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BIOGEOGRAPHY OF THE PUERTO RICAN BANK

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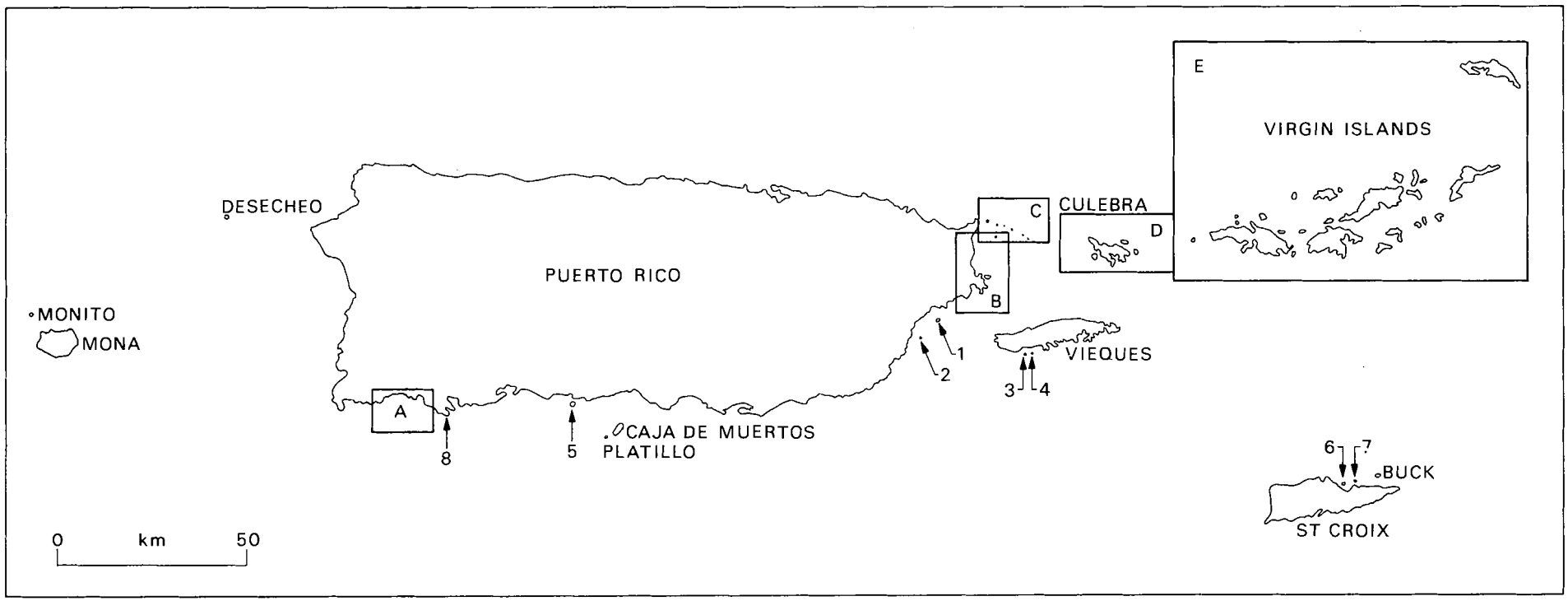

Fig. 1. Map of the Puerto Rican Island Shelf. Rectangles A - E indicate boundaries of maps presented in more detail in Appendix I. 1. Cayo Santiago, 2. Cayo Batata, 3. Cayo de Afuera, 4. Cayo de Tierra, 5. Cardona Key, 6. Protestant Key, 7. Green Key (St. Croix), 8. Caña Azul

ATOLL RESEARCH BULLETIN 251

ERRATUM

The following caption should be inserted for figure 7:

Fig. 7. Temperature in and near a small clump of vegetation on Cayo Ahogado. Dots: 5 cm deep in soil under clump. Circles: 1 cm deep in soil under clump. Triangles: Soil surface under clump. Squares: Surface of vegetation. X's: Air at center of clump. Broken line indicates intervals of more than one hour between measurements.

BIOGEOGRAPHY OF THE PUERTO RICAN BANK

by Harold Heatwole[1], Richard Levins[2] and Michael D. Byer[3]

INTRODUCTION

There has been a recent surge of interest in the biogeography of archipelagoes owing to a reinterpretation of classical concepts of evolution of insular populations, factors controlling numbers of species on islands, and the dynamics of inter-island dispersal. The literature on these subjects is rapidly accumulating; general reviews are presented by Mayr (1963), and Baker and Stebbins (1965). Carlquist (1965, 1974), Preston (1962 a, b), MacArthur and Wilson (1963, 1967), MacArthur *et al.* (1973), Hamilton and Rubinoff (1963, 1967), Hamilton *et al.* (1963), Crowell (1964), Johnson (1975), Whitehead and Jones (1969), Simberloff (1969, 1970), Simberloff and Wilson (1969), Wilson and Taylor (1967), Carson (1970), Heatwole and Levins (1973), Abbott (1974), Johnson and Raven (1973) and Lynch and Johnson (1974), have provided major impetuses through theoretical and/or general papers on numbers of species on islands and the dynamics of insular biogeography and evolution. Other work has dealt with specific problems such as dispersal (Gressitt and Yoshimoto 1963, Carlquist 1966 a-c, 1967, Heatwole and Levins 1972b), interspecific competition (Grant 1965, 1966, 1968, Crowell 1962, 1968, Sheppard *et al.* 1968), effect of disasters (Brattstrom 1963, Sauer 1962), trophic relations (Heatwole 1971, Heatwole and Levins 1972a), colonization (Bassot and Ball 1971, Hunt and Hunt 1974, Becker 1975, Schoener 1975 and Williams 1969), and endemism (Mayr 1965, Heatwole and MacKenzie

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1967, Thornton 1967). In addition there have been a large number of studies treating the distribution and variation of specific groups of organisms on islands and the role of historical factors upon such patterns. With this broadening base of theoretical background and accumulation of information on specific aspects, the first two authors felt it opportune to carry out a comprehensive study of an archipelago containing many islands with a variety of sizes, inter-island distances, topography, vegetation, time of separation, use by humans, and other characteristics, and to study as many aspects of the biogeography of as wide a range of organisms as feasible. Our aim was to look at the subject as a whole and thereby contribute toward a synthetic understanding of the broad aspects of the problem. The original design of the project was presented in an early paper (Levins and Heatwole 1963) and some of the data have been used in general reviews (Levins 1968, 1969, Heatwole 1976a). This paper presents the geography, vegetation, and ecological characteristics of the Puerto Rican Bank and constitutes a background for the rest of the series (some of which have already been published, e.g. Heatwole and Levins 1972b, 1973, Levins and Heatwole 1973, Levins *et al.* 1973), and for papers by a variety of specialists using the material we collected during our study.

GENERAL DESCRIPTION OF THE REGION AND ITS CLIMATE

The area studied consists of all the islands and cays in the part of the Antillean chain making up the political units of Puerto Rico, the American Virgin Islands, and the British Virgin Islands, sometimes referred to as "Greater Puerto Rico" (Thomas and Schwartz 1966). This includes all land masses between latitudes 17° 40' N and 18° 45' N and stretching from the island of Monito (longitude 67° 57' W) to Anegada (longitude 64° 16' W). There are 243 islands and cays in this area (not including those emergent ones periodically washed over by tides and lacking terrestrial vegetation). Of these we surveyed 141, including all of the larger ones. Figure 1 shows a map of the general region and appendix I provides detailed ones of selected areas containing the small cays which were studied. Where possible we followed the official names for islands as listed by the U.S. Department of Commerce, Coast and Geodetic Survey (1962). When no official name could be found, we used names supplied by local fishermen. In cases of nomenclatural disputes among local authorities, we simply chose one of the alternatives. Sometimes we were unable to obtain any name at all and have named islands ourselves.

The climate of the area is tropical and slightly modified by altitude on the larger islands. Rainfall on Puerto Rico is geographically variable, greater in the central mountains than on the coastal plain. In addition, there is a general east-west difference. On the Luquillo Mountains at the northeastern tip of the island, rainfall may exceed 5,080 mm (200 inches) annually; the southwestern lowlands receive less than 750 mm (30 inches) annually (Picó 1954 and see Fig. 2).

The principal Virgin Islands are similar in rainfall to the coastal areas of Puerto Rico; smaller, or more isolated islands represented by Culebra, Vieques, and Mona in figure 2, are more xeric. Mona is drier than its rainfall would suggest, as it is honeycombed with limestone caverns which rapidly drain off surface water.

Temperatures are remarkably uniform seasonally and from year to year in a given locality (Figs. 3, 4). However, on Puerto Rico, temperature follows east-west and altitudinal trends. Guineo Reservoir (elevation 1,000 m) has lower temperatures than Rio Piedras (elevation 15 m) on the northeastern coast. Rio Piedras is in turn cooler than Magueyes Island (10 m) which is representative of the southwestern coast (Fig. 4). The isotherm for mean annual temperatures of 24° C separates the coastal plain and some valleys (below 150 m elevation and where mean annual values exceeding 26° may occur) from the mountains where mean annual values below 20° C are encountered in the highest parts; the highest temperature ever recorded for the island was 39.5° C, the lowest 5° C (Picó 1954). The hotter coastal areas of southwest Puerto Rico have temperatures similar to those of the principal Virgin Islands (Fig. 4).

Very few meteorological data are available for small cays, though it can be said that most are warm and dry. Figure 3 presents data for Magueyes Island. However, this island is so close to Puerto Rico that it is representative of conditions of coastal southwest Puerto Rico rather than that of more isolated islands. Table 1 gives the average conditions on Cayo Ahogado, a small, nearly barren sandy cay about 1 km east of Puerto Rico, during several days in March, 1966. Figures 5-7 show the details of the daily regimen for the two most extreme days, March 10 which was bright and sunny, and March 19 which was heavily overcast with occasional fine rain. The hottest environment on the cay was the soil surface where midday temperatures exceeded 38° C. At 1 cm and 5 cm below the soil surface, temperatures decreased somewhat but even there reached 30° C or above on hot days. Air temperatures near the ground reached 32° C on warm days, temperature decreased with height above ground. However, except for a few flying forms which experience above-ground temperatures, most inhabitants of small cays are exposed to the thermal conditions near the ground. The low vegetation on Cayo Ahogado ameliorates temperatures somewhat (Fig. 7), although on hot days air temperatures near the surface of small clumps of plants reach 32 - 33° C. Surface temperatures of leaves were several degrees lower, presumably because of transpiration. Temperature 1 cm down in the soil was as much as 2° C cooler under vegetation than in the open. At 5 cm depth the difference was as much as 4° C. Although the plants were small and sparsely distributed, and hence did not greatly affect environmental temperatures, the few degrees of difference they caused were in a range that may reduce the insolation directly reaching small animals. The effect of unobstructed radiant energy can be seen from the high black bulb (T_{BB}) temperatures (Fig. 5).

The nearly bare, rocky cays probably have even more extreme conditions than Cayo Ahogado, more heavily vegetated ones are probably

more moderate.

The prevailing winds are from the northeast and apparently have been so at least back into the Pleistocene (Kaye 1959). Marine currents are east to west, although a northward current exists between Mona and Puerto Rico, and there is a northward deflection between Vieques and Puerto Rico (Kaye 1959).

Hurricanes usually travel in a general east to west direction.

VEGETATION

The Puerto Rican and Virgin Island flora has been most recently summarized by Britton and Wilson (1923-30) and by Little and Wadsworth (1964). Ecological treatments of a broad nature have been presented by Gleason and Cook (1927), Cook and Gleason (1928) and Dansereau (1966). Only a few articles have dealt with the plants on the small islands (e.g. Britton 1924, 1933 on Hicacos and Culebra, Heatwole *et al.* 1963 on Cayo Santiago and Cayo Batata, and D'Arcy 1971, 1975 on Anegada). Our records are presented in Appendix II.

Analysis of the vegetation of the islands treated here would be a major project in itself and was not possible within the scope of the present investigation. However, broad vegetation types could be recognized and were grouped on a physiognomic basis into 12 categories, most of which include more than one association, or at least varied somewhat in floristic composition from place to place. The classification is not intended to be phytosociological, but rather a useful description of the type and diversity of available structural habitats for animals. The spatial relationships of the categories to one another and to several major environmental parameters are clarified in Figs. 8 and 9. The categories are as follows:

1. Lack of Vegetation. Extensive areas of bare rock or sand, usually coastal, though occurring locally further inland.

2. Succulent Beach Vegetation. Often nearly pure stands of low, succulent, halophytic herbs. *Sesuvium portulacastrum* and *Philoxeris vermicularis*, usually under 30 cm in height, occur alone or in combination on relatively undisturbed gravelly or sandy beaches[1]. These two species plus *Batis maritima* and *Salicornia perennis* form various combinations after the elimination of mangrove (8), or in otherwise intermittently-flooded, shallow, saline coastal depressions. *Batis* may reach 70 cm in height.

3. Mixed Beach Vegetation. A variable mixture of herbs (*Cakile lanceolata*), small suffrutescents (*Euphorbia buxifolia*), rhizomaceous

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[1] Nomenclature follows Britton and Wilson (1923-30).

grasses (*Sporobolus virginicus, Spartina patens*) and creeping vines (*Ipomoea pes-caprae, Canavalia maritima, Vigna marina*), sometimes with *Sesuvium portulacastrum*. Vegetation usually less than 1 m tall, with low cover. On sand, gravel, or crevices in coastal shelf limestone, fairly resistant to disturbance, and recovers rapidly.

4. Beach Shrubs. Small, scattered shrubs intermixed with herbs and grasses, occasionally containing a high proportion of vines which form a nearly continuous mat. Height usually 1-2 m, found inland from the previous type. Common species are *Suriana maritima, Tournefortia gnaphalodes,* and *Thespesia populnea*, with the species characteristic of the previous type (3) as ground cover. Fairly resistant to disturbance.

5. Graminoid. Stands having the graminoid life form dominant, whether composed of true grasses or of sedges. Usually also contains a number of forbs. Usually 1 m or less high, though taller stands are sometimes found. Found in the interior of intermediate-sized and larger islands. Always a disclimax or successional stage in the climatic zone studied (Richards 1957), maintained by grazing, fire, or periodic cutting or mowing. Various graminoid species cover the full range of moisture and edaphic conditions found in the study region.

6. Scrub. Shrubs of various types, cactus, and vines, frequently intermixed with herbs and grasses. Varies from less than 50% to 100% cover, easily penetrable to impenetrable, and less than 1 m to over 2 m, occasionally higher. Frequent dominants are *Croton astroites, C. rigidus* (both replaced by *C. discolor* in Anegada), *Lantana involucrata, Anthacanthus spinosus,* and *Pithecellobium unguiscati*. A disclimax maintained by overgrazing and overbrowsing, primarily by feral goats, in the interior of intermediate-sized, drier islands and on the leeward (rain-shadow) sides of the largest islands. Shrub stages in the zone where moist forest (10) is climax are successional and consist of more mesomorphic species, often seedlings and saplings of larger, secondary forest trees.

7. Coastal Groves. Stands of small trees or shrubs, inland from (4), ranging from nearly prostrate and less than 1 m in height on windswept coasts and dunes, to 4 m or more in protected sites. Usually provide dense shade with a heavy accumulation of leaf litter. Frequently pure stands of *Coccoloba uvifera* or *Hippomane mancinella,* or mixtures of several to many species; *Elaeodendron xylocarpum, Erithalis fruticosa, Conocarpus erecta,* and the tree-cactus *Opuntia rubescens* are prominent.

8. Mangroves. Stands of mangrove ranging from scattered saplings about 1 m in height to forests over 10 m, providing rather deep shade, in permanently- or intermittently-flooded depressions behind coasts, and along coasts and on old reefs etc. which are sheltered from wave action. *Rhizophora mangle, Avicennia nitida, Laguncularia racemosa* and *Conocarpus erecta,* either as single-species stands or in various combinations.

9. Xeric Forest. Deciduous, open forest, frequently with sparse understory of cactus, thorny shrubs, vines, and annual grasses. Height usually over 8 m. Interior of intermediate-sized islands and leeward (rain-shadow) sides of largest islands. May be absent on the windward (humid) sides of the latter, where mesic forest (10) lies adjacent to coastal formations, except where local edaphic-topographic conditions permit xeric forest. Probably includes Dansereau's (1966) category of Semi-deciduous Forest and Little and Wadsworth's (1964) Dry Coastal and Dry Limestone forests. Dominant trees variable from place to place; *Pisonia subcordata, Torrubia fragrans, Bursera simarouba, Citharexylum fruticosum, Tabebuia heterophylla,* and the giant cactus *Cephalocereus royeni* are representative.

10. Mesic Forest. Includes a variety of moister, altitudinally-zoned types including those called Moist-coastal, Moist Limestone, Lower and Upper Cordillera, and Lower and Upper Luquillo Forest by Little and Wadsworth (1964), and Lowland Rain Forest, Lower Montane Rain Forest, Montane Forest and Montane Scrub by Dansereau (1966). Physiognomy and floristics are variable (see Beard 1944, Richards 1957). Such a variety is included under one heading since in the region studied, these forests occur only on the largest islands, some types only on Puerto Rico. Finer distinctions would be unnecessary for our purposes.

11. Coconut Groves. Usually planted by man in flat, sandy coastal areas. Light shade, understory usually composed of species of the mixed beach vegetation (3) and variable.

12. Other. Any vegetation not fitting any of the above categories, e.g. crops, ruderals, dooryards, or vegetation of other highly modified areas.

During the survey of a particular island, the vegetation types were recorded, and where feasible, the percentage of the island covered by each one estimated and a rough sketch-map drawn. When only a few individual plants were present on an island, complete censuses were made. In some instances, vegetational reconnaissances were made.

The results are presented in Table 2. By way of summary it can be stated that Puerto Rico contains all the vegetation types outlined (1 - 12). Culebra and Vieques have xeric to mesic forests (9, 10); Mona, Caja de Muertos and Desecheo support xeric forest, all five have a variety of the simplest types (1 - 8). Monito has predominantly scrub (6). The small cays near the southern and southwestern coast of Puerto Rico are mostly mangrove islands (8); those further offshore tend to be sandy and nearly bare (1) or with succulents (2) mixed beach vegetation (3), or beach shrubs (4).

The group of cays extending toward Culebra from northeastern Puerto Rico are mostly steep-sided, limestone or cemented sand dunes, although a few low sandy islands also occur. Most support scrub (6),

succulent or mixed beach vegetation (2,3), although the larger ones have shrubs (4) and occasionally trees. The cays south of this chain (east of Puerto Rico) and around Culebra Island are variable, most being either rocky with a beach, or sandy. The larger ones support xeric forest (9), the smaller ones only succulent or mixed beach vegetation (2,3) or scrub (6).

The Virgin Islands, St. John, Tortola and St. Croix have mesic forest plus all other categories (1 - 12). The other principal islands except Anegada, as well as a few somewhat smaller ones such as Guana, Greater Caminoe, Peter, Norman, and Greater Thatch have xeric forest. The remaining cays and small islands plus Anegada are variable. However, few support vegetation more lush than scrub (6), or at most limited areas of xeric forest (9). The available climate and soil data, corroborated by conversation with older inhabitants, indicate that at one time forest was more extensive on both the larger and the smaller islands. Apparently it has been decimated by charcoal burners, cultivators, and feral animals, a widespread phenomenon throughout the Caribbean as indeed in the tropics generally.

GEOLOGY

Rosen (1975) has reviewed the previous history of the Caribbean. Although there is not unanimity among authorities on the topic, he felt that the most reasonable synthesis of the geologic and biogeographic data was the following sequence of events. In the late Mesozoic when South America was separating from Africa, a subduction zone consuming the eastern Pacific sea floor bordered the western coast of both North and South America and the area between them, the latter consisting of a volcanic archipelago, the Proto-Antilles. Subsequently, separate North and South American plates arose by the formation of two decoupling faults on either side of the Proto-Antilles. With the continued relative westward drift of the North American and South American plates, the Proto-Antillean region became displaced eastward towards its present relative position; a new fault zone occurred which separated the Proto-Antilles into two subregions which subsequently became the Greater Antilles and Lesser Antilles. With the continued westward movement of the major American continents, further faulting occurred breaking up the Central American region into an archipelago which subsequently joined to form the present day isthmus; the Caribbean islands aligned themselves into their present relative positions.

If this model is correct, the Greater Antilles have been an archipelago for a long time, contrary to previous opinion that the major Antillean islands were broadly connected (Schuchert 1935). Connections between adjacent banks were rare, the Puerto Rican one never having been connected to the nearest one to the east (St. Maarten) (Butterlin 1956). If it was ever connected to Hispaniola, it lost the connection in the Pliocene or earlier (Mitchell 1954).

The Puerto Rican Bank (Puerto Rico, its outlying islands, the American and British Virgin Islands) resulted from vulcanization in the Cretaceous (Meyerhoff 1933) and became emergent during orogenic movements in the late Eocene (Butterlin 1956). In contrast to the paucity of connections between banks, connections of islands within the Puerto Rican Bank have been extensive and recent. Heatwole and MacKenzie (1967) have shown that the principal islands of the Virgin group (except St. Croix) lost their connection with each other and with Puerto Rico only about 8,000-10,000 years ago, due to eustatic rise in sea level. Culebra lost its connection with Puerto Rico and the Virgins at the same time, although Vieques, Caja de Muertos, and many small cays remained connected to Puerto Rico until about 6,000 years ago. The smaller islands around the principal Virgins were separated from the latter at various times before 8,000-10,000 B.P.

By contrast, Mona, Monito, Desecheo and St. Croix have been isolated much longer, not having been connected to any other islands since at least the Pliocene, if then.

A number of islands were present at various times which have since submerged.

ISLAND AND COASTLINE FORMS

The larger islands are of volcanic origin and consist mainly of igneous and metamorphic rock with quite steep topography. Puerto Rico has, in addition, an extensive northern and a smaller southern strip of cenozoic limestone which has been extensively eroded, giving rise to characteristic low, blocky, vertical-sided hills with many caves. Mona, Monito and the higher islands to the northeast of Puerto Rico are of similar origin, while Anegada is a low, flat limestone shelf, contrasting markedly with all the other islands of the Puerto Rican bank save for a few small cays.

Form of the smaller islands varies considerably, and ranges from low, sandy cays with gently sloping beaches to mushroom-shaped ones surrounded by vertical cliffs undercut at the base by wave action. Many islands have a great proportion of the coastline made up of rock which is neither vertical cliff, nor beach. We termed this "intermediate type". A final coastline type consisted of mangrove swamp. Most large islands have several coastline types, including beach, undercut cliffs, and intermediate type.

METHOD OF SURVEY

Each island surveyed was described as to its vegetation (see above), geological type, soil, presence or absence of standing water, maximum height, area, nature of shoreline, and proportion of each type of coast, proportion surrounded by barrier reef, distance to nearest other land-mass on the Puerto Rican shelf in each of 4 quadrants, degree of

disturbance by humans and time of isolation from other land masses.

Proportions of various shoreline types were obtained by measuring the perimeter on a map or aerial photograph with a Radix map measurer, keeping values for each coastline type separate in accordance with observations made while on the island. Percentages of each type were then calculated. Island areas were obtained either from the literature, from maps using a planimeter, or by direct measurement. Maximum height was obtained from topographic maps, or in the case of small cays by direct estimation or measurement. The other information was obtained by direct observation supplemented by maps, aerial photographs, nautical charts, conversations with inhabitants of various islands, and the literature.

On every island visited, each of the above-defined vegetation categories which was present was searched for the following group of animals; terrestrial isopods, centipedes, millipedes, pseudoscorpions, amblypigids (= phrynichids or tailless whip scorpions), scorpions, spiders, ants, *Drosophila*, land snails, amphibians and reptiles; other groups provided supplementary information on certain aspects. We were opportunistic in that ease of sampling and the probability of obtaining adequate samples in a relatively short time was a consideration in our choice of groups. However, the animal groups we used were chosen to include both eurytopic and stenotopic forms, those with weak and those with strong dispersal powers, and groups with a wide range of suspected evolutionary rates. Specialists in various groups identified (or are in the process of identifying) our material and advised on techniques which would provide as complete a representation of an island's fauna as possible. These methods included use of (1) Tullgren funnel extraction of litter samples transported to the laboratory in plastic bags, (2) sweeping vegetation with an insect net, (3) beating vegetation over a white sheet, (4) examining litter on a white sheet, (5) setting out bait (mixed fruits for *Drosophila*, sugar and tuna for ants, etc.), (6) shooting or noosing (reptiles), (7) careful search of the surface of the ground and vegetation and under rocks and other objects, and (8) breaking open twigs, old termite nests, logs, and other debris.

All data were stored on computer cards. Statistical treatment is discussed later in appropriate papers, as are other special methods used for individual parts of the project. Biogeographic and taxonomic treatments will be published by the various specialists that have received material. The appendices list the results for some groups for which a number of identifications are now available.

SPECIAL NOTES

The island of Sail Rock (Appendix I) requires special mention. It is a mass of rock rising 38 m (125 ft) precipitously out of the sea. It is about 100 m in diameter. The cliffs around it are vertical or nearly vertical and are undercut at the base. It is unusual in that

it completely lacks terrestrial vascular plants and hence no local autotrophic energy base for the surprisingly large number of terrestrial animals. Indeed, the only terrestrial plants observed at all was a green alga in one crevice on the north side. A few individuals of a marine plants, *Sargassum*, collected by sea birds or material was present but did not appear to have any terrestrial animals associated with it or feeding upon it.

We visited the island in May 1966, scaled the cliffs and made an intensive search for organisms on the top.

Numerous cracks and crevices occur in the rock on top, and on the few flat, or nearly flat areas, there are some loose boulders and stones. From these places we collected species of terrestrial vertebrates and one vertebrate (a gekkonid lizard, *Sphaerodactylus macrolepis macrolepis*); many of the species were quite abundant. By far the most abundant arthropod present was a terrestrial isopod. It occurred in surprisingly dense populations and probably served as the basis for much of the rest of the terrestrial food chain which consisted largely of predators, there was 1 species each of centipede, tailless whip scorpion (amblypigid = phrynichid), scorpion and spider. There was in addition one species of ant, several other species of insects, and a land crab. Unfortunately none of the invertebrates were identified to species as our collection was lost in the mail when sent to specialists for identification and we have not had opportunity to visit the island again. However, sufficient is known about the genuine feeding habits of some of the groups to comment on the probable trophic relations.

The top of the island was used extensively by sea birds for nesting and their excrement literally covers the island, giving it a white-washed appearance. These birds feed on fish and hence it is probable that they serve as transfer organisms (Heatwole 1975) obtaining energy from the marine community and depositing a food source for the terrestrial community on the island in the form of guano and on occasions as carrion (dead adults or chicks) or broken eggs. The guano is believed to be the most important source as is carrion was observed and the only species likely to be scavengers that were present was the land crab and possibly the ant. The undercut nature of the island and its height would make work up of marine carrion unlikely. Isopods generally feed on detritus or other finely divided organic matter and we suspect that it fed on guano and in turn was preyed upon by the predatory invertebrates. The larger predators such as scorpion, whip scorpion, and lizards probably eat isopods and some of the invertebrates that prey on isopods. None of the lizards we collected had prey in their stomachs. However, we did obtain three recognizable items from the section of one animal. There were remains of an ant, the head of an insect larva, and surprisingly, parts of a species not otherwise known from the island, a homopteran. The last is a plant feeder and must represent a waif arriving aerially (the nearest vegetated land mass, Culebra Island is 14 km away).

In summary, the probable trophic relations are (1) a transfer of marine-derived energy via sea birds in the form of guano and carrion, (2) its utilization by isopods which (3) serve as prey for a variety of predators, (4) leading to secondary predators. The endogenous prey is probably supplemented by (5) aerial waifs. Complete dependence of an insular terrestrial community upon exogenous, marine-derived energy, although unusual, is not unique. Heatwole (1975) reports communities of several terrestrial species (including predators) on vegetation-free sand cays in the Coral Sea.

The source of the terrestrial fauna on Sail Rock is problematic. Sail Rock became isolated from the once continuous land mass of Greater Puerto Rico (about 8,000 years B.P.) (Heatwole and MacKenzie 1967), and it seems unlikely that the resident species could have maintained themselves on such a small barren island. On the whole the undercut nature of the island's base would suggest that at present flotsam transport would be unlikely and the flightless nature of many of the resident species would militate against aerial transport. The difficulty of access to the island would make human transport unlikely, although there is an automatic light house on top which is periodically serviced. Introduction of so many species by this means, however, seems unlikely.

From the above, it is clear that Sail Rock is especially interesting from the standpoints of island biogeography and community ecology. It would warrant quantitative study by someone in a position to carry out a long-term observation there.

DISCUSSION

The brief description of the general ecology of the archipelago presented above provides a summary of local conditions during the 8-year period in which data were collected. Many ecological characteristics are, however, in the process of rapid change, largely through human influence. An assessment of the nature of such changes is requisite for placing the present study in perspective and for evaluation of future data.

In pre-Columbian times a succession of cultures occurred in the area, especially on the larger islands. However, even those as small as Culebra (about 14 x 6 kms) had at least semi-resident populations, a midden containing various artifacts was found on this island during one of our field trips. Some species, such as useful plants and the edible iguana, may possibly owe their distribution in part to transport by these early residents. In post-Columbian times, man's effect was accelerated through additional clearing of land and establishment of an European-type culture. Domestic animals and a variety of ornamental and edible plants were purposefully introduced as well as various weeds, rodents, insects and other involuntarily-transported species. Feral cats and especially rats have possibly had an adverse effect on the now rare and endangered Puerto Rican

parrot (*Amazona v. vittata*) through depredation of nests (Rodriguez-Vidal 1959). The mongoose was introduced in order to control rodents (unsuccessfully). The role of the mongoose in the decline and extinction of West Indian native fauna may not be as great as is sometimes attributed to it, but it is almost certainly responsible for local extinction of some lizards, snakes and ground-nesting birds (see Barbour 1930, Heatwole and Torres 1967, Philibosian and Ruibal 1971).

The cane toad (*Bufo marinus*) was brought to Puerto Rico to control insect pests of sugar cane in 1920 (Bartlett 1949) and is now abundant on various islands. Cayo Santiago has had a feral band of rhesus monkeys for a number of years. Recently, introduction of some of them into several additional islands was made. These populations will undoubtedly have an ecological effect.

Goats and sheep are perhaps the most destructive of any introduced species, and there are probably few islands in the archipelago which have not been disturbed to some extent by these animals at some time or other. The early custom of releasing goats and other domestic ungulates on small islands and cays for later use by mariners was apparently common (Davis 1971). Mona and Desecheo Islands still maintain local populations originating in this way; the former island serves as a reserve for sportsmen to hunt goats and feral pigs. Many of the cays in the Virgin Islands have goat herds which belong to residents from larger islands and from which individuals are periodically killed for meat. Perhaps the island most affected by feral animals is Salt Island, B.V.I., in which the greater part of the vegetation has been reduced to a low, open strand of *Croton rigidus* and *C. astroites*, species unpalatable even to goats. Except for creeping *Opuntia repens*, the spaces between *Croton* bushes are nearly devoid of other vegetation, and goats have been observed gleaning the tiny grasses and annuals which do appear.

On Salt Island at least, free-roaming sheep and cattle also played a role in decimating once-considerable grassy areas (Mrs. Beatrice Smith, personal communication). These animals died out, since they cannot subsist on a diet of woody dicots as can goats. Observations on exclosures over a three-year period (Byer, in preparation) suggest that once ground cover is eliminated, re-establishment of woody plants is retarded even in the absence of goats. Possibly increased run-off either washes seeds away directly or removes organic matter necessary for their germination.

The degree of disturbance to a small island seems to be related to its geomorphologic type. Monito, which has steep sides undercut at the base, is relatively inaccessible and has probably been visited by humans only a few times (Rolle *et al.* 1964). The same is true of a number of the small islands in the chain just northeast of Puerto Rico. The latter, however, were used for strafing practice during World War II and remnants of shells can still be found embedded in rock on the top of some. Others of the relatively inaccessible steep-sided islands (e.g. Sail Rock) constitute shipping dangers and have light-

houses or other navigational aids which must be periodically serviced.

Many of the small accessible islands are frequently visited for short periods by fishermen who camp on the beach but otherwise have a minimal effect. Some islands containing large colonies of nesting sea birds are periodically visited by egg gatherers (e.g. Frenchcap Cay). A number of the more accessible islands have people living on them, even some as small as Ramos Island (< ½ km in greatest diameter). Lobos Island (slightly more than ½ km in greatest diameter) has a tourist hotel, and Isleta Marine serves as a yacht basin. Most islands with some beach and larger than 1 km in greatest diameter are inhabited either permanently or seasonally. Some inhabited islands show almost no disturbance by their residents (e.g. Guana Island); most however, are clearly modified by agricultural or other practices. Cayo Luis Peña and part of Culebra Island are used for bombing and naval gunnery practice. During World War II, Desecheo was used for bombing practice and bomb fragments can still be found on various parts of the island.

Human effects have accelerated greatly during our study. On many small uninhabited islands in the beginning of the study one was reminded of the proximity of human populations only by the large numbers of bottles, light bulbs, shoes, etc. encountered in the beach drift. Most, however, especially if currently goat-free, appeared in a relatively natural state. Various such islands close to Puerto Rico, were selected for detailed, long-term study (e.g. Cayo Ahogado and Palominitos). It was fortunate that our study was initiated as early as it was because today one would have to select less accessible islands in order to carry out such studies. Those near Puerto Rico with good anchorage for small craft are now visited by large numbers of weekend excursionists, who have turned the cays into veritable garbage and trash dumps and have cut woody vegetation for campfires and tent supports.

It appears that the small, inhabited islands whose owners discourage trespassing are likely to retain some similarity to their natural state, whereas uninhabited, public ones are already being rapidly destroyed.

The larger islands also show an alarming degree of human disturbances to natural communities. For example, in a study contracted by the Puerto Rican government, Heatwole (1970) found that that island had lost a mean of 1.7% of its coverage of mangrove per decade between 1930 and the mid-1960's. Between 1965 and 1970, large tracts were lost, some swamps dying completely. Industrial pollution and interference with drainage patterns by construction activities, dredging, and filling contributed to their demise. Proposed touristic development in the Vacia Talega area will probably eliminate much of Puerto Rico's best remaining mangrove, and is already flooding the island's largest stand of *Avicennia*, near Boguerón, with fresh water in order to convert it into a *Typha* marsh to be used for waterfowl hunting. The flooding was undertaken because all sizeable natural

fresh-water marshes, once thought valueless, had been eliminated some time in the past by agricultural development.

The destruction of habitat with increasing levels of human population is of course, not a problem unique to islands. However, there may be unique aspects arising from insularity. It would appear that three major tasks face island ecologists, (1) detailed study of the functioning of relatively undisturbed insular ecosystems while such are still available, (2) the assessment of the effect of human pressure on such ecosystems, and (3) recommending practices for use of small islands in ways that will not result in their destruction and loss to the human population. The series, to which this paper represents the introduction, concentrates largely on the first of these tasks.

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TABLE 1. TEMPERATURES (MEANS AND RANGES) IN DIFFERENT MICRO-HABITATS ON CAYO AHOGADO, MARCH 16-21, 1966.

			AIR TEMPERATURES			SOIL TEMPERATURES			TEMPERATURES AT A CLUMP OF VEGETATION				
DATE	Rh %	T_{BB}	1 cm	15 cm	1 m	5 cm deep	1 cm deep	Surface	5 cm in soil	1 cm in soil	Soil Surface under Clump	Surface of Vegetation	Center of Clump
16*	--	24.7	25.1	25.2	25.3	25.6	24.1	23.9	24.7	24.4	24.5	24.9	24.9
		24.2-25.5	24.7-25.7	24.8-25.9	24.9-25.9	24.8-27.1	23.4-25.5	23.3-25.0	24.5-25.0	24.0-25.1	24.0-25.3	24.5-25.5	24.5-25.5
17	74	33.5	27.5	27.3	26.6	28.0	29.3	30.4	25.8	26.4	27.6	27.0	27.3
	62-93	24.8-39.0	24.9-30.6	25.2-29.5	25.2-27.7	23.7-30.7	23.6-33.8	24.2-37.9	24.1-26.9	24.8-28.2	25.4-29.9	25.3-28.5	25.3-29.5
18	73	32.1	27.4	26.7	26.3	27.6	28.9	29.9	26.6	27.4	28.0	26.7	27.6
	63-95	22.2-41.1	22.9-32.2	22.5-30.1	22.3-28.4	23.3-31.3	21.5-35.5	21.3-38.2	23.2-29.2	23.2-31.4	22.5-33.2	24.7-29.3	22.2-32.2
19	78	24.1	23.7	23.8	23.6	23.8	22.9	22.8	22.9	22.6	22.9	23.8	23.7
	73-86	22.5-26.9	22.7-25.4	22.3-24.5	22.3-25.2	23.3-24.3	22.0-24.2	21.7-24.5	22.5-23.2	22.0-23.3	22.0-24.0	22.3-25.1	22.4-25.1
20	70	32.0	25.8	25.6	25.2	25.7	27.1	27.3	23.9	24.4	25.2	25.6	25.7
	60-82	23.7-40.8	23.5-28.3	23.4-27.5	23.7-26.7	22.0-28.5	21.4-32.7	21.9-32.6	22.0-25.8	21.9-26.4	22.5-27.5	23.8-27.0	23.7-27.3
21**	87	24.1	23.2	23.5	23.9	23.1	21.9	22.2	----	----	----	----	----
	86-88	22.7-25.5	23.1-23.3	23.1-23.8	23.4-24.4	22.6-23.5	21.7-22.0	21.7-22.7	----	----	----	----	----

* Late evening and night only.

** Early morning only.

Table 2. Vegetation types present on the islands of the Puerto Rican Bank. X indicates presence but cover either not estimated or estimated to have been less than 1%. Where numbers are given, they approximate the percentage of the island's area covered by a given vegetation type. Islands which do not appear, either were not studied from the vegetation standpoint, or will be treated in more detail in future papers. For names of vegetation types see text.

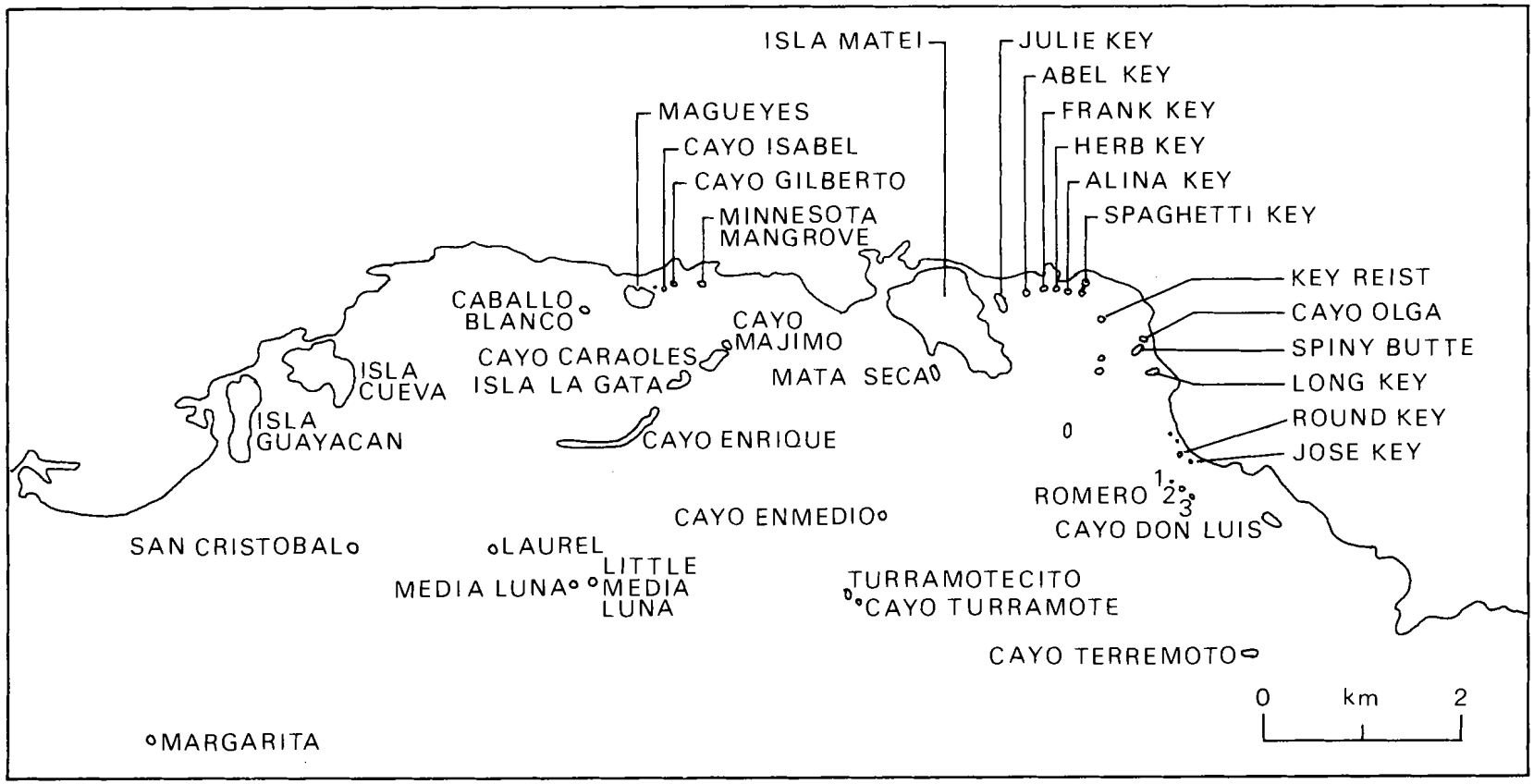
	VEGETATION TYPE											
ISLAND NAME	1	2	3	4	5	6	7	8	9	10	11	12
Abel Key								100				
Alina Key								100				
Anegada	x		x			85	x	5	10			x
Bare Cactus	x				x	x		x	x			
Beef Island	x		x	x	x	x	x	x	x			x
Big Cockroach	10				80	10						
Big Hans Lollick	x		x			x	x		x			
Big Tobago	x				x	60	x		40			
Blanquilla	x	65				35						
Booby Hatch	x	x	x									
Botella	x	5			10	85						
Byer Bache								100				
Caballo Blanco								100				
Cabez de Perro	x	x			x	x						
Caja de Muertos	x		x			x	x		x			
Caña Azul	90	5						5				
Cayo Ahogado	75	25	5									
Cayo Batata	x		x	x								
Cayo Enmedio	20	5						75				
Cayo Enrique	x	x						x				
Cayo Gilberto								100				
Cayo Isabel								100				
Cayo Majimo	5	5						90				
Cayo Norte	x		x	x		x	x		x			
Cayo Olga								100				
Cayo Santiago	x		x		x		x	x	x		x	
Cayo Turramotecito	90	10										
Chicken Island	x				x	x		x	x			
Cooper Island	x		1		4	50	x		40		5	
Cucaracha (Las Cucarachas)	x	x										
Culebra	x	x	x		x	x	x	x	x	x	x	x
Culebrita	x		x	x		x	x		x			
Dead Man's Chest	x				3	48	1		48			
Desecheo	x		x		x	x	x		x			
Diablo	x			x		x						
Double Island	45	50		5								
East Farallón	75	25										

Table 2 cont'd.

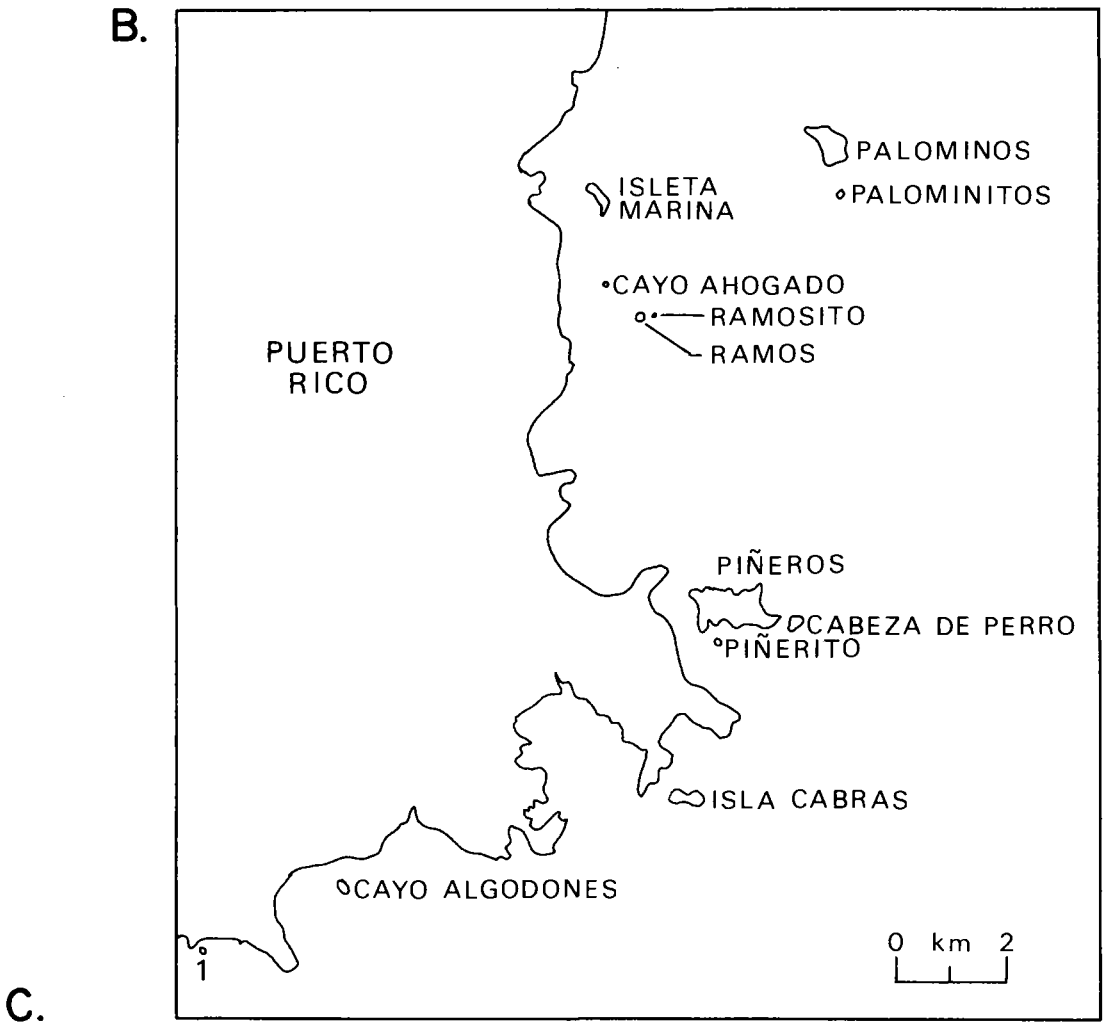
	1	2	3	4	5	6	7	8	9	10	11	12
East Geniquí	10	5			10	50			25			
East Seal Dog	x			x		x	x					
Eustatia	2		1		15	50	1		30		1	
Fallen Jerusalem						x	x		x			x
Frank Key								100				
Frenchman's Cap (French Cap Key)	x			60	37	3						
Frenchman's Cay	x				97				3			
George Dog			2		30	38	x		30			
Ginger Island	x					52	3		45			
Grant Rock	20	80										
Green Cay (Near St. Croix)	x		x	x		x						
Guana	x		x	x		x			x		x	
Gusano	x		x	x								
Herb Key								100				
Hicacos	x		x		x	x	x		x			
Island O								100				
Island Q	40	30						30				
Island R								100				
Isleta Marina	x		x								x	x
José Key								100				
Julie Key								100				
Key Reist								100				
Konyokí	20						60	20				
La Gata (Isla La Gata)	x							x				
Laurel	10							90				
Levin's Rock	x			x								
Little Hans Lollick	x	x	x			50	x	x	50		x	
Little Saba Island					25	75	x					
Little Tobago	x				70				30			
Long Key								100				
Magueyes		x			20	70		x	10			x
Mangrove Key		50						50				
Marina Cay	x	x		x		x	x					x
Mata Seca								100				
Media Luna	95							5				
Minnesota Mangrove								100				
Mona	x		x			x	x		x			
Monito	x					x						
Mosquito Island			4		5		6		80			5
Necker Island	5		x			70	x		25			
Norman Island	2		3			23	2		60	10		
Outer Caracol (Cavo Caracoles)	x	x						x				
Palominitos	20		20			55			5			
Palominos	x				10	90						x

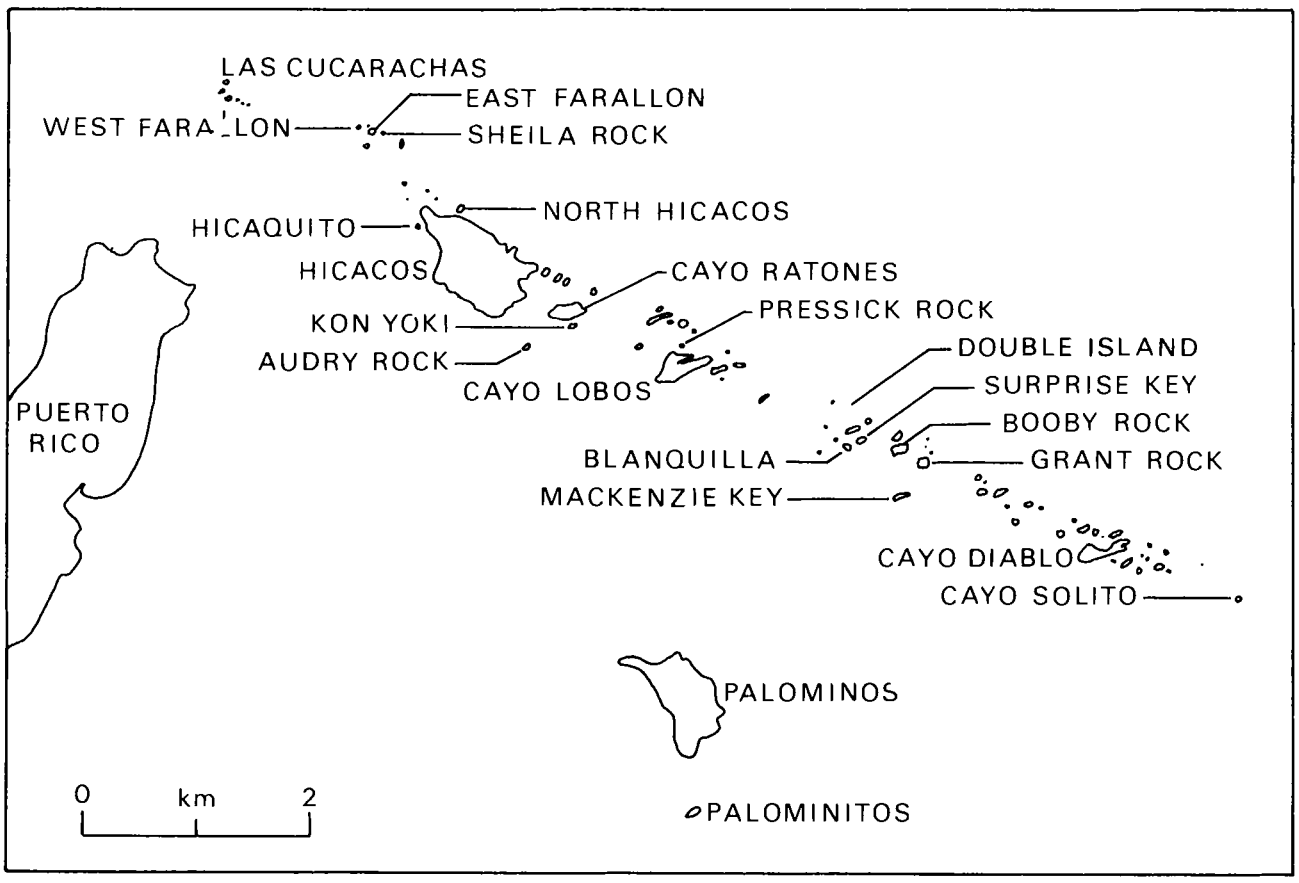
Table 2 cont'd.

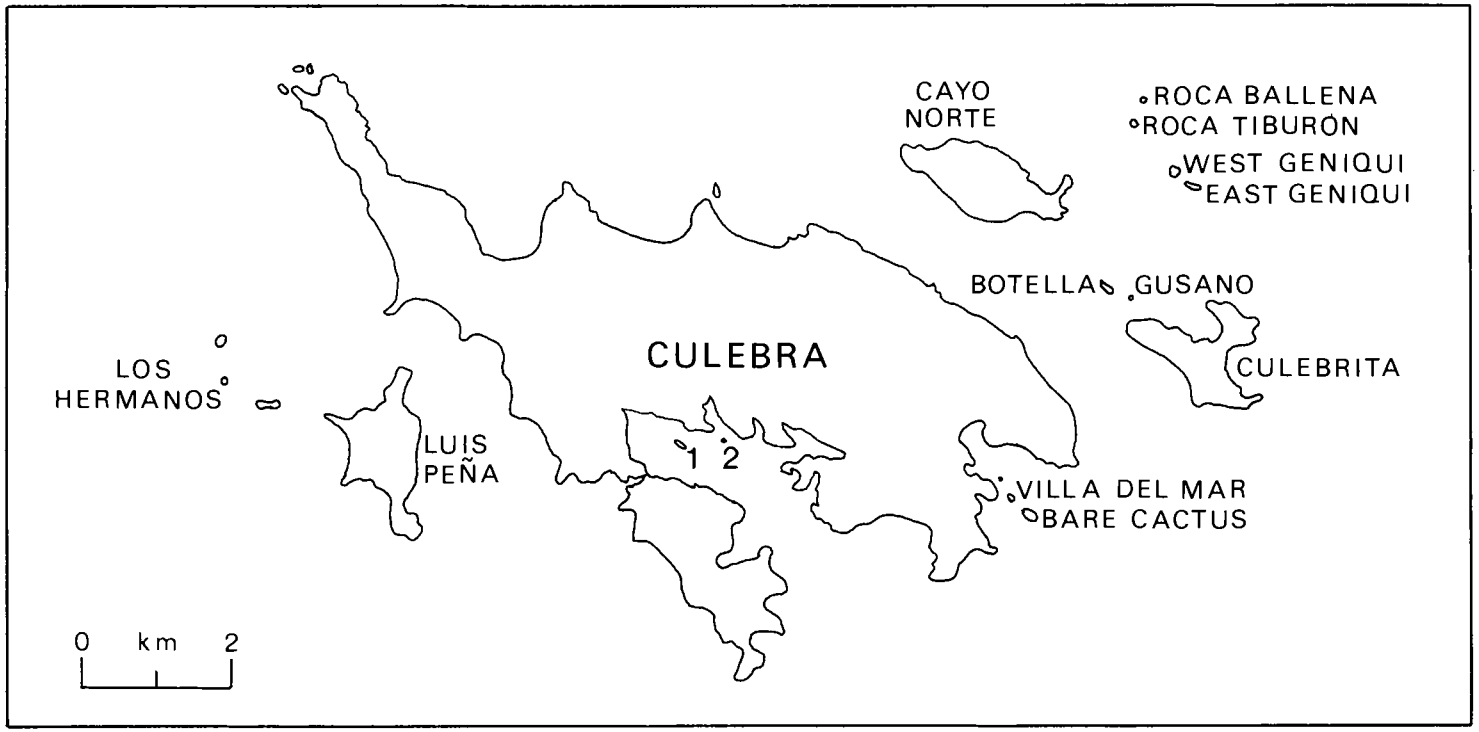
	1	2	3	4	5	6	7	8	9	10	11	12
Pelican Key	90			5		5						
Peter Island	x	x	x	x	x	x	x	x	x			
Platillo	x			x		x	x					
Prickly Pear	x				70				30			
Protestant Key	x			x			x	x			x	x
Puerto Rico	x	x	x	x	x	x	x	x	x	x	x	x
Ramos	x		x			x	x	x			x	x
Ratones (Cayo Ratones)	x		x		x	80	6	4	10		x	
Romero II								100				
Romero III								100				
Round Key								100				
Sail Rock	100											
Salt Island	x		x			80	5	x	10		5	x
San Cristobal	82	15						3				
Sheila Rock	95	5										
Solito (Cayo Solito)	75	25										
Spaghetti Key								100				
Spiny Butte						65		5	30			
St. Croix	x	x	x	x	x	x	x	x	x	x	x	x
St. John	x	x	x	x	x	x	x	x	x	x	x	x
St. Thomas	x	x	x	x	x	x	x	x	x		x	x
Surprise Key	20	50	15		15							
Tortola	x	x	x		x	x	x	x	x	x	x	x
Turramote	25	50						25				
Vieques	x	x	x	x	x	x	x	x	x		x	x
Villa del Mar					90		5	5				
Virgin Gorda	x	x	x	x	x	x	x	x	x		x	x
Watson Rock	90		x	5	5							
West Dog					x	x	x		x			
West Farallón	95	5										
West Seal Dog	x				25	60	15					


ISLA MATEI
JULIE KEY
ABEL KEY
FRANK KEY
HERB KEY
ALINA KEY
SPAGHETTI KEY
MAGUEYES
CAYO ISABEL
CAYO GILBERTO
MINNESOTA MANGROVE
KEY REIST
CAYO OLGA
SPINY BUTTE
LONG KEY
ROUND KEY
JOSE KEY
CABALLO BLANCO
CAYO MAJIMO
CAYO CARAOLES
ISLA LA GATA
MATA SECA
ISLA CUEVA
ISLA GUAYACAN
CAYO ENRIQUE
ROMERO
CAYO ENMEDIO
CAYO DON LUIS
SAN CRISTOBAL
LAUREL
LITTLE MEDIA LUNA
MEDIA LUNA
TURRAMOTECITO
CAYO TURRAMOTE
CAYO TERREMOTO
MARGARITA
0 km 2

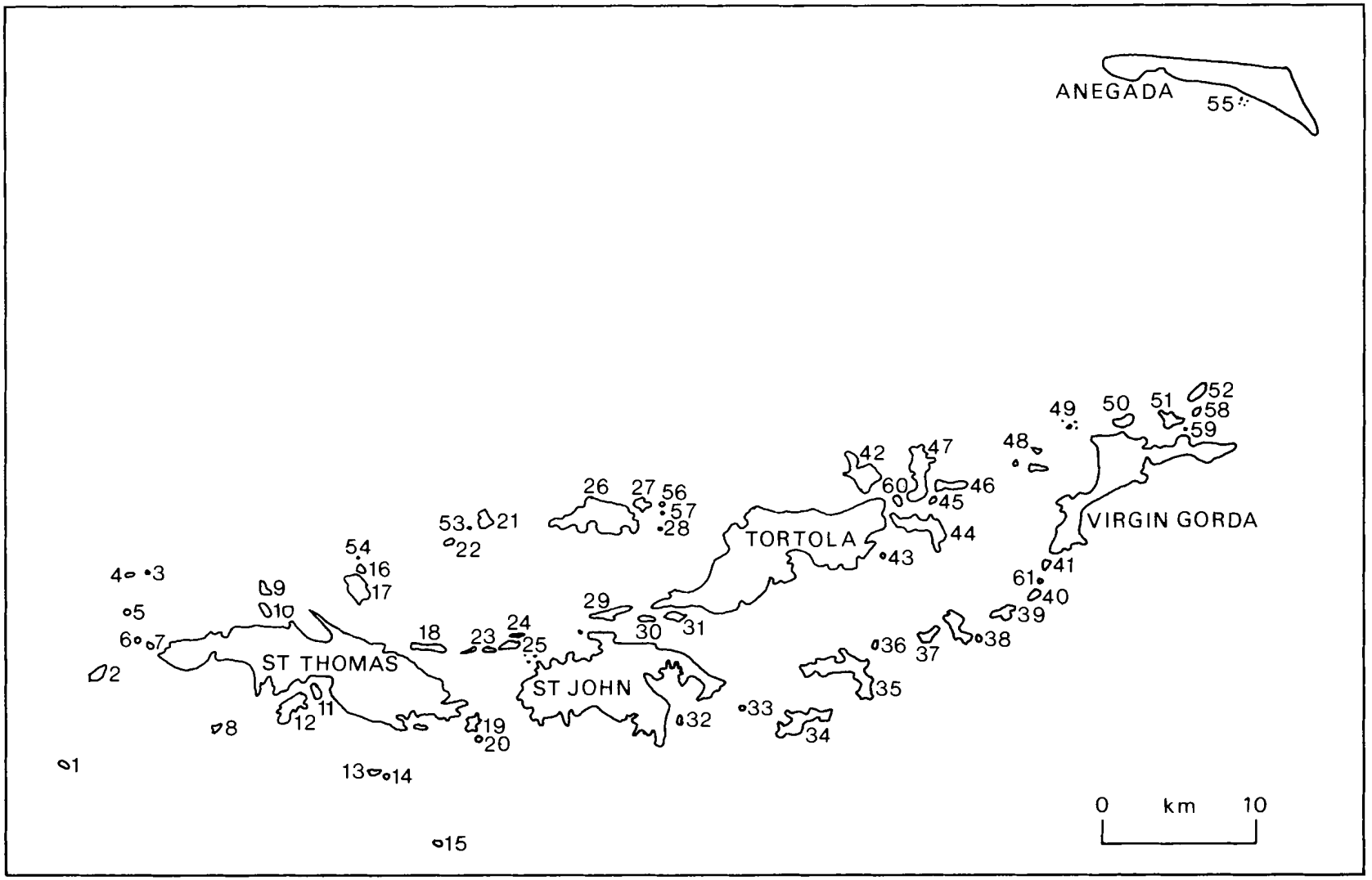
A.


B.
PALOMINOS
ISLETA MARINA
PALOMINITOS
CAYO AHOGADO
RAMOSITO
RAMOS
PUERTO RICO
PIÑEROS
CABEZA DE PERRO
PIÑERITO
ISLA CABRAS
CAYO ALGODONES
1
0 km 2


C.
LAS CUCARACHAS
EAST FARALLON
WEST FARALLON
SHEILA ROCK
NORTH HICACOS
HICAQUITO
HICACOS
CAYO RATONES
KON YOKI
PRESSICK ROCK
AUDRY ROCK
CAYO LOBOS
DOUBLE ISLAND
SURPRISE KEY
BOOBY ROCK
PUERTO RICO
BLANQUILLA
GRANT ROCK
MACKENZIE KEY
CAYO DIABLO
CAYO SOLITO
PALOMINOS
0 km 2
PALOMINITOS


CAYO
NORTE
ROCA BALLENA
ROCA TIBURÓN
WEST GENIQUI
EAST GENIQUI
BOTELLA
GUSANO
CULEBRA
CULEBRITA
LOS
HERMANOS
LUIS
PEÑA
1
2
VILLA DEL MAR
BARE CACTUS
0 km 2

D.


ANEGADA
55
VIRGIN GORDA
TORTOLA
ST THOMAS
ST JOHN
1
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3
4
5
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61
0 km 10

E.

Appendix I. Maps of small islands on the Puerto Rican Bank. Inconsistency in use of "cay" and "key" reflects differences between the American and British Virgin Islands in the way the word is spelled. We prefer the former and use it unless "key" is part of the proper name of an island.

A. Cays in the La Parguera region of Puerto Rico (enlargement of rectangle A in Figure 1).

B. Cays immediately east of Puerto Rico (enlargement of rectangle B in Figure 1). 1. Levin's Rock

C. Cays between Puerto Rico and Culebra Island (enlargement of rectangle C in Figure 1).

D. Culebra Island and its surrounding cays (enlargement of rectangle D in Figure 1). 1. Chicken Island, 2. Mangrove Key.

E. The islands and cays of the American and British Virgin Islands, except for St. Croix and its nearby islets (enlargement of rectangle E in Figure 1).

1. Sail Rock
2. Savanna Island
3. Cricket Rock
4. Cockroach Island (near St. Thomas)
5. Dutchman's Cap
6. Salt Cay
7. West Cay
8. Little Saba Island
9. Outer Brass Island
10. Inner Brass Island
11. Hassel Island
12. Water Island
13. Buck Island (near St. Thomas)
14. Capella Island
15. Frenchman's Cap (French Cap Key)
16. Little Hans Lollick
17. Big Hans Lollick
18. Thatch Key
19. Greater St. James
20. Little St. James
21. Big Tobago
22. Little Tobago
23. Mingo Key
24. Congo Key
25. Lovango Key
26. Jost van Dyke
27. Little Jost van Dyke
28. Sandy Key
29. Great Thatch Island
30. Little Thatch Island
31. Frenchman's Key
32. Leduck Island
33. Flannigan Island
34. Norman Island
35. Peter Island
36. Dead Man's Chest
37. Salt Island
38. Cooper Island
39. Ginger Island
40. Round Rock
41. Fallen Jerusalem
42. Guana Island
43. Buck Island (near Tortola)
44. Beef Island
45. Marina Cay
46. Scrub Island
47. Greater Camanoe
48. The Dog Islands: George Dog, West Dog, Great Dog and Big Cockroach (near Virgin Gorda)
49. Seal Dogs: East Seal Dog and West Seal Dog
50. Mosquito Island
51. Prickly Pear
52. Necker Island
53. Watson Rock
54. Pelican Key

55. A series of tiny cays, R, O, Q and Byer Bache
56. Green Cay (Jost van Dyke)
57. Sandy Spit
58. Eustatia
59. Saba Rock
60. Little Camanoe
61. Broken Jerusalem

Appendix II. Floral lists from some small islands and cays in the Puerto Rican and Virgin Island area. These should be considered as plant records rather than complete floras except for those islands marked with an (*) for which attempts were made to collect all species. Major islands not included; for treatment of their flora and vegetation see Britton and Wilson (1923-30), Gleason and Cook (1927), Little and Wadsworth (1964) and Dansereau (1966). Byer has a long-term, comprehensive study of the flora of small islands of this region in progress.

ANEGADA
See D'Arcy (1971, 1975)

BIG COCKROACH
Cephalocereus royeni
Opuntia dillenii

BIG HANS LOLLICK
Thrinax argentea
Piscidia piscipula
Citharexylum fruticosum
Torrubia fragrans (?)
Pithecellobium unguis-cati
Croton astroites
Agave missionum
Vigna marina
Coccoloba uvifera
Hippomane mancinella
Bursera simarouba
Capparis indica (?)

BIG TOBAGO
Conocarpus erecta
Croton astroites
Bulbostylis vestita
Agave missionum
Cephalocereus royeni
Tabebuia heterophylla
Pithecellobium unguis-cati
Torrubia fragrans
Bursera simarouba
Opuntia repens

CAYO AHOGADO
See Heatwole and Levins (1973)

CAÑA AZUL *
Avicennia nitida
Rhizophora mangle

CAYO BATATA
See Heatwole, Sade and Hildreth (1963)

CAYO ENMEDIO *
Sesuvium portulacastrum

CAYO ENRIQUE *
Sesuvium portulacastrum

CAYO MAJIMO *
Sesuvium portulacastrum

CAYO SANTIAGO
See Heatwole, Sade and Hildreth (1963)

CAYO TURREMOTECITO *
Sesuvium portulacastrum

COOPER ISLAND
- *Bursera simarouba*
- *Cakile lanceolata*
- *Carica papaya*
- *Coccoloba uvifera*
- *Cocos nucifera*
- *Croton astroites*
- *Euphorbia buxifolia*
- *Musa sp.*
- *Sporobolus virginicus*

DOUBLE KEY *
- *Sesuvium portulacastrum*

DEAD MAN'S CHEST
- *Coccoloba uvifera*
- *Croton astroites*
- *Croton sp.*
- *Sesuvium portulacastrum*
- *Sporobolus virginicus*

EAST FARALLON *
- *Sesuvium portulacastrum*

EUSTATIA
- *Bursera simarouba*
- *Cakile lanceolata*
- *Cocos nucifera*
- *Croton astroites*
- *Hippomane mancinella*
- *Sporobolus virginicus*

FALLEN JERUSALEM
- *Bursera simarouba*
- *Coccoloba uvifera*
- *Croton astroites*
- *Tabebuia heterophylla*

FRENCHCAP CAY
- *Canavalia maritima*
- *Clerodendron aculeatum*
- *Cyperus planifolius*
- *Ficus laevigata*
- *Hippomane mancinella*
- *Mollugo verticillata*
- *Portulaca grandiflora*

GEORGE DOG ISLAND
- *Bursera simarouba*
- *Coccoloba uvifera*

GINGER ISLAND
- *Avicennia nitida*
- *Bursera simarouba*
- *Croton astroites*
- *Croton rigidus*
- *Pisonia subcordata*

HICACOS
- See Britton (1924)

ISLAND O *
- *Rhizophora mangle*

ISLAND R *
- *Rhizophora mangle*

ISLAND Q *
- *Borrichia arborescens*
- *Laguncularia racemosa*
- *Rhizophora mangle*
- *Salicornia ambigua*
- *Sesuvium portulacastrum*

LEVINS ROCK *
- *Canavalia maritima*
- *Erithralis fruticosa*
- *Paspalum glabrum*

LITTLE HANS LOLLICK
- *Bursera simarouba*
- *Cephalocereus royeni*
- *Coccoloba uvifera*
- *Croton astroites*
- *Croton discolor*
- *Hippomane mancinella*
- *Jacquinia barbasco*
- *Opuntia dillenii*
- *Opuntia repens*
- *Opuntia rubescens*
- *Pithecellobium unguis-cati*
- *Rivina humilis*
- *Sporobolus virginicus*
- *Thrinax argentea*
- *Torrubia fragrans*

LITTLE SABA
- *Cephalocereus royeni*
- *Conocarpus erecta*
- *Rhizophora mangle*

LITTLE TOBAGO
- *Agave missionum*
- *Bursera simarouba*
- *Cephalocereus royeni*
- *Croton astroites*
- *Jacquemontia jamaicensis*
- *Lantana involucrata*
- *Opuntia dillenii*
- *Pithecellobium unguis-cati*
- *Sporobolus virginicus*
- *Torrubia fragrans*
- *Vigna marina*

MOSQUITO ISLAND
- *Bursera simarouba*
- *Carica papaya*
- *Coccoloba uvifera*
- *Croton astroites*
- *Hippomane mancinella*
- *Sporobolus virginicus*
- *Tabebuia heterophylla*
- *Torrubia fragrans (?)*

NECKER
- *Bursera simarouba*
- *Cactus intortus*
- *Cephalocereus royeni*
- *Coccoloba uvifera*
- *Croton astroites*
- *Croton rigidus*
- *Guilandia crista*

NORMAN ISLAND
- *Amaranthus dubius*
- *Atriplex sp.*
- *Bursera simarouba*
- *Capparis flexuosa*
- *Coccoloba uvifera*
- *Conocarpus erecta*
- *Croton astroites*
- *Euphorbia sp.*
- *Laguncularia racemosa*
- *Pisonia albida*
- *Sporobolus virginicus*
- *Tamarindus indica*

PALOMINITOS *
- *Borrichia arborescens*
- *Cakile lanceolata*
- *Canavalia maritima*
- *Cassytha filiformis*
- *Cenchrus echinata*
- *Cenchrus pauciflorus*
- *Coccoloba uvifera*
- *Conocarpus erecta*
- *Cyperus planifolius*
- *Erethralis fruticosa*
- *Ermodia littoralis*
- *Euphorbia buxifolia*
- *Lantana involucrata*
- *Melanthera nivea*
- *Scaevola plumeri*
- *Sesuvium portulacastrum*
- *Suriana maritima*
- *Vigna marina*
- 3 unidentified

PELICAN KEY
- *Capparis flexuosa*
- *Conocarpus erecta*
- *Laguncularia racemosa* (disappeared again before June 1968)
- *Opuntia repens*
- *Portulaca oleracea*
- *Sporobolus virginicus*

PLATILLO
- *Coccoloba uvifera*

PRICKLY PEAR
- *Agave missionum*
- *Bursera simarouba*

RATONES
- *Coccoloba uvifera*

SAIL ROCK *
- Barren

SALT ISLAND
- *Cocos nucifera*
- *Croton astroites*

SAN CRISTOBAL *
Avicennia nitida
Laguncularia racemosa
Philoxerus vermicularis
Rhizophora mangle
Sesuvium portulacastrum

SHEILA ROCK *
Sesuvium portulacastrum

SOLITO *
Sesuvium portulacastrum

SPINY BUTTE *
Acuan virgatum
Ayenia pusilla
Boerhaavia erecta
Bursera simarouba
Capparis flexuosa
Commelina elegans
Cordia angustifolia
Croton discolor
Croton humilis
Euphorbia berteriana
Hibiscus brasiliensis
Hippomane mancinella
Lantana involucrata
Leptocereus quadricostatus
Molluchia tomentosa
Opuntia dillenii
Panicum maximum
Pectis linifolia
Pithecellobium unguis-cati
Portulaca pilosa
Pteramnus labialis
Rauwolfia lamarckii
Rhizophora mangle
Ruellia tuberosa
Sida glabra
Sida procumbens
Stigmaphyllon lingulatum
3 unidentified

TURREMOTO (CORRAL)
Avicennia nitida
Laguncularia racemosa

WEST DOG ISLAND
Coccoloba uvifera
Conocarpus erecta
Croton rigidus

WEST FARALLON *
Sesuvium portulacastrum

WEST SEAL DOG
Coccoloba uvifera

Appendix III. Reptiles and Amphibians of the Puerto Rico - Virgin Island Archipelago

The islands from which each species was collected are listed first, followed by a listing of all of the herpetofauna for each island. An attempt was made to do a complete survey on each island. These lists are based on our own collections, those of various museums, literature records up to 1970 which we have not verified (*), and our own sight records (**). They do not include the records obtained by other investigators after 1972, and whose collections we have not seen. Some of these later collections add species for islands we have surveyed and present records from a number of islands we did not visit. A complete listing of the known insular distributions of the Puerto Rican - Virgin Island species can be obtained from a combination of the present paper, and the publications of Schwartz and Thomas (1975), Philibosian and Yntema (1976, in press) and Maclean *et al.* (1977). In our list, island names in parentheses indicate that the species in question was recorded from that island but probably does not occur there as a permanently established breeding population. This list corrects that of Schwartz and Thomas (1975) for *Anolis cristatellus cristatellus* and *Anolis cristatellus wileyae* in line with the taxonomic assessment of Heatwole (1976b).

Schwartz and Thomas indicated *A. c. cristatellus* to inhabit many islands east of Puerto Rico, which are in fact inhabited by *A. c. wileyae* instead.

Distribution of Species

LIZARDS

Iguanidae

Anolis acutus

Buck Island (near St. Croix)
Green Key (near St. Croix)
Protestant Key
St. Croix

Anolis cooki

Caja de Muertos
Puerto Rico

Anolis cristatellus cristatellus

Algodones
Caja de Muertos
Cardona Key
(Cayo Ahogado)
Cayo Batata
Cayo Santiago
Isleta Marina[1]
Long Island
Magueyes Island
Platillo
Puerto Rico
Ramos

[1] Also hybrids between *A. c. cristatellus* and *A. c. wileyae*.

Anolis cristatellus wileyae

Algodones
Anegada
Bare Cactus Island
Beef Island (near Tortola)
Blanquilla
Booby Hatch
Botella Island
* Buck Island (near St. Thomas)
Cabeza de Perro
Cayo Lobos
Cayo Norte
Cayo Ratones (near Hicacos)
Chicken Island
Cockroach Island (near St. Thomas)
Cooper Island
Congo Cay
Culebra
Culebrita
Dead Man's Chest

Isleta Marina
Konyokí
Little Camanoe
Little Hans Lollick
Little Jost van Dyke
Little Saba (near St. Thomas)
* Little St. James
Little Tobago
* Lovango Key
Marina Cay
Mosquito Island
Norman Island
Necker Island
Palominitos
Palominos
Peter Island
Piñeros
Piñeritos
Prickly Pear Island
Puerto Rico[1]

Diablo
* Dog Island
* Dutchman's Cap
East Seal Dog
Eustatia
Fallen Jerusalem
George Dog Island
Ginger Island

Grant Rock
* Great Dog Island
Greater Camanoe
Greater Thatch Island
Green Cay (near Tortola)
Guana Island

Hans Lollick
* Hassel Island
Hicacos
* Inner Brass Island
Isla Cabras (near Roosevelt Rds P.R.)
Ramos
* St. James
St. John
St. Thomas
Salt Island
* Salt Key
Sandy Cay (near Tortola)
Sandy Spit
* Savanna Island
Scrub Island
Surprise Key
Tobago
Tortola
Vieques
Villa del Mar
Virgin Gorda
* Water Island
** West Dog Island
West Seal Dog Island

Anolis cuvieri

Puerto Rico
* Vieques

---

[1] Also hybrids between *A. c. cristatellus* and *A. c. wileyae*.

Anolis desechensis

Desecheo

Anolis evermanni

Puerto Rico

Anolis gundlachi

Puerto Rico

Anolis krugi

Puerto Rico

Anolis monensis

Mona

Monito

Anolis occultus

Puerto Rico

Anolis poncensis

Puerto Rico

Anolis pulchellus

Algodones
Anegada
Cabeza de Perro
Caja de Muertos
(Cayo Ahogado)
Cayo Batata
Guana Island
Hicacos
Isleta Marina
* Jost van Dyke
Little Jost van Dyke
* Little St. James
* Lovango Key
Palominos
Peter Island
Cayo Norte
Cayo Ratones (near Hicacos)
Cayo Santiago
Culebra
* Fallen Jerusalem
Greater Camanoe
Piñeros
Puerto Rico
* St. James
St. John
St. Thomas
Tortola
Vieques
Virgin Gorda
* Water Island

Anolis roosevelti

* Culebra

Anolis stratulus

Beef Island (near Tortola)
Cayo Santiago
* Congo Key
Culebra
Fallen Jerusalem
Ginger Island
Greater Camanoe
Greater Thatch Island
Guana Island
* Jost van Dyke
Little Jost van Dyke
* Little Saba (near St. Thomas)
Marina Cay
Necker Island
Norman Island
* Peter Island
Piñeros
Prickly Pear
Puerto Rico
St. John
St. Thomas
* Savanna Island
Scrub Island
Tortola
Vieques
Virgin Gorda
* Water Island

Cyclura cornuta

Mona

Cyclura pinguis

Anegada

Iguana iguana

* Guana Island
* Hassel Island
Hicacos (pers. com. S.D. Garber)
Peter Island
Puerto Rico
* St. Croix
* St. John
* St. Thomas
* Tortola
* Water Island

Teiidae

Ameiva alboguttata

Mona

Ameiva desechensis

Desecheo

Ameiva exsul

Algodones
Anegada
Beef Island
Blanquilla
* Buck Island (near Tortola)
Cabeza de Perro
Caja de Muertos
(Levin's Rock)
Little Camanoe
Little Hans Lollick
Little Jost van Dyke
Little Saba (near St. Thomas)
Little St. James
Lovango Key

* Cardona Key
(Cayo Ahogado)
Cayo Batata
Cayo Lobos
Cayo Norte
Cayo Ratones
Cayo Santiago
Cooper Island
Culebra
Culebrita
Dead Man's Chest
Diablo
* Dutchman's Cap
Eustatia
George Dog Island
Ginger Island
Greater Camanoe
Guana Island
Hans Lollick
Hassel Island
Hicacos
Inner Brass
Isleta Marina
Konyokí
Marina Cay
Mosquito Island
Necker Island
Norman Island
Palominitos
Palominos
Peter Island
Piñeros
Platillo
Prickly Pear
Puerto Rico
Ramos
St. James
St. John
St. Thomas
Salt Island
* Salt Key
Savanna Island
Scrub Island
Tobago
Tortola
Vieques
Virgin Gorda
Water Island

Ameiva polops

Green Key (near St. Croix)
Protestant Key
* St. Croix

Ameiva wetmorei

Caja de Muertos
Magueyes Island
Puerto Rico

Scincidae

Mabuya mabouya sloanei

* Anegada
Buck Island (near St. Thomas)
Cayo Norte
* Culebra
* Culebrita
Dead Man's Chest
** Ginger Island
Hicacos
* Jost van Dyke
* Little Saba (near St. Thomas)
Mona
** Monito
Necker Island
Peter Island
Puerto Rico
* St. John
* St. Thomas
Salt Island
* Vieques (Perhaps now locally extinct)
Virgin Gorda

Anguidae

Diploglossus pleii

Puerto Rico

Gekkonidae

Hemidactylus brooki

Puerto Rico

Hemidactylus mabouia

Culebra
* Jost van Dyke
Mona
Peter Island
Puerto Rico
St. Croix
* St. John
St. Thomas
* Salt Island
Tobago
Tortola
Vieques
* Water Island

Phyllodactylus wirshingi

* Caja de Muertos
* Puerto Rico

Sphaerodactylus beattyi beattyi

Buck Island (near St. Croix)
Green Key (near St. Croix)
St. Croix

Sphaerodactylus beattyi seamani

* St. Croix

Sphaerodactylus gaigeae

Cayo Santiago
Piñeros
Puerto Rico

Sphaerodactylus klauberi

Puerto Rico

Sphaerodactylus levinsi

Desecheo Island

Sphaerodactylus macrolepis ateles

Puerto Rico

Sphaerodactylus macrolepis grandisquamis

Algodones
Cabeza de Perro
Cayo Batata
Cayo Santiago
Puerto Rico

Sphaerodactylus macrolepis guarionex

Puerto Rico

Sphaerodactylus macrolepis inigoi

* Cayo de Afuera
* Cayo de Tierra
Vieques

Sphaerodactylus macrolepis macrolepis

Anegada
Bare Cactus Island
Beef Island
Big Cockroach
Botella
* Buck Island (near St. Thomas)
Cooper Island
* Congo Key
Culebra
Culebrita
Dead Man's Chest
East Geniquí
East Seal Dog
Eustatia
Fallen Jerusalem
George Dog Island
Ginger Island
Great Dog Island
Greater Camanoe
Greater Thatch
Green Cay (near Tortola)
Guana Island
Hans Lollick
Jost van Dyke
Little Camanoe
Little Hans Lollick
Little Jost van Dyke
Little Saba
* Little St. James
Little Thatch Island
Buck Island (near St. Croix)
* Buck Island (near Tortola)
* Cayo Luis Peña
Cayo Norte
Chicken Island
Cockroach (near St. Thomas)
Little Tobago
Marina Cay
Mosquito
Necker Island
Norman Island
Peter Island
Prickly Pear
Sail Rock
St. Croix
St. John
St. Thomas
Salt Island
Sandy Cay (near Tortola)
Sandy Spit
* Savanna Island
Scrub Island
Tobago
Tortola
Villa del Mar
Virgin Gorda
* Water Island
Watson Rock
West Dog Island
West Seal Dog Island

Sphaerodactylus macrolepis mimetes

Puerto Rico

Sphaerodactylus macrolepis phoberus

Puerto Rico

Sphaerodactylus macrolepis spanius

Puerto Rico

Sphaerodactylus macrolepis stibarus

Piñeros

Sphaerodactylus monensis

Mona

Sphaerodactylus nicholsi nicholsi

Magueyes Island
Puerto Rico
Spiny Butte
(Turramote Key)

Sphaerodactylus nicholsi townsendi

Blanquilla
Booby Hatch
Caja de Muertos
* Cayo de Afuera (near Vieques)
* Cayo de Tierra (near Vieques)
Cayo Lobos
Cayo Ratones (near Hicacos)
* Culebra
Diablo
French Cap Key
Grant Rock
Hicacos
Isla Cabras (near Roosevelt Rds., P.R.)
Konyokí
MacKenzie Key
Palominos
Piñeros
Platillo
Puerto Rico
Ramos
Surprise Key
Vieques

Sphaerodactylus parthenopion

Mosquito Island
Virgin Gorda

Sphaerodactylus roosevelti

Caja de Muertos
Magueyes Island
Puerto Rico
* Vieques

Thecadactylus rapicaudus

Necker Island
* St. Croix

AMPHISBAENIANS

Amphisbaenidae

Amphisbaena bakeri

Puerto Rico

Amphisbaena caeca

Puerto Rico

Amphisbaena fenestrata

* Greater Camanoe
Little Jost van Dyke
* St. James
* St. John
* St. Thomas
* Tortola
* Virgin Gorda

Amphisbaena schmidti

Puerto Rico

Amphisbaena xera

Caja de Muertos (called *A. caeca* by Heatwole *et al.* 1965) Puerto Rico

SNAKES

Boidae

Epicrates inornatus

Puerto Rico

Epicrates monensis

* Mona
* Tortola

Colubridae

Alsophis portoricensis

Anegada
* Buck Island (near St. Thomas)
Cabeza de Perro
Caja de Muertos
Cayo Santiago
* Cockroach (near St. Thomas)
Culebra
Ginger Island
Green Cay (near Tortola)
Guana Island
Mona
Mosquito
Necker Island
Norman Island
* Peter Island
Platillo
Puerto Rico
* St. John
* St. Thomas
* Salt Island

* Jost van Dyke
* Little Saba
  Little Tobago
* Savanna Island
* Vieques
  Virgin Gorda

Alsophis sancticrucis

* St. Croix

Arrhyton exiguum

  Anegada
  Cayo Santiago
* Culebra
  Greater Camanoe
* Hassel Island
  Peter Island
  Puerto Rico
* St. John
  St. Thomas
  Tortola
  Virgin Gorda

Typhlopidae

Typhlops granti

Puerto Rico

Typhlops monensis

Mona

Typhlops richardi

  Cayo Norte
* Culebra
  Diablo
  Guana Island
  Little Hans Lollick
  Little Jost van Dyke
  Palominitos
  Puerto Rico
* St. Croix
* St. John
* St. Thomas
  Surprise Key
  Tortola
  Virgin Gorda

Typhlops rostellata

Puerto Rico

TURTLES (excluding marine ones)

Emydidae

Chrysemys decussata stejnegeri

Puerto Rico

Testudinidae

Geochelone carbonaria

* St. John
* St. Thomas
* Tortola
* Water Island

ANURANS

Bufonidae

Bufo lemur

Puerto Rico

Bufo marinus (introduced)

Algodones
Cayo Santiago
Culebra
Puerto Rico
St. Croix
Vieques

Bufo turpis

* Virgin Gorda

Leptodactylidae

Eleutherodactylus antillensis

Culebra
Piñeros
Puerto Rico
St. Croix (introduced?)
St. John
St. Thomas
Tortola
Vieques
Virgin Gorda

Eleutherodactylus brittoni

Puerto Rico

Eleutherodactylus cochranae

* Hassel Island
Puerto Rico
St. John
St. Thomas
Tortola

Eleutherodactylus cooki

Puerto Rico

Eleutherodactylus coqui

Puerto Rico

Eleutherodactylus eneidae

Puerto Rico

Eleutherodactylus gryllus

Puerto Rico

Eleutherodactylus hedrecki

Puerto Rico

Eleutherodactylus karlschmidti

Puerto Rico

Eleutherodactylus lentus

St. Croix St. Thomas

Eleutherodactylus locustus

Puerto Rico

Eleutherodactylus monensis

Mona

Eleutherodactylus portoricensis

Puerto Rico

Eleutherodactylus richmondi

Puerto Rico

Eleutherodactylus schwartzi

Great Dog Tortola
St. Croix (introduced?) Virgin Gorda
St. John

Eleutherodactylus unicolor

Puerto Rico

Eleutherodactylus wightmanae

Puerto Rico

Leptodactylus alibilabris

Algodones	Puerto Rico
Anegada	St. Croix
Cayo Santiago	St. John
Culebra	St. Thomas
Hicacos	Tortola
Piñeros	Vieques

Ranidae

Rana catesbeiana (introduced)

Puerto Rico	Vieques (J.E. Cooper, pers. com.)

Fauna of Islands

Algodones

Ameiva exsul	*Bufo marinus* (introduced)
Anolis cristatellus cristatellus	*Leptodactylus albilabris*
Anolis cristatellus wileyae	*Sphaerodactylus macrolepis grandis-*
Anolis pulchellus	*quamis*

Anegada

Alsophis portoricensis	**Cyclura pinguis*
Ameiva exsul	*Leptodactylus albilabris*
Anolis cristatellus wileyae	**Mabuya mabouya sloanei*
Anolis pulchellus	*Sphaerodactylus macrolepis macrolepis*
* *Arrhyton exigum*	

Bare Cactus Island

Anolis cristatellus wileyae	*Sphaerodactylus macrolepis macrolepis*

Beef Island (near Tortola)

Ameiva exsul	*Anolis stratulus*
Anolis cristatellus wileyae	*Sphaerodactylus macrolepis macrolepis*

Big Cockroach

Sphaerodactylus macrolepis macrolepis

Blanquilla

Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus nicholsi townsendi

Booby Hatch

Anolis cristatellus wileyae
Sphaerodactylus nicholsi townsendi

Botella Island

Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Buck Island (near St. Thomas)

* *Alsophis portoricensis*
* *Anolis cristatellus wileyae*
* *Mabuya mabouya sloanei*
* *Sphaerodactylus macrolepis macrolepis*

Buck Island (near St. Croix)

Anolis acutus
Sphaerodactylus beattyi beattyi
Sphaerodactylus macrolepis macrolepis

Buck Island (near Tortola)

Ameiva exsul
* *Sphaerodactylus macrolepis macrolepis*

Cabeza de Perro

Alsophis portoricensis
Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
Sphaerodactylus macrolepis grandisquamis

Caja de Muertos

Alsophis portoricensis
Ameiva exsul
Ameiva wetmorei
Amphisbaena xera
Anolis cooki
Anolis cristatellus cristatellus
Anolis pulchellus
* *Phyllodactylus wirshingi*
Sphaerodactylus nicholsi townsendi
Sphaerodactylus roosevelti

Cardona Key

Ameiva exsul
* *Anolis cristatellus cristatellus*

Cayo Ahogado

(Ameiva exsul)
(Anolis cristatellus cristatellus)
(Anolis pulchellus)

Cayo Batata

Ameiva exsul
Anolis cristatellus cristatellus
Anolis pulchellus
Sphaerodactylus macrolepis grandisquamis

Cayo de Afuera

* *Sphaerodactylus macrolepis inigoi*
* *Sphaerodactylus nicholsi townsendi*

Cayo de Tierra

* *Sphaerodactylus macrolepis inigoi*
* *Sphaerodactylus nicholsi townsendi*

Cayo Lobos

Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus nicholsi townsendi

Cayo Luis Peña

* *Sphaerodactylus macrolepis macrolepis*

Cayo Norte

Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
Mabuya mabouya sloanei
Sphaerodactylus macrolepis macrolepis
Typhlops richardi

Cayo Ratones

Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
Sphaerodactylus nicholsi townsendi

Cayo Santiago

Alsophis portoricensis
Ameiva exsul
Anolis cristatellus cristatellus
Anolis pulchellus
Anolis stratulus
Arrhyton
Bufo marinus (introduced)
Leptodactylus albilabris
Sphaerodactylus gaigeae
Sphaerodactylus macrolepis grandisquamis

Chicken Island

Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Cockroach (near St. Thomas)

* *Alsophis portoricensis*
Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Cooper Island

Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus macrolepis

Congo Key

* *Anolis cristatellus wileyae*
* *Anolis stratulus*
* *Sphaerodactylus macrolepis macrolepis*

Culebra

Alsophis portoricensis
Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
* *Anolis roosevelti*
Anolis stratulus
Arrhyton exiguum
Bufo marinus (introduced)
Eleutherodactylus antillensis
Hemidactylus mabouia
Leptodactylus albilabris
* *Mabuya mabouya sloanei*
Sphaerodactylus macrolepis macrolepis
* *Sphaerodactylus nicholsi townsendi*
* *Typhlops richardi*

Culebrita

Ameiva exsul
Anolis cristatellus wileyae
* *Mabuya mabouya sloanei*
Sphaerodactylus macrolepis macrolepis

Dead Man's Chest

Ameiva exsul
Anolis cristatellus wileyae
Mabuya mabouya sloanei
Sphaerodactylus macrolepis macrolepis

Desecheo

Ameiva desechensis
Anolis desechensis
Sphaerodactylus levinsi

Diablo

Anolis cristatellus wileyae
Ameiva exsul
Sphaerodactylus nicholsi townsendi
Typhlops richardi

Dog Island

* *Anolis cristatellus wileyae*

Dutchman's Cap

Ameiva exsul
* *Anolis cristatellus wileyae*

East Geniqui

Sphaerodactylus macrolepis macrolepis

East Seal Dog

Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Eustatia

Anolis cristatellus wileyae
Ameiva exsul
Sphaerodactylus macrolepis macrolepis

Fallen Jerusalem

Anolis cristatellus wileyae
* *Anolis pulchellus*
Anolis stratulus
Sphaerodactylus macrolepis macrolepis

French Cap Key

Sphaerodactylus nicholsi townsendi

George Dog Island

Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Ginger Island

Alsophis portoricensis
Ameiva exsul
Anolis cristatellus wileyae
Anolis stratulus
***Mabuya mabouya sloanei*
Sphaerodactylus macrolepis macrolepis

Grant Rock

Anolis cristatellus wileyae
Sphaerodactylus nicholsi townsendi

Great Dog Island

* *Anolis cristatellus wileyae*
Eleutherodactylus schwartzi
Sphaerodactylus macrolepis macrolepis

Greater Camanoe

Ameiva exsul
* *Amphisbaena fenestrata*
Anolis cristatellus wileyae
Anolis pulchellus
Anolis stratulus
Arrhyton exiguum
Sphaerodactylus macrolepis macrolepis

Greater Thatch Island

Anolis cristatellus wileyae
Anolis stratulus
Sphaerodactylus macrolepis macrolepis

Green Key (near St. Croix)

Ameiva polops
Anolis acutus
Sphaerodactylus beattyi beattyi

Green Cay (near Tortola)

Alsophis portoricensis
Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Guana Island

Alsophis portoricensis
Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
Anolis stratulus
* *Iguana iguana*
Sphaerodactylus macrolepis macrolepis
Typhlops richardi

Hans Lollick

Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Hassel Island

Ameiva exsul
* *Anolis cristatellus wileyae*
Arrhyton exiguum
* *Eleutherodactylus cochranae*
* *Iguana iguana*

Hicacos

Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
Iguana iguana (pers. com. S.D. Garber)
Leptodactylus albilabris
Mabuya mabouya sloanei
Sphaerodactylus nicholsi townsendi

Inner Brass Island

Ameiva exsul
Anolis cristatellus wileyae

Isla Cabras (near Roosevelt Rds., P.R.)

Anolis cristatellus wileyae
Sphaerodactylus nicholsi townsendi

Isleta Marina

Ameiva exsul
Anolis cristatellus cristatellus
Anolis cristatellus wileyae
A.c. cristatellus X A. c. wileyae
Anolis pulchellus

Jost van Dyke

* *Alsophis portoricensis*
* *Anolis pulchellus*
* *Anolis stratulus*
* *Hemidactylus mabouia*
* *Mabuya mabouya sloanei*
Sphaerodactylus macrolepis macrolepis

Konyokí

Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus nicholsi townsendi

Levin's Rock

(Ameiva exsul)

Little Camanoe

Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Little Hans Lollick

Alsophis richardi
Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Little Jost van Dyke

Ameiva exsul
Amphisbaena fenestrata
Anolis cristatellus wileyae
Anolis pulchellus
Anolis stratulus
Sphaerodactylus macrolepis macrolepis
Typhlops richardi

Little Saba (near St. Thomas)

* *Alsophis portoricensis*
Ameiva exsul
* *Anolis cristatellus wileyae*
* *Anolis stratulus*
* *Mabuya mabouya sloanei*
* *Sphaerodactylus macrolepis macrolepis*

Little St. James

Ameiva exsul
* *Anolis cristatellus wileyae*
* *Anolis pulchellus*
* *Sphaerodactylus macrolepis macrolepis*

Little Thatch Island

Sphaerodactylus macrolepis macrolepis

Little Tobago

Alsophis portoricensis
Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Long Island

Anolis cristatellus cristatellus

Lovango Key

Ameiva exsul
* *Anolis cristatellus wileyae*
* *Anolis pulchellus*

MacKenzie Key

Sphaerodactylus nicholsi townsendi

Magueyes Island

Ameiva wetmorei
Anolis cristatellus cristatellus
Sphaerodactylus nicholsi nicholsi
Sphaerodactylus roosevelti

Marina Cay

Ameiva exsul
Anolis cristatellus wileyae
Anolis stratulus
Sphaerodactylus macrolepis macrolepis

Mona

Alsophis portoricensis
Ameiva alboguttata
Anolis monensis
Cyclura cornuta
Eleutherodactylus monensis
* *Epicrates monensis*
Hemidactylus mabouia
Mabuya mabouya sloanei
Sphaerodactylus monensis
Typhlops monensis

Monito

Anolis monensis
***Mabuya mabouya sloanei*

Mosquito Island

Alsophis portoricensis
Ameiva exsul
Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis
Sphaerodactylus parthenopion

Necker Island

Alsophis portoricensis
Ameiva exsul
Anolis cristatellus wileyae
Anolis stratulus
Mabuya mabouya sloanei
Sphaerodactylus macrolepis macrolepis
Thecadactylus rapicaudus

Norman Island

Alsophis portoricensis
Ameiva exsul
Anolis cristatellus wileyae
Anolis stratulus
Sphaerodactylus macrolepis macrolepis

Palominitos

Ameiva exsul
Anolis cristatellus wileyae
Typhlops richardi

Palominos

Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
Sphaerodactylus nicholsi townsendi

Peter Island

* *Alsophis portoricensis*
Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
* *Anolis stratulus*
Arrhyton exiguum
Hemidactylus mabouia
Iguana iguana
Mabuya mabouya sloanei
Sphaerodactylus macrolepis macrolepis

Piñeros

Ameiva exsul
Anolis cristatellus wileyae
Anolis pulchellus
Anolis stratulus
Eleutherodactylus antillensis
Leptodactylus albilabris
Sphaerodactylus gaigeae
Sphaerodactylus macrolepis stibarus
Sphaerodactylus nicholsi townsendi

Piñeritos

Anolis cristatellus wileyae

Platillo (Morillito)

Alsophis portoricensis
***Ameiva exsul*
Anolis cristatellus cristatellus
Sphaerodactylus nicholsi townsendi

Prickly Pear Island

Ameiva exsul
Anolis cristatellus wileyae
Anolis stratulus
Sphaerodactylus macrolepis macrolepis

Protestant Key

Ameiva polops
Anolis acutus

Puerto Rico

Alsophis portoricensis
Ameiva exsul
Ameiva wetmorei
Amphisbaena bakeri
Amphisbaena caeca
Amphisbaena schmidti
Amphisbaena xera
Anolis cooki
Anolis cristatellus cristatellus
Anolis cristatellus wileyae
Anolis c. cristatellus X A. c. wileyae
Anolis cuvieri
Anolis evermanni
Anolis gundlacki
Anolis krugi
Anolis occultus
Anolis poncensis
Anolis pulchellus
Eleutherodactylus richmondi
Eleutherodactylus unicolor
Eleutherodactylus wightmanae
Epicrates inornatus
Hemidactylus brooki
Hemidactylus mabouia
Iguana iguana
Leptodactylus albilabris
Mabuya mabouya sloanei
* *Phyllodactylus wirshingi*
Rana catesbeiana (introduced)
Sphaerodactylus gaigei
Sphaerodactylus klauberi
Anolis stratulus
Arrhyton exiguum
Bufo lemur
Bufo marinus (introduced)
Chrysemys decussata stejnegeri
Diploglossus pleii
Eleutherodactylus antillensis
Eleutherodactylus brittoni
Eleutherodactylus cochranae
Eleutherodactylus cooki
Eleutherodactylus coqui
Eleutherodactylus eneidae
Eleutherodactylus gryllus
Eleutherodactylus hedrecki
Eleutherodactylus karlschmidti
Eleutherodactylus locustus
Eleutherodactylus portoricensis
Sphaerodactylus macrolepis ateles
Sphaerodactylus macrolepis grandisquamis
Sphaerodactylus macrolepis guarionex
Sphaerodactylus macrolepis mimetes
Sphaerodactylus macrolepis phoberus
Sphaerodactylus macrolepis spanius
Sphaerodactylus nicholsi nicholsi
Sphaerodactylus nicholsi townsendi
Sphaerodactylus roosevelti
Typhlops granti
Typhlops richardi
Typhlops rostellata

Ramos

Ameiva exsul
Anolis cristatellus cristatellus
Anolis cristatellus wileyae
Sphaerodactylus nicholsi townsendi

Sail Rock

Sphaerodactylus macrolepis macrolepis

St. Croix

* *Alsophis sancticrucis*
* *Ameiva polops*
Anolis acutus
Bufo marinus (introduced)
Eleutherodactylus antillensis (introduced?)
Eleutherodactylus lentus
Eleutherodactylus schwartzi (introduced?)
Hemidactylus mabouia
* *Iguana iguana*
Leptodactylus albilabris
Sphaerodactylus beattyi beattyi
* *Sphaerodactylus beattyi seamani*
Sphaerodactylus macrolepis macrolepis
* *Thecadactylus rapicaudus*
* *Typhlops richardi*

St. James

Ameiva exsul
* *Amphisbaena fenestrata*
* *Anolis cristatellus wileyae*
* *Anolis pulchellus*

St. John

* *Alsophis portoricensis*
Ameiva exsul
* *Amphisbaena fenestrata*
Anolis cristatellus wileyae
Anolis pulchellus
Anolis stratulus
* *Arrhyton exiguum*
Eleutherodactylus antillensis
Eleutherodactylus cochranae
Eleutherodactylus schwartzi
Geochelone carbonaria
* *Hemidactylus mabouia*
* *Iguana iguana*
Leptodactylus albilabris
* *Mabuya mabouya sloanei*
Sphaerodactylus macrolepis macrolepis
* *Typhlops richardi*

St. Thomas

* *Alsophis portoricensis*
Ameiva exsul
Amphisbaena fenestrata
Anolis cristatellus wileyae
Eleutherodactylus cochranae
Eleutherodactylus lentus
* *Geochelone carbonaria*
Hemidactylus mabouia
* *Iguana iguana*
Anolis pulchellus
Anolis stratulus
Arrhyton exiguum
Eleutherodactylus antillensis
Leptodactylus albilabris
* *Mabuya mabouya sloanei*
Sphaerodactylus macrolepis macrolepis
* *Typhlops richardi*

Salt Island

* *Alsophis portoricensis*
Ameiva exsul
Anolis cristatellus wileyae
* *Hemidactylus mabouia*
Mabuya mabouya sloanei
Sphaerodactylus macrolepis macrolepis

Salt Key

* *Ameiva exsul*
* *Anolis cristatellus wileyae*

Sandy Cay (near Tortola)

Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Sandy Spit

Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Savanna Island

* *Alsophis portoricensis*
Ameiva exsul
* *Anolis cristatellus wileyae*
* *Anolis stratulus*
* *Sphaerodactylus macrolepis macrolepis*

Scrub Island

Ameiva exsul
Anolis cristatellus wileyae
Anolis stratulus
Sphaerodactylus macrolepis macrolepis

Spiny Butte

Sphaerodactylus nicholsi nicholsi

Surprise Key

Anolis cristatellus wileyae
Sphaerodactylus nicholsi townsendi
Typhlops richardi

Tobago

Ameiva exsul
Anolis cristatellus wileyae
Hemidactylus mabouia
Sphaerodactylus macrolepis macrolepis

Tortola

Ameiva exsul
* *Amphisbaena fenestrata*
Anolis cristatellus wileyae
Anolis pulchellus
Anolis stratulus
* *Anolis sp.* (giant form)
Arrhyton exiguum
Eleutherodactylus antillensis
Eleutherodactylus cochranae
Eleutherodactylus schwartzi
* *Epicrates monensis*
* *Geochelone carbonaria*
Hemidactylus mabouia
* *Iguana iguana*
Leptodactylus albilabris
Sphaerodactylus macrolepis macrolepis
Typhlops richardi

Turramote Key

(Sphaerodactylus nicholsi nicholsi)

Vieques

* *Alsophis portoricensis*
Ameiva exsul
Anolis cristatellus wileyae
* *Anolis cuvieri*
Anolis pulchellus
Anolis stratulus
Bufo marinus (introduced)
Eleutherodactylus antillensis
Hemidactylus mabouia
Leptodactylus albilabris
* *Mabuya mabouya sloanei* (now probably locally extinct)
Rana catesbeiana (introduced) (J.E. Cooper, pers. comm.)
Sphaerodactylus macrolepis inigoi
Sphaerodactylus nicholsi townsendi
* *Sphaerodactylus roosevelti*

Villa del Mar

Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Virgin Gorda

Alsophis portoricensis
Ameiva exsul
* *Amphisbaena fenestrata*
Anolis cristatellus wileyae
Anolis pulchellus
Anolis stratulus
Arrhyton exiguum
* *Bufo turpis*
Eleutherodactylus antillensis
Eleutherodactylus schwartzi
Mabuya mabouia sloanei
Sphaerodactylus macrolepis macrolepis
Sphaerodactylus parthenopion
Typhlops richardi

Water Island

Ameiva exsul
* *Anolis cristatellus wileyae*
* *Anolis pulchellus*
* *Anolis stratulus*
* *Geochelone carbonaria*
* *Hemidactylus mabouia*
* *Iguana iguana*
* *Sphaerodactylus macrolepis macrolepis*

Watson Rock

Sphaerodactylus macrolepis macrolepis

West Dog Island

***Anolis cristatellus wileyae*
Sphaerodactylus macrolepis macrolepis

West Seal Dog Island

Anolis cristatellus wileyae
Sphaerodactylus macrolepis macrolepis

Appendix IV. Distribution of the scorpion *Centruroides nitidus* and the spider *Gasteracantha tetracantha* on the Puerto Rican Bank

Centruroides nitidus

Anegada
Beef Island
Big Hans Lollick
Big Tobago
Broken Jerusalem
Caja de Muertos
Cayo Diablo
Cayo Norte
Cooper Island
Desecheo
Eustatia
Fallen Jerusalem
George Dog
Great Dog
Greater Camanoe
Great Thatch Island
Guana Island
Hicacos
Jost van Dyke
Little Hans Lollick
Little Jost van Dyke
Little Thatch Island
Little Tobago
Magueyes
Marina Cay
Mosquito Island
Necker Island
Norman Island
Palominos
Peter Island
Piñeros
Prickly Pear
Puerto Rico
Ramos
St. Croix
St. John
St. Thomas
Salt Island
Scrub Island
Tortola
Virgin Gorda

Gasteracantha tetracantha

Anegada
Beef Island
Big Hans Lollick
Big Tobago
Cayo Diablo
Culebrita
Desecheo
Eustatia
George Dog
Ginger Island
Great Dog
Greater Camanoe
Great Thatch Island
Jost van Dyke
Little Camanoe
Little Hans Lollick
Little Thatch Island
Mosquito Island
Necker Island
Norman Island
Piñeros
Puerto Rico
Salt Island
Tortola
Virgin Gorda

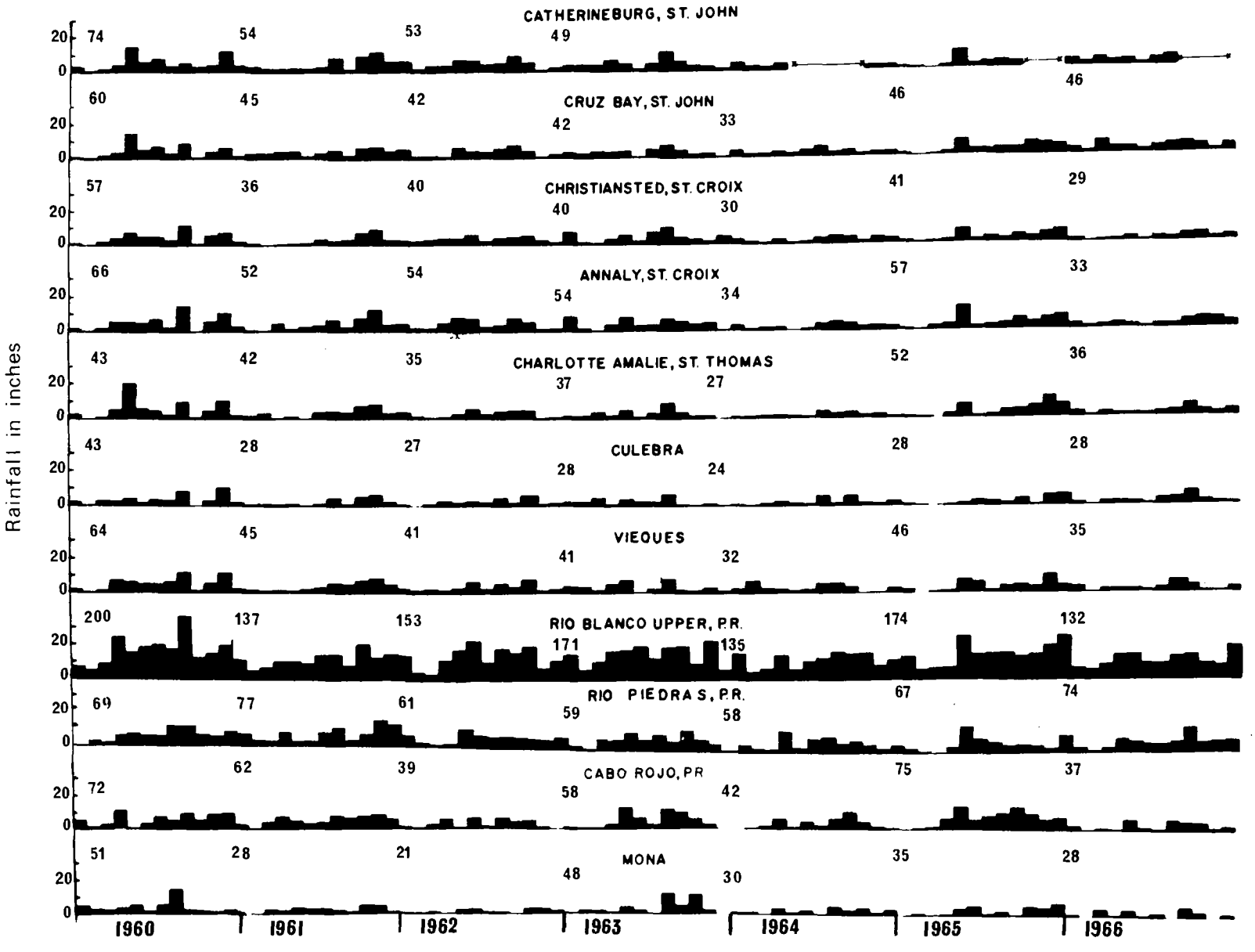


Fig. 2. Rainfall at various localities on the Puerto Rican Bank, 1960-1967. Data from Climatological Data Puerto Rico and Virgin Islands, Vols. 6-12 (1960-1967). Numbers above histograms indicate yearly totals.

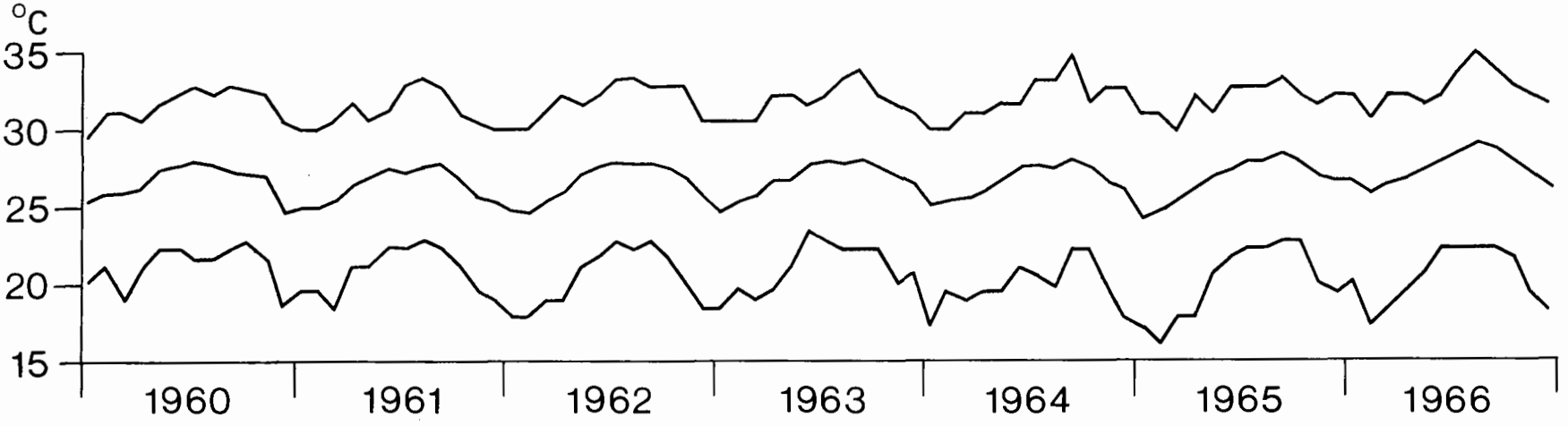


Fig. 3. Temperatures at Magueyes Island, Puerto Rico, 1960-1966. Upper line represents mean daily maxima, middle line the monthly means, and lower line the mean daily minima. Data from same source as that of Figure 2.

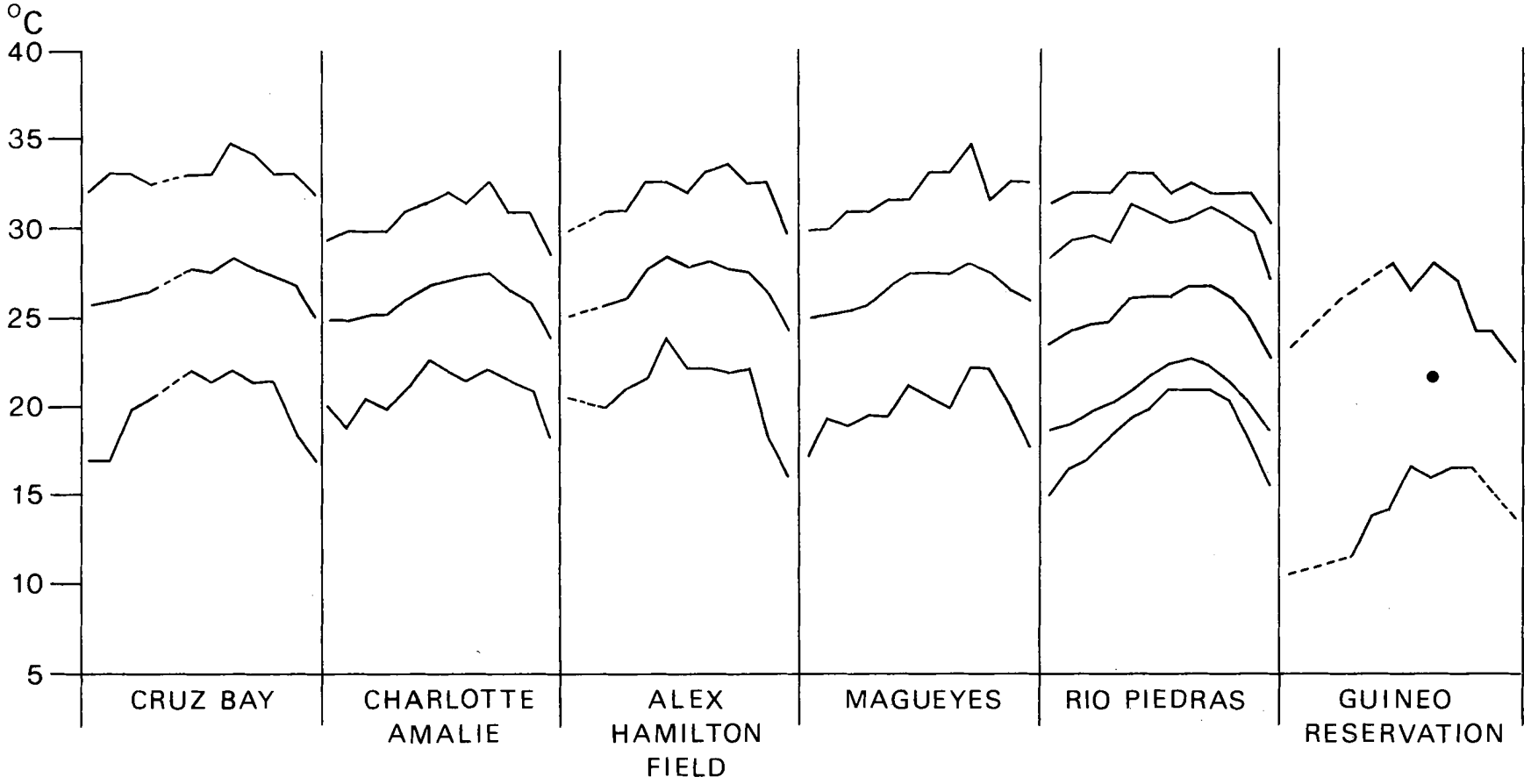


Fig. 4. Temperature at various localities on the Puerto Rican shelf during 1964. Crux Bay, St. John; Charlotte Amalie, St. Thomas; Alexander Hamilton Field, St. Croix; Magueyes Island, Southwest P. R.; Rio Piedras, coastal P. R.; Guineo Reservation, upland P. R. Dotted lines indicate missing data, dot the August mean at Guineo Reservoir. The upper and lower lines for Rio Piedras represent monthly maxima and minima respectively. Other symbols as in Figure 3. Data from Climatological Data Puerto Rico and Virgin Island, Vol. 10 (1964).

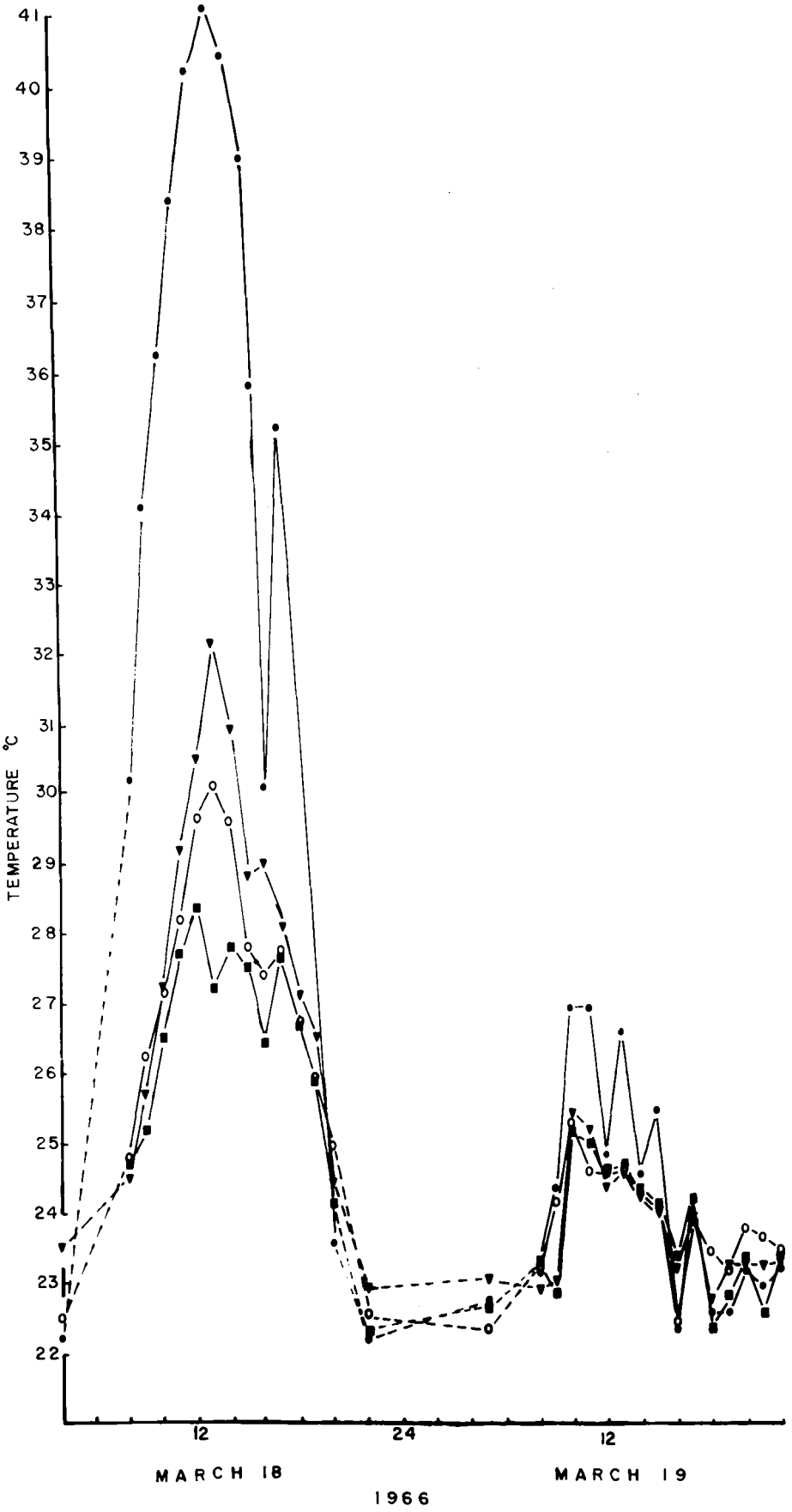


Fig. 5. Air and black bulb temperatures on Cayo Ahogado, P. R. Broken lines indicate intervals of more than 1 hour between measurements. Dots: black bulb temperatures 15 cm above the ground. Triangles: air, 1 cm above ground. Circles: air, 15 cm above ground. Squares: air, 1 m above ground

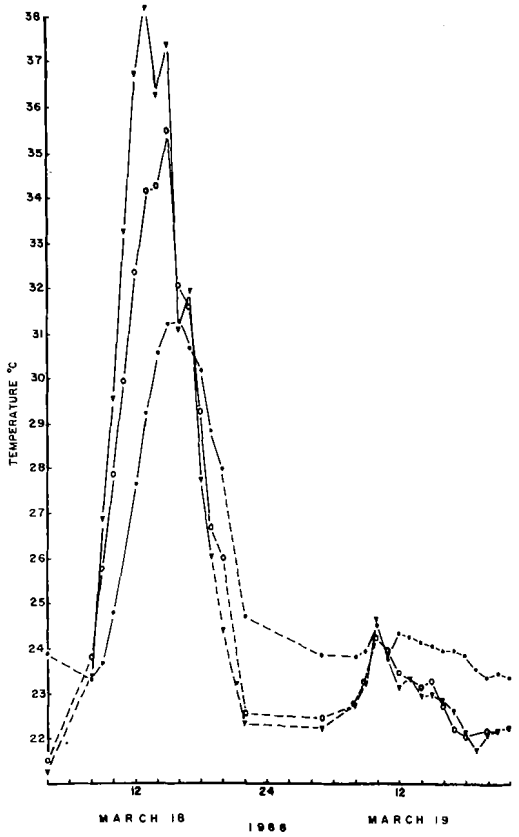
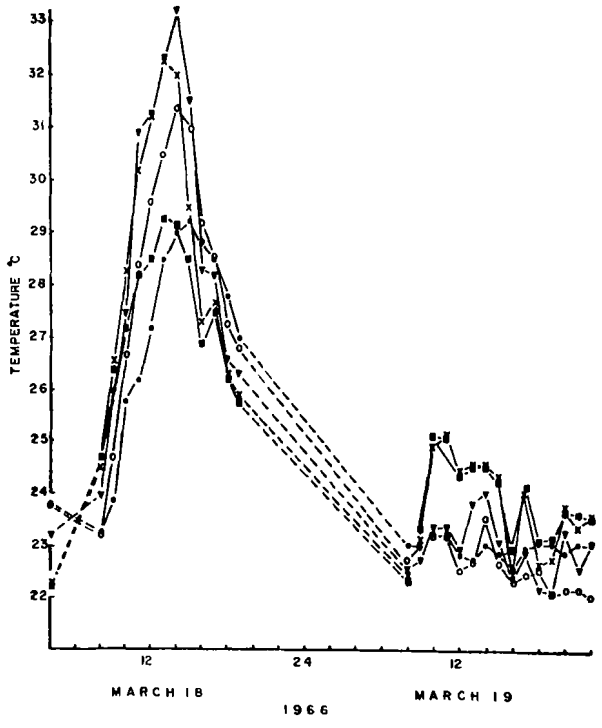


Fig. 6. Unshaded soil temperatures on Cayo Ahogado. Broken lines indicate intervals of more than one hour between measurements. Triangles: at soil surface. Circles: 1 cm deep. Dots: 5 cm deep.



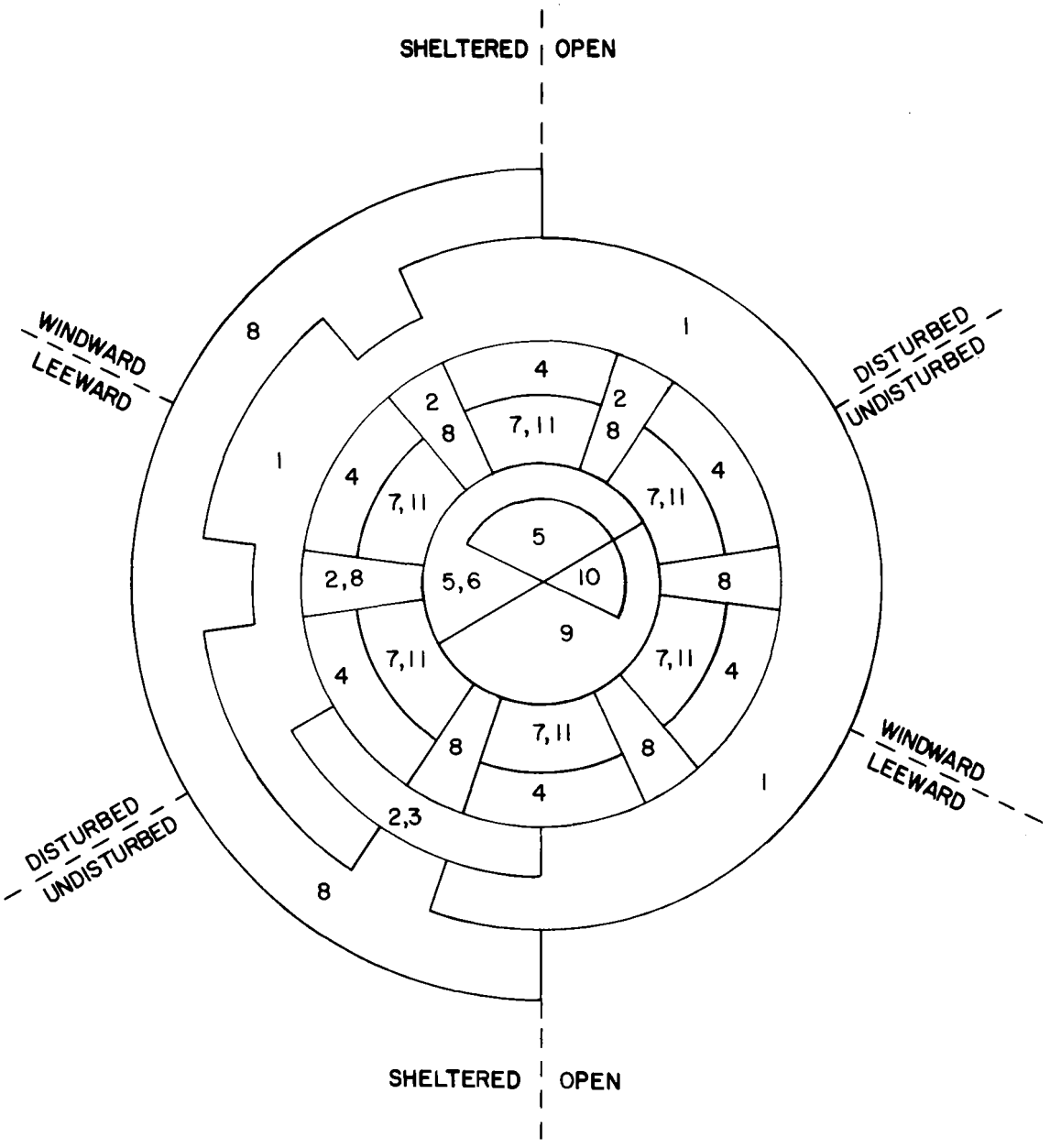


Fig. 8. Diagram-map of hypothetical island showing spatial relationships of numbered vegetation categories (described in text) to one another and to three environmental parameters. Three imaginary straight lines, whose termini are show and labelled, divide the island into two conditions each of wind exposure, wave exposure, and disturbance. Elevation increases towards the center. As islands increase in area and elevation, concentric rings are added from the center, beginning with the most marginal ring not yet present, thus progressively expanding the rings already present toward the outside. Relative areas are not to scale; e.g., most of the area of a large, little-disturbed island might be covered by moist forest (10).

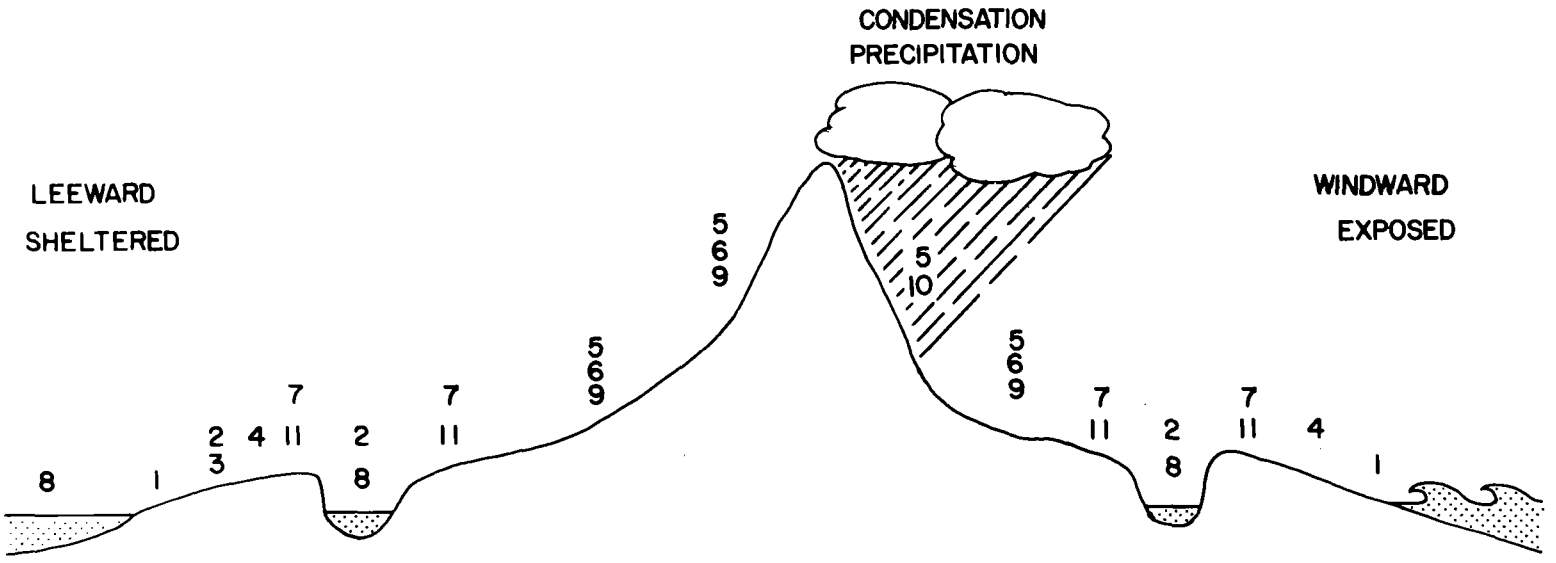


Fig. 9. Vertical section across a hypothetical island showing spatial relationships of numbered vegetation categories (described in text) to one another, distance from the sea, topography, elevation, wind direction, and wave exposure. Not to scale.