beebe, 1909)	0.60	(56)	0.64	(54)
" (Friedmann and Smith, 1950, 1955)	0.65	(117)	0.70	(112)
Highlands:				
Perijá (Phelps, 1943; Gines et al., 1953)	0.95	(245)	1.11	(217)
Rancho Grande (Schäfer and Phelps, 1954)	0.82	(271)	0.97	(242)
Cerro Neblina (Phelps and Phelps, 1965)	0.78	(91)	0.95	(37)
Mt. Duida (Chapman, 1931)	0.85	(48)	0.92	(46)
Mt. Roraima (ibid.)	0.83	(97)	0.86	(95)
Mt. Auyan-tepui:				
460 m. level (Gilliard, 1941)	1.17	(104)	1.37	(97)
1100 m. level (ibid.)	1.02	(117)	1.09	(113)
1500-2200 m. (ibid.)	0.86	(26)	0.92	(25)
Upper Mt. Auyan-tepui (Chapman, 1939)	0.67	(30)	0.71	(29)
Ecuador (Meyer de Schauensee, 1966, 1970)	1.32	(742)	1.36	(713)
Southwest lowlands (Marchant, 1958)	0.62	(42)	0.70	(39)
Peru (Meyer de Schauensee, 1966, 1970)	1.55	(869)	1.57	(837)
Lowlands:				
Apurímac valley (Terborgh and Weske, 1969)	1.27	(134)	1.27	(134)
Depto. Lima (Koepcke, 1964)	0.98	(111)	1.00	(110)

TABLE 7.—Continued

	Total Passerines Ratio	(No. of spp.)	Native Passerines Ratio	(No. of spp.)
Southwest (Hughes, 1970)	0.74	(33)	0.86	(26)
Highlands:				
Urubamba valley (Chapman, 1921)	0.92	(227)	0.94	(223)
Bolivia (Bond and Meyer de Schauensee, 1942-1943)	1.31	(601)	1.34	(593)
Northern lowlands (Gyldenstolpe, 1945b)	1.66	(303)	1.69	(296)
Primarily highlands (Niethammer, 1953-1956)	0.97	(225)	0.99	(223)

TABLE 8.—*Numbers of land species and (a):(b) values in the neotropics* ((a):(b) = passerine-nonpasserine ratio/suboscine-oscine ratio)

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Middle American mainland (Blake, 1953; Eisenmann, 1955)	1145	1035	3.76	3.00
Mexico (Blake, 1953; Edwards, 1968)	776	651	6.28	4.90
" (Beristain and Laurencio, 1894)	739	642	5.36	4.23
" (ibid., keyed to Blake, 1953)	619	534	5.54	4.40
Nontropical Mexico (Edwards, 1972)	542	427	10.2	9.41
Highlands (ibid.)	389	295	11.4	10.6
Northern	282	191	13.6	13.0
Central	313	220	9.62	8.04
Southern	215	142	8.04	6.82
Lowlands (Edwards, 1972)				
Northern Pacific slope	297	186	8.14	4.69
" Gulf "	290	169	6.45	3.80
Central Pacific "	248	158	4.50	2.43
" Gulf "	355	244	3.27	1.90
Southern Pacific "	256	191	2.34	1.46
" Gulf "	352	254	2.74	1.51
Baja California (based on Grinnell, 1928)	200	127	19.4	26.6

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Sonora (van Rossem, 1945; Edwards, 1972)	300	210	10.7	8.18
Tamaulipas (based on Edwards, 1972)	330	218	6.98	5.75
Sinaloa (based on Edwards, 1972)	276	203	7.50	4.95
Colima and adjacent Jalisco (Schaldach, 1963)	279	215	6.54	5.31
Oaxaca (Edwards, 1972; Peterson and Chalif, 1973)	499	413	4.54	3.83
Veracruz (Edwards, 1972; Peterson and Chalif, 1973)	514	413	4.70	3.81
Tropical Mexico-Central America (based on Edwards, 1972; Eisenmann, 1955)	944	832	2.61	1.93
Tropical Mexico, (Edwards, 1972)	563	445	3.98	2.81
Chiapas (based on Alvarez del Toro, 1964)	534	431	3.60	2.71
Southern Veracruz (Wetmore, 1943)	239	180	3.88	2.11
Tabasco (compiled sources)	251	196	2.63	1.43
Yucatan Peninsula (based on Paynter, 1955)	320	227	3.26	1.66
Yucatan (Paynter, 1955)	235	161	4.33	1.98
Campeche (ibid; Storer, 1961)	261	198	3.16	1.64
Quintana Roo (Paynter, 1955)	271	208	3.08	1.64
Isla Cozumel (based on Paynter, 1955)	111	54	8.15	2.42
Central America (based on Eisenmann,1955)	919	807	2.60	1.96
British Honduras-Guatemala (Russell, 1964; Land, 1970)	558	440	3.60	2.40
British Honduras (Russell, 1964)	368	277	3.23	1.85
Gallon Jug	236	180	2.46	1.09
Guatemala (Land, 1970)	547	433	3.62	2.45
" (Griscom, 1932a, keyed to Eisenmann, 1955)	528	409	3.65	2.34
Petén (Smithe, 1966; Land, 1970)	313	241	3.04	1.51
Northern Petén	274	208	2.78	1.33
Tikal	248	177	2.64	1.08
Caribbean lowlands (Land, 1970)	309	239	2.51	1.29
" (Land, 1963)	275	211	2.82	1.51
Arid interior (Land, 1970)	126	86	3.30	1.95
Humid subtropics (ibid.)	380	285	4.55	2.96
Highlands (ibid.)	259	199	6.43	4.27
" (Wetmore, 1941)	141	107	7.70	4.45
Sierra de las Minas (Land, 1962)	158	120	7.10	4.31

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Upper elevations	-	73	-	8.25
Soloma, Huehuetenango (Baepler, 1962)	101	70	13.7	12.2
El Salvador-Honduras (Rand and Traylor, 1954; Monroe, 1968)	556	446	2.70	1.70
El Salvador (Rand and Traylor, 1954)	329	247	3.91	2.35
Arid lowlands (ibid.; Dickey and van Rossem, 1938)	202	147	2.27	1.29
Honduras (Monroe, 1968)	541	432	2.62	1.72
" (Stone, 1932)	347	299	2.71	1.80
Humid Caribbean lowlands (Monroe, 1968)	338	257	2.00	1.06
" (Peters, J. L., 1929)	167	133	2.24	1.05
Subtropical Caribbean slope (Monroe, 1968)	404	321	2.76	1.79
" Pacific " (ibid.)	297	223	3.91	2.41
Highlands (ibid.)	214	179	4.97	3.57
Nicaragua-Costa Rica (Eisenmann, 1955; Slud, 1964a)	710	611	2.40	1.73
Nicaragua (based on Eisenmann, 1955)	512	428	2.49	1.68
Northeast (Huber, 1932)	172	154	2.00	1.68
Southeast (Nutting, 1884; Richmond, 1893; Howell, 1957)	264	218	2.32	1.46
Costa Rica (based on Slud, 1964a)	662	568	2.14	1.55
" (Carriker, 1910)	636	560	2.20	1.68
" (ibid., keyed to Slud, 1964a)	607	535	2.14	1.63
" (Salvin and Godman, 1879-1904)	574	516	2.03	1.76
" (ibid., keyed to Slud, 1964a)	539	474	2.05	1.61
" (Zeledón, 1887)	611	533	2.08	1.55
" (ibid., keyed to Slud, 1964a)	568	494	2.11	1.57
" (Frantzius, 1869)	476	418	2.14	1.63
" (ibid., keyed to Slud, 1964a)	440	384	2.30	1.74
" (Lawrence, 1868-70; Salvin, 1869, 1870)	473	416	2.19	1.63
" (ibid., keyed to Slud, 1964a)	440	384	2.31	1.72
Provinces and zones (Carriker, 1910; Slud, 1964a; compiled sources)				
Provinces				
Alajuela	488	421	2.28	1.72
Cartago	493	421	2.38	1.75

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Guanacaste	407	340	1.91	1.32
Heredia	472	403	2.28	1.66
Limón	360	293	2.16	1.27
Puntarenas	502	431	1.85	1.39
San José	531	453	2.08	1.58
Zones				
Tropical belt	-	443	-	1.47
Subhumid, following map of Holdridge, 1959	-	228	-	1.12
" " Tosi, 1969	-	191	-	1.03
Humid	-	410	-	1.36
Pacific southwest	-	273	-	1.13
Caribbean slope	-	343	-	1.32
Finca La Selva, 1970 (based on Slud, 1960)	324	259	1.97	1.13
" , 1958 (Slud, 1960)	311	250	2.02	1.07
" , 1957 (Slud, unpublished)	236	201	2.24	1.30
Subtropical belt	-	437	-	1.52
Pacific southwest	-	248	-	1.43
Caribbean slope	-	399	-	1.59
Lower Montane belt	-	201	-	2.30
Montane belt	-	84	-	3.38
Costa Rica-Panama (based on Slud, 1964a; Eisenmann, 1955; Wetmore, 1965-1972a)	790	688	2.08	1.52
Panama (based on Eisenmann, 1955; Wetmore, 1965-1972a)	716	622	2.05	1.48
" (Griscom, 1935)	684	608	1.95	1.48
Almirante (Peters, J. L., 1931; compiled sources)	248	197	2.46	1.35
W. Chiriquí highlands (Eisenmann and Loftin, 1967a)	382	324	2.58	1.76
Below 5000 ft.	281	228	2.67	1.61
Above 4000 ft.	202	162	4.67	2.91
Chiriquí Volcano (based on Blake, 1958)	296	260	2.80	2.07
" (Blake, 1958)	227	193	3.58	2.49
Cerro Campana (based on Eisenmann and Loftin, 1967b)	181	148	3.66	2.34
Canal Zone (Eisenmann and Loftin, 1968: definitely known and modern presence)	352	293	1.99	1.22

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
" (ibid.: including doubtful and unusual)	427	348	1.86	1.12
" (Sturgis, 1928)	335	285	1.78	1.15
Barro Colorado I. (based on Eisenmann, 1952)	307	245	1.82	0.97
" (Eisenmann, 1952)	273	229	1.61	0.91
Barro Colorado I. (Chapman, 1938)	228	195	1.63	0.93
" (Chapman, 1929)	192	167	1.55	0.98
Eastern Caribbean lowlands (Griscom, 1932b)	256	220	1.38	0.96
Isla Coiba (Wetmore, 1957)	95	76	2.40	1.23
South American mainland (Meyer de Schauensee, 1970)	2567	2494	1.30	1.19
Northwestern South America (ibid.)	2031	1949	1.40	1.28
Colombia (based on Meyer de Schauensee, 1964)	1425	1351	1.43	1.23
" (Chapman, 1917)	1024	990	1.87	1.73
Zones and sectors (Meyer de Schauensee, 1964)				
Zones				
Tropical	1149	1082	1.30	1.10
Subtropical	570	532	2.33	2.05
Temperate	253	230	2.41	1.92
Paramo	40	37	1.02	0.99
Sectors				
Pacific sector	419	384	1.14	0.99
Guapi (Olivares, 1957-58)	144	137	1.19	1.06
Central mountain sector	896	843	2.00	1.82
Cundinamarca (Olivares, 1969)	552	508	2.04	1.83
San Antonio (Miller, 1963)	165	151	2.84	2.76
Caribbean sector	332	305	1.46	1.09
Atlántico (Dugand, 1947)	212	194	1.39	1.06
Río Frío, Magdalena (Darlington, 1931)	195	174	1.69	0.98
Arid tropical upper Magdalena valley (Miller, 1947, 1952)	168	151	2.07	1.45
Santa Marta area (based on Todd and Carriker, 1922, and keyed to Meyer de Schauensee, 1970)	456	409	1.98	1.46
Eastern sector	718	676	0.96	0.79
Orinoco area	544	509	0.95	0.75

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Meta	473	445	1.12	0.92
Sierra Macarena (Blake, 1962)	304	289	1.04	0.81
Southeast	551	523	0.89	0.74
Vaupés (Olivares, 1955, 1964a, 1964b; Olivares and Hernández, 1962)	318	309	1.07	0.99
Caquetá (based on Meyer de Schauensee, 1964)	371	354	0.84	0.72
Ecuador-Peru (based on Meyer de Schauensee, 1970)	1560	1513	1.23	1.18
Ecuador (ibid.)	1200	1161	1.23	1.17
" (Chapman, 1926)	1223	1191	1.47	1.27
Southwest (Marchant, 1958)	76	70	2.01	1.81
Peru (based on Meyer de Schauensee, 1970)	1334	1291	1.21	1.18
Depto. Lima (Koepcke, 1964)	176	171	1.77	1.80
Southwest (Hughes, 1970)	59	47	1.73	1.45
Northeast (Traylor, 1958)	282	276	0.93	0.94
Apurímac Valley (Terborgh and Weske, 1969)	219	219	1.24	1.24
Urubamba Valley (Chapman, 1921)	343	339	2.15	2.08
Bolivia (based on Meyer de Schauensee, 1970)	1042	1004	1.28	1.27
" (Bond and Meyer de Schauensee, 1942-43)	916	907	1.46	1.41
Northern lowlands (Gyldenstolpe, 1945b)	469	461	1.10	1.06
Primarily highlands (Niethammer, 1953-56)	326	323	2.28	2.25
Venezuela-The Guianas (based on Meyer de Schauensee, 1970)	1198	1132	1.38	1.19
Venezuela (based on Phelps and Phelps, 1958, 1963)	1151	1090	1.41	1.23
Tropical Zone	868	822	1.38	1.18
Subtropical Zone	583	552	1.90	1.70
Temperate Zone	130	124	3.12	2.57
Paramo Zone	27	24	4.00	2.50
Orinoco Region (Cherrie, 1916)	475	463	1.15	1.03
Northeast (Beebe, 1909)	116	114	1.56	1.42
" (Friedmann and Smith, 1950, 1955)	224	218	1.69	1.52
Central Anzoátegui (Smith, F. D., Jr., 1952)	163	154	1.77	1.60
Perijá (Phelps, 1943; Gines et al., 1953)	405	374	1.62	1.25
Rancho Grande (Schäfer and Phelps, 1954)	438	404	1.99	1.54
Highlands				

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Mt. Duida (Chapman, 1931)	73	71	2.27	2.01
Mt. Roraima (ibid.)	137	135	2.01	2.05
Mt. Auyan-tepui (Gilliard, 1941)	284	276	1.42	1.22
469 m. level	104	97	1.11	0.88
1100 m. level	117	113	1.64	1.49
1500-2200 m. level	34	33	3.78	3.39
Cerro Neblina (Phelps and Phelps, 1965)	57	53	3.28	2.44
The Guianas (based on Meyer de Schauensee, 1970)	668	635	1.06	0.96
Guyana-Surinam	654	621	1.07	0.94
Guyana (based on Snyder, 1966)	622	593	1.09	0.95
" (Chubb, 1916-21)	615	597	1.17	1.03
Bartica district (Beebe, 1925; Beebe et al., 1917)	411	394	1.01	0.86
Acary Mts. (Blake, 1950)	151	151	0.80	0.80
Surinam-French Guiana (based on Meyer de Schauensee, 1970)	573	548	0.93	0.84
Surinam (based on Haverschmidt, 1968)	549	524	0.89	0.81
" (Bangs and Penard, 1918)	266	264	0.84	0.80
So. Surinam (Blake, 1963)	273	271	0.93	0.89
French Guiana (based on Meyer de Schauensee, 1970)	526	515	0.83	0.80
" (Berlepsch, 1908)	497	491	0.83	0.80
Trinidad (based on Herklots, 1961)	274	240	1.66	1.23
" (Belcher and Smooker, 1934-37)	252	223	1.49	1.25
No. Brazil-So. Venezuela (Friedmann, 1948)	416	408	1.08	0.97
Brazil (based on Meyer de Schauensee, 1970)	1363	1323	1.02	0.98
" (Pinto, 1938, 1944)	1318	1300	0.90	0.85
" (Ihering and Ihering, 1907)	1391	1391	0.99	0.99
Amazonia (based on Meyer de Schauensee, 1970)	940	916	0.92	0.86
Amazonas-Roraima-Acre	836	816	0.95	0.86
Amazonas	748	729	0.84	0.75
S. Paulo de Olivença (compiled sources)	269	264	0.98	0.92
Tonantíns (ibid.)	216	212	0.93	0.94
Rio Juruá-Rio Purús (Gyldenstolpe, 1945a, 1951)	488	484	0.72	0.69
Upper Juruá-upper Purús (ibid.)	450	445	0.72	0.69
Rio Juruá (Gyldenstolpe, 1945a)	394	387	0.80	0.77

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Upper Juruá (based on Gyldenstolpe, 1945a)	414	406	0.88	0.85
João Pessoa area	386	379	0.90	0.88
Tefé (compiled sources)	255	250	0.78	0.76
Rio Purús (Gyldenstolpe, 1951)	453	449	0.83	0.81
Lr. Middle Purús	314	310	0.91	0.88
Nova Olinda-Arimã	303	299	1.01	0.98
Nova Olinda	200	198	1.06	1.06
Arimã	240	237	1.08	1.03
Middle Purús	345	342	0.78	0.79
Hyutanahã	300	298	0.98	0.98
Manacapuru (compiled sources)	285	281	0.84	0.83
Rio Negro (ibid.)	417	405	0.84	0.74
Lower Rio Negro	203	203	0.90	0.90
Upper Rio Negro	243	243	0.98	0.98
Tahuapunto-Vaupés (compiled sources)	450	432	0.94	0.80
Manaus (ibid.)	253	248	1.19	1.15
Itacoatiara (ibid.)	298	292	1.10	1.07
Parintins (ibid.)	321	320	0.67	0.65
Rio Madeira (Hellmayr, 1910)	424	420	0.71	0.68
Lower Madeira (compiled sources)	433	428	0.63	0.62
Borba area	357	353	0.76	0.75
Borba	300	298	0.75	0.74
Igarapé Auará	207	206	0.84	0.84
Rosarinho area	324	321	0.58	0.58
Rosarinho	264	262	0.63	0.63
Middle to upper Madeira (compiled sources)	338	333	0.81	0.79
Calamá	242	240	0.91	0.91
Acre (compiled sources)	251	250	1.00	0.98
Roraima (based on Pinto, 1966)	379	371	1.38	1.24
Amazonas-Pará (compiled sources)	880	856	0.84	0.77
Lower Amazonia (Griscom and Greenway, 1941)	678	668	0.79	0.76
" (Snethlage, 1914)	947	932	0.73	0.69
Pará-Amapá (based on Meyer de Schauensee, 1970)	726	712	0.81	0.77

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Pará (ibid.)	716	702	0.80	0.77
" (Pinto, 1938, 1944)	657	649	0.79	0.75
Faro (compiled sources)	350	345	0.93	0.87
Obidos (ibid.)	358	354	0.81	0.76
Lower Rio Tapajós (ibid.)	569	559	0.75	0.72
Right bank	522	513	0.71	0.69
Santarém	453	447	0.78	0.77
" (Riker, 1890-91)	234	233	0.74	0.74
Mirituba	198	197	1.24	1.20
Left bank	418	413	0.70	0.68
Itaituba (excluding islands)	202	199	0.81	0.76
Vila Braga	241	239	0.79	0.75
Lower Rio Xingu (compiled sources)	229	227	0.90	0.91
Lower Rio Tocantins (ibid.)	337	336	1.00	1.00
Baião area	288	287	0.87	0.88
Extreme n.e. Pará (ibid.)	437	432	0.73	0.70
Belém (based on Novaes, [MS.])	421	416	0.81	0.77
" (Stone, 1928)	220	219	1.02	1.01
Instituto Agronômico do Norte (compiled sources)	291	291	0.72	0.72
Station "A"	214	214	0.61	0.61
Southeastern Pará (Novaes, 1958)	212	212	1.41	1.41
Amapá (based on Meyer de Schauensee, 1970)	351	349	1.08	1.07
Northeastern Brazil (based on Meyer de Schauensee, 1970)	643	633	0.79	0.78
Maranhão-Piauí-Ceará (ibid.)	457	453	0.85	0.86
" (Hellmayr, 1929)	440	440	0.90	0.90
Piauí through Alagoas (based on Meyer de Schauensee, 1970)	431	428	0.96	0.96
Maranhão	375	372	0.97	0.96
Piauí-Ceará	319	317	0.99	0.99
Piauí	276	275	1.01	1.02
Ceará	198	198	1.19	1.19
Ceará-Paraiba-Alagoas-part of Bahía (Pinto and Camargo, 1961)	274	274	1.28	1.28

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
Pernambuco-Alagoas-Paraiba (based on Meyer de Schauensee, 1970)	335	333	1.21	1.21
Pernambuco	255	254	1.54	1.51
Alagoas	209	209	1.63	1.63
Paraiba (ibid.; Pinto and Camargo, 1961)	196	195	1.68	1.67
Mato Grosso-Goiás (based on Meyer de Schauensee, 1970)	723	705	0.98	0.97
Mato Grosso (ibid.)	657	640	1.06	1.04
" (Pinto, 1938, 1944)	554	543	1.15	1.09
" (Naumburg, 1930)	584	572	1.24	1.18
Northeast (Fry, 1970)	246	237	1.23	1.24
" (Sick, 1955)	217	217	1.09	1.09
Central sector (Pinto, 1940)	215	215	1.70	1.70
Goiás (based on Meyer de Schauensee, 1970)	398	395	1.10	1.12
" (Pinto, 1938, 1944)	357	357	1.28	1.28
Bahía (based on Meyer de Schauensee, 1970)	521	513	0.91	0.89
Southeastern Brazil (ibid.)	681	670	1.05	1.04
Minas Gerais (ibid.)	508	505	0.95	0.94
" (Pinto, 1952)	479	479	0.93	0.93
" (Pinto, 1938, 1944)	448	448	1.08	1.08
Espírito Santo-Rio de Janeiro (based on Meyer de Schauensee, 1970)	517	511	1.08	1.05
Espírito Santo (ibid.)	388	386	1.49	1.45
" (Pinto, 1938, 1944)	304	301	1.51	1.48
Rio de Janeiro (based on Meyer de Schauensee, 1970)	452	446	1.18	1.14
Itatiaya (Holt, 1928; Pinto, 1951; Mitchell, 1957)	249	249	1.23	1.23
São Paulo (based on Meyer de Schauensee, 1970)	561	554	1.05	1.05
" (Ihering, 1898)	499	497	1.07	1.06
Paraná-Sta. Catarina-Rio Grande do Sul (based on Meyer de Schauensee, 1970)	515	505	1.26	1.25
Paraná (ibid.)	357	356	1.27	1.28
" (Pinto, 1938, 1944)	300	300	1.38	1.38
Santa Catarina (based on Meyer de Schauensee, 1970)	228	228	1.11	1.11
" (Pinto, 1938, 1944)	194	194	1.35	1.35
Rio Grande do Sul (based on Meyer de Schauensee, 1970)	415	401	1.31	1.29

TABLE 8.—Continued

	No. of Species		(a):(b)	
	Total Land Birds	Native Land Birds	Total Land Birds	Native Land Birds
" (Pinto, 1938, 1944)	326	322	1.41	1.35
So. South America (based on Meyer de Schauensee, 1970)	771	756	1.29	1.27
Paraguay (ibid.)	535	505	1.20	1.21
" (Laubmann, 1939-40)	484	480	1.23	1.21
Gran Chaco (Laubmann, 1930)	280	278	1.63	1.65
Uruguay (based on Meyer de Schauensee, 1970)	227	196	1.58	1.80
" (Cuello and Gerzenstein, 1962)	213	188	1.79	1.90
Argentina-Chile (based on Meyer de Schauensee, 1970)	747	724	1.32	1.31
Argentina (ibid.)	717	697	1.28	1.28
" (Olrog, 1963)	689	671	1.30	1.25
" (Dabbene, 1910)	692	684	1.27	1.24
Minus subtropical northeast (based on Olrog, 1963)	506	492	1.45	1.38
Misiones (ibid.)	413	362	1.18	1.09
So. Patagonia (Olrog, 1959)	114	108	0.91	0.83
Chile (based on Johnson, 1965-67)	201	176	1.49	1.26
Isla Grande, Tierra del Fuego (Humphrey et al., 1970)	75	31	1.17	1.07

TABLE 9.—*Paramo "islands" of Vuilleumier (1970)* ((a) = passerine-nonpasserine ratio; (b) = suboscine-oscine ratio; (a):(b) = passerine-nonpasserine ratio/ suboscine-oscine ratio)

	No. of Species	Area (km^2)	Distance from "island" no. 1 (km)	(a)	(b)	(a):(b)
Paramo "Islands" of Vuilleumier (1970)						
1. Ecuador	56	3487	1	1.00	1.55	0.65
2. Chiles	28	326	36	1.55	1.83	0.84
3. Las Papas-Coconuco	25	501	234	0.92	1.40	0.66
4. Sumapaz	32	2031	543	1.67	1.00	1.67
5. Tolima-Quindío	32	989	551	1.67	1.50	1.11
6. Paramillo	11	25	773	4.50	0.80	5.63
7. Cocuy	17	2168	801	1.43	2.33	0.61
8. Pamplona	11	217	950	1.20	1.00	1.20
9. Cachira	13	143	958	1.17	0.75	1.56
10. Tamá	14	46	995	2.50	0.43	5.83

TABLE 9.—Continued

	No. of Species	Area (km^2)	Distance from "island" no. 1 (km)	(a)	(b)	(a):(b)
11. Batallón	12	66	1065	2.00	1.00	2.00
12. Mérida	27	1798	1167	2.00	0.80	2.50
13. Perijá	4	167	1182	1.00	0.00	0.00
14. Santa Marta	17	606	1238	3.25	1.67	2.79
15. Cendé	14	70	1380	3.67	0.82	4.40
"Island" Groups (grouped by P. Slud)						
1-3, Central Ecuador to southern Colombia	57	4314	1	1.04	1.42	0.73
4-6, Central Colombia	42	3045	543	1.21	1.09	1.11
7-10, Northeastern Colombia	29	2574	925	1.64	1.25	1.31
11-12, 15, Venezuela	27	1934	1195	2.00	0.80	2.50
14, Santa Marta	17	606	1195	3.25	1.17	2.78

Correlation Coefficients

	No. of Species	Log of Species	(a)	(b)	(a):(b)
Paramo "Islands"					
Distance	-0.73	-0.68	0.44	-0.59	0.42
Square Root of Distance	-0.79	-0.69	0.41	-0.56	0.41
log of Distance	-0.83	-0.65	0.35	-0.44	0.35
Area	0.81	0.69	-0.35	0.49	-0.38
Square Root of Area	0.79	0.71	-0.41	0.54	-0.48
log of Area	0.72	0.68	-0.53	0.56	-0.63
No. of Species	---	---	-0.32	0.50	-0.31
log of Species	---	---	-0.18	0.63	-0.17
"Island" Groups					
Distance	-0.97	-0.92	0.78	-0.70	0.89
Square Root of Distance	-0.95	-0.87	0.69	-0.70	0.79
log of Distance	-0.87	-0.77	0.57	-0.68	0.66
Area	0.97	0.99	-0.95	0.50	-0.93
Square Root of Area	0.93	0.97	-0.98	0.40	-0.92
log Area	0.87	0.94	-0.99	0.29	-0.89
No. of Species	---	---	-0.87	0.52	-0.88
log Species	---	---	-0.95	0.56	-0.91

TABLE 10.—*Comparative distribution of Formicariidae*

	Area (mi²)	Species of Formicariidae	% of Suboscines	% of Passerines	% of Avifauna	Ratio to Oscines
Mexico	763,944	9	10.1	2.3	1.4	0.03
Chiapas	28,729	9	11.8	3.7	2.1	0.05
Yucatan Peninsula	63,034	5	11.4	4.3	2.3	0.07
Central America	228,578	38	19.1	8.0	4.8	0.14
Br. Honduras-Guatemala	50,732	11	13.3	4.5	2.5	0.07
British Honduras	8,688	9	15.0	6.0	3.1	0.10
Guatemala	42,044	11	13.4	4.6	2.6	0.07
Honduras-El Salvador	67,420	19	19.8	8.0	4.3	0.13
Honduras	59,160	19	19.8	8.1	4.5	0.14
El Salvador	8,260	2	4.8	1.5	0.8	0.02
Nicaragua	57,143	21	21.2	8.9	5.0	0.15
Costa Rica	19,238	29	19.0	8.9	5.2	0.17
Finca La Selva	2	20	25.0	13.5	7.9	0.29
Panama	29,224	37	21.2	10.4	6.2	0.24
Canal Zone	372	25	23.1	12.6	7.3	0.27
Barro Colorado I.	6	17	23.3	12.8	7.5	0.28
Colombia	439,825	128	28.5	15.7	9.5	0.35
Vaupés	57,857	40	32.0	20.4	13.2	0.56
Atlántico	1,340	6	12.3	6.1	3.1	0.12
Cundinamarca	9,108	22	14.2	6.9	4.4	0.07
Ecuador-Peru	583,738	144	24.8	14.9	9.6	0.37
Ecuador	101,481	109	26.6	15.3	9.4	0.36
Peru	482,257	118	23.2	14.1	9.2	0.36
Lima	15,052	0	0.0	0.0	0.0	0.00
Bolivia	513,086	69	18.9	10.9	6.9	0.26
Venezuela	352,141	88	23.2	13.1	8.1	0.30
Trinidad	1,864	9	15.3	7.2	3.8	0.14
The Guianas	179,363	53	23.1	14.1	8.4	0.36
Guyana	89,480	48	23.6	14.0	8.2	0.34
Surinam	55,143	47	25.2	15.7	9.1	0.42
French Guiana	34,740	47	25.4	15.9	9.2	0.43
Brazil	3,286,000	159	29.0	18.8	12.1	0.53
Acre	57,153	34	33.4	21.4	13.8	0.60
Alagoas	11,031	16	21.6	11.7	7.8	0.25

TABLE 10.—Continued

	Area (mi^2)	Species of Formicariidae	% of Suboscines	% of Passerines	% of Avifauna	Ratio to Oscines
Amapá	55,489	44	31.4	19.7	12.8	0.52
Amazonas	595,474	92	30.6	20.6	12.7	0.64
Bahía	215,329	23	13.0	7.8	4.5	0.20
Ceará	57,371	11	17.2	9.4	5.6	0.21
Espírito Santo	16,543	37	24.8	14.4	9.7	0.34
Goiás	244,330	16	13.1	7.1	4.1	0.16
Maranhão	133,674	26	18.8	11.5	7.1	0.30
Mato Grosso	485,405	53	24.2	14.1	8.3	0.34
Minas Gerais	226,179	32	17.9	10.8	6.4	0.27
Pará	470,752	78	28.2	18.6	11.2	0.55
Paraiba	21,251	14	20.3	10.9	7.3	0.23
Paraná	82,741	21	15.7	9.2	6.0	0.22
Pernambuco	38,315	18	20.9	11.2	7.2	0.24
Piauí	94,819	12	13.6	7.7	4.4	0.18
Rio de Janeiro	16,372	35	22.4	12.9	7.9	0.30
Rio Grande do Sul	110,150	15	13.0	6.9	4.3	0.15
Roraima	97,438	28	22.0	12.3	7.6	0.28
Santa Catarina	31,118	18	21.2	12.7	8.0	0.32
São Paulo	95,459	34	17.4	10.2	6.2	0.25
Paraguay	157,006	21	12.5	6.9	4.2	0.16
Uruguay	72,172	2	3.6	1.8	1.0	0.03
Argentina	1,072,750	23	9.1	5.3	3.3	0.12
Misiones	11,506	17	16.0	8.5	4.7	0.18
Chile	286,396	0	0.0	0.0	0.0	0.00

TABLE 11.—*Cumulative daily total of species of land birds collected at Obidos, Pará, Brazil, by S. M. Klages in 1920–1921*

Collecting Day	Number of Species		Percentages of Components			
	Cumulative Totals	Daily Increment	Non-passerines / Total	Suboscines / Total	Oscines / Total	Suboscines / Passerines
1.	18	18	11.1	77.8	11.1	87.5
2.	30	12	13.3	73.3	13.4	84.6
3.	44	14	13.6	68.2	18.2	79.0
4.	55	11	20.0	63.7	16.3	79.5
5.	63	8	17.5	66.6	15.9	80.7
6.	66	3	18.2	68.1	13.7	81.9
7.	77	11	23.4	62.3	14.3	81.3
8.	87	10	21.8	63.2	16.0	80.9
9.	94	7	20.2	64.9	14.9	81.3
10.	103	9	20.4	63.1	16.5	79.2
11.	115	12	22.6	59.1	18.3	76.5
12.	117	2	22.2	59.8	18.0	76.9
13.	123	6	24.4	58.5	17.1	77.4
14.	124	1	24.2	58.1	17.7	76.6
15.	129	5	25.6	57.4	17.0	77.0
16.	133	4	26.3	56.4	17.3	76.5
17.	138	5	28.2	54.4	17.4	75.8
18.	142	4	29.6	53.5	16.9	76.0
19.	146	4	28.8	54.1	17.1	76.0
20.	150	4	28.7	54.0	17.3	75.7
21.	151	1	29.1	53.7	17.2	75.7
22.	154	3	29.9	53.3	16.8	75.9
23.	158	4	29.8	53.8	16.4	76.6
24.	160	2	29.4	54.4	16.2	77.0
25.	162	2	29.6	54.3	16.1	77.2
26.	165	3	29.7	53.3	17.0	75.9
27.	168	3	30.4	52.7	17.1	76.0
28.	169	1	30.6	52.3	17.1	76.0
29.	169	0	30.6	52.3	17.1	76.4
30.	172	3	30.6	51.5	17.9	74.2
31.	173	1	30.4	51.8	17.8	74.4
32.	176	3	30.5	51.5	18.0	74.0

TABLE 11.—Continued

Collecting Day	Number of Species		Percentages of Components			
	Cumulative Totals	Daily Increment	Non-passerines / Total	Suboscines / Total	Oscines / Total	Suboscines / Passerines
33.	177	1	30.3	51.2	18.5	73.4
34.	180	3	30.4	50.8	18.8	73.0
35.	181	1	30.2	51.1	18.7	73.2
36.	182	1	30.6	50.8	18.6	73.2
37.	182	0	30.6	50.8	18.6	73.2
38.	186	4	30.0	51.4	18.6	73.3
39.	188	2	30.2	51.4	18.4	73.5
40.	190	2	30.4	50.8	18.8	72.9
41.	190	0	30.4	50.8	18.8	72.9
42.	190	0	30.4	50.8	18.8	72.9
43.	192	2	30.0	50.8	19.2	72.6
44.	193	1	30.4	50.5	19.1	72.6
45.	195	2	30.1	51.0	18.9	73.0
46.	195	0	30.1	51.0	18.9	73.0
47.	195	0	30.1	51.0	18.9	73.0
48.	196	1	29.9	50.8	19.3	72.5
49.	200	4	29.8	50.2	20.0	71.7
50.	201	1	30.0	50.2	19.8	71.9
51.	203	2	30.2	50.2	19.6	72.1
52.	204	1	30.6	50.0	19.4	72.1
53.	206	2	30.8	49.6	19.6	71.5
54.	209	3	31.3	48.3	20.4	71.8
55.	210	1	31.6	49.1	19.3	71.8
56.	211	1	31.4	49.3	19.3	72.0
57.	212	1	31.8	49.1	19.1	72.0
58.	212	0	31.8	49.1	19.1	72.0
59.	213	1	32.1	48.8	19.1	72.0
60.	213	0	32.1	48.8	19.1	72.0
61.	213	0	32.1	48.8	19.1	72.0
62.	213	0	32.1	48.8	19.1	72.0
63.	215	2	32.2	48.9	18.9	72.2
64.	216	1	32.1	49.1	18.8	72.4

TABLE 11.—Continued

Collecting Day	Number of Species		Percentages of Components			
	Cumulative Totals	Daily Increment	Non-passerines / Total	Suboscines / Total	Oscines / Total	Suboscines / Passerines
65.	217	1	32.0	48.8	19.2	71.9
66.	217	0	32.0	48.8	19.2	71.9
67.	217	0	32.0	48.8	19.2	71.9
68.	225	8	31.6	48.7	19.7	71.2
69.	235	10	30.6	48.9	20.5	70.5
70.	242	7	30.5	49.2	20.3	70.8
71.	244	2	30.6	48.8	20.6	70.4
72.	252	8	29.7	49.2	21.0	70.0
73.	256	4	30.0	48.9	21.1	69.8
74.	261	5	29.8	49.5	20.7	70.5
75.	266	5	30.4	48.5	21.1	69.7
76.	272	6	30.1	48.9	21.0	70.0
77.	273	1	30.0	49.1	20.9	70.1
78.	275	2	30.1	49.1	20.9	70.3
79.	279	4	30.7	48.8	20.5	70.4
80.	281	2	31.2	48.5	20.3	70.4
81.	281	0	31.2	48.5	20.3	70.4
10-Day Averages						
1-10.	64	10.3	18.0	67.1	15.0	81.6
11-20.	132	4.7	26.1	56.5	17.4	76.4
21-30.	163	2.2	29.9	53.1	17.0	75.7
31-40.	182	1.8	30.4	51.2	18.5	73.4
41-50.	195	1.1	30.1	50.7	19.2	72.6
51-60.	209	1.2	31.4	49.2	19.4	71.9
61-70.	221	2.9	31.8	48.9	19.4	71.7
71-80.	266	3.9	30.3	48.9	20.8	70.2

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