



THE UNIVERSITY OF CHICAGO PRESS JOURNALS

Taxon Cycles in the West Indian Avifauna

Author(s): Robert E. Ricklefs and George W. Cox

Source: *The American Naturalist*, Vol. 106, No. 948 (Mar. - Apr., 1972), pp. 195-219

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <https://www.jstor.org/stable/2459928>

Accessed: 25-04-2020 18:13 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

The American Society of Naturalists, The University of Chicago Press are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*

TAXON CYCLES IN THE WEST INDIAN AVIFAUNA

ROBERT E. RICKLEFS AND GEORGE W. COX

Department of Biology, University of Pennsylvania, Philadelphia, and
Department of Biology, San Diego State College, San Diego, California

The idea that species or higher taxonomic groups may exhibit “life cycles” analogous to those of individuals is not new (Simpson 1940, 1949; Darlington 1957). From examination of distributional and paleontological evidence, many workers have postulated cycles in which particular groups originate, diversify and spread, and finally decline or become extinct. Analogies between these phases and stages of youth, maturity, and senescence of the individual have been drawn, but they fail to provide meaningful insight into the processes involved (Simpson 1949).

Several authors have recently examined aspects of this problem in the light of modern knowledge of speciation and biogeography (Brown 1957; Carson 1959; Dillon 1966, 1970; Wilson 1961), and a general pattern seems to emerge. Certain species populations may initiate a phase of geographic expansion during which population density is high but morphological differentiation throughout the range of the population is low. Later, correlated with slowed range expansion, the population differentiates into taxonomically recognizable units (subspecies), especially near the margin of the range. With time, divergence within the species increases and extinction occurs in parts of its range, resulting in a discontinuous distribution. Remaining isolated populations tend toward greater ecological specialization and lower population densities than at earlier stages of expansion and differentiation. Finally, descendant populations, often subspecifically or specifically distinct, are restricted to small refugia.

Many interpretations of history based on present distribution patterns are weak because the relative ages of the populations involved are not known independent of their geographic patterns. This weakness may be circumvented in large part through analysis of insular species groups, the relative age of which can be postulated on the basis of divergence from parental mainland populations.

Here, we examine patterns of expansion and restriction in taxa of land birds, exclusive of raptors, within the West Indies. For insular situations, this has been termed by Wilson (1961) the “taxon cycle.” The occurrence of the taxon cycle is verified and documented by examination of the distribution and differentiation of species within the West Indies. We then consider immigration, differentiation, and extinction. Ecological and morphological attributes are compared for species assigned to different stages

of the taxon cycle to determine whether evolutionary changes in populations accompany progress through the taxon cycle. Finally, we postulate that the progress of a species through the taxon cycle reflects effects of progressively reduced competitive ability caused by "counterevolution" of an island biota to that species, coupled with strong competitive pressure from subsequent immigrants. This hypothesis contrasts sharply with current statements (e.g., MacArthur and Wilson 1967) that adaptation to island environments typically increases with time.

THE TAXON CYCLE

Wilson (1961) first formalized the concept of the taxon cycle in island populations. He distinguished expanding and contracting populations of Melanesian ants by their geographical distributions. Geographically widespread or expanding taxa (Stage I) occupied marginal habitats, literally edges of islands, thereby facilitating dispersal over water barriers. Species with reduced or fragmented ranges (Stages II and III) typically inhabited interior and montane forest habitats and exhibited other distinctive features associated with the habitat shift. Wilson postulated that, to have attained their present distributions, Stage II and III species previously must have occupied marginal habitats and behaved as expanding species. Examining other aspects of geographical patterns in this conceptual framework, Wilson concluded that expansion almost always involved movement from larger to smaller land masses, a notion also put forward by Darlington (1957). Similar patterns have been suggested to account for the insular distribution of birds (Greenslade 1968*a*; Ricklefs 1970*a*) and several groups of insects (Greenslade 1968*b*, 1969).

Distributions of nonraptorial land birds of the West Indies are grouped into four stages here, although intermediates and anomalous cases occur. Assignments are based on criteria outlined in table 1. The West Indies are defined here as consisting of the Greater Antilles, including the Cayman Islands, and the Lesser Antilles, but not the Bahama Islands, Trinidad, and Tobago.¹ Our stages do not correspond precisely to Stages I–III of Wilson (1961) and Greenslade (1968*a*) or to Stages I–IV of Dillon (1966), as explained below. Our stages are: (I) Species with widespread or continuous distributions through the islands with little or no subspeciation. Species not known to be moving into the islands but that have reached few islands are also included in this group. (II) Species generally widespread throughout the islands but that show considerable differentiation of populations into subspecies. During this stage, gaps begin to appear in the distribution, presumably through the extinction of populations on small islands. (III) Species with fragmented and reduced distributions and well-differentiated populations. (IV) Species endemic to single islands. Range maps of species representing the first three stages are shown in figure 1.

¹ Islands and species used in this analysis are available on request.

TABLE 1
CRITERIA USED IN DEFINING TAXON CYCLE STAGES FOR LAND BIRD SPECIES OF THE WEST
INDIES, EXCLUSIVE OF HAWKS AND OWLS
A. NONENDEMIC SPECIES (OR SUPERSPECIES GROUPS)

	OVER 10 ISLANDS PER FORM	UNDER 10 ISLANDS PER FORM*			
		No Distributional Gaps and Islands Adjacent to Continental or Other Range of Species		Distributional Gaps Present or Not Adjacent to Continental or Other Range of Species	
		>1 Island/ Species	1 Island/ Species	>1 Island/ Species	1 Island/ Species
Without endemic subspecies	I†	I	I	I	I
With endemic subspecies	I	II	II	III	III

B. ENDEMIC SPECIES (OR SUPERSPECIES GROUPS)

OVER 10 ISLANDS PER FORM	UNDER 10 ISLANDS PER FORM			
	>1 Island per Species			
	No Gaps and Islands Include Both Sizes Above and Below 100 km ²		Gaps or Islands Do Not Cover Sizes Above and Below 100 km ²	
	Monotypic Species	Polytypic Species	One Island per Species	
I	I	II	III	IV

* The term "form" refers to subspecies or monotypic species.

† Roman numerals refer to stages.

Wilson (1961) and Greenslade (1968a) designate only three stages in the cycle; their Stages II and III correspond to our Stages II–IV. Dillon (1966) employs four stages, but his criteria for Stages I and II are the reverse of ours; he states that the first stage of the cycle is well differentiated, on the basis of one detailed study of an "introduced species," the English sparrow, *Passer domesticus* (Johnston and Selander 1964), which now occupies a large part of North America and which demonstrates morphological differentiation among populations. The West Indian data presented here emphatically contradict Dillon's notion. Also, Dillon does not plausibly explain how a well-differentiated population might become monotypic.

The reality of the cycle, that is, the inference that Stages I–IV occur in succession, is supported by data on the level of endemism and degree of subspecific differentiation of species in different stages. The patterns of occurrence on islands and taxonomic differentiation for land birds other than raptorial species (hawks and owls) are presented in table 2. The transition from Stage I to II is clearly not reversible, as this would require the simultaneous convergence of numerous differentiated populations. Also, we may exclude the possibility that IV can be an initial stage, because these species are endemic to the islands and thus cannot be recent immigrants.

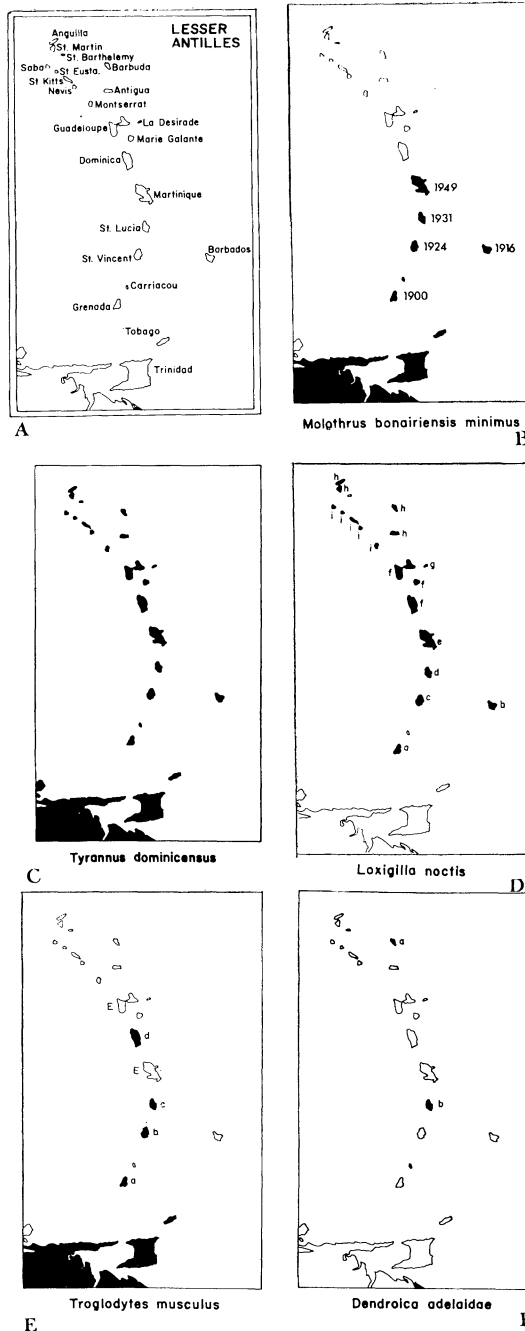


FIG. 1.—Examples of distribution in the Lesser Antilles of birds in different stages of the taxon cycle. *A*, Map of the area. *B*, Early I, *Molothrus bonairiensis*. *C*, Late I, *Tyrannus dominicensis*. *D*, II, *Loxigilla noctis* (representing an expansion within the Lesser Antilles). *E*, Late II–early III, *Troglodytes musculus*. *F*, Late III, *Dendroica adelaidae*. Lowercase letters designate differentiated populations (subspecies); *E* = extinction; dates refer to first colonization.

TABLE 2
PATTERNS OF ISLAND OCCURANCE AND TAXONOMIC DIFFERENTIATION WITHIN THE WEST
INDIES OF SPECIES OF SUPERSPECIES IN VARIOUS STAGES OF THE TAXON CYCLE*

	I	II	III	IV
Number of species	39	21	54	51
Total island populations	428	289	229	57
Total subspecies†	46	117	139	51
Subspecies/species	1.18	5.57	2.57	1.00
Island/species‡	10.97	13.76	4.24	1.12
Islands/subspecies	9.30	2.47	1.65	1.12

* Only land birds, exclusive of raptors, are included. Roman numerals refer to stages.

† Or subspecies plus monotypic species for superspecies.

‡ Or islands/superspecies.

In addition, nearly all of the species occurring within the West Indies, but showing no differentiation from continental forms, have continuous distributions through the islands (as in fig. 1), suggesting a "stepping stone" pattern of immigration. Species currently invading the islands from South America support this view (see below). Virtually no mainland species have undifferentiated populations that occur on single islands in the Carribean, save on Grenada, which is adjacent to South America, and on some of the Greater Antilles. Hence, Stage I is the most likely initial pattern, and IV represents the last possible stage, II necessarily following I.

Whether or not Stage II is a necessary prerequisite to Stage III is a trivial point. The relative number of islands per subspecies for Stage III species suggests, however, that III cannot be derived from I simply by fragmentation of the range through extinction, but also requires extensive morphological differentiation of island populations. Stage I species occupy an average of 10.97 islands and are differentiated into 1.18 subspecies (table 2). If Stage III distributions developed directly from those of Stage I by extinction alone, we would expect a decrease in number of islands per subspecies directly proportional to that in number of islands per species. Thus, we would expect about 3.7 islands per subspecies for Stage III forms, whereas an average of 1.65 is observed. Thus, considerable further differentiation must precede or accompany the development of Stage III patterns. Hence, the simplest explanation of the observed distributional patterns is that species move through the taxon cycle from Stages I to IV.

When discussing changes in the distribution patterns on islands, one must realize that populations on isolated islands are evolutionarily independent. The term "stage" denotes only a particular distributional pattern and a relative time since immigration, and does not assume the species to be an evolutionary unit. All island populations of a species do not disappear from the archipelago as a unit but, rather, isolated populations persist on islands for different periods. Variation in the rate at which sibling populations undergo evolutionary and ecological change emphasizes their independence from each other. Additionally, we should not expect all species to conform to the "typical" taxon cycle. Distribution throughout the islands during expansion may be affected by uneven distribution of barriers

to dispersal, and a certain element of chance must also be present in each step of the cycle.

Extinction is not the only fate of Stage IV species. Many species endemic to the Antilles have Stage I, II, or III patterns, and in view of the rapid differentiation of species recently derived from the mainland, isolated island populations are not likely to evolve in a closely parallel manner for any long period. Early-stage endemic species must represent secondary, and perhaps higher-order, expansions from within the West Indies. We can only surmise the stage from which recycling is most likely to begin, but the general absence of congeneric endemic species, particularly in endemic genera, suggests that new cycles originate from populations belonging to late stages. But, on the other hand, one could not detect secondary expansions of a species within the islands without reproductive isolation of secondarily sympatric populations.

IMMIGRATION

The main paths of immigration into the islands are: from the south, the northern coast of South America, through the Lesser Antilles; from the west, Central America, into the Greater Antilles; and from the north, the peninsula of Florida. Stage I species have several characteristics in common (table 3), although all species with these characteristics are not necessarily good immigrants. Recent invaders into the islands generally have high population densities and inhabit open country on the adjacent mainland. Some of these species frequently flock, and may wander considerable distances during the nonbreeding portions of the year, although this is not a consistent characteristic of the good immigrant. Conversely, few families of birds restricted to inner forest habitats on the mainland, including such important groups as tinamous, antbirds, woodcreepers, and manakins (with the notable exception of woodpeckers), have invaded any of the Caribbean Islands.

TABLE 3
OCCURRENCE AMONG STAGE I TAXA OF CHARACTERISTICS THOUGHT TO BE TYPICAL
OF READILY DISPERSING SPECIES

	OCCURRENCE IN:		
	Surinam*	Colombia†	Trinidad‡
Number of Stage I West Indian species	11	15	15
Characteristic:			
Common or abundant	9	§	9
Inhabits open country, including marshes, savannah, gardens	9½	10¼	9
Gregarious or flocking	2½	§	3

* Data from Haverschmidt (1968).
† Data from DeSchaunsee (1964).
‡ Data from Herklots (1961).
§ Information not available.

The distance species penetrate into the West Indian island chain varies considerably. The number of nonendemic Stage I species per island decreases as distance from the mainland increases (fig. 2). Although South America contains a larger species pool of potential immigrants, and the Lesser Antilles lie closer to the coast of South America, North and Central America have contributed a larger number of birds to the Caribbean avifauna (Bond 1963). Species that have invaded from the south through the small islands of the Lesser Antilles drop off in a fairly regular progression, whereas many northern immigrants stop at Puerto Rico. It seems plausible that the smaller islands to the south filter all except those with remarkable dispersal powers. Also, the Greater Antilles may offer, because of their size, a greater variety of habitats than the Lesser Antilles. The failure of birds to penetrate completely the islands from the south may be attributed either to the fact that the source populations of immigrants from island to island are too small to exhibit strong dispersal power or to the fact that the population exhibits a reduction in its ability to disperse as it spreads through the islands.

Several invading species expanded their ranges in the islands in historical times. The bare-eyed thrush, *Turdus nudigenis*, long present on Grenada and Saint Vincent, has been resident on Saint Lucia, the next island in the chain, since 1951, and in that year was first reported from Martinique, immediately to the north (Bond 1956). By 1965, this species, which is extremely aggressive toward other thrushlike birds, was widespread around settled areas throughout the former island (cf. Bond 1965). The shiny cowbird, *Molothrus bonairiensis*, dispersed rapidly and widely through the islands in recent times. The species was first noted on Grenada and the Grenadines at the turn of the present century, although it may have been introduced to Vieques, off Puerto Rico, earlier, reached Barbados in 1916,

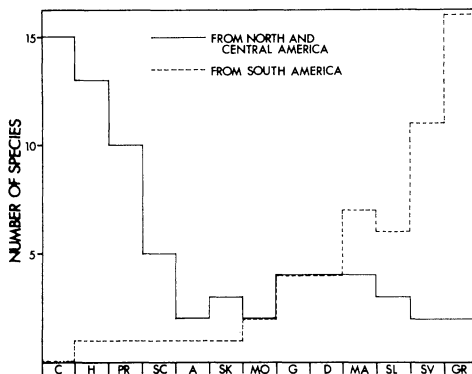


FIG. 2.—The occurrence of nonendemic Stage I species on islands progressively more distant from the source of colonization. C = Cuba, H = Hispaniola, PR = Puerto Rico, SC = Saint Croix, A = Antigua, SK = Saint Kitts, MO = Montserrat, G = Guadeloupe, D = Dominica, MA = Martinique, SL = Saint Lucia, SV = Saint Vincent, GR = Grenada.

and progressively colonized Saint Vincent (1924), Saint Lucia (1931), and Martinique (1949). Recent sight records extend the range to Marie Galante (near Guadeloupe) and Antigua (Bond 1966). The recent invasion of Puerto Rico may have been from an introduced population on nearby Vieques (Bond 1967).

Immigration by some "native" species to the islands, particularly the shiny cowbird, may have been facilitated by man, either through direct introduction or by changes in habitat through cultivation, logging, and urbanization. For example, the smooth-billed ani colonized Swan Island, 200 miles from the nearest source of immigrants, within 50 years after suitable cleared habitat had been created by man (Paynter 1956). Bond (1956) lists 12 species of land birds (other than gallinaceous and raptorial birds) successfully introduced into the West Indies and an additional 18 species of escaped cage birds or introductions that did not thrive. Over and above natural dispersal power and the possibility of introduction in some of the species, much of the West Indies lies within a region of frequent hurricanes that have undoubtedly aided dispersal.

Immigration appears to occur in a stepping-stone fashion, progressing from one island to the next. This model is supported by the uniformly continuous distribution of recent immigrants to the Caribbean and by historical records of species presently expanding in the islands. Also, Hamilton, Barth, and Rubinoff's (1964) analysis of species diversity of birds on islands of the eastern Pacific Ocean showed that diversity on a particular island was strongly influenced by distance to the nearest island, and that distance to the mainland source of colonists had little effect.

DIFFERENTIATION

MacArthur and Wilson (1967) postulated three phases of differentiation once populations became established on an island. The colonizing propagule may differ from the parent population initially due to the "founder effect" (Mayr 1965*a*), because the small number of individuals that immigrate are only a limited sample of the total genetic variability in the mainland population. Because of the remote nature of islands, colonizing species must be good dispersers and are thought to have high intrinsic population growth rates. Initial adjustments of population parameters may involve loss of dispersal power (Carlquist 1966), presumably in return for increased competitive ability on the island. During a second phase, the population adapts more closely to its particular island environment. During this period, marked differentiation of island populations takes place. MacArthur and Wilson's third phase, that of speciation and radiation within the island group, need not concern us here, as it involves secondary cycles of expansion and not the events of a single cycle.

The immediate fate of recent colonists is poorly known, and in general, population parameters affecting a population's capacity to increase are so difficult to ascertain for birds that no definitive statement can be made

about MacArthur and Wilson's first phase. At least some colonists (e.g., the bare-eyed thrush on Saint Lucia) initially were quite restricted on an island before greatly increasing their populations. The saffron finch, *Sicalis flaveola*, introduced in the vicinity of Black River, Jamaica, during the nineteenth century, was restricted to that locality for many years until a sudden period of expansion resulted in its becoming common and widespread throughout the island (Bond 1956). Such rapid population expansion, after an initial "quiescent" period, almost certainly must follow genetic reorganization within the population that results in particularly favorable gene combinations (e.g., Lewontin and Birch 1966). It seems unlikely that changes in environment could be important in the above cases; however, our knowledge of the ecology and genetics of these species is too poor to pursue the point further at this time.

Rate of differentiation appears to be affected by the dispersal of birds among islands. None of the species that are either migratory in the Antilles or that are known to fly frequently between islands (e.g., many doves) exhibit marked differentiation within the islands, and we have designated 10 of 12 of these species as Stage I. Either their dispersal powers prevent their movement through the taxon cycle, or these species are all recent immigrants. Furthermore, distance between islands, presumably a major barrier to dispersal between two islands, strongly reflects the degree of subspecific differentiation among species found on both islands (fig. 3). This relationship is confounded because the largest water gaps tend to occur between the largest islands (presumably between the largest populations), and gene flow must be measured with respect to population size.

Our observations on the relationship between isolation and endemism on islands are consistent with analyses of Hamilton and Rubinoff (1963, 1964, 1967) on Galapagos birds, with Vuilleumier (1970) on birds of montane "islands" of the northern Andes, and with Soulé (1971) on lizards in the Gulf of California. Although Ehrlich and Raven (1969) argued that gene flow has little effect on differentiation within a species, island bird populations do not appear to be completely isolated from one another, and even low levels of gene flow between populations appear to have evolutionary significance. The slowing of differentiation among island forms due to gene flow has little bearing on the general features of the taxon cycle, however, and is ignored here (cf. Udvardy 1970). Interisland movement, and thus gene flow, must be nil in late stages of the taxon cycle, because extinct populations do not appear to be replaced by immigration.

Some populations undergo marked changes on islands, while other island populations of the same species group remain relatively undifferentiated from mainland populations. In most species and subspecies of the *Icterus dominicensis* group of orioles, both males and females are brightly colored. However, females of *Icterus oberi* on the island of Montserrat have become very dull colored, presumably reflecting a major change in the female's role in intraspecific interactions. The opposite has occurred in endemic species of red-winged blackbirds (*Agelaius humeralis* on Cuba and Hispaniola, and

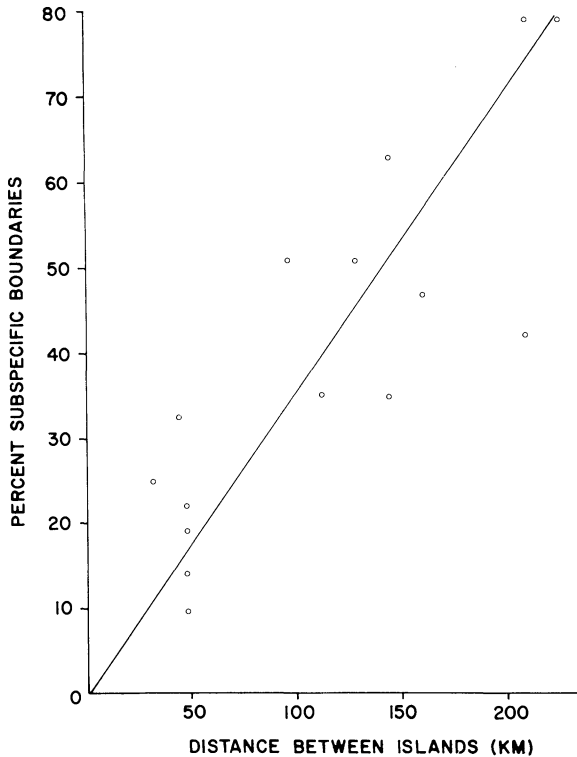


FIG. 3.—Percentage subspecific boundaries as a function of the distance between neighboring islands. Percentage subspecific boundaries was obtained by dividing the number of species held in common by neighboring islands that differ at the subspecific level by the total number of species common to the two islands.

Agelaius xanthornus on Puerto Rico) in which females have evolved a brightly colored plumage and the usual sexual dimorphism of *Agelaius* has almost disappeared. The Barbados race of the widespread bullfinch, *Loxia noctis*, has also lost its dimorphism. Bond (1965) noted distinctive songs in some island populations of widespread species. Songs in the house wren, *Troglodytes aedon*, vary from “comparatively inferior songs of *musculus mesoleucus*” on Saint Vincent and Saint Lucia, where the species is locally distributed, to “beautiful songs of *rufescens*” on Dominica, where wrens are widespread and abundant.

EXTINCTION

The fate of most populations must eventually be extinction. Populations are generally thought to have a higher probability of extinction on small than on large islands, owing to small size and low genetic plasticity of populations (Soulé 1971; Townsend 1952). Extinction may be inferred from

distributional gaps of birds, since recent colonists, as noted above, tend to have continuous ranges.

Many species have become extinct in recent times in the Caribbean, and others are clearly on the brink of disappearance (tables 4 and 5). No population of species designated Stage I on the basis the earliest distribution data has disappeared, and of Stage II species, only the house wren, which is rapidly moving into Stage III, has become extinct in parts of its range. Since many of the Stage III and IV species are restricted in habitat, often to montane forests, one may argue that human disturbance is directly related to their disappearance through destruction of suitable habitat. This certainly may be true of parrots (Psittacidae), which have suffered badly and which bear the additional burden of being edible and prized as pets. The relatively low number of species on Barbados is undoubtedly due to the fact that most of the island is under cultivation and that virtually no natural forest remains. Many Hawaiian endemics are thought to have succumbed to introduced diseases (Warner 1968). However, human disturbance cannot account for the disappearance of the house wren from Guadeloupe and Martinique, and its impending extinction on Saint Vincent

TABLE 4
OCCURRENCE OF EXTINCT AND ENDANGERED SPECIES OF WEST INDIAN LAND BIRDS*

	I	II	III	IV
Extinctions (1850-1925)	0	2	3	2
Extinctions (1925-2000)†	0	2	2	4
Endangered	0	4	7	7
Total species	0	8	12	13
Total island populations‡	428	289	229	57
Percentage	0	2.8	5.2	22.8

* According to stage in the taxon cycle, expressed as number of species and percentage of possible island populations for each stage. Data from Bond (1968).

† Including species likely to become extinct in the near future.

‡ Each population of a species on a different island is counted separately.

TABLE 5
OCCURRENCE OF EXTINCT AND ENDANGERED SPECIES IN RELATION TO ISLAND SIZE*

	LOG ₁₀ OF ISLAND AREA (MILE ²)				
	0-1	1-2	2-3	3-4	4-5
Extinctions (1850-1926)	0	2	2	1	2
Extinctions (1925-2000)†	0	1	6	0	1
Endangered	0	1	10	6	1
Total	0	4	18	7	4
Total island populations:					
Stage IV	0	0	12	24	23
Stage III	6	30	73	45	45
Ratio of extinct and endangered species to total island populations:					
Stage IV	∞	1.50	0.29	0.17
Stage III	0	0.13	0.25	0.16	0.09

* Data from Bond (1968).

† Includes species likely to become extinct in the near future.

and Saint Lucia, where the forest habitat of this species is still plentiful. Nor can habitat disturbance account entirely for the disappearance of such species as the Grand Cayman thrush from an island that has been relatively undisturbed (Johnston 1969).

SPECIES AREA CURVES

One point seems quite clear: probability of extinction is low for species early in the taxon cycle and increases rapidly with stage (table 4). Equally notable is the fact that the probability of extinction decreases with increasing island size (table 5). On the other hand, the rate of colonization in the West Indies is probably independent of island size, owing to the proximity of islands to one another, except that many smaller islands in the Caribbean are extremely distant from sources of colonization.

MacArthur and Wilson (1963) developed a predictive graphical model of the equilibrium number of species on an island, based on rates of colonization and extinction (fig. 4). The colonization curve falls with increased numbers of species on an island because, as the diversity approaches that of the pool of species available to colonize from the mainland, the possibility of new immigrants is reduced. The extinction curve is thought to rise more rapidly than the increasing number of species, owing to increased interspecific competition and reduced population sizes. Neither curve is thought to be linear, for this would require the probability of immigration or extinction of a species to be independent of the number of species on an island. The immigration curve is probably concave because early immi-

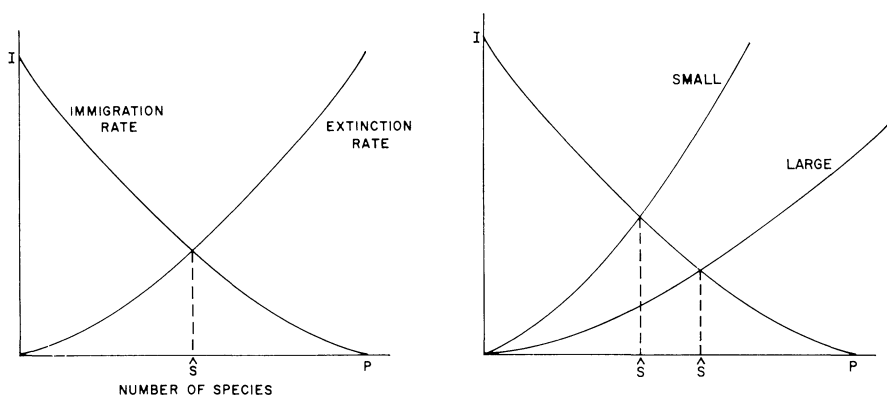


FIG. 4.—MacArthur and Wilson's (1967) model of species diversity on islands. The total number of species on any island is determined by the equilibrium between the immigration rate onto an island and the extinction rate of the local fauna. The immigration rate is zero at p , the total pool of species available for immigration on the mainland. Above the equilibrium point \bar{s} , extinction exceeds immigration and the number of species decreases. Below that point, immigration exceeds extinction and the number of species increases. Small populations are presumed to have a higher probability of extinction than large populations; thus the equilibrium diversity of small islands is lower.

grants represent species that colonize readily. Species now absent from the islands must have a lower probability of becoming colonists than already successful immigrants. As we have observed, some groups appear not to colonize the Caribbean at all, although they are an important part of the mainland species pool.

Because probability of extinction increases with decreasing island size, the number of species per island increases with island size. These patterns are commonly represented as "species-area curves" plotted on logarithmic coordinates (fig. 5). The resulting curve is often described by the equation $S = bA^z$, where S is the number of species on an island, A is the area of the island, and z is the slope of the regression. MacArthur and Wilson (1967) found that z values for many different groups of organisms on islands vary narrowly within the limits 0.20–0.40. Species-area curves on the mainland generally have lower z values (0.12–0.17) because small areas constantly receive immigrants from surrounding areas and thus local extinction is quickly masked by continuous reinvasion. It should be kept in mind that z values are descriptive parameters applied to heterogeneous sets of data (i.e., with varied immigration rates), but also that they are related to the balance between extinction and immigration rates. If immigration to a set of islands is constant, the z value of the species-area curve represents the degree to which extinction rate varies with island size.

The general uniformity of z values raises the ogre of underlying general principles, which always prove to be elusive. We have further found that z values vary with stage of the taxon cycle and with ecological relationships (figs. 6–8). The slope of the species-area relationship increases sharply with

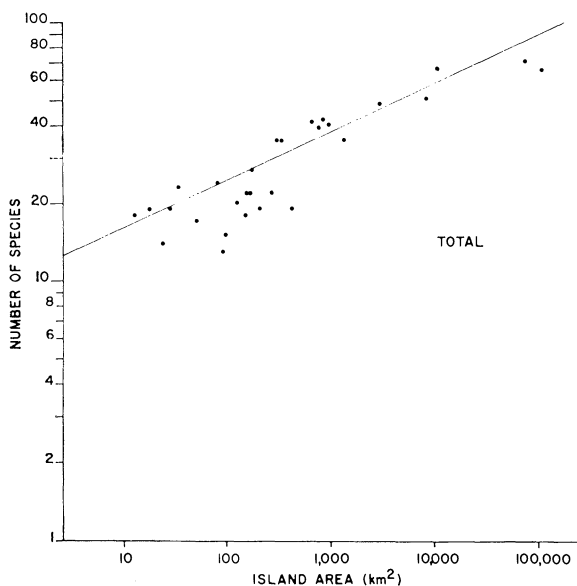


FIG. 5.—Species-area curve for the West Indies. Only land birds, exclusive of raptors, are included. The z value is about 0.22.

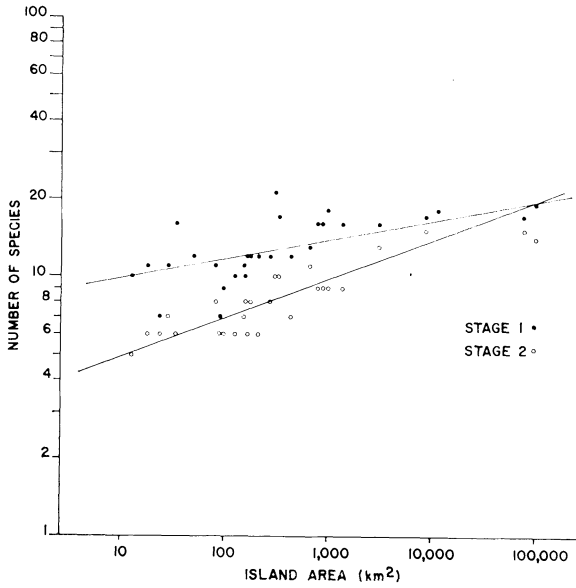


FIG. 6.—Species-area curves for Stage I and II species. The z values are about 0.075 and 0.15, respectively.

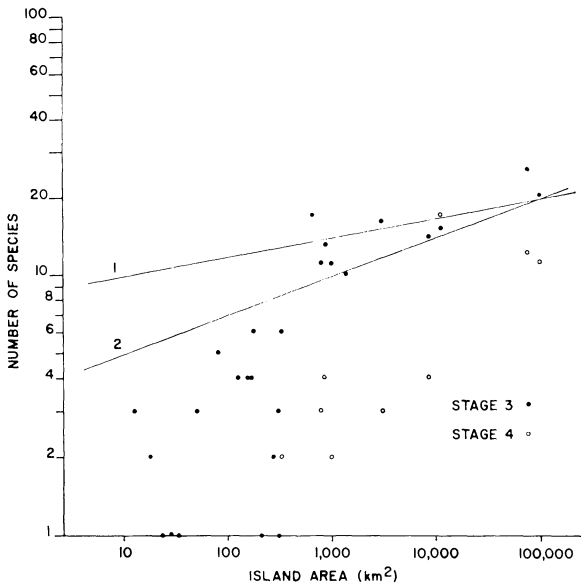


FIG. 7.—Species-area curves for Stage III and IV species. The z values are approximately 0.32 and 0.42, respectively. Species-area curves for Stages I and II are included for comparison.

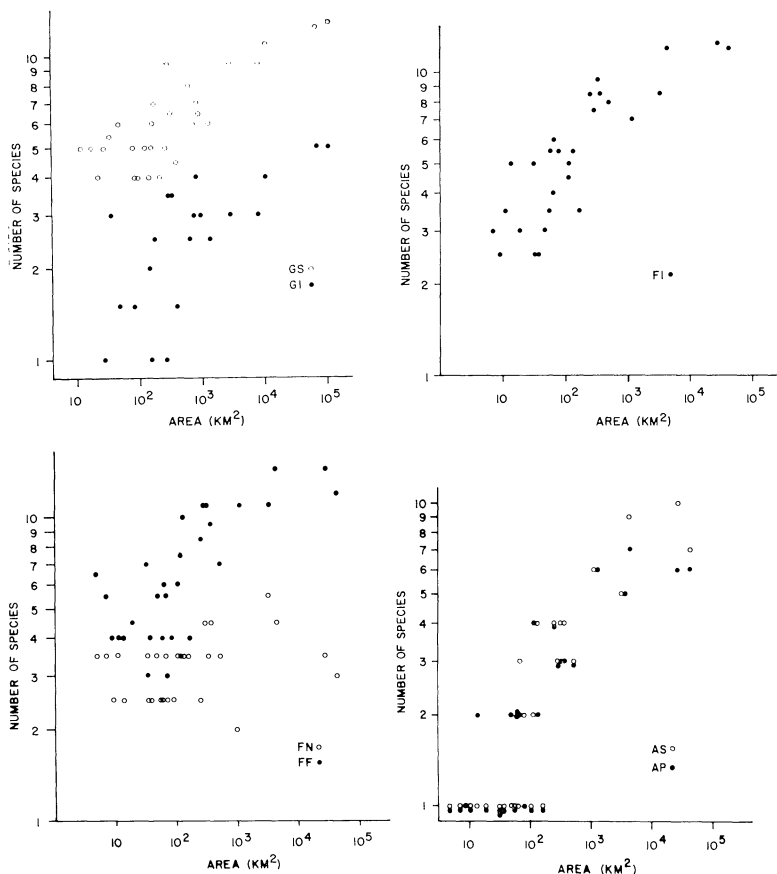


FIG. 8.—Species-area curves for birds grouped according to feeding ecology. The z values are presented in table 6. *GS* = ground searchers, *GI* = ground-feeding insectivorous birds; *FI* = foliage-feeding insectivorous birds; *FN* = foliage-feeding nectivorous birds; *FF* = foliage-feeding frugivorous birds; *AS* = aerially feeding birds that search for prey from perches; *AP* = aerially feeding birds that pursue their prey from the air. Half-species occur because some species are assigned to two feeding categories.

stage of the taxon cycle. Since we believe that there is little or no extinction among first and second stages, the reduced number of Stage I and II species on small islands must be related to their greater distance from mainland sources of colonists. Very small islands close to the mainland, such as Carriacou (34 km²), located between Grenada and Saint Vincent, have as many Stage I species and nearly as many Stage II species as neighboring larger islands (fig. 6).

Slopes of species-area curves also vary according to a group's feeding ecology. In table 6, z values are presented for species grouped according to the scheme of Salt (1957). In general, fruit and nectar feeding species have the lowest z values, followed by those which search for insect food on

TABLE 6
SLOPES OF SPECIES-AREA RELATIONSHIPS, AND EXTRAPOLATED NUMBER OF SPECIES
AT 10⁶ SQUARE KILOMETERS AREA, FOR VARIOUS FEEDING GROUPS, BASED ON FIGURE 10*

Feeding Category (and Representative Species)	Slope (<i>z</i>)	Number of Species at 10 ⁶ km ²
Foliage nectar (hummingbirds, honeycreepers)04	4.5
Ground searchers (doves, some finches)11	16.5
Ground insect (thrushes, some finches)11	6.5
Foliage fruit (some tanagers and icterids)12	20
Foliage insect (warblers, mimids, vireos, some tanagers)16	21
Aerial searchers (flycatchers)21	17
Aerial pursuers (swallows, swifts)21	17

* The species-area curves are biased toward maximum number of species for a given island area to eliminate heterogeneity caused by the relatively great distance of some small islands from a mainland source of colonizers.

the ground or in foliage. Species that actively pursue their food, such as flycatchers, swallows, and swifts, have the steepest species-area curves. The increased slope of the species-area curve may be associated with the relative effort spent in searching for and pursuing prey, but groups with high *z* values also tend to be more specialized in their morphology and feeding habits. Hummingbirds, with a low *z* value, are an exception.

Variation in slopes of species-area curves must be associated with variation in the relationship between extinction rate and island size for each group. Smaller islands may lack habitat diversity to support species groups with particular feeding habits, which may account for variation in species-area curve, but this argument may be countered by pointing out that most of the feeding groups represent within, rather than between, habitat distinctions. Also, gaps in ranges of many species are obviously not due to a lack of suitable habitats. Examination of figures 6–8 further reveals variation in the relative displacement of curves for various groups (table 6), which may result from differences in their immigration rates.

ADAPTATION AND THE CYCLE

Information on adaptive changes in populations as they move through the taxon cycle is meager and mostly indirect. Small land birds do not exhibit great flexibility in fecundity and mortality schedules (Ricklefs 1969, 1970*b*), and thus the changes in population parameters that MacArthur and Wilson (1967) suggest as occurring during early stages of colonization may be difficult to detect. One of the most striking features of recent immigrants onto islands is that of “ecological release,” or the occupancy of a wide range of habitats. Crowell (1962), for example, compared habitat utilization of several North American birds on Bermuda and found greatly increased population densities and broader habitat ranges. This pattern has been further documented by MacArthur, Recher, and Cody (1966) and Cox and Ricklefs (in preparation). Crowell was unable, however, to detect changes in diversity of foraging techniques or use of habitat. Ricklefs (1970*a*) found that expanding taxa on Jamaica

occupied broad ranges of habitats compared with species in later stages of the taxon cycle. Greenslade (1968a) made similar observations on Solomon Island birds.

Greater habitat ranges of early-stage species might lead to increased genetic or phenotypic variation within the population (Soulé 1971). Willson (1969) did not detect systematic differences in morphological variation between species, and island populations generally exhibited low variance in measurable characteristics.

Several species either migrate from the West Indies during the non-breeding season of the year or move widely throughout the islands (e.g., many doves have been seen flying between islands). Most of these are Stage I or II species, and two-thirds of Stage I species not endemic to the islands regularly move from or among islands. This movement may be characteristic of most new colonists or, alternatively, may have delayed their progression through the taxon cycle. Flocking is also less frequent in later stages of the cycle (table 7). Reduced interisland movement and reduced flocking are both consistent with increasing occurrence of birds in mature forest as they move through the taxon cycle (table 7). Although the plumage of many species diverges from characteristic patterns of their taxonomic groups, no consistent trend could be detected with respect to the taxon cycle. Nest construction and placement also did not change with the taxon cycle.

THE CAUSE OF PROGRESS THROUGH THE CYCLE

Progress through the cycle may be an "internal" process of the population uninfluenced by external factors, but if so, the mechanism involved is obscure. Alternatively, the external environment may force populations through the cycle. Competitors, species whose ecological requirements are

TABLE 7
OCCURRENCE OF VARIOUS CHARACTERISTICS OF SPECIES IN DIFFERENT STAGES
OF THE TAXON CYCLE EXHIBITING VARIOUS CHARACTERISTICS

	STAGE			
	I	II	III	IV
Number of species:				
Nonendemic	15	10	17	27
Endemic	4	3	6	17
Percentage of species showing migration or interisland movement:				
Nonendemic	67	20	0	0
Endemic	0	0	0	0
Percentage of species showing flocking behavior:				
Nonendemic	80	40	29	37
Endemic	0	0	0	18
Percentage of species including mature forest among their habitat distribution:				
Nonendemic	20	50	65	82
Endemic	75	33	50	41

so close that they seriously impinge on one another, are most likely candidates for external agents. The role of competitors may be assessed by comparing islands which differ in opportunities for arrival of competing species. Do populations on small islands at which new competitors fail to arrive progress through the ecological changes that occur during the taxon cycle and finally become extinct? Small islands (less than 100 km²) of the Lesser Antilles have few Stage III and no Stage IV species, and are consistently populated by Stage I species that also reach larger islands. Islands of similar size and vegetational characteristics located great distances from the mainland frequently have relatively old populations of birds, often specifically and generically distinct from mainland relatives. Cocos Island (26 km²), west of the coast of Central America, is one such island and has a distinctive member of the Darwin's finch group (*Geospizinae*). The Juan Fernandez Islands, lying 600–800 km off the western coast of South America, also have a number of highly distinctive species (*Spizitornus fernandezianus*, *Aphrastura masafuerae*, *Thamnaste fernandensis*). We cannot say that extinction of established populations does not occur on these islands, but it seems that its rate must be much lower than on similar islands close to source areas of dispersal. On the assumption (not necessarily valid) that these remote islands are ecologically similar to islands close to source areas, excepting the notable lack of close competitors, we must postulate that newly arriving competitors are the major cause of extinction in island bird faunas, aside from the influence of man. Plant and insect species appear to disperse so easily that even remote islands are not particularly depauperate in this respect. Also, with the possible exception of specialized frugivores, birds probably do not distinguish species of plants and insects to any extent (MacArthur and MacArthur 1961).

Mayr (1965b) observed that the percentage of endemic species increased on progressively more remote groups of islands. The percentage of endemic species for islands of similar size was about three times greater on "solitary, well-isolated islands" than on "single islands near mainlands or large archipelagos." The percentage of endemic species for "islands in scattered archipelagos" (including the Greater Antilles) was intermediate. Green-slade (1968a) found similar patterns for selected islands in the Solomons group. If we assume that population differentiation rates on these islands are independent of distance from colonization sources after a certain point, that is, that gene flow has little effect on differentiation, the larger proportion of endemics on remote islands implies that a smaller percentage of their faunas consist of recent immigrants compared with islands near sources of colonists. Thus, two extremes among small islands may be contrasted. On the one hand, islands close to sources of immigration have a relatively large number of recently derived species. At the other end of the spectrum are remote islands with few species, but with a high percentage of endemics and a relatively low turnover rate. Populations on remote islands probably change ecologically, but in the absence of competitors, extinction is infrequent.

Successful immigrants appear to have a definite competitive advantage

over species that have occupied an island for long periods: their population sizes and habitat distributions are greater and their probability of extinction is lower. We may speculate on the nature of the changes that occur in populations as they move through the taxon cycle. As we have mentioned, immigrants typically occupy open habitats and, furthermore, are often widespread and abundant on the mainland. When they arrive on an island, they have had little exposure to the environment of the island, but more important, the environment, which includes the newcomers' potential predators, parasites, food items, and competitors, has had no exposure to them. Thus, the productivity of populations is not greatly inhibited by biological components of the environment, which have not had an opportunity to adapt to the new species. Janzen (1970) and others emphasized that plant species may leave behind their predators and parasites when they invade islands, resulting in dense populations due to release from "pest pressure." Progressively, however, the biotic environment readjusts to the new species through evolutionary responses, often referred to as "counteradaptation" (Ricklefs 1970*b*) or "genetic feedback" (Pimentel 1961). For example, Southwood (1961) showed that tree species in England are infested with species of herbivorous insects in proportion to the abundance and presence of trees through time in the fossil record. Thus, a history of abundance creates the opportunity for profitable specialization.

Recent immigrants onto islands must be particularly susceptible to counteradaptation. Their populations are typically large, and hence they constitute an important part of the environment for many species. Eventually, effects of counteradaptation reduce the relative competitive ability of the new species. If other immigrants colonize the island, some of the original inhabitants will be restricted to those habitats in which their productivity is highest, that is, to which they are best adapted. Breadth of habitat can be maintained only at the expense of productivity, because a widely distributed population is exposed to a variety of selective forces that lead to compromise adaptation.

In the absence of competitors, productivity could be reduced greatly by counteradaptation without seriously affecting the size of the population, because much productivity is absorbed by density-dependent mortality (Lack 1954). Also, intraspecific competition per se cannot lead to the extinction of a population. However, populations of competing species that gain a productive edge will gradually replace the species in all but a few habitats.

Diamond (1970) found that on species-poor (isolated) islands in the southwest Pacific, densities of populations (determined from rates of capture in mist nets) of individual species were similar to those of species-rich islands for "coastal lowland rain forest" habitat, but considerably lower than species-rich islands for "montane forest" and "subalpine mossy forest" habitats. This finding contrasts sharply with Crowell's (1962) observation of increased population densities of species on Bermuda compared with the same species on the North American mainland, with

Diamond's (1969) data for birds of the Channel Islands off southern California, and with Grant's (1966) observations on the Tres Marias Island adjacent to western Mexico. Although Diamond (1970) suggests that the lack of "ecological release" for population densities of birds on small islands in the southwest Pacific may be partly due to "impoverished gene pools, reduced selection pressure, and low degree of endemism," the data are more consistent with our hypothesis that the taxon cycle is driven in part by reduction in competitive ability produced by counteradaptation. For the population-density data cited above, the degree of endemism is least for Bermudan birds; hence, these represent early-stage species whose productivity is high. On smaller islands in the southwest Pacific, montane species, by and large, have progressed further through the taxon cycle (Greenslade 1968*a*) than lowland species, and effects of counteradaptation on population size should be most noticeable there.

In general, as species move through the taxon cycle, they become restricted to montane or mature forest habitats (Greenslade 1968*a*). This may represent a trend toward restriction of populations to the most stable, or perhaps the most abundant, habitats on an island. On the other hand, there are several species on various islands which have been forced into other habitats, such as the Zapata Swamp in Cuba, the arid Hellshire Hills in Jamaica, and semiarid forest areas in Saint Lucia. Thus, habitat specialization may often lead into rare and probably unstable habitats. Habitats occupied by late-stage populations also appear to differ most from those originally occupied when these populations were new colonists from the mainland.

Many of these ideas are brought together into one cohesive model in figure 9. Several factors must be taken into account, the most important of which appear to be rate of immigration to the islands and opportunity for adaptive radiation. We start with potential colonists on the mainland. Some disperse well, and others so poorly that no members of their families are found in the Caribbean. These differences (including ability to establish populations once propagules have reached islands) determine patterns of

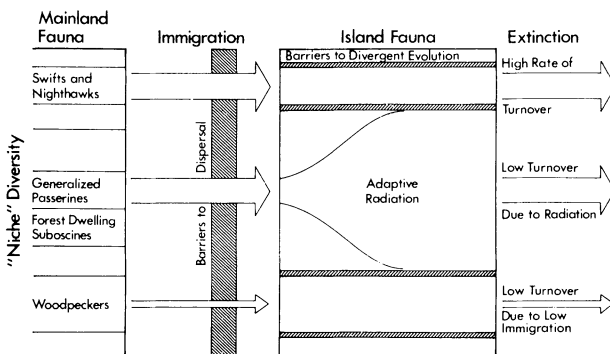


FIG. 9.—A schematic model incorporating the basic components of the taxon cycle. For details see text.

distribution of Stage I species. Once on the island, populations become progressively less able to meet competition from new immigrants. With the arrival of new competitors, the original population may become extinct, or it may meet the challenge by evolving into a different "niche" and thus temporarily avoiding competition.

Some species are so specialized in their habits when they reach an island that they cannot readily evolve to exploit the environment differently. The impact of competitors must be very great upon them. We would expect, because of high extinction rates in these groups, that the slope of the species-area curve would be relatively steep and rate of turnover high. This is true of, for example, swifts and nighthawks, whose morphology is specialized for aerial feeding. This group also appears to have strong dispersal powers. About half its species in the Caribbean are Stage I and the remainder are Stages III and IV. Flycatchers are less specialized for feeding aerially and have radiated into a wide variety of feeding niches. Five of 16 Antillean flycatcher species are Stage I. The large number of foliage gleaners are rather generalized birds that apparently can evolve into new "niches" with relative ease. Of these, only six of 41 species are recent immigrants (Stage I). In the Antilles, their rate of immigration is similar to that of aerially feeding species, but many more accumulate on islands in later stages of the taxon cycle. Also, foliage gleaners are related ecologically to a large number of forest species that do not immigrate to the islands at all, leaving considerable empty "niche" space. The trembler, *Cinlocerthia ruficauda*, is a thrasher (Mimidae) evolved to fill partially a "niche" normally occupied by woodcreepers (Dendrocolaptidae) on the mainland (Zusi 1969).

Woodpeckers are, like aerial feeders, very highly specialized. However, because they are primarily woodland or inner-forest birds, their rate of immigration, and hence turnover rate, is very low. At present, eight of nine species in the Caribbean belong to Stages III and IV.

Although progression through the taxon cycle may often lead to extinction, recycling does occur, for in no other likely way could a series of undifferentiated populations of a species or genus endemic to the island chain have come about. Changes in populations initiating a new cycle within an island group are probably similar to those which occur on the mainland to start an invasion. Recycling may involve escape from constraints imposed upon the population by counteradaptation of the biotic environment. Escape could result from a basic innovation by the population, leading to greater competitive ability, or more likely, from a release of environmental counteradaptive pressures on the population. The population, as it progresses through later stages of the taxon cycle, may become sufficiently rare so that it is no longer important enough to warrant counteradaptation. This model constitutes a negative feedback system which seemingly ought to bring a species into a stable equilibrium rather than cause oscillations that eventually lead to extinction. However, oscillation might be produced by external disturbances, such as immigration of a new species, or by a time lag in the system of counteradaptation. Time lags could result from differ-

ences between processes of adaptation by members of a fauna to one species, when it first appears, and the relaxation of adaptation toward that species as it eventually declines in abundance later in the cycle. The latter would presumably be slower, or occur at lower population levels, because the specific nature of the adaptation places an inherent value on the interaction. The lag is analogous to the documented lags in the development and loss of search images by vertebrate predators (Tinbergen 1960).

The picture we have presented here can only depict a generalized account of what has happened and is happening to the West Indian avifauna. All species of birds differ and cannot be expected to progress through generalized or typical stages. Historical accidents of distribution and evolution must also play a large role in these processes. The climate within the Caribbean and surrounding mainland areas from which colonists are derived has undoubtedly changed during geologically recent history, and must have influenced observed patterns.

Models presented here are empirically based. We believe they represent the simplest interpretation of observed facts, although alternative models could be formulated. As such, however, the models suggest several important areas of research that have received little attention. Of prime importance is the notion that a species progresses through cycles of evolutionary activity and that during these cycles the species undergoes marked changes in its competitive ability. If our notion that this is largely caused by counteradaptation is correct, it points to the basic importance of subtle adjustments among elements of a community to the determination of "niche size" and related aspects of community structure. These hypotheses also suggest the need for considerable detailed fieldwork. Counteradaptation cannot be readily studied in birds because of the relative inflexibility of many of their life history parameters and the fact that mortality is difficult to assess. Other groups of species on the appropriate island chains may well be more amenable to such analyses, and should be sought. Comparable situations in mainland faunas also deserve attention. Although relative ages of populations on mainland areas cannot be determined as in island faunas, we can extrapolate patterns observed on islands and proceed to investigate the ecology of differences in "dominance" or "relative abundance" between species (McNaughton and Wolf 1970; Ricklefs, in preparation).

SUMMARY

Analysis of distribution patterns of land birds in the West Indies supports the empirical theory that once species invade islands they progress through a series of evolutionary changes that eventually greatly increase the probability of extinction.

Species are arbitrarily assigned to four stages of the "taxon cycle" based on their distribution and differentiation within islands: (I) expanding or widespread, with little differentiation into morphologically distinct populations; (II) widespread but highly differentiated; (III) restricted, usually with a fragmented range; and (IV) endemic to one island. These

stages are shown, beyond reasonable doubt, to represent a temporal sequence.

Immigration has been observed to occur very rapidly, and expanding species usually reach most islands in a stepping-stone fashion. Recent colonists usually belong to species that are abundant and distributed in open habitats on the mainland. Once colonists reach islands, differentiation is usually rapid, although hampering effects of gene flow can be recognized. Changes in morphology and ecology also occur during the taxon cycle. In particular, habitat distributions are frequently restricted, often to mature forest. Extinction within recorded history has occurred with much higher frequency among Stage IV species than among species assigned to earlier stages.

Slopes of species-area curves increase with stage of taxon cycle from 0.075 for Stage I species to 0.42 for Stage IV species, demonstrating that extinction rate is more sensitive to island size at progressively later stages of the cycle. Moreover, slopes vary with feeding behavior, from 0.04 for hummingbirds to 0.21 for flycatchers, swallows, and swifts.

On the basis of these and other observations, we postulate that for a particular species the cycle results from progressively reduced competitive ability caused by counterevolution of the island biota toward that species. The cycle is driven by competition from newly arrived colonists that are initially free of a counteradaptive load. The presence of old populations on small remote islands rarely receiving new colonists attests to the importance of competition in the cycle.

We expect groups with differing rates of immigration, differentiation, and extinction to exhibit different patterns of distribution among islands, but that suitable island groups, whose size and spatial patterns normalize these differences, can be found for any group of organisms. Moreover, the concept underlying the taxon cycle undoubtedly applies to mainland faunas and may help explain such patterns as variation in dominance and relative abundance of species.

ACKNOWLEDGMENTS

We are grateful to many individuals who have made comments upon and offered suggestions for improving this manuscript at many stages of writing: D. Anderson, J. Bond, W. L. Brown, Jr., L. I. Dillon, R. Etheridge, F. Gill, P. J. M. Greenslade, H. Hespenheide, D. W. Johnston, J. Karr, R. H. MacArthur, A. S. Rand, N. G. Smith, W. J. Smith, M. Soulé, T. Schoener, I. Waldron, E. E. Williams, and E. O. Wilson. The senior author would like to express special appreciation to R. H. MacArthur, who first introduced him to island biogeography. Parts of this study were supported by a predoctoral NSF fellowship and NSF grant GB-12612, both to Ricklefs.

LITERATURE CITED

- Bond, J. 1956. Check-list of birds of the West Indies. 4th ed. Academy of Natural Science, Philadelphia. 214 p.

- . 1963. Derivation of the Antillean avifauna. *Acad. Natur. Sci. (U.S.A.), Proc.* 115:79–98.
- . 1965. Tenth supplement to the check-list of birds of the West Indies. Academy of Natural Science, Philadelphia.
- . 1966. Eleventh supplement to the check-list of the birds of the West Indies. Academy of Natural Science, Philadelphia.
- . 1967. Twelfth supplement to the check-list of the birds of the West Indies. Academy of Natural Science, Philadelphia.
- . 1968. Thirteenth supplement to the check-list of the birds of the West Indies. Academy of Natural Science, Philadelphia.
- Brown, W. L., Jr. 1957. Centrifugal speciation. *Quart. Rev. Biol.* 32:247–277.
- Carlquist, S. 1966. The biota of long-distance dispersal. II. Loss of dispersibility in Pacific Compositae. *Evolution* 20:30–48.
- Carson, H. L. 1959. Genetic conditions which promote or retard the formation of species. *Cold Spring Harbor Symp. Quant. Biol.* 24:87–105.
- Crowell, K. L. 1962. Reduced interspecific competition among the birds of Bermuda. *Ecology* 43:75–88.
- Darlington, P. J., Jr. 1957. *Zoogeography: the geographical distribution of animals.* Wiley, New York. 675 p.
- DeSchaunsee, R. M. 1964. The birds of Colombia and adjacent areas of South and Central America. Livingston, Narberth, Pa. 430 p.
- . 1966. The species of birds of South America and their distribution. Livingston, Narberth, Pa. 577 p.
- Diamond, J. M. 1969. Avifauna equilibria and species turnover rates on the Channel Islands of California. *Nat. Acad. Sci. (U.S.A.), Proc.* 64:57–63.
- . 1970. Ecological consequences of island colonization by southwest Pacific birds. II. The effect of species diversity on total population density. *Nat. Acad. Sci. (U.S.A.), Proc.* 67:1715–1721.
- Dillon, L. S. 1966. The life cycle of the species: an extension of current concepts. *Syst. Zool.* 15:112–126.
- . 1970. Speciation and changing environment. *Amer. Zool.* 10:27–39.
- Ehrlich, P. R., and P. Raven. 1969. Differentiation of populations. *Science* 165:1228–1232.
- Eisenmann, E. 1955. The species of Middle American Birds. *Trans. Linnean Soc. N.Y.*, vol. 7. 128 p.
- Grant, P. R. 1966. The density of land birds on the Tres Marias Islands in Mexico. II. Distribution of abundance in the community. *Can. J. Zool.* 44:1023–1030.
- Greenslade, P. J. M. 1968a. Island patterns in the Solomon Islands bird fauna. *Evolution* 22:751–761.
- . 1968b. The distribution of some insects of the Solomon Islands. *Linnean Soc. London, Proc.* 179:189–196.
- . 1969. Insect distribution patterns in the Solomon Islands. *Phil. Trans. Roy. Soc. B.* 255:271–284.
- Hamilton, T. H., R. H. Barth, Jr., and I. Rubinoﬀ. 1964. The environmental control of insular variation in bird species abundance. *Nat. Acad. Sci. (U.S.A.), Proc.* 52:132–140.
- Hamilton, T. H., and I. Rubinoﬀ. 1963. Isolation, endemism, and multiplication of species in the Darwin finches. *Evolution* 17:388–403.
- . 1964. On models predicting abundance of species and endemics for the Darwin finches in the Galapagos archipelago. *Evolution* 18:339–342.
- . 1967. On predicting insular variation in endemism and sympatry for the Darwin finches in the Galapagos archipelago. *Amer. Natur.* 101:161–172.
- Haverschmidt, F. 1968. *Birds of Surinam.* Oliver & Boyd, London. 445 p.
- Herklots, G. A. C. 1961. *The birds of Trinidad and Tobago.* Collins, London. 287 p.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Amer. Natur.* 104:501–528.

- Johnston, D. W. 1969. The thrushes of Grand Cayman Island, B.W.I. *Condor* 71:120-128.
- Johnston, R. F., and R. K. Selander. 1964. House sparrows: rapid evolution of races in North America. *Science* 144:548-550.
- Lack, D. 1954. The natural regulation of animal populations. Clarendon, Oxford. 343 p.
- Lewontin, R. C., and L. C. Birch. 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* 20:315-336.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594-598.
- MacArthur, R. H., H. Recher, and M. L. Cody. 1966. On the relation between habitat selection and species diversity. *Amer. Natur.* 100:319-327.
- MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.
- . 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J. 203 p.
- McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. *Science* 167:131-139.
- Mayr, E. 1965*a*. The nature of colonization in birds, p. 29-47. *In* H. G. Baker and G. L. Stebbins [ed.], The genetics of colonizing species. Academic Press, New York.
- . 1965*b*. Avifauna: turnover on islands. *Science* 150:1587-1588.
- Paynter, R. A., Jr. 1956. Birds of the Swan Islands. *Wilson Bull.* 68:103-110.
- Pimentel, D. 1961. Animal population regulation by the genetic feedback mechanism. *Amer. Natur.* 95:65-79.
- Ricklefs, R. E. 1969. Patterns of nesting mortality in birds. *Smithsonian Contrib. Zool.* 9:1-48.
- . 1970*a*. Stage of taxon cycle and distribution of birds on Jamaica, Greater Antilles. *Evolution* 24:475-477.
- . 1970*b*. Clutch-size in birds: outcome of opposing predator and prey adaptations. *Science* 168:599-600.
- Salt, G. W. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. *Condor* 59:373-393.
- Simpson, G. G. 1940. Mammals and land bridges. *J. Washington Acad. Sci.* 30:137-163.
- . 1949. The meaning of evolution. Yale Univ. Press, New Haven, Conn. 364 p.
- Soulé, M. 1971. The variation problem: the gene-flow-variation hypothesis. *Taxon* 20:37-50.
- Southwood, T. R. E. 1961. The number of species of insects associated with various trees. *J. Anim. Ecol.* 30:1-8.
- Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. *Arch. Neerlandaises Zool.* 15:265-343.
- Townsend, J. J., Jr. 1952. Genetics of marginal populations of *Drosophila willistoni*. *Evolution* 6:428.
- Udvardy, M. 1970. Mammalian evolution: is it due to social subordination? *Science* 170:344-345.
- Vuilleumier, F. 1970. Insular biogeography in continental regions. I. The northern Andes of South America. *Amer. Natur.* 104:373-388.
- Warner, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 70:101-120.
- Willson, M. F. 1969. Avian niche size and morphological variation. *Amer. Natur.* 103:531-542.
- Wilson, E. O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Amer. Natur.* 95:169-193.
- Zusi, R. L. 1969. Ecology and adaptations of the trembler on the island of Dominica. *Living Bird* 8:137-164.