THE QUARTERLY REVIEW
of Biology

THE ECOLOGY OF COLONIZATION AS SEEN IN
THE ZOOGEOGRAPHY OF ANOLINE LIZARDS
ON SMALL ISLANDS

BY ERNEST E. WILLIAMS

Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138

ABSTRACT

One group of lizards—the iguanid genus Anolis in the West Indies—is now sufficiently well known to permit an empirical test of ecological theories of colonization in terms of these relatively slowly colonizing forms. Investigation of one special aspect—recent colonization of small distant islands—leads to the following conclusions: (1) Successfully colonizing species are a small and specialized fraction of the number available for colonization. (2) They are “versatile” species—creatures of the ecotone, physiologically and ecologically tolerant of many conditions and requiring of few. (3) Below some critical island size a colonizing species may by ecological release exclude all congeners. In Anolis this size of island is large (e.g., 560 mi²). (4) Coexistence of colonists is possible either if they have been preadapted in sympathy and arrive nearly synchronously, or if the adaptations for coexistence are evolved in situ on complex island banks. (5) Some species have been modified by failed invasions. (6) Coexistence or exclusion, once achieved, is stable unless there is significant environmental change. (7) Exclusion is a very common phenomenon of low visibility. Coexistence is a less frequent but highly visible phenomenon.

INTRODUCTION

MOST current zoogeographic discussion has centered on islands (e.g., MacArthur and Wilson, 1967). The physical circumscription of area, the limited faunas, and the greater probability (as compared with mainlands) of separating the several factors affecting distributions have made islands a natural choice.

The choice of islands is, in the current beginning stage of the newer zoogeography, all but inevitable and certainly desirable. The somewhat simplified phenomena of islands appear to provide the best material for first steps in new interpretations.

Birds have been most frequently regarded as the group of choice for island studies (e.g., MacArthur and Wilson, 1963). The choice of birds, however, has disadvantages. Birds colonize very readily but, as Darlington (1957) has emphasized, it is those groups which colonize with some difficulty that best show the patterns and factors of colonization.
Birds colonize easily because, whether they fly voluntarily or are carried by storms, they are airborne. The hazard for them is distance, not distance plus an unfavorable intervening medium. Yet the latter is the situation for a very important fraction of island colonizers. Much that is said of birds will be untrue for these other groups.

Specifically, the patterns characteristic of birds (or of any other airborne group) will have only limited relevance for mammals, reptiles, or amphibians, most or all of which have rafted to distant islands across salt water. Such cross-water voyages impose special limitations both as to staging areas and ports of entry and provide special hazards during the voyage itself.

It should therefore be useful to compare the ideas that have been derived from birds with the generalizations that arise from groups that have made sea voyages rather than air voyages to distant islands.

Lizards are favorable in this regard. They disperse more readily across water gaps than do snakes or salamanders but, since they are rafted and not blown across, they colonize islands much less easily than birds. Probably because they colonize with greater difficulty, they are more prone to inter-island, as well as intra-island differentiation. The slowness of the colonization process should permit us to observe its stages and the factors involved more completely and in greater depth than in birds.

The group to be studied should be a taxonomic unit at some relatively low level, approximately that of a genus or generic complex; this will minimize the intrinsic diversity which might otherwise make comparison faulty. The taxon studied should be well understood. The number of species should be large and the number of colonizing voyages large enough to insure that we are studying repeated events and not merely unique phenomena. The area should be compact and yet diverse; there must be many opportunities for colonization and these should be of varied sorts.

There is a group and an area which fulfill these requirements to a remarkable degree. The group is the iguanid lizard genus Anolis and the area is the West Indies. The study of this group and area is being actively pursued.

In our study we shall take a close rather than a distant view. We shall deal with individual species and individual cases, sometimes in detail. Much zoogeography deals with data at quite another level: species are ranked in groups which are treated as numbers to be dealt with mathematically; individual species are as a matter of method submerged in the search for significant groupings. This is the "distant" method and, since high generality is sought in such investigations, a legitimate one, although it has its weaknesses. The "distant method" may be employed without any knowledge of the naturalness or artificiality (phyletic, ecological, or physiological) of the groupings; the inferences made from the data may therefore contain hidden assumptions or involve fortuitous or irrelevant correlations. At the least, the distant approach needs to be tested against the "close" approach which, using intimate knowledge of one group, can confidently analyze the relevant factors and make use of them in rising to generalizations. [A short paper by A. S. Rand (1969) deals with some of the data which will be utilized here. It uses the "distant" approach above, however, counting species on islands rather than treating the several cases in detail. This is quite valid for the conclusions it attempts to draw, which parallel some of those stated here.]

The Group Under Study

The iguanid lizard genus or generic complex Anolis has been under intensive study for over ten years and is known as are few other genera. With over 300 available names and perhaps 200 valid species in the southern United States, Mexico, Central and South America, and the Caribbean Islands, it is among the largest of vertebrate genera.

It is the Anolis of the islands that are now taxonomically well worked and ecologically well understood. Although the mainland species are not yet perfectly defined and delimited, major divisions within the genus are very satisfactorily established. Thanks to Etheridge (1960), the osteological characters are now known which sort the genus into clear-cut units. The major osteological character (Fig. 1) is a very simple and apparently trivial one—the presence or absence of transverse processes on
distal caudal vertebrae—but the distribution of this character makes excellent geographic sense:

In the islands of the Caribbean, for example, the two kinds of anoles called by Etheridge alpha (those without transverse processes) and beta (those with transverse processes) sort out in a very striking way. Jamaica has betas only, Cuba both betas and alphas, Hispaniola, Puerto Rico and the Virgin Islands, and the Lesser Antilles only alphas.

It becomes still more interesting when these beta and alpha sections are sorted into primitive and advanced types (see Etheridge, 1960, for definition and documentation). Jamaica has the primitive Antillean betas. The islands to the east have mostly alphas but they are primitive. Hispaniola has both primitive and advanced alphas. Puerto Rico has as one of its ten species an advanced alpha. Cuba has the most advanced betas and the most advanced alphas.

The mainland west, south, and north of the Antilles provides a very interesting frame to the Antillean picture. Mexico has only betas. Central America is overwhelmingly beta with a very few alpha stragglers. South America has a mixed fauna, both alpha and beta. North of the Antilles a single alpha species is widely distributed in the southeastern United States.

A first-level interpretation of this is easy (Fig. 1). We may infer that the betas are Mexican-Central American endemics which have entered the western Antilles but have gone no further. They have successfully invaded the South American mainland, but this has probably happened only since the close of the Panama gap in the late Pliocene. The alphas, on the other hand, are South American endemics. They are the ones that invaded the Lesser Antilles and the eastern Greater Antilles and eventually Cuba and the United States, but they have pushed into Central America in limited numbers, again after the late Pliocene closure of the Panama gap.

Since Etheridge’s osteological study, work on karyotypes and on biochemical characters by George Gorman and collaborators has enriched our knowledge of the group, especially for the animals of the islands. Biochemical characters have proved useful primarily at the species group level (Gorman and Dessauer, 1965, 1966), but karyotypes (Gorman, 1965; Gorman and

![Fig. 1. The Relationship and Dispersal of alpha and beta Anoles](image)

Derived from a first interpretation of the osteological data provided by Etheridge (1960). Inset at upper right shows diagrammatically the major character used: α, an autonomic caudal vertebra without transverse processes; β, such a vertebra with transverse processes.

Atkins, 1966, 1967, 1968, 1969) have provided broader assemblages. They have confirmed in clear fashion Etheridge’s alpha and beta division and have permitted an analysis of apparent evolutionary sequence within some of Etheridge’s subsections (the roquet group in the southern Lesser Antilles and the bimaculatus group in the northern Lesser Antilles and eastern Greater Antilles). The resulting picture of relationships in the Lesser Antilles (Fig. 2) is basically the same as that provided by Etheridge (1960) as interpreted in Fig. 1, but the inferred path of migration has changed direction for the northern Lesser Antilles and has become a pattern of considerable complexity in the southern Lesser Antilles (Gorman and Atkins, 1969).

With the diversity in morphological detail appropriate to so large a group, Anolis combines very important ecological divergencies (Rand, 1962b, 1964, 1967) and a striking homogeneity in basic structure and general habits (Fig. 3).

At least crude habitat and habitat data are available for almost all West Indian anoles (see especially Rand, 1962b, 1964, 1967; Rand and
Reinterpreted on the basis of new biochemical and chromosomal data chiefly from Gorman and coworkers. Broad arrows represent the major landfalls in the West Indies, i.e. first colonizations of an island or island group. Thinner arrows represent subsequent invasions. For the northern Lesser Antilles (center right) the exact sequence of invasions is not known with the same clarity as in those of the southern Lesser Antilles (lower right).

Williams, 1969, and in prep.; Ruibal, 1961; Ruibal and Williams, 1961a,b; Schoener, 1967, 1968; Schoener and Gorman, 1968). Most of this information concerns what Rand (1964) has called “climatic” and “structural niches”—essentially sun-shade and perch preferences. (Differences in these are of high importance for the complex anole communities of the large islands and continents, and will be discussed in a future paper.)

THE CARIBBEAN AS A THEATRE OF COLONIZATION

The West Indian archipelago is famous in zoogeography for the discussions of land connections and transocean transport published in Matthew’s classic volume, Climate and Evolution (1915). It is now taken for granted that for all the islands not now on the continental shelf there was never any mainland connection and that this is abundantly demonstrated by the nature of the West Indian fauna itself (Darlington, 1938; Simpson 1956).

Colonization in the Caribbean area is thus to be understood in the classic sense of invasion and establishment on oceanic islands. A relatively few islands of much size or importance are on the continental shelves: Cozumel off Mexico, Roatan off Honduras, Providencia and San Andres off Nicaragua, and Aruba, Margarita, Trinidad and Toco off Venezuela. It
would be expected that these should have been colonized in a less interesting way, directly overland from adjacent mainlands. We shall see, however, that half (4 of 8) of these islands or island groups have been colonized or partly colonized from the more distant oceanic islands.

The truly oceanic Caribbean islands vary in size from small, low islets to Cuba—an area of 40,000 sq. mi. (104,000 km²). The very smallest of these have no permanent population of anoles, but on islands above the size of the most miniscule of rocks and sand bars anoles are omnipresent in the Caribbean.

The ages of the oceanic and continental islands are very different. The largest and most mountainous of both classes are oldest and have certainly been above water since at least the later Tertiary. Thus, although at times their areas may have been much contracted, some of their fauna may be relatively ancient. The lowest islands were submerged several times during the latest Pleistocene emergences. Indeed, a number of the islands now emergent are only the peaks of submerged banks. In such cases discussion should be of the faunas of the banks and not of those of the individual islands.

There are also many banks which are now wholly submerged which did surface at various times during the Pleistocene and so have surely been of high importance zoogeographically. Fig. 4 displays both the submerged and the partially emergent banks of the West Indies. It will be seen that they are numerous, and it will be later demonstrated that they are important. Note also that certain of the Bahama banks are extremely large and would, were their total area above water, compete in size with the Greater Antilles; the Great Bahama Bank in fact exceeds Jamaica and Puerto Rico and vies with Hispaniola and Cuba.

Ecologically the West Indies are very diverse. In contrast to many of the islands of the East Indies, most have within short distances very wet and very arid portions. Nearly all have recently been very much disturbed by man with a consequent marked increase in open formations and eroded barren areas.

The Caribbean area is thus a remarkably rich and varied one ecologically and physiographically. There is, however, even a geometric sense in which it is of special interest:

![Image of Anolis porcatus from Oriente, Cuba]

This is the characteristic habitus of the genus *Anolis*; note the diagnostic adhesive dilations of the toes (well seen on the left hind foot).

the West Indies is surrounded on three sides by land; it may therefore be colonized from many directions. It is important that many of the multiple possibilities have been realized.

Table 1 lists the oceanic Caribbean islands which have received *Anolis*, the number of species known on each and the minimum number of invasions required to explain the present *Anolis* fauna.

The island *Anolis* comprise nearly half the number of known taxa belonging to the genus. As is inevitable on islands, there is some obscurity still as to whether some island taxa are full species or not. But this problem is less difficult than might be imagined: level of differentiation is a matter of great importance in the analysis of colonization, and the existence of equivocal cases is an important item in that analysis. Table 1 indicates that the most probable count of species on Caribbean islands off the continental banks is 78. This is almost certainly a minimal count. In particular, in the case of the Greater Antillean islands, the species enumerated are unquestionably distinct, and it is known that there are still new species to be described. However, the number of invasions to and between the islands which has produced the Greater Antillean species is much less (11) than the number of valid species (59)
The submerged portions of the island banks are shown out to the 100-fathom contour (most of each bank is much shallower than this). The continental shelf is indicated by a contour line at the same level.

because of the great amount of intra-island speciation on the larger islands. For all Caribbean islands smaller than the Greater Antilles, the number of invasions required is exactly the number of species present on these islands.

Table 1 records within parentheses those species which are poorly differentiated (i.e., not clearly distinct) from species known on other islands. In the West Indies these poorly differentiated species are confined to islands that have one, two, or a maximum of four species per island. There are only two cases of non-endemic species on the larger faunally richer islands, one species in 21 in Hispaniola and one in 7 in Jamaica. In the other cases of poorly differentiated species the islands they inhabit are small, low, and were submerged during the later Pleistocene interglacials and hence have faunas that arrived relatively recently. None of these low small islands has a non-endemic species coexisting with an unequivocal endemic species.

In contrast, the species of the Greater Antilles, namely, those of the large islands (regarded as including the smaller islands on their banks) are, except for the two cited above, strongly differentiated endemics; there can be no informed doubt about their specific distinctness.

Twenty-three islands or banks in the Greater Antillean subregion (those listed as Bahamas and Western Caribbean in Table 1) belong to the category of low small islands and exhibit faunal newness. Examination of the affinities of the anoles of these 23 landfalls shows (Table 2) that only 6 species account for the new colonizations.
### TABLE 1
Colonization of oceanic islands of the Caribbean area (understood to include the Bahamas)

<table>
<thead>
<tr>
<th>Greater Antillean Subregion</th>
<th>Number of Species</th>
<th>Number of Colonizations (minimum)</th>
<th>Number of Recent Colonizations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greater Antilles</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cuba</td>
<td>22</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td>Hispaniola</td>
<td>20+[1]</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Puerto Rican Bank</td>
<td>11</td>
<td>5†</td>
<td>1</td>
</tr>
<tr>
<td>Jamaica</td>
<td>6+(1)</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>St. Croix</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Bahamas</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great Bahama Bank</td>
<td>(4)</td>
<td>22</td>
<td>22</td>
</tr>
<tr>
<td>Little Bahama Bank</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Cay Sal</td>
<td>(2)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Rum Cay</td>
<td>(2)</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Watlings (San Salvador)</td>
<td>(2)</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Crooked Bank</td>
<td>(2)</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Conception</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Atwood (Samana)</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Plana West</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Plana East</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mayaguana</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Caicos</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Turks</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Little Inagua</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Great Inagua</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Western Caribbean</td>
<td></td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>one endemic species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grand Cayman</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Little Cayman</td>
<td>(2)</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Cayman Brac</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Swan Island</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Providencia</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>San Andres</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Navassa</td>
<td>(1)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Southern Caribbean Subregion</td>
<td></td>
<td>3 endemic species</td>
<td>0</td>
</tr>
<tr>
<td>Curacao</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Bonaire</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Blanquilla</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Lesser Antillean Subregion</td>
<td></td>
<td>probably 14 endemic species</td>
<td>18</td>
</tr>
<tr>
<td>Anguilla Bank</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>St. Kitt's Bank</td>
<td>1+(1)</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Antigua Bank</td>
<td>1+(1)</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

1. \[1^1\] 2. \[5^2\]
### TABLE 1—Continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Colonizations (Minimum)</th>
<th>Number of Recent Colonizations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saba</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Redonda</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Montserrat</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Guadeloupe</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Dominica</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Martinique</td>
<td>(1)</td>
<td>1</td>
</tr>
<tr>
<td>St. Lucia</td>
<td>1+2</td>
<td>0+2</td>
</tr>
<tr>
<td>St. Vincent</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Grenada</td>
<td>1+(1)</td>
<td>1</td>
</tr>
<tr>
<td>Barbados</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

1 There is a documented record of a considerable population of the Puerto Rican species *A. cristatellus* at La Romana on the south of Hispaniola. La Romana is a port, and this may be a case of successful though accidental human importation.

2 The number of colonizations within the Greater Antilles requires elaborate discussion for the support of any view. This will be provided in a later paper.

3 *A. concolor* on San Andres and Providencia was described from “Nicaragua.” However, no recently collected specimens validate the supposed mainland distribution.

4 The status of the anoles from Anguilla to Dominica listed here as full species is less clear-cut than that of the species from Martinique to Barbados which have been more completely studied.

( ) indicates non-endemic species or a taxon equivocal as to species status

[ ] indicates human importation

Total species endemic to Caribbean area = 78

Total colonizations = 62

Total number of recent non-endemic colonizations = 36

In the Lesser Antilles poorly differentiated or undifferentiated colonizations are much less frequent. In the northern group of Lesser Antilles one species does occur on 3 of the 8 banks, but the other anoles of these 8 banks are readily recognizable endemics (though sufficiently close that most of them were considered a single species by Underwood, 1959). In the southern group of islands one species occurs on 3 of the 5 banks, another on 2 of the 5 banks, but these two species nowhere overlap. The specific distinctness of 3 other forms, endemic each to a single bank, is fully demonstrated (see biochemical and karyotypic data summarized by Gorman and Atkins, 1969).

The pattern here is more complex than that shown in the small satellites of the Greater Antilles, and with more grades of differentiation. Quite evidently the fauna of the Lesser Antilles is in general more differentiated (inherently older) than that of the small isolated islands of the Greater Antillean region. Nevertheless, it should still be noted that invasions by only three stocks will explain all complications found in the Lesser Antilles.

The islands of Curaçao, Bonaire, and Blanquilla adjacent to the South American mainland show still another picture. Two related endemic species occur on Bonaire and on Blanquilla and appear to be derived from the southern Lesser Antilles, and a different one, sharply endemic and of uncertain affinities, occurs on Curaçao (and on Aruba on the continental shelf).

San Andres and Providencia, near the coast of Nicaragua and just off the continental shelf, share a single endemic species derived apparently from the adjacent mainland.
VISIBLE AND INVISIBLE HISTORY

Several levels and ages of colonization are obvious in the Caribbean. The older are somewhat obscured by the fog of time, and there may have been much “invisible history” antecedent to present conditions. We have therefore a methodological problem to face. We can deal with invisible history only when it has had visible effects. Those past colonizations which have genuinely disappeared without trace are beyond consideration. This fact places limitations upon our generalizations and our theorizing, but does not defeat them. We may not talk about absolute numbers of colonizations but (as in Table 1) about minimum numbers, not about real patterns of colonization but probable ones. [There is also a reasonable expectation that any invader population which lasted an appreciable time would, even if now extinct, have left its effect on the still surviving species. We shall have occasion (p. 381 ff.) to discuss cases that may be interpreted in this way.]

There are, however, conclusions from visible data which may be beyond contradiction by additional evidence. It is important to be able to recognize these secure conclusions when they exist. It will illustrate the problem if we look at the colonization of the islands satellite to the Greater Antilles in terms of two alternative hypotheses. First, these islands may have received their anoles from the mainland, and the close relationship of Greater Antillean and satellite island anoles is an indication only that these smaller islands were stepping-stones on the way from the mainlands to the Greater Antilles. According to this hypothesis, the immediate ancestors of the satellite and of the Greater Antillean anoles were once on the mainland but are extinct there now, having been pushed out by better, modernized competitors. Second, the anoles of the islands satellite to the Greater Antilles may have been colonized outward from the big islands, on each of which an endemic fauna has evolved in situ.

The first of these hypotheses is plausible on its face. For many persons, it has been the hypothesis of choice—in the absence of detailed evidence. This hypothesis is, however, incorrect.

It is quite true that the West Indian islands in the first instance received their anole fauna from the adjacent mainlands. But since the work of Etheridge (1960) it has become clear that once that fauna arrived and differentiated, almost all that has happened on the Caribbean islands has been an internal matter. Even the islands near the mainland, and even some of the continental shelves themselves, have received their fauna from the islands and not from the mainland.

This is contrary to the expectation of many zoogeographers (e.g., Darlington, 1957). It is a statement which not many years ago we could not have made at all. Now, with every increase in information and with every improvement in analysis, the conclusion becomes more securely demonstrated. The Etheridgean analysis of osteology already implied and required this conclusion. The data provided by Gorman, Thomas, and Atkins (1968) on chromosomes supports and develops the same proposition.

<table>
<thead>
<tr>
<th>SPECIES OR SPECIES COMPLEX</th>
<th>AREA INVADED</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>A. carolinensis</em></td>
<td>Cay Sal, Great Bahama Bank, Crooked Bank, West Plana Cay, Navassa, Little Cayman; and on the continental shelf: Bay Islands (Roatan, etc.), Half Moon Cay; southeastern United States</td>
</tr>
<tr>
<td>3. <em>A. grahami</em></td>
<td>Grand Cayman</td>
</tr>
<tr>
<td>4. <em>A. distichus</em></td>
<td>Grand Bahama Bank, Rum Cay, San Salvador</td>
</tr>
<tr>
<td>5. <em>A. cristatellus</em></td>
<td>Great Inagua, Little Inagua, Caicos, Mayaguana, E. Plana Cay</td>
</tr>
<tr>
<td>6. <em>A. angusticeps</em></td>
<td>Great Bahama Bank</td>
</tr>
</tbody>
</table>
Alternative interpretations of patterns of colonization requiring extinct populations on the mainland now seem frivolous; the now tightly knit web of evidence rejects them. The sequences of differentiation may still be read within the islands—this is the critical point—and only a Ptolemaic complication of ad hoc hypotheses could read the facts in terms of waves of invasion from the mainland.

This major conclusion will not, I think, be falsified by any evidence to come. New species may yet be discovered within the Antilles, fossils may be discovered on islands and on the mainland, but the evidence of intra-island radiation and of colonization from the large islands has too much internal coherence to be refuted.

There is at present no evidence to indicate that extinction as a continuing or continual process has had the importance for Anolis in the West Indies that Mayr (1965a, b) finds for it in island birds or that MacArthur and Wilson (1963, 1967) have postulated it generally has for island faunas. One major extinction and subsequent recolonization and radiation seem adequate to explain West Indian anoline lizards. The sole survivors of an early anole invasion of the Greater Antilles are two highly differentiated and quite different genera—the giant Chamaeleolis, with 2 species widespread on Cuba (Etheridge, 1960; Garrido and Schwartz, 1968), and the dwarf Chamaelinarops, with a single species (Etheridge, 1960; Thomas, 1966) confined to the south island (Williams, 1961) of Hispaniola. These alone of the present anole fauna of the West Indies may antedate the early Miocene inundation of the area (Schuchert, 1935; Woodring, 1954; Mencher, pers. commun.), an inundation great enough that one may be more surprised that the two genera survived than feel compelled to make ad hoc hypotheses to explain the absence of a larger old anole fauna. All other anoles of the Greater Antilles may be accounted for by a very limited number of rather recent invasions plus extensive intra-island differentiation (see above), and extinction seems rarely required as an explanation of present faunal composition or distribution. There are not, as there are said to be in birds, any significant gaps in the levels of differentiation. This difference, if it be real, may relate to the differing importance of intra-island differentiation, as compared with multiple invasions, in lizards and in birds.

**THE FIRST APPROACH**

The easiest, plainest story is that provided by the non-endemic island colonizers. For the non-endemic species of the small, recent, distant islands, the situation seems particularly clear. The time since invasion has been short; the faunas and the islands themselves are simple. Both the fog of time and the complexities introduced by the multiple interactions of a multispecies fauna are reduced or eliminated.

We can define a "small" island by the presence of a substantial gap between this class and the next larger in size. In the Caribbean area the largest island belonging to the class "small" will then be Great Inagua Island, about 560 sq. miles (the bank would be bigger). Jamaica, in contrast, is 4,450 sq. miles, Puerto Rico about 3,420 sq. miles (but including its bank, larger than Jamaica); these are the smallest of the Greater Antilles.

The islands to be studied are not only "small," they are low. Their highest elevations are a few hundred feet (tens of meters) at most; and they are therefore "recent," that is, newly emergent after repeated Pleistocene inundations.

They are also "distant." This term requires definition. No island on a submarine bank is distant from any other element of that bank. Each one was in fact at least once during the Pleistocene connected to every other portion of the bank by dry land. The Isle of Pines thus is a part of Cuba, Vieques is part of Puerto Rico, Gonave is part of Hispaniola. Such islands clearly are not "distant." Beyond this clear demarcation, however, it is difficult to find a satisfactory break in a virtual continuum of distances from rather near (ca. 10 miles = 16 km) to very far (200–400 miles = 300–600 + km). In practice we shall arbitrarily use the term "distant" to mean "never connected by dry land, but always requiring a cross-water voyage of at least 10 miles (> 15 km) for colonization."

Many Caribbean islands fall in one way or another outside our category of "small, recent, and distant." All the Lesser Antilles would in terms of size fall well within the category small, but all the Lesser Antillean banks except Som-
brero (see below) have elevations over 1,000 feet and surely were never totally submerged in the Pleistocene inundations. They are thus not recent. We shall, however, consider some recent colonizations that have occurred on them.

In addition, two of the Lesser Antillean banks—St. Vincent and Grenada—are not distant from one another even by the excessively liberal definition we have here employed. We shall discuss this case also in order to compare it with more typical cases.

On the other hand, both the Great and Little Bahama Banks are recent but are large in undersea extent. The Great Bahama Bank, the larger of the two (though some of its emergent peaks such as Bimini are tiny), is separated from Cuba by only 10 miles (16 km)—the smallest degree of distance. Likewise, the Little Bahama Bank is only 20 miles (32 km) from the Great Bahama Bank, which is the only land mass that matters; since it is effectively blocked off from colonization from other sources by the Great Bahama Bank on the one hand (see Fig. 4) and the Gulf Stream on the other. (The latter carries drift past the Little Bahama Bank rather than to it.)

The Greater Antilles are distant with relation to both the mainlands and each other (always more than 50 miles = 80 km) but are neither small nor recent.

The exclusion of so many islands reduces the heart of the present study to the truly simplest cases: we shall deal with small, recent, and distant islands in which there is colonization without strong differentiation and without intra-island radiation.

Even without strong differentiation or intra-island radiation the anole faunas of these small, single, recent, distant islands all demonstrate vagility, i.e., special ability to invade across barriers, and some demonstrate coexistence and some apparently demonstrate exclusion. The sample, if not very large, is yet adequate for some discussion of the factors which may underlie each of these three phenomena.

Let us begin with the most successful of all anole colonists—the Anolis carolinensis group.

THE Anolis carolinensis complex

The common green anoles, Anolis carolinensis, of the southeastern United States are like nothing else in the fauna of temperate North America. Anolis carolinensis extends well into Texas (Brown, 1950) and its Mexican congeners extend northward along the coast with one species extending into Tamaulipas (Smith and Taylor, 1950), where they approach the border of the United States. There seems, however, to be a gap devoid of all Anolis between Anolis carolinensis and its Mexican congeners.

Mexican anoles belong to the beta section of Etheridge and are thus not close to A. carolinensis, a member of Etheridge’s alpha section. Instead, the relationships of A. carolinensis are Caribbean, and it is clearly a derivative of a western Caribbean species complex. Thus the Texas-Mexican gap in the genus Anolis appears not to be a gap in an originally continuous distribution but, on the contrary, an interval remaining as two stocks approach each other from opposite directions.

Anolis carolinensis in the southeastern United States is a very successful species. It is of particular interest since, coming from a tropical Caribbean island, it has invaded in a very substantial way the more complex fauna of a subtropical to temperate mainland area. This is in contrast to the pattern that Darlington (1957, 1959) has emphasized as a general rule of movement of animals out from continents, and which Simpson (1956) has stated even more emphatically (for mammals) for the Greater Antilles.

To speak of firm knowledge is not to say that all problems of anoline lizards or of the carolinensis group are solved. It is, for example, uncertain whether the mainland Anolis carolinensis is really a single species or not; it certainly possesses a high variability. It is quite uncertain whether, as suggested by Oliver (1948), the Bahaman carolinensis-like populations should be treated as subspecies of A. carolinensis or as full species. In Cuba there are at least two, possibly three, carolinensis-like species (Ruibal and Williams, 1961a); whether any of these is conspecific with the mainland A. carolinensis is a very open question. The specific status, similarly, of the carolinensis-representatives on Little Cayman and on Navassa Island is in doubt. It is important to realize that for present purposes it is possible to treat the carolinensis complex as a complex and not to worry about every detail within it.
Definition of the carolinensis complex

In any event, the carolinensis complex in no case rises much above the level of the superspecies. Only in central Cuba are two members of the complex sympatric. This is a very close-knit group.

These are anoles with wide adhesive dilations of the toes (see Fig. 3); they are always arboreal and usually green. (Despite the apparent implication of toe dilation that arboreality is primitive, some anoles are not arboreal and many are not green.) The anoles of the carolinensis complex are distinguished by a rather sharp snout (this is somewhat variable), by variable ridging of the snout area, by uniformly granular dorsal squamation with larger keeled ventral scales which are in transverse rows, and by the number of scales between the nasal and rostral scales (Fig. 5). They are of moderate size, up to ca. 91 mm from snout tip to vent. Only the whole of this suite of characters taken together will identify a member of the complex. On Cuba itself two species not members of the complex are quite close to it: A. angusticeps (which occurs also in the Bahamas) and A. isolepis (a small and rare species); these differ in size, color, and in details of squamation.

Many of the characters of the carolinensis group appear to be strongly correlated with their usual habitat on the upper trunks and crowns of trees and recur in distantly related species with the same ecology.

The distribution of the carolinensis complex

Cuba is the geographic center of the carolinensis complex. It is the only large island involved and has mountains rising to 6000 feet above sea level. Alone of the islands on which the carolinensis species group occurs, Cuba was probably never totally submerged during any part of the Tertiary. It has certainly been largely emergent since the Miocene (though perhaps broken into smaller islands during the Pleistocene — Woodring, 1954).

As mentioned above, the taxonomy of the carolinensis group on Cuba is not fully worked out. It is fully established, however, that the most distinct member of the carolinensis group, certainly a full species, A. allisoni, occurs in central Cuba and is there sympatric with another species of the same group (Ruibal and Williams, 1961a). Confusion arises in regard to the populations in western and eastern Cuba which are structurally similar to this second central Cuban species (Ruibal and Williams, 1961a). Anolis allisoni differs in ear shape, head ridging, and scale size from the other Cuban populations, which are similar enough to be usually lumped under the name Anolis porcatus and which are closer to North American carolinensis than to partly sympatric allisoni. These other Cuban populations differ among themselves primarily in color.

To the northeast of Cuba lie the Bahamas, an archipelago of 29 small islands plus thousands of yet smaller cays and rocks. All the present islands are the exposed portions of larger (sometimes much larger) banks now under shallow seas. Not only are the larger portions of these banks now submerged, but no existing Bahaman island exceeds 220 feet (67 m) in height and most are lower. These islands were surely wholly under water in the Pliocene and early Pleistocene and suffered periodic floodings or submergences during the Pleistocene.

Four distinguishable populations of the carolinensis group have been named in the Bahamas: A. fairchildi, A. smaragdinus, A. bruneus and A. lernerii. These differ in scale size, snout shape, and color, as well as in other minor ways, but, because they are all allopatric, their status as species or subspecies is very variously estimated. Again, they are all rather close to the North American mainland carolinensis and to Cuban porcatus, and are not as close to allisoni.

Due south of Guantanamo, Cuba, and between Jamaica and Hispaniola, lies the very
small island of Navassa, 2 miles (3.2 km) long
and about one mile (1.6 km) wide and rising
to a height of only 100 feet (30 m). This again
harbors a carolinensis representative—a long-
nouted one, and hence named A. longiceps; it
is more distinct than the Bahaman populations
but not as distinct as A. allisoni.

Due south of western Cuba lie the Caymans,
a set of three islands on a submarine ridge but
separated by troughs deep enough so that they
were never united during the Pleistocene. Two
of these, Cayman Brac and Little Cayman, are
much closer to each other than to the third,
Grand Cayman, but all three seem to have re-
cieved their anoles independently (see further
discussion below). Little Cayman, the middle
of the three, is about 9 miles (14.5 km) long; its
maximum width is about one mile (1.6 km), and
its highest point is only 48 feet (15 m) above the
sea. It has a long-snouted carolinensis represen-
tative which has received the name A. maynardi.

Southwest of Cuba, off the north coast of
Honduras, lie the Bay Islands. It was on the
largest of these, Roatan, that A. allisoni—cited
above for central Cuba—was first discovered.
Specimens have more recently been taken also
on Bonaca and Helene Islands and on Half
Moon Cay, which lies 100 miles (160 km) north-
west of the Bay Islands, off the coast of British
Honduras. These islands off Honduras and
British Honduras are likewise low. Like all the
islands peripheral to Cuba on which representa-
tives of the carolinensis species group occur,
they were submerged during part of the Pleisto-
cene.

The last area in which anoles of the caroli-
nensis group occur is the mainland of the south-
eastern United States including the Florida keys.
The present distribution is probably as exten-
sive to the north as temperature permits and
as extensive to the west as humidity permits.
Probabilities point to a landfall in Florida dur-
ing some period of Pleistocene emergence. At
this time the expanding outlines of Florida and
of Cuba would have diminished the transocean
distances and hence have very substantially en-
harmed the probability of a cross-water voyage.

The context of Anolis carolinensis

It is necessary to put the Anolis carolinensis
complex in a proper taxonomic and phyletic
context before its history can be traced. Barbour
(1928), in his description of A. allisoni from the
Bay Islands, had defined a carolinensis group,
compact and very similar in form, color, and
habits. With the carolinensis species group as
I define it, he unequivocally included one of
the green anoles of Hispaniola, A. chlorocyanus.
With less certainty he included the green anoles
of Jamaica. He went on to assert that “pattern
and color may be more conservative and less
given to variation by isolation than, for in-
stance, the form of the skull.”

In this account Barbour is both right and
wrong. Etheridge (1960) has shown that A.
chlorocyanus (and its sister species A. coelesti-
nus) are clearly related to carolinensis, but are
more primitive than the carolinensis species
group and probably ancestral. In this instance,
the resemblance in color is truly phyletic; how-
ever, in the Jamaica anoles—all in Etheridge’s
beta group—the green color is convergent only,
like certain features of habitus and ecology.

The skeletal analysis by Etheridge (1960) has
permitted a sure assessment of relationship and
provides a clear ancestry. The carolinensis spe-
cies group belongs to a subsection of the alpha
anoles distinguished by specialized characters
of the shoulder girdle (Fig. 6). The primitive
members of this subsection are on the eastern
Greater Antilles, and the common green anoles
of Hispaniola, A. chlorocyanus and A. coelesti-
nus, are relatively unspecialized examples.
Structurally, both externally and internally, and
in their green color and arboreal habit, they are
almost ideal ancestors for the carolinensis group
and for the other alphas of Cuba.

The major currents in the Caribbean sweep
westward; so do the currents to the north of
Hispaniola. It is easy to imagine some animal
very like A. coelestinus (but more primitive in
having one more bone, a splenial, in the lower
jaw) carried across the rather narrow channel
between Hispaniola and Cuba and thereafter
filling a tree-crown niche on Cuba.

The carolinensis group (sensu stricto) on
Cuba is one twig of the extensive Cuban al-
pha anole radiation, which is ecological as well
as morphological (Fig. 7). The members of
the carolinensis group are themselves relatively
primitive anoles in being primarily tree-lizards.
At least the adult males take their stations well
up on the trunks of trees or in the crowns, and characteristically flee upwards when disturbed. The giant anole _A. equestris_ is rather similar. All eleven other members of the radiation to which _carolinensis_ belongs differ strikingly from the _carolinensis_ group in habitat and behavior. One (_vermiculatus_), though more than twice the snout-vent length of even _allisoni_, is found on bushes and small trees over water, tending, because of its size, to lie across the branches (Schwartz, pers. commun.) and, as many have reported, to dive into the water when disturbed. Others (_loysiana, argillaceus, angusticeps, argenteolus_) live on certain types of tree trunks and do not invade the crown. (_A. angusticeps_ occurs also on bushes and _A. argenteolus_ is said to occur on limestone.) _A. isolepis_ has been found on the leaves of the canopy. Three (_spectrum, cyanopleurus, alutaceus_) are grass-lizards. _A. lucius_ and _A. hartschi_ live on rock walls in or near caves or (_luci_ of the fissured trunks of large trees. Of this whole radiation the _carolinensis_ species group (sensu stricto) has relatively broad ecological tolerance and, in contrast to the very spotty distribution of the other species, seems almost omnipresent.

**FOSSILS AND ANOLINE HISTORY**

The general place of the _carolinensis_ complex in the anole story is easy to make out. It is a Cuban endemic derived from more primitive forms to the east. Were there a good fossil record for _Anolis_, it might be possible to be more precise about the ancestry of _carolinensis_. The fossil record of _Anolis_, however, is pitifully inadequate. The oldest fossil is an _Anolis_ in amber of Miocene or Oligocene age (Lazell, 1965)—a species of very uncertain affinities preserved as scales and not as skeleton. To be compared with this are only fossil or subfossil skeletal fragments, usually mandibles, of latest Pleistocene or sub-Recent age from Cuba (Koopman and Ruibal, 1955), Hispaniola (Etheridge, 1965), Barbuda (Etheridge, 1964), and Florida (Auffenberg, 1956; Holman, 1958, 1959a,b, 1967; Gut and Ray, 1963). The Floridian records reveal _A. carolinensis_ as a rather common Illinioian, Wisconsin, and post-Wisconsin fossil. The West Indian finds, besides known species of sub-Recent age, doubtfully provide one extinct form on Barbuda in the late Pleistocene.

These few finds neither add to nor detract from the scheme provided by Etheridge's osteological information for Recent forms. His scheme remains the basis for working out the origin and dispersal of _Anolis carolinensis_, as of every other anole.

**THE DISPERAL OF THE **_**carolinensis** SPECIES GROUP**

The _carolinensis_ species group, once it had originated in Cuba as a relatively primitive derivative of the early arboreal _alpahas_ and once it had differentiated into the _carolinensis_ and _allisoni_ stocks, dispersed from there in many directions across water, sometimes over considerable distances. Table 3 shows some of the distances from Cuba to the points of arrival. Fig. 8 maps the dispersal of _carolinensis_.

In one way Table 3 may overestimate these distances: if the distances were calculated from the edges of the bank surrounding Cuba to the edge of the bank on which the port of arrival stands, the distances in the table would be reduced. However, this overestimation is more than compensated for by error in the reverse direction which is far less easy to correct. Table 3 underestimates the distances actually traversed in two ways: (1) the distances are straight-line distances to the nearest shore of Cuba, and this is unlikely to have been the real point of departure. This is particularly true in the case of the _allisoni_ populations on Half Moon Cay and the Bay Islands. The nearest point is Cabo Corrientes (370 mi = 592 km) in extreme west-

---

**TABLE 3**

_Distances from Cuba to areas colonized by the carolinensis group_

<table>
<thead>
<tr>
<th>AREA COLONIZED</th>
<th>MILES (Km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cay Sal</td>
<td>451 (72)</td>
</tr>
<tr>
<td>Key West (Mainland U.S.)</td>
<td>90 (144)</td>
</tr>
<tr>
<td>Andros Is. (Great Bahama Bank)</td>
<td>951 (152)</td>
</tr>
<tr>
<td>Navassa Is.</td>
<td>105 (168)</td>
</tr>
<tr>
<td>Acklins Bank</td>
<td>110 (176)</td>
</tr>
<tr>
<td>Mainland Florida</td>
<td>135 (216)</td>
</tr>
<tr>
<td>Little Cayman Is.</td>
<td>135 (216)</td>
</tr>
<tr>
<td>Half Moon Cay</td>
<td>370 (592)</td>
</tr>
<tr>
<td>Roatan Is.</td>
<td>400 (640)</td>
</tr>
</tbody>
</table>

1 The distances in these cases are much less bank to bank. See Table 4.
Fig. 6. Shoulder Girdle Differences in Two Anoles and in a More Distantly Related Iguanid

In (a), Enyallosaurus quinquecarinata, note the arrow-shaped interclavicle shown in black, its arms strongly bent away from the clavicles with which it is in contact only medially. In (b), Anolis bimaculatus, a primitive alpha anole, the interclavicle is in more extensive contact with the clavicles but distal portions of its arms are still free. In (c), Anolis carolinensis, the arms of the interclavicle are applied in their whole length to the clavicles. Modified from Etheridge (1960).

Fig. 7. The Ecological Radiation of alpha Anoles in Cuba, Shown as Primarily a Matter of the Perch Chosen
ern Cuba, far from the present distribution of *allisoni*. The straight-line distances to the central Cuban-Cienfuegos area where *allisoni* is known are about 600 and 560 miles (960 and 896 km) respectively. (2) Straight-line distances are not reasonable biological distances for lizards carried from one island to another. Straight-line distances apply—if at all—to airborne animals. Lizards are characteristically carried on surface rafts and hence their journeys are guided by major surface currents. Since these currents flow between islands and not from one to another, a raft voyage from one island to another will be an oblique voyage influenced primarily by the direction of the current and its speed.

Vegetational rafts, even "tree islands" with abundant life upon them, are documented not only for large rivers such as the Orinoco or the Magdalena (Darlington, 1957) but also for such relatively small low-gradient rivers as the Rio Tortugero in Costa Rica (King, 1962). In addition, hurricanes create masses of vegetation and carry them partially through the air, partially on surface currents.

Hurricane paths, however, though like the major Caribbean currents possessing a general east-west direction, have greater twists toward the north and more erratic and unpredictable courses. If hurricanes have been important in transport between the individual Antilles and from the Antilles to the mainland, they introduce an element of uncertainty in the length of the voyages traversed during colonization.

In any case, we are here less concerned with exact distances than with orders of magnitude. It is sufficient to know that the distances successfully traversed by *carolinensis* group animals have sometimes been considerable. Quite as interesting are the distances over which colonization has failed. The *carolinensis* group has, for example, colonized the tiny island of Na-
vassa between Jamaica and Hispaniola, but neither of these vastly larger targets. As inspection of Fig. 8 indicates very clearly, the carolinensis group has been limited in its dispersal by something other than distance. Two questions may therefore be raised:

1. What factors have in some instances promoted the dispersal of the carolinensis group over very great distances?
2. What factors have sometimes prevented colonization over much shorter distances?

The longest of the voyages postulated in Table 3 for carolinensis colonists cannot be significantly reduced by any sea level changes. The shortening of distances between the edges of the continents and the edges of the islands during periods of low sea level was simply not enough to be important. We must admit that really long voyages, with their attendant extreme rigor for the rafted colonizer, indeed occurred. It follows that successful colonizers must be in general very hardy animals—resistant to the physiological hazards of the voyage and of arrival.

Major among these physiological hazards is desiccation. Starvation during these voyages is not a primary danger for any cold-blooded animal—unless it is in poor condition before it starts, and such an animal is, of course, quite out of the running. But water is a problem. Sea water will be only another kind of desiccation. Perhaps if the voyager is hurricane-carried in whole or in part, the fresh water provided by the storm will relieve this problem (but the battering of the storm will provide another kind of danger and damage).

In the end, the inadvertent voyager must land upon a beach. This is not, for an arboreal lizard, a welcoming environment. The perils of desiccation exist here too, and the lizard is no longer passively transported. It must seek out and find—soon—a favorable environment, or the colonization will have failed. Thus, there can be no question that any colonizer making one of the long raft voyages across an ocean will arrive in very unfavorable physiological condition on an inhospitable shore. If, then, the colonizer always arrives in a wretched physiological condition, it presumably cannot afford any further disadvantage, and in particular not the presence of competitors.

From the vantage point of these considerations let us now canvass the colonizations of the carolinensis group, counting every landfall within the range established by the longest verified voyage (that to the Bay Islands, ca. 400 miles = 640 km).

Table 4 lists for the areas successfully colonized by the carolinensis group two additional facts: (1) The number of other species of anoles present there; and (2) whether or not this land area was above water during the whole of the Pleistocene. Table 5 provides the same two facts for areas which the carolinensis group could in theory have colonized, but on which, if any colonist arrived, no colony has survived.

The relevance of two additional bits of data should be quite clear: (1) By accepted ecological theory, competition should be severest between closest relatives. Thus, for the first test of competitors of the carolinensis group, we look to its congeners. (2) The fact of the emergence and subsidence of so many of the smaller islands during the Pleistocene provides us a contrast of two conditions: (a) the continental mainland and the large islands (Jamaica, Hispaniola), since they were never submerged during the Pleistocene, had a complex fauna which any Pleistocene invader would have had to confront, while (b) the islands which at some time in the Pleistocene were submerged were, when they re-emerged, available almost for the taking, or quite without contest. The first comer surely had no problem on one of the newly emergent islands—as soon as it had regained the minimal ecology necessary to anoles. Any second comer might or might not have difficulty, depending on the ecology of the island, the degree of overlap between the newcomer's niche and that of the resident species, and the special circumstances at the moment of invasion.

A comparison of Tables 4 and 5 shows that colonization by the carolinensis group succeeded in the case of the continental mainlands and large islands only in a single case—the United States mainland—in which no congeners were present to compete with the colonist. (The late Pleistocene fossil record for the southern United States is probably not adequate, but as far as it goes, it testifies to the absence of anoles other than A. carolinensis.)

The continental mainlands and the large is-
TABLE 4
Cases of successful colonization by the carolinensis group in the western Caribbean

<table>
<thead>
<tr>
<th>LANDFALL (IN APPROXIMATE ORDER BY AREA)</th>
<th>OTHER ANOLES</th>
<th>EMERGENT DURING WHOLE OF PLEISTOCENE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mainland U.S. (90 mi = 144 km)</td>
<td>None¹</td>
<td>+</td>
</tr>
<tr>
<td>Great Bahama Bank (Andros, New Providence, etc.) (bank to bank = 10 mi = 16 km)</td>
<td>3 (sagrei, distichus, angusticeps)</td>
<td>-</td>
</tr>
<tr>
<td>Bay Islands (Roatan etc.) (400 mi = 640 km)</td>
<td>1 (lemurinus)</td>
<td>-</td>
</tr>
<tr>
<td>Crooked Bank (115 mi = 184 km)</td>
<td>1 (sagrei)</td>
<td>-</td>
</tr>
<tr>
<td>Cay Sal (bank to bank = 25 mi = 40 km)</td>
<td>1 (sagrei)</td>
<td>-</td>
</tr>
<tr>
<td>Little Cayman (135 mi = 216 km)</td>
<td>1 (sagrei)</td>
<td>-</td>
</tr>
<tr>
<td>Navassa (105 mi = 168 km)</td>
<td>0²</td>
<td>-</td>
</tr>
<tr>
<td>Half Moon Cay (370 mi = 692 km)</td>
<td>1 (sagrei)</td>
<td>-</td>
</tr>
</tbody>
</table>

(Figures in parentheses are approximate minimum distances from Cuba)

¹ Except scattered, possibly man-dispersed colonies of two additional species (A. sagrei, A. distichus) in southern Florida. A. carolinensis occurs with no other anole over most of its North American range.

² The supposed second species on Navassa (A. latirostris) is probably a locality-mislabelled Haitian A. coelestinus (Thomas, 1966).

lands are of course exactly the areas which were always dry land during all the Pleistocene and therefore they are the areas in which an old resident fauna was always in possession.

The smaller islands were, on the contrary, submerged at some time during the Pleistocene. Their subsequent emergence opened them to colonization, each as a tabula rasa on which a completely new faunal history could be written. The carolinensis group has colonized many of these smaller islands. Sometimes it occupies islands quite alone, sometimes it shares them with other anole species (in one instance with as many as three others), and at yet other times it seems not to have succeeded in occupying an island which has only one congener.

Such successes and failures by carolinensis would seem at first sight random. However, let us take a closer look.

(1) The only examples of small islands shared by carolinensis with three other species are Bahaman and all are in fact on the Great Bahama Bank, including the tiny islet of South Bimini. This bank, though at present largely under water, has an enormous area — a greatest width of 225 miles (360 km) and a length of 415 miles (249 km) (see Fig. 4). It was totally emergent at certain periods of the Pleistocene; at others, totally submerged. It presumably received its present fauna during the last period of emergence, when it was both very close to Cuba and provided a great expanse of living space for invading species.

Three of the anoles that invaded this area were of Cuban affinities (A. carolinensis, A. angusticeps, A. sagrei) and one (A. distichus) was of Hispaniolan affinity. All four are on the Great Bahaman Bank, but the smaller banks have only one or two species. There is only sagrei on the Little Bahama bank, sagrei and carolinensis on Acklins Bank, and only distichus and sagrei on Rum Cay and San Salvador (Watlings Is.).

Clearly it is the former, and not the present, area of exposed land that has allowed four anole species to coexist in the area of the Great Bahama Bank. In particular, South Bimini is ridiculously small to have permitted colonization by four species if its area at the time of colonization had been the same as it is now. It is very probable that the great area of the emergent bank made possible a landfall by
several species without immediate and direct competition, and that thereafter space provided the opportunity for coadjuvment of four species (not all from the same source) into an ecological complex which could survive a diminution in the land area, at least for a significant period of time.

(2) When the Great Bahama Bank is eliminated, carolinensis is found to share islands with only two other species, Anolis sagrei and A. lemurinus, and never with more than one of these. In the six successful small island colonization, A. carolinensis shares the islands with sagrei in four cases, with lemurinus in one. The coexistence of lemurinus (a mainland beta anole) may be a chance phenomenon. The Bay Islands are on the continental shelf and lie very close indeed to the present mainland. In such circumstances, colonization of the islands by some mainland stock is to be expected. A. lemu

rinus is ecologically different from carolinensis and seems, in fact, to be a mainland analog of A. sagrei.

Published information on the ecology of mainland Anolis is all but lacking and, where it exists, is far more casual and less careful than that which is now available for the majority of West Indian anoles. However, for A. lemurinus I have collected personal reports by L. C. Stuart and Douglas C. Robinson. Stuart says of the species: "highly tolerant. Found in monte, forest, etc., generally on tree trunks close to the ground. Tends to return to ground when startled rather than climb higher." Robinson reports it as "commonly encountered five to six feet above ground on the branches of small trees 10–20 feet in height." These observations seem to imply that it is found in more shaded situations than those typical of sagrei. A. lemurinus may therefore be most nearly equivalent to shade-prefering (but noncolonizing) members of the sagrei series in Cuba.

TABLE 5

<table>
<thead>
<tr>
<th>LANDFALL (IN APPROXIMATE ORDER BY AREA)</th>
<th>OTHER ANOLES</th>
<th>EMERGENT DURING WHOLE OF PLEISTOCENE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yucatan (120 mi = 192 km)</td>
<td>7 (incl. sagrei, coastal only)</td>
<td>+</td>
</tr>
<tr>
<td>Hispaniola (50 mi = 80 km)</td>
<td>20</td>
<td>+</td>
</tr>
<tr>
<td>Jamaica (90 mi = 144 km)</td>
<td>7 (incl. sagrei, western half only)</td>
<td>+</td>
</tr>
<tr>
<td>Little Bahama Bank *</td>
<td>1 (sagrei)</td>
<td>−</td>
</tr>
<tr>
<td>Caicos Bank (130 mi = 208 km)</td>
<td>1 (scriptus)</td>
<td>−</td>
</tr>
<tr>
<td>Inagua (55 mi = 88 km)</td>
<td>1 (scriptus)</td>
<td>−</td>
</tr>
<tr>
<td>Gonave (an island on the Hispaniolan bank) (100 mi = 160 km)</td>
<td>4</td>
<td>−</td>
</tr>
<tr>
<td>Mayaguana (155 mi = 248 km)</td>
<td>1 (scriptus)</td>
<td>−</td>
</tr>
<tr>
<td>Cozumel (140 mi = 224 km)</td>
<td>1 (sagrei)</td>
<td>−</td>
</tr>
<tr>
<td>Mona *</td>
<td>1 (monensis)</td>
<td>−</td>
</tr>
<tr>
<td>Grand Cayman (180 mi = 288 km)</td>
<td>1 (conspersus)</td>
<td>−</td>
</tr>
<tr>
<td>Cayman Brac (125 mi = 200 km)</td>
<td>1 (sagrei relative)</td>
<td>−</td>
</tr>
<tr>
<td>Swan Island (290 mi = 464 km from Isle of Pines)</td>
<td>1 (sagrei)</td>
<td>−</td>
</tr>
<tr>
<td>Providencia (510 mi = 816 km)</td>
<td>1 (concolor)</td>
<td>−</td>
</tr>
<tr>
<td>San Andres (570 mi = 912 km)</td>
<td>1 (concolor)</td>
<td>−</td>
</tr>
</tbody>
</table>

Figures in parentheses are approximate minimum distances from Cuba.

* Island "blocked off" by intervening islands or banks; reference to Fig. 4 will show that these islands could be reached from Cuba only by devious routes around the intervening islands or from the intervening island or bank.
The presence of \textit{saurei} with \textit{carolinensis} is too frequent to be random. \textit{A. saurei}, like \textit{carolinensis}, is of Cuban origin. This is a fact of prime importance. The \textit{carolinensis} complex and \textit{saurei} are sympatric throughout Cuba, and both are very common. It is clear that on Cuba they are well adjusted to one another. As would be expected, there is a clear niche difference on Cuba and elsewhere — \textit{carolinensis} on the trunk and in the crown of trees, \textit{saurei} lower on the trunk and on the ground. They differ also in size, especially head size, and may take different insect prey (Schoener, 1968).

(3) The small islands, emergent since the later Pleistocene, on which \textit{carolinensis} is absent, are instructive also. About half of them have only \textit{saurei} and the several other cases involve just four other species — \textit{A. conspersus} of Grand Cayman, \textit{A. scriptus} of Inagua, the Caicos Bank, Mayaguana and East Plana Key, \textit{A. monensis} of Mona Island, and \textit{A. concolor} of San Andres and Providencia.

\textit{A. conspersus} is an ecological analog of \textit{carolinensis}. It is a green anole with a similar niche but derived from \textit{A. grahami} of Jamaica (like \textit{A. saurei}, a member of the \textit{beta} series). Ecological exclusion here is an obvious interpretation.

The reasons for exclusion are not so immediately clear with \textit{A. scriptus}, but the fact of exclusion is especially dramatic in East and West Plana Keys, which lie just at the border of the island ranges of \textit{carolinensis} and \textit{scriptus}. These two tiny islands, just east of Acklins Island and closer to each other than to any other land area, are inhabited by different anoles. On West Plana Key is a race of \textit{A. carolinensis}; on East Plana Key is a race of \textit{A. scriptus} (Fig. 9).

Exclusion of \textit{carolinensis} from Mona Island between Hispaniola and Puerto Rico really requires no ecological explanation. Access to the island is too difficult for the \textit{carolinensis} group, the more so since the major currents in the area sweep westward. Similarly, the exclusion of \textit{carolinensis} from Providencia and San Andres would appear to be merely a matter of distance, currents, and the time available for colonization by \textit{A. carolinensis}. Providencia, the nearer of the two islands, is 500 miles (800 km) from the nearest point on Cuba. Again, the westward sweep of major currents tends to transform a voyage from these islands to Cuba from a very improbable event to one effectively impossible.

To summarize now what has thus far been said about the \textit{carolinensis} group:

(1) This species group is nowhere known to have invaded an integrated complex of anoline species. It is, indeed, a very vigorous, far-ranging invader, it has reached the Bay Islands and Half Moon Cay, the islands fringing the continent, but we know of no instance of capture of even the continental margins in the presence of a resident anoline fauna. It has been a spectacular invader in the southeastern United States, but it is precisely there that it met no prior resident anole fauna.

(2) Given its distant successful voyages, the \textit{carolinensis} group has surely more than once tested all the closer islands. If it has failed to colonize these close islands, that is a very impressive and instructive failure. But before discussing this point further, let us examine other successful colonizers.

\textit{Anolis saurei}, PARALLEL AND COMPETITOR

Only \textit{A. saurei} of all island anoles has a record of success in colonization comparable to that of \textit{carolinensis} (Table 6, Fig. 10). Like \textit{carolinensis}, it has reached the Great Bahama, Cay Sal, and Crooked Banks, Little Cayman, the Bay Islands, and Half Moon Cay. It has gone beyond \textit{carolinensis} to the Little Bahama Bank, Rum Cay and San Salvador, and to Cayman Brac; it has invaded the margin of the Mexican mainland on and near Cozumel, and the British Honduras mainland near Half Moon Cay, and has inserted itself into the western part of Jamaica. On the other hand, it has sometimes failed where \textit{carolinensis} succeeded. It has not
reached Navassa or Inagua and it has not, even with possible human aid, achieved more than scattered coastal landfalls on the Floridian mainland and has nowhere gone beyond south Florida (Ruibal, 1964; King and Krakauer, 1966).

Like *A. carolinensis*, *A. sagrei* is a creature of the sun rather than the shade. More than any *carolinensis* it is a superabundant animal wherever it occurs. If any anole were to be singled out as a “dominant” species, *A. sagrei* would be that species.

The similarities and contrasts of the colonization patterns of *carolinensis* and *sagrei* are extremely interesting and revealing.

*A. sagrei* is a *beta* anole, one of 8 species of this major section of the genus on Cuba. It is not the most primitive of this section, but a central member, moderately specialized. In contrast to the Cuban *alphas*, the Cuban *betas* are a relatively tight-knit group, varying primarily in dewlap color, extent of keeling on their scales, and shade-sun preferences.

Fig. 11 displays the niche variation within the Cuban *beta* anoles. In temperature preference the divergence is extreme— from deepest shade to brightest sun. In perch site the original and still most frequent type is the trunk-ground niche seen in *A. sagrei*. (Compare this with the Cuban *alpha* radiation and the trunk-crown niche of Cuban *carolinensis*, Fig. 7). Two departures from the trunk-ground niche of the Cuban *betas* are the use of boulders as centers of territory by *Anolis mestrei* in western Cuba, and the ground habit of *A. ophiolepis* in open grassland.

The *beta* anoles of Cuba are, as a group, surely invaders from Jamaica, where more primitive (and more structurally varied) *beta* anoles are present (Etheridge, 1960). Thus *sagrei*, rather like *carolinensis*, is, it must be emphasized, a central, not highly specialized member of an advanced segment of a colonizing stock.

**A. sagrei on Jamaica**

The most extraordinary feature of the distribution of *A. sagrei* is its occurrence over a great part of western Jamaica. The presence of *sagrei*
on Jamaica is, in the present stage of geographic patterns in West Indian anoles, a unique phenomenon — the sole instance of extensive invasion of a species from one to another Greater Antillean island. The direction of colonization is clear: *A. sagrei* is a Cuban species that has recently invaded Jamaica; it is a back-invader from a stock originally Jamaican in origin.

If the Jamaican population of *sagrei* differs at all in morphology or color from all Cuban populations, the difference is at a very low level. Size does differ; the Jamaican animals are smaller than those in all Cuban populations. In behavior there also appears to be a difference, in that the Jamaican populations are more often found on the ground than those of Cuba. Jamaican *sagrei* is in fact called "ground lizard" in western Jamaica, where the large ground teiid lizard *Ameiva* is very local and unfamiliar to many of the people. *A. sagrei* in western Jamaica is a creature of the open, the sun, and the ground.

In western Jamaica *sagrei* is in contact with 5 of the 6 endemic anole species, but it is in substantial competition with none of them. Five of the 6 sympatric species are more arboreal than *sagrei* — typically spending little or no time on the ground. Only one of the sympatric species has the same perch and foraging habits as Cuban *sagrei* — perching low on tree trunks, foraging on the ground. But in western Jamaica this potentially competing species — *A. lineatopus* — does not in fact compete, since it is more of a shade animal than *A. sagrei*. The two species seek and inhabit different microclimates and so avoid competition.

In Jamaica the endemic species *A. lineatopus* occurs in two types of climate — wet and dry — and has races adapted to each (Underwood and Williams, 1959). The western end of Jamaica is distinctly wetter than the south central coast and the *lineatopus* there is greenish and tolerant of wetter conditions and greater shade than the
brown animals of the south central coast or of the north and northwest coast.

Yet dry-country-adapted *sagrei* has invaded the wet west end of Jamaica. Presumably it has done so because secular increase in desiccation has left drier open areas for it to dwell in, and man has, of course, accelerated this process by ruthlessly clearing away the forest.

We have no timetable for the advance of *sagrei* into Jamaica. Without reliable old records we cannot be sure that it has advanced in historical times, but human action in opening up its habitat has almost surely permitted an advance. We do have some information. In 1939 (Grant, 1940a) *sagrei* was known to occur as far as Williamsfield at the east end of the Mandeville plateau—a wet area at about 2,000 feet (600 m) elevation, but largely deforested—in which green *lineatopus*, as the subspecies *neckeri*, can be found only in the deepest shade. Into this same east end of the plateau, the nominate brown subspecies had penetrated in the open sunlit places, and here it overlapped *sagrei*. Now almost three decades later, collections along the road below the plateau on the flat hot Liguanea Plain demonstrate that *sagrei* has now invaded this plain. A. S. Rand and E. Williams in 1961 saw *sagrei* at Clarendon Park at the extreme west edge; in 1968 R. Trivers and E. Williams found a substantial population occurring with *lineatopus* along the road just before Four Paths some distance to the east and a few *sagrei* individuals were seen and one taken still further east beyond May Pen (Fig. 12). This is a substantial advance eastward on the southern edge of *sagrei*’s distribution. It appears to be paralleled by a similar advance in the northern part of *sagrei*’s range. George Gorman and Richard Thomas (pers. commun.) independently report that *sagrei* occurs with *merope*, the northern brown race of *lineatopus*, at Ocho Rios.

So far it is not clear that the advance has occurred except along the main roads. On the southern prong of the distribution, investigation of two roads south from the vicinity of Four Paths encountered only *lineatopus*.

Although *sagrei* and brown *lineatopus* may

---

**Fig. 11. The Ecological Radiation of beta Anoles on Cuba**

This is primarily a matter of thermal habitat, but involves perch in two instances—*A. mestrei* on rocks and *A. ophiolepis* on grass and ground.
now be encountered on adjacent fence posts along a road in the south, there are indications from observations in the vicinity of Four Paths that the two species may be maintaining ecological differences that will permit coexistence: sagrei, smaller, in more open sunny situations, more often on the ground and on smaller lower perches; lineatopus, larger, in better-shaded situations, infrequent on the ground, and occurring on larger, somewhat higher perches. These limited observations require confirmation, however, and the whole situation may be a very labile one which will bear careful watching.

In the north Thomas Schoener (pers. comm.) has reported habitat differences between the two species in their overlap area east of Montego Bay. There sagrei is found in the natural beach vegetation and lineatopus further inland.

The relation between sagrei and its ecological near-equivalents, the brown races of lineatopus, is surely not yet at equilibrium. It illustrates the dynamic situations that may arise once a colonizing species has achieved that first essential step — establishment. The relation, on the other hand, between sagrei where it coexists with green lineatopus in western Jamaica is in keeping with the conditions of stable coexistence everywhere and with the special conditions prerequisite to the first step in successful colonization — i.e., establishment.

A. sagrei in Central America

In Mexico and British Honduras limitation of sagrei to coastal areas coincides with total exclusion of carolinensis. Yet carolinensis (as allisoni) and sagrei coexist on Half Moon Cay off British Honduras. The easiest explanation here may be the following. Coastal sagrei is long established and has undergone some "ecological release," i.e. broadening of its niche, such that it now excludes carolinensis on the coast of the mainland. A. sagrei on Half Moon Cay, on the contrary, is a recent arrival on a newly emergent islet; since it is so recent, it is ecologically Cuban, hence adjusted to coexistence with carolinensis, which has also arrived quite recently and is likewise ecologically Cuban.

THE MINOR COLONIZERS

No other anoles are comparable to sagrei or carolinensis in their wide success as colonizers. All others have established themselves on one or a few islands.

(1) A. grahami of Jamaica has provided a daughter species, A. conspersus, to the single island of Grand Cayman, 190 miles (304 km) to the northwest (see Fig. 10). A. grahami is a beta anole, one of an endemic Jamaican radiation more primitive than the sagrei radiation of Cuba. It is a green anole roughly the ecological equivalent of carolinensis (especially the Cuban porcatus) and like the latter is a relatively un-specialized arboreal animal, characteristic of rather open country. On Jamaica A. grahami is very infrequently found on the ground.

A. conspersus on Grand Cayman differs very little morphologically from A. grahami. The most striking difference is a blue rather than yellow or orange dewlap. Chromosomally it is distinct, however; in fact, it is more primitive in this respect than grahami (Gorman and Atkins, 1966), and has presumably reached the species level. Ecologically it resembles grahami in tolerance of open conditions, but the females and juveniles are, at least in the dry season, more terrestrial, and do not consistently range as high in the trees as grahami females do in Jamaica.

The geographic context of conspersus is worth examination. Grand Cayman is the largest of the three Cayman Islands, about 70 miles (112 km) from Little Cayman, which is only 5 miles (8 km) from Cayman Brac. The distance of the Caymans from Cuba is no greater than from Jamaica, and the herpetofauna is partially of Cuban and partially of Jamaican.
origin. The anole fauna of the two smaller Caymans is in fact wholly Cuban (on Little Cayman, *carolinensis* and *sagrei*; on Cayman Brac, *sagrei* only).

In terms of currents, Jamaica has a definite advantage as a staging area for the Caymans, in that the currents sweep westward and a bit northward and lead quite directly toward the Caymans. Nevertheless, Cuba has provided more colonists to the Caymans than Jamaica.

The propinquity of the three Cayman Islands would lead to the expectation of a great similarity in their faunas. This is in general true (Table 7; Grant, 1940b). There may or may not be minor differentiation of the same colonizing stock on some or all of the islands, and colonists may not have reached (or not have persisted on) one or two of the islands, but *Anolis* is the only genus in which three different stocks have colonized one or more of the islands and also the only genus in which two stocks are sympatric on one island. In genera other than *Anolis* there is apparently a high probability that a first landing on any Cayman island will provide a stepping stone to colonization of the other Caymans. For one *Anolis* this may have been true (*sagrei* on Little Cayman and Cayman Brac). With the *carolinensis* derivative (*maynardii*) and the *grahami* derivative (*conspersus*), however, it is clearly untrue. The picture instead is one of exclusion by an ecological equivalent.

Even in the one case — *sagrei* — which might be interpreted as colonization within the island group, this explanation may not apply, since here, in spite of the nearness of Cayman Brac to Grand Cayman and especially to Little Cayman, neither *conspersus* nor *maynardii* has invaded Cayman Brac. We may well have to infer here an older *sagrei* invasion with "ecological release" such that *carolinensis* and *grahami* stocks, in spite of their trunk-crown rather than trunk-ground adaptation, have been excluded.

(2) Puerto Rican *Anolis cristatellus* is a more impressive colonizer than *A. grahami*, since it

### TABLE 7

*The herpetofauna of the Cayman Islands*

<table>
<thead>
<tr>
<th></th>
<th>GRAND CAYMAN</th>
<th>LITTLE CAYMAN</th>
<th>CAYMAN BRAC</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SALIENTIA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hyla septentrionalis</em></td>
<td>C</td>
<td><em>H. septentrionalis</em></td>
<td>C</td>
</tr>
<tr>
<td><em>Eleutherodactylus ricordii</em></td>
<td>C</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SAURIA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aristelliger praesignis</em></td>
<td>J</td>
<td><em>A. praesignis</em></td>
<td>J</td>
</tr>
<tr>
<td><strong>Sphaerodactylus lewisi</strong></td>
<td>J</td>
<td><em>S. bartschi</em></td>
<td>J</td>
</tr>
<tr>
<td><strong>Anolis conspersus</strong></td>
<td>J</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyclura macleayi lewisi</em></td>
<td>C</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Leiocephalus varius</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SERPENTES</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Typhlops caymanensis</strong></td>
<td>C</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Tropidophis caymanensis caymanensis</strong></td>
<td>C</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Alsophis cantherigerus caymanensis</strong></td>
<td>C</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>TESTUDINES</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chrysemys terrapen granti</em></td>
<td>J</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>CROCODILIA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Crocodylus acutus</em></td>
<td>C</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

C, Cuban affinity; J, Jamaican affinity.
* Endemic subspecies; ** endemic species. Species on the same line are closely related.
has populated several distinct banks, in part over very considerable distances (Fig. 13). It is perhaps possible to dismiss as trivial the colonization by this species of the two islands of Mona and Desecheo between Puerto Rico and Hispaniola. Mona, it is true, is clearly on a bank of its own, now 40 miles (64 km) away, but when a drop in sea level extended Puerto Rico to the west, the distance from the emergent mass to Desecheo and Mona was minor (Heatwole and MacKenzie, 1967).

The situation is quite different, however, for the cristatellus derivative, scriptus, which occupies Great and Little Inagua (400 mi=640 km distant), the Caicos Bank (320 mi=512 km distant), and Mayaguana and Atwood Cay (both of them colonized from intervening islands). The distances are quite impressive.

The case for relationship is, however, unsailable. Not only are scriptus and cristatellus morphologically so close that scriptus was at one time (Barbour, 1914) synonymized with cristatellus and only recently rehabilitated as valid (Rand, 1962a), but Gorman and Atkins (1968) have now provided clinching karyotypic evidence. Mouchoir Bank, Silver Bank, and Navidad Bank between Puerto Rico and Caicos, although at present under shallow water, undoubtedly provided way stations at times during the Pleistocene (Schwartz, 1968).

Anolis cristatellus is an alpha anole, a member of a special Puerto Rican radiation. The series is distinguished by a chromosomal specialization peculiar to it, and the series on Puerto Rico displays variability in both microclimatic (both dry- and wet-adapted species) and in structural trunk-ground and bush-grass niches (Rand, 1964).

A. cristatellus, a relatively unspecialized trunk-ground species, tends toward a dry sunny microclimate. It is the most abundant and widespread Anolis on Puerto Rico. It is therefore not surprising that of all the species on Puerto Rico this is the one that has colonized the southern Bahamas.

The colonization was also favored by the westward drift of the currents in the area and, as before mentioned, by intervening banks. It is less peculiar that cristatellus should have colonized the south Bahaman banks, however, than it should be the only Anolis to have done so. Cuba, with 22 or more anoles, and Hispaniola, with 20 or more, appear to offer to such an island as Great Inagua a far greater possibility of colonization. Mayaguana and the Inagua Bank, though small by comparison with the four Greater Antillean islands, are by no means tiny; and the Caicos Bank, when fully emergent, must have offered a still larger target. Yet each of these island banks has the single anole, Anolis scriptus, differing from A. cristatellus only in the most minor scale characters (Rand, 1962a) and in bolder coloration (dark brown markings on light brown). It would appear inescapable that in some fashion A. scriptus has excluded all later colonists.

(3) Hispaniolan A. distichus has sent representatives to the Great Bahama Bank, and thence to several adjacent banks (Fig. 14). It has also colonized the Floridian mainland, perhaps from the Bahamas (Schwartz, 1968).

A. distichus is a small alpha anole of mesic forests in Hispaniola. It lives on tree trunks between the trunk-ground species and the trunk-crown species (Rand, 1962b). It has a dry-country sibling (brevirostris) in part of its home island.

The distributional anomaly of distichus is a double one: (a) its insertion in the Bahamas into the midst of a fauna of three other species, all of them Cuban; (b) its bypassing of the island of Inagua which intervenes directly between its source island, Hispaniola, and the more distant Great Bahama Bank.

Surely the entrance of distichus into the oth-
erwise wholly Cuban anole fauna of the Great Bahama Bank is an insinuation permitted by its peculiar ecology on Hispaniola. As we said, *carolinensis* is a trunk-crown animal, *sagrei* a trunk-ground animal, *angusticeps* is a crown-vine-bush animal. In both size and structural niche preference, *distichus* is preadapted to insert itself between *carolinensis* and *sagrei*, to fit within the pattern.

The bypassing of Inagua is perhaps most readily understood had Inagua not been available for colonization when *distichus* made its single successful voyage to the Bahamas. But given the closeness of Great Inagua to Hispaniola, and given the greater distance to the Great Bahama Bank, it is probable that if *distichus* made the distant voyage, it made the closer one much more often. If that be true, then a single broadly adapted anole population (in this case, *A. scriptus*) would appear to be more resistant to invasion than a somewhat more complex fauna of specialists.

(4) *Anolis angusticeps* — an alpha anole — is one of the Cuban anoles that has invaded the Bahamas. It is known, however, only from the Great Bahama Bank, where in appropriate environments it is moderately abundant.

Schoener’s quantified observations on Bimini (Schoener, 1968) modify those of Oliver (1948) for the same area. The occurrence of *angusticeps* is usually high in the tree crown on branches of quite small diameter and mostly on light bark. This does not correspond well to any part of the recorded structural niches for the same species’ island-wide range in Cuba. However, data for Cuba are based on equally careful and documented studies. The Cuban situation indeed requires further study. That there is niche variation appears to be unquestionable (Barbour and Ramsden, 1919; Collette, 1961; Ribal, 1964; Hardy, 1966), but how much is individual variation and how much is geographic remains uncertain. The special interest of this species, then, is that it may well exemplify the sort of niche variation that is necessary for the intra-island evolution of distinct species from a single immigrant stock.

The three remaining colonizers require very little discussion: (a) *A. luciae* — an alpha anole — is the most interesting of these, primarily because, according to Gorman (1968), it represents the basal stock of all the roquet group in the southern Lesser Antilles. Beyond this, it is interesting only because it has colonized over a considerable distance: Blanquilla, its first landing, is already over 200 miles (320 km) from St. Lucia; and Bonaire, presumably colonized from Blanquilla, is another 200 miles (320 km) further west. Colonization was strongly favored in this instance, however, by the general westward drift of Caribbean ocean currents. (b) *A. lineatus* — a beta anole — is of interest in two respects. Although on an island very close to the continent, it is quite unlike any living species on the neighboring mainland and, in fact, it has colonized Aruba on the continental shelf and excluded from that island all present-day mainland stocks. Rand and Rand (1967) have discussed the structural habitat of *lineatus* on Curacao and have demonstrated that it is somewhat broader than that found on such a multi-anole island as Puerto Rico. Again, the colonization of Aruba has been favored by the westward drift of currents, but it is remarkable that a distinctive species appears to have originated, and has certainly maintained itself, on islands so close to the coast. (c) The anoles on Providencia and San Andres are referred to the species *A. concolor*, which was described from “Nicaragua” but without precise locality. No mainland specimens have been taken since the types, and it seems likely that the type locality is itself in error. It would certainly be a zoogeographic anomaly if an island species, abundant on two well-separated islands, over 50
miles (= 80 km) apart, should be conspecific with so rare a mainland species that out of a very large anole fauna it has not been taken on the mainland in more than 100 years since its description. [Specimens in the British Museum from the mainland of Nicaragua have been referred to A. concolor (Dunn, 1930; Dunn and Saxe, 1950). These, however, were misidentified. They are in fact A. rhombifer Boulenker (distinguishable from concolor by the characters cited by Schmidt in Barbour, 1934) and A. sericeus auct. = sallaei.] It is much more probable that concolor, like lineatus, is an island endemic. It is, however, related to and derived from the neighboring mainland fauna. Zoogeographically this is plausible, since the islands are on a continental bank, and yet the fauna appears to be a waif fauna. The forms on the two islands are distinguishable in size and, according to reports, in color. It is not possible at present to evaluate the level of difference, but it is certain that each is the closest relative of the other.

THE FAILURE OF MAINLAND SPECIES TO BE RECENT COLONIZERS

The great arc of the mainland which surrounds the Caribbean is rich in anole species, and certainly Central America and South America did originally provide the anoline stocks that have populated the Caribbean area. Why have these mainland stocks provided no recent invaders of the newly emergent small Caribbean islands except lemurinus on the Bay Islands and no recent invaders of the larger and more stable islands at all?

For the small, distant, recent islands two factors seem of some importance—distance and currents. The distance from South America is in the case of the islands very important. The shorter distances from the Antilles to the newly emergent islands promoted the early capture of these islands by Antillean species. As for Central America, the westward drift of Caribbean currents has made invasion from thence to the small Caribbean islands relatively difficult and has again permitted earlier capture by Antillean species.

In the Gulf of Mexico the eastward drift of currents might bring propagules to Cuba from Central America, but the already complex anole fauna of that island would then presumably exclude them.

Yet drift and distance even for the small islands cannot constitute the full story. A. carolinensis has come to the very edge of Central America, and A. sagrei occupies a portion of the coast. The mainland fauna seems to a certain degree vulnerable; in this genus we must assume some colonization failure on the part of the mainland species. The question of the reason for colonization failure leads us directly to the factors of vagility.

THE FACTORS OF VAGILITY

What are the factors which make one species better than another in cross-water colonization? We can describe A. carolinensis and A. sagrei as "vagile," but we have not conveyed much information until we determine why and how they are so. It may be profitable to look at some of the characters and ecologies held in common by the expanding species of anoles.

(1) The anoles that have recently expanded their range to small recent islands appear to be animals of open forest or savanna areas. A. carolinensis and A. allisoni are so. A. sagrei, in most present island environments, is conspicuously a fence-post lizard; it does not require forest at all. A. angusticeps is an arboreal or bush lizard, but not in dense forest. A. grahami, the ancestor of A. conspersus, is an arboreal form but again is characteristic of open, not of dense, forest. A. distichus in the Bahamas is a member of a species complex which on Hispaniola has both mesic and arid-adapted elements; the Bahaman populations are surely nearer the arid pole in their adaptations. A. scriptus and A. monensis are not only derivatives of dry-adapted lowland A. cristatellus, but occur on very arid islands.

(2) It is the other side of this coin that none of these expanding anole species is a deep shade, rain forest, or montane form. The shade-loving relatives of A. sagrei—A. homolechis, A. allogus, A. ahli, A. mestrei—have either made no cross-water voyages or none that were successful. A. gundlachi, a wet area, highland relative of cristatellus, has no representatives outside Puerto Rico, though A. cristatellus has both scriptus and monensis.

(3) We have already noted neither A. caro-
**linensis** nor **A. sagrei** is the extreme specialist of its respective radiation. The specialists, even when widespread, have done much less well. **A. ophiolepis** is a species related to **sagrei** but more specialized. It is widespread in the grasslands of Cuba but has gone nowhere else. (It is true that successful rafts do not ordinarily form in the habitat of **ophiolepis**, but see below.)

(4) We have noted the very limited number of species that have achieved successful colonizations and the monotonously repetitive occurrence of the same species on newly colonized island after island. We have noted also, as the obverse, that except on the four stable Greater Antillean islands there were, because of recent emergence, no endemic residents to dispute possession with the invading forms.

This picture is somewhat like that which Wilson (1959, 1961) described for his Stage I (expanding) species of Melanesian ants. The phenomenon of "expanding" species is, of course, by no means limited to anoles or ants, but Wilson provided a detailed analysis which permits cross-comparison.

In the Melanesian ants Wilson found Stage I species to have the following major characteristics: (1) a greater concentration in marginal habitats (open lowland forest, savanna, and littoral); (2) rarely limited to montane or rain forest habitats; (3) individual occurrence in a greater range of major habitats; (4) occurrence in a higher proportion on islands and archipelagos satellite to the main theatres of evolution; and (5) the species within the same genus tend to be markedly different from one another in morphology, ecology, and behavior.

There are resemblances here to the anole story, and also discrepancies. The remarkable fact is that there are resemblances. Why should there be? Look again at the nature of the colonization voyage. I have stressed the rigors of the voyage — the hazards of desiccation, especially for animals which, like lizards, are carried on rafts. For wet-adapted rain forest species, the desiccation hazard implicit in rafting should be an insuperable horror. Only if rain forest or montane species can avoid rafting — by travelling by winds or hurricanes — would the problem be lessened. Presumably that is possible for ants; yet even in their case most colonizations have been made by species that could survive drier habitats and not by those species restricted to rain forest or mountains.

The physiology of cross-water invasion may thus be a primary point to consider. Is it, however, all? In each of the four Greater Antillean islands there are some species highly adapted to arid conditions — e.g., **A. whitemani** on Hispaniola, **A. poncensis** on Puerto Rico. None of these has been a successful colonist. Is this chance? Or must cross-water colonization presuppose subtler adaptations than resistance to desiccation? We do not have enough information. The anole colonists are few. We should feel some hesitation about generalizing from a colonizing sample of six species, even though the sample of non-colonizers is very much greater.

If, however, the total West Indian lizard fauna is considered (in order to provide us with a larger base for discussion), it is possible to come up with at least hints that vagility — the good-traveler quality of expanding species — is not wholly a matter of the physiology of cross-water invasion.

If we look at the fauna of Costa Rica, which lies in the center of the land colonization routes between North and South America, we find there the northern limits of certain South American genera which have been good, though not superlative, invaders from that continent, as well as the southern limit (or close to it) of certain North American genera which have proven to be weak invaders in the other direction. Some other genera from both sources have invaded about as far as climate has permitted.

Table 8 lists these three groupings. It demonstrates that the genera which are widespread on land are precisely those which have colonized the West Indies. The good travelers on land are the same as those that have travelled well across seas.

It will in no way assist our understanding of this phenomenon to describe the genera which have achieved wide ranges on land and across oceans as "dominant." That would be to name without explaining. We need to find the factors which are genuinely responsible for the phenomenon. The phrase "dominant" is in fact an unfortunate term. It is a metaphor and has
### TABLE 8

*Costa Rican lizard genera*

<table>
<thead>
<tr>
<th>LIMITED TOWARD THE S</th>
<th>WIDESPREAD</th>
<th>LIMITED TOWARD THE N</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Gekkonidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coleonyx</td>
<td>Gonatodes [GA]</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Sphaerodactylus</em> [GA, LA]</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Phylodactylus</em> [GA, LA]</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Thecadactylus</em> [LA]</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Lepidoblepharis</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Iguanidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basiliscus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corythophanes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ctenosaura *</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sceloporus</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Iguana * [LA — 2 stocks]</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Anolis</em> [GA, LA — 2 stocks]</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Polychrus</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Teiidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Gymnophthalmus</em> [LA]</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Ameiva</em> [GA-LA]</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Cnemidophorus</em>**</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Lepsoma</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Anadia</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Psychochlossus</em></td>
<td></td>
</tr>
<tr>
<td><strong>Anguidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barisia</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Diploglossus</em> [GA]</td>
<td></td>
</tr>
<tr>
<td><strong>Xantusiidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Lepidophyma</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Scincidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leiolopisma</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eumeces</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Mabuya</em> [GA, LA]</td>
<td></td>
</tr>
</tbody>
</table>

GA = Greater Antilles  
LA = Lesser Antilles  
Widespread = occurring north of Costa Rica and extensively in South America as well  
* Related genus in Greater Antilles.  
** Related genus in Cuba.  
*** This genus is probably a synonym of *Ameiva.*

---

an emotional content; it appears to imply conquest. Zoogeographically, it seems to imply competitive replacement. But in the expanding species we have examined here, we have seen no competitive replacement. There is no demonstration whatsoever that *carolinensis* or *sagrei* have “replaced” anything. They have, however, with the utmost effectiveness seized open ground.

In the seizure of open ground, expanding species resemble “fugitive” species, as they do also in their dispersal powers. They would appear to differ from fugitive species, as classically defined, however, in their ability to hold their ground once taken. They offer a sturdy resistance to change or, better, they adapt to it. They are, in fact, not so much “dominant” as “versatile.” They are generalists rather than specialists; they tolerate many conditions; they require few. This last distinguishes them importantly from the specialist non-expanding species; the specialist has little tolerance and rigid requirements. I owe the term “versatile” to R. Ruibal, who in a letter to me confessed himself impressed with the “versatility” of *A. watts* — the one expanding species in the northern Lesser Antilles. I count as a virtue of the term over “generalist” or “non-special-
ist” (so often stigmatized as a “jack of all trades”) that it implies breadth and tolerance and not just non-extreme or “average.” The connotation of non-specialist and even “generalist” is too negative; it lacks affirmation that this is a kind of adaptation, probably genetically no easier to attain than specialization, and perhaps, with its implication of buffering and tolerance of extremes even more difficult to achieve, and hence rarer. The obtrusiveness in some respects of these colonizing species may lead to an erroneous impression of commonness (and by an implication inherent in language and not in biology, of vulgarity); but resilience such as these species manifest may be both rare and, when achieved, immensely successful, while specialization may be the sink to which all species tend unless special circumstances prevent.

These generalizations I take to be a mere description of the evidence before us. Among others, I have tended to divide anoles into sun and shade animals with sometimes several grades to be recognized in each (e.g., the sagrei series in Cuba—see Ruibal, 1961). This is, in fact, a simple description of the circumstances in which we found the several species; it certainly implies that each species tolerates the conditions in which it is found, and presumably tolerates those conditions better than adjacent species do. The assumption was too easily made, however, that tolerance implies some requirement, which in turn, implies a genetic bias which is not easily overturned. This assumption is, in fact, fallacious. Schoener’s recent careful explorations of the differing habitats and habitats of sagrei on several islands (Schoener, 1968; and in prep.) have made clear that animal’s climatic versatility (Table 9). Albert Schwartz (pers. commun.) had already cautioned that in his very extensive field observations sagrei was “everywhere.”

Note that versatility is not perfect adaption to any environment; it is, rather, the ability to use what is available. If shade is fully occupied on Jamaica or Cuba by other species, sagrei will be in the sun. If the trunks and crowns of trees in Jamaica and Cuba or Little Cayman are occupied by grahami in the one instance and carolinensis in the other two, sagrei will be restricted to the ground and low trunks to an extent that it apparently is not in Cayman Brac. A versatile species can be and is restricted by the presence of other species. If any species is long restricted to a given habitat, selection will tend to adapt it genetically more perfectly to that habitat.

But this is decay of versatility. We may expect that versatile species will spawn populations adapted to local conditions; these populations may become ultimately non-versatile, non-vagile species. There will be constant selective pressure to local adaptation, with all its consequences. This is again the “sink of specialization.” [This phenomenon of alternation of vagile and non-vagile phases (or populations) is clearly the same as the “taxon cycle” described by Wilson (1961) in Melanesian ants. It is presumably a quite general phenomenon. See also Lewontin (1965) in the discussion of Wilson (1965), and Mayr (1965a). There is a major discussion in MacArthur and Wilson (1967, Chapter 7).]

Let us look again at carolinensis and sagrei. They are in present-day Cuba the most abun-

<table>
<thead>
<tr>
<th></th>
<th>CAYMAN BRAC</th>
<th>BIMINI AND LITTLE CAYMAN</th>
<th>JAMAICA</th>
</tr>
</thead>
<tbody>
<tr>
<td>♂♂ and juveniles</td>
<td>relatively low on trees, but perhaps not as low as on other islands</td>
<td>always to an important degree terrestrial (even holes in rock)</td>
<td>most terrestrial on Jamaica if on trees, hardly ever on trees of large diameter</td>
</tr>
<tr>
<td></td>
<td></td>
<td>sometimes on trees of large diameter</td>
<td></td>
</tr>
<tr>
<td>♀♀</td>
<td>highest on Cayman Brac</td>
<td>definitely higher than Jamaica</td>
<td>lower than elsewhere</td>
</tr>
</tbody>
</table>

Information from Schoener (1968 and pers. commun.).
dant of *Anolis* species. But R. Ruibal has shown me maps of former forest in the province of Camaguey. In the past forest was the prevalent biome. When it was so, the anoles of the shaded forest must have been far commoner, and *sagrei* and *carolinensis* must have been far rarer, occurring only at the edges and in clearings. It is only because man has made edges and clearings prevalent that *carolinensis* and *sagrei* are now numerically dominant.

What are the ecological characteristics of edges and clearings? They are rather unstable. They are the areas of "combat between two competing extreme ecologies. Species that inhabit them must therefore have some of the characteristics of "fugitive" species. They must at the same time have a high tolerance of isolation and yet must disperse readily through habitats occupied by species adapted to shade. They are neither restricted to nor very closely adapted to extreme ecologies. Such animals are obviously preadapted to colonize: they are tolerant and good dispersers, i.e., they are "versatile" generalists, and, in the present, they are abundant.

This matter of abundance requires careful consideration. Abundance should be a requirement for colonizing species (Levins and Heatwole, 1963), and especially for those which colonize across so hazardous a barrier as the sea. We have said above (1) that *carolinensis* and *sagrei* are more abundant now than they were in the past, and (2) we have commented previously on the apparent earlier colonization of the mainland by *carolinensis* rather than *sagrei*.

Are there explanations for these two phenomena?

1. There is a contrast between *carolinensis* and *sagrei* that may have affected their abundance in the past. *A. carolinensis* is a creature in large part of the tree crown; to the extent that the sun reaches the crown, *A. carolinensis* is in ecologically "edge" situations; any advantage it might have over other species with respect to sun tolerance would come into play when it seeks the sun at the top of the crown; it is not inherently trapped by shade. As a tree-crown-dweller, it may be at least a modest denizen of most forests, whether there are many real clearings or not, and it may therefore be rafted out of even fairly dense forests. Once on a raft, its tolerance of desiccation, rare among forest animals, permits it to be a colonizer. (It may be very significant that the anoles judged most primitive according to Etheridge's 1960 scheme are also animals with strong affinities for the crowns of trees, and hence are similar to *carolinensis*.)

In contrast, *A. sagrei* is an anole of the lower trunk and the ground. If its competitive advantage is only in situations in which sun reaches the lower trunk and ground, it is obviously restricted to true clearings—natural or man-made—and unless these clearings are abundant, *A. sagrei* will not be abundant. In any island situation, therefore, in which forest is an important part of the total island flora, *A. carolinensis* should be more abundant than *A. sagrei* and have a greater opportunity to colonize.

2. Much about the history of the West Indies suggests that these islands have suffered a progressive drying out. The anole fauna itself seems to imply this, since the primitive species, despite the fact that they may have come across water, seem to be true forest species, while the dry, open country species evolved in situ, and appear to be late and specialized forms. (This story will be documented in a later paper.) If the West Indies were formerly wetter and more heavily forested, the apparent temporal sequence of colonizers, first *carolinensis* and then *sagrei*, becomes plausible. Colonization would thus have begun when forests were still overwhelmingly characteristic of the West Indies (as they are of the East Indies today), and thus when *carolinensis* was optimally abundant. It then continued during a period of drying out of forests that heightened the later abundance of *sagrei*, a phenomenon that man's action has merely accelerated.

**THE FACTORS OF EXCLUSION AND COEXISTENCE**

The population of any colonizing species is at first very small. The most probable fate of any very small population is extinction. If the colonizing species is only one fertilized or pregnant female, the species is indeed on the verge of extinction. When, therefore, we estimate the probability of colonization, we ask in effect under what circumstances a very improbable event
— the expansion of a very small population — will take place.

Given a small initial population, it is crucial that the budget of advantages and disadvantages not be negative, even momentarily, until several generations have raised the population numbers beyond the level at which there is a significant risk of extinction. The problem is the old one of the gambler with too little capital. He must have a run of luck in order to stay in the game. Fortunately, the gambler-colonist, if she can reproduce and her progeny can reproduce, has before her the possibility of exponential increase, and thus a greater assurance with every new generation of escaping the “final solution” — extinction. With vertebrates, however, reproductive increase is relatively slow, and many generations may be required before the population reaches the level of safety.

In the first phases of colonization the gambler-colonist obviously cannot afford to play against an established opponent, i.e., a species with a large effective capital in territory and population. If the larger, established population interferes in any way with the small invader colony in its initial stages (and it cannot easily be imagined that a congener will not so interfere), the long odds are increased that the invasion will come to nothing.

If invasion is made to seem an extraordinarily difficult and improbable event, I feel I do not overstate the case. Colonization characteristically depends on a vast number of attempts, most of which fail. Those that fail are not ordinarily on record. It is the very rare successes that are conspicuously displayed before us.

Success in invasion must then depend upon advantages. What sorts of advantages can a colonist have which will permit it to overcome its basic disadvantage of small numbers? Among them are the following: (1) existence of an unoccupied area, i.e., a physical area actually devoid of competing animals; (2) a “vacant niche,” i.e., an unutilized aspect of the environment to which the invader is already adapted; and (3) direct competitive advantage within the same niche.

Of these three possible advantages, it is the third which is conventionally emphasized. However, I consider that the disadvantage of initial small population size is so great that even a large competitive advantage within a niche is of little use to a colonist unless it has also advantages (1) or (2), or both. At least in territorial animals, such as the anoles of the West Indies, invasion which has involved competitive conquest of terrain already occupied by an established species has yet to be demonstrated. For these animals, then, the two other advantages need to be stressed.

If, in a formal and ideal model, any territorial species occupied all suitable sites on an island evenly and continuously, it is easy to see that a species of similar if not identical ecology, without any physical vantage point and with a small population, has no possibility of incursion. We have stressed above that this model is quite unrealistic: typically, neither ecologies nor animals are evenly and continuously distributed. However, some anole species on some small islands approach the condition of the model amazingly closely, occupying essentially every portion of their island that has any erect vegetation, e.g., \textit{A. conspersus} on Grand Cayman.

Any distribution other than complete occupation offers physical vantage points for the invader. However, since discontinuity in ecology is at least part of the reason for species limitation or disjunction (including microdisjunction), very possibly the invader that successfully seized the unoccupied spaces would differ in at least part of its ecology from the resident species. Thus advantage (1) above (physical space available) will often imply advantage (2) (ecological space available) as well.

This certainly is the apparent situation for the presence of \textit{sagrei} in western Jamaica, where it appears to have colonized areas that were open in two senses, open to the sun and open physically and ecologically, i.e., unoccupied. As we have suggested, the very existence of areas open in these two senses may be a recent phenomenon and \textit{sagrei}'s invasion a very recent affair.

It is tempting to regard the case of \textit{sagrei} in Jamaica as paralleling \textit{sagrei}'s invasion of the Mexican coast but as going a bit further. Very likely \textit{sagrei}, when first in Jamaica, held only dry coast localities, just as on the mainland. Then the opening up of the forests of western
Jamaica, naturally and by man, permitted the infiltration of *sagrei* inland, until now it occupies all suitable habitats in the western half of Jamaica.

Jamaica, however, is a large island. Its western coast could provide a sufficiently spacious invasion base to permit a build-up of a “safe” population — one that could escape the hazards of limited initial population size. The beaches of truly small islands do not provide comparable invasion bases.

Here we confront again the islands of the Great Bahama Bank for the information they provide us. Four species still coexist on one fragment of the Great Bahama Bank — South Bimini — fantastically smaller than the areas which on Great Inagua and Grand Bahama support only a single species.

Clearly South Bimini as such was never invaded by four species, nor did four species ever establish themselves on so small an area. On the contrary, the four resident species invaded and became established on an enormous island (Fig. 2) on which the four species had both geographic space because of the huge size of the emergent Great Bahama Bank and ecological space because these four species were preadapted to coexist.

The preadaptation was of two sorts: *carolinensis, sagrei, and angusticeps* could coexist because they had long been coadapted on Cuba. *A. distichus* from Hispaniola could join them because it came to the Great Bahama Bank already adapted to a part of the environment that the other species did not fully use.

Again I must point out the importance of geographic area. Enormous as the emergent Great Bahama Bank was, it could not have been occupied all at once. Indeed, coming from a different direction, *distichus* was most likely to land on the Great Bahama Bank at a different time and in a different area than those of the arrival of the three Cuban species. It should then have had ample time to develop safe population levels by the time it met and inserted itself among the Cuban invaders.

In this story it would seem that not only geographic area and not only ecological preadaptation, but also favorable arrival time is important. We might therefore consider this factor as a fourth advantage that might assure a successful invasion. In fact, however, favorable arrival time is a mere restatement of the availability of geographic space for a population build-up. This is easily seen to be true in cases of coexistence. Thus, *distichus* and *sagrei* have each successfully colonized such very small banks as Rum Key and El Salvador. This success is most readily explained if the two species arrived almost simultaneously from the Great Bahama Bank. If they did so in slightly different areas, as is highly probable, each would initially occupy space empty of the congener and thus the problems of unavailable space and of disparity in population size should not be a hazard for either of them. Their colonies would grow until they met and then, since they were already coadapted on the Great Bahama Bank, they would be expected to fit together on these smaller banks also.

In cases of exclusion, the close relation of space to time is again apparent. Exclusion seems to occur when a species has achieved full spatial occupation of an island before a second invader lands (e.g., *Anolis conspersus*). Arrival time appears to be significant precisely because it provides open ground to the first invader and denies it to the second. In the cases of exclusion on small islands, there are two especially interesting aspects: the frequently large populations of the single species on small islands; and the breadth of adaptation that such single species display. These are in fact aspects of the same small-island effects that result in exclusion and single-species islands. Thus on a very small island, the physical area necessary to maintain a permanent population of any species may be a genuine problem. For an animal of a given size and given feeding and reproductive demands, there will be a definite spatial limit — given the most favorable ecology — in which a population can indefinitely be maintained at a large enough level to be reproductively “safe.” (For *Anolis* this limit for isolated islands may possibly be a mile square = 2.6 km².) In contrast, on larger islands and on continents, even disjunct ecologies may with sufficient interpopulational migration sum up to a sufficient physical area for the maintenance of a safe population. Thus, even if the individual areas of disjunct but similar ecology might fluctuate in size, a “rare” species may successfully perpetuate itself if the
total available area is above a certain limit. On a small island, however, a species cannot afford to be rare; the sparse population of a tiny area cannot be replenished from outside: invasion is just too harsh and chancey a process.

To be abundant over all of a small island a species must, unless the island is very uniform in ecology, be in some way broadly adapted. Ruibal and Philobosian (in mss.) have demonstrated that breadth of thermal adaptation in the single species of a one-anole island (e.g., *A. oculatus* on Dominica) may encompass the total thermal adaptation of several species on a multispecies island such as Cuba (Fig. 15). They found that one local population of *A. oculatus* might differ very strikingly in body temperature if the thermal habitat was diverse, accepting passively a range of temperatures that in Cuba or Puerto Rico (Ruibal, 1961; Rand, 1964) would be divided among the separate thermal micro-habitats of two or three mutually exclusive species of anoles.

The achievement of such breadth of adaptation as *oculatus* reveals implies the absence of the effective biotic pressures which restrict adaptation. It implies that a species is alone within the relevant ecological space. Once achieved, however, breadth of adaptation maintains and is maintained by high populations. These high populations again prevent population build-up in any invader and thus prevent the invasions that could provide restrictive biotic pressures.

In summary, colonization is itself a difficult process, difficult even for a first invader. Exclusion therefore should be very easy, coexistence enormously difficult. And in fact, we have found on small recent islands only two situations applicable to congenic invading species: either one is excluded or if they are preadapted for sympatric existence, they may continue to coexist. Is coexistence possible then only if there is prior coadaptation? Are there no cases anywhere of the evolution of coexistence in situ? Such cases are unquestionably known on continents and large islands. But are there any such on small islands? In reality, yes—in the Lesser Antilles, although there we take leave of small, recent, simple islands and advance a step towards the problem of large islands and speciation on them.

THE LESSER ANTILLES: ONE STEP BEYOND SMALL RECENT ISLANDS

Most of the Lesser Antilles, the islands from Sombrero to Grenada, though of uncertain age, are certainly too old and have too many peaks well over 1,000 feet high to be a part of the story of small recently emergent islands. The northernmost island, Sombrero, is very low, however. It is only about 40 feet (12 m) high at the highest point; certainly it is one of the recently emergent islands. It deserves comment if only because it is not clear that it has any native population of anoles. Lazell (1964b), who first recorded an anole there, is uncertain whether the species he found was not recently introduced. At all events, the anoles differ from *A. gingivinus*, of the Anguilla Bank directly to the southwest, only in the constant presence of a color pattern which occurs in 10 or 20 per cent of Anguilla Bank populations, and not at all in basic morphology. Because the island is without trees, *A. gingivinus* is a ground lizard on Sombrero, in contrast to its tree-bush habitat on the Anguilla Bank (Lazell, 1964b).

The absence of a truly endemic species of

---

**Figure 15.** The Thermal Range (in MBT, Mean Body Temperature) of *Anolis oculatus* of Dominica, Compared with that of Several Cuban Anoles and *Uta stansburiana*

Modified from Ruibal and Philobosian (in mss.). The numbers in parentheses are the numbers of samples used in determining the ranges of MBTs.
anole on Sombrero is extraordinary and in strong contrast with the Bahaman islets, e.g. Bimini, quite as small but with a far better fauna. The problem is the greater because Sombrero is the remnant of a much larger bank and once had tortoises and a large iguanid — Iguana or Cyclura (Julien, 1866; Williams, 1952).

It is difficult to suppose that Sombrero is so recently emergent that anoles have had no time to get there, since the island does support an endemic ground lizard, Ameiva, not only melanistic but well-differentiated in scale characters (Baskin and Williams, 1967). It is preferable to believe that the present absence of trees is correlated with the absence of any permanent anole colony. The absence of trees and shrubs itself implies an exceptionally rigorous environment. The factors which have eliminated trees may equally prevent long continuance of anole populations, while not harming to the same extent the larger, hardier Ameiva, which is characteristically a ground-dweller. Very probably when tortoises and larger iguanids lived on the Sombrero Bank, anoles lived there also. The absence of anoles in a Caribbean herpetofauna of even very modest proportions would be anomalous indeed.

All the other Lesser Antilles do have native anoles. In the Leewards each island bank, though not each island, has its own distinctive anole, usually considered to be of full species status.

In addition to gingivinus on Sombrero and the Anguilla Bank, two other species (or subspecies) of Lesser Antillean anoles occur on more than one bank, are nearly undifferentiated, and are therefore presumably very recent colonists. Anolis watti occurs on the Anguilla Bank, the St. Kitts-Nevis-Statia Bank and the Antigua-Barbuda Bank. Anolis richardi, far to the south, occurs on both St. Vincent and the Granada Bank, and on Tobago on the continental shelf.

The distances involved in the colonizations are in these cases very small — 10 to 20 miles (16 to 32 km) between banks, rarely 30 miles (48 km), apart. Even the distance between emergent islands, e.g., Bequia on the Grenada Bank and St. Vincent (7 miles = 11 km), is ridiculously small in comparison with the voyages made by carolinensis, sagrei, scriptus, grahami, or even distichus. The difficulties of colonization may have been somewhat greater, however, since the major oceanic currents flow westward between the island banks and, in addition, in the case of both watti and richardi there is good reason (Gorman, 1968) to believe that colonization came southward from a more northern point of origin and not in the expected fashion northward from the continent. There is the further point that both colonizations were effected in the presence of an endemic resident anole species.

The short distances between Lesser Antillean island banks certainly imply that attempted invasions between these banks must be vastly more frequent than attempted invasions by carolinensis or sagrei of their distant landfalls. The shortness of distance may indeed have been essential to the successful assault by richardi or watti on an island held by a competing congener.

There may have been another factor: the physical complexity of the land masses invaded. All the islands invaded by watti, for example, are on complex banks which have to varying degrees been emergent and submerged. The present condition of these banks is intermediate, showing neither maximum emergence nor maximum submergence but perhaps near-maximum complexity. Thus the Anguilla and St. Kitts Banks are now represented by three major islands each, the Antigua Bank by two.

The possible importance of this will be seen if we confront again the problem of new colonizers invading an occupied island. We have seen that even superlative colonizers such as sagrei or carolinensis seem sometimes to be excluded, and that in the Greater Antillean area there is in fact no instance of a colonizer coexisting on a small island with a prior invader unless (1) the coexisting species have had prior coadapted niches on their home island (e.g. carolinensis and sagrei), or (2) the species which insinuates itself is preadapted to do so by the special qualities of its niche adaptation on its home island (e.g. distichus on the Great Bahama Bank, sagrei in Jamaica). There is in the Greater Antillean area no example at all of very closely related species sequentially colonizing the same island.
Yet in the Lesser Antilles, both in the northern and in the southern islands, the recent invaders are quite closely related to the species whose islands they invade. This is a very anomalous fact unless two special features of the Lesser Antilles are important: the closeness of the islands and the presence of microarchipelagos consisting of the islands of a single bank.

In these cases the matter of space — critical in all colonization — may be decisive. The most difficult problem for an invader once he has arrived, as we have suggested, is population build-up. Until its population is permitted by the circumstances surrounding its invasion to reach a safe level, the most probable fate of any invader is extinction. Thus, to permit invasion of any occupied area by a species closely related to one already present, we must find physical space for the invading population. If there is space to permit a safely large population, there can be interaction between the invader and the resident species with the build-up of the essential character difference ("character displacement") that will permit their coexistence. In the Lesser Antilles it is clear that size difference is one of the character differences developed between recent invaders and resident species. [To judge from the size of anoles on the one-anole islands, in most cases both species have changed in size.] Where has this character difference evolved? It seems plausible that the emerging land surface of complex banks, resurgence after a period of maximum submergence, might provide the vacant land surface both on emerging separate islands and emerging parts of islands on which an invader could build up its population to the point where contact with the resident species would result in stimulation to selection for difference rather than in stress upon a small population to the point of its extinction. (I emphasize that the area of these islands is small, probably not many times greater than the dispersal range of individuals within a species. Character displacement occurring at the contact between species has therefore the probability of affecting entire populations, as it might not be able to do in populations with relatively enormous ranges on continents or even large islands.)

To make the issues clearer, let us consider the effect of failed invasions. Assume that an invader, fully isolated reproductively from a resident species, has frequently made temporary incursions into the range of the resident. Assume also that the invasions fail because of competition, and that for both invader and resident species competition is severest between those fractions of each population which are most similar in all ecologically relevant parameters. The significant point here is that, if the invader has been able to seize an island of a bank or part of a newly emerging island, the stress of the invasion applies not only to the invader population but also to the resident. The elements of the resident population which are ecologically most similar to the invader are likely to be under selective erosion; their reproductive potential has the highest probability of being diminished by contact and competition with the invader, and their genes ultimately eliminated. By this process, at least temporarily, one segment of the variability of a species, for example, variability in size, may be diminished or eliminated and during the period of invasion stress the resident species is nudged toward one side of its curve of variability.

Remove the stress imposed upon the resident species by the invader and the balance of selective forces which had imposed the former curve of variability would act to restore the original lost frequencies. The resident species would "recover." But if invasions reached a critical frequency, the resident species would not in fact have time to "recover"; it would be permanently altered by even the failed invasion.

It follows that permanent alteration of the resident species would relieve the competitive stress upon the invader, and would heighten the probability of its survival for a longer period. This, in turn, would increase the pressures upon the resident, probably increasing the magnitude of the alteration of the resident, and heighten the competitive efficiency of the invader so that at some point a permanent invader colony might be established.

Once effectively continuous contact was established, character modification (character displacement) would proceed exactly as it is expected to occur upon continents. But important here for the island story are (1) the effects of even failed invasions, (2) the existence of a critical invasion frequency, and (3) the depen-
dence of this critical invasion frequency upon a critical distance.

Consider now the presence of an invader species on one newly emergent element of an island bank which already has a resident on another more permanently raised portion of the same bank. The timing of such an event is critical, since the resident should have by far the greater chance to colonize islands of its own bank. But other factors may favor the invader: currents which favor one direction above another; a decay of colonizing ability in the resident, which is now closely adapted to local conditions; etc. In any event, if the two species do become established on one bank, the coadaptation of the species follows inevitably. Once adjustment has been achieved on one island (e.g., by the colonization-prone species becoming changed in size, as in the case of A. wattsii, of the northern Lesser Antilles), this species is then preadapted to invade other islands (as wattsii has, in fact, done).

This hypothesis remains vague in its details and is a priori clearer for the complex banks of the northern Lesser Antilles than for the St. Vincent-Grenada banks in the southern islands. In the latter case, Gorman (1969) seems to have clearly shown that the distribution of biochemical and other characters seems to require a double invasion of St. Vincent from St. Lucia. St. Vincent itself has too simple a bank and is too far from St. Lucia to be in accord with the hypothesis outlined above. Only if we involve in some way the Grenadines of the Grenada Bank do we introduce the needed complexity. At the moment it does not seem possible to work out this conundrum in a satisfactory way. It needs to be pointed out, however, that it is on this St. Vincent-Grenada complex of two banks (Fig. 16), so nearly contiguous as to be almost one, that, according to Gorman (1969), the major evolutionary changes within the roquet group of the southern Lesser Antilles have taken place — in size, in climatic adaptation, in chromosomes, and in biochemistry.

The fact that in both the northern and southern Lesser Antilles double invasion has occurred only on banks (or pairs of banks) that are complex is what we have attempted to explain here. The obverse is that in all the Lesser Antilles the simple banks — Saba, Redonda, Montserrat, Dominica, Martinique, St. Lucia, and Barbados (let us include here unconventionally St. Croix) — have all resisted a second invasion. Some of them, namely, Martinique and Dominica, are of moderate size and display considerable ecological diversity. Neither small size nor ecological uniformity will explain the failure of a second invader to have achieved a foothold. The examples are a bit too numerous to permit a facile explanation by coincidence.

There is one Lesser Antillean island complex still unmentioned: the Guadeloupean archipelago. Here we have the double island of Guadeloupe itself, and on the same bank with it, in addition to some tiny islets, Desirade. Very close indeed, but apparently separated by some deep water, are the twin islands of Les Saintes. Not quite as close is Marie Galante, on its own bank. This is a true microarchipelago (Fig 17).

The puzzle in the Guadeloupean archipelago is the size of the anole on Marie Galante, cur-
rently called *A. marmoratus ferreus* Cope. It is larger than any other anole living alone on an island. This seemed no anomaly until quite recently, since a second anole (*A. speciosus* Garman) was reported from the island, and Garman has recorded the two species (*ferreus* as the synonym *asper* Garman) from the island on the faith of the same collector, W. B. Richardson. Recent collectors (Lazell, 1964a; Schwartz, pers. commun.) have taken only *ferreus*. Lazell (1964a) has also presented evidence that appeared to imply that *ferreus* was not specifically distinct from the other anoles of the Guadeloupe archipelago, and that in fact *ferreus* was connected to the anoles of Guadeloupe proper by intermediate populations on islands to the northeast (*A. marmoratus chrysops* and *A. m. desiradei*). *A. speciosus* Garman was further identified by Lazell with a population on Grand Terre, the northeast portion of the double island of Guadeloupe, and the locality of Marie Galante given by Garman for *speciosus* was regarded by Lazell as erroneous.

A possibility not expressly considered by Lazell (but implicitly discarded through his affirmation of conspecific status for *speciosus* and *ferreus*) is that of a former population of *speciosus* on Marie Galante, or of a failed invasion, as implied in the hypothesis elaborated above. The great size of *ferreus* and the striking development of tail crest in adult males are readily explainable if at any time it has been in contact and competition with another species; they are not readily explainable, however, in a rassenkreis of intergrading populations (Fig. 17). In no other case among anoles does size vary intraspecifically in so radical and unexpected a fashion. In particular this phenomenon is unique in anoles of one-anole islands. Schoener (in press) has convincing evidence that the anoles of one-anole islands convergently approximate an optimal moderate size. Lazell’s decision to regard *ferreus* of Marie Galante as conspecific with *marmoratus* of Guadeloupe, Desirade, and Les Saintes will therefore bear reexamination. It may be more reasonable to see in *ferreus* an example of the “nudge” effect which we postulate to occur when each of a pair of related full species has a refugium of its own that is geographically so close to the other that contact has an evolutionary effect on both species.

A LAST WORD: COLONIZERS AND CONTINENTS

The heavy emphasis of this paper has fallen on the difficulty of establishment — the initial hazards faced by founder individuals or populations. We have only casually and incidentally alluded to the subsequent history of such populations once they have achieved a safe population size by finding a physical or ecological refugium.

In the initial phase of colonization it should make little difference whether the invasion is of a small island or of a continent — the essential question is: can physical or ecological space be found which will permit establishment? If the answer is no, exclusion has occurred. If the answer is yes, what will happen later is another story, and one that is at a very different and more complex ecological level. One of the things that very probably may happen is that “ecological release” may be reversed and that species may instead face “ecological compression” (MacArthur and Wilson, 1967). Without so naming it, we have inferred that this has occurred on many of the Lesser Antillean islands. As for the continent, the most suggestive evidence has been furnished by Wayne King (in mss.) who has observed that mainland *A. carolinensis*, which generally occupies both sun and shade, appears whenever it is in contact
with long-established colonies of *A. distichus* in Florida to be restricted in its ecology to the sunnier areas of shrubs and open ground, and to avoid the well-shaded trees in which *distichus* has its home.

The interaction of species on large islands and on continents, where space and complex ecology permit complex interaction, should of course go far beyond this simple reversal of ecological release. Biotic pressures when complex will compel specialization, may compel diversity, and may create very strange and unexpected specialists. We shall elsewhere describe and trace the history of just such specialists on the four Greater Antillean islands. On these islands (which I infer to have been largely unentained by lizards when anoles arrived) the anoline lizards were on their own and found first open space and then biotic pressure, which was almost wholly that of the congeners.

The best of the colonizers here described — *A. carolinensis* — has indeed been able to invade and establish itself on a continent and to colonize it widely, but it has not diversified. Why not? Most probably because it is held within relatively narrow limits by biotic pressures, but in this case not those of congeners. *A. carolinensis* was able to find vacant ecological space. Nothing very much like it existed on the North American mainland when it came. But to diversify, it would have needed the physiographic or ecological barriers that promote speciation and also would have had to find still unutilized ecological space. It has not found these on the North American continent. Ecological space is clearly more closely packed in the continental area, but we do not see too clearly what it is that restricts *carolinensis*.

**SUMMARY: METHODS AND RESULTS**

This paper has tried stubbornly to derive all its statements from an empirical base. The data and the methods used are simple indeed. We have considered island size and island distance, have taken into account some very elementary data on ocean currents, and have added the available information on one group of animals, their distribution, their phyletic relationships, and their most basic ecology.

We have presented these data for a set of especially simple cases — small, recent, distant islands. From this examination we have emerged with conclusions about the nature of colonizing species and about the principles of exclusion and coexistence. These conclusions, though derived from a single group, are stated below in terms of greater generality. The justice of such generalizations will, of course, require testing.

1. Effective colonizers are at any given time a small fraction of existing species. (In the Greater Antilles 6 of 56 species have colonized the recently available small islands.)

2. Colonizing species tend to be repeated colonizers. (The 6 Greater Antillean colonizers have colonized 23 separate banks.)

3. Colonizing species are neither primitive species nor extreme specialists; their primary quality is versatility, i.e., they are physiologically and ecologically tolerant of many conditions, and require few. They appear to be creatures of the ecotone — the "edge" between ecologies — and resemble "fugitive species" in their ability to seize upon temporarily open habitats. They apparently differ from fugitive species in their powers of persistence, perhaps because their ecological tolerance permits rapid adaptation to local conditions.

4. There appears to be some critical island size below which a colonizing species may exclude every other congener. (In anoles it is clear that this critical size is relatively large. Great Inagua, the Caicos Bank, and the Little Bahama Bank are of very substantial dimensions.)

5. "Ecological release" is a demonstrable phenomenon and, given an island below the critical size, is the effective agent in exclusion. (*A. conspersus* and *A. scriptus* both show "release" and both exclude other *Anolis* species from large islands that are quite close to rich major source islands.)

6. Coexistence of colonists is possible if the colonizing species have been preadapted in sympathy on more complex source islands and if, arriving nearly synchronously, they maintain essentially the same ecological relationships they had on the source islands. (*A. carolinensis, A. angusticeps,* and *A. sagrei* were preadapted because of coadaptation on the source island; *A. distichus* was preadapted because its speciali-
zations happened to coincide with an available vacant niche.)

(7) Coexistence may be evolved in situ in the special circumstances of complex geography, including complex island banks (A. wattsi in the northern Lesser Antilles; A. richardi in the southern).

(8) Certain species may have been modified by failed invasions (e.g., A. ferreus on Marie Galante).

(9) Even on small islands the phenomena of exclusion and coexistence appear to be relatively stable, once achieved. The resulting stable equilibrium will most probably be changed only by significant environmental change (e.g., change of climate, change of area by rise or fall of sea level, change of surface relief, and such) or if a new invader is able to insinuate itself into some unutilized aspect of the available ecological space.

(10) Exclusion is an extremely common phenomenon but one of low visibility. Coexistence is a less frequent but highly visible phenomenon.

These conclusions are not wholly new. Such general works as MacArthur and Wilson (1967) and Baker and Stebbins (1965) contain much that will instantly be recognized as consonant with these conclusions, as well as some dissonant concepts. I do not attempt to review them in depth here. It is too early to do so. The ecology of colonization is a nascent field in which much in both data and theory are still largely crude. Nevertheless, a few of the most striking points of difference between recent theories of island colonization and the generalizations derived from anoline lizards may be mentioned.

(a) The Anolis evidence suggests that island species are not necessarily competitively inferior, as Darlington (1957) has implied. As we have seen, recently emergent islands, open to colonization de novo, even when very close to continents, have been occupied by island endemics rather than by adjacent mainland species: carolinensis and sagrei are the most aggressive of the colonizers that have spread outward from the islands toward or onto the mainland.

(b) Contrary to Carquist's (1966) expectation, the successful colonizations by lizards of distant islands are rare single events. Lizards are rafted, the chance of rafting to distant islands is very low, and the chance of multiple rafting is far lower. Much of the difference between the zoogeography of lizards and other rafter animals, on the one hand, and those that fly or are blown, on the other, must depend upon this fact of rare colonization. Exclusion depends upon the time interval between colonizations.

(c) Island size has not the simple relation to faunal size that has sometimes been postulated. Utilizing in somewhat different fashion the same evidence that has been presented here, Rand (1969) has made the point very clear. It is of course quite certain that there are effects of island size—e.g., complex faunas exist only on large islands. Among the West Indian islands inhabited by anolines, however, "small" may mean 560 square miles. In such cases, a simple relationship between faunal complexity and island size is no longer clear.

The fauna of small islands on the same bank as a large island does correlate rather closely with size, as Rand has shown. It does so by extinction of part of a rich fauna. On islands never connected to other islands, however, the facts of importance are likely to be "ecological release" and "exclusion," and these are independent of island size, up to a point. The phenomena occurring on the two sorts of islands are very distinct. One is erosion of an already existing diversity by reduction of extent and variety of habitats. The other is the interruption of the build-up of diversity by evolution of broad adaptations in a small fauna. It is not surprising that a single formulation cannot deal plausibly with both.

(d) Turnover, i.e. extinction on islands, does not appear for lizards to be so automatic or so regular a process as MacArthur and Wilson (1963, 1967) or Mayr (1965b) have postulated it to be for birds and insects. Here the mode of colonization may be important for interpretation of the data.

For birds and insects the difficulties of arrival appear to be less than for lizards, and the possibility of temporary establishment far greater. Hence the visibility of the sequence—arrival, limited time of survival, eventual replacement—is high; consequently, cases of such temporary colonization and replacement are well documented (MacArthur and Wilson, 1963, 1967).
No comparable documentation exists for lizards. Extinction of unsuccessful colonists must ordinarily occur, quite invisibly and before they have left any record, on the beaches of the invaded islands. In these terms, the difference may be a matter of documentation only. From this point of view, I would not want at all to deny the importance of extinction for lizards. In fact, exclusion, which we have repeatedly shown to occur, might in MacArthur and Wilson's terms be described as a phenomenon that maximizes the extinction rate of late-arriving propagules.

For the phenomenon of replacement, however, the difference between birds and insects, on the one hand, and Anolis and other rafted animals, on the other, may be very real. Replacement is not only not documented for lizards, it is not even theoretically very probable. Most established Anolis species appear to be in the situation described by MacArthur and Wilson (1967, p. 77): population size near carrying capacity; time to extinction, very long.

I disregard here competitive extinction, i.e., extinction by the direct competition of a superior competitor in the same niche. I do so because this again is not documented for Anolis. We have seen above the contact of sagrei and brown lineatopus in Jamaica, where what seems to have happened, at least for a short period, is a mutual accommodation, a subdivision of available ecological space, and not replacement.

I emphasize again the strong empirical bias of this paper. MacArthur and Wilson (1967) have in erecting an extraordinarily interesting superstructure of theory lamented the lack of more and better empirical data to test all theories. I have tried to provide some of the needed data.

The merit claimed here (and the weakness here recognized) is that of a "close" rather than a "distant" view—the intimate analysis of information concerning a single group of lizards on one archipelago. Even so, I have thus far utilized only a small part of the available information. The whole phenomenon of intra-island radiation on large islands requires fuller discussion, as does the interplay of random and non-random forces in the inferred history of the group. A future paper is planned to deal with these phenomena.

A final caveat: this paper has taken as a primary datum changes in sea level in the near past which have first submerged small islands and then raised them again for new colonization. Such changes affected much more than small islands. We need to remember that all present distributions and faunal numbers surely reflect the disturbed conditions of the Pleistocene. The present is barely 10,000 years post-Pleistocene and that period was a special period of earth history with especially rapid changes of sea level and of climate (and hence of island size and of vegetational belts). It will not do to suppose that turnover or any sort of faunal change in the tropics or in any other part of the world was uninfluenced by the changes of this period. Even the classic tropical rain forests must now be admitted to have been gravely affected (Moreau, 1966; Haffer, 1969). Until proper account is taken of the Pleistocene and its consequences, all discussions of island diversity, extinction, and related phenomena in this latest period of geological time will lack in realism.

ACKNOWLEDGMENTS

The study of Anolis has been for some years the preoccupation of a privileged few. A great deal of information has long been the private possession of this special group. Discussion and the interchange of ideas has been constant and vigorous within a narrow circle, and it is now no longer possible for any one of us to give full credit where credit is due. It must suffice to list the names of these consultants, collaborators, and coworkers in alphabetical order: R. Etheridge, G. Gorman, A. S. Rand, R. Ruibal, T. Schoener, and P. Vanzolini.

Outside this circle many have assisted in the field, in museums, and in individual discussion. Their help does not go unappreciated although it must go unrecorded, since there are literally too many to mention.

An early version of this paper was read by G. Simpson, E. Mayr, E. O. Wilson, R. MacArthur, R. Levins, H. Heatwole, H. Horn, R. Ruibal, R. Etheridge, B. Patterson, T. Frazzetta, and M. Willson. Much of the final version has been read by T. Schoener and B. Patterson. R. Trivers and J. Gilmartin have made suggestions.

This paper and the investigations on which it is based have been supported by Grant GB-6944 and previous grants from the National Science Foundation.
LIST OF LITERATURE


Hardy, J. D., Jr. 1966. Geographic variation in the West Indian lizard Anolis angusticeps with


