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ECOLOGICAL ANALYSIS OF THE CAYMAN ISLAND AVIFAUNA

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ECOLOGICAL ANALYSIS OF THE CAYMAN ISLAND AVIFAUNA

DAVID W. JOHNSTON¹

SYNOPSIS: Ecological studies of the avifauna carried out over the past eight years in the three Cayman Islands of the Caribbean Sea revealed the presence of 151 species, mostly transients. Grand Cayman has 39 species of breeding birds (26 terrestrial), Little Cayman 29 (17 terrestrial), and Cayman Brac 30 (20 terrestrial). Each island also supports an additional 40 North American migrants in winter. Seasonal occurrences and relative abundances of birds are described, particularly for seven upland ecological formations in which the greatest breeding species diversities occur in logwood-thatch palm-red birch and limestone forests. In one series, from pastureland through limestone forest, bird species diversity and total abundance increase with age of the community. High species diversity and density in the limestone forest are associated with some semblance of stratification but more so with a greater number of feeding niches. For the most part, the land birds breed in May and June at the onset of a rainy season.

In the past 30-40 years, two bird species have become extinct on Grand Cayman, whereas two others have at least attempted colonization. The problems of inter-island distributional patterns are discussed in an attempt to explain the presence and absence of different species on different islands. No evidence was found to support the idea that the absence of one species on an island permitted another one on that same island to broaden its ecological niche; rather, the absence of woodpeckers, a tanager, flycatcher, dove, finch, and others on the two small islands strongly suggests vacant niches on those islands.

Competition for environmental resources among the resident terrestrial birds was analyzed, especially between congeners and between species of similar ecologies. The four (or five) sympatric dove and pigeon species are separated chiefly by habitat and food differences; the two woodpeckers by food; four flycatchers by combinations of bill size, habitat, feeding height, and food type; the vireos by body size and bill size; and two *Dendroica* warblers by habitat and feeding height.

With the exception of the scarce Barn Owl, no significant vertebrate predators on birds occur on these islands. The largely ornithophagous owl probably represents the greatest single biological control of the avifauna.

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Feeding ecologies, habitat distribution, and taxon cycles are specified, where known, for all the resident terrestrial species. Taxon cycles appear to be similar to those of other insular avifaunas, despite the absence of montane refugia on the Caymans. Species in Stage I (evidently the recent colonizers) are more common in early seral stages ("marginal habitats"), whereas the endemic subspecies (Stage IV) are more abundant in the mature forests. Because of the relatively large number of available habitats, Grand Cayman has 3.8 habitats per species, an exceptionally high figure when compared with mainland and other insular populations. This value plus other data indicate a remarkable generalization for the Cayman Island birds.

The large number of wintering species appears to influence the residents very little because the wintering forms usually occupy feeding niches different from the residents. It is suggested that the winter is characterized by an abundant food supply (chiefly insects) that is incompletely exploited by the resident avifauna.

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INTRODUCTION

Despite the recent burgeoning of interest in island biogeography, few complete ecological investigations have been conducted on insular forms of virtually any taxon level. Theoretical treatments of insular population biology (e.g., MacArthur and Wilson 1967) necessarily relied heavily upon many literature sources in the construction of species-area curves, extinction-immigration curves, and other ecological models. This is not meant to imply that such derived models are necessarily incorrect or inadequate, but simply to underscore the need for more raw data on island

populations so that ecological models and generalizations might be more rigorously tested, amended, or even rejected. Since complete data for avian insular populations are particularly sparse, scattered in the literature, and often incomplete, the ecological model-builder or synthesizer must consult a multitude of scientific papers by different authors, each using different techniques and reporting usually single ecological parameters from widely different islands. For the entire complex of West Indian Islands, not one island has yet been subjected to a thorough, comprehensive investigation of its avifauna, despite the distributional survey by Bond (1971) and the general assessments of taxon cycles by Ricklefs and Cox (1972).

Accordingly, this report is an assemblage of published data, several years of personal field experience and collecting, and a thorough analysis of as many ecological parameters as possible for a single insular avifauna, namely that of the three small isolated Cayman Islands. Attention is focused on "standard" ecological parameters such as population densities, competitive interactions, food and feeding behavior, reproductive cycles, predation and other population controls, habitat and stratal distribution, and secondary succession. Even this comprehensive report, which corroborates and augments ideas from other insular studies, is admittedly incomplete in one important aspect—the impact on resident bird populations by a large contingent of North American birds that overwinter in these islands.

ACKNOWLEDGMENTS

Through the years a number of organizations have provided financial support for these investigations. They include a Biomedical Institutional Support Grant from the Division of Sponsored Research of the University of Florida, the Bradley Fisk Fund, the American Philosophical Society (Johnson Fund, Penrose Fund), and National Science Foundation (GB-2114). Partial subsidy for publication came from the Bradley Fisk Fund and the Division of Biological Sciences, University of Florida. Assistance in field observations and collections came from Jon C. Barlow, Charles H. Blake, Donald W. Buden, Alexander Cruz, Erma J. Fisk, and Albert Schwartz. David May made the insect identifications and Albert Laessle most of the fruit and seed identifications. Walter Auffenberg, Pierce Brodkorb, and Ronald Pine kindly assisted in the identification of vertebrate prey items. I am particularly indebted to Alexander Cruz, Daniel Simberloff, Carmine Lanciani, and Robert Ricklefs for spirited and helpful discussions that shed much insight on ecological problems concerning insular avifaunas. C. D. Hutchings, Chief Agricultural officer, and R. F. Pocock, Chief of Police of the Cayman Islands, were both cooperative in many ways especially in the collecting of birds. Finally, of inestimable value has been the lifelong field experiences of the islands' principal naturalist, Ira Thompson.

GENERAL DESCRIPTION OF THE ISLANDS AND THEIR AVIFAUNA

The three Cayman Islands (Grand Cayman, Little Cayman, Cayman Brac) lie in the northwestern Caribbean Sea where, as a group, their remote position is rather extreme among the many West Indian islands. Grand Cayman ($19^{\circ}20'N, 81^{\circ}20'W$) is approximately 290 km (180 mi.) south of Cuba, about the same distance northwest of Jamaica, and 480 km northeast of Honduras, the nearest point in Central America. Cayman Brac ($19^{\circ}43'N, 79^{\circ}50'W$) is 89 km east of Grand Cayman and 8 km east of Little Cayman. These three limestone islands are of similar geological structure and represent the projecting peaks of the ancient submarine Cayman Ridge extending from near British Honduras to Cuba (Richards 1955). Steep-sided submarine slopes occur around the islands, with a 100-fathom line lying only a few hundred meters offshore. Bartlett Deep, a 6,200 m trench, is found just south of Grand Cayman. Further indications of the isolation of these islands are the many well-marked animal species and subspecies that have been described from them, including birds (Johnston *et al.* 1971), insects (Clench, H. 1964), mollusks (Clench, W. 1964), and reptiles (Grant 1940).

These islands are typically low and flat. Much of Grand Cayman (185 km²) is less than five meters in elevation, although an east-west forested ridge on its north side reaches 20 m in places. Low-lying lagoons and inland swamps abound (Fig. 1). Chiefly because of a beautiful beach of coral sand on its western side, most of the human popula-

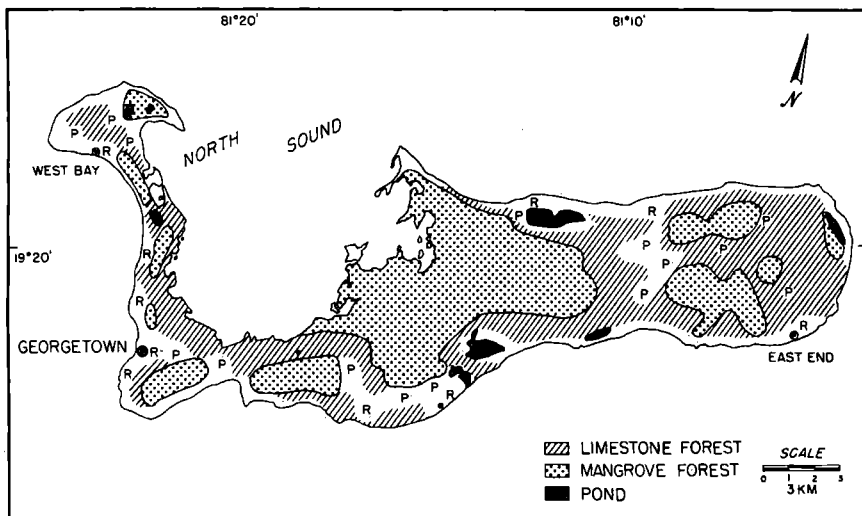


FIGURE 1.—Map of Grand Cayman showing general distribution of major forest types and ponds. P=pasturelands/clearings; R=residential areas.

tions are currently on that portion of the island, namely at Georgetown or West Bay or between the two. (In the early 1970s, however, an extensive construction "program" was rapidly expanding eastward and progressively engulfing formerly untouched natural communities.) Except along the western "seven-mile beach" a typical coral reef fringes the island. A honey-combed bluff limestone formation, often with an intermittent ridge and swale effect, characterizes the central, eastern, and southern parts of the island, whereas "ironshore" formation is especially prominent adjacent to the shoreline (Doran 1954). Pockets and crevices in the underlying rock frequently include a reddish soil formed by erosion of the original limestone.

Topographically and geologically, Little Cayman (24 km²) resembles Grand Cayman (cf. Fig. 1 and Fig. 2), except that relatively few places on the smaller island are over 4 m in elevation and the highest point is only 14 m. The few human inhabitants, largely clustered at the southwest end, have disturbed Little Cayman very little. A recently constructed road nearly encircling the island's shoreline forebodes "development."

Cayman Brac (31 km²) differs physiographically much from the other two islands, chiefly by the presence of an ascending (west to east) plateau with bluffs that reach 43 m at the island's eastern end. Abutting both the north and south sides are bluffs (Figs. 3 and 4). Closely associated with the existence of the high bluffs is a marked reduction in lagoons and mangrove swamp forests on Cayman Brac. The human popu-

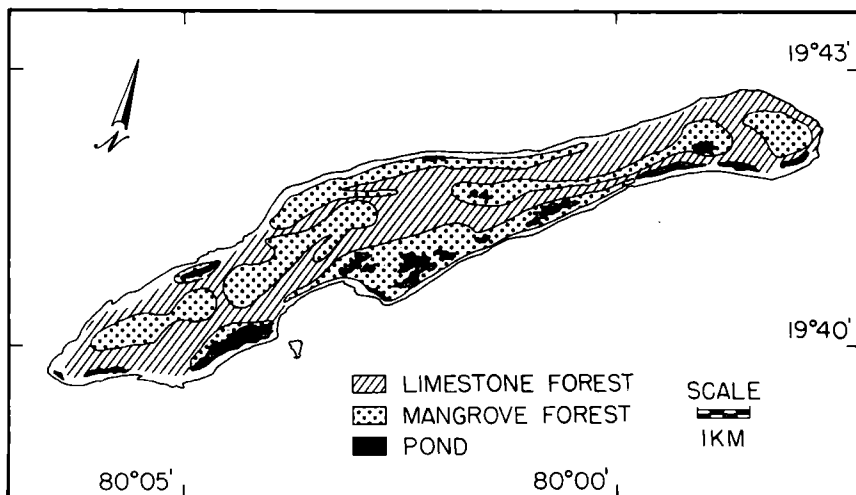


FIGURE 2.—Map of Little Cayman. Legend as in Figure 1.

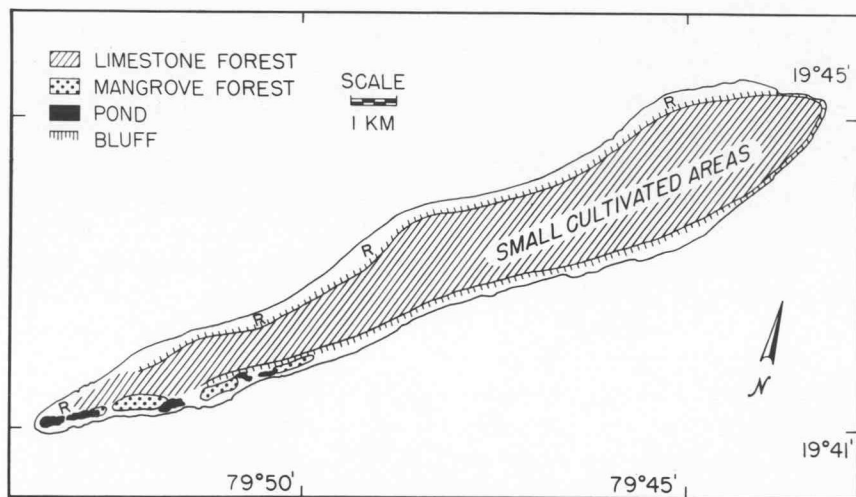


FIGURE 3.—Map of Cayman Brac. Legend as in Figure 1.



FIGURE 4.—Precipitous bluff on east end of Cayman Brac; sole breeding sites of *Sula leucogaster* and *Phaethon lepturus* in the Cayman Islands.

lation of a few hundred persons is now chiefly restricted to the north coast and western tip, although coconut plantations were once common on both coasts. Largely because of their relative inaccessibility, the bluff or limestone forests in the central highlands of the island have been little disturbed, except for scattered, small cultivations of vegetable crops.

The climate of the Cayman Islands is characterized by mild to hot temperatures and a distinct dry season. A weather station maintained at Owen Roberts airfield on Grand Cayman provided the temperature and rainfall data in Table 1. From the data supplied by the weather station personnel, the mean annual high temperature was calculated to be 30°C. Seasonal fluctuations in temperature are not extreme. On the other hand, both rainfall (annual mean of 154.9 cm) and prevailing winds do change seasonally. From May to October the prevailing winds are easterly, but through the winter months they tend to be from the northeast or northwest. A dry season extends from November through April, and periods of drought are frequent at other times. Despite an annual wet season during the summer and autumn months, the islands' low relief, desiccating winds, shallow soils, and porosity of the limestone formation preclude the humid, tropical, luxuriant vegetation characteristic of many West Indian islands. In fact, much of the natural upland vegetation (see later discussion), including the introduced species, takes the form of low xerophytic scrub, many of the plants possessing sharp spines and small leaves. Occasional autumnal hurricanes buffet the islands, and their effects may be quite severe, as was the hurricane of October 1944.

TABLE 1.—TEMPERATURE AND RAINFALL MEASUREMENTS AT OWEN ROBERTS AIRFIELD, GRAND CAYMAN, 1957-1970.

	Mean temperatures (C)				Mean rainfall (cm)
	maximum		minimum		
	mean	extreme	mean	extreme	
January	28	32	21	13	4.39
February	28	31	21	11	3.30
March	29	32	21	13	1.57
April	30	32	21	15	4.52
May	30	33	22	14	19.25
June	31	34	24	21	23.93
July	32	33	24	21	15.06
August	32	33	23	22	15.82
September	31	33	23	20	21.16
October	30	32	23	21	27.25
November	29	31	22	15	12.70
December	28	30	22	14	7.11

Through 1971, 151 species of birds had been recorded from the Caymans (Johnston *et al.* 1971). Most of these are North American migrants either in-transit or overwintering in the islands. A breakdown of the avifauna is as follows:

	Grand Cayman 185 km ²	Little Cayman 24 km ²	Cayman Brac 31 km ²
known or suspected breeding species:			
a. aquatic	13	12	10
b. terrestrial	26	17	20
total	39	29	30

These data fall within the expected ranges on a species-area curve determined by Ricklefs and Cox (1972) for small West Indian islands. Species numbers (12-47) for the small (18-658 km²) satellite islands off Hispaniola also generally conform to this species-area curve (Schwartz 1969).

Bond (1934: 345) believed that "Grand Cayman has received most of its bird life from Jamaica and Cuba, whereas Little Cayman and Cayman Brac have derived theirs from Cuba alone. . . ." Certainly the breeding terrestrial avifauna of Grand Cayman has many species in common with Cuba or Jamaica. But of the two smaller islands only one species (*Mimocichla rubripes*), which is restricted to Cayman Brac, has affinities with Cuban birds, whereas the remaining 18 species on the smaller islands have affinities with forms occurring in both Cuba and Jamaica. Furthermore, the Grand Cayman avifauna includes more species related to the Cuban avifauna than do the smaller islands.

The extent to which the origins of all the Cayman Island avifauna can be assessed accurately will always be speculative, partly because such an evaluation would depend upon the taxonomic level under consideration. For example, most biogeographers consider the family Parulidae to be of North American origin (Mengel 1964), but *Dendroica petechia eoa*, the Cayman Island form, also occurs on Jamaica. So, did this Yellow Warbler reach the Caymans from North America (perhaps via Cuba) and then spread to Jamaica, or follow the opposite route, or neither one? We really do not know the answer to this and related questions. It is nevertheless possible to assess affinities of avifaunas in a general way, as Bond (1934, 1966a) has attempted, and one would have to agree with Bond that by and large the Cayman Island avifauna probably originated chiefly from Central American elements. In this group, I would include the Columbidae, Cuculidae, Vireonidae, Coerebidae, Icteridae, and some Fringillidae. On the other hand, the closest relatives to the Caymanian *Amazona*, *Mimocichla*, *Colaptes*, *Centurus*, and *Melopyrrha* are presently Cuban. Contributions from Jamaica depend partly upon one's viewpoint but quite likely these include *Chordeiles minor*, most or all of the four species of Tyrannidae, *Dendroica petechia*, and perhaps *Spindalis* and *Quiscalus*.

My own field work and collections on these islands were initiated in 1965 and have continued intermittently for eight years, covering all seasons and all three islands, although most of the data were taken on Grand Cayman. Additional valuable field notes, specimens, bird stomachs, and other experiences on the islands in the past decade have been kindly shared with me by Albert Schwartz, Erma J. Fisk, Alexander Cruz, Ronald Pulliam, Jon C. Barlow, and Donald W. Buden.

ECOLOGICAL FORMATIONS

So that the distribution of the avifauna can be analyzed generally, major ecological formations for the islands are proposed, defined, and delineated here. Fundamental to the definition of the formations are major and minor plant associations, distinctive topographic features, and pertinent geologic, edaphic, and hydrologic conditions. These ecological formations are similar to, if not identical with, some of the major plant communities described by Asprey and Robbins (1953) from Jamaica. Implied for each formation are those general and specific niche requirements essential to the successful occurrence of each of its avifaunal components, including food and other trophic relationships, available nesting and feeding sites, and protective cover. In addition to the plant community analyses by Asprey and Robbins (1953), other reports have proven valuable in the definitions of these formations, namely those by Doran (1954) and Richards (1955) on geology, and Swabey and Lewis (1946) on forestry.

In evaluating insular avifaunas it is sometimes useful and desirable to include a "marine littoral element," essentially pelagic birds depending upon offshore waters for food and the island for breeding sites. Although this contingent is not considered here as a distinct, important ecologic formation, it is emphasized that at least four species of birds breeding on the Cayman Islands would be considered pelagic during the non-breeding season—*Phaethon lepturus*, *Sula leucogaster*, *S. sula*, and *Fregata magnificens*.

FRINGING REEFS AND LAGOONS.—For the most part the three islands possess fringing coral reefs that enclose shallow lagoons or sounds (Fig. 5), although on Cayman Brac the reefs are limited to the southwestern tip. The reefs, usually 30 to 100 m offshore, typically vary from about 0.5 m below sea level to about 0.3 m above. Water in the enclosed lagoons may be 3 m or more deep but is usually less than 1 m deep. Despite the incessant pounding of surf on the reefs and water depth of the lagoons, both are visited periodically for food by some herons, egrets, and terns, plus an occasional shorebird, especially at low tide.



FIGURE 5.—Typical fringing reef, lagoon, and sand-coral beach, Grand Cayman.

A distinctive feature of Grand Cayman is its immense North Sound (Fig. 1), embracing some 64 km² and partially separated from the open sea to the north by a broken reef and shoals. The greatest depth of the sound (near its center) is only about 6 m; much of its shallow floor abounds in turtle grass (*Thalassia testudinum*). Although the boundary of the North Sound with land is not always clear-cut, nonetheless much of its periphery is composed of red mangroves (*Rhizophora mangle*), with occasional mangrove islands in the sound. The sound and its fringing red mangroves are not generally used by aquatic birds, but at least one island (Booby Cay) is a well-known heron rookery, whereas other small mangrove islands provide temporary roosting sites for frigate birds, herons, and egrets.

SAND-CORAL BEACH.—The coastlines of the islands are composed of coral cobbles, sandy beaches, or steep bluffs. The beaches are best developed for about 5 km on the western end of Grand Cayman, a popular resort area. Steep bluffs (6-30 m) dropping off into deep water are best developed along the northeast coast of Grand Cayman and at the eastern end of Cayman Brac.

The sand-coral beach formation (Fig. 5) consists of blown coral sand and well-rounded coral fragments piled up and worn by winds, waves, storms, and hurricanes. This formation, some 3-10 m wide, has little covering vegetation, but some pioneer plants grow on it including

Sesuvium portulacastrum, *Ipomea* sp., and *Sporobolus virginicus*. On the landward side the sand-coral beach formation is continuous in many places with a rugged, irregular shore platform termed "ironshore." It slopes gradually to a height of 4-5 m, may extend inland some 10-50 m, and also possesses sparse or no vegetation, except in certain areas where woody thickets of *Caesalpinia bonduc* have developed.

SEA GRAPE-ALMOND WOODLAND.—This coastal vegetation formation is characteristic of the West Indies ("strand woodland" of Asprey and Robbins). From the "ironshore" or, where it is absent or poorly developed, from the sand-coral beach formation, the gradually ascending beach ridge supports a distinctive plant community dominated by *Coccoloba uvifera*, *Terminalia catappa*, *Thespesia populnea*, *Casuarina equisetifolia*, *Chrysobalanus icaco*, *Tournefortia gnaphalodes*, and other salt-resistant shrubs and forbs (Fig. 6). Commonly the trees are wind-pruned, desiccated in appearance, and no more than 5 m tall. On Grand Cayman, at least, this arboreal community usually does not exceed 30 m in width, but it does extend as a distinctive coastal band nearly around each of the islands. It has offered shade and sheltered sites for human habitations for many generations.

MANGROVE SWAMPS.—Extensive areas of Grand Cayman and Little Cayman are covered with mangrove or buttonwood swamps (see Figs. 1



FIGURE 6.—Sea grape-almond woodland with Australian pines behind beach on Grand Cayman.

and 2). In wetter and more saline places, as around North Sound, *Rhizophora mangle* predominates (Fig. 7), but farther inland at somewhat drier sites (at least seasonally) other mangroves (*Laguncularia racemosa* and *Avicennia nitida*) combine to form a thick-canopied forest (Fig. 8). At even drier sites, buttonwood (*Conocarpus erectus*) and mahogany (*Swietenia mahagoni*) dominate this formation. On the interior eastern side of North Sound these mangrove swamps attain their greatest development; the trees often reaching heights of 18-20 m. As will be demonstrated later, these swamps are important communities for wintering birds.

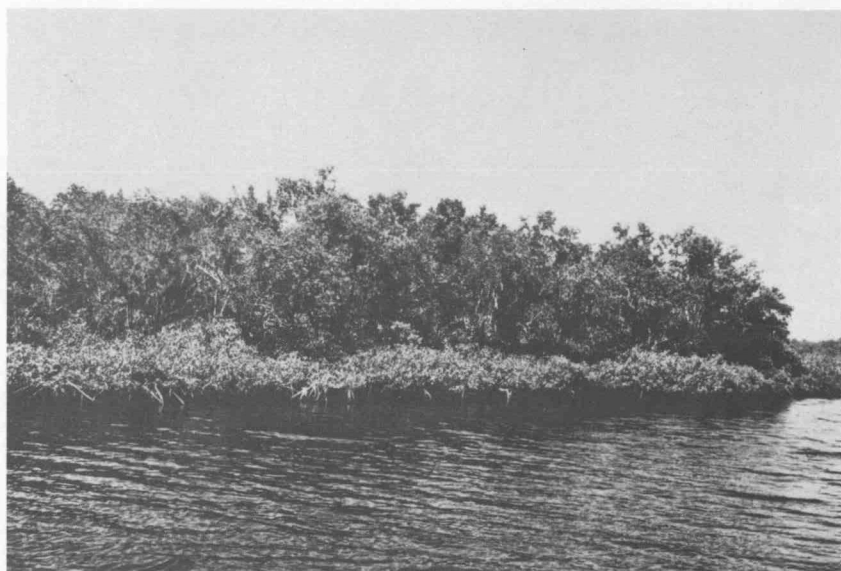


FIGURE 7.—Red (foreground) and black (background) mangroves beside North Sound, Grand Cayman.

PASTURES AND CULTIVATED AREAS.—Characteristically, for many years the Caymanian people have depended upon small cultivations for staples such as yam, cassava, potato, papaya, and bananas. Small cultivated areas, hewn and burned out of the limestone forests, are chiefly at inland sites, such as at the interior eastern end of Grand Cayman and on the bluff of Cayman Brac where pockets of red earth support the meager crops. Formerly coconuts (*Cocos nucifera*) were extensively cultivated, especially at coastal sites on Little Cayman and Cayman Brac, but a bud-rot disease has virtually eliminated the once flourishing coconut industry.

The "bush" has also been traditionally cleared for pastures especially



FIGURE 8.—Black and white mangrove forest, Grand Cayman.

on Grand Cayman (Figs. 9 and 10). Important introduced grasses of these pastures are Guinea grass (*Panicum maximum*) and Seymour grass (*Andropogon metusus*), and there are also scattered shrubs, such as *Comocladia dentata* and trees such as *Bursera simaruba*, *Roystonea* sp., and *Mangifera indica*. Maintenance of the pastures (i.e., the arresting of natural secondary succession to a woody community) is effected chiefly by sporadic man-made fires. These small, scattered fires are important, though not essential, ingredients in stirring up insects for anis, egrets, and swallows.

LOGWOOD FOREST OR SCRUB WOODLAND.—Pastures and other cleared areas, if not maintained as such, quickly revert to a woody community with the invasion of a variety of plants (Fig. 11). The latter include maiden plum, red birch, and especially the introduced logwood (*Haematoxylon campechianum*). Open and, later, dense stands of nearly pure logwood develop and are common on Grand Cayman on drier upland sites (Fig. 12). Local people often refer to the dense logwood as "scrub woodland." These stands, depending upon their age and other variables (soil and water), frequently include in later stages thatch palm (*Thrinax argentea*) and red birch, the combination woodland averaging about 6 m in height and forming a nearly impenetrable forest (Fig. 13). This formation is restricted to Grand Cayman and is most frequent in the middle section of the island.



FIGURE 9.—Partially cleared pastureland with scattered trees, Grand Cayman.

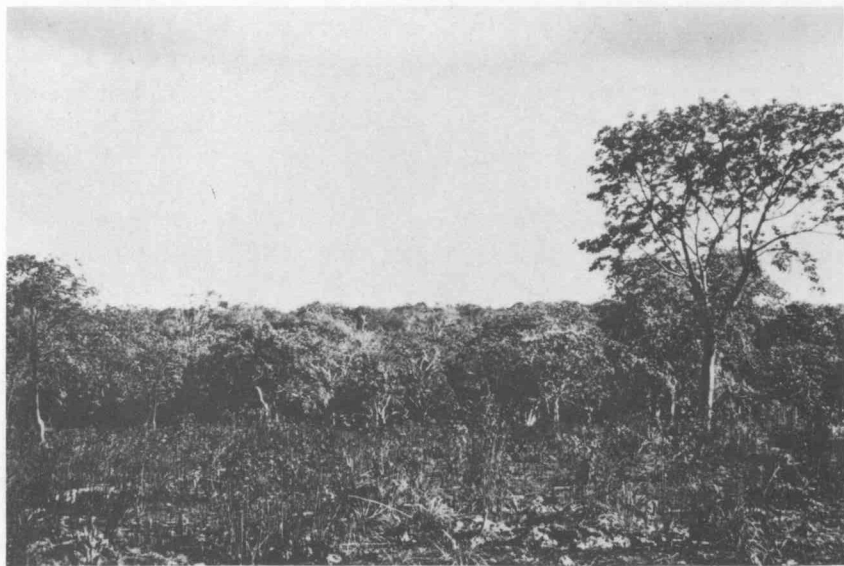


FIGURE 10.—Inland clearing for cassava, potato, and other vegetables with dense limestone forest in background, Grand Cayman.

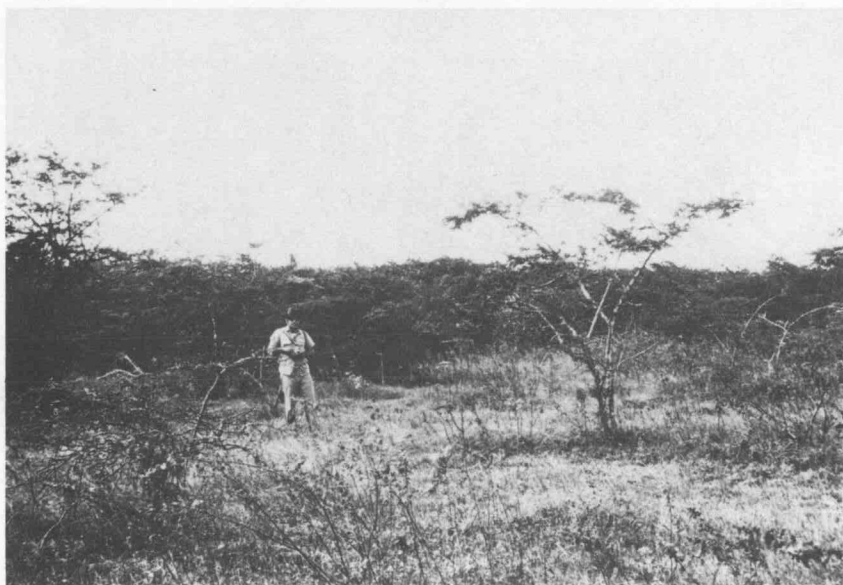


FIGURE 11.—Early logwood succession, Grand Cayman. Note interspersed grassy plots.



FIGURE 12.—Pure logwood forest (5 m high), Grand Cayman.



FIGURE 13.—Dense logwood-thatch palm-red birch forest (8 m high), Grand Cayman.

LIMESTONE FOREST.—Originally, this type of forest must have covered most of the drier upland portions of Grand Cayman (Swabey and Lewis 1946), especially on the northern and eastern sections where limestone ridges are common. These ridges, oriented in an east-west direction, commonly reach heights of 2-8 m, typically possess jagged honey-combed rocks, and are difficult to traverse except for a very few trails. With some red soil deposited, especially in intervening swales, the limestone ridges support a dense hardwood forest (Fig. 14), which has been selectively cut over as a source of lumber and other wood products for many years. The larger mahogany trees, in particular, have been removed, but even today this type of forest contains *Hippomane mancinella*, *Clusia flava*, *Cedrela odorata*, *Bursera simaruba*, *Eugenia* sp., *Ficus populnea*, and other hardwoods. Swabey and Lewis (1946) list some 30 species of trees as characteristic of this forest. The forest on Grand Cayman may reach a height of 14 m. Apparently the limestone forest formation on the Cayman Islands is of the same structure as that described for the wet limestone forest of Jamaica by Asprey and Robbins (1953).

The bluff limestone forest on Cayman Brac (Fig. 15) is of the same general character, except that mahogany is absent and cedar abounds due to the well-drained terrain. *Agave americana* is a conspicuous plant of



FIGURE 14.—Interior of dense limestone forest, Grand Cayman.

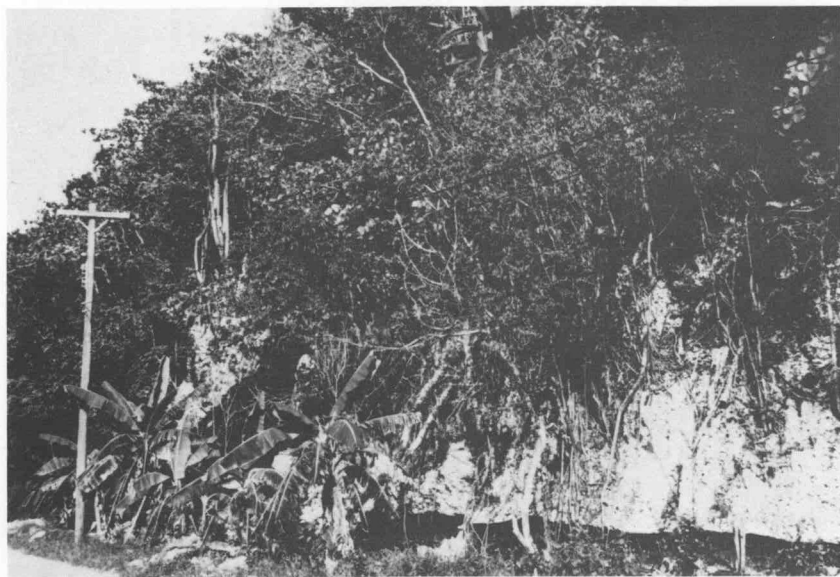


FIGURE 15.—Bluff limestone forest, Cayman Brac.

these bluffs. On Little Cayman the limestone forest of the inland sites is lower in height (6 m or less) and appears to be denser, with a greater frequency of mahogany and *Cereus* cacti.

INLAND LAGOONS AND PONDS.—Although no streams occur on these islands, to some degree all of them possess brackish lagoons (Fig. 16) just behind the coastal ridges. Farther inland on Grand Cayman and Little Cayman in lowlands are rain-fed ponds, chiefly brackish in nature and surrounded by mudflats or mangroves. These ponds are breeding sites for the abundant mosquito populations, but also support small fish (chiefly *Limia caymanensis* and *Gambusia p. puncticulata*) and crabs available to the piscivorous avifauna. Except for one large lagoon and a few ponds in mangrove swamps on the southwestern portion, Cayman Brac with its large central bluff is devoid of standing water.

TOWN AND HOUSE SITES.—Where the native vegetation has been cleared for houses, an important and distinctive ecological community has developed. House sites, for example, include clearings for small gardens, cultivated flowers and introduced shrubs, fruit-bearing trees, scattered shade trees, and ruderal areas (Fig. 17). The spread-out towns of Georgetown and West Bay on Grand Cayman are typical of this community with its introduced plants, which are attractive to certain bird species. Particularly attractive to birds are flowers of *Bougainvillea glabra*, *Delonix regia*, and *Nerium oleander* and fruits of *Coccoloba*



FIGURE 16.—Inland lagoon and mudflats with fringing mangroves, Little Cayman.

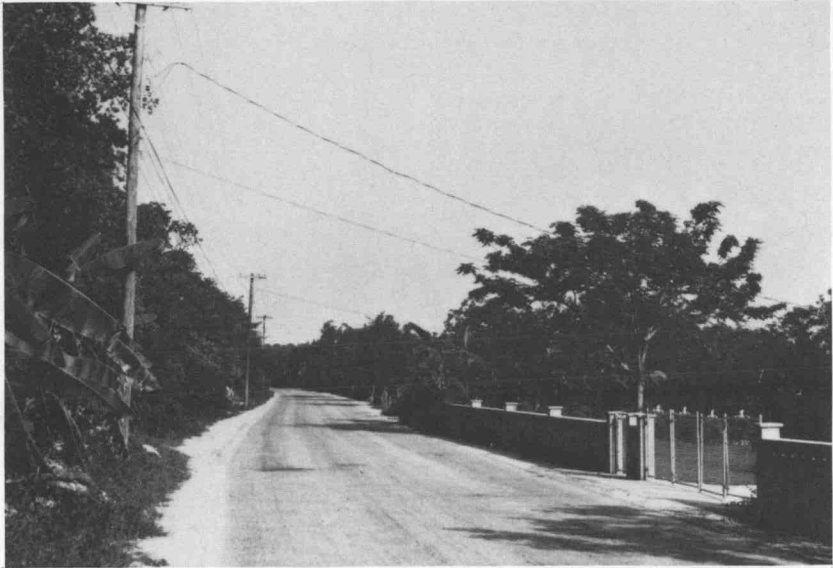


FIGURE 17.—Typical roadside and house-site habitat, Cayman Brac.

uvifera, *Bursera simaruba*, *Mangifera indica*, *Carica papaya*, *Psidium guajava*, and *Manilkara zapoda*. Included in this formation is the so-called "roadside community" which contains powerlines, poles, and fence lines. Because there is currently a small resident human population on Little Cayman (about 20), this ecological formation is virtually absent from that island.

AVIFAUNAL DISTRIBUTION IN THE ECOLOGICAL FORMATIONS

The impenetrability of most of the wooded formations on the Cayman Islands, the exceedingly rough and uneven terrain, and the absence of trails for accurately measuring distances made it possible to obtain precise quantitative measures of the terrestrial avifauna, except in unusual instances (see census data presented later). Thus, traditional techniques for measuring bird population densities, such as a transect-count or the territory-mapping technique, could not be employed in these investigations. A semi-quantitative method was devised, however, to provide relative indices of abundances of species populations. The method was used on all three islands, although most of the censuses were taken on Grand Cayman. Ten censuses, each of about two hours duration in early morning hours, were taken in representatives of each of the major ecological formations during the month(s) indicated in the accompanying tables.

After a count was made of all individual birds recorded during each census, relative scores were derived as follows:

U (uncommon)—5-20 individuals/20 hr.
FC (fairly common)—20-100 individuals/20 hr.
C (common)—100-300 individuals/20 hr.
VC (very common)—300 individuals/20 hr.

Excluded from the following summary tables are the rare or accidental species, that is, those observed less than five times in the total counts.

As a rule, bird species diversity is a positive function of vegetational complexity (MacArthur, Recher, and Cody 1966). Foliage height diversity is believed to be a good and reasonably accurate indicator of bird species diversity, particularly for tropical avifaunas. In the Cayman Islands, however, use of vegetation as an indicator was impractical for two major reasons: (1) with the exception of some limestone and inland mangrove forests, a given habitat studied for its avifaunal composition usually did not exceed 5 m in height; and (2) the honey-combed limestone terrain with its exceedingly dense vegetation (often impenetrable and thorny) precluded attempts to accurately measure vegetational strata and the organisms occurring in presumed strata. Rather, as will be indicated later, attention was given to average relative feeding heights of only potential competitors, especially congeners.

BIRDS OF FRINGING REEFS, LAGOONS, AND SAND-CORAL BEACH.—Table 2 summarizes the relative abundances of birds in this formation. It is important to note that few species are ever common here. *Thalasseus maximus* is the most common year-around inhabitant of the reef-lagoon-beach area where fish are plentiful in the shallow waters. Actually, no birds breed in this formation in the Cayman Islands; the summer occurrences of *Phaethon lepturus*, *Sula leucogaster*, *S. sula*, and *Fregata magnificens* represent birds feeding or flying over from nest-sites on nearby bluffs or lagoons farther inland. Otherwise, most of the 18 species in Table 2 are either migrants or winter residents that feed on the marine fauna (chiefly invertebrates and small fishes) found in this formation. Forms such as *Florida caerulea* and *Hydranassa tricolor* breed elsewhere on the islands and make only occasional visits to the beach area.

Of all the ecological formations studied here, this one has the lowest bird species diversity (10 in summer, 13 in winter) and the smallest populations.

BIRDS OF SEA GRAPE-ALMOND WOODLAND.—As stated earlier, this formation forms a belt around most of the islands and is an important woody, terrestrial community for birds because it provides (a) suitable nesting sites for 5-7 species, (b) a dependable food supply, and (c) at

TABLE 2.—BIRDS OF FRINGING REEFS, LAGOONS, AND SAND-CORAL BEACH.

Species	Island: Date:	GC December	GC Apr-June	LC August	CB June-Aug
<i>Phaethon lepturus</i>					C
<i>Sula leucogaster</i>				U	C
<i>Sula sula</i>				VC	
<i>Fregata magnificens</i>		U	FC	VC	FC
<i>Ardea herodias</i>		U			
<i>Florida caerulea</i>		U	U	U	
<i>Hydranassa tricolor</i>		U			
<i>Pandion haliaetus</i>			U	U	
<i>Squatarola squatarola</i>		FC	U	U	U
<i>Arenaria interpres</i>		FC	U	U	U
<i>Actitis macularia</i>		U	U		
<i>Tringa solitaria</i>		U			
<i>Catoptrophorus semipalmatus</i>		U	U		
<i>Larus atricilla</i>		FC	U		
<i>Sterna hirundo</i>		FC			
<i>Thalasseus maximus</i>		C	C		
<i>Ceryle alcyon</i>		U			
<i>Hirundo rustica</i>			C		
Total species		13	10	7	5

least a temporary first landfall for migrants. Three breeding forms (*Elaenia martinica*, *Dendroica petechia*, and *Coereba flaveola*) are common there throughout the year (Table 3). The very interesting *Nyctanassa violacea*, known locally as "crabcatcher," stalks small land crabs (chiefly *Gecarcinus lateralis* and *Cardiosoma guanhumi*) on the ground among the *Coccoloba* and *Terminalia* trees. Fruits of these and other trees are important seasonal dietary items of *Columba leucocephala* and both of the *Zenaida* species. In winter this formation supports at least 10 additional species of North American migrants, for the most part foliage-gleaning warblers (Parulidae).

BIRDS OF MANGROVE SWAMPS.—Although mangrove swamps differ floristically according to the dominant plant species (*Rhizophora mangle* or *Laguncularia racemosa* and *Avicennia nitida* or *Conocarpus erectus*), as a whole this formation teems with bird life, especially in the winter (Table 4). Noticeably high concentrations of North American warblers (12 species) utilize mangrove swamps in the winter months (see later analysis of the winter avifauna). Field observations of a non-quantitative nature suggest that insect food supplies also peak at this season. Even during the breeding season 10 bird species regularly inhabit this formation, with *Dendroica petechia* being exceptionally common at all seasons.

BIRDS OF PASTURES AND CULTIVATED AREAS.—Pastures, grasslands, and cultivated fields are well-known for relatively low densities of breeding

TABLE 3.—BIRDS OF SEA GRAPE-ALMOND WOODLAND.

Species	Island: Date:	GC December	GC June	GC August	LC August	CB June-Aug.
<i>Nyctanassa violacea</i>		U	U		U	
<i>Columba leucocephala</i>						C*
<i>Zenaida aurita</i>					FC*	
<i>Zenaida asiatica</i>					U	U
<i>Columbina passerina</i>		U	U	U	U	U
<i>Coccyzus minor</i>			U			U
<i>Coccyzus americanus</i>					FC*	
<i>Colaptes auratus</i>		FC	U*	U		
<i>Centurus superciliosus</i>			U			
<i>Sphyrapicus varius</i>		C				
<i>Tyrannus dominicensis</i>			U		C*	C*
<i>Tyrannus caudifasciatus</i>		FC		FC		
<i>Myiarchus stolidus</i>			FC*			
<i>Elaenia martinica</i>		FC	VC*	VC	VC*	VC*
<i>Mimus polyglottos</i>		U	U	U	FC*	U*
<i>Mimocichla plumbea</i>						U
<i>Vireo altiloquus</i>						U
<i>Vireo magister</i>		U				
<i>Mniotilta varia</i>		FC				
<i>Parula americana</i>		C				
<i>Dendroica petechia</i>		VC	VC*	VC		
<i>Dendroica tigrina</i>		U				
<i>Dendroica caerulescens</i>		U				
<i>Dendroica fusca</i>		U				
<i>Dendroica palmarum</i>		C				
<i>Geothlypis trichas</i>		U				
<i>Setophaga ruticilla</i>		FC				
<i>Coereba flaveola</i>		VC	VC*		VC*	C*
<i>Quiscalus niger</i>		U	U	C	FC*	
<i>Passerina cyanea</i>		U				
<i>Melopyrrha nigra</i>		U	U			
Total Species		21	13	7	10	10
* known or suspected breeders			5		7	5

birds in North America (Johnston and Odum 1956), and census data from the Cayman Islands are not an exception to this rule (Table 5). Only six species were found breeding in this formation. Some of these birds required nesting sites in low trees and shrubs at the edge of or in a partially cleared pasture. During the nonbreeding season an additional 10 species occurred at times in this formation, none of them (except *Ardeola ibis*) ever recorded as common.

BIRDS OF LOGWOOD FORESTS.—The dense logwood forests of Grand Cayman support 10 breeding species (Table 6), some of these being common or very common (*Vireo magister*, *Dendroica vitellina*, *Coereba flaveola*, and *Quiscalus niger*). As in other terrestrial formations discussed here, a significant number of migrant species (12) regularly inhabit this formation in the winter.

TABLE 4.—BIRDS OF MANGROVE SWAMPS.¹

Species	Island: Date:	GC December	GC June	GC August	LC August	CB June-Aug.
<i>Butorides virescens</i>		FC	U*	FC		
<i>Gallinula chloropus</i>			U*	U	U*	
<i>Columba leucocephala</i>		C	FC*	C	C*	
<i>Zenaida asiatica</i>			U			
<i>Ceryle alcyon</i>		U				
<i>Colaptes auratus</i>		FC	FC*	U		
<i>Centurus superciliosus</i>		U		U		
<i>Tyrannus caudifasciatus</i>		FC	U*			
<i>Myiarchus stolidus</i>		FC				
<i>Elaenia martinica</i>		U	C*	C	C*	VC*
<i>Poliophtila caerulea</i>		U				
<i>Vireo crassirostris</i>		U				
<i>Vireo magister</i>		FC	FC*	FC		
<i>Mniotilta varia</i>		U				
<i>Parula americana</i>		C				
<i>Dendroica petechia</i>		VC	VC*	VC	VC*	VC*
<i>Dendroica tigrina</i>		U				
<i>Dendroica caerulescens</i>		FC				
<i>Dendroica virens</i>		U				
<i>Dendroica dominica</i>		U				
<i>Dendroica discolor</i>		U				
<i>Dendroica palmarum</i>		C				
<i>Seiurus aurocapillus</i>		U				
<i>Seiurus noveboracensis</i>		U				
<i>Geothlypis trichas</i>		U				
<i>Setophaga ruticilla</i>		C				
<i>Coereba flaveola</i>		FC	C*	FC	C*	C*
<i>Spindalis zena</i>			U			
<i>Quiscalus niger</i>		C	C*	C	C*	
<i>Total Species</i>		26	12	10	6	3

* known or suspected breeders

10

6

3

¹ exclusive of roosting herons and egrets

BIRDS OF LOGWOOD-THATCH PALM-RED BIRCH FORESTS.—As plant species diversity increases from a logwood forest to this formation, so do the breeding and wintering bird populations (Table 7). Probably the *Haematoxylon-Thrinax-Bursera* formation contains a greater food diversity and more strata and feeding niches to support the avifaunal complex. This formation contains, among other forms, two breeding species of doves, two woodpeckers, three flycatchers, two vireos, and two warblers. Partitioning of food resources by these pairs will be discussed in a later section. Again, a significant invasion by wintering warblers is characteristic of this formation.

BIRDS OF LIMESTONE FORESTS.—As a whole, the limestone forests of the Cayman Islands support a relatively great variety of breeding birds (Table 8). For all three islands, 17 bird species breed in this formation;

TABLE 5.—BIRDS OF PASTURES AND CULTIVATED AREAS.

Species	Island: Date:	GC December	GC Apr-May	LC August	CB June-August
<i>Ardeola ibis</i>		C	C	FC	U
<i>Circus cyaneus</i>		U			
<i>Falco columbarius</i>		U			
<i>Falco sparverius</i>		U			
<i>Zenaida asiatica</i>		FC	FC		U
<i>Columbina passerina</i>		FC	FC*	C*	U*
<i>Amazona leucocephala</i>		U	U		U
<i>Coccyzus minor</i>		U	U		
<i>Crotophaga ani</i>		C	C*	FC*	FC*
<i>Chordeiles minor</i>			U*		U*
<i>Tyrannus dominicensis</i>				C*	U*
<i>Mimus polyglottos</i>		C	C*	FC*	U*
<i>Dendroica palmarum</i>		VC			
<i>Quiscalus niger</i>		FC	FC	U	
<i>Dolichonyx oryzivorus</i>			U		
<i>Tiaris olivacea</i>		FC	FC*	U*	U*
<i>Passerina cyanea</i>		U			
<i>Melopyrrha nigra</i>		U			
<i>Passerculus sandwichensis</i>		U			
<i>Ammodramus savannarum</i>		U			
<i>Total Species</i>		16	9	7	8
* known or suspected breeders			5	5	6

this represents 63 percent of the breeding terrestrial avifauna for the islands. Furthermore, during the breeding season the total population in this formation exceeds that of any other formation on the islands, with the exception of the town-house site-roadside formation. In winter, the limestone forests clearly do not attract as high a contingency of North American migrants as do the logwood, logwood-thatch palm-red birch, and mangrove forests. This may be partially explained by the so-called "irregularity principle," as discussed by Willis (1966), namely the tendency for migrants in the tropics to avoid extensive forests but to favor "irregular" or "peripheral" habitats, such as montane forests or isolated areas or those disturbed by man.

BIRDS OF INLAND LAGOONS AND PONDS.—In winter and spring migration periods, a large variety of birds is attracted to this formation (Table 9). This is due to (1) the abundant food supply (small fish, crustaceans, etc.) and (2) varying water depths that can accommodate both small wading birds, such as sandpipers, and birds feeding in deeper waters, such as occasional diving ducks. The low but dense mangroves surrounding such ponds provide nesting sites for herons and egrets.

BIRDS OF TOWNS, HOUSE SITES, AND ROADSIDES.—Areas subjected to human disturbance generally possess such a great variety of plant species

TABLE 6.—BIRDS OF PURE LOGWOOD FORESTS.

Species	Grand Cayman	
	December	June
<i>Zenaida asiatica</i>	FC	
<i>Colaptes auratus</i>	U	U*
<i>Centurus supercilii</i>	U	
<i>Tyrannus caudifasciatus</i>	C	
<i>Myiarchus stolidus</i>		U*
<i>Elaenia martinica</i>	U	U
<i>Mimus polyglottos</i>	FC	FC*
<i>Dumetella carolinensis</i>	C	
<i>Vireo crassirostris</i>	U	FC*
<i>Vireo magister</i>	C	C*
<i>Mniotilta varia</i>	U	
<i>Helmitheros vermivorus</i>	U	
<i>Parula americana</i>	FC	
<i>Dendroica petechia</i>	U	U*
<i>Dendroica tigrina</i>	U	
<i>Dendroica caerulescens</i>	U	
<i>Dendroica vitellina</i>	C	VC*
<i>Dendroica palmarum</i>	VC	
<i>Seiurus aurocapillus</i>	U	
<i>Seiurus noveboracensis</i>	U	
<i>Geothlypis trichas</i>	C	
<i>Setophaga ruticilla</i>	U	
<i>Coereba flaveola</i>	C	VC*
<i>Quiscalus niger</i>	U	C*
<i>Tiaris olivacea</i>		U*
<i>Melopyrrha nigra</i>	U	
Total Species	24	10
* known or suspected breeders		10

for nest sites and foods that birds are equally attracted. It is not surprising, therefore, to note the high number of bird species and their abundances found here (Table 10). Considering breeding birds alone, this formation supports the greatest species diversity and populations of all the terrestrial ecological formations on the Cayman Islands. Although this formation is relatively high in wintering migrants, these birds reach higher populations in other formations (for example, mangrove swamps and logwood forests). The avian population data from this disturbed formation, therefore, do not necessarily conform to the "irregularity principle" mentioned above.

POPULATION DENSITIES ON CAYMAN BRAC

A large area physically suitable for precise quantitative evaluation of bird populations was difficult to find on these islands. Such an area, however, was located at one relatively undisturbed site on Cayman Brac.

TABLE 7.—BIRDS OF LOGWOOD-THATCH PALM-RED BIRCH FOREST.

Species	December	Grand Cayman	
		Apr-May	August
<i>Columba leucocephala</i>	U		U
<i>Zenaida aurita</i>	U	U*	
<i>Zenaida asiatica</i>	U	U*	U
<i>Colaptes auratus</i>	FC	U*	U
<i>Centurus superciliosus</i>	U	FC*	FC
<i>Tyrannus caudifasciatus</i>		FC*	FC
<i>Myiarchus stolidus</i>	U	FC*	U
<i>Elaenia martinica</i>	C	VC*	C
<i>Dumetella carolinensis</i>	C		
<i>Vireo crassirostris</i>	FC	FC*	FC
<i>Vireo magister</i>	FC	FC*	U
<i>Mniotilta varia</i>	U		
<i>Helmitheros vermivorus</i>	U		
<i>Parula americana</i>	FC		
<i>Dendroica petechia</i>	U	U*	U
<i>Dendroica tigrina</i>	U		
<i>Dendroica discolor</i>	FC		
<i>Dendroica vitellina</i>	VC	VC*	VC
<i>Dendroica palmarum</i>	C		
<i>Seiurus aurocapillus</i>	U		
<i>Geothlypis trichas</i>	C		
<i>Setophaga ruticilla</i>	U		
<i>Coereba flaveola</i>	VC	C*	C
<i>Spindalis zena</i>		U*	
<i>Quiscalus niger</i>	C	FC*	FC
<i>Tiaris olivacea</i>	U		
<i>Melopyrrha nigra</i>	FC	U*	
Total Species	25	15	13

* known or suspected breeders

15

One side of a road contained 2.4 acres of limestone bluff forest and the other side, 4.8 acres of a scrubby woodland (not a logwood forest, however), including some house sites (Table 11). The limestone forest contained seven bird species, virtually the same species composition as observed in censuses of limestone forests at inland sites (Table 8) on this island. Furthermore, with the exception of *Columba leucocephala*, there is good agreement between the density figures in Table 11 and the relative abundance scores in Table 8. Both methods revealed high populations of *Elaenia martinica*, *Coereba flaveola*, and *Dendroica vitellina*, with lower values for *Zenaida asiatica* and the two vireos. The "scrub woodland" census showed high numbers of *Coereba flaveola*, *Dendroica vitellina*, *Elaenia martinica*, and *Tiaris olivacea*. The presence of *Tiaris*, *Mimus polyglottos*, *Columbina passerina*, and *Ardeola ibis* indicates a disturbed community from which the native trees and shrubs have been partially cleared, resulting in grassy or bare areas utilized by and essential

TABLE 8.—BIRDS OF LIMESTONE FORESTS.

Species	Island: Date:	GC December	GC Apr-May	GC August	LC August	CB June-Aug
<i>Columba leucocephala</i>			U*	FC	FC*	FC*
<i>Zenaida aurita</i>		U	U*		FC*	
<i>Zenaida asiatica</i>			U			FC*
<i>Columbina passerina</i>				U	C	U
<i>Leptotila jamaicensis</i>		U	U*	U		
<i>Amazona leucocephala</i>			FC*	U		U*
<i>Coccyzus minor</i>						U
<i>Tyto alba</i>			U			
<i>Colaptes auratus</i>		C	FC*	U		
<i>Centurus superciliosus</i>		C	FC*	FC		
<i>Tyrannus dominicensis</i>					U	
<i>Tyrannus caudifasciatus</i>				U	U	
<i>Myiarchus stolidus</i>			FC*	U		
<i>Elaenia martinica</i>		VC	VC*	VC	VC*	VC*
<i>Dumetella carolinensis</i>		U	U			
<i>Mimocichla plumbea</i>						U
<i>Vireo crassirostris</i>		FC	U*	U		U*
<i>Vireo altiloquus</i>					U*	FC*
<i>Vireo magister</i>		C	C*	FC		
<i>Mniotilta varia</i>		U				
<i>Parula americana</i>		U				
<i>Dendroica petechia</i>			U			
<i>Dendroica virens</i>			U			
<i>Dendroica vitellina</i>		C	FC*	C	C*	FC*
<i>Setophaga ruticilla</i>		U	U			
<i>Coereba flaveola</i>		VC	VC*	VC	VC*	VC*
<i>Spindalis zena</i>		U	FC*	U		
<i>Quiscalus niger</i>			U*	U	FC*	
<i>Melopyrrha nigra</i>		C	FC*	FC		
Total Species		15	21	16	10	11
* known or suspected breeders			15		7	8

to the feeding behavioral patterns of these four species. The avifaunal composition of this "scrub woodland" census is most closely comparable to that of the relative abundances for towns, house sites, and roadsides in Table 10.

BIRD POPULATIONS AND UPLAND SECONDARY PLANT SUCCESSION

Although detailed studies of secondary plant succession have not been carried out in the Cayman Islands, apparently some of the major ecological formations (plant communities) discussed above should be considered as climax: sea grape-almond woodland, mangrove forests, and limestone forest. (Some of the relatively dry buttonwood areas may not be climax.) At any rate, all the evidence from these islands, and chiefly from

TABLE 9.—BIRDS OF INLAND LAGOONS AND PONDS.

Species	Island: Date:	GC Dec.	GC Apr-May	GC Aug.	LC Aug.	CB June-Aug.
<i>Podilymbus podiceps</i>		C	U*	U	U*	U*
<i>Butorides virescens</i>		U	FC*	U	U*	U*
<i>Florida caerulea</i>		FC	FC*		U*	U*
<i>Ardeola ibis</i>		U	U*			U*
<i>Casmerodius albus</i>		U				
<i>Egretta thula</i>		VC	FC*	C	FC*	U*
<i>Hydranassa tricolor</i>		FC	VC*	VC	FC*	U*
<i>Plegadis falcinellus</i>		U				U
<i>Dendrocygna arborea</i>		U	U*	U	U*	
<i>Anas discors</i>		VC				
<i>Anas americana</i>		U				
<i>Aythya affinis</i>		U				
<i>Porphyryla martinica</i>			U	U		
<i>Gallinula chloropus</i>		VC	FC*	C	C*	U*
<i>Fulica americana</i>		VC			U*	
<i>Charadrius semipalmatus</i>						U
<i>Charadrius wilsonia</i>						U
<i>Squatarola squatarola</i>			U			FC
<i>Arenaria interpres</i>		FC	U		U	C
<i>Himantopus himantopus</i>		C	C*	C	C*	U*
<i>Capella gallinago</i>		U				
<i>Actitis macularia</i>		U	U		U	U
<i>Tringa solitaria</i>		U				
<i>Tringa melanoleuca</i>		U	U	U	U	
<i>Tringa flavipes</i>		U				
<i>Catoptrophorus</i>						
<i>semipalmatus</i>		U			U	U
<i>Calidris canutus</i>		U	U			
<i>Calidris pusilla</i>			U			FC
<i>Crocethia alba</i>			U			
<i>Limnodromus griseus</i>		U				
<i>Larus atricilla</i>			U			U
<i>Sterna hirundo</i>		U				
<i>Sterna albifrons</i>			FC*	FC	U*	C*
<i>Ceryle alcyon</i>		U				
<i>Riparia riparia</i>			U			
<i>Hirundo rustica</i>			VC	U		U
<i>Petrochelidon pyrrhonota</i>			U			
<i>Stelgidopteryx ruficollis</i>			U			
<i>Total Species</i>		26	23	11	14	19

* known or suspected breeders

10

10

9

Grand Cayman, points to one conspicuous secondary sere—from a pasture or cultivated field to logwood forest to logwood-thatch palm-red birch forest to a climax limestone forest. The time involved in each seral stage is unknown and is obviously subject to local variations, especially edaphic influences and drainage patterns, but certainly reversion of pastureland to logwood forest probably occurs within a few years

TABLE 10.—BIRDS OF TOWNS, HOUSE SITES, AND ROADSIDES.

Species	Island: Date:	GC December	GC Apr-May	GC August	CB June-August
<i>Ardeola ibis</i>					U
<i>Falco sparverius</i> **		U			
<i>Columba leucocephala</i>		U	U*	U	C*
<i>Zenaida aurita</i>					U
<i>Zenaida asiatica</i>		C	C*	U	
<i>Columbina passerina</i>		C	C*	C	C*
<i>Crotophaga ani</i>		C	C*	C	
<i>Colaptes auratus</i>		U	U*	U	
<i>Centurus superciliosus</i>		U	U*	U	
<i>Sphyrapicus varius</i>		U			
<i>Tyrannus dominicensis</i>			U*	U	C*
<i>Tyrannus caudifasciatus</i>		U	U*	C	
<i>Myiarchus stolidus</i>			U*	U	
<i>Elaenia martinica</i>		U	C*	C	C*
<i>Hirundo rustica</i> **		VC	C		
<i>Mimus polyglottos</i>		C	C*	C	FC*
<i>Dumetella carolinensis</i>		U			
<i>Mimocichla plumbea</i>					FC*
<i>Vireo crassirostris</i>			U*		U*
<i>Vireo magister</i>			FC*		
<i>Dendroica petechia</i>		FC	FC*		
<i>Dendroica vitellina</i>		U			FC*
<i>Dendroica palmarum</i>		VC			
<i>Coereba flaveola</i>		VC	VC*	VC	VC*
<i>Spindalis zena</i>			FC*		
<i>Quiscalus niger</i>			C*		
<i>Dolichonyx oryzivorus</i> **			U		
<i>Tiaris olivacea</i>		FC	FC*	FC	FC*
<i>Passerina cyanea</i>		U			
<i>Melopyrrha nigra</i>		FC	FC*	FC	
<i>Passerculus sandwichensis</i> **		U			
<i>Total Species</i>		21	21	14	12

* known or suspected breeders

** species typical of roadside only

because the seedlings of *Haematoxylon* are fast-growing.

By selecting representatives of these seral stages, it is then possible to assess the progression of the attendant avifaunal populations, especially during the breeding season (Table 12). As might be expected from similar analyses of secondary succession and bird populations on the North American mainland (Johnston and Odum 1956), with advancing ecological age and increasing complexity of the plant communities, there is a concomitant increase in breeding bird composition, at least through the subclimax (logwood-thatch palm-red birch) formation. Similarly, total density figures show an increase. On the other hand, if one considers the wintering populations (inclusive incidentally, of the

TABLE 11.—ROADSIDE CENSUSES ON CAYMAN BRAC.*

Species	Limestone Bluff Forest (2.4 acres)	Scrub Woodland** (4.8 acres)
<i>Elaenia martinica</i>	60***	16
<i>Mimus polyglottos</i>	0	4
<i>Coereba flaveola</i>	44	28
<i>Mimocichla plumbea</i>	0	6
<i>Vireo crassirostris</i>	4	6
<i>Vireo altiloquus</i>	6	0
<i>Dendroica vitellina</i>	12	24
<i>Tiaris olivacea</i>	0	16
<i>Tyrannus dominicensis</i>	0	6
<i>Columbina passerina</i>	0	2
<i>Zenaida asiatica</i>	8	4
<i>Coccyzus minor</i>	4	0
<i>Ardeola ibis</i>	0	2

* Average number of birds seen per five 1-hour censuses in late June 1970

** Included three house sites and yards

*** All density figures are converted to a 10-acre basis

TABLE 12.—BIRDS OF PROBABLE SUCCESSIONAL STAGES ON GRAND CAYMAN.

Breeding Species	Pastures and Cultivated Areas	Logwood Forest	Logwood- Palm-Birch	Limestone Forest
<i>Columbina passerina</i>	FC			
<i>Crotophaga ani</i>	C			
<i>Chordeiles minor</i>	U			
<i>Mimus polyglottos</i>	C	FC		
<i>Tiaris olivacea</i>	FC	U		
<i>Dendroica petechia</i>		U	U	
<i>Vireo crassirostris</i>		FC	FC	U
<i>Colaptes auratus</i>		U	U	FC
<i>Vireo magister</i>		C	FC	C
<i>Dendroica vitellina</i>		VC	VC	FC
<i>Coereba flaveola</i>		VC	C	VC
<i>Quiscalus niger</i>		C	FC	U
<i>Myiarchus stolidus</i>		U	FC	FC
<i>Zenaida asiatica</i>			U	
<i>Tyrannus caudifasciatus</i>			FC	
<i>Zenaida aurita</i>			U	U
<i>Centurus superciliosus</i>			FC	FC
<i>Elaenia martinica</i>			VC	VC
<i>Spindalis zena</i>			U	FC
<i>Melopyrrha nigra</i>			U	FC
<i>Amazona leucocephala</i>				FC
<i>Columba leucocephala</i>				U
<i>Leptotila jamaicensis</i>				U
Total breeding species	5	10	15	15
Abundance index*	11	22	29	30
Total wintering species	16	24	25	15
Abundance index	30	42	47	32

* Obtained by summations of equivalent values: U=1, FC=2, C=3, VC=4.

resident breeding complement) separately, it is apparent that the climax limestone forest does not support the densest population in this sere. An explanation for the relative decrease in winter in this climax formation may be found in part in the "irregularity principle" cited earlier (Willis 1966). Perhaps, in turn primary productivity is higher annually in the subclimax logwood-thatch palm-red birch formation than in the limestone forest.

Note should also be made of the changing proportions between seral stages of uncommon and fairly common species to the common and very common ones. In early seral stages common and very common species represent 66 percent of the birds, but in the subclimax and climax stages these classes comprise only 25 percent of the breeding avifauna. Conversely, in the climax seral stage the proportion of uncommon and fairly common species increases. A completely satisfactory explanation of this phenomenon cannot be provided at the present time, but several factors are influential. First, in both the subclimax and climax stages, there is an obvious increase in niches available to the avifauna, the niches markedly influenced by increasing tree species diversity and attendant stratification of the foliage. Second, among the species found only in the limestone forest and yet ranked only as uncommon or fairly common are *Amazona leucocephala*, *Columba leucocephala*, and *Leptotila jamaicensis*. All these birds are large in body size and from numerous field observations appear to have large home ranges. Thus, on a unit area basis each of these species would maintain lower densities than smaller birds with smaller territories. Finally, a factor undoubtedly influencing the habitat distribution of these three species is food. All are frugivores and on Grand Cayman their preferred fruiting trees during the breeding season are most abundant in the limestone forests (see Appendix III).

BREEDING SEASONS

Breeding seasons of tropical and equatorial birds have received the attention of biologists especially interested in elucidating causative factors underlying the seasonality. There is a dearth of published information for insular avifaunas, so the present data from the Cayman Islands should be of value despite their geographic location north of the equator.

Few concerted efforts have been made by any single investigator to obtain quantitative breeding data for any species on these islands, although such long-term efforts would certainly be rewarding for the analysis and interpretation of annual population fluctuations, natality, mortality, and population controlling mechanisms. Indeed, it is a sad commentary that no one ever recorded breeding data for the extinct Grand

Cayman Thrush (*Mimocichla ravidia*), although the species was observed and collected by ornithologists over a span of some 50 years. Contemporary data on breeding seasons of birds of the Cayman Islands are summarized in Table 13, the data having been derived from the scanty literature, from my own experiences, and those of Donald W. Buden who spent five continuous months on Grand Cayman in the spring of 1970.

A number of features in Table 13 merit special mention. *Sula leucogaster* shows a bimodal breeding season, a characteristic of this species well-known from several previous reports on other islands (Schreiber and Ashmole 1970). *Tyto alba*, although not studied in detail throughout the year, clearly shows some peak of breeding activity in mid-winter. *Mimus polyglottos*, from fragmentary observations and reports, has a protracted breeding period in the spring. *Coereba flaveola* apparently breeds in every month of the year.

The annual breeding cycles of land birds on the Cayman Islands conform generally to Immelmann's description (1971: 348-9): "Most birds of regions with a regular change between one long dry and one long wet season per year . . . breed around the rainy season with only a few specialists laying during the dry period." In Table 13, it is evident that peak breeding on the Caymans is in May and June; in each of these months 54 percent of the land birds are breeding and, for June, 55 percent of all the breeding species. By referring to Table 1, it can be seen that this peak in breeding activity coincides with the onset of the wet season. Tentatively, then, it would appear that rainfall is an important proximate factor in regulating breeding, a conclusion similarly reached by Snow and Snow (1964) for Trinidad. Obviously, the wet season (May-October) is the period in which resident birds should reach their highest annual population densities and should make their greatest demands on food resources. Quantification of food resources was not made in this study, but it is quite likely that the wet season is a time of maximum food availability. The quantitative report by Dingle and Khamala (1972: 220) at African localities is relevant here: "Most savanna and dry country birds breed during the long rains; this breeding is correlated with a major increase in the availability of insect food." (On the other hand, as discussed later, the dry winter months must also be a season of abundant foods, especially small insects, to support the influx of North American migrants, many of which glean insects from leaf surfaces in the mangrove and limestone forests.)

The "specialists laying during the dry period" (Immelmann 1971) should more properly be called generalists in this sense, especially if they breed during both dry and wet seasons. Among the Cayman avifauna in this category are *Crotophaga ani*, *Tyto alba*, *Coereba flaveola*, and prob-

TABLE 13.—BREEDING TIMES OF BIRDS ON THE THREE CAYMAN ISLANDS.*

Species	J	F	M	A	M	J	J	A	S	O	N	D
<i>Podilymbus podiceps</i>							Y					
<i>Phaethon lepturus</i>						N						
<i>Sula leucogaster</i>						Y					Y	Y
<i>Sula sula</i>			N			N	Y					
<i>Fregata magnificens</i>						N	Y					
<i>Florida caerulea</i>				Y								
<i>Ardeola ibis</i>						Y						
<i>Hydranassa tricolor</i>		Y	Y									
<i>Nyctanassa violacea</i>						Y						
<i>Gallinula chloropus</i>				Y								
<i>Fulica americana</i>							Y					
<i>Himantopus himantopus</i>				N	NY							
<i>Catoptrophorus semipalmatus</i>						N						
<i>Sterna albifrons</i>					NY	NY		Y				
<i>Columba leucocephala</i>								N				
<i>Zenaida aurita</i>							N					
<i>Amazona leucocephala</i>			N	N	Y	Y						
<i>Coccyzus minor</i>					Y							
<i>Crotophaga ani</i>				Y							Y	Y
<i>Tyto alba</i>												Y
<i>Chordeiles minor</i>					Y							
<i>Colaptes auratus</i>							Y	Y				
<i>Centurus supercilii</i>			N	N	N							
<i>Tyrannus dominicensis</i>						N						
<i>Tyrannus caudifasciatus</i>						N						
<i>Myiarchus stolidus</i>		N	N	N								
<i>Elaenia martinica</i>					N	N						
<i>Mimus polyglottos</i>	?	?	?	?	N	N						
<i>Mimocichla plumbea</i>					N	N						
<i>Vireo crassirostris</i>						N						
<i>Vireo magister</i>					N	Y						
<i>Dendroica petechia</i>				NY	NY	Y						
<i>Dendroica vitellina</i>				N	Y	Y						
<i>Coereba flaveola</i>	N	N	NY	N		N	N	N	N	N		N
<i>Spindalis zena</i>			N		NY							
<i>Quiscalus niger</i>							Y					
<i>Tiaris olivacea</i>			N		N	N						
<i>Melopyrrha nigra</i>					Y	Y						Y
Totals (N and/or Y)	1+	2+	8+	11+	15	21	8	4	1	1	2	5

*includes all breeding species for which data are available, based upon nests (N) and/or dependent young (Y).

ably *Mimus polyglottos*. *Crotophaga* is obviously an omnivore (see Appendix III), *Tyto* preys on birds and rodents, and *Coereba* is chiefly a nectarivore. Considering the small populations of *Tyto* on these islands, an apparently adequate food supply, and the absence of a competitor, the breeding season of this owl should not *a priori* be restricted by either a wet or dry season. *Crotophaga* is more abundant, occurring in scattered but small and discrete groups in many ecological formations; because of its omnivorous habits, it too would hardly be restricted in breeding by wet or dry seasons. Perhaps a similar argument could be made for *Mimus*, but less is known of this species' annual cycle. *Coereba* is an interesting case, because throughout its range in the Caribbean region it is renowned for a protracted breeding season. In the absence of hummingbirds (at least for the Cayman Islands) this Bananaquit can utilize a unique food resource (nectar and tiny insects) to support a large and widespread population at all seasons.

INTER-ISLAND DISTRIBUTIONAL PATTERNS

Archipelagos are renowned for their interrupted distributional patterns among the avifauna. In this context, examples are found in individual species of Galapagos finches (Geospizidae) and Hawaiian honeycreepers (Drepaniidae). However, patterns above the family level, although often well known for a given archipelago, have largely been overlooked in the literature, and since the Cayman Island avifauna contains conspicuous examples of distributional "anomalies," an analysis of these distributional patterns is discussed here and summarized in Table 14.

One is faced, of course, with the obvious question—why is species A restricted to a given Cayman island and yet species B, whether a congener or not, occurs on all three islands? At the outset, several basic premises must be recalled and at least temporarily accepted: (1) the three Cayman islands are of a similar geological age; (2) with relatively minor exceptions (introduced logwood and its scattered stands limited to Grand Cayman), ecological formations or habitat structures appear to be identical, or nearly so, among the three islands (see previous discussion); (3) the three islands are each approximately the same distances from both Cuba and Jamaica, the potential if not actual sources of most of the avifauna; (4) Grand Cayman has a much greater land area than the smaller islands, and certainly the areal expanse of each ecological formation is far greater on the larger island; and (5) there is no evidence that hurricane tracks or wind or water currents are extraordinarily restricted to any one of the islands.

Pertinent to these disjunct distributions are the statements by Whitehead and Jones (1969: 176): "... if one assumes that the rate of move-

TABLE 14.—SOME INTER-ISLAND BREEDING DISTRIBUTIONAL PATTERNS.

Species	Grand Cayman	Little Cayman	Cayman Brac
<i>Phaethon lepturus</i>			breeds
<i>Sula leucogaster</i>		+ *	breeds
<i>Sula sula</i>		breeds	
<i>Fregata magnificens</i>	+	breeds	+
<i>Dendrocygna arborea</i>	breeds	breeds	
<i>Columba leucocephala</i>	breeds	+	breeds
<i>Leptotila jamaicensis</i>	breeds		
<i>Amazona leucocephala</i>	breeds	+	breeds
<i>Colaptes auratus</i>	breeds		
<i>Centurus superciliosus</i>	breeds		
<i>Myiarchus stolidus</i>	breeds		
<i>Mimocichla plumbea</i>	+		breeds
<i>Vireo altiloquus</i>	+	breeds	breeds
<i>Vireo magister</i>	breeds		
<i>Spindalis zena</i>	breeds		
<i>Quiscalus niger</i>	breeds	breeds	+
<i>Melopyrrha nigra</i>	breeds		
Totals = 17	11	5	6
Breeding endemic on only one island	7	2	3

* + = present, but contemporary breeding unconfirmed

ment of propagules . . . across a given segment of ocean surface is essentially constant through time, it follows that larger islands will intercept a larger number of disseminules per unit time." On this basis one would expect Grand Cayman to support a larger resident avifauna (39 species) than the two smaller islands (Cayman Brac 30, Little Cayman 29). This is only a partial explanation, however, because habitat areal expanse and standing water with its concomitant mangrove swamps are also important factors supporting a diversity of bird life.

With these ideas in mind, we can initiate an analysis of the interesting, interrupted distributional patterns as summarized in Table 14. *Phaethon lepturus* and *Sula leucogaster* prefer or require for breeding the high bluffs occurring only on Cayman Brac. *Sula sula* and *Fregata magnificens* currently maintain a moderate-sized breeding colony in the landward mangrove fringe of a large shallow lagoon on Little Cayman. The physiognomy of this lagoon site appears similar to those on Grand Cayman, but these birds have not bred on Grand Cayman, at least in historical times. Perhaps quite local prevailing winds and the lack of human disturbances are primary factors in the restricted breeding distributions of these two species on Little Cayman. *Dendrocygna arborea* is evidently confined as a breeding bird to Grand Cayman and Little Cayman where mangrove swamps and ponds are common (cf. Figs. 1, 2,

3); breeding of this species has not been confirmed for Cayman Brac, an island where open water and mangrove swamps are quite limited.

Columba leucocephala and *Amazona leucocephala* evidently do not currently breed on Little Cayman, although both species are at least moderately common on the other two islands. Longtime human residents of Little Cayman report that both of these species breed on Cayman Brac and that small flocks of each undertake daily round-trip flights to Little Cayman for feeding purposes only. *Leptotila jamaicensis*, a large ground-feeding dove, is a species with one of the most restricted ranges of all the Cayman Island avifauna, being found only in the remote inland limestone forests of Grand Cayman. Why it does not occur on the other two islands is unknown. *Quiscalus niger*, a ubiquitous and conspicuous resident of both Grand Cayman and Little Cayman, is virtually unknown on Cayman Brac. Small groups sometimes fly back and forth between the two smaller islands (8 km) but there is presently no rational explanation for its absence as a breeding bird on Cayman Brac.

The eight remaining species in Table 14 present puzzling distributional patterns among the three islands. Why are *Colaptes*, *Centurus*, *Myiarchus*, *Vireo magister*, *Spindalis*, and *Melopyrrha* all restricted to Grand Cayman? Why does not *Mimocichla plumbea* occur permanently on Grand Cayman and Little Cayman, the latter only 8 km from Cayman Brac? Apparently, favorable habitats for this species would be the same for all three islands. One is tempted to explain these patterns by suggesting that the original successfully breeding pair(s) reached only one island (usually the largest) from the source population. In subsequent times, perhaps fortuitously, propagules have failed to reach the other islands, and the populations now established on the single island became sedentary. This could be the explanation for these eight species. Is it probable, however, that of the four forms with definite Cuban affinities (*Colaptes*, *Centurus*, *Melopyrrha*, and *Mimocichla*), all but the latter one should colonize only Grand Cayman?

In reviewing all these distributional patterns, I am inclined to support a chance-colonization hypothesis for a number of reasons. In the first place, preferred ecological formations on Cayman Brac, for example, appear to be potentially suitable to all these terrestrial species currently restricted to Grand Cayman, and it is likely that they simply never reached the other islands. Alternatively, populations could have become extinct. Second, two species (*Zenaida asiatica* and *Mimus polyglottos*) have within quite recent years spread from island to island and now maintain breeding populations on islands where each was absent as recently as 25 years ago. Third, *Mimocichla plumbea* has been recorded as a vagrant on Grand Cayman (Johnston 1969) where an unmated fe-

male, previously unrecorded from this island, even constructed unsuccessful nests in at least two successive years. The point is that with the possible exception of the congeneric vireos in which competitive exclusion may be an important limiting factor (see discussion beyond), most if not all of the terrestrial birds currently restricted to a single island could probably successfully colonize any of the other islands (contra Bond 1934: 345-346). Perhaps the sedentary habits of species now restricted to Grand Cayman and the distance (97 km) to the other islands have served as barriers to their dispersal to the smaller islands. This latter point, emphasizing a "poor" immigration rate of birds such as woodpeckers, is in substantial agreement with the views of Ricklefs and Cox (1972: 215).

Among the most curious distributional features of the Cayman Island avifauna is the absence of resident hummingbirds. This fact is especially anomalous when it is recalled that (1) every other major island and land mass east, west, and north of the Caymans all have several resident hummingbird species (Moynihan 1968; Bond 1971), (2) hurricane paths in the past argue for the possibility of widespread dissemination of birds in the Caribbean region, and (3) occasional hummingbirds are known to migrate through Grand Cayman (Johnston *et al.* 1971). Collectively, these points tend to negate an hypothesis that hummingbirds could not or have not reached the islands in the past. The problem is, I believe, whether or not conditions are currently favorable for their existence in the islands. The absence of breeding hummingbirds is related to two factors, a dependable food supply and the possible role of potential competitors.

As pointed out elsewhere in this paper, the small size, low relief, desiccating winds, sparse soils, and porous limestone base of the Caymans preclude the support of luxuriant tropical vegetation, despite the moderately heavy, though seasonal, rainfall. The extensive expanses of limestone and mangrove forests of the Caymans (Figs. 1, 2, 3) are not characterized by the diversity, distribution, or abundance of flowering trees and shrubs that one finds elsewhere in the West Indies. Although quantitative support cannot be marshalled for this statement on plant diversity and distribution for the Cayman Islands, it is obvious that most of the favorite hummingbird nectar-bearing plants of Jamaica (*Hibiscus*, *Bougainvillea*, *Nerium*, *Tamarindus*, *Psidium* and many others) are at best limited chiefly to scattered and relatively sparse house sites on the Caymans. Thus, I believe that even if potentially immigrant hummingbirds did currently find their way to the Caymans, a dependable food supply would not be available.

Another consideration in the lack of hummingbirds is the possibility of

competition specifically with the ubiquitous Bananaquit (*Coereba flaveola*). Throughout the rest of the West Indies and Central America where hummingbirds and *Coereba* are sympatric, there is much evidence that hummingbirds dominate *Coereba* at food sources (see, for example, Wetmore 1927). Furthermore, hummingbirds and these bananaquits generally feed in different fashions, though often utilizing the same food source simultaneously. None of these features suggest that competition does or would play a significant role in explaining the absence of hummingbirds on the Caymans.

Intriguing questions on niche breadth, occupancy, and vacancy are invoked by these inter-island distributional patterns. Characteristic timber-probing woodpeckers (*Colaptes* and *Centurus*) are absent from the two smaller islands. For these woodpeckers island size and habitat diversity are important limiting factors. Three species that are frugivorous in low trees or on or near the ground surface on Grand Cayman are *Leptotila*, *Spindalis*, and *Melopyrrha*. Are these feeding niches simply vacant on the smaller islands? They probably are, but not enough is known of comparative feeding behaviors of species with similar feeding patterns where a competitor is absent. For example, it is possible, though not documented, that *Elaenia* has a broader feeding niche on Cayman Brac (both qualitatively and quantitatively) than on Grand Cayman, where it undoubtedly competes with *Spindalis*, *Melopyrrha*, and other species for small fruits. Similarly, the absence of the foliage-gleaning insectivorous *Myiarchus* on the two small islands might release potential competitors (*Vireo*, *Dendroica*) to the extent that their feeding behavior patterns are broadened on Little Cayman and Cayman Brac. These and related points certainly merit future intensive studies.

IMMIGRATION AND EXTINCTION

An equilibrium model for the number of species on an island was developed by MacArthur and Wilson (1967), who predicted that the number of species on an island is determined by a balance between immigration and extinction rates. Our current knowledge of the Cayman Island avifauna provides some concrete examples in support of this model, despite the fact that few bird species and a relatively short period of time are involved. There is sufficient evidence, for example, that two birds (*Mimocichla ravidia* and *Icterus leucopteryx bairdi*) are now extinct on Grand Cayman, where formerly (1900-1916) both were moderately common and were last observed in the 1930s (Johnston *et al.* 1971). Unfortunately, no precise information is available on the causes of their extinction, whether by hurricanes, partial habitat destruction, human dis-

turbance, or a combination thereof. Another thrush, *Mimocichla plumbea rubripes*, became extinct on Swan Island, possibly because of forest destruction (Paynter 1956). Both species on Grand Cayman, incidentally, were undoubtedly in Stage IV of a taxon cycle because, among other characteristics, each was highly restricted in habitat distribution, the thrush probably to limestone forests and the oriole to sites on the northern coast. (*I. l. leucopteryx* is still common on Jamaica as is *I. l. lawrencii* on St. Andrews Is.) Conversely, the White-winged Dove (*Zenaida asiatica*) has invaded all three Cayman Islands since about 1935 and is now a well-established and common resident, especially in more peripheral habitats of the islands. A spurious attempt at colonization by an unmated female *Mimocichla plumbea* on Grand Cayman was earlier documented by Johnston (1969). If one can include this last occurrence as a bona fide instance of immigration, then within the last 40 years Grand Cayman alone has experienced two instances of avian extinction and two of immigration. Even if one considers the *Mimocichla* incident as being an unsuccessful immigration, the data still fit the MacArthur-Wilson model for a small island where the probability of extinction increases with decreasing island size.

Immigration and extinction are not well documented for birds on the smaller islands (Cayman Brac and Little Cayman), chiefly because few ornithologists have carefully studied the birds of these islands until recently (Johnston *et al.* 1971). The interrupted distribution of certain species on these islands is both curious and unexplained (see Table 14), especially since histories underlying the current distributional patterns are largely unknown, and little information is available on food, habitat, and other ecological factors. Evidently *Amazona leucocephala* does not presently breed on Little Cayman (if it ever did, despite old specimens and observations to the contrary), but small flocks regularly fly over from Cayman Brac during the day to feed on ripe fruits. Conversely, the older ornithological records indicate that *Quiscalus niger* was once common on Little Cayman and Cayman Brac; today, small flocks fly from Little Cayman to Cayman Brac to spend the day feeding, but evidently this grackle does not now breed on Cayman Brac. *Mimocichla plumbea* is moderately common at least on the lowland perimeter of Cayman Brac (Table 11); yet it has never been recorded from nearby Little Cayman but has attempted to breed on Grand Cayman.

As late as 1956, the Mockingbird (*Mimus polyglottos*) was unknown from both Little Cayman and Cayman Brac (Bond 1956), even though the species has been a common resident of ruderal and roadside habitats on Grand Cayman at least since the earliest days of ornithological investigations in 1886. By 1956 Mockingbirds were reported on Cayman

Brac by C. H. Blake (Bond 1958), and the species became well established on that island around "inhabitated areas" by 1966 (Harvey, *in* Bond 1967). Harvey also noted the species on Little Cayman in the same year. In the summer of 1971, I recorded nine well-spaced individuals on Little Cayman during two hours of observation along 8 km of that island's newly constructed perimeter road. It is apparent that construction of this road has created open habitats preferred by this species. The mockingbird probably immigrated to the two smaller islands from Grand Cayman where it continues to increase in number, probably in response to continued clearing of mangrove swamps and logwood forests, thus increasing its preferred habitat.

As discussed elsewhere in this paper, the distribution of the genus *Vireo* on these islands is curious, because *V. crassirostris* occurs on all three islands with either *V. magister* (Grand Cayman) or *V. altiloquus* (Little Cayman and Cayman Brac). No more than two species of *Vireo* are sympatric on a given island. Bond (1966b) mentioned a single old record of two *V. altiloquus* on Grand Cayman that probably represented vagrants.

The fragmentary data available on the ecology of *Mimocichla ravidia* (English 1916) and *Icterus leucopteryx* on Grand Cayman conform to Mayr's (1965) belief that small population sizes and probable genetic uniformity have made such populations exceptionally vulnerable to the smallest environmental change. This is another way of invoking genetic drift as a contributing factor in the extinction of these two forms on Grand Cayman. Both existed in quite restricted habitats (thus reducing gene flow), and their population densities in any one year probably never exceeded 100 breeding pairs. In these small populations, by genetic drift some alleles favored by selection could have been lost and less favored ones, perhaps lethals, could have increased in frequencies. These birds might not have been able to adapt to ensuing environmental changes. As stated before, the nature of that change, or changes, is unknown, but possibilities would include some habitat disturbance or hurricane effects. Furthermore, each of these small Cayman Islands appears to exemplify Mayr's statement (1965: 1587) "... that the smaller the island the lower the percentage of endemic species. . . ." In fact, plotting data from these small islands on Mayr's figure 2, the linear relationship between double logarithmic plottings for island area on percent of endemic species would become curvilinear, the line extrapolating to zero endemic species with an island area of approximately 70 square miles or less. According to this interpretation, none of the Cayman Islands should have any endemic species, and currently they do not.

In the first analysis of the birds of these islands, Cory (1886) de-

scribed 13 new species from Grand Cayman alone, and subsequently, three other species were recognized by early systematists from the other two islands (for a list, see Johnston *et al.* 1971). Later taxonomists (e.g., Ridgway and Friedmann 1901-1950) synonymized all of these other West Indian forms, except for *Mimocichla ravidia*. Consequently, a modern treatment (Johnston *et al.* 1971) recognized no current endemic species from the islands, but 16 endemic subspecies. This latter figure appears to be high for small West Indian islands and suggests a relatively long period of isolation for the resident avifauna, with little or no recent immigration.

A similar example of insular equilibrium between extinction and immigration is Diamond's (1969) analysis of the Channel Islands of California. Those islands lie from 8 to 61 miles from the mainland. Between 1917 and 1968 from 17-62 percent of the breeding bird species disappeared, but an approximately equal number of new immigrants became established.

COMPETITION FOR ENVIRONMENTAL RESOURCES AMONG THE RESIDENT TERRESTRIAL AVIFAUNA

Ecological isolating mechanisms, the avoidance of competition, and related phenomena in birds have been discussed by numerous investigators and were summarized recently by Lack (1971). The thesis of Lack and others is that contemporary bird species can coexist in the same area only if they differ in some ecological factor(s). If an investigator interested in sympatric forms (genera, species) A and B looks long and hard enough, presumably he will discover that their coexistence is made possible by differences in habitat, food, feeding methods, stratification, or the like, because the only other alternatives are competitive exclusion or extinction (i.e., coexisting species will have different ecological niches). Theoretically, at least, the more niches available in a given community, the more species of birds that can actually or potentially coexist in that community. Interesting cases are those of insular birds with quite similar niches; these have been the subject of intensive studies among the closely related resident Cayman Island birds.

A morphological indication of reduced interspecific competition between closely related birds is difference in bill size, which, in turn, presumably reflects differences in food particle size and hence partitioning of food resources. Grant (1968, 1969), for example, demonstrated that sympatric congeneric species of birds on islands differ in bill length and avoid competition by feeding in different habitats or by having different feeding habits. Schoener (1965), in developing this theme quantitatively,

suggested that a character difference (ratio of larger to smaller bill length) greater than 1.14 was typical of sympatric congeneric insular birds. Congeners with such bill length differences would reduce competition by selecting different-sized food particles. Of the five congeneric pairs of birds on the Cayman Islands, two have a bill character difference less than 1.14: *Dendroica petechia*-*D. vitellina* (1.01) and *Tyrannus dominicensis*-*T. caudifasciatus* (1.02) (bill measurements taken chiefly from Ridgway 1901-1950). In the two *Dendroica* species stomach analyses revealed few qualitative differences in food choices (see discussion beyond and Appendix III); competition between these forms is avoided primarily by differences in habitat choice as well as feeding heights. The *Tyrannus* species, although possessing similar bill lengths, (1) take different foods, (2) are found in different habitats, and (3) obviously feed in different fashions. Bill size differences are, therefore, not always the most important means of avoiding competition in all the Cayman Island congeners. As will be discussed later in this paper, congeners and other closely related forms clearly have evolved a spectrum of mechanisms that in various combinations facilitates coexistence. It should be noted that in the relatively short time that birds have been studied on these islands, there is no assurance that competition is not causing a gradual exclusion of one species or a slow transition into a new ecologic niche for another.

DOVES AND PIGEONS (COLUMBIDAE).—A nearly linear relationship exists between island size and number of species of Columbidae in the West Indies (A. Cruz, pers. comm.). Island size is not necessarily the prime factor, however, because certainly habitat diversity and distance to the source population are of major importance. The largest West Indian islands support the highest numbers of species of Columbidae (Jamaica 10, Cuba 11, Hispaniola 10), but these islands also have greater relief and habitat diversities than are found on more xeric, flatter West Indian islands, such as the Caymans. Furthermore, on no island are the several dove and pigeon populations and densities necessarily the same; *Columba inornata* and *Geotrygon passerina* of Jamaica are both relatively rare, as compared with the common *Columbina passerina* and *Columba leucocephala* on that island. Relative population densities of the doves and pigeons on the Cayman Islands seem to be, in decreasing order of abundance: *Zenaida asiatica*, *Columba leucocephala*, *Columbina passerina*, *Z. aurita*, and *Leptotila jamaicensis* (the latter restricted to Grand Cayman). Thus in terms of a given island, it is ecologically misleading merely to enumerate species without also considering relative or absolute abundances and habitat diversity.

The question posed here is: how can each of the Cayman Islands support its complement of four or five species of columbids? Or, how do

these columbids partition resources so as to permit (1) sympatry on the island and (2) syntopy in given ecological formations? It is initially important to admit the paucity of information on their breeding habits, seasonality of breeding (see Table 13), and feeding behavior. Nevertheless, from the available information summarized in Table 15, it appears that the columbid species partition resources in two principal fashions—by habitat selection and by food type. As breeding birds, no more than three species are found in a given ecological formation (Tables 3-10). All these species are basically frugivorous and, for the syntopic species, limited stomach analyses (see Appendix III) do not indicate any marked interspecific differences in food habits.

TABLE 15.—NICHE CHARACTERISTICS OF DOVES AND PIGEONS ON GRAND CAYMAN.

1	<i>Leptotila jamaicensis</i>	1			
2	<i>Columba leucocephala</i>	BS FH	2		
3	<i>Zenaida aurita</i>	(H),BL FT	BS,BL FH,FT	3	
4	<i>Zenaida asiatica</i>	BL,H FT?	(BS) FT?	BL,(BS) FT?	4
5	<i>Columbina passerina</i>	BS,BL H, FT	BS,BL H,FH FT	BS,BL FT	BS,BL (H),FH FT

Key: BS (body size), BL (bill length), H (habitat), FH (feeding height), FT (food type). A symbol in parentheses indicates that the difference is poorly developed.

WOODPECKERS (PICIDAE).—The two resident woodpeckers (*Colaptes auratus* and *Centurus superciliosus*) of Grand Cayman were earlier believed to be ecologically separated, chiefly on the basis of habitat, with *Colaptes* supposedly being a bird of the mangrove swamps and *Centurus* most common around human habitations (Johnston 1970). Subsequent intensified study by Alex Cruz and me showed, however, that these species were not necessarily separated by habitat differences. As seen earlier in the distribution analyses of birds in the various ecological formations (Tables 3-10), clearly both woodpeckers occur together in most of these wooded formations, although *Colaptes* predominates in mangrove swamps. Overall, the differences in habitat choice between these two woodpeckers are only of minor importance (Table 16).

The principal niche differences between these species are in feeding methods and food type. *Colaptes* is essentially a probing and drilling

TABLE 16.—NICHE CHARACTERISTICS OF CLOSELY RELATED RESIDENT BIRDS OF THE CAYMAN ISLANDS.

		body size	bill length	habitat	feeding height	feeding methods	food** type
<i>Colaptes auratus</i>	}	1*	2*	2	1	3*	4*
<i>Centurus supercilii</i>							
<i>Tyrannus dominicensis</i>	}	1	1	4	4	4	3
<i>Tyrannus caudifasciatus</i>							
<i>Elaenia martinica</i>	}	3	4	1	4	4	4
<i>Myiarchus stolidus</i>							
<i>Vireo magister</i>	}	GC	4	2	2	?	2
<i>Vireo crassirostris</i>							
<i>Vireo altiloquus</i>							
		LC	4	2	2	?	?
		CB					
<i>Dendroica petechia</i>	}	2	1	4	4	1	1
<i>Dendroica vitellina</i>							

* Differences: (4) strongly developed, (3) moderately well developed, (2) poorly developed, (1) absent or negligible.

** Based chiefly upon percent differences in animal and vegetable material and not upon different species of animals or plant materials consumed.

woodpecker, whereas *Centurus* spends much of its time in gleaning arthropods (especially in bromeliads) and taking small fruits. Analyses of stomach contents indicate differences in foraging techniques. From Appendix III it can be seen that 19 *Colaptes* fed heavily (97% of the diet) on arthropods, mostly on ants and termites. Although *Centurus* has a diet high in insects (56%), especially beetles, approximately one-half of its diet is fruit. In fact, the frequent occurrences of this woodpecker at house sites are closely connected to the fruit-bearing trees, especially papaya, cultivated there. Of interest also are the "herptiles" taken by *Centurus*, the *Hyla* most likely captured by probing into bromeliads.

FLYCATCHERS (TYRANNIDAE).—Of all the closely related birds on the Cayman Islands, the four resident species of Tyrannidae possess the most interesting sets of ecological isolating features. No two species-pairs have evolved precisely the same mechanisms, which are based on differences in habitat choice, feeding height, feeding methods, and food types (Table 16). Of particular significance is the fact that one of these "flycatchers," *Elaenia martinica*, is chiefly a frugivore (Appendix III), and as such does not compete with the other three insectivorous tyrannids. Also, *Tyrannus caudifasciatus* consumes both lizards and frogs, a predatory habit not shared with the other tyrannids. *Elaenia martinica* is one of the most widespread and abundant members of the resident

avifauna (Tables 3-10) and is also extremely belligerent both intra- and interspecifically. In the hundreds of interspecific behavioral encounters I observed, it appeared that *Elaenia* was always dominant. Among the four species, within-habitat feeding strata clearly differed from species to species (Figure 18); in no case did two species spend more than about 20 percent of the time feeding at the same stratum, and even when they did, each selected different foods.

In summary, the tyrannids provide a classic case of the partitioning of environmental resources such that coexistence of four resident forms is possible on Grand Cayman. *Elaenia* is chiefly a frugivore, whereas the others are chiefly insectivorous; *Tyrannus dominicensis* is a large insectivore feeding at tree-top levels in open sites around towns and

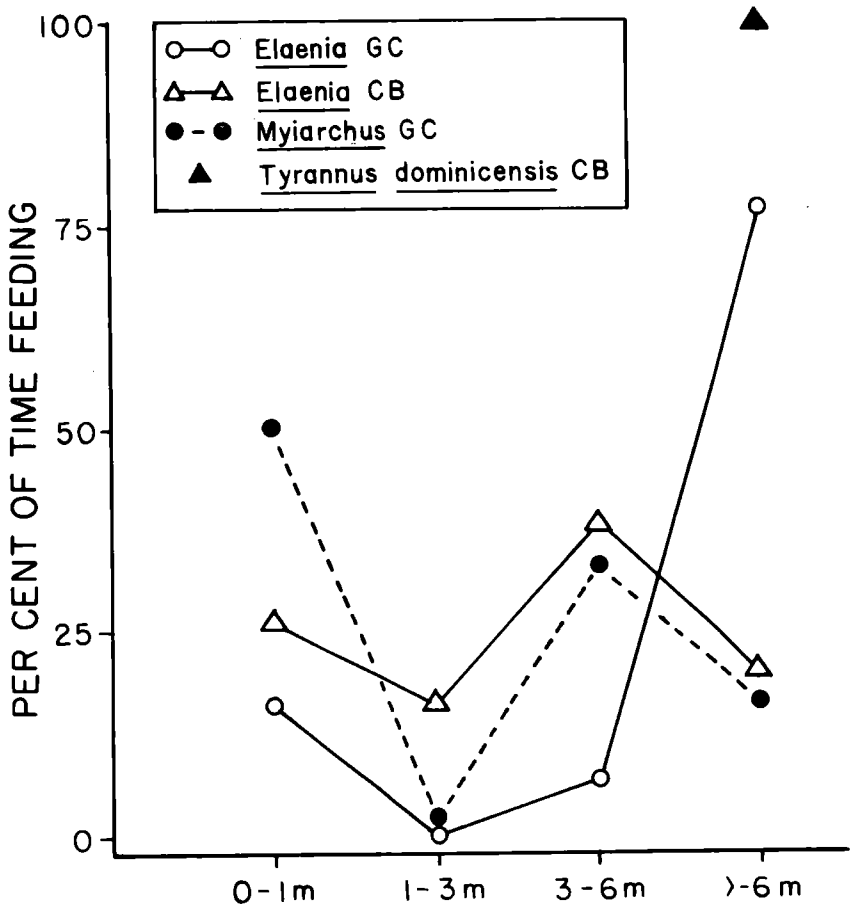


FIGURE 18.—Feeding heights and percentages of time feeding for flycatchers.

houses; *T. caudifasciatus* is common in wooded formations where it consumes large insects and small vertebrates; *Myiarchus* is an intermediate-sized woodland and "edge" species that is more generalized in food habits (insectivorous and frugivorous) than the other species.

VIREOS (VIREONIDAE).—The three resident vireos of the Caymans proved difficult to analyze for interspecific ecological differences, and the present summary should be considered tentative. As is true elsewhere in the distribution of the genus *Vireo* where sympatry and/or syntopy are evident, the usual case is the presence of an arboreal member of the subgenus *Vireosylva* and a thicket-inhabiting member of the subgenus *Vireo* (Hamilton 1962). Presumably these stratal and perhaps other differences effectively minimize interspecific competition.

Over the years of observations on Grand Cayman, however, it became apparent that *V. crassirostris*, although the only vireo inhabiting thickets and shrubby fields, coexisted with *V. magister* in early logwood successional stages. A similar relationship existed between *V. crassirostris* and *V. altiloquus* on the other two islands. Indeed, through the seral stages into a climax limestone forest formation, both forms could be found. Frequently both species were observed or collected in the same strata between 3 and 5 m. As a rule, *V. crassirostris* was most frequently encountered below about 4 m, whereas both *V. magister* and *V. altiloquus* tended to prefer foraging positions from 5 to 15 m.

The relatively large number of stomachs examined (11 for *V. crassirostris* and 9 for *V. magister*) and taken at the same season revealed food differences that (1) reinforce feeding strata differences and (2) provide the key to avoidance of interspecific competition (see Appendix III). *V. crassirostris* consumes a higher percentage (77%) of animal food than *V. magister* (51%). Probably the species of Coleoptera or other taxa mutually eaten by both vireos were in fact different, although the insect fragments found in their stomachs could not be identified below the family level.

Thus, the two vireo-pairings on these islands showed closer ecological niche characteristics than the other closely related resident avifauna, and should certainly be subjected to a more detailed scrutiny.

WOOD WARBLERS (PARULIDAE).—The two resident warblers (*Dendroica petechia* and *D. vitellina*) were initially believed to be habitat restricted, with *D. petechia* being a mangrove swamp species and *D. vitellina* occurring principally in thickets, shrubland, and early logwood forests. Further observations showed that habitat separation was not complete because *D. petechia* is now known to be more widespread, occurring as a breeding bird in six of the upland ecological formations (Tables 3-10). On the other hand, *D. vitellina* is found in only four of

these. Attention must be given to the relative population densities of each species in each formation: where *petechia* is very common (sea grape-almond woodland and mangrove swamps), *D. vitellina* is absent; where *D. vitellina* is fairly or very common (logwood, logwood-thatch palm-red birch, and limestone forests), *D. petechia* is at best uncommon. To some extent then, these species are segregated by habitat.

Feeding heights of these warblers are also important, *D. vitellina* choosing the lower strata up to about 3 m, and *D. petechia* usually occurring from 3 m upwards. At present no available data support an hypothesis that the two species either have different foraging habits or select different foods.

PREDATION AND POPULATION CONTROL

Of special importance for the bird populations of the Cayman Islands is the obvious paucity of vertebrate predators. Grant (1940) documented systematics of the herpetofauna but devoted little attention to their biological features. He did note (p. 49), however, that the colubrid snake *Alsophis angulifer* is "diurnal, active, feeds on lizards, frogs, birds . . . Lewis took a number of specimens in the tops of trees, one over 30 feet off the ground . . . [where they were feeding on] *Hylas*." On Cayman Brac a specimen of this snake, reported by Grant (p. 50), had a honeycreeper in its stomach. In my several years of observing and collecting on these islands, I never encountered an *Alsophis* pursuing birds or with a bird in its stomach, nor did any of the local people indicate an ornithophagous habit for this species. Still, Grant does provide some evidence that the snake at least occasionally preys on birds. The abundant *Anolis* lizards, especially *A. conspersus*, might prey on birds' eggs (there is no concrete evidence) because elsewhere in the West Indies *Anolis* occasionally eats eggs of honeycreepers (Biaggi 1955). No mammalian carnivores occur on the Caymans. Both *Mus musculus* and *Rattus* (mostly *R. rattus* but some *R. norvegicus*) are found, but they are only locally abundant. Specimens of these mammals have been collected or observed chiefly in areas of human habitation and not in the "wilder" portions of the islands.

A conspicuous hiatus in the avifaunal trophic structure is a diurnal predator. In winter an occasional hawk (*Circus cyaneus*, *Falco sparverius* and *F. columbarius*) does visit the islands (Johnston *et al.* 1971). The food habits of these predatory birds in the Caymans are unknown, although elsewhere birds do constitute some portion of their diets. But even if they did prey on an occasional (or more) land bird in winter, the small numbers and infrequent occurrences of these hawks would

tend to minimize their predation pressure on the avifauna. On the other hand, the resident Barn Owl (*Tyto alba*) has been shown recently to be a potent predator on birds (Johnston 1972), even though its numbers are low. The regurgitated pellets of these owls taken from five widely scattered sites on Grand Cayman, and quite likely representative of five different individuals, revealed a high proportion of avian remains among their prey, ranging in size from a medium-sized egret (*Egretta*) to a honeycreeper (*Coereba*). Furthermore, the prey items included at least eight genera of the resident birds. These data suggest that of the actual or potential vertebrate predators on the avifauna only *Tyto alba* is especially important, and I suspect this predator represents the greatest single biological control of the resident avifauna.

The ubiquitous hermit and land crabs are clearly potential scavengers or predators of any terrestrial animal life. Only the Nighthawk (*Chordeiles minor*) is a consistent ground-nesting bird on the Caymans, however, and because this species is scarce and breeds only in bare fields where crabs are also scarce, it appears highly unlikely that even this bird, its eggs, or young would be preyed upon by the crabs. Interestingly, where land crabs are most abundant on the islands (rocky barren roadsides and limestone forests), no ground-nesting birds are known, unless it is a very occasional dove (*Columbina passerina* or *Zenaida aurita*).

The widespread and abundant *Coereba flaveola* is conspicuous throughout the Caymans and elsewhere in its range. In most West Indian island avifaunas, it is the most abundant terrestrial resident species. Controlling mechanisms for this species were documented by Gross (1958) and include bird predators (*Quiscalus*, *Crotophaga*) as well as ants and lizards. In the absence of concrete evidence, we can only assume that similar predators prey on *Coereba* in the Cayman Islands. *Coereba* is an occasional victim of the uncommon Barn Owl (Appendix III).

The extent to which other biological and physical factors exercise any control on population size of birds is as yet unassessed. For example, for the Caymanian avifauna no quantitative data are available on annual population fluctuations, clutch size, hatching success, fledging success, or, indeed, natality rate for any bird species especially in comparison with other insular or mainland populations. Two species are increasing in numbers and range in the Caymans, *Mimus polyglottos* and *Zenaida asiatica*. Conversely, the only documented recent losses there are of *Mimocichla ruficauda* and *Icterus leucopteryx bairdi*; causative factors bearing on their extinctions have been discussed in an earlier section.

A GENERAL ASSESSMENT OF FEEDING ECOLOGIES AND HABITAT DISTRIBUTIONS

It is instructive now to generalize and summarize data on feeding ecologies or feeding niches of the resident terrestrial avifauna. As shown in Table 17, most of the bird species (57%) are arboreal foragers, either on arthropods or fruits. Furthermore, with the expected exception of pastures and cultivated areas, these same species are each widely distributed in the seven upland formations and have comparable frequency of occurrence and relative abundance therein. Conversely, ground-feeding forms (21%) are relatively less common as a whole in the Caymans and are virtually restricted to the non-forested formations. The latter distribution strongly suggests the scarcity of insects and seeds on the ground in the several forest formations. Indeed, ground cover is noticeably scarce in the several forest formations due to a combination of factors (edaphic karst topography, light penetration). The relatively high proportion of arboreal insectivores and frugivores, augmented by the timber-probing and -gleaning woodpeckers would be expected on islands, such as the Caymans, where forest formations of several types predominate in areal extent (see Figs. 1-3).

Bird species diversity is a known function of habitat or plant species diversity. Although plant species diversity was not determined quantitatively in the present study, it is nonetheless empirically true that in the comparisons of avifaunal compositions of the several ecological formations, bird species diversity does attain its peak in those forest formations with the greatest plant diversity. Complexity of floristic composition (presence of many codominant trees vs. one or two dominants, height of vegetation, some semblance of stratification, etc.) may be sequentially arranged in descending order (number of bird species in parentheses) as follows: towns and house sites (20), limestone forests (17), logwood-thatch palm-red birch forest (15), sea grape-almond woodland (16), mangrove swamps (11), pure logwood forests (11), and pastures and cultivated areas (11). A relationship between number of terrestrial bird species and habitat complexity is implied by these data.

TAXON CYCLES

A subject of recent interest to some island biogeographers is that of taxon cycles, and for the West Indian avifauna these have been explored generally and in detail by Ricklefs and Cox (1972). Whether an analysis of taxon cycles for individual small islands or archipelagos is meaningful (see Ricklefs 1970, for Jamaica) is a moot point because of great areal and relief differences in large island groupings, but an attempt at

TABLE 17.—FEEDING ECOLOGIES AND HABITAT DISTRIBUTIONS OF RESIDENT TERRESTRIAL SPECIES ON GRAND CAYMAN.

Feeding Ecology	Total Species Available	Pastures & Cultivated Areas	Towns and House sites	Sea Grape-Almond Woodland	Pure Logwood Forests	Logwood-Thatch Palm-Red Birch Forest	Limestone Forests	Mangrove Swamps
Predator on vertebrates	1	1	1					
Aerial Insectivore	2	1(3)*	1(1)	1(1)				
Foliage feeding-nectar	1		1(4)	1(4)	1(4)	1(3)	1(4)	1(3)
Foliage feeding-arthropods (chiefly insects)	8	2(3)	6(10)	4(8)	6(14)	7(15)	7(11)	4(10)
Foliage feeding-fruits/seeds	8	2(3)	5(11)	5(11)	1(1)	5(8)	7(13)	4(7)
Timber probing-insects	2		2(2)	2(2)	1(1)	2(3)	2(4)	2(2)
Ground feeding-arthropods (chiefly insects)	3	3(9)	2(6)	1(1)	1(2)			
Ground feeding-other invertebrates	1			1(1)				
Ground feeding-seeds	2	2(4)	2(5)	1(1)	1(1)			

*Figure in parentheses = sum of number of species X total abundance scores (see footnote of Table 18)

such an analysis for the three Cayman Islands has been undertaken, a summary of which appears in Table 18. There appears, first of all, to be only a weak correlation between feeding ecology and early stages of the taxon cycle, namely that the presumed recent colonizers (Stage I) are mainly either frugivores or omnivores. On the other hand, other characteristically frugivorous birds, plus some insectivores, have also been classified as Stage IV forms. As a rule, specific feeding ecology cannot be closely correlated with a stage in the taxon cycle, at least for the Cayman Island avifauna. There is, unfortunately, no available information on food habits of *Mimocichla ravida* and *Icterus leucopteryx*, the two recently extinct birds from these islands, although it is certainly true that if this study had been made 40 or more years ago, both of these birds would have been in Stage IV using the criteria of Ricklefs (1970). Both were known, for example, to be quite restricted in habitat preferences and areal distribution on Grand Cayman.

Some problems arise in subjectively assigning a given bird species to a given stage in the taxon cycle, especially as regards Stage IV. Ricklefs (1970: 475) gives this definition: "The last stage of the cycle, before going extinct or recycling, is the endemic population. As the cycle progresses, populations move from marginal coastal habitats into more central and montane habitats." Similarly, Ricklefs and Cox (1972: 195) note: "Finally, descendant populations, often subspecifically or specifically distinct, are restricted to small refugia." The problems in diagnosing taxon cycle stages for the Cayman Island avifauna condense to two major points. First, as described previously, these islands have neither montane habitats nor discreet small refugia, unless in the latter case one considers the mature, more-or-less inland limestone forests. Second, these three islands currently have no endemic species of birds, but, according to Bond (1956) and Johnston *et al.* (1971), do contain 13 species with endemic subspecies. It is of interest to recall that earlier taxonomists (for example, Cory 1886) regarded seven of these as distinct species. Based upon the contemporary belief that these (see Table 18) are all well-marked, distinct subspecies, endemic to one or more of the three islands, I am tentatively assigning the 13 forms to Stage IV in the taxon cycle. Their occurrences on the individual islands were outlined earlier by Johnston *et al.* (1971).

Taxon cycles for the Caymanian avifauna may be compared, albeit with some qualification, with those of Jamaican birds (Ricklefs 1970) and Solomon Island birds (Greenslade 1968). Although the Cayman Islands currently contain no endemic species, Jamaica does have 26 such species, many of which (a) occur in the interior montane forests and (b) are in Stage IV. Ricklefs (1970) gave 14 as the number of Stage IV endemics,

TABLE 18.—FEEDING ECOLOGIES, STAGES IN TAXON CYCLE, AND ABUNDANCE OF RESIDENT TERRESTRIAL SPECIES.

Species	Feeding Ecology†	Stage in Taxon Cycle	Total‡ Abundance	Average Abundance	No. of§ habitats
<i>Columba leucocephala</i>	FF	I	8	2.0	4
<i>Zenaida aurita</i>	FF	I	4	1.3	3
<i>Zenaida asiatica</i>	FF(?)	I	6	3.0	3
<i>Columbina passerina</i>	GS	II	5	2.5	2
<i>Leptotila jamaicensis</i>	FF	IV	1	1.0	1
<i>Amazona leucocephala</i>	FF	IV	2	2.0	1
<i>Coccyzus minor</i>	FI,GI(?)	II	2	1.0	2
<i>Crotophaga ani</i>	GI,CV,GS	I	6	3.0	2
<i>Chordeiles minor</i>	AI	I	1	1.0	1
<i>Colaptes auratus</i>	TPI,FF	IV	8	1.3	6
<i>Centurus superciliosus</i>	TPI,FF,TV	IV	5	1.7	3
<i>Tyrannus dominicensis</i>	AI	I	7	2.3	3
<i>Tyrannus caudifasciatus</i>	FI,TV,FF	IV	4	1.3	3
<i>Myiarchus stolidus</i>	FI,FF	III	8	1.6	5
<i>Elaenia martinica</i>	FF,FI	IV	17	3.4	5
<i>Mimus polyglottos</i>	GI,GO,GS	I	10	2.5	4
<i>Mimocichla plumbea</i>	unknown	IV	2	2.0	1
<i>Vireo crassirostris</i>	FI,FF	II	6	1.5	4
<i>Vireo altiloquus</i>	unknown	I	2	2.0	1
<i>Vireo magister</i>	FI,FF	IV	12	2.4	5
<i>Dendroica petechia</i>	FI	II	10	2.0	5
<i>Dendroica vitellina</i>	FI,FF	IV	12	3.0	4
<i>Coereba flaveola</i>	FN,FI	IV	22	3.7	6
<i>Spindalis zena</i>	FF	IV	5	1.7	3
<i>Quiscalus niger</i>	FI,TV,FF	IV	13	2.2	6
<i>Tiaris olivacea</i>	GS	II	5	1.7	3
<i>Melophryrha nigra</i>	FF,FI	IV	5	1.7	3

† Adapted from Salt (1953, 1957) and Orians (1969): AI, aerial insectivore; PV, predator on vertebrates; PI, predator on invertebrates; FN, foliage feeding on nectar; FI, foliage feeding on insects and spiders; FF, foliage feeding on fruits (and/or seeds); TPI, timber probing for insects; TV, timber gleaning for vertebrates; GV, ground feeding on vertebrates; GI, ground feeding on insects and spiders; GO, ground feeding on other invertebrates (crustacea, mollusks); GS, ground feeding on seeds. When two or more feeding ecologies are given for a bird, the predominant type is listed first.

‡ Scored by conversion of U (uncommon)=1, FC (fairly common)=2, C (common)=3, VC (very common)=4. See individual census tables for each habitat concerned.

§ Seven habitats available during breeding season.

	Stage of Taxon Cycle			
	I	II	III	IV
Number of species and subspecies	8	5	1	13
Mean number of habitats occupied	2.6	3.2	5.0	3.6
Mean total abundance	5.5	5.6	8.0	8.4
Mean of the average local abundance	2.1	1.7	1.6	2.1

but his censuses did not include the endemic columbids, parrots, cuckoos, and hummingbirds. Ricklefs' 14 Stage IV forms, as compared with the Caymanian 13, were less widespread in habitat occupancy and less abundant than Stage I types. The converse is true for the Cayman birds (Table 18). Probably these differences are at least partially explicable in terms of the likelihood that the Jamaican avifauna is older than that of the Cayman Islands, has available well-developed refugia in the montane forests, and occupies a much larger island with greater relief and habitat diversity.

An interesting ecological question is whether or not immigrating and hence colonizing species on islands are found chiefly in "marginal habitats." Because so many factors potentially determine the success of colonization (competition, adaptability of the propagule, niche availability, etc.), it is important to speculate on, or document, an ecological habitat that fits the needs of most immigrating forms. Another way of examining this problem is to assess the habitat distribution of species in Stage I of a taxon cycle. Do they, indeed, "occupy marginal habitats at the center of their expansion . . . [and] exhibit 'ecological release' on small islands due to lack of competition" (Ricklefs 1970)? For Solomon Island birds, Greenslade (1968) concluded that "the habitats of the species suggest that expansion occurs mainly in coastal situations while the rest of the cycle involves a shift to lowland rain-forest and, increasingly in the final stage, to montane forest."

The Cayman Islands have neither rain forests nor montane forests. In terms of secondary succession they do have fields and pastures, early logwood forests, logwood-thatch palm-birch forests, and a (presumed) climax limestone forest. If one can equate the fields and pastures (many of which are at least near the coast) with marginal or coastal habitats as used by Greenslade, Ricklefs, and others, then the distribution of breeding birds of each taxon cycle stage in this and later successional stages should provide answers to the questions posed above. From data in Tables 12, 17, and 18 it can be determined that 50% of the Stage I birds breed in the fields and pastures and the other 50% occur in the later forested seral stages. All of the Stage II birds are restricted to early seral stages, and at least 75% of the Stage IV types are in the later seral stages. Thus even in the absence of montane forest refugia on the Cayman Islands, the ecological distributions of the resident avifauna partially support the idea that the most recent colonizing species are found primarily in so-called marginal habitats, and the "older" endemics are more characteristic of interior forests.

On the other hand, colonization of these islands has yet a different facet. What considerations should be given to the presently forest-

adapted Stage IV species such as the *Centurus* woodpecker, *Amazona* parrot, and vireos? At the time that each form invaded these islands, did each undergo a taxon cycle beginning in a marginal habitat and ultimately become associated with the mature limestone forest? Contemporary data do not support such a possibility. Rather David Lack (in litt.) appears to have a more plausible explanation to the effect that potential colonists on nearby islands would have to be best adapted to conditions on the Cayman Islands. For example, the *Amazona* parrot on the Caymans is especially characteristic of limestone forests (Table 8); on Cuba its conspecific is found in remote woodlands from mountains to sea level. *Elaenia martinica*, so widespread and abundant in the Caymans, is adapted to arid lowland woodlands elsewhere in the Caribbean region. *Mimocichla plumbea* of Cayman Brac, Cuba, and Hispaniola is a bird of forested regions, plantations, and gardens. These and other examples strongly support the contention that colonization of new islands is not necessarily restricted to Stage I species but could be successful for species in any taxon cycle stage, provided they were pre-adapted to and could find suitable ecological conditions on a new island.

HABITAT DISTRIBUTIONS OF INSULAR AND MAINLAND BIRD POPULATIONS

The extent to which breeding bird species occupy all habitats available to them has been discussed at least in part by MacArthur and Wilson (1967, Chap. 5). Clearly, some combination of competition, predators, immigration, vegetational complexity, and other factors play significant roles in restricting bird species to given habitats. In some insular avifaunas that have been investigated intensively (e.g., those of Puerto Rico) individual bird species have undergone an ecological expansion into many habitats, whereas species in the Panamanian tropical forests are much more restricted to a small number of habitats. As a rule, if an avifauna can specifically occupy all or most of the habitats available, it can be described as eurytypic or "generalized;" if the species occupies only a small number of available habitats, it can be considered stenotypic or "specialized."

Some interesting figures emerge from the habitat distribution of the Grand Cayman avifauna. Considering seven upland terrestrial formations (Tables 3-10), the distributions of the 24 species occurring therein (exclusive of the wide-ranging Barn Owl and Nighthawk) are as follows:

- 1 species, in only 1 formation
- 5 species, in only 2 formations
- 5 species, in only 3 formations
- 5 species, in only 4 formations

3 species, in only 5 formations
4 species, in only 6 formations
1 species, in all 7 formations

By extrapolation one arrives at an average figure of 3.9 habitats per species. Data for mainland populations (Fig. 19) are in sharp contrast; for example in Georgia the figure is 1.6 habitats per species (Johnston and Odum 1956) and for Panama about 1.3 (MacArthur *et al.* 1966). On Puerto Rico the value is 2.5 (Recher 1970) and Jamaica 2.9 (Ricklefs 1970). For Grand Cayman the relatively large number of habitats occupied by each species indicates either reduced interspecific competition *per se*, the evolution of mechanisms to avoid competition, or both. These properties are discussed at length in the previous section on competition.

To exemplify these features more generally, a number of published breeding censuses from typical island and mainland populations have been reviewed with respect to number of available habitats occupied by the species. This assessment is graphically summarized in Figure 19. In regions where relatively few habitats are available (three or four), mainland bird populations tend to be specialized, and as more habitats become available (five or six), the mainland populations tend to become even more specialized. Large islands, such as Puerto Rico and Jamaica, include bird populations that are intermediate between the extremes of generalization and specialization. On small islands (including Grand Cayman) the bird populations reach peaks in generalization. Grand Cayman is unique in this feature by having the highest known value of mean number of habitats per species, namely 3.9.

Lack concluded (1969: 207) that "... the small numbers of resident bird species on islands are due ... to ecological limitations, to which the islands' birds are often specially adapted, and which enable fewer species with broader niches to exclude a greater number of specialists." If I interpret this sentence correctly and if "ecological limitations" are chiefly those of habitat diversification, then the graphic presentation of Figure 19 supports his contention only for small islands. In fact, with respect to number of habitats occupied by each species, the larger islands of Puerto Rico and Jamaica, with their large number of available habitats, resemble the mainland populations. Grand Cayman, Bermuda, and St. John each tend to have (fewer?) species with "broader niches." The extent to which such ecological generalization might "exclude a greater number of specialists" is certainly undemonstrable from present evidence.

Another, yet different, approach to this subject is Simberloff's species/genera ratios (1970). Similar S/G values for large and small islands would indicate, for example, that competition is at least as intense on the

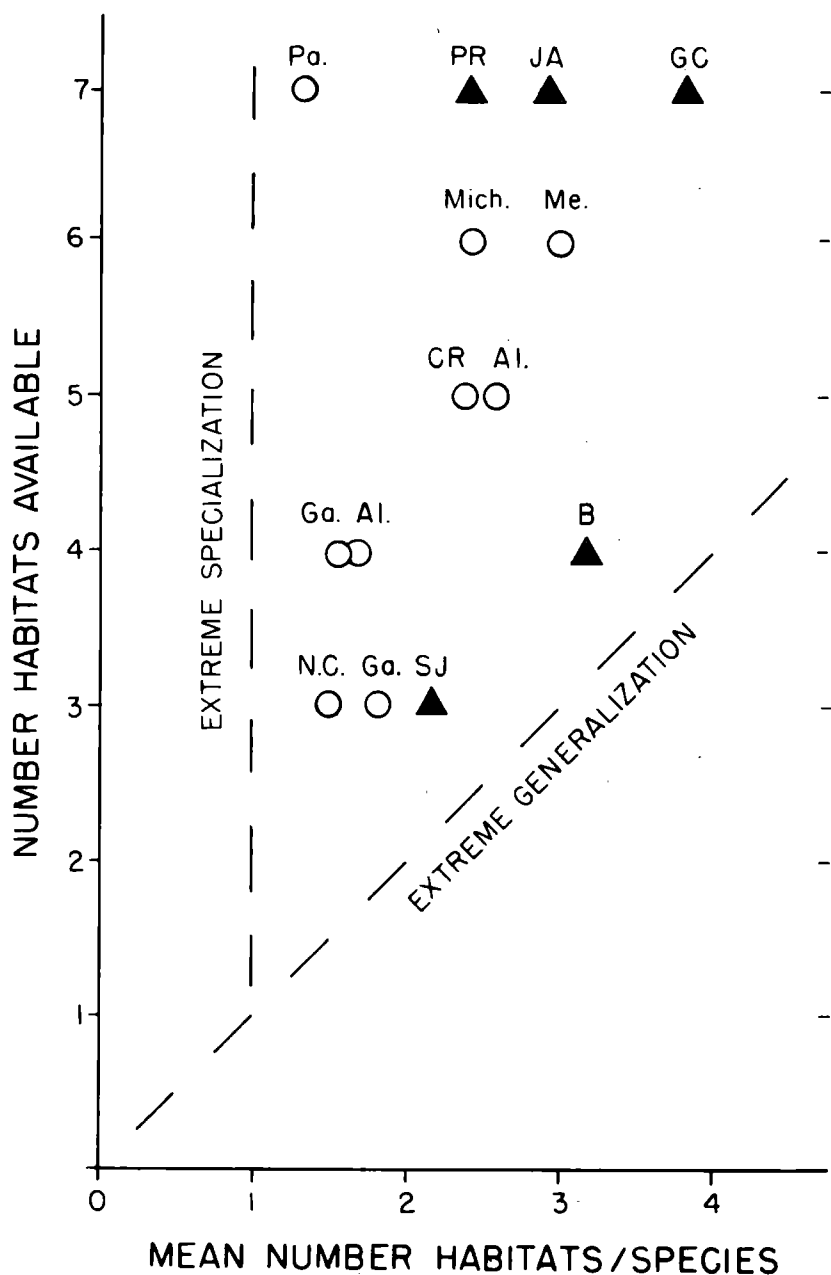


FIGURE 19.—Habitat distributions of insular and mainland bird populations. Pa.=Panama (MacArthur, Recher, and Cody 1966); PR=Puerto Rico (Recher 1970); JA=Jamaica (Ricklefs 1970); Mich.=Michigan (Kendeigh 1948); Me.=Maine (Stewart and Aldrich 1952); CR=Costa Rica (Orians 1970); Al.=Alaska (Kessel and Cade 1958, Williamson *et al.* 1966); Ga.=Georgia (Johnston and Odum 1956); B=Bermuda (Crowell 1962); N.C.=North Carolina (Odum 1950); SJ=St. John (Robertson 1962).

small islands. Therefore, based on comparative data for the Caymans (Grand Cayman=1.18, Little Cayman=1.25, Cayman Brac=1.27) and those of Cuba ($S/G=1.26$) competition is of about equal intensity on the Caymans and Cuba. As Simberloff indicated, small islands can support many similar species, and insular avifaunas will likely contain species that occupy more habitats because of less competition within habitats.

THE WINTER AVIFAUNA

Influences of the many North American migrant birds on a resident tropical avifauna have not been widely investigated (but see, for example, Eaton 1953 and Willis 1966). Despite intensive studies by a few investigators, most of the major questions remain unanswered or poorly documented. Thus the interrelationships permitting coexistence between migrants and residents require close scrutiny, but on a protracted basis in the field. On the Cayman Islands a detailed investigation was not undertaken, but a number of general and interesting ecological features have been at least partially elucidated.

As indicated elsewhere in this paper, the resident terrestrial avifauna of all the Caymans includes some 27 species; in winter at least an additional 20 reasonably common species also occur. Some 10 other species are currently known from three or fewer winter records (c.f. Johnston *et al.* 1971), but in time some of these forms might prove to be more common. For the most part the wintering birds occur in loose mixed-species flocks (especially parulid warblers), a habit also reported for Cuba (Eaton 1953) and Puerto Rico (Recher 1970). Whether any individuals are sedentary and maintain winter territories remains unproven for the Cayman Islands, but observations of at least the *Seiurus* warblers suggest this to be the case. The 20 wintering species are found on the islands mainly in the wooded ecological formations—logwood and limestone forests, mangrove swamps, and the sea grape-almond woodland. Some of these birds occur in smaller numbers in the town-and-house site formation, whereas the two wintering sparrows (*Passerculus sandwichensis* and *Ammodramus savannarum*) are both restricted to pastures and grassy fields. In the wooded formations an observer is immediately impressed by the quantitative predominance of the North American migrants. In Table 4, for example, note that the terrestrial migrant species outnumber the breeding residents by 13:8 in mangrove swamps. From these data and field observations, some immediate questions arise. What ecological features permit coexistence between migrants and residents? What role does seasonal availability of food play? How do

the two groups, corporately and individually, partition food resources? To what extent is behavior (territoriality, if it exists, and aggression) important in these syntopic relationships?

In the first place, the augmentation of a rather depauperate resident population in the mangrove swamps by wintering migrants strongly suggests two things: (1) during the breeding season there are probably unoccupied feeding niches or limited food resources in mangrove swamps, assuming that (2) a reasonably constant annual food supply is available. No data have been assembled on food resources; however, it may be noted, by way of example, that in mangrove swamps foliage-gleaning insectivores are represented in summer by one resident (*Dendroica petechia*), whereas in winter *D. caerulescens*, *Parula americana*, *Setophaga ruticilla*, and others also occur. (Multispecific warbler flocks in winter are well known from other Caribbean islands, such as Puerto Rico [see Recher 1970: E-78].) This winter increase of the avifauna at a single trophic level strongly suggests an abundant insect food supply during that season. Furthermore, in the mangrove swamps a number of feeding niches are filled only in winter—trunk and branch-gleaning for small insects (by *Mniotilta varia*), aerial-feeding small insectivores (*Setophaga ruticilla*, *Poliophtila caerulea*), ground-feeding insectivores (*Seiurus noveboracensis* and *S. aurocapillus*). Possibly insects are less abundant in these swamps in summer than in winter, but I suspect there is a high annual insect population that is simply underexploited by the resident birds in summer. In other words, some feeding niches are unfilled during the summer. Similar arguments might be made, incidentally, for the other ecological formations.

Competition for food, at least in the form of overt aggressive pursuits, does not appear to be very evident between the residents and migrants. The reason for this is at least partially explained by the fact that feeding ecologies of residents and migrants are generally dissimilar. The resident insular birds such as doves, woodpeckers, cuckoos, the parrot, flycatchers, and the bananaquit, have virtually no competitors among the wintering migrant birds. When active pursuits were observed, they were infrequent, of short durations, and appeared to involve intraspecific actions among the residents (such as two *Dendroica petechia*) or interspecific and intraspecific actions among the migrant warblers or other species. (Chases were often so rapid that neither bird could be positively identified.) Also central, localized feeding (fruiting) trees so characteristic of other tropical forests are apparently not an important ecological component in any of the Cayman Island formations; hence, competition at such a localized site is virtually nonexistent.

In summary, it appears that the large number of wintering birds in-

fluence the resident species very little, chiefly because the wintering forms usually occupy different feeding niches than the residents. That is, migrants rely upon a food resource not fully exploited by the residents, a feature previously noted in tropical regions by Morel and Bourliere (1962) and Willis (1966). On the other hand, migrants in the Caymans do not necessarily favor secondary habitats or disturbed areas; hence, they do not conform to the "irregularity principle" of Willis (1966) except with reference to a supposed abundant winter food supply. Nevertheless, the wintering birds, many of which are insectivorous, probably do play a significant trophic role in controlling insect populations.

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APPENDIX I: SCIENTIFIC AND COMMON NAMES
OF BIRDS APPEARING IN TEXT¹

- Podilymbus podiceps* (Linnaeus). Pied-billed Grebe.
Phaethon lepturus Daudin. White-tailed Tropicbird.
Sula leucogaster leucogaster (Boddaert). Brown Booby.
Sula sula sula (Linnaeus). Red-footed Booby.
Fregata magnificens Mathews. Magnificent Frigatebird.
Ardea herodias Linnaeus. Great Blue Heron.
Butorides virescens maculatus (Boddaert). Green Heron.
Florida caerulea (Linnaeus). Little Blue Heron.
Ardeola ibis ibis (Linnaeus). Cattle Egret.
Casmerodius albus (Linnaeus). Common Egret.
Egretta thula (Molina). Snowy Egret.
Hydranassa tricolor ruficollis (Gosse). Louisiana Heron.
Nyctanassa violacea (Linnaeus). Yellow-crowned Night Heron.
Plegadis falcinellus (Linnaeus). Glossy Ibis.
Dendrocygna arborea (Linnaeus). West Indian Tree Duck.
Anas discors Linnaeus. Blue-winged Teal.
Anas americana (Gmelin). American Widgeon.
Aythya affinis (Eyton). Lesser Scaup.
Circus cyaneus (Linnaeus). Marsh Hawk.
Pandion haliaetus (Linnaeus). Osprey.
Falco columbarius Linnaeus. Pigeon Hawk.
Falco sparverius Linnaeus. Sparrow Hawk.
Porphyrio martinica (Linnaeus). Purple Gallinule.
Gallinula chloropus cercheris Bangs. Common Gallinule.
Fulica americana Gmelin. American Coot.
Charadrius semipalmatus Bonaparte. Semipalmated Plover.
Charadrius wilsonia Ord. Wilson's Plover.
Charadrius vociferus Linnaeus. Killdeer.
Squatarola squatarola (Linnaeus). Black-bellied Plover.
Arenaria interpres morinella (Linnaeus). Ruddy Turnstone.
Himantopus himantopus (Müller). Black-necked Stilt.
Capella gallinago Linnaeus. Common Snipe.
Actitis macularia (Linnaeus). Spotted Sandpiper.
Tringa solitaria Wilson. Solitary Sandpiper.
Tringa melanoleuca (Gmelin). Greater Yellowlegs.
Tringa flavipes (Gmelin). Lesser Yellowlegs.
Catoptrophorus semipalmatus semipalmatus (Gmelin). Willet.
Calidris canutus (Linnaeus). Knot.
Crocethia alba (Pallas). Sanderling.
Limnodromus griseus hendersoni (Gmelin). Short-billed Dowitcher.
Larus atricilla Linnaeus. Laughing Gull.
Sterna hirundo hirundo Linnaeus. Common Tern.
Sterna albifrons antillarum (Lesson). Least Tern.
Thalasseus maximus maximus (Boddaert). Royal Tern.
Columba leucocephala Linnaeus. White-crowned Pigeon.
Zenaida aurita zenaida (Bonaparte). Zenaida Dove.
Zenaida asiatica (Linnaeus). White-winged Dove.
Columbina passerina insularis (Ridgway). Ground Dove.
Leptotila jamaicensis collaris (Cory). White-bellied Dove.
Amazona leucocephala Linnaeus. Cuban Parrot.
Coccyzus minor (Gmelin). Mangrove Cuckoo.
Coccyzus americanus americanus (Linnaeus). Yellow-billed Cuckoo.

¹ Nomenclature from Johnston *et al.* (1971).

Crotophaga ani Linnaeus. Smooth-billed Ani.
Tyto alba furcata (Temminck). Barn Owl.
Chordeiles minor (Forster). Nighthawk.
Chaetura pelagica (Linnaeus). Chimney Swift.
Archilochus colubris (Linnaeus). Ruby-throated Hummingbird.
Ceryle alcyon (Linnaeus). Belted Kingfisher.
Colaptes auratus gundlachi Cory. Flicker.
Centurus supercilii *caymanensis* Cory. West Indian Red-bellied Woodpecker.
Sphyrapicus varius (Linnaeus). Yellow-bellied Sapsucker.
Tyrannus tyrannus (Linnaeus). Eastern Kingbird.
Tyrannus dominicensis dominicensis (Gmelin). Gray Kingbird.
Tyrannus caudifasciatus caymanensis (Nicoll). Loggerhead Kingbird.
Myiarchus stolidus sagrae (Gundlach). Stolid Flycatcher.
Contopus virens (Linnaeus). Wood Pewee.
Elaenia martinica caymanensis Berlepsch. Caribbean Elaenia.
Progne subis subis (Linnaeus). Purple Martin.
Progne dominicensis (Gmelin). Martin.
Riparia riparia (Linnaeus). Bank Swallow.
Stelgidopteryx ruficollis (Vieillot). Rough-winged Swallow.
Hirundo rustica erythrogaster Boddaert. Barn Swallow.
Petrochelidon pyrrhonota (Vieillot). Cliff Swallow.
Petrochelidon fulva (Vieillot). Cave Swallow.
Mimus polyglottos orpheus (Linnaeus). Mockingbird.
Dumetella carolinensis (Linnaeus). Catbird.
Mimocichla plumbea coryi Sharpe. Red-legged Thrush.
Mimocichla ravida Cory. Grand Cayman Thrush.
Poliophtila caerulea caerulea (Linnaeus). Blue-gray Gnatcatcher.
Vireo crassirostris crassirostris (Bryant). Thick-billed Vireo.
Vireo griseus (Boddaert). White-eyed Vireo.
Vireo altiloquus (Vieillot). Black-whiskered Vireo.
Vireo magister caymanensis Cory. Yucatan Vireo.
Mniotilta varia (Linnaeus). Black-and-white Warbler.
Helmitheros vermivorus (Gmelin). Worm-eating Warbler.
Parula americana (Linnaeus). Parula Warbler.
Dendroica petechia eoa (Gosse). Yellow Warbler.
Dendroica tigrina (Gmelin). Cape May Warbler.
Dendroica caerulescens caerulescens (Gmelin). Black-throated Blue Warbler.
Dendroica virens (Gmelin). Black-throated Green Warbler.
Dendroica dominica dominica (Linnaeus). Yellow-throated Warbler.
Dendroica discolor discolor (Vieillot). Prairie Warbler.
Dendroica vitellina Cory. Vitelline Warbler.
Dendroica palmarum palmarum (Gmelin). Palm Warbler.
Seiurus aurocapillus (Linnaeus). Ovenbird.
Seiurus noveboracensis notabilis Ridgway. Northern Waterthrush.
Geothlypis trichas (Linnaeus). Common Yellowthroat.
Setophaga ruticilla (Linnaeus). Redstart.
Coereba flaveola sharpei (Cory). Bananaquit.
Spindalis zena salvini Cory. Stripe-headed Tanager.
Quiscalus niger (Boddaert). Greater Antillean Grackle.
Icterus leucopteryx bairdi Cory. Jamaican Oriole.
Dolichonyx oryzivorus (Linnaeus). Bobolink.
Tiaris olivacea olivacea (Linnaeus). Yellow-faced Grassquit.
Passerina cyanea (Linnaeus). Indigo Bunting.
Melopyrrha nigra taylori Hartert. Cuban Bullfinch.
Passerculus sandwichensis savanna (Wilson). Savannah Sparrow.
Ammodramus savannarum (Gmelin). Grasshopper Sparrow.

APPENDIX II: SCIENTIFIC AND COMMON NAMES
OF PLANTS APPEARING IN TEXT¹

Thalassia testudinum Koenig and Sims. Turtle Grass.
Sporobolus virginicus (L.) Kunth. Dropseed.
Panicum maximum Jacq. Guinea Grass.
Andropogon metusus L. Seymour Grass.
Cocos nucifera L. Coconut Palm.
Thrinax argentea L. Thatch Palm.
Agave americana L. Century Plant.
Musa sp. L. Banana.
Casuarina equisetifolia Forst. Australian Pine.
Ficus populnea Willd. Fig.
Coccoloba uvifera (L.) L. Sea Grape.
Bougainvillea glabra Choisy. Bougainvillea.
Sesuvium portulacastrum (L.) L. Sea Purslane.
Prunus myrtifolia L. West Indian Cherry.
Chrysobalanus icaco L. Coco Plum.
Haematoxylon campechianum L. Logwood.
Tamarindus indica L. Tamarind.
Caesalpinia bonduc Roxb. Cockspur.
Delonix regia (Bojer) Raf. Royal Poinciana.
Bursera simaruba (L.) Sarg. Gumbo Limbo or Red Birch.
Cedrela odorata L. Cedar.
Swietenia mahagoni (L.) Jacq. West Indian Mahogany.
Hippomane mancinella L. Manchineel.
Ceratiola sp. Michx. Rosemary.
Mangifera indica L. Mango.
Comocladia dentata Jacq. Maiden Plum.
Muntingia calabura L. Strawberry Tree.
Thespesia populnea (L.) Seaside Mahoe.
Hibiscus sp. L. Hibiscus.
Clusia flava Jacq. Balsam.
Passiflora sp. L. Passionflower.
Carica papaya L. Papaya.
Cereus (L.) Mill. Cactus.
Rhizophora mangle L. Red Mangrove.
Conocarpus erecta L. Buttonwood.
Terminalia catappa L. Almond.
Laguncularia racemosa Gaertn. F. White Mangrove.
Calypttranthes pallens Griseb. Pale Lidflower.
Psidium guajava L. Guava.
Eugenia sp. L. "Strawberry".
Myrtus sp. L. Stopper.
Ardisia escallonioides Schlecht & Cham. Marlberry.
Manilkara zapoda (L.) Naseberry.
Nerium oleander L. Oleander.
Ipomoea sp. L. Morning Glory.
Tournefortia gnaphalodes (L.) B. Br. Sea Lavender.
Avicennia nitida Jacq. Black Mangrove.
Cirsium sp. Mill. Thistle.

¹ Nomenclature from Swabey and Lewis (1946), Asprey and Robbins (1953), or Long and Lakela (1971).

APPENDIX III: STOMACH CONTENTS OF CAYMAN ISLAND BIRDS

The birds utilized in these analyses were collected in either April or August, chiefly from Grand Cayman. The numbers in parentheses represent the numbers of bird stomachs examined, A = animal food, V = plant food, and an asterisk (*) indicates a predominant food item. When more than one stomach was examined, the percentages for A and V are mean values. Nomenclature for the insect items follows that of Borror and DeLong (1964) and for plant foods, that of Asprey and Robbins (1953) or Long and Lakela (1971).

Butorides virescens (2). A, 100% Isopoda; Odonata, Libellulidae; Orthoptera, Acrididae, Cyrtacanthacridinae; Hemiptera, Belostomatidae, *Belostoma* (?)*; Coleoptera, Carabidae*, Dytiscidae.

Porzana carolina (1). V, 100%. Sedge seeds.

Columba leucocephala (1). V, 100%. Elaeocarpaceae, *Muntingia**.

Zenaida aurita (1). V, 100%. Cyperaceae, *Scleria**, *Rhynchospora**; Poaceae, *Panicum*; legumes; Empetraceae, *Ceratiola*; Myrtaceae, *Eugenia*; Asteraceae, *Cirsium*.

Columbina passerina (2). V, 100%. Cyperaceae, *Scleria**; Commelinaceae, *Commelina**; Asteraceae, *Cirsium*.

Leptotila jamaicensis (1). V, 100%. Cyperaceae, *Scleria*; Convolvulaceae, *Ipomoea*; legumes; Elaeocarpaceae, *Muntingia*; Rosaceae, *Prunus*; Empetraceae, *Ceratiola*.

Amazona leucocephala (2). V, 100%. Caricaceae, *Carica*.

Crotophaga ani (3). A, 87%; V, 13%. Arachnida, Araneida; Orthoptera, Acrididae, Cyrtacanthacridinae; Odonata, Coenagrionidae(?), Aeshnidae(?); Lepidoptera, Noctuidae, Nymphalidae(?); Coleoptera, Scarabaeidae, Chrysomelidae(?), Curculionidae*, Tenebrionidae; Homoptera, Cicadellidae; Hemiptera, Pentatomidae, Coreidae(?), Scutelleridae*, *Chelysoma*; Diptera head; Hymenoptera, Vespidae*. Vertebrate: *Anolis conspersus*.

Sedge seeds; Passifloraceae, *Passiflora*.

Tyto alba (ca. 50 pellets). Invertebrate- Paguridae, *Coenobita cylpeatus*; Coleoptera; Reptilia- *Aristelliger praesignis*; Aves- *Egretta thula*, *Centurus supercilialis*, *Elaenia martinica*, *Mimus polyglottos*, *Dumetella carolinensis*, *Dendroica* sp.?, *Coereba flaveola*, *Quiscalus niger*, *Melopyrrha nigra*; Mammalia- *Rattus rattus**, *R. norvegicus*, *Mus musculus**, *Brachyphylla nana*, *Artibeus jamaicensis*.

Colaptes auratus (19). A, 97%; V, 3%. Arachnida, Araneida; Coleoptera, Cerambycidae, Bostrichidae(?); Hymenoptera, Formicidae, *Formica**; Isoptera, Rhinotermitidae*.

Unidentified fruit fragments.

Centurus supercilialis (16). A, 56%; V, 44%. Arachnida, Araneida, *Seytodes fusca*; Orthoptera, Gryllidae, Acrididae*; Coleoptera, Curculionidae, Otiorhynchinae, Tenebrionidae; Hymenoptera, Formicidae, Vespidae(?).

Hyla septentrionalis, *Sphaerodactylus lewisi*.

Moraceae, *Ficus*; Caricaceae, *Carica**.

Tyrannus dominicensis (1). A, 100%. Homoptera, Cicadidae*.

Tyrannus caudifasciatus (5). A, 96%; V, 4%. Orthoptera, Gryllidae; Coleoptera, Curculionidae*, Carabidae, Buprestidae, *Polycesta*; Hymenoptera, Vespidae, *Vespula*(?), Formicidae, Myrmicinae. *Hyla septentrionalis*, *Anolis conspersus**. Burseraceae, *Bursera simaruba*; Passifloraceae, *Passiflora*.

Myiarchus stolidus (4). A, 89%; V, 11%. Arachnida, Araneida; Orthoptera, Gryllidae; Lepidoptera; Coleoptera, Cerambycidae*, Oedemeridae*; Hemiptera, Scutelleridae, *Chelysoma*(?)*; Hymenoptera, Tiphiidae(?), Andrenidae, Colletidae, *Colletes*, Vespidae(?).

Burseraceae, *Bursera simaruba*; unidentified seeds.

- Elaenia martinica* (9). A, 6%; V, 94%. Coleoptera, Curculionidae; Homoptera, Flatidae.
Moraceae, *Ficus**; Burseraceae, *Bursera simaruba*; Passifloraceae, *Passiflora*; many unidentified seeds*.
- Mimus polyglottos* (1). A, 87%; V, 13%. Crustacea, crab parts, Isopoda; Coleoptera, Scarabaeidae, *Dyscinetus*(?); Hemiptera, Pentatomidae; Hymenoptera, Formicidae, *Solenopsis*.
Unidentified seeds.
- Vireo crassirostris* (11). A, 77%; V, 23%. Arachnida, Araneida*; Orthoptera; Lepidoptera larva*, Microlepidoptera, Geometridae; Neuroptera, Chrysopidae; Coleoptera*, Curculionidae*, Oedemeridae, Cerambycidae*, Staphylinidae(?), Elateridae(?), Chrysomelidae; Hymenoptera, Formicidae, Vespidae; Hemiptera, Pentatomidae, Phymatidae.
Burseraceae, *Bursera simaruba*; many unidentifiable seeds.
- Vireo magister* (9). A, 51%; V, 49%. Arachnida, Araneida; Orthoptera, Gryllidae; Lepidoptera larvae*, Geometridae; Neuroptera, Chrysopidae; Coleoptera*, Tenebrionidae, Chrysomelidae, Curculionidae*, Cerambycidae, Scarabaeidae(?); Oedemeridae; Hemiptera, Pentatomidae; Homoptera, Flatidae; Homoptera leg; Hymenoptera, Ichneumonidae, Formicidae, *Cryptocerus*.
Burseraceae, *Bursera simaruba*; many unidentified seeds.
- Dendroica petechia* (3). A, 100%. Coleoptera*, Curculionidae, Oedemeridae*; Hymenoptera, Formicidae.
- Dendroica vitellina* (7). A, 97%; V, 3%. Arachnida, Araneida*; Lepidoptera larvae; Orthoptera, Gryllidae(?); Coleoptera, Curculionidae*; Homoptera*, Aphidae, Fulgoridae*, Ceropidae; Diptera, Muscidae; Hymenoptera, Formicidae.
Few unidentified seeds.
- Coereba flaveola* (6). A, 50%; V, 50%. Lepidoptera larvae*; Coleoptera, Chrysomelidae, Chalcidinae, Curculionidae; Homoptera, Cercopidae(?); Hymenoptera, Chalcidoidea.
Unidentified flower parts.
- Spindalis zena* (4). V, 100%. Myrsinaceae, *Ardisia*; many unidentified seeds.
- Quiscalus niger* (8). A, 87%; V, 13%. Arachnida, Araneida; Orthoptera, Tetrigidae, Gryllidae(?), Blattidae; Lepidoptera, Noctuidae; Coleoptera, Carabidae*, Oedemeridae, Curculionidae*, Alleculidae; Homoptera, Cicadidae; Hemiptera, Pentatomidae, Scutelleridae(?); Hymenoptera, Formicidae; Diptera, Culicidae(?).
- Hyla septentrionalis**, *Anolis conspersus**.
Moraceae, *Ficus*; unidentified seeds and plant fragments.
- Tiaris olivacea* (3). V, 100%. Poaceae, *Panicum**; many unidentified seeds.
- Melopyrrha nigra* (4). A, 39%; V, 61%. Lepidoptera larvae*; Coleoptera*; Chrysomelidae(?).
Unidentified seeds.

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