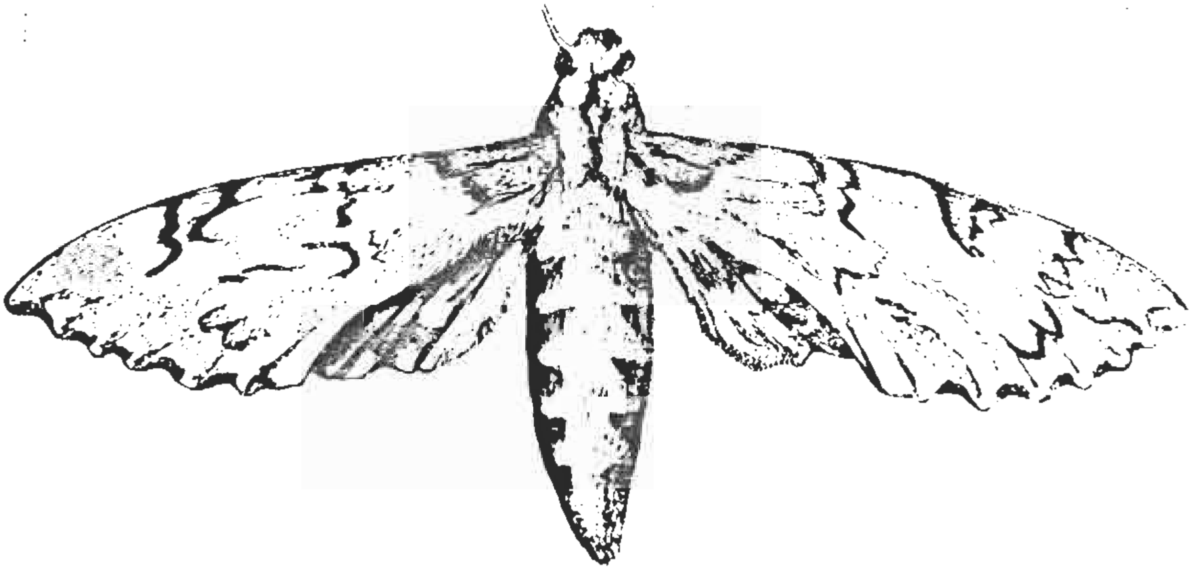
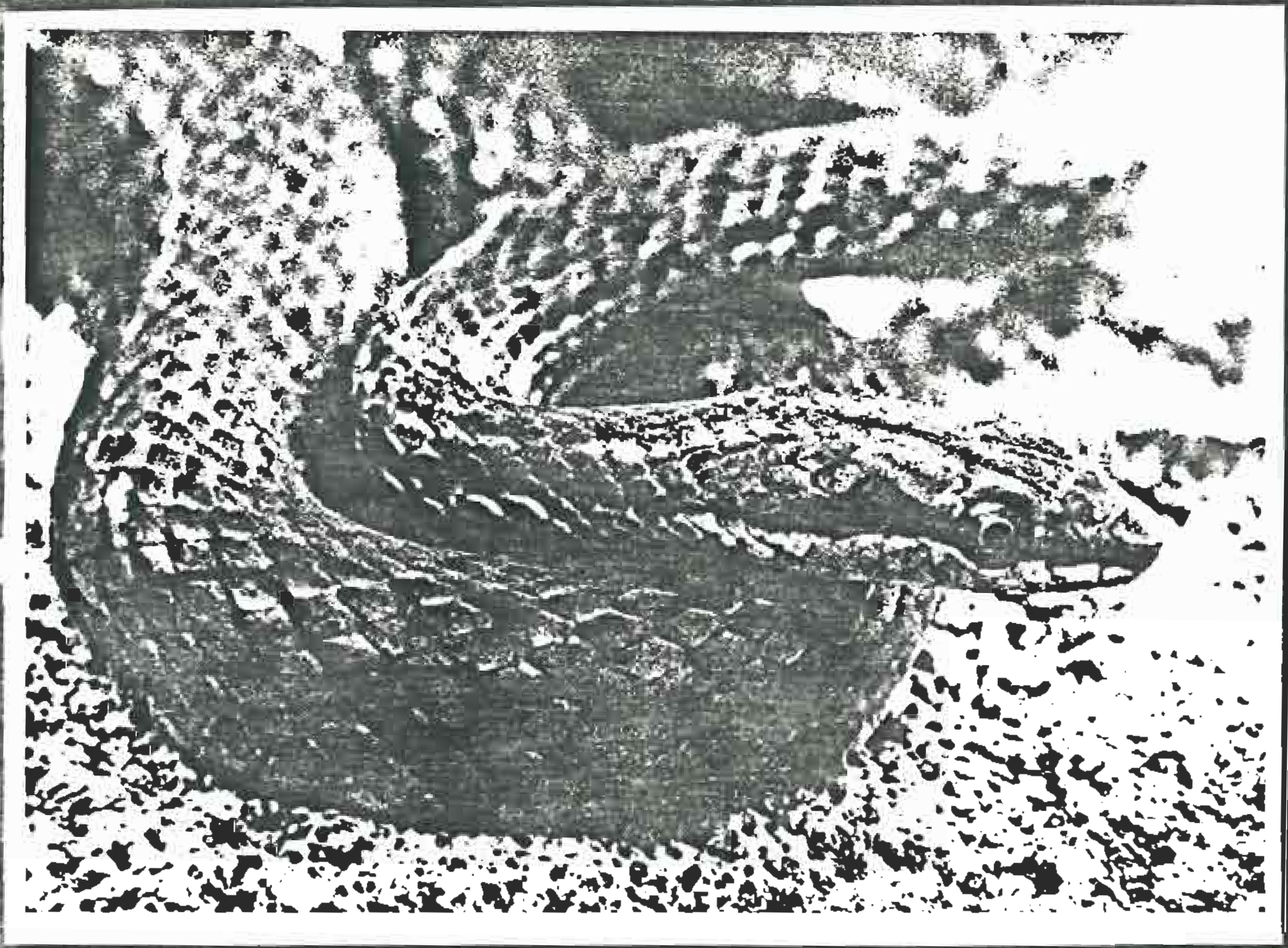
NATURAL HISTORY ON GUANA ISLAND



by J.D.Lazell



NATURAL HISTORY

ON

GUANA ISLAND

by

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"The richness and variety -- in a word, the diversity -- of natural ecological communities have never been more highly valued than they are now, as they become increasingly threatened by the environmental crisis. Students of what has come to be known as 'ecological diversity' realize that their work now has practical importance (indeed, urgency) in addition to the academic interest it always had."

Pielou, 1975.

"...empirical science is fundamentally a democratic process open to all who choose to acquaint themselves with the data."

McLoughlin, 1979.

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Front Cover: The great sphinx moth, *Pseudosphinx tetrio*, whose caterpillar, the Princeton worm, feeds on Guana's frangipani. Drawn by Ann Payne, life-size.

And the common snake, *Liophis portoricensis anegadae*. Photo by Jan Soderquist, 1½ life-size.

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  G. Evelyn Hutchinson: Homage to Santa Rosalia *or* Why Are There So Many Kinds of Animals?

  John W. Terborgh and John Faaborg: Saturation of Bird Communities in the West Indies.

  Robert M. May: The Role of Theory in Ecology.

  John A. Endler: Problems in Distinguishing Historical from Ecological Factors in Biogeography.

Back Cover: The Guana palm snail, *Hemitrochus nemoralinus intensus*, which disappeared from 1889 until 1982. Photo by Robert Ginsberg, four times life-size.

And the agglomeratic tuff formation called 'Guana Head, from which the Island takes its name. It really does look like a giant lizard's head. Photo by Jan Soderquist.

I. INTRODUCTION

Guana Island is a small, arid, essentially desert island with about four times as many species of animals naturally occurring on it as the emergent science of theoretical ecology predicted. These animals can have come to the island by any of three ways: they can have crossed water from other islands (and ultimately from continents); they can have been stranded here as sea level rose after the last glacial period; or they can have evolved here in isolation. The last alternative requires that their ancestors got here by one of the first two methods.

In 1859 the science of evolution emerged from natural history with the publication of Charles Darwin's _The Origin of Species by Means of Natural Selection_. There had been murmurings and false starts before Darwin, of course, but no one had set forth a rational, testable, provable scheme accounting for the diversity of life on earth until Darwin. A century later, in 1959, the science of ecology emerged from natural history with the publication of G. Evelyn Hutchinson's _Homage to Santa Rosalia or Why Are There So Many Kinds of Animals_? (See Appendix.)

Darwin provided the answer to the _how_ of species diversity by demonstrating a method which produces such diversity. Hutchinson asked the question _what sustains_ such diversity. He had inklings of answers, but a single, overall answer -- such as Darwin's natural selection -- remains elusive.

I cannot claim to have found it on Guana Island, but Guana is a most remarkable island because it harbors a far greater diversity of animal and plant species than has heretofore been thought likely for an island of its size. Guana's setting within the Virgin Island complex of the Greater Puerto Rico Bank places it in one of the most dynamic theaters of evolution on the planet today. Thus, Guana would seem to be ideal for an in-depth scientific study of natural history.

The Nature of the Task

"...why are there not more different kinds of animals?"

Hutchinson (1959)

"Practice has caught up with theory in ecology."

Odum (1971)

"...empirical studies lag far behind theory...."

Grant and Price (1981)

"...ecological theory...often runs ahead of observation."

May (1982)

A basic observation of field biologists and practical ecologists is that complex, natural ecosystems are more stable than simple and/or unnatural ones. This observation is a cornerstone of the conservation movement and underlies arguments for habitat and species preservation, no matter how pragmatically those arguments are styled (Ehrlich and Ehrlich, 1970; Harcombe and Marks, 1976; Myers, 1976; Eisner _et al_., 1981).

There are immediate problems, of course, in refining that observation. What is an "ecosystem"? What is "stability"? What is"natural" _vs_ "unnatural"? How many species make a system "diverse" _vs_ "simple"? A number of excellent books deal with these questions (Odum, 1971; Hutchinson, 1978; Krebs, 1978; Goudie, 1982), and a general, working concensus seems to have emerged, at least in qualitative terms. The undoubtedly apocryphal case of the snail and the sprig of pond weed sealed in a test tube, and exposed daily to sunlight, is much too simple and much too artificial an ecosystem to maintain stability for more than a few days. (In fact, even that system is vastly more complex than its describers pretended: snail, weed, and water are all necessarily hosts to a plethora of interacting, if microscopic, life forms.) A tract of Amazonian rain forest, on the day the first field biologists arrive, is certainly an example of a diverse and natural ecosystem. New England woodlots, or islands like Guana, fall somewhere in between. And we can be pretty reasonable about deciding on Guana's ecosystem status: it has an edge.

Unstable ecosystems are "bad" because they are apt to undergo increasingly turbulent oscillations in species and individual numbers, often with unpredictable corollary effects, and eventually "crash" to a condition of lifelessness, or greatly diminished life-supporting capacity. Humans vastly prefer stable ecosystems to unstable ones, because we rely on predictability for planning our lives, and because we are high-level consumers and do best in a life-rich environment. At a simple (and very artificial) level, we see modern agriculturists constantly exhorting their colleagues in more primitive or "less developed" countries to diversify agriculture. We believe, with excellent reasons based on historical precedents, that diversity in agriculture leads to greater stability in food resource availability and economics. Nevertheless, humans are the principal perpetrators of disastrous ecosystem simplification (often through agriculture). Krebs (1978) has given explicit consideration to many of the most infamous cases because they are de facto experiments in ecosystem instability and simplification.

Rigorous proof, in terms of mathematics and symbolic logic, for the diversity-stability relationship remains elusive. Indeed, no rational engineer or physicist would predict that a highly diversified system, complexly heterogeneous in both space and time, laced and bound by myriad interdependencies, would be more stable than a simple system. Therein lies one of the major dilemmas in trying to reconcile physical and biological scientists. Hutchinson (1959) noted of simple, natural, but highly unstable ecosystems such as the arctic tundra that cyclic instability "...may be due in part to the communities not being significantly complex to damp out oscillations." He believed MacArthur (1955) had produced a "proof" of the damping abilities of complex systems, but MacArthur was often wrong in his math, and was so in this case (MacArthur, 1972). May (1973) devoted an entire book to the problem. Gordon (1981) posed the admirable question of just what theoretical ecology has done to enable us to understand the real world (but does not answer it). Brown (1981) has articulated the general disappointment of theoretical ecologists at their failures, but points to brighter horizons. Indeed, Smith (1980) has considered the effects of environmental diversity (elevation, temperature, and humidity gradients) on animal diversity and stability; Tilman (1980) has explained some aspects of stable coexistence of species competing for resources; and McNab (1980) has explicitly dealt with energetics (but Brown, 1981, seems to have missed this paper). Probably the best available theoretical discussion is that of Lawlor (1980), who demonstrates that Monte Carlo and other models fail because real species interact in competitive ways that are very far from random. May (1976) shows some of the problems inherent in models; May (1982) also argues for the immediate pragmatic successes (despite occasional failures) of theoretical ecology.

While Guana Island is far more diverse than theory (e.g. MacArthur and Wilson, 1967) predicts -- and more diverse than most ecosystems actually studied in the past -- it is small enough for us to hope to come to grips with it. If there are to be real successes in theoretical ecology, which is after all nothing less than humanity's rational effort to comprehend life on earth, then those successes will probably emerge through study of places like Guana Island.

Methods

I first visited Guana Island with George Marler on 24 March, 1980, examined and photographed snakes, collected some lizards, noted the condition of the vegetation (fine, big trees in the ravines, but "overgrazing...severe"), and wrote down what people said about other sorts of animals and birds which I did not encounter. I returned with Dr. Robert Chipley, an ornithologist with The Nature Conservancy, on 11 April, 1980, and stayed (with trips off to the Camanoes, Scrub, and Marina Cay) through 13 April. We compiled more notes on lizards and birds, collected voucher specimens of the former, and explored some ravine woodland.

I returned to Guana on 3 March, 1982, and stayed until 10 April. I set up a pit trap grid in the woods at White Bay on 8 March, and, with the help of various Jareckis and friends, another in the North Bay woods by 16 March. Both grids were maintained until 9 April, when the pits were filled. Pit traps were checked at least every other day. Accompanied by various Jareckis, Guana Club guests, and occasionally staff, I hiked and scrambled over the island daily with the intention of visiting every part of the island at least three times. Some areas I only managed to get to twice, and some very steep slopes I did not traverse at all. Several people provided photo documentation of animals and habitats, especially Jan Soderquist, Robert Ginsberg, and Lee Durrell.

In all, we obtained specimens of two bats, a snake, and a lizard not previously recorded from the island, rediscovered a tree snail described in 1889 but without known geographic provenance, compiled notes on habitat, behavior, and ecology of seven species of reptiles, made estimates of four reptile populations by mark-and-recapture, located the second proven pelican nesting area in the British Virgins, collected numerous spiders, scorpions, centipedes and other invertebrates, and generally noted birds, vegetation, and other aspects of natural history. By April of 1982 I was quite convinced that Guana is even more interesting than I had thought it to be in March of 1980.

II. GEOLOGY, GEOGRAPHY, AND BIOGEOGRAPHY

Guana Island is steep-to and fairly rugged, rising to about 266 meters (m) at the highest peak, called Guana Peak or Sugarloaf. The planar area -- that is, calculated from linear dimensions off a flat map -- is about 297 hectares (ha). Thus the island falls on the curve projected by MacArthur and Wilson (1967) with those islands in the West Indies that should have three species of reptiles and amphibians. Since Guana certainly has 11 species, probably 12, and possibly even more as yet unsuspected, the island is immediately more interesting than most.

Theoretical ecology may not be a precise science, but neither is the world chaos. A wave-washed rock in the sea supports no land animals (like the lizards, snakes, and frog of Guana). A big island, like Puerto Rico, supports dozens of species (one can hear 14 species of frogs calling at one time in the rain forest of El Yunque). Surely it is sensible to predict that Guana Island falls somewhere in between. Of course it does. MacArthur and Wilson (1967) just failed (by a factor of four) to figure out where. In failing, these two did some scientifically quite unforgivable things -- like cull the data, selecting numbers that fit and discarding those that didn't (<u>cf</u>. Darlington, 1957, and Lazell, 1964). They also neglected some very important things about islands such as actual, <u>vs</u> planar, area.

Virtually all population biologists calculate animal (or plant) densities by planar areas. Obviously, it is much easier than getting involved in the abstruse realms of topology necessary to calculate real areas. On Guana, I have done this myself. I laid out trap grids on flat plains at White and North Bays; I figured snake numbers for the whole island and densities for the planar 297 ha. However, one should not be so simplistic. From elementary geometry (take a 3, 4, 5 right triangle, for example), we see that for smooth slopes between 35° and 40° the surface area increases about 20 percent. At a little over 45° of slope the area has increased 40 percent. At a bit over 57° of slope, the actual land surface (if smooth) is double what the planar area off a map would indicate. A cliff can have a lot of surface area, and be important habitat, but we cannot compute its area from its foot length and its 90° slope; we have to know its vertical dimension.

In theory, a computer should be able to give us a reasonable figure for actual surface area given an accurate topographic map (and integral calculus). In practice, I have found it some help to modify MacArthur and Wilson's (1967) simple formula

$$S = CA^z$$

(where S is the number of species, A is island area, and C and z are constants dependent on the sorts of animals considered -- such as birds vs frogs). I added in E for elevation (Lazell, 1983):

$$S = C_1A + C_2E + C_3AE + C_4$$

The third item, C_3AE, implies that there is some synergistic effect of elevation and area, greater than the simple additive effect. (Even so, my formulation is not any too accurate in the British Virgin Islands.)

The most apparent synergistic effect of elevation on area I could envision is the development of ravines on high, steep islands. Thus we would do well to consider the ravine effect on Guana. The most obvious thing the ravines on Guana have that the other slopes lack is an abundance of big trees. These produce shade, which conserves moisture. The ravines also accumulate humus and topsoil to a greater extent than the open slopes; this is both a cause and an effect of the big trees.

Plant Communities

The basic and focal reference to the flora of the British Virgin Islands is Beard (1945). This paper was published in February, 1945, in Trinidad. At that time German U-boats still lurked in the Caribbean, the French islands, at least, were still in essentially enemy hands, and supplies for printing and disseminating forestry bulletins were scant indeed. Very few copies of this work were apparently printed, and the only one to reach the U.S. seems to be that housed at the Yale Forestry Library (I have my own now, thanks to Xerox).

A reference which borrows heavily from Beard (1945) is Little, *et al*. (1976), describing Virgin Gorda. D'Arcy (1967) provides lists of plants for Tortola, many of which also occur on Guana.

Originally, most of Guana was covered by deciduous seasonal forest in two storys. The upper story, forming a canopy at 10-15 m, was probably dominated by "turpentine" or "gumbo-limbo", *Bursera simaruba*, and "dogwood", *Lonchocarpus latifolius*. Beard (1945) lists twelve principal species in this upper story forest, all present on Guana today. I tabulate them below, with the caveat that the vernacular names given are local and have nothing whatever to do with similar names given to North American temperate-climate trees.

TABLE I

Upper Story Forest Trees

Bursera simaruba (turpentine)
Pisonia subcordata (loblolly)
Lonchocarpus latifolius (dogwood)
Melicocca bijuga (genip)
Citharexylum fructicosum (fiddlewood)
Tabebuia pallida (white cedar)
Cordia sebestina (wild nut)
Hymenaea coubaril (locust)
Cordia alliodora (manjack)
Cordia sulcata (hog plum)
Tamarinda indica (tamarind)
Spondias mombin (prickle)

Three additional tree species are important on Guana today. The strangler fig, *Ficus citrifolia* (it is not clear in Little, *et al.*, if this is the same as their "bearded fig") and mammee apple, *Clusia rosea*, occur especially on the higher slopes, often in exposed, rock-jumble sites. In the lower ravines and on the flats behind the beaches one may still find manchineel, *Hippomane mancinella*. This tree is toxic to touch for some unlucky people, and its little green apples will kill any man. War was waged on it almost everywhere and survivors are few (there is a fine stand on the flat of Green Cay, on the way to Jost Van Dyke).

The understory in deciduous seasonal forest is of evergreen shrubs and dagger-like ground plants. I cannot attest to the presence of all those in Table 2 (below) on Guana, because I cannot identify some of them. Two species, however, the broom palm and the pinguin, form very special subcommunities on Guana and are given consideration under "Guana palm snail" and "frogs", respectively. Once again, beware of vernacular names.

TABLE 2

Understory Shrubs, Vines, and Ground Plants

Eugenia axillaris (white stopper)
Eugenia cordata (lather-berry)
Psidium amplexicaule (guava)
Leucaena glauca (white bush)
Pithecellobium unguis-cati (cat claw)
Guettarda scabra (greenheart)
Acacia macracantha (acacia)
Coccoloba uvifera (sea grape)
Chrysobalanus icaco (coco plum)
Randia aculeata (box briar)
Bumelia obovata (bitch)
Thrinax morrisii (broom palm)
Smilax coriacea (leather briar)
Dalbergia ecastophyllum (wood vine)
Agave missionum (dagger)
Bromelia pinguin (pinguin)
Fagara spp. (wild tamarind)
Croton spp. (marawn)

The last two of these, wild tamarind and marawn (or mechicky or croton) combine with several species of *Lantana* (*e.g.*, *L. urticifolia*, *camara*, and *involucrata*) and coarse grass, *Sporobolus virginicus*, to domin- parts of the island where the forest has been destroyed and over-grazing by sheep has prevented recovery.

A second natural community is cactus scrub. Formerly this dominated steep slopes, cliffs, and headlands. Destruction of the forest has benefited this community and it is more widespread on Guana than it naturally would be. Some very characteristic species are:

TABLE 3

Cactus Scrub Dominants

Cephalocereus royenii (tree cactus)	Urechites lutea (wild wist vine)
Opuntia dillenii (beavertail cactus)	Plumeria alba (frangipani)
Opuntia repens (jumping cactus)	Agave missionum (dagger)
Melocactus intortus (turks head)	Croton discolor (mechicky)

A third natural plant community, much persecuted and reduced on Guana, is mangrove swamp. It must once have dominated the salt pond, and battered examples of its characteristic trees (now mere bushes) survive. Conventional wisdom has it that mangroves harbor biting insects, and should thus be destroyed. Maybe so, but I don't know of any scientific documentation for that belief. Following Gleason and Cook (1927), there are five major species of trees and three succulent species of ground cover. The latter can be seen in profusion in the openings in the woods inside North Bay.

TABLE 4

Mangrove and Salt Flats

Rhizophora mangle (red mangrove)	Annona palustris (pond apple)
Avicennia nitida (black mangrove)	Batis maritima (brine bush)
Laguncularia racemosa (white mangrove)	Sesuvium portulacastrum (camphor)
Conocarpus erectus (buttonwood)	Portulaca oleracea (portulaca)

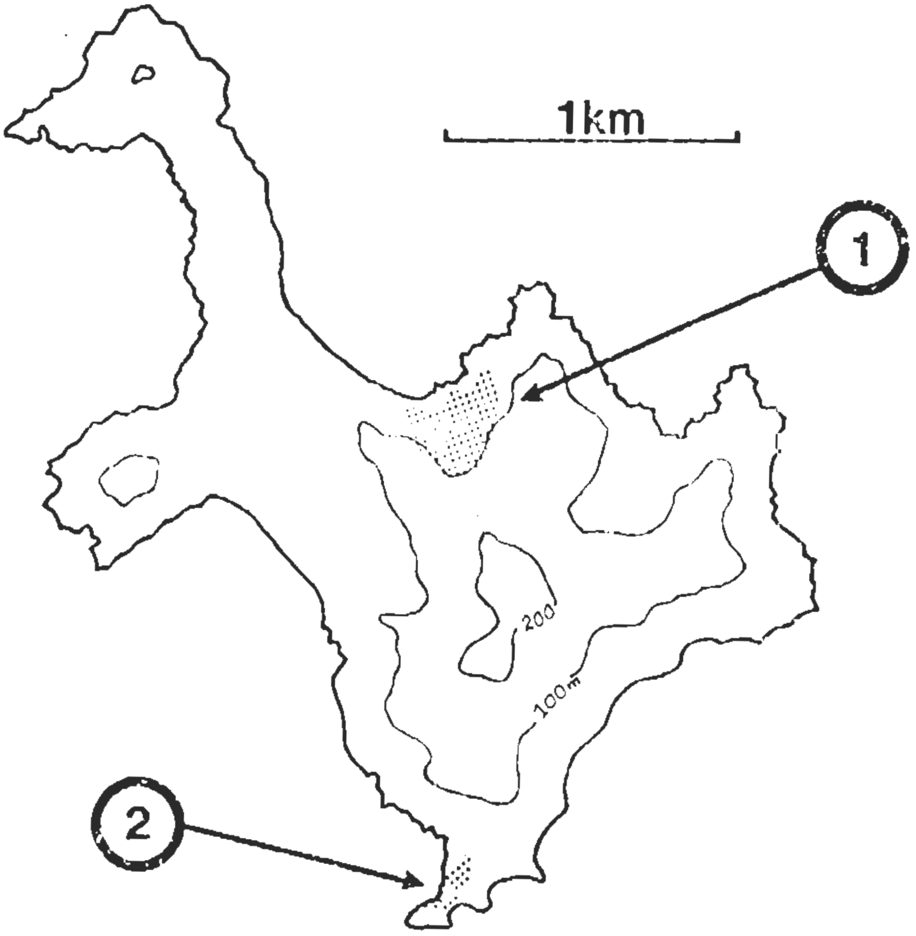
Several highly interesting components of the flora may be mentioned. The sword fern, Nephrolepis exaltata is listed by Little, et al., as a rare plant. It is fairly common on Guana, with beautiful big specimens growing from the moister depths of rock outcrops and jumbles right to the Peak.

Everywhere in the forest and cactus scrub one sees a profusion of wild pines, the bromeliad Tillandsia recurvata (North American spanish "moss" belongs to the same family and genus).

The woods on the North Bay flats are dominated by seagrape, *Coccoloba uvifera*, home to huge colonies of termites. I suspect this woods was once dominated by manchineel and that the seagrape giants are a fortuitous expansion. The situation is, however, unusual in the Antilles.

The only endemic species of plant yet described from the British Virgins is "mountain croton", *Croton fishlockii*. It was first discovered by an Englishman, Walter Charles Fishlock (1875-1932), in May, 1919, on Gorda Peak, Virgin Gorda. Fishlock ran the Agricultural Experiment Station in Road Town, Tortola, for many years. The plant was named in his honor by Nathaniel Lord Britton in 1920. I would not bother to mention this botanical oddity except that it has recently been discovered on Great Camanoe (Little, *et al.*, 1976). It thus may very well occur on Guana. Some enterprising botanist ought to find out how to identify it and conduct a search.

In general, the vegetation of Guana is far better preserved than is that of most of the world's dry islands. Apparently much of the steeper portions escaped clearing for agriculture in the heydays of the seventeenth and eighteenth centuries, and goats have been off the island for nearly half of this century. The good condition of the vegetation may well have a direct bearing on the diversity of animal species found on Guana.



Two unusual plant zones on Guana:

1. Broom palm understory subcommunity (Thrinax morrisii).
2. Pinguin thicket; pinguin (Bromelia pinguin) is a tough, rather brittle, large, and very thorny ground-dwelling bromeliad or wild pine.

Geology

I am not at all a geologist, but fortunately Dr. Ed Olsen, Curator of Geology, Field Museum of Natural History, was on Guana during part of my 1982 stay. He collected samples of rock from the top of Sugarloaf, the Pyramid, the bat caves, and North Bay outcrops. I am indebted to Dr. Olsen for his identification of these samples and his analysis of geological processes on Guana.

The island is largely made of Upper Cretaceous igneous extrusives -- rocks resulting from volcanic activity so long ago that the classic morphologies of the volcanoes are long gone. Thus, we do not see craters or calderas; there are no fumaroles or sulfur vents; and there are no basalt spires such as one sees in the Lesser Antilles proper (where many volcanoes are still active). Most of Guana's rocks are more than seventy million years old. Dr. Olsen identified three major sorts of rocks:

1. Andesite flows. -- This rock is related to basalt on the one hand and rhyolite on the other. It is produced directly from eruption on the surface of magma from the Benioff or seismic zone beneath the crustal plates of the earth's surface. The normal pattern is for the sedimentary shell of continental strata to be reworked by upwelling magma (Holmes, 1978; Berkner and Marshall, 1972). The greater the depth of origin of the andesite flow, the greater the amounts of silicon dioxide (SiO_2) and potash (K_2O) in the andesite (Holmes, 1978, p. 664-5).

Andesites vary from 55-60 percent SiO_2 and from $<$ 1-4 percent K_2O. Basalts are dark, rich in ferromagnesian minerals, and poor in SiO_2 . Rhyolites are pale, poor in ferromagnesian minerals, and rich in SiO_2. Andesite is intermediate (Holmes, 1978; Stearns, 1972). The Guana andesite contains the mineral augite -- basically calcium, magnesium, iron, and silicondioxide -- Ca (Mg, Fe) SiO_2 -- with aluminum added. Augite andesites are the abundant flow rocks of the Virgin Islands and are not rich enough in aluminum or other valuable metals to be worthy of mining effort. The question of the origin of these rocks vis-a-vis plate tectonics and biogeography will be addressed below. Andesites are porous and trap ground water (Stearns, 1972).

2. Tuffs. -- These very abundant rocks are made of volcanic ash, often with bits of larger debris. They may look like conglomerate (or concrete with pebbles in it). Dr. Olsen recognized two sorts: welded tuffs, in which the ash was so hot at time of formation that it is cemented into durable rock, and agglomeratic tuffs -- which contain chips of andesite and other minerals. The tuffs are of the same age as the andesite, or slightly younger (for those which contain andesite chips).

Stearns (1972, and works cited therein) reports tuffs -- especially the agglomeratic ones -- to be very differentially porous to water. Thus one would expect very different rates of erosion, expansion, and contraction within areas or seams of a given bed. This feature is presumably responsible for such striking geological features of Guana Island as the undercut ledges -- like Guana Head -- and the numerous dome caves -- like the bat caves. The climate of the Antillean region -- indeed of the tropics in general -- was far wetter during a period of great glaciation, such as the Würm or Wisconsin glaciation of about 50-12 thousand years ago. Since then we have experienced "climatic deterioration" (Lazell, 1966, and works cited therein): the tropics have got drier (and possibly hotter, too). Since the last great glaciation was only one of a vast succession of similar cyclic climatic phenomena, presumably more or less spanning Tertiary time, and the last 70 million years at least, there has been ample opportunity for the caves and ledges to form.

Why Dr. Olsen and I reject sea level rise and wave erosion as the architect of the caves will be apparent below.

3. Conglomerates. -- These are true sedimentary rocks and scarce on Guana. They are made of wave-worn, rounded rocks and pebbles cemented in a sandy or limestone matrix. They can form very rapidly (Higgins, 1968; Ginsburg and James, 1974). During previous interglacial periods sea level was considerably higher than it is now. Coralline algae, corals themselves, calciferous bacteria, and sand overlay areas now dry land, and in these areas conglomerates could form. The slow way is by simple compaction of material beneath water and an overburden of less consolidated sediments. The fast way is by cementation using organic materials in the algal and bacterial cells themselves -- essentially glue. In either case, the true conglomerates visible on Guana today are all relatively close to present sea level, and best developed at the edges of the flats at White and North Bays. They were both largely created and largely preserved in shallow areas of high sedimentation and low turbulence.

There are several peculiar features of Guana's geology that one might wish to ponder. For example, there is a large scree of coral on the southeast side of Long Point at about 100 m elevation. Since sea level never stood this high, and since any traces of the last interglacial's corals would surely have washed away (rain water is always slightly acidic and coral dissolves very quickly if exposed to it), <u>somebody</u> must have put all that coral up there rather recently. I wonder who and why.

If we have explained the erosional collapses that made the bat caves (and similar features), we have not explained what emptied the caves out.

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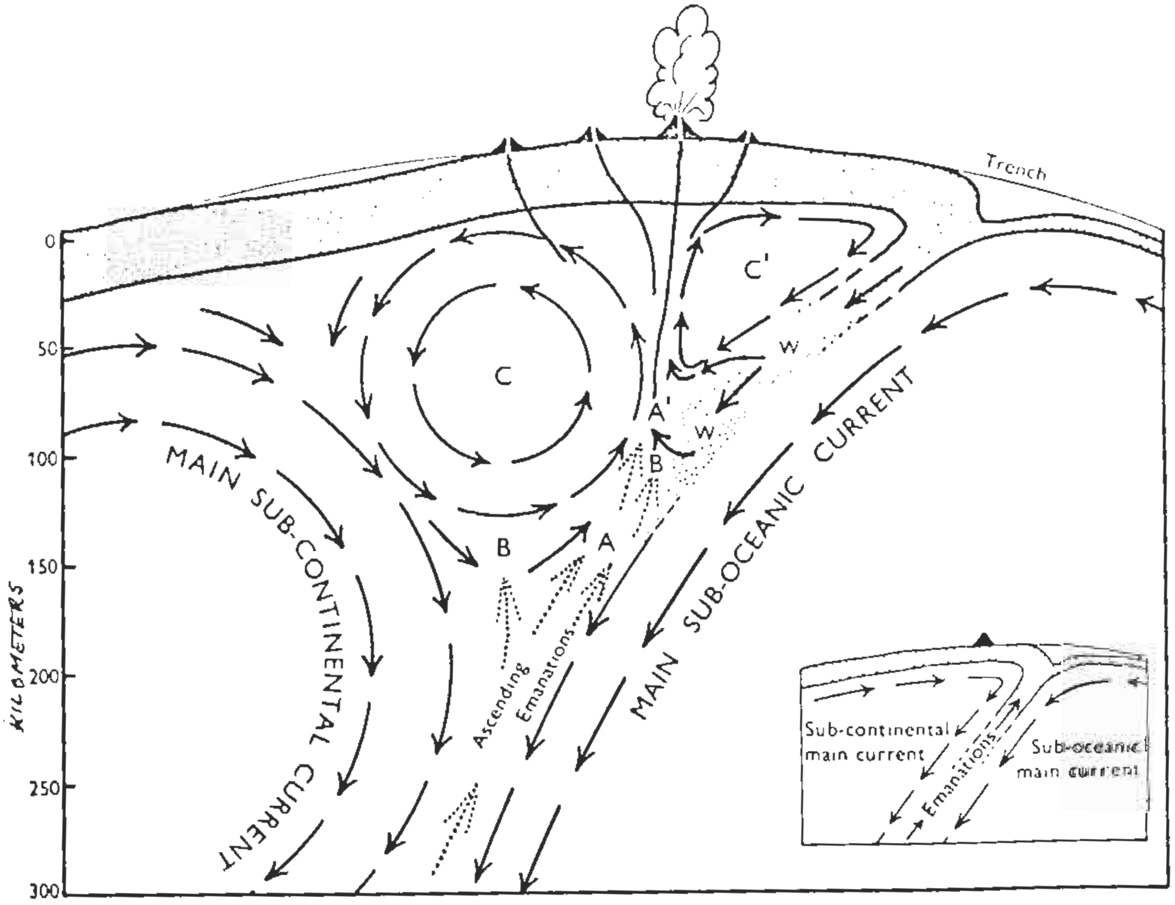
Why do we today find them with relatively smooth, often earthen floors? Why are they not just filled boulder jumbles inside?

Since sea level did indeed stand higher during the last interglacial -- called the Sangamon -- by as much as ten meters, for as long as 60 thousand years (Flint, 1971, e.g., p. 455), why do we see so little evidence of it? In most parts of the world there are obvious benches cut by higher sea level and flattened by wave action. Often large caves standing well back at the inland edges of old, stranded, beach flats attest earlier sea level and wave action. Guana's numerous caves appear at all elevations, quite without beach flats or shelves before them, and often (as with the bat caves) far higher than sea level could ever have stood. The sea seems to have had rather little effect on Guana Island.



(explanation, next page)

Diagrammatic section across the Andesite Line and a typical island arc to illustrate a speculative arrangement of convection currents which might account for the origin of andesitic lavas and their associates.

The small inset diagram indicates the downturn of the major currents along the belt of intermediate and deep earthquakes. Eventually the lighter and more mobile materials converge through a considerable range of depth, such as AA', to generate andesite. Being light and highly charged with gases, these will rise in a more nearly vertical direction to form the radial axis of a subsidiary convection cell CC'. Most of the crustal rock of basaltic composition is likely to be carried deeper into the mantle, but some, in situations like B, will become basaltic magma which may contribute to the generation of andesite.

From Holmes and Holmes (1978)

Biogeography

There is no quicker way to the heart of the fray that is theoretical biology than biogeography: consideration of the geographical distributions of living things. Charles Darwin got his start as a practical biogeographer. So did Alfred Russel Wallace, Darwin's co-author of the first evolution publication. And Dr. Hutchinson's poser is a biogeographical one: for us, 'why are there so many different kinds of animals on Guana Island?' The question has three broad facets.

The first, as we have seen, Darwin handily answered. Evolution by means of natural selection can generate vast numbers of species, given diverse selection pressures and ample opportunity for spatial isolation of populations for selection to operate on. Speciation can, in fact, be thought of as a natural result of the Second Law of Thermodynamics: increasing entropy. Nothing could be better for species production (called "radiation") than an archipelago of islands in a fluctuating sea. The West Indies in general, the Puerto Rico Bank in particular, and the British Virgin Islands in microcosm are great species producers.

The second facet, what sustains diversity, is Hutchinson's realm. We will work on it in Sections IV and V particularly.

The third facet is the realm of biogeographers: how did they get there? Many theories of biogeography, particularly of islands, have been developed in recent years. Endler (1982a) presents a succinct discussion of the major ones which (as a biogeographer) I feel I can further refine into five main threads of thought. Threads, of course, because they will eventually begin to interweave.

1. The deterministic view. -- This picture of the distribution of life argues that the kinds and numbers of species in any given place (island) are determined by a set of physical parameters such as length of time of isolation, distance to nearest neighbor, and -- especially -- area. MacArthur and Wilson (1967) were the initial proponents of this view, which they built by culling data from Darlington (1957), who had noticed rough trends in species numbers relative to island areas. This view instantly became immensely popular because -- if true -- it would enable us to understand biogeography in terms of simple, mensurable, physical (as opposed to biological) things: time, distance, size. It soon became apparent that time and distance really did not matter very much, because area really

determines species numbers (they argued). Species are highly prone to extinction on islands: just look at the historical record since the poor dodo. Similarly, species rapidly colonize islands and begin evolution towards new species. Undeniably true. So, theoretically, the longer an island (or swamp, or woodlot, or mountain) is isolated, and no matter how great its distance of isolation, sooner or later it will come to have the "right" number of species for each group of living things. An equilibrium between extinction and colonization will eventually develop.

2. The biological view. -- Within a few months of MacArthur and Wilson's publication many seasoned field biologists -- infuriated by this simplistic view of life -- rallied to show, in case after case, that the theory was not applicable. None did so better than David Lack (1976), the ornithologist who had made his name studying Darwin's Galapagos finches. MacArthur and Wilson drew heavily on data for birds, reptiles, and amphibians, especially from the West Indies. Lack dealt with the land birds of Jamaica. I (Lazell, 1976) dealt with reptiles and amphibians of New England, and subsequently (Lazell, 1983) the same two groups in the British Virgins. The viewpoint developed was that the presence of a particular species in a given place has to do with the special features of that species (i.e., ability to stand salinity, or cold, or dry spells), the ecological relationships of the species to others it encounters (i.e., who it eats, who eats it, who competes with it), and vast amounts of highly chancy history. This view is repugnantly unpopular because it says, in effect, all theories are worthless; only empirical observations will do. No two cases are the same. Everything imaginable matters, or might. At the very least, to explain lizard distributions in the West Indies, I need an annotated time table,

with charts, for all hurricanes during the Würm glacial maximum, ca 50-12 thousand years ago, when sea level was 100 m lower, land areas were much larger, and distances were very short.

3. The classic view. -- This is the view promoted by the great biogeographers of our century, such as Simpson (1965), Darlington (1957), and Romer (1966). Darwin would have felt right at home with this school of thought. These are men with incredible knowledge of animal life -- vertebrate and invertebrate -- geology, and the fossil record. They acknowledged great changes in the earth: glacials and interglacials; mountain building revolutions and trench making folds and faults; and the emergence and submergence of land areas. They assumed that some land areas, like Siberia and Alaska, would be broadly united by dry land at some times in history, but other land areas, like the Virgin Islands and the Bahamas, could never have been connected by dry land. They explained the distribution of life on earth by the origin of new, well-adapted species succeeding numerically and territorially, radiating into novel genera and families, dispersing and displacing competitors, and -- in turn -- giving way to newer, even better adapted models. Of course, since things change, those well adapted today may be hopelessly maladapted tomorrow, just by failing to change. And, all sorts of seemingly maladapted oddities might survive on islands, at the tips of long peninsulas, or up in some remote mountain range, just because their novel competitors failed to reach them.

Proponents of this view would usually find it easy to distinguish between a truly oceanic island's fauna and that of a land bridge island. The former would tend to have fewer species, all of groups that colonize over and across water well, and would be apt to have radiations of closely related species, occupying diverse niches, paralleling to some extent the mainland situation of communities of distantly related species. Any area open to colonization across dry land -- a land bridge island -- would tend to have a larger representation of mainland species including some, like salamanders, ungulates, carnivores, and primates which are essentially incapable of crossing sea water; radiations of close relatives are not at all likely here.

The Galapagos are, in the finest classical sense, oceanic islands. Their animals seem derived from a small number of single colonization events: a finch, a tortoise, an iguana, etc. These few colonizers, in a virtual competitive vacuum, underwent radiations producing an assortment of species occupying diverse ecological niches.

The northeastern coastal islands off the United States -- Long Island, Martha's Vineyard, Nantucket, and a dozen smaller neighbors -- are classic land bridge islands. They have salamanders, deer, foxes, raccoons, etc. -- and previously had wolves and bears in some cases. There has been some differentiation of populations since isolation, but no great radiations.

4. Bridge builders. -- Of course land bridges have been and are very real. The Panama land bridge has kept North and South America united for some millions of years now. The Bering land bridge must connect Asia and North America every time sea level drops during a glacial period. In general, all land areas separated by seas shallower than about a hundred meters become continuous with each other at a glacial maximum. Thus, the Virgin Islands (except St. Croix) are at times one with Puerto Rico (but Puerto Rico cannot, by this method, connect to Hispaniola, St. Croix, or even Mona: the water is too deep). The dedicated bridge builders, however,

are far from satisfied with such readily demonstrable land continuities. They argue for major tectonic events in the earth's crust that have produced dry land over great areas of today's deep water. They claim the presence of a single species on a remote island is evidence of a previous land bridge. In the West Indies the geologist Schuchert (1935) was a major architect of grand land bridges of the past. Two biologists, Thomas Barbour of Harvard (a bridge builder) and W. D. Matthew of the American Museum, New York (a classicist) developed a lengthy polemic over just what the animals of the Antilles do indicate about the geological history of the area. A summary work (Matthew, 1939) includes the major relevant papers of both. Matthew seemed clearly to have won, but he couldn't have known what would pop up next.

5. The proponents of continental drift. -- In the last few years continental drift has enjoyed a vast resurgence in popularity as an explanation for the distributions of plants and animals. No one doubts that continental drift has occurred, but the timing is crucial. Hurlburt (1976) provides an account of the now current and popular view, which bases the continental unity on fossils of a reptile, Mesosaurus, which flourished about 250 million years ago. It is interesting to note that much of the geological evidence depends on this fossil reptile as a starting point. If Mesosaurus were 600 million years old, the geologists would calculate very different (less than one-half speed) rates of sea floor spreading and drift.

Mesosaurus represented an order of primitive aquatic reptiles attaining lengths of about a meter (Romer, 1966: 116-117). Given the facts that much smaller, highly terrestrial lizards like skinks and geckos -- as well as much larger, but less aquatic crocodiles -- occur in both Africa and the New World tropics today, some of us do not think Mesosaurus a very good indicator organism.

Whatever the histories of Africa and South America with respect to each other, the notions of continental drift become important in the Antillean-Caribbean region only because of the theories of Rosen (1975). He maintains that the islands of the West Indies are fragments of a great Central American land mass which broke up just a few million years ago, while drifting eastward. He envisions his land barges (my term) carrying with them the mammals, reptiles, amphibians, birds, and even inshore fishes that live in the West Indies today. This view maintains that the animals did not disperse to the islands, but rather the islands -- carrying animals -- dispersed to where we find them today. Rosen uses exactly the same evidence for his theory that the bridge builders used, and that the classicists used to defeat the bridge builders. Whenever there is no evidence to support Rosen's view, which is most of the time, he merely points out that this lack reflects the lethargy and ineptitude of those of us who should be out in the field collecting more evidence.

III. THE SPECIES STUDIED

I have concentrated my efforts on native land animals, and especially reptiles and mammals. Although I know little about invertebrates, I did collect some of the larger and more dramatic ones for distribution to my colleagues who work on them. This has produced some remarkable results, noted below. I have also taken an interest in birds, especially those which nest on Guana (or might be expected to nest here). I give some consideration to exotic introduced animals (like rats and sheep) because they have affected the Guana ecosystem considerably.

Anole Lizards (Family Iguanidae)

By far the most conspicuous native land animals on Guana are lizards. There are very common ones and very rare ones, big ones and small ones, very well-studied ones and some we know virtually nothing about. All of them are found elsewhere in the British Virgins and elsewhere on the Greater Puerto Rico Bank.

Lizards' tails break off easily, and new tails -- regenerated, we say -- grow back again. Regenerated tails are not as big as the originals. Because of this, we do not usually worry much about the total length of a lizard -- tail included. We generally consider the snout-to-vent length (SVL): tip of the snout to cloacal (or "anal") opening or vent.

I did not collect series of specimens of lizards on Guana Island because I was studying the animals alive. Thus, my comments on size, stomach contents, etc., are based on specimens collected from other, close-by islands (and often collected years ago). First I consider those lizards often called "chameleons" (an African group in reality), but properly known as anoles.

Crested anole: Anolis cristatellus wileyae. -- If this is not the most abundant animal on Guana Island it is certainly the most conspicuous. The males grow to about 70 mm SVL, and females to about 50 mm. Tail included, a big male goes about 160 mm (less than seven inches). The adult males average a little less than five grams, and females average less than two grams.

Adult males of the crested anole perch, often in a head-down position, on trees, shrubs, walls, and like, often in very conspicuous places. They are basically brown, and can show a fair amount of pattern. They have grand, sail-like crests on their original tails (which do not grow back on regenerated tails). They can voluntarily elevate another crest on the neck called the nuchal crest. Courtship, combat, and territorial defense are accompanied by extension of a large throat-fan or dewlap; it is yellow-green with a crimson border.

Display of the throat-fan is usually accompanied by push-ups, head-bobbing, and tail lashing -- especially when one male's display is answered by another's and tempers (over who owns which rock or tree trunk) flare. Anoles in general are among the finest animals in the world in which to study territorial behavior.

Female crested anoles -- much smaller -- also have throat-fans, similarly colored. They do not have much of a tail crest and scarcely any nuchal crest. Like the males, they are brown, but they have a well-defined ashy-white or buff stripe down the middle of the back (so do juvenile males). Most people mistake male and female crested anoles for two different species. Females also bob and display their little fans, and are only a bit less territorial than the big males.

The tails of anoles are thoroughly worthy of study. Not only do they break off readily and writhe and flip, but they are a great aid (prior to detachment) in balance. Ballinger (1973) studied the tail as a balancing organ in the crest-less Anolis carolinensis. He also considered (Ballinger, 1981) the role of the detached tail: see house gecko, below.

Stomach contents of 10 specimens (four adult males, four adult females, and two juveniles) from Peter Island were mostly ants 2-5 mm in length (mostly 3 mm). They also contained beetles (including beetle grubs up to 18 mm), an orthopteran (? cricket), leaf-hoppers, whip-scorpion pincers (did the anoles eat whole whip-scorpions or just wrench off pincers?), small pebbles (1-1.5 mm), and plant material. The diet seemed to be less than ten percent plant material by item count, though about 12 percent by volume. Pebbles were less than four percent by count and only a fraction of a percent by volume.

Anolis cristatellus wileyae was originally described from Isla Culebra, east of Puerto Rico, by Major Chapman Grant in 1931. He named the form for Ms. Grace Olive Wiley. Both Major Grant and Ms. Wiley were prominent herpetologists and important contributors to our knowledge of New World reptiles, especially. Dr. Harold Heatwole studied geographic variation in anoles of the cristatellus assemblage throughout the Greater Puerto Rico Bank islands and on the Mona Bank. He concluded that all of the insular populations west of the immediate coastal cays off Puerto Rico proper -- throughout the Virgins to Anegada -- belong to the form A. c. wileyae. In my 1980 survey (Lazell 1980, 1983) I found this lizard on every rock and cay that supported any sort of lizard at all except on Carrot Rock, south of Peter Island. On Carrot Rock A. c. wileyae is replaced by a closely related, but differently colored and much larger, species: Anolis ernestwilliamsi Lazell (1983). This remarkable new species was photographed on Peter Island (where it may now be extinct) by Dr. Heatwole in 1960. He saw only one specimen, and lost it. It remained a mystery for 20 years until I climbed onto Carrot Rock in April, 1980. There it was in abundance.

I checked The Monkey just to be sure, but it's classic Anolis c. wileyae there too -- no surprises.

Saddled anole: Anolis stratulus. -- This species is also very common on Guana, but not very conspicuous. It prefers tree trunks; it does not perch for long periods in obvious places. Males grow to about 55 mm SVL, and females may approach 50 mm. The sexes are similarly colored, although young specimens often show a pale middorsal stripe. The basic color is pale greenish-grey or pale olive with short, dark saddles across the back. When disturbed, these anoles can turn dark brown; in this phase they usually show a reticulate (net-like) pattern of lighter brown, and the transverse saddles are nearly black. Both sexes have lovely orange throat-fans with rich yellow borders (smaller in the female), but are essentially crest-less.

Saddled anoles are vigorously territorial and show all the elaborate display techniques typical of the genus Anolis.

I weighed five saddled anoles from Puerto Rico and five from Norman Island (five of each sex); there was no arithmetically significant difference in weight (or SVL length) between the two localities. Males averaged 2.08 grams and females 1.35 grams. In general, sexual dimorphism is much less in A. stratulus than in A. c. wileyae; no one would mistake the sexes for different kinds of lizards, and most people have trouble telling the sexes apart.

Although saddled anoles were too scarce in the pit trap grids to develop any population density estimates, these little creatures were seen actively hunting food in great numbers in the big ravines, on rocks and low on tree trunks, especially early in the morning.

I checked stomach contents of ten specimens from the Puerto Rican mainland at Mayaguez (four adult males, four adult females, and two juveniles). Their diet was about 90 percent ants of $<$ 1 to 4 mm (average 3.5 mm). They also ate beetles, spiders, and orthopterans (crickets?) up to 12 mm. Plant material was about three percent of their diet by item count, but about ten percent by volume.

No one seems to have considered geographic variation in _Anolis stratulus_, first described by Edward Drinker Cope, of the Academy of Natural Sciences in Philadelphia, in 1861, on the basis of specimens taken on St. Thomas. In my survey (1980) I noted considerable variation in the degree of greenness, with some individuals being rather bright, light green. In 1982 I noticed some throat-fan color differences between Guana Island specimens and those seen alive south of Ciales in Puerto Rico. There is a very real possibility that a thorough study of this species would result in the description and naming of a new form or two; somebody ought to do it.

The name _stratulus_ is Latin and the diminutive form of _stratus_: saddle. It alludes to the little saddles -- the short, dark, transverse bars on the back so characteristic of this species. I invented the English name "saddled anole."

Grass anole: _Anolis pulchellus_. -- The status of this pretty little species (and that is exactly what _pulchellus_ means in Latin) on Guana is enigmatic. I have never encountered it. I found it only rarely on Tortola, but Gorman and Harwood (1977) found up to 20,000 individuals per hectare, with a biomass of 10 kg, on mainland Puerto Rico. Thus, in some localities, it may rank as the most abundant lizard on earth.

In grass anoles the sexes are rather similar. Males reach about 50 mm SVL, females about 45 mm. Puerto Rican males average 1.97 grams, females 1.33. These lizards have large heads and very long tails. They are basically yellow and brown, with a bold light stripe along the side of the body. The general Gestalt is elongated and slender. The throat fan, well-developed only in males, is bright red studded with white to rich yellow scales.

As their name implies, grass anoles perch on stems of grass, and on small shrubs and bushes. I have often noticed them only when they leapt from one stem to another. Their striped pattern blends in very well.

Major Chapman Grant (1932) collected a specimen of *A. pulchellus* from Guana Island in April, 1932. It is now in the University of Michigan Museum of Zoology (UMMZ), number 73904. The fact that I failed to find this species in my 1980 and 1982 surveys, however, means little because I worked during the dry season. *A. pulchellus* are probably rather short-lived little lizards, prone to great seasonal fluctuations in population. A thorough search of grassy areas on the White Bay flats in the wet season might well produce good numbers of this species. Of course, Grant caught his at the height of the dry season, too.

Stomach contents of six Tortola specimens (two adult males, three adult females, and one juvenile) were far more diverse than in the two previous *Anolis* lizards. Ants were about half the total by item count, but less than 40 percent by volume. *A. pulchellus* ate big ants, too: 2 to 6 mm individuals (average 4 mm). Flies and fly larvae were about ten percent of the diet by both count and volume. There were also a spider, a thrip, a true bug (Order Hemiptera), a grasshopper 13 mm long, and 16 unidentified insects 4 to 16 (average 5) mm long.

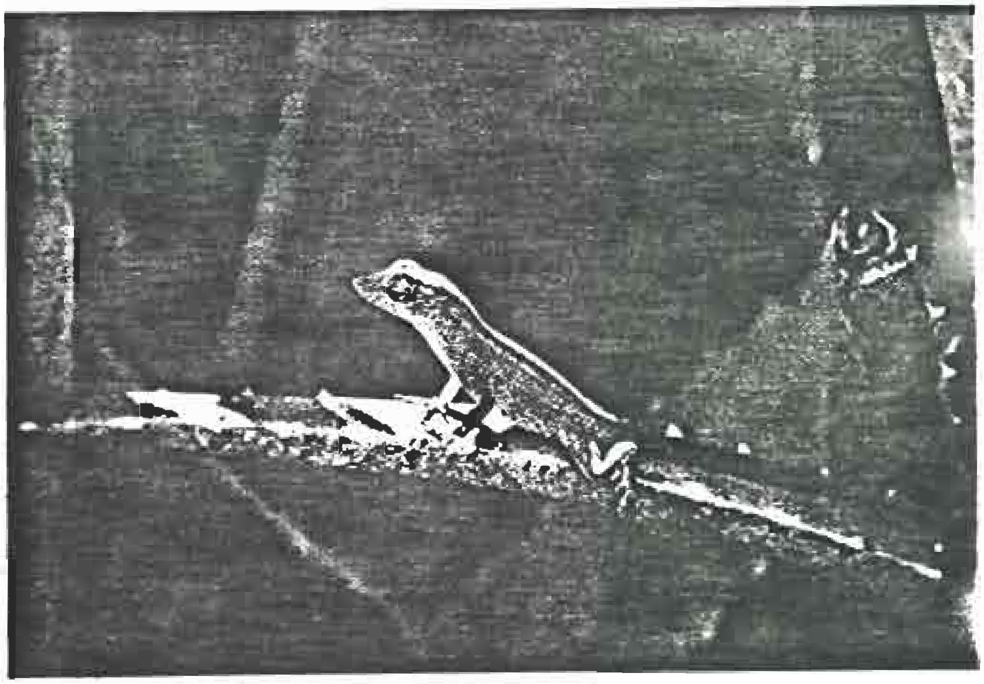
Anolis pulchellus is known from numerous specimens on the larger Virgins: Tortola, St. Thomas, St. John, and Virgin Gorda.

GUANA ISLAND LIZARDS I: THE ANOLES

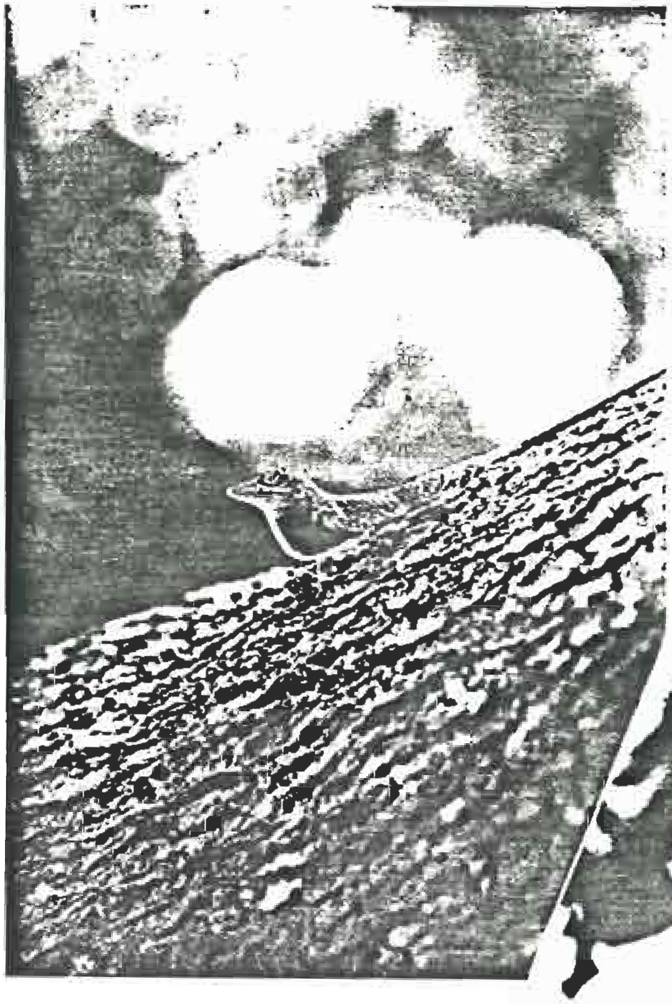
The crested anole, *Anolis cristatellus wileyae*. Adult male to the left, adult female below.

The male is "throat-fanning" in territorial display.

Both photos were taken on Guana by Jan Soderquist.



GUANA ISLAND LIZARDS I: THE ANOLES



The saddled anole, Anolis stratulus.

Adult male "throat-fanning."

Photo on Guana by Jan Soderquist.

Another adult male saddled anole. Data as above.

GUANA ISLAND LIZARDS I: THE ANOLES

The saddled anole, Anolis stratulus. This species usually frequents tree trunks and rocks, but this adult male has been caught out on a limb. The females look similar, but have smaller throat-fans. Photo on Guana by Jan Soderquist.

GUANA ISLAND LIZARDS I: THE ANOLES

The grass anole, Anolis pulchellus. This adult male was photographed "throat-fanning" by Dr. William MacLean on St. Thomas. The species is known from Guana only on the basis of Major Chapman Grant's specimen, UMMZ 73904, captured in April, 1932. It should be looked for in grass and low shrubs.

Geckos (Family Gekkonidae)

This family is virtually worldwide -- except in cold climates. Our two species are rather fleshy, tender creatures, apt to rip and tear easily when grabbed. Their tails may be dropped or flipped off even when not grabbed. Many geckos -- including ours -- lack movable eyelids, just like snakes. Some have external ears, some do not. Our house gecko has them, but not all woodslaves do -- or there may be an ear on one side, but none on the other. They have big toes.

House gecko: _Hemidactylus_ _mabouia_. -- This is a large pallid fellow (to _ca_ 8 cm, or _ca_ 3 inches, SVL) who would much rather be inside than out. Its generic name means "halved toe" and refers to the fact that broad scales under toes are divided down the middle into two ranks; these scales are called _lamellae_ and provide great grip for the lizard. The species name, variously spelled, is a standard Antillean Creole word for lizard and may have come from Africa. Indeed, the origin of the house gecko is believed to be the Old World tropics and it is not known (or at least hotly debated) how long it has been present in the West Indies. The prevailing view is that it got here on ships in post-Columbian time. It is said that it did not reach Anegada until the importation of building supplies a mere decade ago (Carey, 1972). In any case, this house gecko is now found virtually throughout the tropical and subtropical world. Its dispersal has certainly been one of the great biogeographic feats of all time; to quote Roger Conant (1975): "The speed with which this species has expanded its range...in recent years is even more remarkable than the spread of the cattle egret. The bird has wings...."

Although certainly not unexpected, the house gecko was the first reptilian new record I got on Guana, in 1980.

The sexes of house geckos are very similar; males have the tail base swollen, especially at the sides of the ventral surface, where the paired copulatory organs -- hemipenes -- lie. In females the tail tapers smoothly. The average weight of five adults (mixed sexes) from Tortola was 5.3 grams. Stomach contents for this series included less than ten percent ants, but more than 20 percent dipterans (flies and mosquitoes). House geckos take large prey, up to a 13 mm roach and a 10 mm grasshopper. Other identified items included a 6 mm robber fly and a 2.5 mm beetle. The average prey size was 4.6 mm. No vegetable matter was found in the stomachs of house geckos.

These geckos have remarkable tails. Ballinger (1981) has effectively questioned the standard belief that detached tails wiggle and writhe to attract the attention of the predator -- so that the lizard itself may escape. He notes an iguanid lizard species in which the tail does not writhe, contains very little fat, and is not eaten by the lizard who lost it. He notes a skink (another lizard family) which has a tail that does writhe on autotomy, contains 20 percent fat, and is usually eaten by the lizard. The skink returns to the location of tail loss after the predator has moved on. This suggests that tail writhing after autotomy serves to attract the tail's original owner, who eats it, and thus mitigates his loss.

Geckos have very fat tails which autotomize very easily, but I have never seen one return to eat the lost tail. However, in all fairness, I do not usually give them a chance: if I decide to catch a house gecko I do so because I want the specimen. It gets pickled, usually tail and all.

This is our most nocturnal lizard. Cloudsley-Thompson (1961) points out ways in which nocturnalism mitigates both predation and competition. Certainly the house gecko enjoys a rich food source attracted to lights at night, and has it all to itself: no other lizard species competes. Bustard (1970) studied the activity cycle of the very closely related Hemidactylus frenatus. He found the peak of activity was between dusk and midnight. In his species there was a daytime, afternoon subpeak of activity. This has never been reported in H. mabouia. Being nocturnal makes for problems in energetics: lizards need a fair amount of heat, and most get it by basking in the sun. Bustard (1970) found that a natural temperature regime exaggerated the activity peak pattern, while a laboratory-controlled, constant temperature regime damped it out. This is presumably because the natural temperature regime allowed the geckos to heat up in the afternoon, and they remained warmest in the early hours of the night. Their activity diminished -- as we would expect -- as they cooled. Given no temperature variation, it would not matter -- energetically -- when they were active.

Frankenberg and Werner (1981) transported some Hawaiian Hemidactylus to Israel. Those kept in total darkness maintained their Hawaiian activity cycle, but those allowed to adjust did so extremely rapidly: more rapidly than any imaginable travel time needed to colonize such a distance via, for example, a surface vessel.

House geckos are the stars of many wondrous folk tales in the West Indies. If one drops on a woman -- some say -- she is instantly pregnant. Should one get on you, it will stick so tightly that it must be removed with a red-hot knife. In Jamaica, however, these geckos are loved and revered for their insect-eating habits -- an altogether saner attitude.

Woodslave: Sphaerodactylus macrolepis. -- This very pretty, tiny, ground-dwelling lizard is also a gecko. Its names mean sphere-toed and big-scaled. Woodslaves act rather like North American salamanders, but are no relation to them. They are easily found all over Guana by simply turning over vegetation or loose rocks. They seem most common in the seagrape woodlands and thickets bordering the beaches.

This species is extremely variable, both individually and geographically, and subspecies have been described; ours is the nominate form, S. m. macrolepis. Even within this subspecies local populations vary quite a bit. On Guana, males tend to have blue-grey heads and brown bodies with little pattern. Females are rich brown all over, marbled with near black, often in a longitudinal pattern. Usually the females have a "target" -- a black area with one or two white dots in it centered on the shoulders. Because of their highly distinctive markings, individual woodslaves can easily be recognized when seen again, so one hardly needs to further "mark" them in mark-recapture studies.

The sexes are similar in size and weigh about half a gram. A specimen in excess of 25 mm (an inch) SVL is a big one.

These tiny creatures eat rather large prey. Six from Buck Island south of Tortola contained only 17 prey items averaging 2.7 mm in length. The biggest item eaten was a 12 mm earwig (Dermaptera). About 30 percent of their diet was roaches, and another near-twenty percent of their diet was small spiders. Their food also included a beetle grub and only one ant. I was amazed to find no termites or termite larvae in this Buck Island sample. On Guana, woodslaves frequent termite nests and lay their eggs in them. It is hard for me to imagine that the geckos do not avail themselves of such a succulent potential food supply. Perhaps the problem is Buck Island. When I visited it in 1980 it was one of the most devastated islands I have ever seen. The woodslaves whose stomach contents I examined were caught by Major Grant about 1930; I don't know what Buck Island was like then. Today there are no big trees, no shady woods, and very few termites accordingly. This is the clearest case in which I suspect off-island data may not be valid for the same species on Guana.

There are two other sphaeros (as I call woodslaves) in the Virgin Islands, and quite a number on the Greater Puerto Rico Bank (Thomas and Schwartz, 1966). The smallest living vertebrate animal in the world is probably the Virgin Gorda dwarf gecko, _Sphaerodactylus parthenopion_ (see Lazell, 1980, for details). This species has recently been found on Tortola, and might occur on Guana.

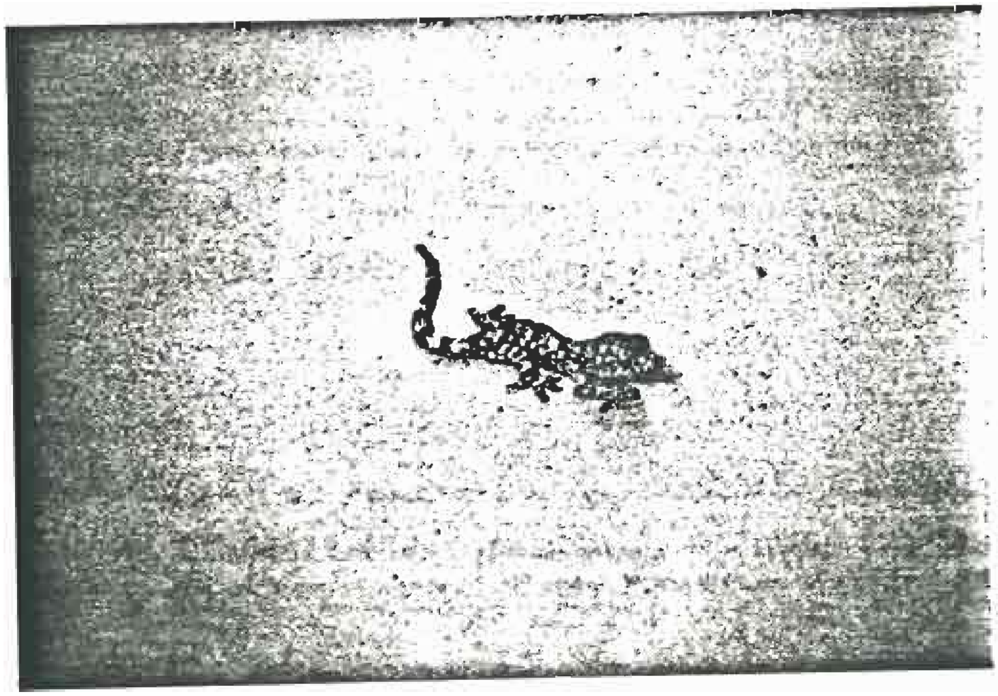
A fascinating situation exists on St. Croix, where our _S. macrolepis_ occurs with the similar-sized _S. beattyi_. MacLean and Holt (1979) found evidence of a dynamic replacement cycle between these species, which seem to compete so fiercely as to exclude each other. _S. beattyi_ resists water loss more effectively than _S. macrolepis_, so holds the dry territory. Wet seasons, and series of wet years, allow _S. macrolepis_ to expand; drought cuts them back again. This is a remarkable situation because usually one of two things happens in a case like this: one species out-competes the other and drives it to extinction; or, ecological accommodation _via_ behavioral or character divergence takes place, and the two evolve out of severe competition. MacLean and Holt show a fine graphic way of presenting data on carrying capacities of habitats for these competing lizards. Although we have only one proven species of sphaero on Guana, the techniques presented might be highly applicable to anole lizards, or even the ground lizard-skink pair.

GUANA ISLAND LIZARDS II: THE GECKOS

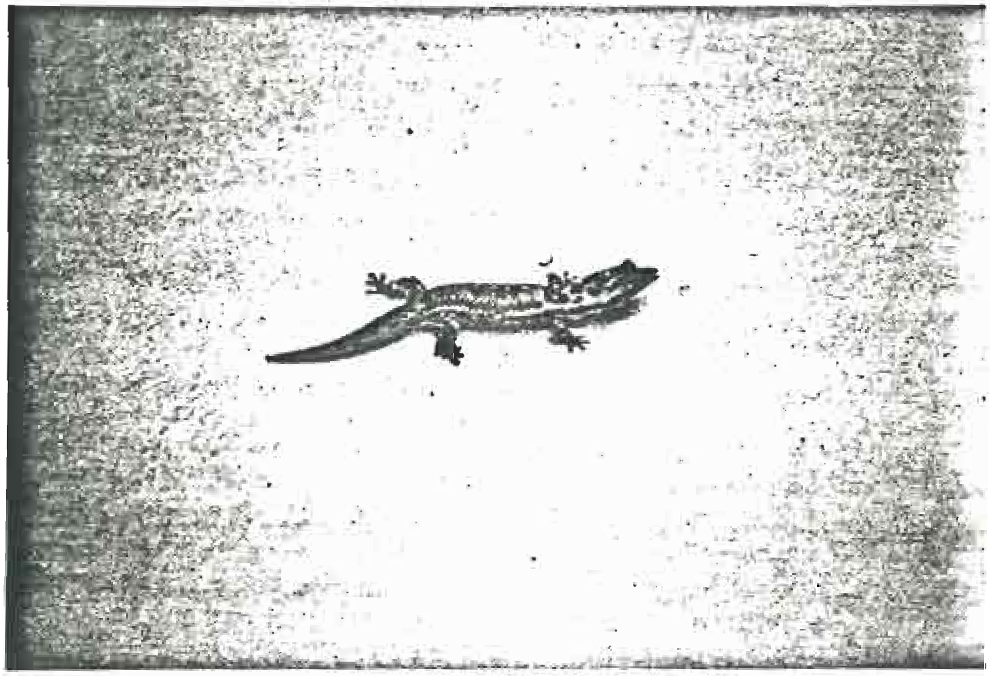
The house gecko, Hemidactylus mabouia. Left, close-up of the head of an adult showing the huge eye and very small ear.

Below, a hatching showing about as much color pattern as these pallid creatures normally have.

Photos by Robert Ginsberg and Jan Soderquist.



GUANA ISLAND LIZARDS II: THE GECKOS



The woodslave or sphaero (Sphaerodactylus macrolepis), a tiny, ground-dwelling gecko of great abundance on Guana. It scurries in shady leaf litter or retreats beneath logs and rocks. This one is a female; males have blue-grey heads.

Photo by Jan Soderquist.

Big Ground Dwellers (Families Teiidae and Scincidae)

These are Guana's biggest lizards. One is very common, one very rare. If you are going to explore around the island, it is a good idea to learn how to tell them apart, because the rare one is a wonderful beast indeed.

Ground lizard: Ameiva exsul. -- This is a member of the strictly New World family Teiidae. These fellows can attain an SVL of 30 cm -- a foot -- and a total length well over two feet. They do not seem to get very large on Guana, but 20 cm SVL is not remarkable. When young, they are rich rust red on the back and face, with whitish or yellow stripes along each side of the back, set off by near-black borders. Their sides may be flecked with sky-blue, and their bellies are washed with blue or blue-grey. With age, the blue-grey coloration tends to spread over the dorsal surfaces, beginning at the front end. Very old adults may be cloudy blue-grey all over. Females do not grow as large as males, but at the sizes usually seen on Guana they seem quite similar. The sexes are distinguished by the swollen tail base of the male, containing the hemipenes.

Ground lizards are as strictly diurnal as house geckos are nocturnal. They do not venture out from their shelters in crab holes or under logs or stones until the day is very hot. Then they bask in the sun until they reach body temperatures exceeding 38°C, or 100°F. At these temperatures, notably higher than even "warm-blooded" mammals, they are able to zoom around with spurts of speed up to 30 mph. If undisturbed, a hot, foraging ground lizard moves along in a series of jerky scuffles, flicking out the tongue like a snake, and searching beneath all manner of surface debris for its animal food. On spying a potential enemy (like a human), the ground lizard stops, looks, and strokes the ground with its forefeet. If it takes fright, it goes from 0 to 30 in about a quarter of a second, running bipedally on its hindlegs.

Catching ground lizards is great sport. It can be done with a monofilament noose on a fairly long (2 m) pole. Often the lizard will cock its head and listen with rapt attention to a wavering whistle. While thus entranced it pays little attention to the noose going over its head. A quick whip of the pole may catch it, but keep the tension and get the lizard to hand instantly: ground lizards reach up with their dextrous hands and pull the noose off their heads.

The average weight of ten adults from Anegada was about 19 grams; these are about the same size as Guana individuals. Five of these were checked for stomach contents and contained 15 items averaging 12 mm in length. More than a third of their diet was roaches and another 15 percent was crickets. They had eaten a weevil, a large beetle larva, a trichopteran (insect), and a 35 mm cicada. Probably the largest item was a woodslave; from the bits of it left, I estimated it to have been a 40 mm adult. I suspect these little geckos make up far more of the diet of ground lizards than my small seven percent sample indicates.

I have always believed ground lizards to be strict carnivores, but these contained a plant seed and a 6 mm piece of stem. I wonder if these were swallowed inadvertently when gulping down some hapless animal.

Ameiva _exsul_ is found on most of the islands of the Greater Puerto Bank, and has differentiated into forms that have been named subspecies on some. The status of these, however, is rather questionable in view of overall variation in the species. The whole thing needs critical reevaluation.

Ground lizards seem to be wide-ranging and not very territorial. They avoid each other, but I have never seen them react antagonistically towards one another the way anoles do all the time. Despite their abundance, not one ever fell into one of my pit traps, so I have no good population or home range estimates.

The name Ameiva seems to be an Amerindian word from South America. The species name exsul is Latin for "exiled," referring to its island origin. Ameivas are widespread in the New World tropics and so closely related to North American racerunners (called Cnemidophorus) that many of us question the validity of a generic separation.

The slippery-back or Sloane's skink: Mabuya sloanei. -- This remarkable and beautiful lizard is internationally endangered, but the British Virgin Islands are its stronghold. Once found on most of the islands from Jamaica to the Anegada Passage, this species seems to have been a victim of the mongoose. Mongooses were imported to the West Indies from Java in mid-nineteenth century explicitly for the purpose of killing rats. There never were any particularly venemous snakes in the Greater Antilles, and the Javan mongoose, Herpestes auropunctatus, is not the renowned snake-killer that the Indian house mongoose -- Riki-tiki-tavi -- is, anyway. Quite a few of the larger Antillean snakes eat mongooses, in fact. Of course, the mongoose had no effect on rats, far preferring the easy prey of ground-dwelling and ground-nesting birds, and the tame, slow-moving, harmless island creatures like the slippery-back.

The slippery-back was named for Sir Hans Sloane, who, around the turn of the nineteenth century, travelled extensively in the Antilles and chronicled their natural history. The generic name Mabuya is Creole (or African) for lizard.

The sexes are so similar I cannot separate them without dissecting the animal. Ten adults from Culebra averaged more than 12 grams; they attain an SVL of ca 10 cm. Unlike the ground lizard, this skink is shiny. It has large, imbricate (overlapping) scales rather than a granular skin. It is proportionately stouter, too, though never attains such great size. Slippery-backs move slowly, anticipating no harm -- at least from humans -- and are fairly easy to catch by hand. They are rich metallic copper or bronze on the back with three bold, light stripes on their dark brown napes. They are our only lizard that has both dorsolateral and mid-dorsal stripes, and these are confined to the neck region.

Slippery-backs are our only live-bearing lizard, and one of the few live-bearing (viviparous) lizards in all the lowland tropics of the world. Fitch (1970) says they bear in July and August. A female 88 mm SVL from Culebra (no exact date of collection) contained four fully-formed young averaging 33 mm SVL. These relatively huge babies took up so much space inside the mother that her stomach was compressed flat and quite empty. Gravid female reptiles often do not, or are unable to, eat.

Five other Culebra adults contained 16 food items averaging over 6 mm in length. Crickets and cricket eggs were 75 percent of the diet. The only other insects eaten were roaches -- two for 12.5 percent. There was some plant stem material, too; judging from the way a 20 mm stem was chewed and folded, it must have been ingested purposefully. The largest insects eaten were both 18 mm, a cricket and a roach. No other lizard in this study had such a restricted diet.

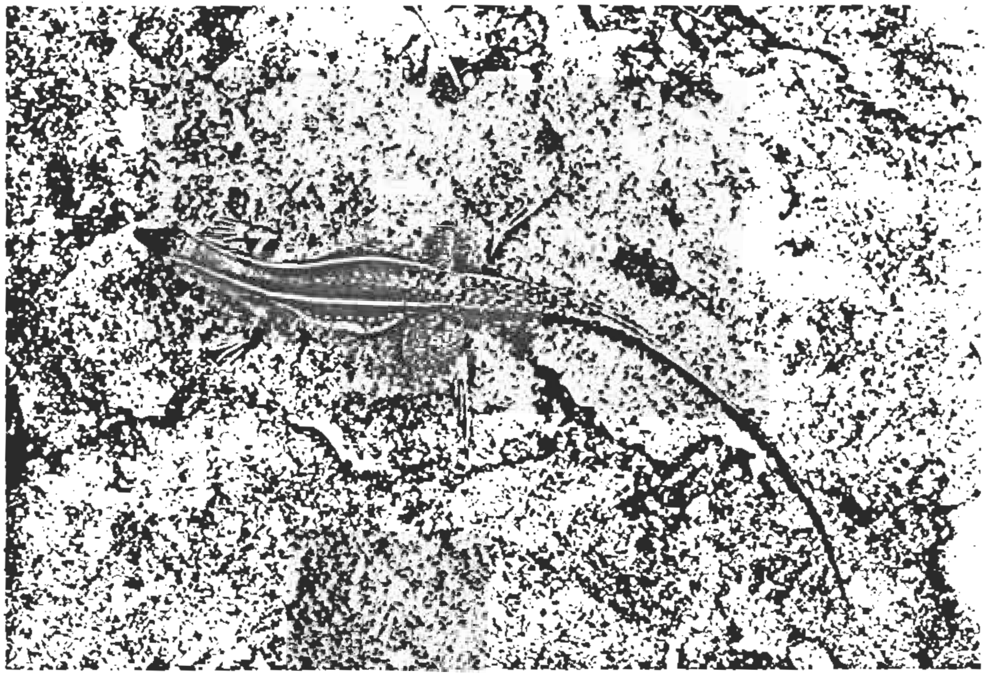
I have yet to see a Guana slippery-back and -- with no extant voucher specimen -- its presence here remains unofficial. Grant (1932) did not record it here, either. Nevertheless, the species is so distinctive and well-known that I cannot doubt the numerous sight records.

The skinks of the genus Mabuya are widespread in Africa, the Indian Ocean islands, southeast Asia, the West Indies, and tropical South America. They are absent from the Pacific islands. This is a peculiar distribution in view of notions about continental drift. As a group, Mabuya is close-knit and shows normal patterns of speciation. For example, Mabuya mabuya of the Lesser Antilles is very closely related to M. sloanei (some classify them as subspecies), just as one would expect of close neighbors. However, Mabuya has not fragmented -- or radiated -- into many species as have Anolis or Ameiva or Sphaerodactylus. Thus, one might guess they have not been here as long as those genera, nor as short a time as Hemidactylus mabouia (which has not speciated at all). Certainly they are not human introductions like the house gecko. The older radiations -- Anolis, Ameiva, Sphaerodactylus -- have no close relatives in Africa or southeast Asia. Mabuya is small and quite terrestrial; compared to Mesosaurus, it is a very poor candidate for long-distance, over-water dispersal.

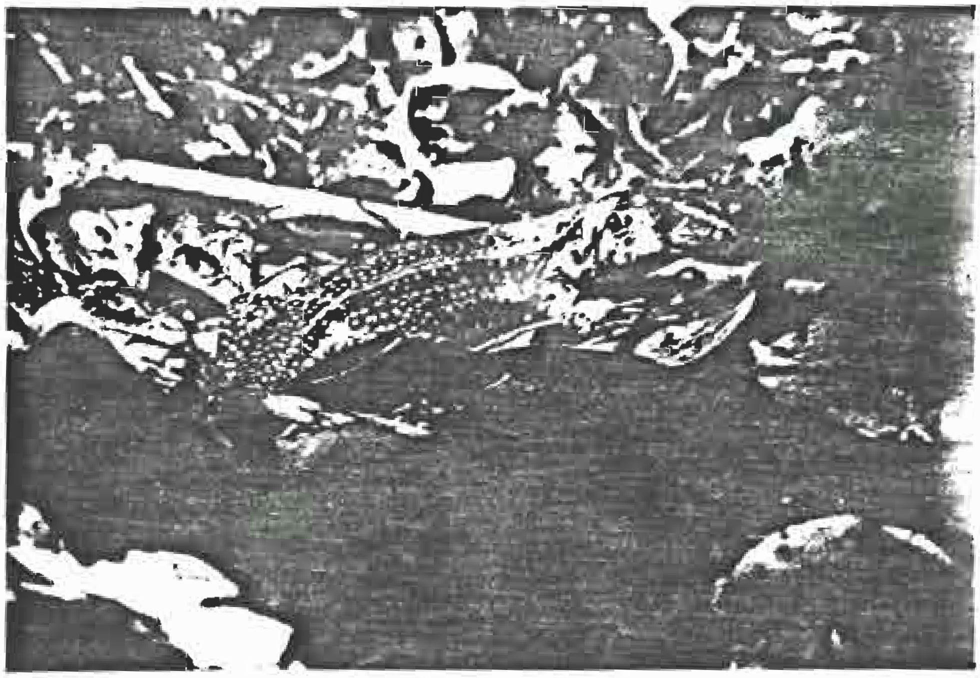
Using the reasoning of the proponents of continental continuity at the time of Mesosaurus, one can easily argue that continental drift has not yet commenced. The Atlantic Ocean is merely a cartographer's error. The Mabuya-bearing lands of the world must still be solidly contiguous.

Basing the time of break-up of the continents on evidence from the fossil record is most unwise, unless and until a relatively vast amount of better evidence becomes available. Single genera such as Mabuya (or Mesosaurus, or Crocodilus, or the geckos of the genus Tarentola) are not valid indicators -- not today, not 200 million years ago.

GUANA ISLAND LIZARDS III: BIG GROUND DWELLERS

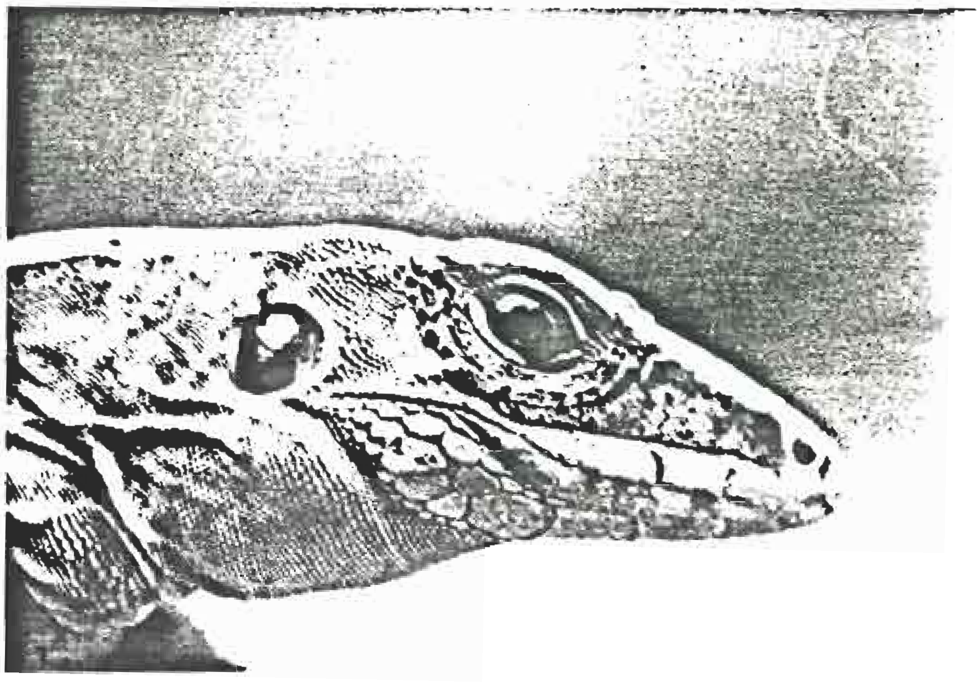


Ground lizard, Ameiva exsul: a young female from Guana. Photo by Jan Soderquist.



The same species, Ameiva exsul, but a big old male from Sandy Cay. Photo by Richard Taylor.

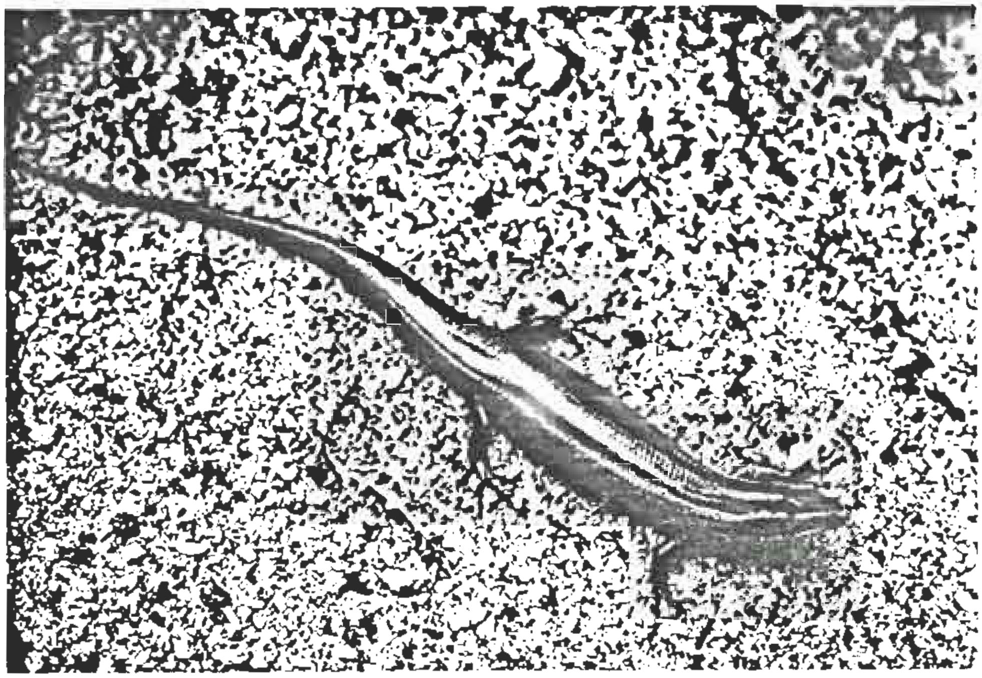
GUANA ISLAND LIZARDS III: BIG GROUND DWELLERS



Ground lizard, Ameiva exsul: a female from Guana. Note the large ear opening with the clear, cellophane-like tympanum. The large head scales grade abruptly into tiny body granules that give the animal a rough, sandpapery look. The pupil is hour-glass shaped, constricting in the middle from top to bottom. This seems to be an adaptation to strong sunlight, but I do not know how it works.

Photo by Robert Ginsberg.

GUANA ISLAND LIZARDS III: BIG GROUND DWELLERS



The slippery-back, or Sloane's skink, Mabuya sloanei. This specimen is not from Guana, but from Little Tobago Cay, where a population was just discovered in 1980.

The stronghold for this internationally endangered species is the British Virgin Islands.

Photo by George Marler.

Snakes

Three species of snakes have been recorded on Guana. One is very common. One is probably much more common than it seems, but it is a tiny burrower and we only discovered its presence in March, 1982. The third is known from Guana only on the basis of a published report. It is internationally endangered and very rare everywhere. Even the common snake belongs to a species restricted to the Puerto Rico Bank and a subspecies endemic to the British Virgins. So, all of Guana's snakes are interesting. All are also beneficial members of the ecosystem. It is a bad idea to be bitten by the common one, because reactions have been reported occasionally from bites of its Puerto Rican relative, but no adverse effect has ever been recorded on Guana, and the snakes bite me all the time.

Common snake: Liophis portoricensis anegadae. -- This meter-long species has other names. I invented "Anegada ground snake" in my 1980 report, and have since regretted it: it is not confined to Anegada, and does climb trees a bit. The generic name "Alsophis" is in widespread use for this species and some of its large relatives. I looked into the matter in detail when preparing my 1983 paper. I concluded there were no anatomical grounds for separating "Alsophis" from Liophis, and that the small and large forms of the Puerto Rico Bank (L. portoricensis and L. exiguus) are very closely related, just as are the Anolis species cristatellus and pulchellus. I do not know what Liophis means, except that ophis is Greek for snake. The species name signifies of the Puerto Rico Bank, and the subspecies name means of Anegada. This subspecies occurs on all the larger British Virgins north of Tortola.

These snakes are diurnal, fast-moving, and alert. The sexes are similar in size; adults average almost exactly one meter. The largest I measured, a male, was 108 cm. All are basically grey-brown with indistinct side stripes and faint cross-barring. Some have a lot of yellow on throat and sides. The males have hemipenes, just like lizards, and these show in the prominently swollen tail base. In females the tail tapers abruptly at the cloacal opening (vent).

Liophis is a genus of the family Colubridae, the huge, worldwide family of "harmless" snakes. Coluber itself is the genus of the common North American and Eurasian racers. Not all colubrids are utterly harmless, however. The great herpetologist Dr. Karl P. Schmidt died of the effects of boomslang bite. The boomslang is a big, arboreal colubrid of Africa. No expert believed before Dr. Schmidt's death that any colubrid could be deadly. In Puerto Rico, Drs. Heatwole and Banuchi (1966) observed and reported on very serious effects of the bite of the common snake, Liophis portoricensis. The bite was not lethal, but it was more than just painful. There was apparent envenomation. Subsequently, similar effects have been noted by Dr. A. S. Rand and Dr. Richard Thomas, who told me about the incidents.

However, Liophis portoricensis is a common snake indeed, and bites are a daily occurrence. Something like one in a thousand must produce adverse effects. The only way I know to catch these snakes is to leap on them when you see one. I'm pretty good at it, but I only get about half I see. I grab them by whatever I can get -- body, tail, whatever. I never seem to get them just behind the head. They usually do bite me. I've been catching Liophis ever since I was 17 years old, which, as of this writing, makes more than a quarter of a century. Nothing bad ever happened to me, and I am not going to quit catching them now.

Liophis p. anegadae eats lizards. I have watched them stalk Anolis stratulus in the early morning in Guana's big ravines. I made one disgorge a 10 cm SVL adult Ameiva -- fresh caught, too, in the heat of the day. That was on the trail just south of the North Bay flat, where snakes are abundant, and Ameiva hardly scarce. Judging from the abundance of snakes, they must be very good lizard catchers. Perhaps this accounts for the apparent fact that ground lizards rarely seem to grow old (and large) on Guana.

These snakes almost certainly eat mice and frogs too, but that will be hard to prove, because mice and frogs are scarce on Guana.

I found Liophis active from sunrise to sunset, with peaks of activity in mid-morning and late afternoon. I saw and caught them virtually everywhere I went on the island. With the help of numerous leaping enthusiasts, I managed to mark 35 snakes in 30 days, and got two recaptures, for a total of 37 captures. These figures provide very weak population estimates by mark-recapture calculations, but about two or more snakes per planar hectare, and a total of about 650 on the island, seems reasonable.

Blind snake: Typhlops cf. richardi. -- The snakes of the genus Typhlops -- which means blind-appearing -- range from tiny to small in size. They belong to their own family, Typhlopidae, and are nearly worldwide in distribution, at least in the tropics (tropicopolitan, we say). Hawaiians like to claim they have no snakes, but Typhlops braminus is abundant there (and Pelamis platurus, a sea snake of the cobra family -- one of the deadliest on earth -- regularly occurs in Hawaii, too). Typhlops are widespread, often abundant, and -- judging by their radiation into many species and subspecies -- ancient residents of the West Indies.

The classification of Typhlops, at least in the Virgin Islands, is in a state of limbo, or at least transition. Dr. Richard Thomas, University of Puerto Rico, is the authority on the group. He originally recognized three forms in the British Virgins, all subspecies of Typhlops richardi (named for some man named Richard -- as are several other Antillean species -- but not Richard Thomas). These were nominate richardi of Tortola and Beef Island, naugus of Virgin Gorda and Prickly Pear Cay, and catapontus of Anegada. Then, Thomas's researches indicated that the species richardi was the same as the Puerto Rican T. platycephalus, and the scale count characteristics of the Virgins forms were compromised by variation in Puerto Rico. So, in their synthetic work on the West Indies, Schwartz and Thomas (1975) did not recognize any of the Virgins forms. Subsequently, fresh material has indicated that other characters besides scale counts may be significant, and the apparent overlap of Puerto Rican and Virgins forms may be convergence or coincidence, rather than a reflection of true relationship.

In any case, it came as something of a surprise when, on 6 March 1982, I turned up a Typhlops on Guana. Two days later we scored a double: Gerald Durrell and I each caught one on 8 March. It looked like it was going to be a bonanza of blind snakes, but in the next month no one saw another one. Dr. Thomas has the specimens (which now belong to the Museum of Comparative Zoology at Harvard), but he has not yet decided just what form they are. Of course, they might be a new form all their own, endemic to Guana Island.

Typhlops are fossorial, which means they live their lives under ground. One finds them by turning over rubbish, logs, rocks, and such items. Thomas and Thomas (1978) conducted experiments on Typhlops that indicate they can distinguish light from dark, but cannot resolve images. They are rigidly nocturnal. If their tiny eyes are surgically removed, they remain entrained to the light cycles of their original regime, and that activity cycle. (Compare to the house geckos kept in total darkness and those which could see and accommodate, described above.) Thomas and Thomas found nocturnalism was most strongly pronounced in xeric (dry) country forms of Typhlops, although they did not think predation could be a significant factor for these incredibly tough little animals (cf. Cloudsley-Thompson, 1961). Typhlops eat nothing, they say, except termites, so competition cannot be a major factor in their lives either. Presumably water loss in hot circumstances is sufficient to account for their nocturnality.

We need to know lots more about Typhlops on Guana and elsewhere in the Virgins (it has been reported, for example, on Great Camanoe). The only way to find out about these creatures is to search for them, find them, keep them, and record the circumstances. We who travel on the surface can never endanger cryptic creatures like these merely by collecting them: we cannot find a tenth of a percent of them.

Virgin Island boa: Epicrates monensis granti. -- Major Chapman Grant (1932) first reported this pretty little constrictor, saying it "inhabits rocky cliffs on Tortola and Guana Island." He seemed to have only one specimen, however, a rather battered carcass from Tortola. He turned it over to Dr. Olive G. Stull, a woman who specialized in snakes of the boa-python family (Boidae). Stull (1933) described it and named it for Major Grant. She believed it was related to the much larger, somber Puerto Rican forest boa, Epicrates inornatus. Sheplan and Schwartz (1974) showed the Virgins form to be closely allied to the equally small Mona boa, and it is now classified as a subspecies of that form. They had six specimens, all from St. Thomas except Stull's original type-specimen collected by Grant on Tortola.

Nellis and MacLean (1983) obtained five more on St. Thomas and concluded that the species is largely arboreal, feeding on warm-blooded prey such as mice (Sheplan and Schwartz found one in a stomach) and small, roosting birds. Theirs was nocturnal. They describe the snake as "...striking. The blotches are dark chocolate brown with light grey-brown in between. Conspicuous blue-purple iridescence was observed...." The Virgin Islands boa has 61-73 body blotches and 20-22 tail saddles or bands; Mona boas have 47-56 and 10-14, respectively (Sheplan and Schwartz, 1974). These little boas are not yet known to attain even a meter in length, though one might hope to find one that big. They present no danger whatsoever to anything bigger than a small rat -- although, for their size, they are powerful constrictors. No boas or pythons are venemous.

All boas and pythons have pelvic spurs: small horn-like appendages near the sides of the cloacal (vent) opening. These are biggest in males; Gillingham and Chalmers (1982) report the spurs are used by the male to position the female during courtship, at least in the Burmese python.

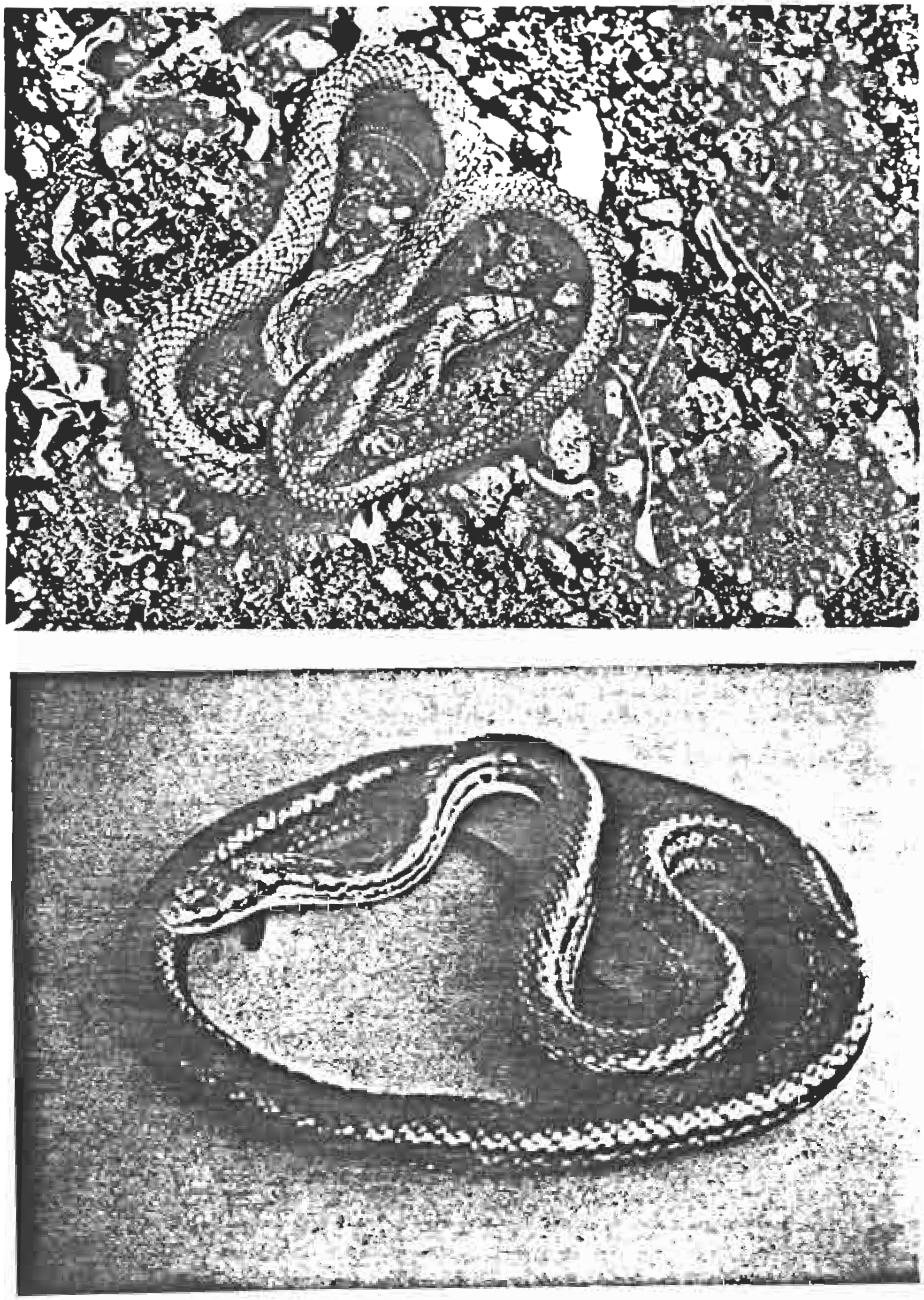
Any snake with bold markings, or more than 2 m up in a tree, or active at night, is likely to be this rare creature. There is a pickled one on Great Camanoe, and people claim to have seen them several times on Necker Island (Lazell, 1980). If a specimen can be obtained, it should be held in captivity (a cloth bag is best) until a biologist like Dr. MacLean, at College of the Virgin Islands, can examine it. The question of preserving it as a museum specimen or releasing it is tricky. In the American islands to kill one is a federal violation. Britain is signatory to the IUCN endangered species conventions, and the BVI are supposed to be thereby included as a Crown Colony. In fact, none of the IUCN conventions are respected in the BVI, where sea turtles, for example, are still killed regularly and (supposedly) legally.

It cannot endanger a population on an island the size of Guana to take out one specimen of a cryptic species like E. m. granti, and it would certainly be a huge scientific benefit to have another specimen -- especially a voucher from another island (remembering, the Great Camanoe specimen is not in any museum at this time).

Ideally, perhaps, the thing to do would be to maintain a Guana individual alive in captivity (it would need a good cage of glass and wood), tempt it with various food items, and record its behavior. Most boas are females and they store sperm, so there is a good chance a single captive would produce a litter (they are live-bearers). Then we could scale-and-blotch count, examine, and photograph a whole batch of individuals. Then pickling one would not be such a big deal. A pickled (or frozen) specimen can be turned over to Dr. MacLean, or any biologist, who can then put it in an appropriate museum (such as MCZ at Harvard, which has the greatest Antillean collections).

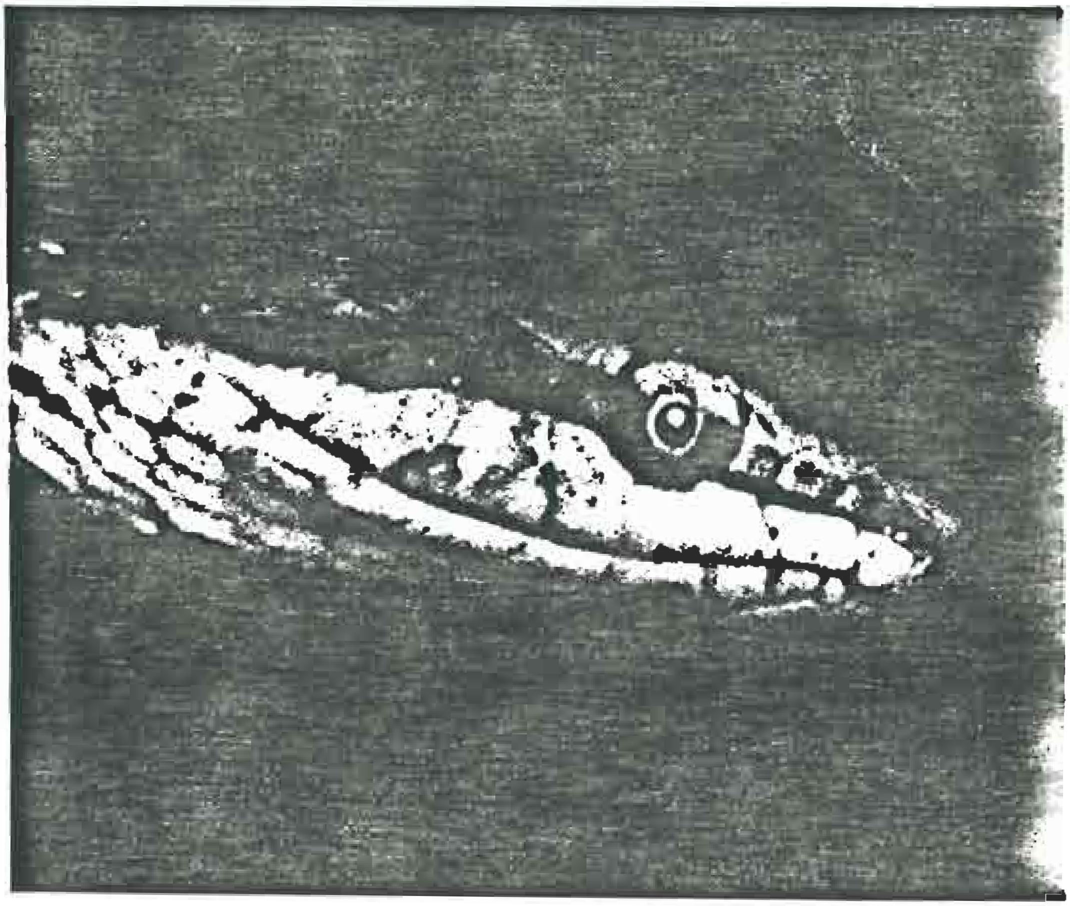
But the big problem with the Virgin Island boa on Guana is not legalities, or cage, or food -- it is to find one....

GUANA ISLAND SNAKES



Common snake, Liophis portoricensis anegadae. Both photographed on Guana by George Marler (top) and Jan Soderquist (bottom).

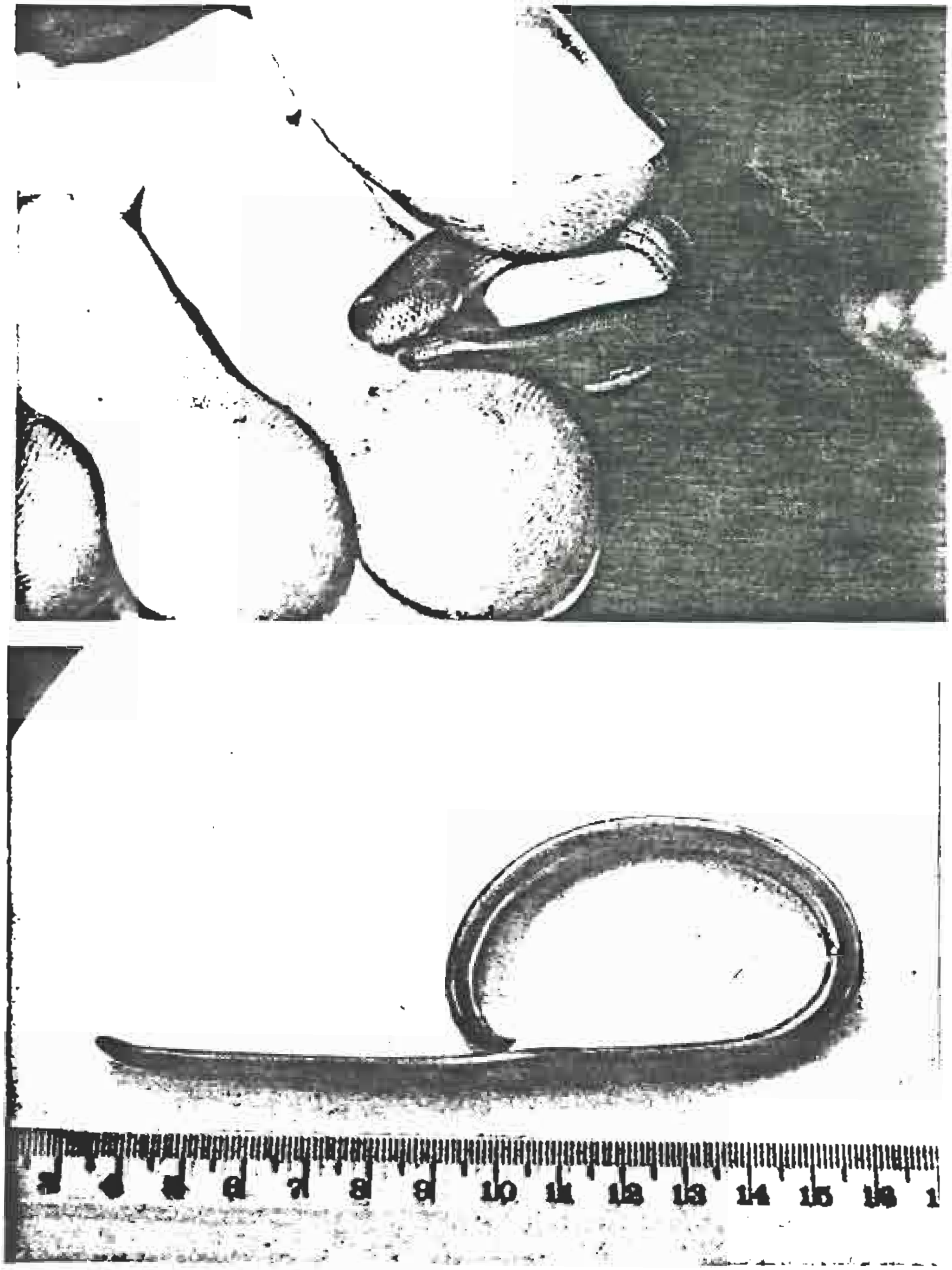
GUANA ISLAND SNAKES



Common snake, Liophis portoricensis anegadae. Snakes have no movable eyelids and no external ear openings. This species sees very well, and all pick up vibrations in the substrate. They rely on taste, conveyed to the Jacobsen's organ in the roof of the mouth by the forked tongue, in addition to sight for hunting.

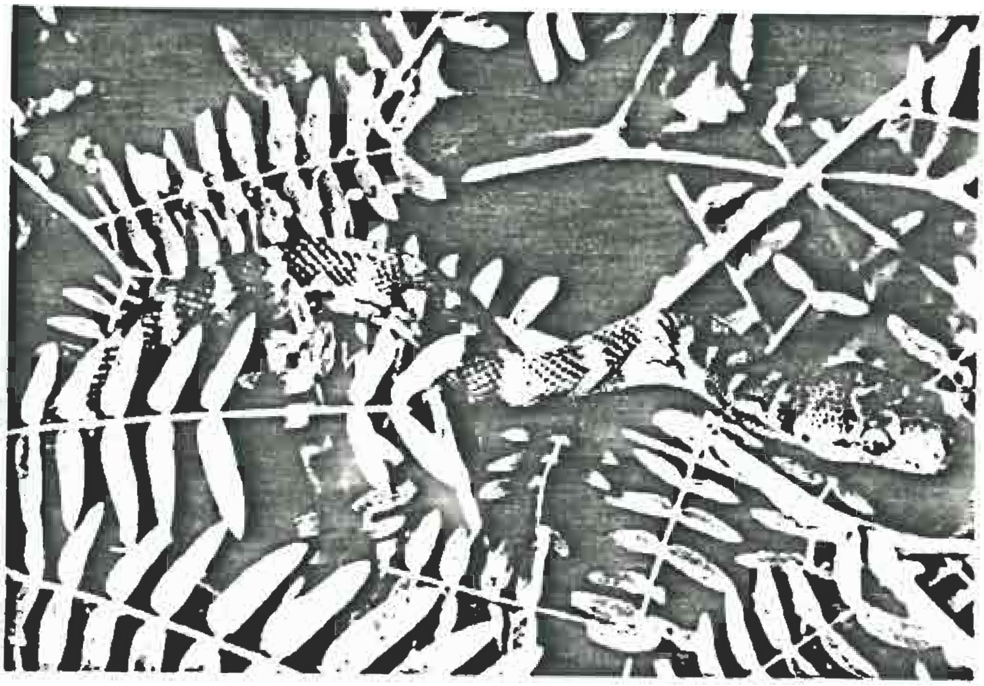
Photo by Jan Soderquist of a Guana individual.

GUANA ISLAND SNAKES



Blind snake, Typhlops cf. richardi. Note the tiny eyes beneath the scales on the hand-held one. The scale on the other, larger one is a millimeter rule. Photos by Lee Durrell, on Guana.

GUANA ISLAND SNAKES



Virgin Island boa, Epicrates monensis granti. Note the bold pattern and distinctive head shape (boas are called Tet'chien -- dog-head -- in Creole).

This is a diminutive species known from less than a dozen specimens in the world. It is internationally endangered. It is absolutely harmless. There are specimens from Tortola, Great Camanoe, and St. Thomas (where this one was photographed), but only an old published report of them on Guana (Grant, 1932).

Photo by Dr. William MacLean.

Mammals

> "While I amused myself with this wonderful quadruped, I saw it several times confute the vulgar opinion, that bats, when down on a flat surface, cannot get on the wing again, by rising with great ease from the floor. It ran, I observed, with more dispatch than I was aware of...."
>
> Gilbert White, 1774.

I have considered in this study only land mammals, of which bats are the only known native representatives. Rats and mice, imported from Eurasia, occur too, as do humans (in season) and their domestic commensals.

Watson (1981), in a fine work, indicates that no fewer than 27 kinds of cetaceans (whales, porpoises, and dolphins) occur in Caribbean waters east of Puerto Rico. Humpback whales and spinner dolphins may be regularly seen around Guana. Once there was a seal -- _Monachus tropicalis_, the Caribbean monk seal. It was a peculiar, otter-like form which shed its skin regularly, like a snake. None have been seen since 1954, and we conclude the species is extinct. It was called _lobo del mar_ -- seawolf -- in Spanish; the males were called "dogs" in English; the memory of the Caribbean monk seal lingers on in the names of small, remote cays where it once hauled out and pupped.

Antillean fruit bat: _Artibeus jamaicensis_. -- This is a large, absolutely tail-less bat with a wingspread well over a foot (45 cm on Guana). It has a large, lance-shaped nose leaf, rising about 1.5 cm from the upper lip. The pelage is brown and grey-brown. _Artibeus_ belongs to the family Phyllostomatidae (or "Phyllostomidae"), whose name means leaf-mouthed.

This species, and the nominate subspecies _A. j. jamaicensis_, is widespread in the Antilles. It feeds mostly on fruit, but also takes insects and probably other small animals if it can overpower them. This is the common bat of Guana, and a good colony of more than a dozen roost in the bat caves above the White Bay flat. We made two bat collecting forays in March, 1982. The first, led by Oscar (who knew the way), featured Alan Gray as chief batcatcher (I shouted encouragement), and resulted in two fine specimens of this species. The second expedition was better equipped and staffed; I can't remember everyone present. The basic plan was that Gerry Durrell and I would enter a given cave, armed with tennis rackets. Lee Durrell, Didi and Lianna Jarecki would haul up a big piece of Mary Randall's bird-excluding plastic netting (it works very well: no birds have ever gotten inside the bales of it in the storage room).

This plan was not such a hopeless failure as a rational human might have predicted. Four fine specimens were secured, although the details of how it all happened remained obscured in the dim light and pitch darkness of the arena. All these bat specimens went to the American Museum of Natural History in New York, except for one, which went to the Institute of Zoology, Academia Sinica, Beijing, China.

But there is more to catching bats than just the bats. These bats had remarkable little beasties living on them. There are two families of peculiar, highly modified flies (Order Diptera) that are external parasites on tropical bats: the Streblidae and the Nycteribiidae. One has little wings and looks sort of like a tiny cricket. The other has the wings reduced to invisible flaps and looks sort of spider-like. I do not know which is which, but I got both from the Guana fruit bats. Maa (1971) considered the meager evidence and literature available on these batflies, but cited no evidence that they had ever been recorded before in the Virgin Islands. I gave the Guana specimens to Dr. Kerv Hyland, parasitologist at the University of Rhode Island. If he has managed to identify them yet, I haven't heard so.

The economics of thermoregulation in tropical bats was the subject of a fascinating paper by McNab (1969). I will say more about mammals vs. reptiles in terms of energetics and ecological implications under The Ecological Community, below.

Cave bat: Brachyphyllum cavernarum. -- This is also a big, tail-less bat of the family Phyllostomatidae, but it has a very small nose leaf (Brachyphyllum means short-leaf). It seems nowhere to be as common as Artibeus, and is known from Guana on the basis of a single specimen spotted by Alan Gray on that first bat-catching expedition. This specimen (also now in AMNH) was dead and mummified (but in excellent condition, fur and all). It was hanging next to a jack spaniard nest, and had great swellings on the wings indicating that the wasps may have stung it to death. Brachyphyllum seems to favor cave habitats (Artibeus will live under most any shelter) and is insectivorous. Apparently, it has no close relatives. In a paper obviously written by a committee (Baker, et al., 1981) it is concluded that the subfamily Brachyphyllinae is confined to the Antilles, and that none of its other members are closely related to Brachyphyllum itself. The subfamily characters are very weak or inconsistent, and each expert on the committee seems to have arrived at different conclusions after examining different sorts of data (e.g. anatomy vs. blood proteins). I am able to conclude from their hodgepodge principally that the cave bat is a very interesting species in need of much more study.

There is also present on Guana a tiny bat with a tail. It is certainly insectivorous, based on its hawking behavior over the terrace at night. It seems much smaller than any bat (like a freetail or a mastiff bat) ever recorded in the Greater Puerto Rico region. It will certainly prove to be a remarkable new record, if not a new species -- when and if someone manages to catch one. (I thought I saw small bats zooming out of the caves on the first visit, but not the second.) The little bat remains a great mystery, but easily seen practically every night during March of 1982.

Rats and mice: family Muridae. -- We will probably never know for sure where the various species of rats and mice now so integrally a part of the human environment originally came from. They were quite unknown in the New World until post-Columbian Europeans brought them. In fact, their pre-Columbian absence from, for example, Amerindian midden sites is one of the best lines of evidence against pre-Columbian expeditions to the New World. If Scandinavians or Phoenicians -- or whoever -- really got here, how come they didn't bring rats and mice, quite by accident, in their vessels, the way every ship beginning with the _Nina_, the _Pinta_, and the _Santa Maria_ did?

The species involved are three: the house mouse, _Mus musculus_, possibly of temperate European origin; the black or fruit rat, _Rattus rattus_, possibly of Mediterranean origin; and the brown or Norway rat, _Rattus norvegicus_, strangely enough probably of Chinese origin. Only the first two are known to occur on Guana, and I saw only _Rattus rattus_, which is common. Not only do _Rattus_ live around human habitations, but they have colonized the wilds, too. The large stick nests in the bat caves yielded _Rattus rattus_ to my snap traps.

Rattus rattus carries bubonic plague, _Rattus norvegicus_ rarely does so, and _Mus musculus_ seemingly never. It may now be impossible to wipe out

Rattus and Mus from our habitations except by wiping the habitations and ourselves out too. But almost everyone thinks you can wipe them out; everyone seems to immediately have the same thought: get a cat.

Well, that has never, ever, anywhere worked yet. Nowhere. Rats and mice occur absolutely everywhere cats occur in the world, and are never wiped out by them. Why, confronted with an entire planet chock-full of evidence to the contrary does anyone still persist in believing cats will eliminate rats and mice?

The first, most elementary Rule of ecology codifies predator-prey relations: No Predator that has Evolved in Sympatry with its Prey can Eliminate that Prey Species. Just like No Disease Organism Kills its Natural Host. Of course not. Those are rules, so someone may be able to find a weird, rare, bizarre exception, but I will bet every exception involves some artificial, third-party, human interference.

Anyway, Eurasian rats and mice and Eurasian house cats evolved in sympatry -- together. So, the cat, as predator, will merely hone the rat or mouse population to a fine edge: the rats and mice will be sharper, stronger, better adapted in general. At first, while the unfit are being harvested, one may notice a nice drop in the prey population. But not in the long run. Soon, the prey species returns to its optimal number for the habitat, and the predator settles down for an easy life of skimming off the surplus who would just die anyway. Most individual prey animals that natural predators harvest are the very young, unfit ones, or the senescent old.

Buck Island, south of Tortola, was, when I was there in April, 1980, the best example I've ever seen of the cat-rat relationship. It was almost impossible to imagine so many cats and rats in one small area. Cats cause healthy, fecund rats. Charlie Darwin pointed out exactly how that works in 1859.

Wourms (1981) studied the predator-prey relationship of house mice, Mus musculus, and house roaches, Blattus germanicus. House mice are vigorous predators on insects and other small animals. 26 mice in Wourms' study attacked roaches 170 times in 31 trials. But European mice and European roaches evolved together. The former isn't going to seriously diminish the latter. Indeed, 78 percent of Wourms' roaches escaped.

Of course, introducing a novel predator into an environment where its potential prey species have evolved in its absence can be very different. The mongoose has done vast damage to native island species of birds and small mammals since its introduction from Java a century ago. House cats -- and even rats, which are very carnivorous when they have the chance -- have devastated the faunas of many small islands, including those in the West Indies. In summary, introduced exotic predators, such as cats, rats, and mongooses in the Antilles, never do what you want them to do, and do all sorts of other horrible things instead.

The best ways to control rats and mice are on a very local, small scale: traps and species-specific poison. I believe covered poison-bait stations would work well in the garden plots, although poisoned rats will head for water, so the cisterns must be effectively protected. Snakes and kestrels can handle house mice, which probably accounts for their relative scarcity. Snakes can also probably effectively raid rat nests and consume the young. The only native predators which can handle adult Rattus are the red-tailed hawk and maybe the owl. A limiting factor for these birds on Guana may be lack of nest sites. I will say more about that under Birds and Prospects for Future Work, below.

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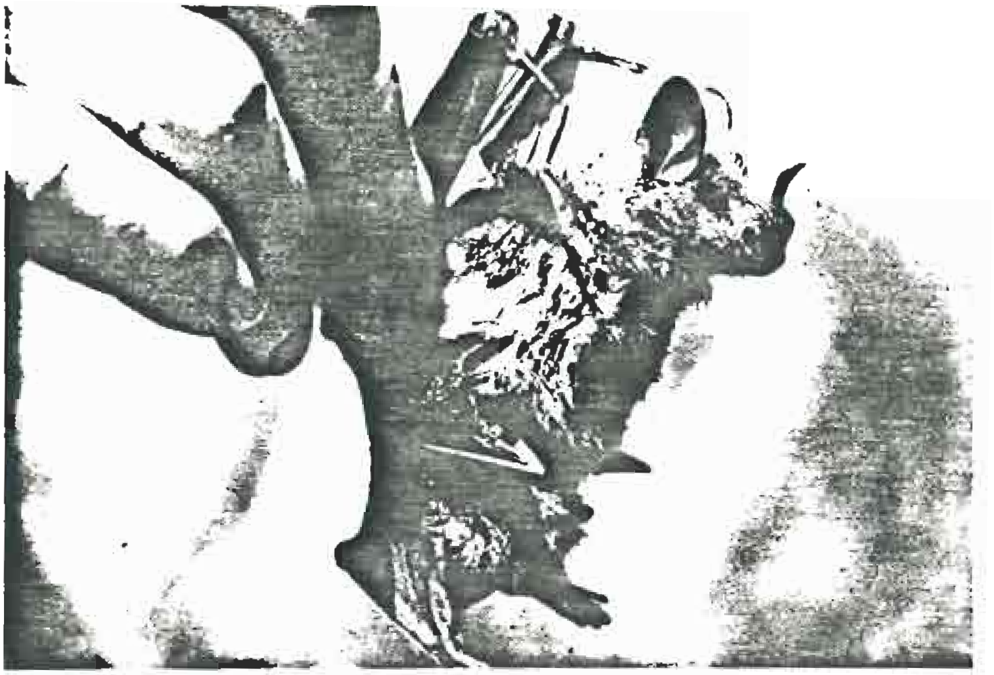
Sheep: Ovis aries. -- I do not know much about sheep except how to skin and roast them. I recommend that on a large scale. Just a quick comparison of the fenced, sheep exclosures (around the buildings it is very leaky, but the garden plots on White Bay flat are better) reveals the extent of sheep influence on the vegetation.

The rule of thumb is a thousand pounds of sheep on an acre of improved pasture (Goudie, 1982). That makes Guana look sick indeed. Surely, if sheep are desired, it would only make the most elementary economic sense to improve a few acres of pasture and confine the sheep to them. I have spent a lot of time in Australia, Tasmania, and New England -- where sheep are successfully raised for profit. I never saw a more wretched, miserable example of sheep-raising than Guana. It's nothing to do with being too hot and dry, either -- ever seen South Australia? It's to do with not knowing how to raise sheep and not bothering to find out. If it was me, I would either get rid of the sheep or decide to raise them right.



Antillean fruit bat, <u>Artibeus j. jamaicensis</u>, from the Guana bat caves. Photo by Jan Soderquist.

Close-up of the head of an Antillean fruit bat from the Guana bat caves.

Photo by Lee Durrell.

Birds

Birds are no doubt the most popular class of wildlife and the most studied and noted by visitors to Guana. I am no ornithologist (rather agreeing with Oscar Wilde's sentiments about birds uncooked), but several species present, or potentially present, on the island deserve special consideration, so I have tried to find out about them.

The known history of birding on Guana goes back to the days of the Bigelows, when Mrs. Erma J. (Jonnie) Fisk, now a master bird bander on Cape Cod, annotated the Guana library's old copy of Bond's *Field Guide to the Birds of the West Indies* (the most recent edition is Bond, 1971). Various people have identified and listed birds since, notably Dr. Robert Chipley, a Cornell ornithologist now with The Nature Conservancy, in 1980. Mary Randall has kept track of ornithological doings, and the list below is a composite of all known sources. Chipley listed 32 species definitely known from the island, and that has been increased by nine, to 41, in two years.

BIRDS RECORDED ON GUANA
(N indicates known nesting)

Red-billed tropic bird, N
Brown pelican, N
Brown booby, N
Magnificent frigatebird
Great blue heron
Little blue heron
Cattle Egret
White-cheeked pintail, N
Blue-winged teal
Caribbean coot
Red-tailed Hawk
Kestrel, N
Wilson's plover
Black-bellied plover
Killdeer
Ruddy turnstone
Greater yellowlegs
Oystercatcher
Black-necked stilt, N
Spotted sandpiper
Roseate tern, N
Royal tern
Sandwich tern
Red-necked pigeon, N
Zenaida dove, N
Common ground dove
Bridled quail dove
Mangrove cuckoo
Smooth-billed ani
Bare-foot screech owl
Green-throated carib
Antillean crested hummingbird
Caribbean martin
Grey kingbird
Caribbean elaenia
Mockingbird
Pearly-eyed thrasher, N
Yellow warbler
Palm warbler
Bananaquit, N
Black-faced grassquit, N

BIRDS EXPECTED ON GUANA

White-tailed tropic bird
Green heron
Yellow-crowned night heron
Semipalmated plover
Golden plover
Snipe
Whimbrel
Solitary sandpiper
Lesser yellowlegs
Willet
Red knot
Pectoral sandpiper
White-rumped sandpiper
Least sandpiper
Semipalmated sandpiper
Western sandpiper
Sanderling
Dowitcher
Stilt sandpiper
Laughing gull
Gull-billed tern
Common tern
Forster's tern
Bridled tern
Sooty tern
Least tern
Black tern
Brown noddy
White-crowned pigeon
Belted kingfisher
Yellow-bellied sapsucker
Barn swallow
Black-whiskered vireo
Black-and-white warbler
Prothonotary warbler
Cape May warbler
Black-throated blue warbler
Blackpoll
Black-throated green warbler
Yellow-throated warbler
Myrtle warbler
Prairie warbler
Ovenbird
Northern waterthrush
American redstart

BIRDS THAT MIGHT OCCUR ON GUANA

Audubon's shearwater
Blue-faced booby
Great egret
Snowy egret
Tricolored heron
Black-crowned night heron
Glossy ibis
Roseate spoonbill
Roseate flamingo
Fulvous tree duck
Black-bellied tree duck
Gadwall
Northern pintail
Green-winged teal
American wigeon
Shoveler
Ring-necked duck
Lesser scaup
Ruddy duck
Masked duck
Hooded merganser
Marsh hawk
Osprey
Peregrine falcon
Merlin
Clapper rail
Sora
Common gallinule
Snowy plover
Upland sandpiper
Black skimmer
Caribbean parakeet
Yellow-billed cuckoo
Black-billed cuckoo
Nighthawk
Black swift
Antillean mango
Stolid flycatcher
Bank swallow
Cliff swallow
Worm-eating warbler
Magnolia warbler
Bay-breasted warbler
Louisiana waterthrush
Connecticut warbler
Common yellowthroat
Glossy cowbird
Stripe-headed tanager
Lesser Antillean bullfinch
Indigo bunting

Ten bird species (at least) deserve a few lines of special attention.

Red-billed tropic bird. -- This species was not listed as breeding in the British Virgins by Mirecki (1977), the most recent major report on the islands' birds. George Marler and I found a number of nest sites on various cays, and Robert Chipley and I spotted them nesting on the north face of Long Point, all in 1980. I published a popular note on them: Lazell (1981). The white-tailed species also nests in the BVI (although not found by Mirecki and his group), and should be looked for on Guana.

Brown pelican. -- This species has been disastrously reduced by pesticides throughout its range in tropical and subtropical America. Mirecki (1977) reported only one nesting site in the BVI. We were delighted to be able to confirm the sight records of nesting for Guana in April, 1982. It wasn't easy, however. On 20 March, 1982, the younger Jareckis, with friends, Jan Soderquist, and I undertook to reach the presumed nesting area over land. We got close, and both Didi and Lianna thought they could see nests, but could not be positive. Then, on 3 April, Albert led a party by sea that included Mary, Pam, me, and Robert Ginsberg. We landed and got there quite easily. The young pelicans revealed themselves by squawking, or we might have missed them in the dense vegetation. The hardest part was getting Robert to climb a tree so he could photograph the downy young. Something went wrong with getting home again, too. In summer it is said that nests are much more plentiful and easier to find.

Brown booby. -- Not recorded nesting on Guana by Mirecki (1977). At least two dozen pairs nest on the north face of Long Point in March and April. This may be off-peak season nesting, so counts should be made at other times of year.

Red-tailed hawk. -- These magnificent birds soar over Guana frequently, but are not known to nest here. Because they are superb ratters (and European <u>Rattus</u> are not well adapted to avoiding them), it might be worthwhile to try to attract a pair. I would try erecting a fifty-foot pole with two 24 inch crossed two-by-fours, to which an assortment of natural branches were nailed. I would erect this nest-mimic on the slope above the main garden patch, about half-way up, at least. It should be below ridge-level, so as to be sheltered from the wind, but far enough in the woods to prevent human activity on the flat from scaring off the hawks. I assume that at one time there were really big trees on the White Bay flat which provided natural nesting habitat for red-tails. I would argue that erecting a nest platform was part of restoring the original habitat.

White-cheeked pintail. -- This species, <u>Anas bahamensis</u>, is often called the Bahama pintail. It is rare in the world, and the BVI seem to be a real stronghold for it. Thus the nesting colony on the salt pond, even though only one or two pairs, is an important resource, potentially supplying young pintails to recolonize other areas from which they were extirpated in years past by unregulated hunting.

Flamingo. -- These magnificent -- if gaudy -- birds formerly nested in the British Virgins by the thousands. Their main nesting area was Anegada (LaBastille and Richmond, 1973), but they were reported to nest around many salt ponds, such as those of Virgin Gorda and Tortola. They were entirely extirpated as breeding birds early in this century by indiscriminate gunning. The ecological effect of their absence from the salt pond ecosystem can only be guessed or imagined, but it must be profound. Surely it would be a good idea to re-establish flamingos in the BVI. It would be good for the flamingos -- much diminished throughout their range, good for tourism, and good for the ecosystem. George Marler and the Caribbean Wildlife Society (Box 108, Road Town, Tortola) have been trying to develop a plan for reintroduction, using a mix of Bahamian and Floridian (Hialeah) stock. I do not know that any flamingos certainly nested on Guana's salt pond, but find it hard to imagine that they did not. I would recommend releasing a couple of pairs of pinioned stock, and see what happens.

Roseate tern. -- This lovely species is in bad shape worldwide. Mirecki (1977) reported a colony of several hundred on Guana in 1976, but we found none in 1980 or 1982. Maybe we were too early in the season. They should be looked for along the southern beaches: Monkey Point, Long Grey, and Bigelow Bay.

Bridled quail dove. -- Robertson (1962) painted a gloomy picture for the survival of this handsome species of ground-dwelling dove. Mirecki (1977) did little better, and did not find the species on Guana. However, records of their presence here go back for as long as records have been kept, and Robert Chipley was delighted to find a pair in the big ghut rising from the south end of the White Bay flat. In 1982 we spotted a pair or two in most of the big ravines, including "Fresh Water Ghut," which drains onto the south end of North Bay beach, and "Grand Ghut," between North Point and North East Point. No one knows whether -- or how far -- the birds move within or between optimal habitats. There might be three or four pairs on the island, or only one. Nesting remains unproven, but presumably these doves do nest on Guana, although it is possible that they only travel here from Tortola.

This species is very localized and confined to the Virgin Islands. Any observations on its life-history and behavior would be valuable additions to ornithological knowledge, and a good, detailed study would surely be publishable.

Bare-foot screech owl. -- This little species, Otus nudipes, belongs to the same genus as the North American screech owl, but lacks ear tufts and feathered feet (nudipes means bare-foot). It has been seen and heard on Guana, most often on the roof of the main building. Neither Chipley nor I managed to observe one. For many years the existence of the Virgin Islands form, named O. n. newtoni, was in question. Mirecki (1977) reported hearing it on Tortola, but not until Nellis (1979) actually saw two on St. Croix was it firmly established as still surviving at all. Surely, it must be considered among the rarest and least known of birds; even its taxonomic status is questionable.

The nominate form from Puerto Rico (Puerto Rican screech owl, O. n. nudipes) is fairly common, and seems to survive well in forested areas -- for example, at Luquillo. Dr. James Wiley, U.S. Fish and Wildlife Service (P. O. Box 21, Palmer, Puerto Rico 00721), has kindly supplied me with a lot of information on these owls. The problem seems to be that the really big trees, likely to have suitable nesting cavities, have been cut down virtually throughout the range of the Virgin Islands form. The owls take readily to artificial nest sites -- such as boxes -- however.

A nest box needs to be at least 30 cm (a foot) deep and sheltered from rain. The diameter needs to be about 20 cm (or greater than 15 x 15 cm square). Wood duck boxes would seem to be ideal. Wiley says these owls usually lay but one egg, and less than 10 percent lay two. Owls seem to compete successfully with pearly-eyed thrashers for nest cavities, so that abundant species should not prove to be a problem. In good habitat on Puerto Rico a square kilometer supports a pair, and two pairs may occur in three km^2. Thus, Guana could easily support two pairs of these owls.

They eat insects, other invertebrates, lizards, frogs, and rodents. Rarely they have been recorded taking small birds (Wetmore, 1916). Not only would a resident population presumably do well on Guana, it would be a benefit in terms of mouse control. Establishing such a population, or augmenting that already present, would certainly be ecosystem restoration, as in the cases of red-tailed hawk and (probably) flamingo. The benefits to ornithology from helping this rare bird, and to some enterprising ornithologist who could then study it, would be immense.

Yellow-bellied sapsucker. -- Dr. Chipley listed this species as rare, but its occasional presence on Guana is solidly attested by the numerous signs of its work: rows of bore holes on the trunks of the larger trees. It is presumably the only woodpecker ever present on the island.

In general, the birds of Guana will repay greater study. Terborgh and Faaborg (1980) have produced a fascinating overview of the numbers and characteristics of bird species on Antillean islands, and their generalizations are especially relevant to a very small island in good ecological condition (i.e., still relatively natural and not terribly modified by humans), like Guana. They found that species numbers were low compared to similar-sized mainland areas at similar latitudes. They found individual species tended to have broader niches than their closest mainland relatives. They found several guilds (see below for a discussion of animal species guilds), especially the insect gleaners, depleted or absent. Most interestingly, they found that a large number of "tramp" species, like pearly-eyed thrashers and bananaquits, seemed far better at colonizing small, ecologically poor islands than mainland birds. Such species even took over coastal cays much closer to the homes of their mainland relatives. In general, one may conclude that -- as with reptiles and mammals -- insular bird species are very different in behavior and ecology (not just taxonomy) from continental forms, and not necessarily at a competitive disadvantage.

GUANA BIRDS

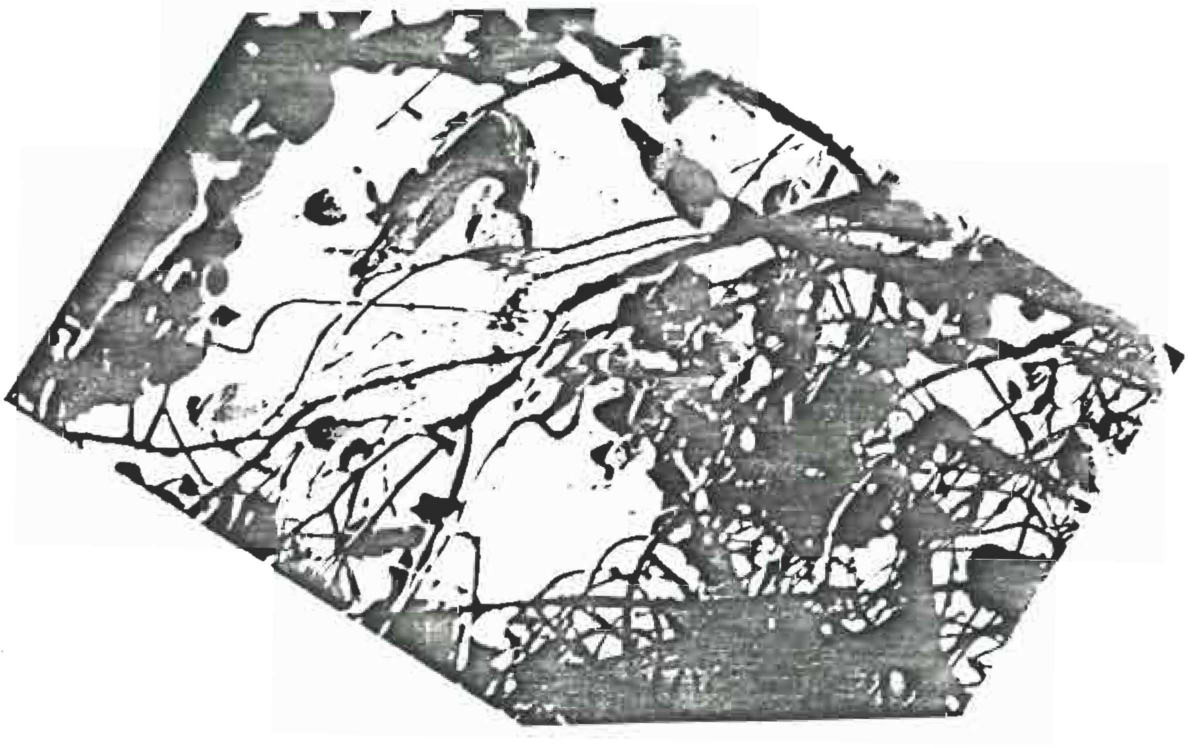
Above, the oystercatcher, a bird just recorded from Guana in March, 1982, frequents the rocky coast.

Photo by Richard Taylor at Green Cay.

At left, ruddy turnstones flock to Guana's salt pond in April, prior to their migration to the arctic.

Photo by Robert Ginsberg.

GUANA BIRDS



Brown pelican -- in the fluffy white condition of the downy young -- which proves the species really is nesting. This one was photographed between North East East End and South East East End, 3 April, 1982, by Robert Ginsberg.

This species was severely reduced everywhere by pesticides, but seems to be making a comeback.

Selected Invertebrates

There is no way I could begin to deal with all the myriad insects and other invertebrates which inhabit Guana in a comprehensive way. What I have tried to do is pick certain ones which are very conspicuous, or seem to attract great interest, and find out a little about them. Two -- a butterfly and a snail -- seem to be especially important from a conservation standpoint. Two others are so abundant and conspicuous that they amaze and befuddle many visitors to the island unused to these tropical habitats.

Those two are the termites of the genus Nasutitermes and the soldier, or hermit, crab, Coenobita clypeatus. The termites build large, dark brown nests of processed wood -- like a sort of spongy or honey-combed masonite. These nests may be two meters in diameter. They may be on the ground or as high up in trees as the trunks will support them. Between nests and feeding areas, the termites make tunnels -- covered runways -- also of processed wood pulp, but mixed with sand or soil. Inside the termite nests dwell scorpions and woodslaves and blind snakes -- as well as other things I have not identified. The termites convert dead wood to humus, and are themselves converted into reptilian and avian protein.

The soldier crabs take over old snail shells, often the size of a softball. Although it is said that they must return to the sea to breed, they occupy all habitats on land, including the tree tops. When alarmed they simply let go and pull into their stolen shells. Falling soldier crabs are more dangerous than falling coconuts on Guana: there are more of them. They concentrate in low areas on the ground, too -- often by the hundreds. Their great pincer is brilliant purple and wine-red, and can produce a most painful pinch. Occasionally, one may find a soldier crab who croaks when picked up;

I have known them most of my life, but I don't have any idea why or how they do that. Soldier crabs are scavengers and fruit seems to make up the bulk of their diet. When changing snail shells they are very vulnerable, and herons and egrets are able to feed on them. Their aquatic larvae are a mainstay in the food supply of the inshore fish nursery. I bet soldier crab pincers -- "claws" -- would be just as good as those of the stone crabs so avidly sought in south Florida and the Bahamas.

Spiders. -- I did not encounter any potentially lethal spiders on Guana, although the black widow, Latrodectus mactans, could easily occur here. The most fearsome is the great tarantula, whose scientific name I do not know. I collected a batch of these for my colleagues at Harvard who study spiders, but have never received a determination. These spiders live in holes in the ground. They can be caught by turning over rocks, or by "fishing" with a grass lure. Mary or Albert can demonstrate this technique. Any big spider could potentially give a painful bite, including these. However, I have never heard of one bothering anybody -- certainly not if left alone.

The most colorful of Guana's spiders are three very common orb-weavers, Family Araneidae. They are named for their well-made webs characterized by radiating strands which support the catching strands in concentric orbits. The biggest is the hammock spider, Nephila clavipes. It attains a head-body length of about three centimeters -- well over an inch. It appears somber until looked at closely. Then one sees an intricate pattern of silver, gold, and green on lustrous black and maroon. The long legs are black with fuzzy yellow joints. The hammock spider likes shade. It is most often found hanging in its web sloth-like or upside down. The web is the messiest and least symmetrical of our orb-weavers. Like all orb-weavers, the female hammock spider is the big, obvious one. The males are tiny and hang around the edges of the web; they can be very difficult to find.

The next in decreasing order of size is the silver orb-weaver, Argiope argentata. It builds a classic, highly symmetrical web, usually low and in the open. The web usually displays a distinctive signature of thickened, white silk strands in the middle. The silver orb-weaver female usually hangs vertically, bat-like with its head down.

The smallest orb-weavers are several star spiders, or spiny spiders, of the genus Gasteracantha (which means spike-bellied). A big one is a centimeter across the wide abdomen from horn to horn (or spike to spike). They are brilliantly colored in yellow, red, silver, green, and so on, varying with the species. The commonest on Guana I found was yellow and red. These seem to love to build their fine, rather well-made webs right at face-height in the woods, especially across trails. I walk into them all the time.

I have never heard of any orb-weaver biting anyone, but I wouldn't just grab a big Nephila. All spiders belong to the Phylum Arthropoda, as do insects (and crabs), and the Class Arachnida. The Arachnida differ from the Insecta in having four pairs of walking legs instead of three (eight legs vs. six). The following are in Class Arachnida too.

Scorpions and whipscorpions. -- These have pincers -- properly called chelicers or chelae -- rather like those of crawfish. Then they have eight walking legs behind those. The true scorpions are elongate and have long, segmented tails ending in a hook-like stinger. They can sting, but it's not any worse than a bee sting (no where near as bad as a jack spaniard -- the common wasp). Whipscorpions are broad -- to five centimeters or two inches -- and tailless. Their second pair of walking legs are modified into great, elegant whips which both grip by wrapping and sense things tactilely. Whipscorpions are perfectly harmless so far as I know (and I've caught them all my life). I never succeeded in nabbing a really big, adult whipscorpion on Guana. That's a good project for someone. They live under things and inside old stumps and logs. The little ones I did get were such juveniles they could not be identified.

Dr. Jorge Santiago Blay, Calle 33 ZG-9, Riverview Bayamon, Puerto Rico 00619, is the authority on the scorpions and whipscorpions of the Greater Puerto Rico Bank, including the Virgin Islands. He identified two species on Guana in my material:

Centuroides _g._ _griseus_ is the biggest and commonest. I found it almost everywhere. It is rich yellow and amber, long and slender, with elongate, delicate chelae. Dr. Santiago Blay believes this species was mistakenly reported as "_Centuroides_ _nitidus_" in a Smithsonian Atoll Research Bulletin, number 251, in July, 1981. That probable misidentification was the only scorpion record for Guana previous to March, 1982.

Heteronebo _yntemai_ (named for Y. A. Yntema, a St. Croix biologist) is a new record for the island. We found it fairly common in and around the pinguin thickets just north of the Monkey (see map following Plant Associations, above). This is a small, somber, brown scorpion with very plump, round chelae. Unlike _Centuroides_, which climbs well, this species seems entirely terrestrial.

Both of our scorpions were first scientifically described and named in 1980. Perhaps there are more, as yet unnamed.

Centipedes and millipedes. -- These belong to Phylum Arthropoda also, the Classes Chilopoda and Diplopoda, respectively. Centipedes have one pair of walking legs per body segment and a pair of horizontally-oriented fangs under their heads. Millipedes have two pairs of legs per segment and no fangs. Most millipedes curl up when disturbed, and many secrete a strong iodine solution which is distasteful to predators (and stains clothing and fingers). I know little about these creatures and mention them here only because I collected quite a few on Guana, sent them to experts who claimed they wanted them, and have yet to hear a word from them (either the specimens or the experts). No millipedes are at all dangerous and none can bite or sting. The very large (to 15 cm, or six inches), dark slaty millipedes which climb trees are conspicuous on Guana. Often clusters of them may be found in a wild pine (bromeliad) or a trunk cavity, or just draped on twigs.

Some of the larger Antillean centipedes are potentially dangerous, but none I found on Guana. The biggest I got were lovely blue, blue-green, and rosy fellows, about eight centimeters (three inches) long. Centipedes like to live under rocks and logs in inaccessible places.

Moths. -- Two species of very large, nocturnal moths are conspicuous Guana residents (and no doubt hundreds of smaller ones). The first is _Erebus_, the cave moth. It likes dark, sheltered places -- like caves and little-used buildings. It is dark in color and looks black in dim light, but is really quite lovely in shades and details: see photo, below.

The second big moth is the adult of the famous "Princeton worm," _Pseudosphinx tetrio_. The larva, or caterpillar, grows to about 15 cm (six inches) and is velvety-black with an orange head and yellow bands (sometimes chartreuse). The name "Princeton worm" was invented on Guana, so far as I know, because of those colors (suits me; I'm a Harvard man and on the staff at Yale). The caterpillars feed on frangipani, _Plumeria alba_, and can strip an entire tree in a couple of days. The adult is a large, delicately patterned sphinx moth (or hawk moth, or hummingbird moth). There is a photo of a Princeton worm below, and the adult moth, drawn from a Cuban specimen by Ann Payne, is on the front cover of this report.

Butterflies. -- There is a good field guide to West Indian butterflies: Riley (1975). Because of Dr. Lorimer, an amateur lepidopterist who has done much work on Tortola, I was able to include certain special butterfly species in my earlier report: Lazell (1980). One of these, the lovely flambeau, _Dryas juliae juliae_, occurs on Guana. This is an orange and black species with elongate wings (somewhat like the common black and yellow "zebra" or _Heliconia_ in shape). Alan Gray caught one (I don't know how -- he didn't have a net and neither did I) on 12 March, 1982. He got it in the south-slope ravine just west of the peak of the island (or between the two peaks). It has gone to Harvard. This flambeau differs from others in having three narrow, parallel, wavy, black lines near the edge of the hindwing. It is rare, may produce a brood only once a year, and very little-known. It is an important addition to the fauna, of great significance for conservation because it was first described from Tortola and remains known only from the Virgin Islands.

The enterprising butterfly enthusiast might do very, very well for himself on Guana Island. A fascinating paper on New World tropical butterflies with _aposematic_ coloration is that of Brown (1982). Aposematic coloration is "warning" colors -- _e.g._, orange and black. These colors often warn off predators and signal distasteful or actually toxic species. Of course, evolutionary convergence may produce look-alikes -- mimics of the toxic species which benefit from similar colors although harmless themselves. No butterfly can hurt you if you do not eat it.

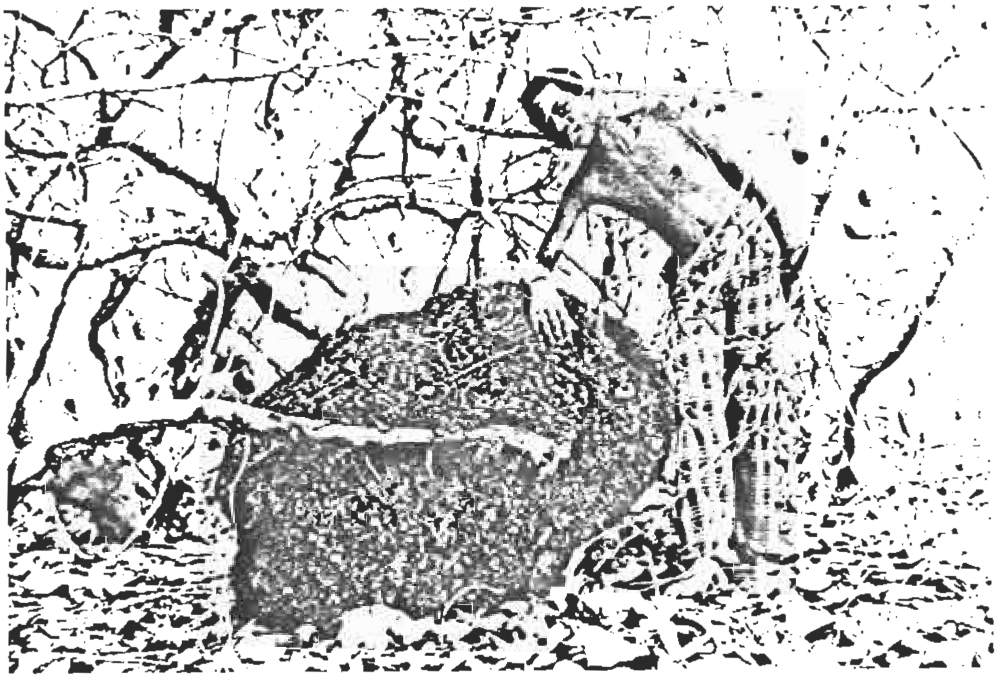
Guana palm snail: Hemitrochus nemoralinus intensus. -- There are lots of snails on Guana: little, olive-pit-like brown ones; long, white, unicorn-horn-like ones; -- dozens. I don't pay any attention to ordinary West Indian snails any more than I pay attention to soldier crabs: they are part of the background. Unless they are not part of the background; unless they are funny-looking. I am very proud of myself for spotting a very peculiar snail on Guana in March, 1982, and for trusting myself that it was -- in fact -- very peculiar, and for having sense enough to collect a good batch of them. I sent a live one to Harvard and Gerry and Lee Durrell took a bunch back to Jersey, in the Channel Islands. No one reacted; no one wrote enthusiastic letters urging me to get more.

But I've been on a few of these cays, and I've seen a snail or two, and these didn't look right to me. I went back and got more -- lots more. I sent them to Dr. Fred Thompson at Florida State Museum. By damn, that got me my enthusiastic letter back.

Seems they were first described by Dr. H. A. Pilsbry in his classic Manual of Conchology (which is not a Florida Keys sociology text) in 1889. Pilsbry didn't know where his specimens had come from -- just somewhere in the West Indies. No one ever mentioned the species again in published literature, so Dr. Thompson said. Til that day, no one ever knew where Pilsbry's little snails had come from. They come from the north side of Guana Island. They especially like to live on the fronds of the little broom palm, Thrinax morrisii, itself a remarkable component of the biota (see Plant Associations, above). The first one I found was on a rotting log in the ravine on 6 March. On 20 March, on the otherwise ill-fated first pelican nest expedition, we found lots on the palms in the same area. I went back after a good rain on 28 March and got the lot that are now Florida State Museum UF 40044. A paper on this snail has been submitted to The Nautilus, journal of the American Malacological Society.

There is just no telling what someone who was interested in snails might find.

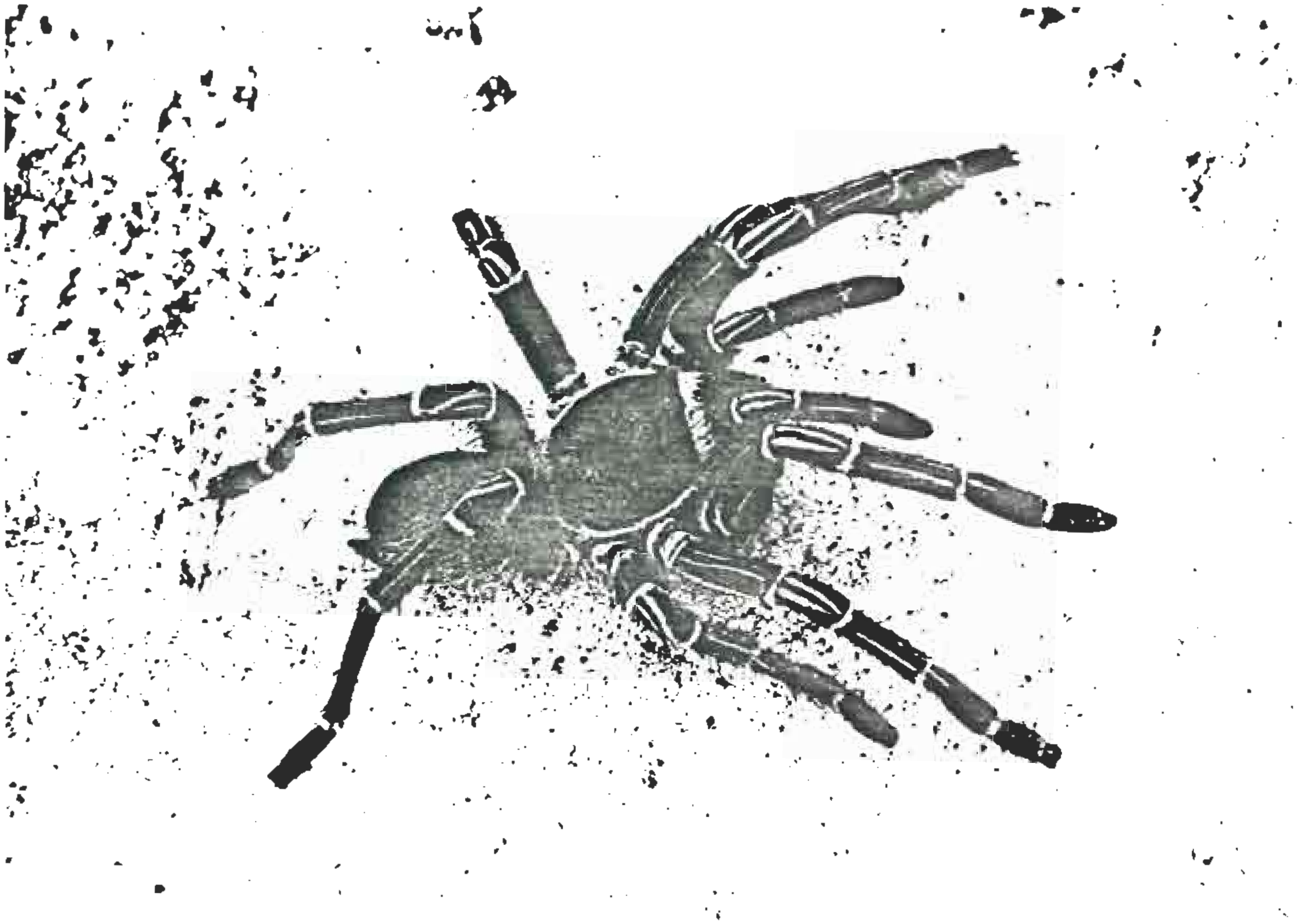
GUANA INVERTEBRATES



A fair-sized termite nest, genus Nasutitermes. This species is extremely abundant on Guana, where it makes much larger nests, often high in the trees.

This one was photographed on Sandy Spit, a tiny bit of land south of Green Cay, by Richard Taylor.

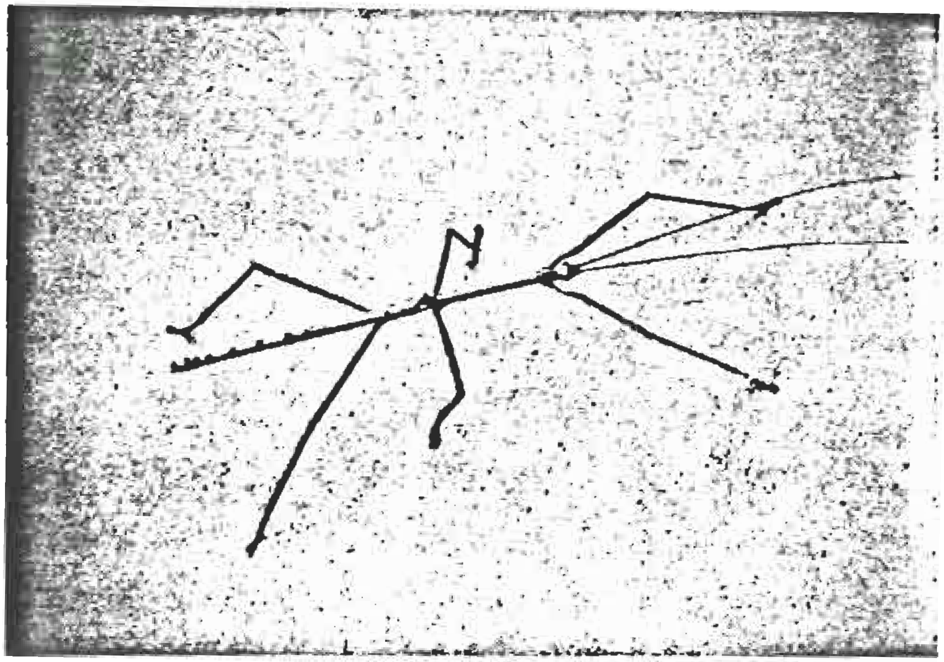
GUANA INVERTEBRATES



A typical Guana ground spider, or "tarantula." These live in holes, often under rocks or logs. They can be caught with a grass lure, as Mary Randall or Albert Penn (for example) can demonstrate. Once you have caught one, what will you do with it? Please do not harm it, because it is a major member of the Obnoxious Insect Control Patrol.

This one is about life-sized; photo by Jan Soderquist.

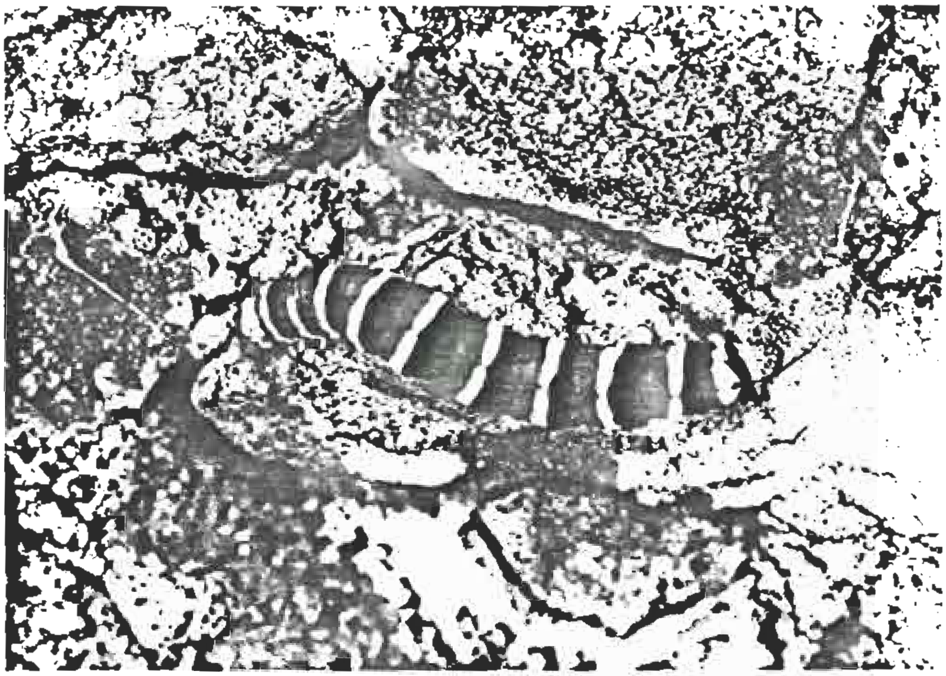
GUANA INVERTEBRATES



A Guana walking stick. This harmless and rather charming insect reaches a length of about 18 cm (seven inches). It belongs to the Family Phasmidae, Order Orthoptera. That is about all I know about it, except that its photo was taken by Jan Soderquist.

A cave moth, genus Erebus, wingspread about 18 cm (seven inches), appropriately photographed in the Guana bat caves by Robert Ginsberg.

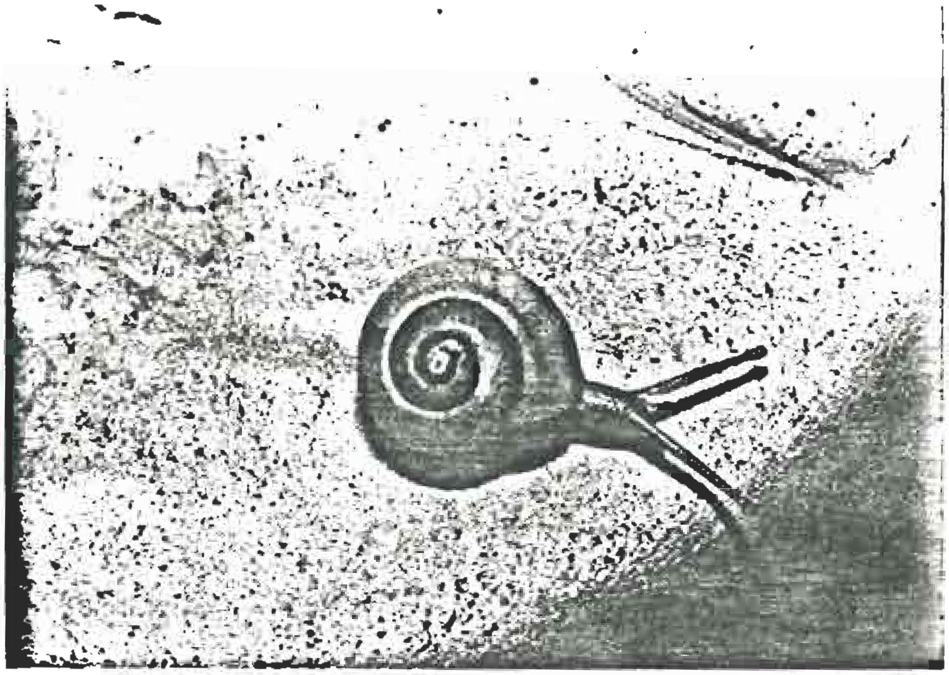
GUANA INVERTEBRATES



The famous Guana "Princeton worm," here shown a bit smaller than life-size for a big one. This is the caterpillar of the sphingid (sphinx) moth, <u>Pseudosphinx tetrio</u>. It feeds on frangipani.

The adult moth is shown on the front cover. Photo by Robert Ginsberg.

GUANA INVERTEBRATES



The Guana palm snail, Hemitrochus nemoralinus intensus, described by Pilsbry in 1889 on the basis of specimens without known geographic origin. I rediscovered it on 6 March, 1982. It was sitting on a rotting log in deep shade about 100 m up the Fresh Water Ghut. It was a big one, about 6 mm in diameter (a quarter of an inch). Anybody would have plainly recognized its scientific importance and realized they had made a Real Find.

Photo by Robert Ginsberg.

IV. POPULATION BIOLOGY

> "Every specimen, whether of diatom, moth, bird or elephant, will have required a certain amount of space for its development. The number of specimens, provided we stick to a single taxonomic group, gives in a certain sense, a measure of the space needed by the successful members of that species."
>
> G. Evelyn Hutchinson, 1953

Population biology is the cornerstone of all modern life science, although the biochemists and biophysicists may not have figured that out yet. It is population biology that tells how many individuals of each species are living, what the turnover or recruitment rate is, how many will be living at some specified future time, and what the ultimate, theoretical limits to any population are. Because that turnover or recruitment rate is the mechanism by which species change, population biology is the heart of evolution. Because the changes that matter have to be heritable -- capable, at least in theory, of being passed on via genetic material -- the parameters of population biology determine biochemical and biophysical properties.

Mathematics is truly the hand maiden of population biology, but chemistry and physics have little to offer it. Biological systems are so utterly remote from the fundamental physical systems from which physical scientists learn their methodology and develop their patterns of mentation as to seem utterly magical. The physical scientist looking at the daily work of the evolutionary biologist -- i.e. population biology -- must utter the ultimate Yankee instruction: "You can't get there from here."

Nevertheless, you can get there. The first person to do it was Charles Darwin, of course, and it is worth going over -- in paraphrase -- just what it was that Darwin said about life -- populations -- that made him so different. Hutchinson (1953) has said: "What we call knowledge appears to consist of a series of known relationships between unknown elements." Here, then, is Ultimate Knowledge about populations and evolution:

1. All populations are limited.
    a. no population can increase indefinitely.
    b. each population achieves stability, even if that equals zero.
2. Stability (above zero) means maintenance of the same average population mean over many generations, where generational variations from the average mean are trivial compared to the number of offspring produced in that generation.
3. Therefore within every population far more offspring are produced than are needed to maintain the stable population.
4. Evolutionary change is nothing more than one individual of one generation with a certain genetic constitution replacing another individual of a previous generation with a different genetic constitution.

That last point is crucial: individuals must replace individuals; genes do not move through populations by osmosis or diffusion.

Let us look at an ideal situation in which there is no environmental change over time. Here a population of organisms reaches stability at N individuals, all perfectly genetically attuned to their stable environment. Let us imagine that, over time, they have achieved such genetic perfection that no predator is able to catch one, no disease organism can strike one down, and they are even so agile and careful that no serious accident ever befalls one of them. All that happens to them is that they eventually die peacefully of old age. Would it not be possible for these organisms in this population living in this ideal environment to produce only as many offspring as were needed to replace each dying generation? Could not, simply put, the birth rate equal the death rate?

Fortunately, fundamental physical science is here able to supply the answer (I gave it away with that line about dying of old age): No. Not unless you can get around the Second Law.

The Second Law of Thermodynamics is the law of entropy. Entropy is the inexorable process of breakdown: of each and every system losing energy and organization to the universe outside that system. The Second Law covers the replication of DNA, the genetic material, just like it covers everything else. It ensures that DNA cannot replicate itself precisely, every time: there will be faults and screw-ups and mistakes -- no matter what.

Of course, the Second Law guarantees mortality, and wipes out our first postulate, above: no environment can possibly remain the same. The Second Law guarantees inexorable change and necessitates that, to survive, all generations of all organisms must produce far more offspring than are needed to replace them. The birth rate must always vastly exceed the death rate.

But, to even remain adaptively at zero -- to simply run in place evolutionarily -- the vast majority of those offspring produced must fail to reproduce themselves. In natural populations, this means that the vast majority of offspring produced must die before they reach sexual maturity. Anybody who thinks Nature isn't blood-red in tooth and claw simply hasn't observed much Nature.

(Aside: no doubt some of you blessed with missing elementary physics are wondering just what in Hell that First Law is. It's a good one, too. It is called the law of conservation, and simplistically states that the total amount of stuff in the universe is conserved. That is, you can shuffle it around, alter its shape and order and arrangement, but there will always be just as much stuff in the universe as there ever was or ever will be. It is sort of encouraging to know that the stuff of the universe cannot really be destroyed: we can't lose any. But it's sort of discouraging to realize we can't get any, either. No gain is possible. There is a Third Law, too. It is a little duller. It just says that everything in the universe has to obey the first two laws, always, forever, no matter what, no exceptions. I think it was Howard Platt, at Germantown Friends School in Philadelphia, at least thirty years ago, who first presented me with a biologist's version of the Three Laws of Thermodynamics: (1) You can't win. (2) You have to lose. (3) You can't get out of the game.)

The implications of basic, evolutionary, population biology for the species <u>Homo sapiens</u> are utterly staggering. Obviously, we are doing everything wrong. The senescent males who control our social systems simply do not seem to be able to figure that out. Too bad, but I am no more interested in the fate of <u>Homo sapiens</u> that I am in that of starlings, Norway rats, or gonococcus bacteria. Organisms have to be fairly scarce, or at least restricted in range and habitat, to interest me (which is exactly why people who are interested in gold or diamonds are not much interested in mud and sand).

Back to Guana Island, where all of the species studied have to produce more offspring than are needed to maintain stable populations, or become extinct. Because such an unexpectedly large number of species seem to manage this in the Guana ecosystem, it's just got to be worthwhile and interesting to try to figure out how they do it.

Reproductive Strategies

The cornerstone of population biology is reproduction. For a species to survive, or a population to remain stable, not only must lots of offspring be produced but some have to survive to reproduce again. There are two extremes of reproductive strategy, each garnered from the logistic of Verhulst as presented by MacArthur and Wilson (1967):

$$\frac{dN}{dt} = r\ N\ (1-N/K)$$

where N is the number of individuals in the population, r the Malthusian parameter or intrinsic rate of increase (a function of life-history), K is the carrying capacity of the habitat or asymptotic population (a function of the environment), and t is time. These extremes are called r-selection and K-selection (MacArthur and Wilson, 1967).

Species which are r-selected produce huge numbers of offspring and put as little parental investment into them as possible. An insect like the roach is classically r-selected. It lays a zillion eggs, utterly ignores them, and doesn't even get around to hoping for the best or wishing them well. Species which are K-selected produce fewer offspring and indulge relatively great investment of time and energy in the development of those offspring. Humans are a fine example of K-selection, as are the skinks called slippery-backs, <u>Mabuya sloanei</u>.

One can clearly see that there are advantages to each extreme. The simple fact that the European house roach, <u>Blattus germanicus</u>, and the human, <u>Homo sapiens</u>, are perched at the opposite extremes, but both are essentially worldwide in distribution, agregiously abundant, and still increasing exponentially, is evidence enough that one strategy is not, <u>per se</u>, better than the other. Most organisms, including those studied on Guana, fall somewhere between these two extremes.

In addition to the first chapter of Hutchinson (1978), excellent short articles on r and K selection are provided by Pianka (1970) and Green (1980). Fitch (1970) documents reptilian reproductive patterns empirically, and Tinkle, et al. (1970) consider theory. A good overview is provided by Turner (1977).

Determination of reproductive strategy for each species is absolutely crucial not just to population biology, but to understanding its ecology. It must be done empirically, by actual observation.

Population Sizes

The imperative question, without whose answer we can do nothing further, is what is N, the population size. Initially, we will have to try to determine N at one set time. Then, we can attempt to learn if N changes seasonally, or cyclically from year to year, or if N is in long-term flux leading to stability at some much higher number -- or zero.

The simplest first approximation involves the "corks-in-a-barrel" approach. The habitat is like a barrel; it is opaque. We cannot simply see how many lizards (or corks) there are, and count them. But we can reach in and pull some out. We can do it with a lizard noose, or a trap of some sort, or a leaping grab. But since we cannot realistically expect to reach in and pull them all out, what good does that do us?

Well, if we mark each cork (or lizard, or snake) we take out, and then put it back in, and then reach in again and grab some more corks (or lizards, or snakes) will that help? You bet! I have forgotten just who the Lincoln of the Lincoln Index was (I've forgotten, too, who Student of Student's t-test was). I did once know. Anyway, it wasn't the founder of the Republican Party. It was the fellow who pointed out that:

$$N = \frac{Mn}{X}$$

Where N is the population (number of corks in the barrel), M is the number you managed to mark, X is the number you grabbed the second time (your recaptured, marked ones), and n is the total number grabbed (i.e., the number marked plus the number recaptured).

The earliest paper I do remember is that of Schumacher and Eschmeyer (1943), dealing with as close to corks in a barrel as you can get: fish in a pond. Hayne (1949) applied the technique to mammals. Bailey (1952) and De Lury (1958) made improvements, and Overton (1971) sums up with the best simple formulae and tables enabling one to calculate 95 percent confidence limits on the values obtained for N.

The basic Lincoln Index of Overton (1971) is what I used on Guana in 1982 because I could assume in a very short-term study that births, deaths, emigration, and immigration were essentially nil. Those assumptions become invalid as soon as the time of study gets long enough to include a breeding season, or a severe drought, or the sort of predictable environmental change that can lead to animal movements or migrations. What is realistic for corks in a barrel becomes silly when applied to animals over time.

In 40 days I got data to which I could apply the Lincoln Index on just three species of Guana's reptiles. These data are given in a table at the end of this section.

In a longer-term study we would need to employ more sophisticated techniques. Jolly (1965) included factors for death and immigration. Otis, et al. (1978) produced a monograph with seven models taking into account many variables. Dixon and Chapman (1980) and Mares, et al. (1980) dealt with necessity of determining home range and individual movements of the animals to develop accurate population inferences. Lin and Lu (1982) provide an excellent study of the population of a Taiwanese lizard, quite up-to-date in these respects.

There is another standard way to estimate populations: the line transect census. There is a fine, sophisticated Wildlife Monograph on line transect censusing, written by Burnham, et al., about 1980, and published by the Wildlife Society. I cannot now cite it because I have not got it handy, and I am on a small, virtually uninhabitated cay ca 120 km north of Havana. Ah, well....

Anyway, a first-approximation, simple method of transect censusing is to lay out a line. Travel that line at regular intervals and count every individual on it during each traverse. Find the average number of individuals on the line (the more traverses, naturally, the better), and square it to get the number in an area equal to the square of the linear dimension -- the line. I did this (as well as Lincoln Index) for the common snake. I took 100 m of the trail from the driveway to Anegada House to the col just above the North Bay flat (confluence of North Bay road and the Jarecki's driveway). I walked this 11 times, counting from zero to five snakes, average 1.7 (there are only two significant figures in the calculation). This yields an estimate of 2.9 per hectare (a hectare is 100 m on a side, or 10,000 m^2). For a very sloppy method, this compares favorably with the very vague Lincoln Index result. Estimations such as these are best described as mellor que nada: better than nothing.

Another way to estimate populations is an areal census. In theory, this should be the best way, because you actually count animals. It does not, in fact, work very well, as you can demonstrate to yourself pretty quickly. Small animals, like Guana's lizards and snakes, are cryptic: you just cannot see them to count. Nevertheless, for some species this works pretty well. You can really census the ducks on the salt pond, or the number of pelican nests. You can also take a reasonable shot at a lizard with a very restricted habitat, like the house gecko.

I estimated the number of resident house geckos in the main room at three. I then added up all the similar wall areas (discarding those in air-conditioned rooms, etc., as unsuitable), and calculated there might be something like 70 house geckos on Guana. That is just barely _mellor que nada_, and will make a fine target for someone to shoot at with a better technique.

I did similar calculations for two other lizards that were common enough to count, and have used these slightly-educated guesses in making the second table, below. I repeat, these estimates are basically just informed guesses, and should be used only to compare with better data at a later date.

GUANA REPTILE POPULATIONS I:
SOME MARK-RECAPTURE ESTIMATES.

These estimates are based on data collected in March and April, 1982, using the Lincoln Index and 95 percent confidence limits from Overton (1971). These data are much too poor to publish, indicating a much longer study would be required to develop accurate estimates.

Species	Site and Area	Calculated N	Minimum	Maximum
Woodslave	White Bay/100m^2	40	13	103
"	North Bay/100m^2	7	1	15
Crested anole	Both sites/100m^2	5.4	1	20
Common snake	Island-wide	648	101	3,649
"	per hectare	2.2	0.3	12

GUANA REPTILE POPULATIONS II:
EXTRAPOLATIONS, ESTIMATES, AND GUESSES

The figures for crested anole, _Anolis c. wileyae_, are extrapolated from the combined mark-recapture calculation for 100 m^2. The figures for woodslave, _Sphaerodactylus macrolepis_, result from assuming 12/100 m^2 to be a fair and conservative point between the disparate mark-recapture calculations and extrapolating that. The figures for saddled anole, _Anolis stratulus_, ground lizard, _Ameiva exsul_, and house gecko, _Hemidactylus mabouia_, are scarcely more than informed guesses.

All these figures should be used as targets for future, more sophisticated studies to try to shoot down.

Species	per hectare	Island-wide
Crested anole	5,400	1,566,000
Woodslave	12,000	3,480,000
Saddled anole	500	145,000
Ground lizard	100	29,000
House gecko	---	70
Common snake	2-3	648

Life Histories

The culmination of any population biology study is the writing of a life history. One hopes, or wishes, to be able to write a life history for every member of the community, but in practice one cannot do this, even for a relatively small ecosystem like Guana. In a 40-day study very little can be gleaned about life histories of even the commonest species.

A good life history consists of basic demographic data: density, home range, territory if any is defended, longevity, recruitment, reproductive strategy, and so on. It also involves ecological features such as diet, predation, and competition. Ultimately one can perceive evolutionary rates. Complete life histories are available for a number of insect species, especially those of economic importance like fruit flies and mosquitoes (I am not interested enough in these very common creatures to know the literature on them: mud and sand, again). Vertebrate biologists are only just beginning to get going on this, and often a single species will take several generations of biologists to even begin to study.

Tinkle (1976) provides a demographic life table for a spiny lizard, Family Iguanidae, which might be quite comparable to that of our commonest iguanid, the crested anole (Anolis c. wileyae). Here is what a good life table should look like:

X	l_X	m_X	$l_X m_X$
0	1.0	0	0
1	0.2	0	0
2	0.1	5	0.50
3	0.04	7	0.28
4	0.02	7	0.14
5	0.01	7	0.07

Here, X is age in years, l is survivorship or the number surviving (subscripted for X, the age at a given year), m is the number of female offspring per female produced (similarly subscripted), and the last column (the product of survivorship times maternity) measured reproductive success. In our example, some lizards lived to be about five years old. Most failed to reach sexual maturity at age two (ninety percent, in fact, failed to make it). Maternity was higher at age three than at two, and stayed as high for the rest of the lizards' lives. This says that all the lizards in the population died while still reproductively active. (Since they didn't die of concussions falling off their trees, you can bet somebody ate them.)

In the bibliography, I have cited dozens of good papers which could and should be read if and when data for Guana begin to deserve detailed comparisons and analysis. Meantime, we have gleaned some life history data, summarized here.

Species on Guana for which there are data can be divided into three groups:

1. All-aged. -- Three species, crested anole (Anolis c. wileyae), saddled anole (Anolis stratulus), and woodslave (Sphaerodactylus macrolepis) were encountered at all ages from eggs to old adults. The notion that these are year-round breeders, with each female laying one egg at a time, at an interval of something like two weeks, accords well with the published evidence (e.g. Lazell, 1972).

2. Even-aged. -- Two species, the ground lizard (Ameiva exsul) and the common snake (Liophis p. anegadae) were pretty much of a size during the study. This implies seasonal breeding; since both species were encountered as adults, it implies that we were not on the ground during that season.

3. Bimodal. -- Two species, the house gecko (Hemidactylus mabouia) and the fruit bat (Artibeus j. jamaicensis) were encountered at two discrete sizes or ages: full adults or infants (includes eggs, embryos, hatchlings, and nursing young). One cannot conclude that these are seasonal breeders and we were present at that season: our encounters with these species were far too few. All one can conclude is that these two species produce young at least during the season of our study, which is the driest season of the year.

Some details are worthy of explicit note. Common snake. -- This species lays shelled eggs which can be palped in the body. A female with six eggs was palped on 9 March; she measured 753 mm. A female with three eggs was palped on 10 March; she measured 891 mm. A female who seemed to contain five or six as-yet-unshelled eggs was palped on 20 March; she was 816 mm.

We can set up some very weak hypotheses about common snake reproduction and hope someday to collect data which will corroborate or refute them. Most female common snakes (11 of 14) contained no palpable eggs. Therefore, it seems likely that these snakes begin to lay about April. If the eggs take about a month to hatch, we should expect to see the first hatchling common snakes in May. The peak of laying will be notably later -- let's guess late May or June. The peak for hatchling observation should then be about the first of July through that month, or into early August. That is a warm, rainy season.

House gecko. -- These pallid, rather translucent lizards lay snow-white shelled eggs measuring 9.5 - 10 mm in length (measured 25 and 28 March: four eggs total). A female with two shelled eggs clearly visible inside her on 11 March was held in captivity and laid those eggs on 25 March. Eggs found in a drawer of a desk (they lay them in the damndest places) hatched on 27 and 28 March. The eggs turned dark prior to hatching. The hatchlings measured 22 mm SVL and 46 mm total (with their perfect, unregenerated tails).

Fruit bat. -- A female with a very large, surely near-full-term embryo, was collected on 11 March. A female carrying a nursing infant was collected on 18 March.

Evolutionary rates are of great importance to those of us interested in conservation. They tell us about how rapidly a given species can accommodate to environmental change. Often, as demonstrated by the dodo, the auk, the quagga, and the passenger pigeon, not nearly fast enough. I published the simplest formula for evolutionary rate (Lazell, 1972), developed by a high school student of mine who took no further interest in the subject after getting her A for the course. It is:

$$X^g = N$$

where X is the number of offspring produced per individual per generation, g is the number of generations, and N (as before) is the number of individuals in the stable population. Put another (and easier to deal with) way:

$$g = \log N / \log X$$

This formula also yields the minimum number of generations required for a colonizing species to reach its optimum, stable population beginning with a single propagule. A propagule is the number of individuals needed to found a population. It could be a pair or just a gravid (or pregnant) female (in sexually reproducing species). The formula is true for expanding colonies because they are just like evolutionary changes in requiring new individuals. For evolutionary change, of course, a new individual must replace an old one.

In practice, one must modify the variables. Only a fraction, on the average, of an individual's offspring will inherit a given gene present in the parent. Often, this fraction is something like one half, so one usually assumes an X divided by two. As life history data get better, other, more realistic ways to modify the variables become available. Eventually, one needs a computer to model populations and evolutionary rates.

V. THE ECOLOGICAL COMMUNITY

> "In terms of niche specificities the observed local faunas... could be accommodated by a hyperspace with four or five dimensions, the coordinates divided into 10 lengths, each representing the possible minimum and maximum values for tolerances or requirements of a single species. This is obviously far too formal a way of trying to put nature together, but indicates the kinds of magnitudes that might be involved."
>
> G. Evelyn Hutchinson, 1978.

In this section I will discuss ways to build on the data from population biology to develop ecological models involving competition, cooperation, predator-prey relations, behavior, and evolutionary adaptations. The math and theory get tougher, but fortunately we have so little data we cannot get too far bogged down. This will be a brief review of the state of the art.

The concept of niche is integral to community ecology. As developed by the early naturalists, the notion of niche was rather vaguely thought of as a species' place in the system relative to all the other species and the physical environment. Long before the niche notion got itself quantified and codified formally, naturalists had perceived the Law of Competitive Exclusion. This simply states that no two species can occupy the same niche at the same time. It is not very different from the physical law that no two objects can occupy the same place at the same time, except that physics deals only with three or four dimensions, while ecology -- and niches -- are n-dimensional: one can easily quantify a dozen or more dimensions of a lizard's ecological niche. It has only been in the last quarter century, since the late 1950's, that niche has become a mensurable quantity, even though measuring perch heights, prey sizes, activity hours, temperatures, and so on might seem to you and me (in retrospect) to be childishly simple and elementary.

One of the nice things about niches is that, although they could be infinitely complex and unfathomable, they usually sort out very quickly along rather simple, easily perceived and measured dimensions.

As I have said before, Guana Island is a wonderful potential theater for the study of community ecology because it is small enough and homogeneous (physically) enough to be comprehensible, yet it has a far greater species diversity -- especially among those terrestrial vertebrates the reptiles -- to be quite different from any system yet studied anywhere else. Fine review papers include Mayhew (1968),Schoener (1969), Pianka (1973, 1977), and Lawlor and Smith (1976) deal specifically with the concept of ecosystem stability in the face of competition.

Schoener and Schoener (two papers in 1971) deal with Antillean lizards, but beware the excellent critical work of Simberloff and Boecklin (1981). Pacala and Roughgarden (1982) look at two species of Virgin Islands anole lizards (only one of which occurs on Guana). In tabular form at the end of this section I have presented an assortment of relevant, comparative literature to multi-species systems (single-species literature is cited in Population Biology section of the bibliography). I have rather arbitrarily decided that works on the major islands of the Greater Antilles (Puerto Rico, Hispaniola, and Jamaica) are dealing with "mainlands," not "small islands" in the sense of Guana.

Niche Breadth. -- Diversity and competition combine to determine just how much of each resource a species may utilize; physiology and competition combine to set the physical parameters of the species' niche. The breadth of a species' niche may be determined for each dimension of its niche. Thus, a lizard may survive and function between a measurable low and a measurable high temperature. Below the low, it becomes torpid and too sluggish to catch food or escape predators. Above the high it cannot thermoregulate well enough to carry on; its very biochemistry begins to break down. Within the temperature range, there will probably be an optimum, at which the species functions best. Thus, the thermal dimension of a niche, like most others, is *stochastic* -- deviating, at any one time of measurement, within some reasonable distance from the optimal point.

A strictly diurnal lizard, like the ground lizard *Ameiva exsul*, and a strictly nocturnal species, like the house gecko *Hemidactylus mabouia*, could easily live in the same place, eat the same food items, and overlap each other in a multitude of their niche dimensions, but scarcely impinge upon or compete with each other at all, so different is their thermal niche dimension.

The standard measure of niche breadth for a given species is the Shannon-Wiener Index: H, or B', where:

$$H = \log B' = -\sum p_{ih} \log p_{ih}$$

Here, p is the proportion of the niche dimension used by the species in question, i symbolizes the i-th species in the system, and h is the instantaneous measure of the resource or physical feature. So, for any species S_i, p_{ih} is that proportion of the whole surviving at temperature h, or eating food of size h, and so on. One can express this Index -- a raw number as given above -- in the units of information theory, depending on whether one uses as the base of one's logarithms the binary system, 2 -- giving *bits*; the decimal system, 10 -- giving *decits*; or the Napierian or natural base e, 2.718 -- giving *nats*.

In a completely censused community, diversity is determined as:

$$H = \frac{1}{N} \log \frac{N!}{\prod N_i!}$$

where N is (as before) the total number of individuals, N! (N factorial) is N (N-1) (N-2)..., and $\prod N_i!$ is the product of all the values of factorial $N_1 \ldots N_i \ldots N_s$, where s is the total number of species present. Finally, I is a characteristic of all lines and curves, which can be plotted relative to x and y axes, such that

$$I = X\ (dy/dx)$$

which means that I is X times the derivative -- or rate of change -- of y with respect to x. One will need a computer just to deal with the numbers generated here by several million reptiles belonging to the ten species known from Guana. So far, our empirical data do not justify computer time, but we can hope they someday will.

The Food Web. -- Who could say it better:

> "The complexity introduced into animal nature by the elaboration of the food web is probably the most obvious cause of biological diversity."
>
> G. Evelyn Hutchinson, 1978.

If by "diversity" we mean something more than just a list of the species present (and we do), the first area to consider will be the elementary species interactions involved in who eats whom. Two generalizations seem to have repeatedly impressed ecologists who attempted to correlate number of species present and food web relations. First, islands have disproportionately fewer species than do comparable sized pieces of mainland. Second, life becomes disproportionately more abundant as one goes down latitudes towards the tropics. To quote Paine (1966):

> "Though longitudinal or latitudinal gradients in species diversity tend to be well described in a zoogeographic sense, they are poorly understood phenomena of major ecological interest. Their importance lies in the derived implication that biological processes may be fundamentally different in

> the tropics, typically the pinnacle of most gradients, than in temperate...regions.... Understanding of the phenomenon suffers from both a specific lack of synecological data applied to particular, local situations and from the difficulty of inferring the underlying mechanism(s) solely from descriptions and comparisons of faunas on a zoogeographic scale."

Living things are divided into three major trophic sorts (trophic refers to how they get food energy -- in the case of animals, eat). Producers convert solar energy into molecular bonds. They make their own food, and in so doing make food for everything else, too. Plants (and some bacteria and other protists) are producers. Consumers eat producers and their products. These are the herbivores of the world. Predators eat consumers or other predators. One may have many trophic levels between the first predator (like a woodslave) who eats a consumer (like a beetle grub) and a red-tailed hawk (*e.g.*, woodslave is eaten by ground lizard, ground lizard is eaten by snake, snake is eaten by hawk).

Paine (1966) goes on to make five generalizations about food webs:

1. Diversity is higher if production is uniform throughout the year, rather than seasonally peaked, because competitive displacement of consumers can be mitigated by consumer species specializing on portions of the production.

2. Therefore, stability of production is directly proportional to diversity, other things being equal.

3. The upper limit of diversity is set by some combination of stability of production and rate of production.

4. Diversity should also be directly proportional to the number of predator species present, because these will tend to specialize within the consumers and thus prevent any one prey (consumer) species from monopolizing a resource.

5. Increased stability may lead to increased capacity to sustain predators.

The reptile community of Guana is one of remarkable diversity of predators. Because Guana is tropical, there is good production year round, but because Guana is dry, there will be a wet season peak. Production on Guana could never approach that of tropical wet forest because of aridity. A basic, comparative study of production and consumption on Guana would be fascinating.

I note, however, that the reptile community on Sage Mountain, Tortola -- a fine moist forest community with very little seasonality -- is not known to be nearly as diverse as is Guana's: many of the reptiles involved are specifically adapted to arid lowlands (Nellis and MacLean, 1983).

Laughlin (1966), in a doctoral dissertation I have not seen published, studied food webs and niche overlap in several species of temperate-climate lizards. His techniques would require updating, but his approach makes a good model. Very recently, Rubenstein (1982) has presented a review of a symposium on feeding strategies, including ecological, ethological (behavioral), and even psychological approaches.

Guilds. -- The reptile -- especially the lizard -- community on Guana is one of the finest cases imaginable of an ecological subcommunity which is receiving great and deserved attention: a guild. Root (1967) developed the concept of a guild while studying gnatcatchers -- small, insectivorous birds who fit into a group of such species exploiting a particular habitat. A guild is a group of comparable -- though not necessarily closely related -- species who compete for a particular resource. There are seven species of insectivorous lizards on Guana. Because of their differences in activity patterns, prey size, foraging elevations, and so on, they epitomize a guild system. There are no herbivorous lizards on Guana, and none that eat any significant amount of anything else except insects (and some arachnids like spiders). Dr. Hutchinson's great question can here be honed to a keen edge: Why are there so many species of insectivorous lizards on Guana Island?

Pianka (1970) studied guilds of widely separated desert lizards (western U.S., southern Africa, and Australia). He found fine examples of niche segregation within each guild, but was surprised that the guilds in the different places were not composed of ecologically comparable species. Each guild seemed to have evolved independently and irrelevantly to the others. Pianka, *et al*. (1979) expanded this work; Pianka (1977) provides a very useful formulation for diversity within a guild (it does not fit a whole community because it does not consider, for example, primary production). Here, D_s is total species diversity

$$D_s = D_r/D_u \quad (1 + C\bar{\alpha})$$

where D_r is the diversity of resources, D_u the diversity of resource utilization by the average species (thus, average niche breadth per niche dimension), C is a measure of the number of neighbors in a given niche space, and $\bar{\alpha}$ is the average niche overlap.

Hairston (1981) attempted to study a guild of small carnivores (Appalachian salamanders) in some ways quite comparable (size, diet) to Guana's lizards. He removed the commonest species or two from selected plots and looked at what happened to those remaining. He decided that competition was insufficient to explain the results. It seemed that predation on some members of the guild (from outside of it) better explained some sorts of niche differences than competition. He concluded that "experimental tests are needed even in widely accepted examples of guild organization."

Life history changes. -- Another factor influencing diversity of communities can be life history changes within a species. Naturally, the amphibians -- whose name tells us that they lead two lives -- provide the best examples. Bruce (1980) studied a salamander comparable in size to a slippery-back (and wholly carnivorous, too). He found the larvae of the species had much broader diets than the adults, and were very variable in life histories between themselves. Some indulged in long larval lives, some in short ones, for example. Christian (1982) studied small frogs and found, similarly, that the young (not larvae in this case) had broader diets. Size was a critical factor in prey selection at all ages, with individuals specializing on larger -- but rarer -- prey as they grew older. In this study stomach content analyses were quantitatively compared to relative abundance -- an excellent innovation.

Guana has only one known amphibian, the mysteriously missing frog. However, evidence from some reptiles, such as common snakes and crested anoles, suggests that the young may occupy very different niches from the adults.

Energetics. -- I have scarcely noted what is surely a major factor in species diversity, especially for animals like reptiles who must maintain their body temperatures by behavior (they do not generate much metabolic heat, physiologically, like we do). Times of activity can tell us a great deal about lizard energetics, because insolation is the animals' source of heat. I have graphed these below (using data for house gecko from Anegada and Tortola, as well as Guana, and data from Puerto Rico for grass anole).

Huey (1974), Hertz (1979), and Henderson (1982) have produced comparative studies dealing with lizards and snakes with very close relatives on

Guana. Snyder (1975) provides a model for the study of heating and water loss in a single species. Lawton (1981) provides a broad overview of the questions of endotherms vs ectotherms and r-selected vs K-selected species. He points out that ectotherms (like reptiles) are an order of magnitude more efficient energetically than endotherms (like us) because they are not using food consumption as a source of heat energy.

Community Evolution and Biogeography. -- Appropriate here is a quote from a highly provocative book by J. T. Bonner (1980):

> "...there are many sophisticated evolutionary biologists who will point out that there are really no new or revolutionary ideas; what I have to say is essentially what they knew all along. That is likely the case; yet they have not put it all quite this way."

And another from Splendid Isolation, the classic by G. G. Simpson:

> "It might be expected that faunas living in...quite complete isolation would reach an approximately stable equilibrium within, say, two or three million years.... On a continental scale, at least, evolution in isolation does not soon (geologically speaking), if ever, lead to an approximately stable equilibrium."

Small, insular ecosystems (like Guana) evolve rapidly to stability. They are characterized by species which are physiologically very tough: able to resist and rebound from catastrophic vicissitudes like severe droughts and hurricanes. Yet these species are poor competitors with continental forms, at least on continents. They tend to have broad niches. They tend to travel well and colonize other islands, but undergo rapid evolution to form novel forms tightly adapted to each specific island. This means that no two small, insular ecosystems will be much alike in close detail and that finding viable generalizations will require unusual insight. But viable generalizations surely will be there.

Small islands and continents are at opposite poles of the ecosystem spectrum, with large islands combining features of both. Strangely enough, however, if we are ever to comprehend continental ecosystems, as we have come to comprehend continental evolution, we will probably do so *via* the route of comprehending small island ecosystems -- as we did with evolution, too.

On Guana we have bulges of species diversity called guilds. I have paid most attention to the lizard guild, but there are clearly a bat guild, a shorebird guild, a predatory bird guild (which includes kestrel, red-tailed hawk, mangrove cuckoo, owl, and cattle egret -- for example), and lots more. Are these guilds relatively stable over time, as I have suggested they should be? Or are colonizations and extinctions taking place on Guana which will someday bring its fauna to a MacArthurian "equilibrium" at a diversity far lower than today's, and more in line with previous biogeographic predictions?

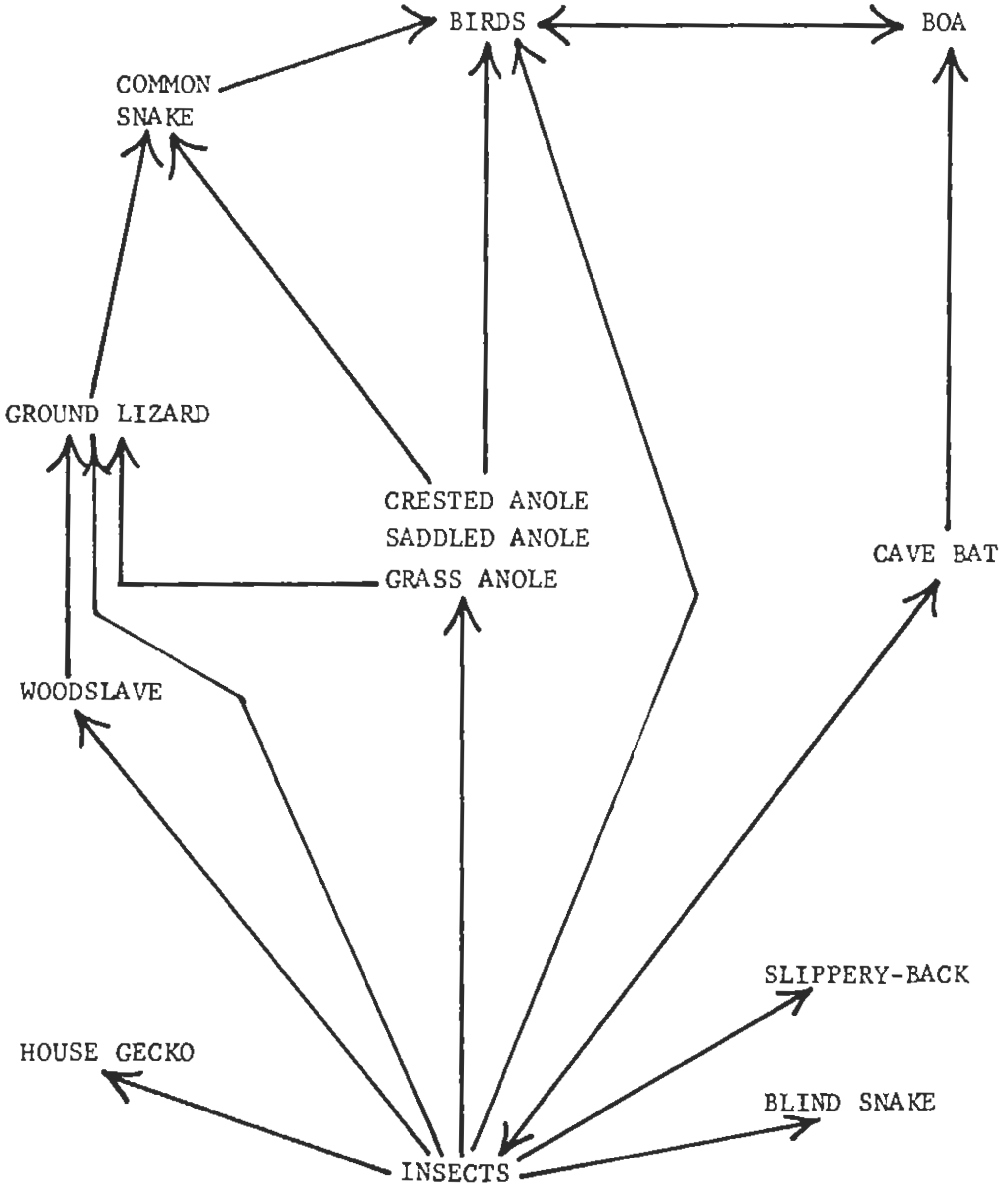
SOME COMPARATIVE ECOSYSTEM LITERATURE

(Single species works are cited in Population Biology section)

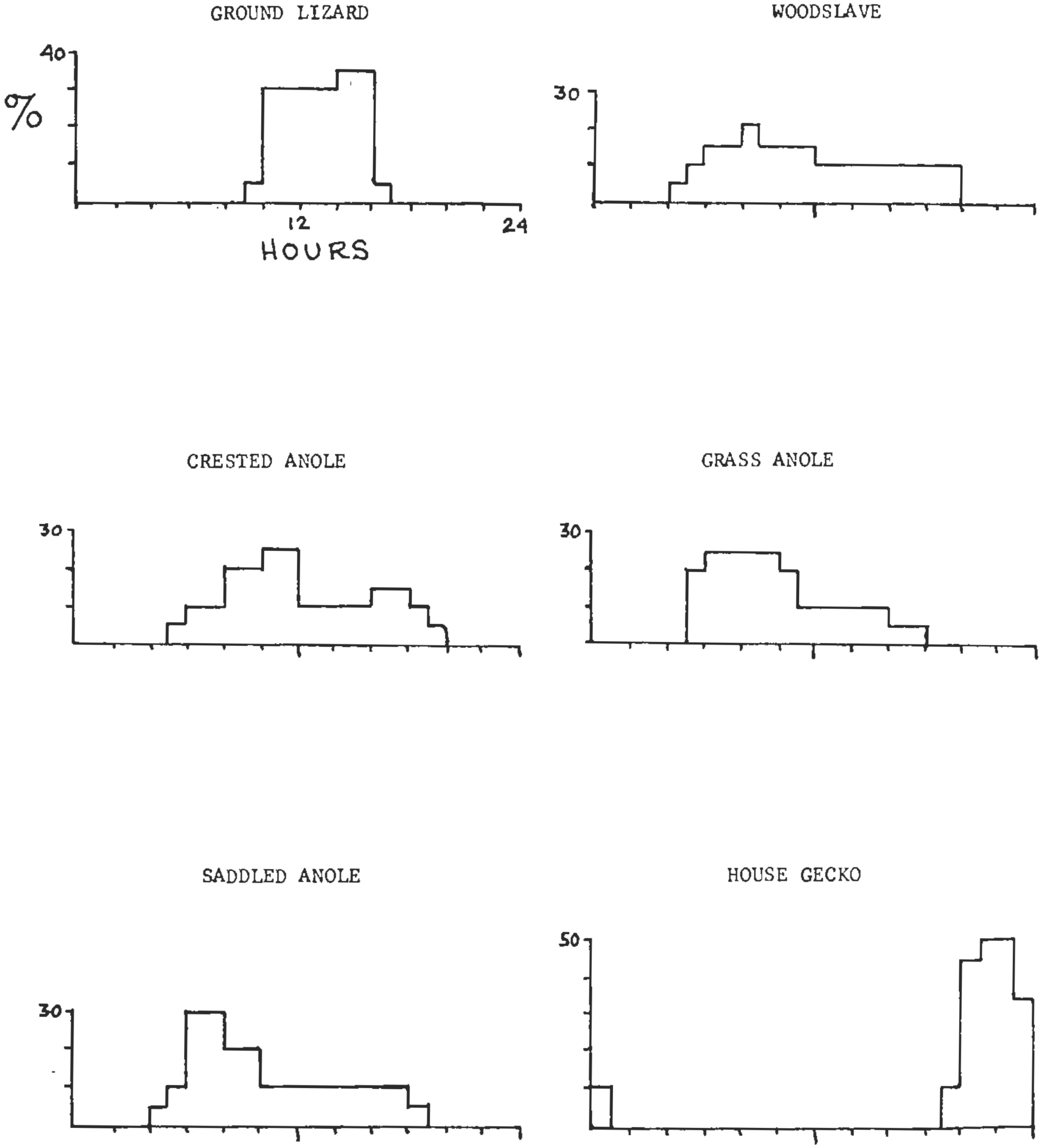
<table>
<tr><th></th><th></th><th colspan="4">TROPICAL</th></tr>
<tr><th></th><th>TEMPERATE</th><th colspan="2">MESIC (WET)</th><th colspan="2">XERIC (DRY)</th></tr>
<tr><th></th><th></th><th>Mainland</th><th>Small Island</th><th>Mainland</th><th>Small Island</th></tr>
<tr><td>Amphibians</td><td>Wrobel, et al. (1980)
Hairston (1981)</td><td>Heyer & Maxson (1982)</td><td></td><td>Heyer & Maxson (1982)</td><td></td></tr>
<tr><td>Birds</td><td>MacArthur (1958)
Root (1967)
Humphreys, et al. (1982)</td><td></td><td colspan="2">Terborgh & Faaborg (1980)</td><td></td></tr>
<tr><td>Reptiles: 2-4 species</td><td>Laughlin (1966)
Pianka, et al. (1979)</td><td>Hirth (1963)
Schoener & Schoener (1971)
Barbault (1976)</td><td></td><td>Schoener & Schoener (1971)
Hertz (1979)</td><td>Lister (1976)
Henderson (1982)
Pacala & Roughgarden (1982)</td></tr>
<tr><td>Reptiles: 5 or more species</td><td></td><td colspan="2">Hardy (1982)</td><td></td><td>THIS STUDY</td></tr>
</table>

A GUANA FOOD WEB

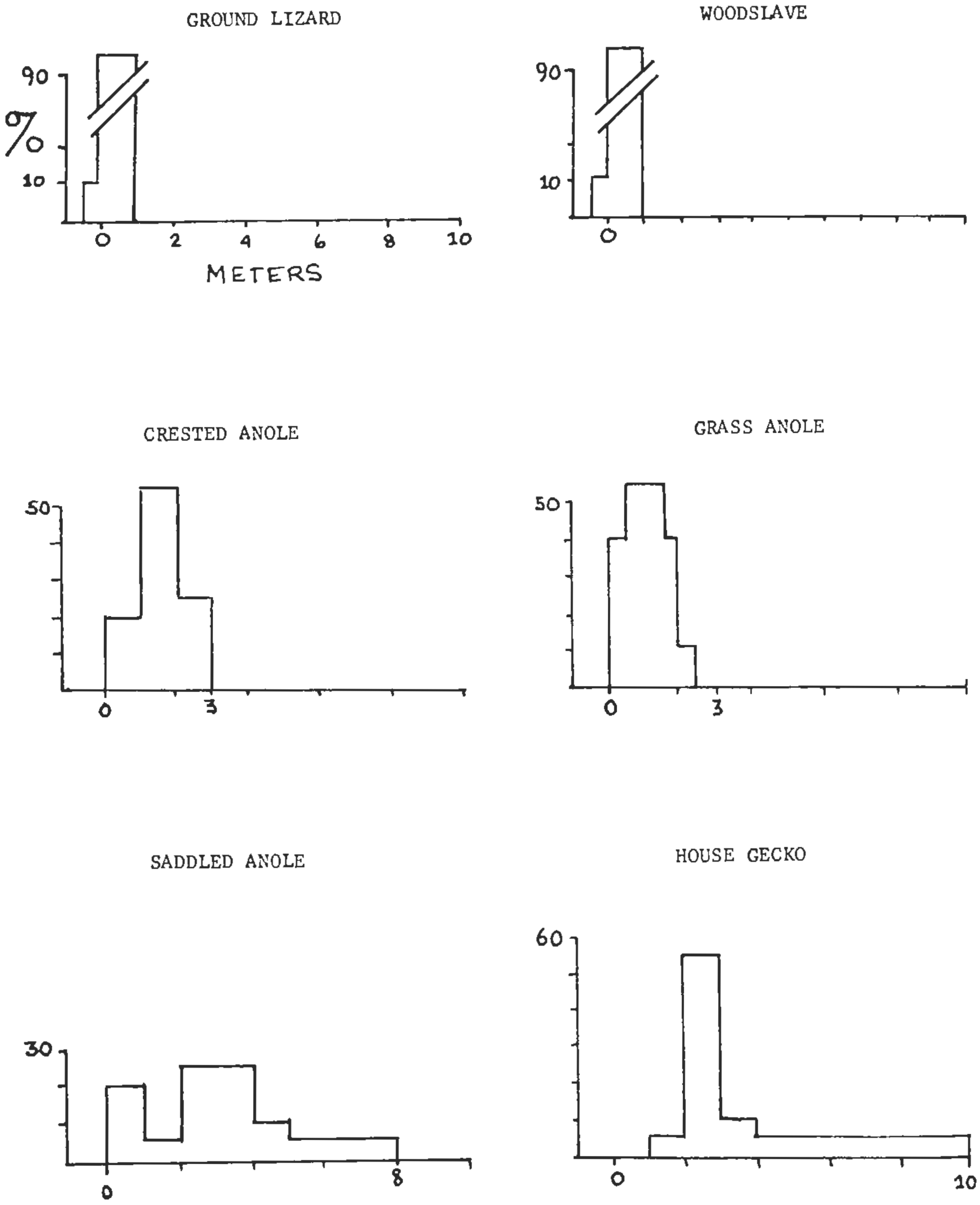
This is a highly simplified, herpetologist's view of a Guana food web. An ornithologist would sort out warblers (eaten by boas) and red-tailed hawks (which eat boas). An entomologist would be aghast (but I did not forget streblids and nycteribiids). House geckos, slippery-backs, and blind snakes seem immune from direct predation. The former because of habitat, the other two because of their heavy dermal armour. See text.



GUANA LIZARD NICHES I:
Daily (diel) activity cycles

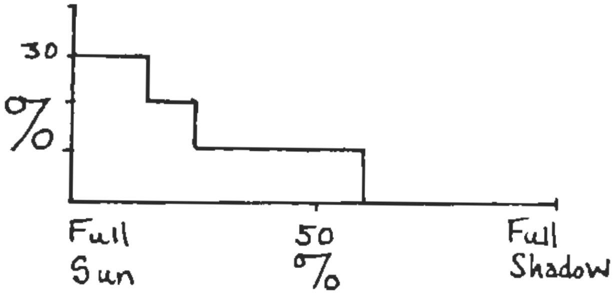


GUANA LIZARD NICHES II:
Foraging and perching heights

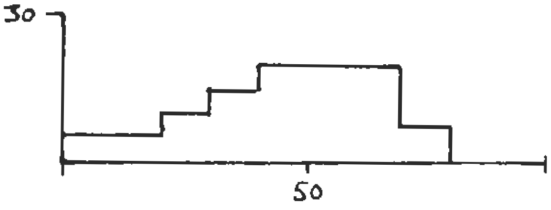


GUANA LIZARD NICHES III:
Insolation: percentage of direct sunlight on activity areas during times of activity, the latter estimated in percent.

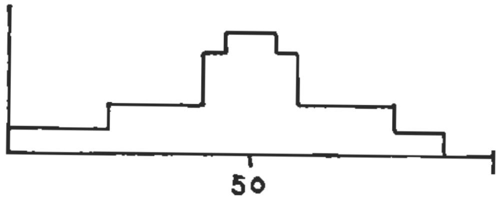
GROUND LIZARD



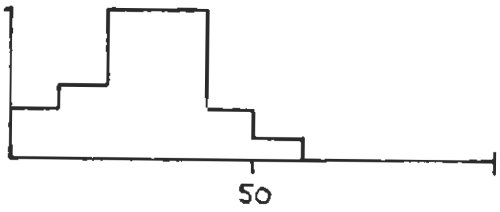
WOODSLAVE



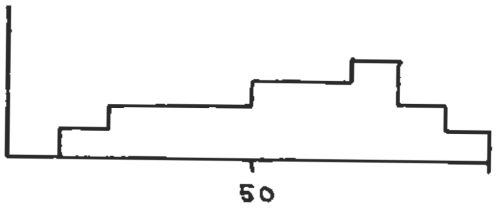
CRESTED ANOLE



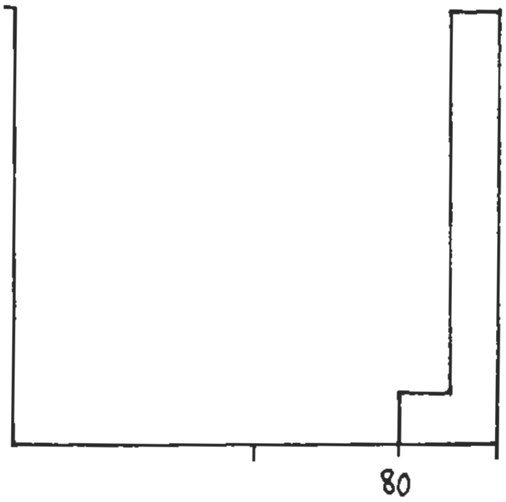
GRASS ANOLE



SADDLED ANOLE



HOUSE GECKO



VI. PROSPECTS FOR FUTURE WORK

"Behold, I have set before you an open door."

That is the motto of the high school I went to, and I am embarrassed to say I do not know its origin. Good line, though.

There are at least a dozen major, important papers to be got out of continued study on Guana, given supervision and direction. These may vary all the way from student term papers for particular courses, possibly resulting in short journal articles, to doctoral dissertations and ecological monographs. In producing this report I have tried to make a veritable Sierra out of incidence, inference, and reference -- in ascending order. The data accumulated on the ground in forty days are not all trivial. There is more than a mole hill, but we are still far from publishable results about any but the most remarkable single finds, like the palm snail (Lazell, 1983).

I would like to see Guana Island become a center for biological and ecological research. I do not see that role conflicting significantly with its role as site of a hide-away hotel, or as a retreat from world turmoil. The latter roles might well be complemented by the results of some of the biological research. For example, plant ecology of the island cries out for better management or elimination of the sheep. This would benefit all native wildlife including snakes, hawks, and owl -- all of which tend to reduce exotic pests. It would also increase water-retention capacity via increased ground cover, humus, and soil. Simple short cuts would include nest boxes for owls and nest platforms for red-tailed hawks which would tend to decrease exotic pests right away.

I personally wish to pursue investigation of the reptile community. This means maintaining the pit-trap grid, expanding other mark-recapture efforts, flagging off selected sites for detailed animal study (e.g. diets, reproductive condition, morphological characteristics), and searching for the rare and "missing" species.

It is the lure of rare species that truly compels me. I am an animal hunter. The veneer of population biologist, taxonomist, or theoretical ecologist that appears on me was applied in hours: course hours in academia on the boy-years and man-years of australopithecus hunting his prey. I mostly learned to be a discriminating hunter: rare things are better than common things, "extinct" things are better than rare things, when rediscovered alive, and new living things -- never before known to science -- are best.

I also learned that I do not want to wipe out my prey, and that sometimes I am capable of it. I could probably eat all the Guana palm snails there are in a few hours, and be the first and last man on earth to eat any at all. I love snails, too. But I want them to live -- probably, a psychiatrist would say, because I always want to be able to go back and get some more: reinforce pleasant memory (that is exactly why I tend to reorder seafood platters and filets mignon bleu; it is less likely to explain why I did not simply shoot my ex-wife).

Guana has an impressive list of rarities -- animals so rare I haven't been able to find them yet. Grant's 1932 paper is most interesting in this respect, for he lists three species I have not found. For one of the three, the grass anole, <u>Anolis pulchellus</u>, Grant's word is unimpeachable: he collected the specimen; it is in the Museum of Zoology, University of Michigan. No doubt about it. For another, the common iguana, <u>Iguana iguana</u>, Grant seems certainly to have been in error. Iguanas are conspicuous creatures. They climb trees and rocky cliffs and bask in the sun. They grow to be six feet long and run -- very fast -- through the woods sounding like a rhinoceros. If they were here, we would know it. If they were here in 1932, Oscar would know it. He says they weren't.

Iguanas are widespread in the Virgin Islands. They occur on Tortola, but are scarce there. They are common on Peter Island and the northeast end of Virgin Gorda. I studied them in considerable detail in preparing my revision (Lazell, 1973). I concluded that patterns of geographic variation indicated that the Virgin Islands populations are native. So iguanas may once have occurred on Guana. They nest in sand, where they bury their eggs much as sea turtles do. They would have to nest along White Bay beach; North Bay and the other, smaller beaches do not provide enough of a dune ridge, in my opinion. Iguanas might have been extirpated from the island during the agricultural years between 1740 and 1890. One might hope to find their bones in caves.

Grant's third species is the most important. The little boa occurs nowhere else on earth except the Virgin Islands, and it is everywhere very, very rare. Since it certainly occurs on both Tortola and Great Camanoe, I have no reason to doubt Grant's word that it occurs on Guana. Nellis and MacLean (1983) report that "specimen yield," the rate at which biologists find these boas (on St. Thomas, where most have been found), has accelerated from two per decade in the early 1960's to about one per year now. With data like that I have no reason to doubt that boas are as common on Guana as they are anywhere else in their range. One of these days (or nights) we'll find one. It is a matter of international importance that we do.

Another species which is rare in the world and regarded as internationally endangered is the slippery-back skink. I believe the numerous people who claim to have seen this lizard on Guana, but I couldn't find one. I certainly want to resume the search.

The only amphibian reported from Guana is a frog -- some sort of frog. It does not sound, from the description, like a toad, although the bizarre toad _Bufo lemur_ (someone has recently put it in a separate genus, but I haven't got the paper to cite) occurs on Virgin Gorda. The white-lipped frog, _Leptodactylus albilabris_ occurs on Anegada, Tortola, Jost Van Dyke, and several American islands. It lays its eggs in fresh water, like most frogs, and they hatch out as tadpoles and breathe with gills. They could live on Guana because fresh water does stand long enough in the big ravines to permit their tadpoles to develop. A few weeks would do. But the habitat is temporary and marginal. Perhaps the most likely sort of frog for Guana is one of the species of _Eleutherodactylus_ called "bo-peeps." These are small, nondescript frogs with expanded toe disks for climbing. They lay their eggs in foam nests in moist pockets on land, and their larvae develop directly into little froglets.

Three species of _Eleutherodactylus_ occur on Tortola: _antillensis_, _cochranae_, and _schwartzi_. Both _antillensis_ and _schwartzi_ occur on Virgin Gorda. People claim some sort of "bo-peep" occurs on Peter Island, but I couldn't find that one either. No other _Eleutherodactylus_ populations have been recorded in the British Virgins, so Guana would be by far the smallest island to support one. Thus, a Guana population would have great significance.

These frogs are interesting in all sorts of ways. Almost nothing is known about their life-histories or behavior. We do not know, and cannot imagine very clearly, where they go when they are not out on wet nights, conspicuously calling and courting. We almost never find them otherwise, despite intensive searches under rocks and logs in moist ravines, and in such lovely damp places as the leaf axills of bromeliads like wild pine and pinguin. These would be ideal subjects for radio telemetry study.

Radio telemetry provides a wonderful way to learn animal behavior, home ranges, and -- in combination with mark-recapture -- population biology. It is not cheap, but we could probably gear up to telemeter most of Guana's species for less than two thousand dollars. In addition to frogs (when found), telemetry would be ideal for the study of snakes, ground lizards, and slipperybacks (when found).

Another "missing" and most mysterious species is the little bat. We saw it repeatedly. On grounds of size alone it cannot be any of the species of bats presently known to inhabit the Virgin Islands. One thinks immediately of the North American migratory bats, like red and hoary, but they are too large. The only possible North American migratory candidate is the very rare silver-haired bat, *Lasionycteris noctivagans*, and I think it is too big. How could we catch this creature? It would take a crack shot with a light shotgun (*e.g.* a .410) to hit one, and then it must be killed directly over the terrace so we can retrieve it. Mist nets sometimes catch bats, but only when placed in a tight opening or over water, where that bat is concentrating its sonar on other things and fails to pick up the net. I can't see a mist net working over Guana's terrace. Dr. Karl Koopman, at the American Museum of Natural History in New York, is the authority on Virgin Islands bats. We need to get a specimen and send it to him.

For me, then, the reptiles, amphibians, and mammals are focal. I would like to spend up to two months per year on them, preferably one month in the wet season (say, August through October) and one month in the dry season. I need one full-time assistant and can supervise up to three students, providing they are highly motivated, self-starting, and willing to accept responsibility for specific projects. I think three Liannas and a Didi would do fine.

It would also be extremely worthwhile to involve other biologists with other interests. I think immediately of an ornithologist, an entomologist, a botanist, and a littoral marine biologist. They will predictably have similar assistant/student needs and capacities, so the demand for Liannas and Didis will increase accordingly. I can see a community of three to five biologists, each with three or four assistants and students, churning out research that would make Guana Island famous throughout the scientific world.

Barro Colorado, an island formed in Gatun Lake when the Panama Canal was made, is in some ways comparable. It is a field station staffed by Smithsonian biologists. They have produced a wealth of published work over the years, but the island is utterly different from Guana. It is wet and lush -- covered with rain forest. It has a typically continental fauna and flora. It is an artificial island with a recently stranded biota. The Darwin Station in the Galapagos has produced some work of the sort I envision. The Galapagos are dry islands with a classically oceanic island biota. However, their species are so different that the studies produced there could only be exemplary and comparative for us.

Funding is the obvious problem. Biologists are notoriously poor, as are most students. I don't seem to be quite as bad-off as most of my colleagues, but nobody -- including IRS -- can figure out why, since I have no visible means of support. I quit working when I was 39 and plan never to do another lick of it. Of course, some regard my little strolls around Guana -- or writing reports like this -- work, but that's their opinion. But, even I would need some financial support to keep going.

Big government grants are an unlikely solution. Generally, they only go to a select group of scientists who became established at major universities in the 1950's or early 1960's. What big government money there is gets distributed rather incestuously nowadays; it's a difficult party to crash. The best prospect is to find a patron. This has to be someone with a large enough income to benefit from deductible losses in the thousands. This has to be someone who feels amply rewarded by acknowledgement in a growing body of published work, and who looks forward to the sort of immortality that comes when a new species or subspecies bears his or her patronym. There are predictably new forms to be described as work on Guana proceeds. The little bat, the frog, or the blind snake (with three fine specimens already in hand) are possible candidates. Some common species, like the saddled anole, may well represent as yet unnamed forms. In the realm of invertebrates the probabilities become virtual certainties.

In my opinion, the best thing to do is set up a revokable, timed trust under the auspices of a non-profit corporation. The capital would have to be large enough to generate sufficient interest to fund the research, and one would entertain applications from scientists and students to do the work. You would get plenty of applicants; someone would have to cull out the best ones and oversee the entire project. I will apply for that job. The trust would be set up so that the capital could not be touched, and would revert to the donor (unless the trust were renewed), at the end of some time period -- for example, a decade.

It's just a little, scrub-covered lump of desert with four times as many kinds of snakes and lizards on it as theory supposed there should be. Some, like the tiny, delicate, iridescent boa are among the niftiest species of animals on earth. Some we know are there we haven't even caught yet. It's just a little island, but it could easily make us more than famous; it could make us immortal.

VII. BIBLIOGRAPHY

To facilitate learning more about particular subjects, I have listed works by section. I include not only references cited in the text, but other literature I believe to be relevant and useful. The information explosion of the last few years has been especially vast in the fields of population biology and theoretical ecology, so I have surely missed some important works. Journal abbreviations are those used in university libraries. The two quotations on the title page are from:

McLoughlin, J. C. 1979. Archosauria. Viking Press, New York.

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I. Introduction

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VIII. APPENDIX OF SELECTED PUBLISHED WORKS

Santa Rosalia is the patron saint of Palermo, on the island of Sicily. Little is known of her, but the cave in which her bones rest (or rested) presides over a small pool which supports vast numbers of aquatic beetles. Dr. Hutchinson went to the pool at the cave to collect those beetles. He mused on the fact that three-quarters of the described species of animals on earth are insects, and a disproportionate number of those insects are beetles. He mused also on the remark of the great British biologist J.B.S. Haldane, who, asked by a group of theologians what a scientist could deduce about the Creator from studying His Creation, said "An inordinate fondness for beetles."

An inordinate fondness for *Anolis* lizards, geckos, frogs, bats, birds, and lots more too -- it would seem. Hutchinson's musings on Haldane's remark led to the framing of the question which has haunted ecologists ever since, and which has driven ecology from simple, qualitative, observational natural history in the far realms of arcane science. I have here included four papers which I believe give good insight into the state of that science at the present time.

HOMAGE TO SANTA ROSALIA
or
WHY ARE THERE SO MANY KINDS OF ANIMALS?*

G. E. HUTCHINSON

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When you did me the honor of asking me to fill your presidential chair, I accepted pethaps without duly considering the duties of the president of a society, founded largely to further the study of evolution, at the close of the year that marks the centenary of Darwin and Wallace's initial presentation of the theory of natural selection. It seemed to me that most of the significant aspects of modern evolutionary theory have come either from geneticists, or from those heroic museum workers who suffering through years of neglect, were able to establish about 20 years ago what has come to be called the "new systematics." You had, however, chosen an ecologist as your president and one of that school at times supposed to study the environment without any relation to the organism.

A few months later I happened to be in Sicily. An early interest in zoogeography and in aquaric insects led me to attempt to collect near Palermo, certain species of water-bugs, of the genus *Corixa*, described a century ago by Fieber and supposed to occur in the region, but never fully reinvestigated. It is hard to find suitable localities in so highly cultivated a landscape as the Concha d'Oro. Fortunately, I was driven up Monte Pellegrino, the hill that rises to the west of the city, to admire the view. A little below the summit, a church with a simple baroque facade stands in front of a cave in the limestone of the hill. Here in the 16th century a stalactite encrusted skeleton associated with a cross and twelve beads was discovered. Of this skeleton nothing is certainly known save that it is that of Santa Rosalia, a saint of whom little is reliably reported save that she seems to have lived in the 12th century, that her skeleton was found in this cave, and that she has been the chief patroness of Palermo ever since. Other limestone caverns on Monte Pellegrino had yielded bones of extinct pleistocene *Equus*, and on the walls of one of the rock shelters at the bottom of the hill there are beautiful Gravettian engravings. Moreover, a small relic of the saint that I saw in the treasury of the Cathedral of Monreale has a venerable and

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*Address of the President, American Society of Naturalists, delivered at the annual meeting, Washington, D. C., December 30, 1958.

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petrified appearance, as might be expected. Nothing in her history being known to the contrary, perhaps for the moment we may take Santa Rosalia as the patroness of evolutionary studies, for just below the sanctuary, fed no doubt by the water that percolates through the limestone cracks of the mountain, and which formed the sacred cave, lies a small artificial pond, and when I could get to the pond a few weeks later, I got from it a hint of what I was looking for.

Vast numbers of Corixidae were living in the water. At first I was rather disappointed because every specimen of the larger of the two species present was a female, and so lacking in most critical diagnostic features, while both sexes of the second slightly smaller species were present in about equal number. Examination of the material at leisure, and of the relevant literature, has convinced me that the two species are the common European *C. punctata* and *C. affinis*, and that the peculiar Mediterranean species are illusionary. The larger *C. punctata* was clearly at the end of its breeding season, the smaller *C. affinis* was probably just beginning to breed. This is the sort of observation that any naturalist can and does make all the time. It was not until I asked myself why the larger species should breed first, and then the more general question as to why there should be two and not 20 or 200 species of the genus in the pond, that ideas suitable to present to you began to emerge. These ideas finally prompted the very general question as to why there are such an enormous number of animal species.

There are at the present time supposed to be (Muller and Campbell, 1954; Hyman, 1955) about one million described species of animals. Of these about three-quarters are insects, of which a quite disproportionately large number are members of a single order, the Coleoptera.[1] The marine fauna although it has at its disposal a much greater area than has the terrestrial, lacks this astonishing diversity (Thorson, 1958). If the insects are excluded, it would seem to be more diverse. The proper answer to my initial question would be to develop a theory at least predicting an order of magnitude for the number of species of 10^6 rather than 10^8 or 10^4. This I certainly cannot do. At most it is merely possible to point out some of the factors which would have to be considered if such a theory was ever to be constructed.

Before developing my ideas I should like to say that I subscribe to the view that the process of natural selection, coupled with isolation and later mutual invasion of ranges leads to the evolution of sympatric species, which at equilibrium occupy distinct niches, according to the Volterra-Gause principle. The empirical reasons for adopting this view and the correlative view that the boundaries of realized niches are set by competition are mainly indirect. So far as niches may be defined in terms of food, the subject has been carefully considered by Lack (1954). In general all the indirect evi-

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[1] There is a story, possibly apocryphal, of the distinguished British biologist, J. B. S. Haldane, who found himself in the company of a group of theologians. On being asked what one could conclude as to the nature of the Creator from a study of his creation, Haldane is said to have answered, "An inordinate fondness for beetles."

dence is in accord with the view, which has the advantage of confirming theoretical expectation. Most of the opinions that have been held to the contrary appear to be due to misunderstandings and to loose formulation of the problem (Hutchinson, 1958).

In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum "eat or be eaten," but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view.

FOOD CHAINS

Animal ecologists frequently think in terms of food chains, of the form *individuals of species* S_1 *are eaten by those of* S_2, *of* S_2 *by* S_3, *of* S_3 *by* S_4, etc. In such a food chain S_1 will ordinarily be some holophylic organism or material derived from such organisms. The simplest case is that in which we have a true *predator chain* in Odum's (1953) convenient terminology, in which the lowest link is a green plant, the next a herbivorous animal, the next a primary carnivore, the next a secondary carnivore, etc. A specially important type of predator chain may be designated Eltonian, because in recent years C. S. Elton (1927) has emphasized its widespread significance, in which the predator at each level is larger and rarer than its prey. This phenomenon was recognized much earlier, notably by A. R. Wallace in his contribution to the 1858 communication to the Linnean Society of London.

In such a system we can make a theoretical guess of the order of magnitude of the diversity that a single food chain can introduce into a community. If we assume that in general 20 per cent of the energy passing through one link can enter the next link in the chain, which is overgenerous (cf. Lindeman, 1942; Slobodkin in an unpublished study finds 13 per cent as a reasonable upper limit) and if we suppose that each predator has twice the mass, (or 1.26 the linear dimensions) of its prey, which is a very low estimate of the size difference between links, the fifth animal link will have a population of one ten thousandth (10^{-4}) of the first, and the fiftieth animal link, if there was one, a population of 10^{-49} the size of the first. Five animal links are certainly possible, a few fairly clear cut cases having been in fact recorded. If, however, we wanted 50 links, starting with a protozoan or rotifer feeding on algae with a density of 10^6 cells per ml, we should need a volume of 10^{24} cubic kilometers to accommodate on an average one specimen of the ultimate predator, and this is vastly greater than the volume of the world ocean. Clearly the Eltonian food-chain of itself cannot give any great diversity, and the same is almost certainly true of the other types of food chain, based on detritus feeding or on parasitism.

Natural selection

Before proceeding to a further consideration of diversity, it is, however, desirable to consider the kinds of selective force that may operate on a food chain, for this may limit the possible diversity.

It is reasonably certain that natural selection will tend to maintain the efficiency of transfer from one level to another at a maximum. Any increase in the predatory efficiency of the n^{th} link of a simple food chain will however always increase the possibility of the extermination of the $(n-1)^{\mathrm{th}}$ link. If this occurs either the species constituting the n^{th} link must adapt itself to eating the $(n-2)^{\mathrm{th}}$ link or itself become extinct. This process will in fact tend to shortening of food chains. A lengthening can presumably occur most simply by the development of a new terminal carnivore link, as its niche is by definition previously empty. In most cases this is not likely to be easy. The evolution of the whale-bone whales, which at least in the case of *Balaenoptera borealis*, can feed largely on copepods and so rank on occasions as primary carnivores (Bigelow, 1926), presumably constitutes the most dramatic example of the shortening of a food chain. Mechanical considerations would have prevented the evolution of a larger rarer predator, until man developed essentially non-Eltonian methods of hunting whales.

Effect of size

A second important limitation of the length of a food chain is due to the fact that ordinarily animals change their size during free life. If the terminal member of a chain were a fish that grew from say one cm to 150 cms in the course of an ordinary life, this size change would set a limit by competition to the possible number of otherwise conceivable links in the 1-150 cm range. At least in fishes this type of process (metaphoetesis) may involve the smaller specimens belonging to links below the larger and the chain length is thus lengthened, though under strong limitations, by cannibalism.

We may next enquire into what determines the number of food chains in a community. In part the answer is clear, though if we cease to be zoologists and become biologists, the answer begs the question. Within certain limits, the number of kinds of primary producers is certainly involved, because many herbivorous animals are somewhat eclectic in their tastes and many more limited by their size or by such structural adaptations for feeding that they have been able to develop.

Effects of terrestrial plants

The extraordinary diversity of the terrestrial fauna, which is much greater than that of the marine fauna, is clearly due largely to the diversity provided by terrestrial plants. This diversity is actually two-fold. Firstly, since terrestrial plants compete for light, they have tended to evolve into structures growing into a gaseous medium of negligible buoyancy. This has led to the formation of specialized supporting, photosynthetic, and reproductive structures which inevitably differ in chemical and physical properties. The ancient Danes and Irish are supposed to have eaten elm-bark, and sometimes sawdust; in periods of stress, has been hydrolyzed to produce edible carbohydrate; but usually man, the most omnivorous of all animals, has avoided almost all parts of trees except fruits as sources of food, though various individual species of animals can deal with practically every tissue of many arboreal species. A major source of terrestrial diversity was thus introduced by the evolution of almost 200,000 species of flowering plants, and the three quarters of a million insects supposedly known today are in part a product of that diversity. But of itself merely providing five or ten kinds of food of different consistencies and compositions does not get us much further than the five or ten links of an Eltonian pyramid. On the whole the problem still remains, but in the new form: why are there so many kinds of plants? As a zoologist I do not want to attack that question directly, I want to stick with animals, but also to get the answer. Since, however, the plants are part of the general system of communities, any sufficiently abstract properties of such communities are likely to be relevant to plants as well as to herbivores and carnivores. It is, therefore, by being somewhat abstract, though with concrete zoological details as examples, that I intend to proceed.

INTERRELATIONS OF FOOD CHAINS

Biological communities do not consist of independent food chains, but of food webs, of such a kind that an individual at any level (corresponding to a link in a single chain) can use some but not all of the food provided by species in the levels below it.

It has long been realized that the presence of two species at any level, either of which can be eaten by a predator at a level above, but which may differ in palatability, ease of capture or seasonal and local abundance, may provide alternative foods for the predator. The predator, therefore, will neither become extinct itself nor exterminate its usual prey, when for any reason, not dependent on prey-predator relationships, the usual prey happens to be abnormally scarce. This aspect of complicated food webs has been stressed by many ecologists, of whom the Chicago school as represented by Allee, Emerson, Park, Park and Schmidt (1949), Odum (1953) and Elton (1958), may in particular be mentioned. Recently MacArthur (1955) using an ingenious but simple application of information theory has generalized the points of view of earlier workers by providing a formal proof of the increase in stability of a community as the number of links in its food web increases.

MacArthur concludes that in the evolution of a natural community two partly antagonistic processes are occurring. More efficient species will replace less efficient species, but more stable communities will outlast less stable communities. In the process of community formation, the entry of a new species may involve one of three possibilities. It may completely displace an old species. This of itself does not necessarily change the stability, though it may do so if the new species inherently has a more stable population (cf. Slobodkin, 1956) than the old. Secondly, it may occupy an unfilled niche, which may, by providing new partially independent links, increase stability. Thirdly, it may partition a niche with a pre-existing species. Elton (1958) in a fascinating work largely devoted to the fate of species accidentally or purposefully introduced by man, concludes that in very diverse communities such introductions are difficult. Early in the history of a community we may suppose many niches will be empty and invasion will proceed easily; as the community becomes more diversified, the process will be progressively more difficult. Sometimes an extremely successful invader may oust a species but add little or nothing to stability, at other times the invader by some specialization will be able to compete successfully for the marginal parts of a niche. In all cases it is probable that invasion is most likely when one or more species happen to be fluctuating and are underrepresented at a given moment. As the communities build up, these opportunities will get progressively rarer. In this way a complex community containing some highly specialized species is constructed asymptotically.

Modern ecological theory therefore appears to answer our initial question at least partially by saying that there is a great diversity of organisms because communities of many diversified organisms are better able to persist than are communities of fewer less diversified organisms. Even though the entry of an invader which takes over part of a niche will lead to the reduction in the *average* population of the species originally present, it will also lead to an increase in stability reducing the risk of the original population being at times underrepresented to a dangerous degree. In this way loss of some niche space may be compensated by reduction in the amplitude of fluctuations in a way that can be advantageous to both species. The process however appears likely to be asymptotic and we have now to consider what sets the asymptote, or in simpler words why are there not more different kinds of animals?

LIMITATION OF DIVERSITY

It is first obvious that the processes of evolution of communities must be under various sorts of external control, and that in some cases such control limits the possible diversity. Several investigators, notably Odum (1953) and MacArthur (1955), have pointed out that the more or less cyclical oscillations observed in arctic and boreal fauna may be due in part to the communities not being sufficiently complex to damp out oscillations. It is certain that the fauna of any such region is qualitatively poorer than that of warm temperate and tropical areas of comparable effective precipitation. It is probably considered to be intuitively obvious that this should be so, but on analysis the obviousness tends to disappear. If we can have one or two species of a large family adapted to the rigors of Arctic existence, why can we not have more? It is reasonable to suppose that the total biomass may be involved. If the fundamental productivity of an area is limited by a short growing season to such a degree that the total biomass is less than under more favorable conditions, then the rarer species in a community may be so rare that they do not exist. It is also probable that certain absolute limitations on growth-forms of plants, such as those that make the development of forest impossible above a certain latitude, may in so acting, severely limit the number of niches. Dr. Robert MacArthur points out that the development of high tropical rain forest increases the bird fauna more than that of mammals, and Thorson (1957) likewise has shown that the so-called infauna show no increase of species toward the tropics while the marine epifauna becomes more diversified. The importance of this aspect of the plant or animal substratum, which depends largely on the length of the growing season and other aspects of productivity is related to that of the environmental mosaic discussed later.

We may also inquire, but at present cannot obtain any likely answer, whether the arctic fauna is not itself too young to have achieved its maximum diversity. Finally, the continual occurrence of catastrophes, as Wynne-Edwards (1952) has emphasized, may keep the arctic terrestrial community in a state of perennial though stunted youth.

Closely related to the problems of environmental rigor and stability, is the question of the absolute size of the habitat that can be colonized. Over much of western Europe there are three common species of small voles, namely *Microtus arvalis*, *M. agrestis* and *Clethrionomys glareolus*. These are sympatric but with somewhat different ecological preferences.

In the smaller islands off Britain and in the English channel, there is only one case of two species co-occurring on an island, namely *M. agrestis* and Clethrionomys on the island of Mull in the Inner Hebrides (Barrett-Hamilton and Hinton, 1911-1921). On the Orkneys the single species is *M. orcadensis*, which in morphology and cytology is a well-differentiated ally of *M. arvalis*; a comparable animal (*M. sarnius*) occurs on Guernsey. On most of the Scottish Islands only subspecies of *M. agrestis* occur, but on Mull and Raasay, on the Welsh island of Skomer, as well as on Jersey, races of Clethrionomys of somewhat uncertain status are found. No voles have reached Ireland, presumably for paleogeographic reasons, but they are also absent from a number of small islands, notably Alderney and Sark. The last named island must have been as well placed as Guernsey to receive *Microtus arvalis*. Still stranger is the fact that although it could not have got to the Orkneys without entering the mainland of Britain, no vole of the *arvalis* type now occurs in the latter country. Cases of this sort may be perhaps explained by the lack of favorable refuges in randomly distributed very unfavorable seasons or under special kinds of competition. This explanation is very reasonable as an explanation of the lack of Microtus on Sark, where it may have had difficulty in competing with *Rattus rattus* in a small area. It would be stretching one's credulity to suppose that the area of Great Britain is too small to permit the existence of two sympatric species of Microtus, but no other explanation seems to have been proposed.

It is a matter of considerable interest that Lack (1942) studying the populations of birds on some of these small British islands concluded that such populations are often unstable, and that the few species present often occupied larger niches than on the mainland in the presence of competitors. Such faunas provide examples of communities held at an early stage in development because there is not enough space for the evolution of a fuller and more stable community.

NICHE REQUIREMENTS

The various evolutionary tendencies, notably metaphoetesis, which operate on single food chains must operate equally on the food-web, but we also have a new, if comparable, problem as to how much difference between two species at the same level is needed to prevent them from occupying the same niche. Where metric characters are involved we can gain some insight into this extremely important problem by the study of what Brown and Wilson (1956) have called *character displacement* or the divergence shown when two partly allopatric species of comparable niche requirements become sympatric in part of their range.

I have collected together a number of cases of mammals and birds which appear to exhibit the phenomenon (table 1). These cases involve metric characters related to the trophic apparatus, the length of the culmen in birds and of the skull in mammals appearing to provide appropriate measures. Where the species co-occur, the ratio of the larger to the small form varies from 1.1 to 1.4, the mean ratio being 1.28 or roughly 1.3. This latter figure may tentatively be used as an indication of the kind of difference necessary to permit two species to co-occur in different niches but at the same level of a food-web. In the case of the aquatic insects with which I began my address, we have over most of Europe three very closely allied species of Corixa, the largest *punctata*, being about 116 per cent longer than the middle sized species *macrocephala*, and 146 per cent longer than the small species *affinis*. In northwestern Europe there is a fourth species, *C. dentipes*, as large as *C. punctata* and very similar in appearance. A single observation (Brown, 1948) suggests that this is what I have elsewhere (Hutchinson, 1951) termed a fugitive species, maintaining itself in the face of competition mainly on account of greater mobility. According to Macan (1954) while both *affinis* and *macrocephala* may occur with *punctata* they never are found with each other, so that all three species never occur together. In the eastern part of the range, *macrocephala* drops out, and *punctata* appears to have a discontinuous distribution, being recorded as far east as Simla, but not in southern Persia or Kashmir, where *affinis* occurs. In these eastern localities, where it occurs by itself, *affinis* is larger and darker than in the west, and superficially looks like *macrocephala* (Hutchinson, 1940).

This case is very interesting because it looks as though character displacement is occurring, but that the size differences between the three species are just not great enough to allow them all to co-occur. Other characters than size are in fact clearly involved in the separation, *macrocephala* preferring deeper water than *affinis* and the latter being more tolerant of brackish conditions. It is also interesting because it calls attention to a marked difference that must occur between hemimetabolous insects with annual life cycles involving relatively long growth periods, and birds or mammals in which the period of growth in length is short and of a very special nature compared with the total life span. In the latter, niche separation may be possible merely through genetic size differences, while in a pair of ani-

TABLE 1

Mean character displacement in measurable trophic structures in mammals (skull) and birds (culmen); data for Mustela from Miller (1912); Apodemus from Cranbrook (1957); Sitta from Brown and Wilson (1956) after Vaurie; Galapagos finches from Lack (1947)

	Locality and measurement when sympatric	Locality and measurement when allopatric	Ratio when sympatric
Mustela nivalis	Britain; skull ♂ 39.3 ♀ 33.6 mm.	(*boccamela*) S. France, Italy ♂ 42.9 ♀ 34.7 mm. (*iberica*) Spain, Portugal ♂ 40.4 ♀ 36.0	♂ 100:128 ♀ 100:134
M. erminea	Britain; " ♂ 50.4 ♀ 45.0	(*hibernica*) Ireland ♂ 46.0 ♀ 41.9	
Apodemus sylvaticus	Britain; " 24.8	unnamed races on Channel Islands 25.6–26.7	100:109
A. flavicollis	Britain; " 27.0		
Sitta tephronota	Iran; culmen 29.0	races east of overlap 25.5	100:124
S. neumayer	Iran; " 23.5	races west of overlap 26.0	
Geospiza fortis	Indefatigable Isl.; culmen 12.0	Daphne Isl. 10.5	100:143
G. fuliginosa	Indefatigable Isl.; " 8.4	Crossman Isl. 9.3	
Camarhynchus parvulus	James Isl.; " 7.0 Indefatigable Isl.; " 7.5	N. Albemarle Isl. 7.0 Chatham Isl. 8.0	James 100:140:180 100:129
C. psittacula	S. Albemarle Isl.; " 7.3 James Isl.; " 9.8 Indefatigable Isl.; " 9.6	Abington Isl. 10.1 Bindloe Isl. 10.5	Indefatigable 100:128:162 100:127
C. pallidus	S. Albemarle Isl.; " 8.5 James Isl.; " 12.6 Indefatigable Isl.; " 12.1 S. Albemarle Isl.; " 11.2	N. Albemarle Isl. 11.7 Chatham Isl. 10.8	S. Albemarle 100:116:153 100:132
			Mean ratio 100:128

mals like *C. punctata* and *C. affinis* we need not only a size difference but a seasonal one in reproduction; this is likely to be a rather complicated matter. For the larger of two species always to be larger, it must never breed later than the smaller one. I do not doubt that this is what was happening in the pond on Monte Pellegrino, but have no idea how the difference is achieved.

I want to emphasize the complexity of the adaptation necessary on the part of two species inhabiting adjacent niches in a given biotope, as it probably underlies a phenomenon which to some has appeared rather puzzling. MacArthur (1957) has shown that in a sufficiently large bird fauna, in a uniform undisturbed habitat, areas occupied by the different species appear to correspond to the random non-overlapping fractionation of a plane or volume. Kohn (1959) has found the same thing for the cone-shells (Conus) on the Hawaiian reefs. This type of arrangement almost certainly implies such individual and unpredictable complexities in the determination of the niche boundaries, and so of the actual areas colonized, that in any overall view, the process would appear random. It is fairly obvious that in different types of community the divisibility of niches will differ and so the degree of diversity that can be achieved. The fine details of the process have not been adequately investigated, though many data must already exist that could be organized to throw light on the problem.

MOSAIC NATURE OF THE ENVIRONMENT

A final aspect of the limitation of possible diversity, and one that perhaps is of greatest importance, concerns what may be called the mosaic nature of the environment. Except perhaps in open water when only uniform quasi-horizontal surfaces are considered, every area colonized by organisms has some local diversity. The significance of such local diversity depends very largely on the size of the organisms under consideration. In another paper MacArthur and I (Hutchinson and MacArthur, 1959) have attempted a theoretical formulation of this property of living communities and have pointed out that even if we consider only the herbivorous level or only one of the carnivorous levels, there are likely, above a certain lower limit of size, to be more species of small or medium sized organisms than of large organisms. It is difficult to go much beyond crude qualitative impressions in testing this hypothesis, but we find that for mammal faunas, which contain such diverse organisms that they may well be regarded as models of whole faunas, there is a definite hint of the kind of theoretical distribution that we deduce. In qualitative terms the phenomenon can be exemplified by any of the larger species of ungulates which may require a number of different kinds of terrain within their home ranges, any one of which types of terrain might be the habitat of some small species. Most of the genera or even subfamilies of very large terrestrial animals contain only one or two sympatric species. In this connection I cannot refrain from pointing out the immense scientific importance of obtaining a really full insight into the ecology of the large mammals of Africa while they can still be studied under natural conditions. It is indeed quite possible that the results of studies on these wonderful animals would in long-range though purely practical terms pay for the establishment of greater reservations and National Parks than at present exist.

In the passerine birds the occurrence of five or six closely related sympatric species is a commonplace. In the mammal fauna of western Europe no genus appears to contain more than four strictly sympatric species. In Britain this number is not reached even by Mustela with three species, on the adjacent parts of the continent there may be three sympatric shrews of the genus Crocidura and in parts of Holland three of Microtus. In the same general region there are genera of insects containing hundreds of species, as in Athela in the Coleoptera and Dasyhelea in the Diptera Nematocera. The same phenomenon will be encountered whenever any well-studied fauna is considered. Irrespective of their position in a food chain, small size, by permitting animals to become specialized to the conditions offered by small diversified elements of the environmental mosaic, clearly makes possible a degree of diversity quite unknown among groups of larger organisms.

We may, therefore, conclude that the reason why there are so many species of animals is at least partly because a complex trophic organization of a community is more stable than a simple one, but that limits are set by the tendency of food chains to shorten or become blurred, by unfavorable physical factors, by space, by the fineness of possible subdivision of niches, and by those characters of the environmental mosaic which permit a greater diversity of small than of large allied species.

CONCLUDING DISCUSSION

In conclusion I should like to point out three very general aspects of the sort of process I have described. One speculative approach to evolutionary theory arises from some of these conclusions. Just as adaptative evolution by natural selection is less easy in a small population of a species than in a larger one, because the total pool of genetic variability is inevitably less, so it is probable that a group containing many diversified species will be able to seize new evolutionary opportunities more easily than an undiversified group. There will be some limits to this process. Where large size permits the development of a brain capable of much new learnt behavior, the greater plasticity acquired by the individual species will offset the disadvantage of the small number of allied species characteristic of groups of large animals. Early during evolution the main process from the standpoint of community structure was the filling of all the niche space potentially available for producer and decomposer organisms and for herbivorous animals. As the latter, and still more as carnivorous animals began to appear, the persistence of more stable communities would imply splitting of niches previously occupied by single species as the communities became more diverse. As this process continued one would expect the overall rate of evolution to have increased, as the increasing diversity increased the probability of the existence of species preadapted to new and unusual niches. It is reasonable to suppose that strong predation among macroscopic metazoa did not begin until the late Precambrian, and that the appearance of powerful predators led to the appearance of fossilizable skeletons. This seems the only reasonable hypothesis, of those so far advanced, to account for the relatively sudden appearance of several fossilizable groups in the Lower Cambrian. The process of diversification would, according to this argument, be somewhat autocatakinetic even without the increased stability that it would produce; with the increase in stability it would be still more a self inducing process, but one, as we have seen, with an upper limit. Part of this upper limit is set by the impossibility of having many sympatric allied species of large animals. These however are the animals that can pass from primarily innate to highly modifiable behavior. From an evolutionary point of view, once they have appeared, there is perhaps less need for diversity, though from other points of view, as Elton (1958) has stressed in dealing with human activities, the stability provided by diversity can be valuable even to the most adaptable of all large animals. We may perhaps therefore see in the process of evolution an increase in diversity at an increasing rate till the early Paleozoic, by which time the familiar types of community structure were established. There followed then a long period in which various large and finally large-brained species became dominant, and then a period in which man has been reducing diversity by a rapidly increasing tendency to cause extinction of supposedly unwanted species, often in an indiscriminate manner. Finally we may hope for a limited reversal of this process when man becomes aware of the value of diversity no less in an economic than in an esthetic and scientific sense.

A second and much more metaphysical general point is perhaps worth a moment's discussion. The evolution of biological communities, though each species appears to fend for itself alone, produces integrated aggregates which increase in stability. There is nothing mysterious about this; it follows from mathematical theory and appears to be confirmed to some extent empirically. It is however a phenomenon which also finds analogies in other fields in which a more complex type of behavior, that we intuitively regard as higher, emerges as the result of the interaction of less complex types of behavior, that we call lower. The emergence of love as an antidote to aggression, as Lorenz pictures the process, or the development of cooperation from various forms of more or less inevitable group behavior that Allee (1931) has stressed are examples of this from the more complex types of biological systems.

In the ordinary sense of explanation in science, such phenomena are explicable. The types of holistic philosophy which import *ad hoc* mysteries into science whenever such a situation is met are obviously unnecessary. Yet perhaps we may wonder whether the empirical fact that it is the nature of things for this type of explicable emergence to occur is not something that itself requires an explanation. Many objections can be raised to such a view; a friendly organization of biologists could not occur in a universe in which cooperative behavior was impossible and without your cooperation I could not raise the problem. The question may in fact appear to certain

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types of philosophers not to be a real one, though I suspect such philosophers in their desire to demonstrate how often people talk nonsense, may sometimes show less ingenuity than would be desirable in finding some sense in such questions. Even if the answer to such a question were positive, it might not get us very far; to an existentialist, life would have merely provided yet one more problem; students of Whitehead might be made happier, though on the whole the obscurities of that great writer do not seem to generate unhappiness; the religious philosophers would welcome a positive answer but note that it told them nothing that they did not know before; Marxists might merely say, "I told you so." In spite of this I suspect that the question is worth raising, and that it could be phrased so as to provide some sort of real dichotomy between alternatives; I therefore raise it knowing that I cannot, and suspecting that at present others cannot, provide an intellectually satisfying answer.

My third general point is less metaphysical, but not without interest. If I am right that it is easier to have a greater diversity of small than of large organisms, then the evolutionary process in small organisms will differ somewhat from that of large ones. Wherever we have a great array of allied sympatric species there must be an emphasis on very accurate interspecific mating barriers which is unnecessary where virtually no sympatric allies occur. We ourselves are large animals in this sense; it would seem very unlikely that the peculiar lability that seems to exist in man, in which even the direction of normal sexual behavior must be learnt, could have developed to quite the existing extent if species recognition, involving closely related sympatric congeners, had been necessary. Elsewhere (Hutchinson, 1959) I have attempted to show that the difficulties that *Homo sapiens* has to face in this regard may imply various unsuspected processes in human evolutionary selection. But perhaps Santa Rosalia would find at this point that we are speculating too freely, so for the moment, while under her patronage, I will say no more.

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SATURATION OF BIRD COMMUNITIES IN THE WEST INDIES

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The concept of faunal saturation goes back at least to Elton (1950), who stated that "the number of different kinds of animals that can live together in an area of uniform type rapidly reaches a saturation point." Other authors have subsequently employed the term in a variety of contexts, some peculiar to island biogeography, and some more pertinent to continental situations.

MacArthur and Wilson (1967) regarded an insular fauna as saturated when immigration and extinction were in balance, i.e., "the equilibrial condition." Earlier (1963), in discussing the distance effect on insular faunas, they referred to "degree of saturation" as the species number of a far island expressed as a fraction of the number of species on an equal-sized near island. Abbott and Grant (1976) used the same phrase, but their frame of reference was the ultimate source of colonists, rather than a near island of equivalent physical characteristics. The term has thus been used to refer to three situations in island biogeography: the equilibrium condition, the effect of distance, and the proportion of species relative to the source, a measure that incorporates the effects of distance, area, and probably other factors as well.

Students of continental diversity patterns have similarly thought of saturation in a variety of contexts. Points of view have differed in accordance with whether measured species diversities were perceived as reflecting inelastic limits to species packing (e.g., Cody 1966) or evolutionary history. MacArthur (1965) expressed the dichotomy thusly: ". . . if the areas being compared are not saturated with species, an historical answer involving rates of speciation and length of time available will be appropriate; if the areas are saturated with species, then the answer must be expressed in terms of the size of the niche space . . . and the limiting similarity of co-existing species." However, neither MacArthur nor, to our knowledge, any other author has proposed a set of operational criteria by which a saturated community could be distinguished from an unsaturated one. The issue is of no small importance to diversity studies because differences in the number of species occupying a series of habitats could be due to the availability of disparate numbers of appropriately adapted taxa just as well as to differences in the measured features of the habitats.

How can saturation be demonstrated? Ideally, one would like to be able to

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control the habitat and vary the number of species available to exploit it. In fact it is possible to do just this by selecting comparable tracts of vegetation on a series of islands that differ widely in size, and hence in the number of species they contain. Insular species pools of landbirds vary within the West Indies from about 10 on small, remote islands (Mona, Navassa) to 79 on the largest islands (Hispaniola, Cuba). By comparing the bird communities of matched sites on islands differing widely in size, we show that saturation exists within West Indian habitats. Our task is to understand what it implies for evolution and ecology.

METHODS

We censused the bird species present in uniform tracts of vegetation by two means, netting and direct observation. Nets were strung end-to-end in lines of 16 or 20 and operated from dawn to dusk on 3 to 5 consecutive days. Details of the procedure have been published (Terborgh and Faaborg 1973). The nets provide samples of the bird populations using a standard horizontal slice of the vegetation, 0.1–2.0 m above the ground.

The procedure was repeated at 17 sites on 12 islands ranging in size from Terre de Haut (4.6 km^2) to Hispaniola (80,000 km^2). Study sites were located in the largest, most homogeneous tracts of vegetation available. Species lists and details of the elevation, vegetation, etc., of the sites are given in other publications (Terborgh and Faaborg 1973 for Mona, Puerto Rico; Terborgh et al. 1978 for Lesser Antilles; Terborgh and Faaborg 1980 for Hispaniola).

The sites represent the two most extensive vegetation formations in the Antilles: humid lower montane forest (hereafter, rainforest; mean elevation was ca. 400 m) and coastal sclerophyll scrub. The latter occurs in the lowlands of nearly all islands and covers virtually the entire surface of many low islands (e.g., Mona, Virgin Islands, Guadeloupe satellites, etc.). It is particularly extensive in karstic regions (Puerto Rico, southern Hispaniola). Rainforest is more limited in total extent and more patchy in its distribution. Appreciable areas of it exist only on islands possessing elevated interiors. The physiognomic and floristic features of the two vegetation types have been described by Beard (1949), Hodge (1954), and others.

RESULTS

Our results are contained in figure 1, which shows the numbers of species censused and netted at 17 sites in relation to the total number of landbird species present on each island (= species pool). Both the census and net results fit typical "saturation" curves in the sense employed in physiology. A plot of the rate of an enzymatic reaction versus the concentration of its substrate, for example, describes a curve of this form, as does photosynthetic rate against light intensity. Such curves are interpreted to indicate a functional dependence on the independent variable up to a critical level of concentration, beyond which the process is limited by the state of some other variable (e.g., the concentration of the enzyme). The analogy to birds on islands should probably not be carried beyond the shape

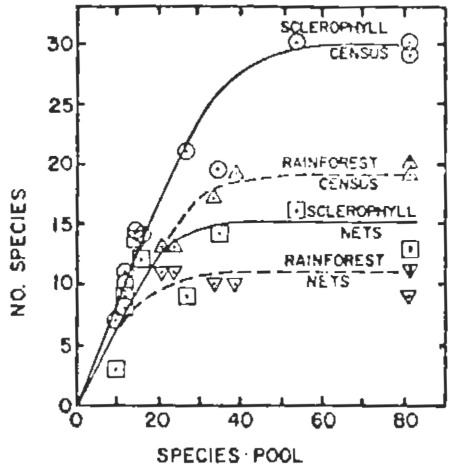

FIG. 1.—Total census and no. of species captured in netted samples at 17 sites on 12 Greater and Lesser Antillean islands. Tracts of sclerophyll vegetation were studied on Mona, Beata, Saona, Terre de Bas, Terre de Haut, La Desirade, Guadeloupe, Puerto Rico, and Hispaniola (2 sites). Rainforest was studied on St. Kitts, Montserrat, Guadeloupe, Dominica, and Hispaniola (3 sites). The abscissa represents the number of breeding land bird species per island (figures given in Appendix B). Net samples are based on a standard effort of roughly 60 net-days. Because of appreciable variation in avian density between the sites, this meant that no. of individuals captured per sample spanned a wide range of values (48–209 for rainforest sites; 62–446 for scrub sites). However, there is no discernible relationship between no. of species per island and no. of individuals captured. Hence, to the extent that the no. of species per sample is influenced by variation in capture rate, the variation contributes only to scatter in the points and does not systematically bias the result.

of the curve itself. What is suggested is that there are two stages in the interaction of birds and island habitats, a linear stage at low species numbers in which species are added to any habitat in proportion to the number present on the island, and an independent stage in which habitats appear to be filled. Once the latter stage has been attained additional numbers of species per island are accommodated through a finer partitioning of habitats, rather than through further increases in the level of syntopic coexistence. Just such results were anticipated, though never demonstrated, by MacArthur. "As the fauna of the island becomes quite large, it will contain a representative of each phenotype category and no further increase in the number of species per habitat will take place. Each new species will, instead, cause a further subdivision of the habitats" (MacArthur 1965, pp. 522–523). Why this should be so is not at all obvious. Before considering possible reasons, we should like to point out some additional features of the results.

1. When fewer than 15 species occur on an island, they all coexist in the predominant vegetation. When more than 15 species are present, some will show restricted habitat distributions (Terborgh et al. 1978).
2. A maximum number of about 30 species coexists in sclerophyll scrub on islands containing more than 50 species.
3. A maximum number of about 20 species coexists in rainforest on islands containing more than 40 species.

4. Netted species numbers reach saturation ahead of the total census for the habitat (i.e., at smaller pool sizes).

5. There is little vertical stratification of bird species within the vegetation in small faunas (≤20 spp.), regardless of whether the habitat is tall rainforest or low scrub. This is indicated by the convergence of the netted and census curves at low pool size.

6. Vertical stratification becomes appreciable on islands containing more than 20 species. Roughly 50% of the species present in both habitat types are captured in the larger faunas, notwithstanding the considerably greater height of rainforest (ca. 30 m vs. ≤ 12 m for scrub).

HYPOTHESES

We now enumerate a set of hypotheses which, though they are not mutually exclusive, specify four distinct mechanisms that could account for the observed saturation of species numbers in habitats.

Hypothesis 1.—All the "niche space" is filled at saturation; the species are as much alike as they can be without breaching the limits of similarity.

Hypothesis 2.—The West Indian avifauna consists largely of habitat specialists. A habitat is saturated when it contains all the appropriately adapted species in the available pool of colonists. A corollary of this is that the species area curve is mainly attributable to the addition of new habitats on larger islands.

Hypothesis 3.—Members of the West Indian species pool have become coadapted to tolerate a maximum level of interspecific competition, namely that which prevails on the largest islands. Since small islands are nearly always colonized from larger neighbors, species accumulate until the competitive pressure approximately equals that on the source islands.

Hypothesis 4.—Habitat occupancy broadens under reduced interspecific competition. As the number of species per island drops, the species present invade additional vegetation types to maintain constant diversity until all segregation by habitat disappears. (This is the antithesis of hypothesis 2.)

Although one could perhaps think of additional ways to account for the observations, we feel that the most biologically plausible mechanisms are incorporated in the four listed above. Further explanations could, of course, be generated by recombining elements of the hypotheses already stated.

Evaluation of the Hypotheses

Hypothesis 1.—That West Indian bird communities are packed to the limits of similarity seems improbable in view of the fact that analogous mainland habitats contain much higher diversities. Rainforest communities in Central America typically include more than 100 species (Howell 1957; Slud 1960), and those in Amazonia may accommodate in excess of 200 (O'Neill and Pearson 1974; O'Neill 1974).

Nevertheless, it is still possible, in spite of the structural similarity of island and mainland vegetation, that the insular habitats offer a greatly reduced array of resources. Perhaps this is what Lack (1976) meant when he attributed the low species number on Jamaica (as compared to adjacent Honduras) to "ecological impoverishment."

Certain categories of species are clearly missing from the West Indian fauna: ant-following birds (no army ants); large raptors (no large mammalian prey); large frugivores > 1,000 g (paucity of large fruits). However, even discounting these, there remain big disparities in the richness of island and mainland communities at the same latitude.

It is not clear how ecological impoverishment could be measured or recognized other than through its association with low species numbers, but this is circular. Avian populations do not seem depressed in the West Indies. A series of lowland habitats in Hispaniola, for example, contained between 14 and 20 pairs per ha J. W. Terborgh, unpublished censuses), values that would be normal to high for comparable mainland sites. Moreover, net yields on a number of Greater and Lesser Antillean islands are neither systematically lower nor higher than on the mainland (Terborgh et al. 1978; Terborgh and Faaborg 1980). The carrying capacity of island habitats for birds thus appears to be undiminished. If the island habitats are ecologically impoverished, the impoverishment might take the form of missing categories of resources and/or truncated resource spectra, rather than of reduced resource productivity.

It is strikingly apparent that West Indian bird communities are organized differently from those on the mainland. This is most conspicuous in the fact that the largest guilds are of frugiovores rather than of insectivores (Terborgh 1977; Terborgh et al. 1978). On either the North or South American mainlands, 70%–90% of the biomass of netted samples of forest bird communities is composed of insectivores; frugivores make up less than 20%. In the West Indies the proportions are reversed (table 1).

The paucity of gleaning and hovering insectivores in the Antilles is truly remarkable. A tall rainforest in Hispaniola, for example, had only four: the bananaquit, which is equally a nectarivore; the narrow-billed tody; the Hispaniolan lizard cuckoo; and the black-whiskered vireo (scientific names are given in Appendix A). In contrast, these guilds were represented by 59 species in a structually similar Amazonian forest (Terborgh 1979*a*, 1979*b*). In most of the lowland vegetation of Hispaniola and Puerto Rico there is no small gleaning counterpart of a warbler or antwren (Terborgh and Faaborg 1980). In view of the prominent role played by such birds in mainland communities, it is hard to believe that this absence is due to chance. A partial explanation may be in the finding that insect densities are systematically lower on Caribbean islands than they are in comparable sites in Costa Rica (Janzen 1973; Allan et al. 1973). Insectivorous *Anolis* lizards are much more abundant in West Indian than in mainland habitats, but this could be a consequence, just as well as a cause, of a scarcity of avian competitors (Andrews 1976). Paradoxically, large numbers of North American warblers winter in the West Indies, more than doubling the biomass of insectivorous birds in many habitats on the nearer islands (Emlen 1980; Terborgh and Faaborg 1980). Though it is far from clear how all these facts can be reconciled, the anomalous deficiency of insectivores in the West Indian avifauna seems beyond dispute. This has further repercussions on the issue of low insular species diversity because insects as a

TABLE 1

TROPHIC STRUCTURE OF NETTED SAMPLES OF INSULAR AND CONTINENTAL FOREST BIRD COMMUNITIES

	WEST INDIES			TROPICAL SOUTH AMERICA		TEMPERATE NORTH AMERICA
Net Sample	Dominica	St. Kitts	Hispaniola	Peru	Peru	Maryland*
Locality						
Elevation (m)	290	505	450	180	690	20
No. individuals	48	108	106	141	264	431
No. species	10	11	13	44	64	29
% Sample biomass						
Gleaning insectivores	7.8	6.5	15.7	76.4	63.1	86.6
Hawking insectivores	0	2.7	4.5	14.8	12.9	2.9
Nectarivores	2.9	1.4	1.2	.5	2.4	0
Frugivores	82.9	78.4	74.0	8.3	17.4	6.8
Seedeaters	6.4	10.9	4.6	0	4.2	3.7

* Data from Stamm et al. 1960.

resource can be partitioned in many more ways than fruit (Orians 1969; Diamond 1973; Terborgh 1977, 1979*a*). A community that is low in insectivores and high in frugivores will inevitably contain fewer species than one in which the proportions are reversed. It is in this circumstance that we find further qualified support for Lack's (1976) hypothesis of ecological impoverishment.

It does not automatically follow from the fact that island communities are composed of relatively few species that such communities are loosely packed in an ecological sense. The packing itself should be separately examined, something we have done in other publications (Faaborg 1977; Terborgh et al. 1978; Terborgh 1979*a*). Weight ratios of neighboring guild members are substantially greater on small than on large West Indian islands, and far greater on islands than on the Neotropical mainland. From these results it is apparent that the species in Antillean bird communities are not pushing the limits of similarity in any absolute sense.

Hypothesis 2.—West Indian birds are habitat specialists. As a categorical statement this is clearly false. MacArthur et al. (1966) showed that species turnover along a habitat gradient was markedly less in Puerto Rico than in North America or Panama. Lack (1976) found that the number of habitats occupied per species in Jamaica was far greater than in nearby Honduras, notwithstanding the greater array of habitats available in the mainland area. Montane birds in Hispaniola occupy a median elevational range of 1,820 m, a value that is 2.5 times greater than that exhibited by Andean birds in Peru (J. W. Terborgh 1971 and unpublished). Similarly, a number of Hispaniolan species are able to occupy the entire lowland moisture gradient from xeric thorn scrub to rainforest, while no Venezuelan species does so (J. W. Terborgh, unpublished). Roughly estimated, the median Hispaniolan species occupies 5–10 times the gradient space occupied by its South American counterpart (increased amplitude on elevation gradient × increased amplitude on moisture gradient).

This raises the counterargument that island birds have already expanded their habitat spectra as far as physiologically possible, and hence are habitat specialists in the sense that they are unable to respond to opportunity. While this may be true for some species it is not true for all, as we showed in comparing the habitat spectra of species on a pair of source islands (Guadeloupe, Dominica) with those of derived populations on a nearby pair of target islands (St. Kitts, Montserrat; Terborgh et al. 1978). Several species that were restricted to coastal scrub on the richer source islands had expanded into the montane forests of the target islands in the absence of trophic counterparts present in the forest communities of the source islands. Thus at least some West Indian birds are capable of broadening their habitat spectra where the density of competitors is sufficiently low.

Although a few counter-examples may discredit the hypothesis as a universal generality, they do not eliminate the possibility that a substantial number of West Indian species are habitat specialists. We now ask whether the corollary of hypothesis 2 holds, that is, whether there is a strong dependency of insular species number on the number of available habitats. We do this by asking how many major vegetation formations are represented on each of the islands we have visited. A few islands we have not seen have been included on the strength of descriptions available in the literature. Only broad habitat categories are included, e.g., sclerophyll scrub, elfin thickets, etc. Further details are provided in Appendix B. Figure 2 shows that the regression of species against number of habitats closely parallels the species area curve.

The slope of figure 2 implies that about 10 species are added per habitat. Because the number of habitats per island is intimately correlated with island area ($r = .91$), the extent to which the trend strictly relates to habitat diversity is unclear. Familiarity with the distribution of birds on Hispaniola allows a closer inspection of the underlying details. Habitats that are generously represented ($\geq$ 10% of the island's area), e.g., pine forest, humid montane forest, typically harbor 5–10 stenotopic species. Poorly represented vegetation types (mangroves, savannah) contain smaller numbers of specialists. Thus only a part of the trend shown in figure 2 is directly explained by increased numbers of stenotopic species. Much of the remainder can be explained by the fact that each new vegetation type increases the number of habitat combinations that may be exploited. Taken together, these two correlates of increased habitat diversity explain most of the increase of species with area in the West Indies on islands large enough to contain two or more major vegetation formations.

Hypothesis 3.—Members of the West Indian species pool have become adapted to species poor communities and are incapable of invading uphill on diversity gradients. There is a good deal of circumstantial evidence that is consistent with this statement. Many West Indian species that have wide distributions in the Antilles and Bahamas have not succeeded in colonizing southern Florida, which has a climate and vegetation comparable to those of the northern Bahamas at the same latitude. A considerable number of these birds have been recorded one to several times in Florida but have not succeeded in establishing new populations (Zenaida dove, Key West quail dove, Cuban emerald, Antillean palm swift, Bahama swallow, thick-billed vireo, bananaquit, stripe-headed tanager, black-faced grassquit; Bond 1971). Some of these may be excluded by close competitors (e.g., the thick-billed vireo by the white-eyed vireo), but others (e.g., bananaquit) have no evident counterparts in Florida. A few species have colonized the mainland from the West Indies (white-crowned pigeon, Antillean nighthawk, smooth-billed ani, grey kingbird, black-whiskered vireo), but all except one of these, the grey kingbird, is restricted to the sclerophyllous vegetation of extreme south Florida and the keys. Moreover, two of them, the ani and kingbird, nest on the Neotropical mainland, and hence are not island endemics. What prevents further colonizations? Perhaps it is the higher resident species density in Florida: 65 species south of Lake Okeechobee versus 36 in Grand Bahama and Andros.

Another biogeographical anomaly that supports the hypothesis is the occurrence of a predominantly West Indian fauna on the marginal Caribbean islands of Swan, Providencia, and San Andres. These are remote little dots in the sea, farther from the Antilles than from the Central American coast. The fact that West Indian endemics have colonized these islands suggests two things: first, that some insular species have the dispersal potential to reach the mainland, and second, that continental birds are terrible overwater colonists. Additional populations of Antillean endemics have established themselves on a number of other far-flung islands around the Caribbean, some of them so close as to be within sight of the mainland (Cozumel, Mujeres, The Bay Islands, Bonaire, Horquilla). If the birds in

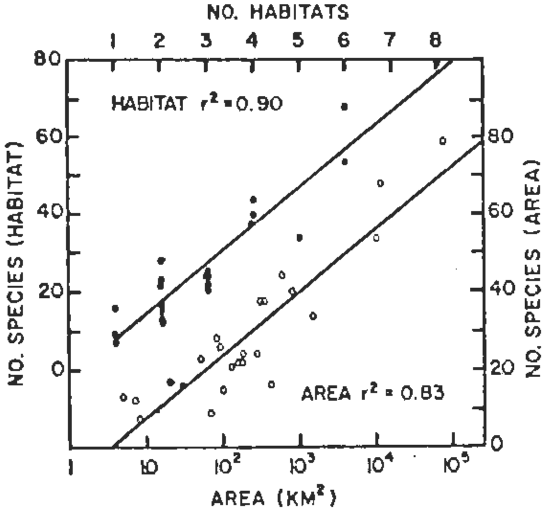

FIG. 2.—The relation between no. of breeding land birds and no. of distinct habitats present on islands in the Greater and Lesser Antilles. Further details provided in Appendix B.

question were actually capable of invading the mainland, we suggest that such distributions would not exist.

Nearly three-quarters of the breeding landbirds of the West Indies are endemic to the archipelago, notwithstanding that the northernmost and southernmost islands lie only 105 and 140 km from the North and South American mainlands, respectively (Bond 1971; Lack 1976). It follows that successful colonizations in either direction between the islands and the continents must be exceedingly rare events. This conclusion is supported by the extreme paucity of West Indian records of vagrant landbirds from the Neotropical mainland. Bond (1971) lists only three: a cuckoo (Grenada, 1963), and two hummingbirds (Carriacou, 1904, and Grenada, 1962). In contrast, West Indian records of stray birds from North America and even Europe are comparatively numerous.

Like the islands of the southwest Pacific, the Caribbean archipelago contains several "supertramps," bird species that ply the trade of fugitives on small, low diversity islands (Diamond 1974, 1975; Diamond and Marshall 1976). Of a number of probable cases, three are especially clear. One of these, the pearly-eyed thrasher, shows evidence of having invaded the Bahamas and Greater Antilles from the Lesser Antilles (Bond 1948). It occurs on numerous small islands but on none larger than Puerto Rico. The western extremity of its range is Beata Island, a rough 35 km² block of limestone just 5 km off the south coast of Hispaniola. It has not been recorded on Hispaniola itself. The Bahama mockingbird displays a similar pattern. The center of its range is in the Bahamas, where it occupies a contiguous group of islands; but in addition it has established two disjunct populations, one in a restricted region of arid vegetation in southern Jamaica and the other on some small cays just a few km off the north coast of Cuba. Within the Bahamas it is curiously missing from the two richest islands, Grand Bahama and Abaco, although it is present on tiny mangrove cays just to the north (Bond 1948). Exclusion by the northern mockingbird cannot be the whole explanation because

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the two birds coexist on several Bahamian islands and in Jamaica, but on the latter island they do not share the same habitat. The final and perhaps most extraordinary case is that of the bananaquit, a bird that has reached virtually every speck of land in the Caribbean. It does not, however, inhabit Cuba, though individuals have been sighted there a number of times. Exclusion by the red-legged honeycreeper seems doubtful, as the latter bird appears to be scarce and local in Cuba (Barbour 1943). The existence of the bananaquit on the Neotropical mainland does not preclude its status as a supertramp in the West Indies because of the possibility of local adaptation (Emlen 1978). That such adaptation has occurred is suggested by the recognition of 16 insular races of the bananaquit in the Caribbean (Bond 1956).

The majority of endemic West Indian species could be regarded as supertramps in the sense that they appear to be restricted to landmasses that are small and faunistically impoverished relative to the surrounding mainlands. The three cases described above are only extreme and instructive examples of what must be a general phenomenon: a strong resistance of rich communities to potential colonists originating from low diversity faunas (Terborgh 1973).

Hypothesis 4.—Broadening of habitat spectra under reduced interspecific competition is a well documented response of bird populations (Crowell 1962; Keast 1970; Diamond 1971; MacArthur et al. 1972; Terborgh and Weske 1975). We have already mentioned the example of the Lesser Antillean scrub species that expanded into the montane forests of two smaller species poor islands. An additional form of niche broadening is the expansion of vertical foraging zones. Our Lesser Antillean comparisons provide some good examples of this as well. Among the most frequently captured species in the humid forests of St. Kitts and Montserrat are the pearly-eyed thrasher, scaly-breasted thrasher, trembler, and bananaquit. All of these are common in the montane forests of Guadeloupe and Dominica where they live almost entirely in the canopy. In the forest understory of these larger islands four additional species fill similar trophic roles: the forest thrush, rufous-throated solitaire, house wren, and plumbeous warbler. The presence of these more typical understory species apparently confines the first group to the canopy; on the smaller islands where the understory species are missing, the canopy species descend and are freely captured in nets (Terborgh et al. 1978).

Examples of broadened habitat utilization, expanded vertical foraging zones and compensatory increases in abundance (ecological release: Terborgh and Faaborg 1973; Cox and Ricklefs 1977) under conditions of reduced species density all point to the likelihood that versatility and opportunism are far more prevalent among West Indian birds than is rigid habitat specialization. That the illustrative examples are few in number is much more a reflection of the limited opportunities to test responses (small islands tend to have low, uniform vegetation), than it is of a behavioral reticence on the part of the birds.

SYNTHESIS

It is apparent from the evaluation of the four hypotheses that all of them are at least partially correct. Lack's notion of ecological impoverishment is supported by the absence of certain mainland guilds and by the gross underrepresentation of others, especially insectivorous guilds. Large islands harbor more species than small islands, mainly because they tend to offer a greater range of habitats, though the tight intercorrelation of variables precludes a quantitative separation of the contributions of area and number of habitats to total species number. A good deal of anecdotal and circumstantial evidence favors the notion that species are adapted to live in communities having certain diversity levels, and that invasion of richer communities is thereby precluded. Last, where circumstances permitted the appropriate tests, most species responded opportunistically in expanding their habitat and/or foraging ranges in the absence of probable competitors.

Because of the variety of underlying responses and the difficulty of examining them on a species-by-species basis, the interpretation of the saturation phenomenon in the West Indies must necessarily remain somewhat ambiguous. Hypothesis 1 (ecological impoverishment) undoubtedly contributes to the drastically reduced community diversities of the islands in comparison with the Neotropical mainland, but does not seem to be a factor in interisland comparisons. Hence, saturation as it is manifested within the Antillean archipelago must be attributable to other causes. The suggestion of hypothesis 2 that a diversity ceiling is reached because the habitats contain all available species with appropriate adaptations is very doubtful in view of the substantial differences in community composition that may occur in adjacent large islands. The total number of scrub-dwelling species in the West Indies is well over twice the 30 or so that anywhere occur together, and for rainforest species the disparity is even greater. Thus an insufficiency of appropriate colonists in the avifauna of the archipelago as a whole is not the answer.

The most plausible explanation is offered by hypothesis 3 (upper limit to tolerance of competitors), which more directly than any of the others predicts the observed result. As reviewed above, the evidence for a decreased tolerance of competitors on the part of island birds, while scattered and admittedly indirect, is in the aggregate quite convincing. Hypothesis 3 in itself, however, provides only a partial explanation of the results. Broader habitat utilization and reduced vertical stratification in the presence of small species pools are features of hypothesis 4 (opportunistic responses to ecological release). Flexible habitat utilization by many species maintains the flatness of the total census curves over wide ranges of pool size, and vertical adjustments maintain the constancy of netted diversities over even wider ranges. Thus we deduce that a limit to the tolerance of competitors imposes the ceiling on diversity (saturation), and that opportunistic behavior provides the mechanism which accounts for the detailed shapes of the curves in figure 1.

SCLEROPHYLL SCRUB VERSUS RAINFOREST

One feature of the results contradicts the findings of many previous studies of the relation between habitat structure and bird species diversity. It is the occurrence of substantially greater species numbers in low scrub vegetation than in tall stratified rainforest. On mainlands the richest bird communities are generally those of mature forests; scrub habitats typically hold only half or two-thirds as many species (MacArthur and MacArthur 1961; MacArthur et al 1966; Karr and Roth 1971; Recher 1969; Terborgh and Weske 1969; Terborgh 1977; Cody 1975). The pattern is clearly reversed in the West Indies. Why? Are Caribbean rainforests somehow "impoverished" relative to scrub? We doubt it. Aggregate densities of birds may be high in West Indian rainforests (21 pairs/ha in one Hispaniolan plot vs. 14 and 20 pairs/ha in two sclerophyll plots on the same island). The representation of trophic guilds—frugivores, granivores, gleaning insectivores, nectarivores—is about the same as in sclerophyll communities; and the size range represented by the species is as great or greater. Instead, it appears that the guilds within the sclerophyll community are more tightly packed (Terborgh et al. 1978). This could be understood if the scrub were subject to more intense invasion pressure.

It may be that this is true as a consequence of the following circumstances. The extent of rainforest over the entire archipelago is small relative to that of sclerophyll scrub. Many islands are too dry. Where it occurs, rainforest tends to be surrounded by alien habitats and sheltered from prevailing winds. Within the island chain, distances between adjacent patches of rainforest average greater than those between patches of scrub. Stenotopic rainforest species show a pronounced tendency to endemize (Ricklefs and Cox 1972, 1978), a fact that lends further support to the notion of restricted interisland dispersal of these species. Scrub species, in contrast, readily disperse to small isolated islands and rarely endemize.

A reversal in the expected relationship between complexity of the habitat and the number of bird species living in it would result if the habitats were subject to separate immigration-extinction equilibria. As the area and accessibility to propagules of rainforest within the Caribbean are both considerably less than those of scrub vegetation, the necessary conditions pertain.

Even if this is the correct interpretation, we must still wonder why numbers of species do not invade the Antillean rainforests from adjacent habitats to bring the total diversity at least up to the level characteristic of scrub vegetation. The answer appears to be that scrub species are severely disadvantaged in rainforest. In the Lesser Antilles we found that where scrub species had invaded mountain forests in the absence of stenotopic forest dwelling counterparts they attained relatively lower population densities than the species they had replaced (Terborgh et al. 1978). One must presume that a full complement (ca. 20 species) of appropriately adapted forms occupy adjacent habitats.

Reduced numbers of species in forests relative to adjacent scrub have also been found in several south temperate studies (Chile, Cody 1970, 1975; Patagonia, Vuilleumier 1972; New Zealand, Kikkawa 1966; Tasmania, Ridpath and Moreau 1966). The forests of these regions are rich in relict tree species (e.g., *Nothofagus*, *Aracaria*, etc.) and thus must have had a continuous existence for millions of years; yet they contain surprisingly few birds (typically 15–20 species), notwithstanding their considerable structural complexity and sometimes robust stature (50–60 m trees in Tasmania). It may be, just as in the West Indies, that the comparatively small areas of these forests and their geographical isolation from other forested regions are responsible for their low avian diversities.

DISCUSSION: AN EVOLVED UPPER LIMIT TO COMPETITIVE ABILITY?

Community saturation is manifested as a ceiling on the number of species per habitat as more and more species are added to the local fauna. Once this ceiling has been reached, additional species are accommodated, as MacArthur (1965) supposed, by progressively finer sorting into different habitats. What is so striking about the results we present here is the abruptness with which the ceiling is reached and its constancy over a wide range of pool sizes (number of species per island). West Indian bird communities apparently become noninvadable when they contain 20 (rainforest) to 30 (scrub) species, not just gradually more resistant to invasion as more and more species are available in other habitats on the same island.

To understand this, it is necessary to have an appreciation of the mechanism by which species are distributed in different habitats. Two extreme situations are possible. Habitat selection could be noninteractive, that is, determined only by properties intrinsic to the habitat and the species in question; or, it could be interactive, that is, flexible within broad or narrow limits in response to the presence of competitors. Where competitors are many habitat utilization will be closely restricted, and where there are few it will be broad. In theory the distinction is easily tested, but in practice large scale tests are not possible in the West Indies because small islands have few habitats and large islands have many. Species number, area, and number of major habitats are all highly intercorrelated with $r > .9$ for every pairwise combination. Where we have been able to conduct appropriate tests (in the Lesser Antilles, fully reported in Terborgh et al. 1978; see also Diamond 1971; Terborgh and Weske 1975) the results emphatically supported the interactive mechanism. When presented with opportunities to expand into species-poor but uncharacteristic habitats, a majority of the species present did so. This implies that under normal circumstances (i.e., mainlands or large islands) the habitat distributions of many, if not most, species are restricted by direct or diffuse competitive exclusion.

However, even if the habitat distributions of most species were interactive, one might still expect the number of species per habitat to increase, though perhaps slowly, with increasing pool size. That this apparently does not happen we interpret as indicative of the existence of a coevolved upper limit of tolerance to interspecific competition.

If we assume such a ceiling to competitive ability, and take into account the fact that small islands are generally colonized from their larger neighbors, the form of the saturation curve can be rationalized as follows. Species dispersing from the principal islands of the archipelago (Cuba, Hispaniola, etc., in the Greater Antilles; Dominica, Guadeloupe, etc., in the Lesser Antilles), easily colonize (empty) smaller islands, often exhibiting various forms of ecological release. Little resistance to further successful colonizations develops until within-habitat species numbers approach those characteristic of the source island(s). At this point community resistance increases sharply as each new species is obliged to force ecological adjustments upon already established species (contractions of abundance, habitat spectra, vertical foraging zones) in order to become established itself. The resilience of these compensatory responses is what allows within-habitat species numbers to remain stable over so wide a range of pool sizes.

If, as we are proposing, competitive ability is a coevolved property of regional faunas, there would have to be both a reason why competitive ability should decline in species poor environments, and in the particular case of West Indian birds, time for the necessary adaptive adjustments to occur. Diminished competitive ability is implicit in the broad habitat amplitudes of insular species. As previously mentioned, the median species in Hispaniola occupies 5–10 times the gradient space that a species in South America does. Species invading a depauperate island system from a rich mainland fauna encounter a relatively competitor free environment and respond by expanding their habitat distributions, as has been demonstrated not only for islands, but for isolated mountain peaks in New Guinea and the Andes as well (Diamond 1969; Terborgh and Weske 1975). In the absence of selective reinforcement of competitive ability, selection will favor an improved ability to exploit a wide array of habitats. The adaptive trade-off will continue until a new balance is reached between versatility and competitive status in the new milieu.

Is it reasonable to suppose that West Indian bird species have had enough time to become coadapted on a fauna-wide basis? We think this is implied by the facts that nearly three-quarters of the resident landbird species are endemic to the archipelago and that more than 90% are at least subspecifically distinct from their nearest mainland relatives. One or two successful invasions per millennium would probably be adequate to maintain these proportions at a steady state. If so, the median residence time would be on the order of tens or hundreds of thousands of years, presumably long enough for local adaptation to occur (Johnson and Sclander 1964).

If our interpretation is right, it carries further implications for a number of issues in biogeography and ecology. (1) Invasion of regions of low species diversity (e.g., islands) is essentially irreversible, that is, unidirectional. (2) This could provide a mechanism for driving the taxon cycle (Ricklefs and Cox 1972, 1978), and possibly the latitudinal diversity gradient as well (Terborgh 1973). It also (3) clarifies the status of supertramps (Diamond 1974) and (4) helps to account for the orderliness of island community structure, i.e., "assembly rules" (Diamond 1975). Finally (5), it suggests that the variation in species number among islands of a given size and habitat configuration should be strongly damped on the high side.

The problem of the evolution of competitive ability is of central importance to community ecology, though very elusive at the empirical level. We hope that these tentative beginnings will help to encourage further inquiry.

SUMMARY

The paper is directed to interpreting the set of data displayed in figure 1, which shows that the number of bird species in two widespread West Indian habitats reaches a ceiling (saturation) that holds over a wide range of island species numbers. Four hypotheses are evaluated in an effort to understand the result. (1) Island communities are as tightly packed as they can be without breaching the limits of similarity; (2) island bird species are habitat specialists; (3) island species display an upper limit of tolerance of interspecific competition; (4) island species respond to reduced competition by broadening habitat spectra and other forms of ecological release.

West Indian guilds are found to be less tightly packed than their mainland counterparts, eliminating hypothesis 1 in the sense of absolute limits to packing, but not foreclosing the possibility that island species are competitively excluded at lower packing levels than mainland species. The number of species per island increases in tight correlation ($r^2 = .90$) with the number of available habitats, and large islands do contain numbers of species with restricted habitat ranges. Nevertheless, when tested with the opportunity to expand into atypical habitats containing reduced numbers of competitors most species do so, suggesting that habitat ranges in rich faunas are largely delineated by diffuse interspecific competition. A good deal of evidence suggests that island species are unable to invade richer mainland communities or, in some cases, even the richest large islands.

We speculate that the evolution of ecological versatility at the expense of competitiveness leads to coadaptation of the fauna throughout the archipelago for the level of diffuse interspecific competition characteristic of the largest islands. Various forms of ecological release (expansion of abundance, habitat spectra, vertical foraging ranges) could then serve on smaller islands to maintain the observed constancy of within-habitat species numbers over a wide range of island species numbers.

ACKNOWLEDGMENTS

As the fieldwork was accomplished on many trips undertaken over a 6-yr period, it is impractical to name all those who helped. However, we are especially grateful to the following: H. J. Brockmann, A. and D. Dod, D. Howell, J. S. Weske, Alcoa Corporation, and Gulf and Western Industries. Two anonymous reviewers made helpful suggestions on the manuscript.

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APPENDIX A

SCIENTIFIC NAMES OF BIRDS MENTIONED IN THE TEXT (from Bond 1971)

White-crowned pigeon (*Columba leucocephala*)
Zenaida dove (*Zenaida aurita*)
Key West quail dove (*Geotrygon chrysia*)
Smooth-billed ani (*Crotophaga ani*)
Hispaniolan lizard cuckoo (*Saurothera longirostris*)
Antillean nighthawk (*Chordeiles gundlachii*)
Antillean palm swift (*Tachornis phoenicobia*)
Cuban emerald (*Chlorostilbon ricordii*)
Narrow-billed tody (*Todus angustirostris*)
Grey kingbird (*Tyrannus dominicensis*)
Bahama swallow (*Callichelidon cyaneoviridis*)
House wren (*Troglodytes aedon*)
Northern mockingbird (*Mimus polyglottos*)
Bahama mockingbird (*Mimus gundlachii*)
Scaly-breasted thrasher (*Margarops fuscus*)
Pearly-eyed thrasher (*Margarops fuscatus*)
Trembler (*Cinclocerthia ruficauda*)
Forest thrush (*Cichlherminia l'herminieri*)
Rufous-throated solitaire (*Myadestes genibarbis*)
Thick-billed vireo (*Vireo crassirostris*)
White-eyed vireo (*Vireo griseus*)
Black-whiskered vireo (*Vireo altiloquus*)
Plumbeous warbler (*Dendroica plumbea*)
Bananaquit (*Coereba flaveola*)
Stripe-headed tanager (*Spindalis zena*)
Black-faced grassquit (*Tiaris bicolor*)

Islands visited
Mona .....
Beata .....
Terre de Hat

Terre de Bas
La Desirade
Saona .....

St. Martin
Barbados ..
Marie Galant

Barbuda ...
Nevis ......
St. Kitts ...

Antigua ....
Montserrat
Dominica ..

Guadeloupe
Puerto Rico
Hispaniola .

Not visited
Navassa ...

St. John ...
Grenada ...

St. Vincent
St. Lucia ..
Jamaica . ..

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APPENDIX B

DISTINCT HABITATS AND NUMBER OF BREEDING LAND BIRDS ON ISLANDS IN THE GREATER AND LESSER ANTILLES

	Sclerophyll Scrub	Cultivated Land	Humid Forest	Montane Thicket	Mangroves	Xeric Thorn Scrub	Savannah	Pine Forest	Island Area (km^2)	No. Habitats	No. Land Birds	References
Islands visited												
Mona	×								65	1	9	
Beata	×								30	1	16	
Terre de Haut ...	×	×							5	2	13	
Terre de Bas	×	×							7	2	12	
La Desirade	×	×							20	2	17	
Saona	×	×							80	2	28	
St. Martin	×	×							100	2	15	
Barbados	×	×							430	2	16	
Marie Galante ...	×	×							160	2	22	
Barbuda	×	×			×				160	3	22	
Nevis	×	×	×						130	3	21	
St. Kitts	×	×	×						180	3	24	
Antigua	×	×					×		280	3	24	
Montserrat	×	×	×						85	3	26	
Dominica	×	×	×	×					800	4	40	
Guadeloupe	×	×	×	×	×				1,500	5	34	
Puerto Rico	×	×	×	×	×		×		10,000	6	54	
Hispaniola	×	×	×	×	×	×	×	×	76,000	8	79	
Not visited												
Navassa	×								8	1	7	Wetmore & Swales (1931)
St. John	×	×							50	2	23	Robertson (1962)
Grenada	×	×	×	×					310	4	38	Lack and Lack (1973)
St. Vincent	×	×	×	×					350	4	38	Lack et al. (1973)
St. Lucia	×	×	×	×					600	4	44	Diamond (1973)
Jamaica	×	×	×	×	×	×			11,400	6	68	Lack (1976)

NOTE.—Here we provide the information used to construct figure 2. Habitats were regarded as being present on an island when the total extent of the habitat was estimated to exceed 1% of the island's area or 1 km^2, whichever was the larger. Thus, islands having only a few scattered copses of mangroves (Dominica) or one exposed peak (Nevis, St. Kitts) were not counted as having mangroves or montane thickets, respectively. The habitat divisions are intentionally coarse. Further subdivision of the major vegetation types would alter the slope of figure 2 without substantially altering the amount of explained variation in bird species number. (One could, for example, distinguish lowland and montane humid forest. This would merely add one habitat to all of the mountainous islands, as no island possesses humid lowland forest that does not also have a mountainous interior.)

The data on habitat diversity come from 17 islands we have inspected ourselves and from 6 others that are adequately described in the literature. Landbird species lists (raptors, vultures, and pigeons through passerines) were extracted from Bond (1971). Recently extinct birds were counted, while introductions were not.

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The Role of Theory in Ecology[1]

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SYNOPSIS. Theory can have many different kinds of use in illuminating ecological research. The examples sketched in this paper include: the uses and short-comings of population models currently used in setting catch quotas for whales and for fisheries; the rich array of behaviour displayed by nonlinear equations and its relevance to understanding natural and managed populations; models for the interaction between populations (particularly the regulation of natural populations by diseases); and some general patterns of community organization. The paper concludes with some remarks on the contrasts between public pieties about "The Scientific Method" and the way scientists actually work, from Darwin's day to our own.

INTRODUCTION

Ecological theory comes in many forms. This fact is well illustrated by the papers presented at the American Society of Zoologist's special symposium on theoretical ecology. Some of the work (exemplified here by the papers by Levin and Oster, and by parts of those by Grant and Werner) deals with mathematical models in the traditions of theoretical physics or classical applied mathematics. Such models range from simple, general models aimed at explaining some of the similarities and differences among observations on a range of organisms, to relatively complicated and detailed models aimed at putting a theoretical curve through a collection of data points. Other work (exemplified by Pattern's paper; see also Allen, 1981) borrows from systems analysis or hierarchy theory, in the hope of providing transcendent ways of describing pattern and process in complex communities, or of providing recipes for appropriate ways of aggregating variables. Not all theorizing, however, need be cast in mathematical terms; a lot of useful theory takes the form of verbal models. Such verbal models or schema (exemplified by the papers of Fox and Brown, not to mention Darwin) range from sets of ideas giving coherence to a body of data and making sense of observed patterns, to questions and speculations that stimulate empirical studies. It is, indeed, possible for the same idea to appear, and to be pursued independently, in two or more of these different theoretical styles; Jackson shows in historical detail how this has happened for "niche theory" (where earlier "verbal models" anticipated many of the essentials of the later, and independently developed, mathematical models of Hutchinson, MacArthur and others).

My own work is mainly in the idiom of applied mathematics. What follows is an eclectic set of examples, illustrating the diverse ways in which such ecological theory can be helpful in advancing our understanding of the natural world. These examples reflect my own interests, and not any absolute judgment about what problems are important; some serve merely as fables, or as points of departure for opinionated comment. The examples are described *very* briefly, because the details are available in easily-accessible journals and unnecessary repetition is undesirable.

THEORETICAL ECOLOGY AND WHALING QUOTAS

Theoretical population biology has, for many years, played an explicit role in many areas of resource management. In particular, the concept of maximum sustainable yield (MSY), framed by Graham (1952) and Schaefer (1957), has—at least in principle—been the basis for management of most fishing and whaling industries since World War II.

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[1] From the Symposium on *Theoretical Ecology*, presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1980, at Seattle, Washington.

Following the lead provided by its "Committee of Three Scientists" (Allen, Chapman, Holt) in 1960, the Scientific Advisory Committee to the International Whaling Commission (IWC) has recommended sustainable catches for baleen whale species computed from a population equation of the form:

$$N(t+1) = (1-\mu)N(t) + \tfrac{1}{2}(1-\mu)^T N(t-T) \cdot \{P + Q[1 - (N(t-T)/K)^z]\}. \qquad (1)$$

Here N(t) is the population of sexually mature, adult whales in year t. The corresponding population one year later, N(t + 1), consists of the surviving fraction, $(1-\mu)N(t)$, plus those newly recruited into the adult population from births T years ago; T is the time taken to attain sexual maturity. The other parameters are: K, the unharvested equilibrium density of the whale population; P, the per capita fecundity of females at this pristine equilibrium point, N = K; Q, the maximum increase in per capita fecundity of which the whales are capable as population densities fall to low levels; and z, a phenomenological constant measuring the severity with which this nonlinear, density dependent response in fecundity is manifested. From equation (1) and a knowledge of the actual magnitude of the whale population density over the T preceding years, it is in principle possible to establish maximum sustainable yields. Notice that the quantities T, μ, P, Q and K all have direct biological interpretations, and are susceptible (albeit with some difficulty) to direct measurement. The parameter z, however, is essentially a fudge factor, describing the extent to which density dependent responses appear to be concentrated in the neighborhood of K, rather than being manifested in a simple logistic way ($z = 1$); the IWC uses $z = 2.4$ in most of its recent computations. (For a more full and mathematically explicit discussion, see May, 1980.)

The IWC thus mixes biology and frankly heuristic curve-fitting in using equation (1) to set annual quotas. The sorry story of massive overexploitation of baleen whale stocks throughout the 1960s and early 1970s derives not from faults in equation (1), but rather from the IWC consistently ignoring the advice of its own Scientific Advisory Committee and setting quotas too high. The underlying dynamics of this process comes from economic considerations, which (unlike the biological tenets of MSY) discount future yields; a superb exposition of these bioeconomic factors is by Clark (1976, 1981).

Recent theoretical work is modifying the IWC deliberations in three main ways.

First, whale population densities are typically estimated from data on the catch per unit harvesting effort (CPUE), it being usually assumed that stock density is linearly proportional to CPUE. Borrowing from recent developments in the theory of insect prey-predator interactions (Hassell, 1978), Beddington, Holt, Chapman and others (Anonymous, 1979, 1980) have recently shown that incorporation of the effects of finite "handling times," and of aggregation of predators (whaling ships) around clumps of prey (whales), makes for nonlinearities in the relation between stock density and CPUE; the upshot is reduced estimates of stock density, and lowered quotas. I regard this as a tangible accomplishment for ecological theory.

Second, conventional MSY theory assumes that recruitment relations and the like are deterministic curves. But natural populations are subject to all manner of environmental fluctuations and vagaries, such that we necessarily must deal with probability distributions, not unique deterministic relationships. This points the way to the next generation of management rules, which ask questions not merely about the maximum sustainable average yield, but also about the associated level of fluctuation in stock and yield; we need to pay more deliberate attention to designing "risk averse" management strategies. (For a more full discussion see Beddington and May, 1977; May *et al.*, 1978, and references therein.)

Third, as harvesting pressures intensify, the assumption that whale species can each be treated as a single population, ignoring biological interactions with other species, increasingly breaks down. In a massive, ill-documented and unintentional experiment in "competitive release," it is likely that minke whale populations have roughly doubled as their main competitor, the blue whale, has been virtually removed (Anonymous, 1978, 1979, 1980). Such multispecies considerations become even more complicated and pressing when harvesting takes place simultaneously at more than one trophic level. This is beginning to be the case for baleen whales and krill in the Southern Ocean. May *et al.* (1979) have used simple, general models to give a qualitative analysis of the effects of various management regimes in such multispecies situations; although admittedly abstract and lacking detailed realism, this work has, *faut de mieux,* become the basis for the principles of managment included in the draft Convention of the Southern Ocean.

These practical problems differ from many other, more academic, areas of ecology in that decisions simply must be made, often (to use Clausewitz's telling metaphor) "in the fog." Well-designed procedures could reduce this fog, and enable more information to be gathered about the interplay between theory and reality. For example, the IWC could (as Holt has often suggested) use different parameters or different decision rules in different areas of the oceans, thus having, as it were, more experimental "controls." Too often, other considerations overrule scientific good sense.

THEORETICAL ECOLOGY AND FISHERIES

Most of the conventional work in fisheries management assumes that recruitment is essentially independent of stock density, and seeks to determine the minimum age at which fish should be harvested (set, for example, by mesh size on nets) in order to produce the maximum sustainable catch. The concern is to avoid "growth overfishing." Recently, however, with the collapse of several major fisheries, it appears that "recruitment overfishing" can occur, with overexploitation leading to a collapse in recruitment.

As a result, several people are investigating theoretical models for the recruitment process in fish stocks, paying especial attention to factors that might serve to herald the imminence of collapse in recruitment (Cushing, 1973, 1977; Gulland, 1979; for a review and some new ideas see May, 1980). One outcome of this research could be a more quantitative understanding of why typical fish populations have "forward peaked" recruitment curves (with recruitment essentially independent of stock density around pristine population values), while typical marine mammal populations have pronouncedly "backward peaked" curves. It is even possible that one could end up with a biological basis for equation (1), complete with an understanding of the factors determining the value of z (May, 1980).

Of course, multispecies considerations are also important in many fisheries, particularly as industries move to harvest new species, usually lower on the trophic ladder. Some such practical problems and theoretical work are reviewed by May *et al.* (1979).

DYNAMICAL BEHAVIOR OF SINGLE POPULATIONS

Over the past seven years or so, mathematical studies have shown that the simple, deterministic equations proposed by practical entomologists, epidemiologists and fishery managers as descriptions of the way particular populations change over time are capable of exhibiting an astonishingly rich array of dynamical behavior (May and Oster, 1976).

The most fully studied and most fully understood such equations are those for univoltine insects and other single populations with discrete, nonoverlapping generations. The population dynamics of such creatures are appropriately described by first-order difference equations, of the general form

$$N(t + 1) = F(N(t)). \qquad (2)$$

Here the nonlinear function $F(N)$ typically corresponds to the population increasing from one generation to the next at low densities, and decreasing at high densities, with the severity of this nonlinear propensity to "boom and bust" tuned by one or more biological parameters. Specific examples are the relation $F = \lambda N \exp(-aN)$, propounded for particular insect and fish populations (see references in May and

Oster, 1976), or the simplest such nonlinear function, $F = aN(1 - N)$, which is the "canonical form" adopted by mathematicians for studies of these equations. If the nonlinearities are not too pronounced, such equations describe populations that settle to a stable equilibrium value (with disturbances dying away either exponentially, or as damped oscillations). As the nonlinear tendency to boom and bust steepens, however, the stable point gives way to stable cycles in which the population steadily alternates between high and low values in successive generations (in detail, a cascading sequence of bifurcations gives a hierarchy of such stable cycles, with periods 2, 4, 8, 16, . . . , 2^n), and eventually to a regime of apparent chaos, in which the dynamical trajectories are effectively indistinguishable from the sample function of a random process.

More recently, it has been realized (Mackey and Glass, 1977; May, 1980) that similar phenomena arise for populations with continuously overlapping generations. These populations are appropriately described by differential equations in which, however, recruitment rates and other density dependent processes typically involve time lags. The simplest such differential-delay equations have the form

$$dN/dt = -\mu N + R(N(t - T)). \qquad (3)$$

Here μ is a per capita death rate, $R(N)$ some recruitment term, and T the time lag (derived from maturation times, resource renewal lags, or other delay effects). As nonlinearities become more marked (and/or time lags lengthen), these differential-delay equations also unfold the panoply of stable points, stable cycles (with cascades of period doubling) and chaos; for very severe nonlinearity, the chaotic dynamical regime appears, puzzlingly, to collapse back to a unique stable cycle.

Given that the opposite extremes of discrete, nonoverlapping generations (first-order difference equations) and continuously overlapping generations (first-order differential-delay equations) manifest similar ranges of behavior, it seems likely that the common intermediate case of populations with discrete but overlapping generations does too.

This work is of interest for many reasons, some of them external to population biology as such. The bifurcation processes in first-order difference equations are now well understood, and their intricate details—especially in the apparently chaotic regime—are of intrinsic mathematical interest (for a mathematically oriented review, see May, 1976). Current knowledge of the apparently analogous phenomena in first-order differential-delay equations rests on numerical studies, and an understanding of the underlying mechanisms remains a challenging mathematical problem. On another tack, this work is finding applications in the theory of turbulence: this is the first time that physics has borrowed mathematical techniques developed in a biological context, which I find a pleasing inversion of the usual order of things.

In biology, the work is important in showing the unexpected range of dynamical behavior that can arise from nonlinearities in simple, deterministic models. This range includes apparently stochastic behavior; when this happens we have the paradoxical situation that long-term prediction is impossible, even though we have a simple and fully deterministic model. Notice that this understanding is important for its own sake. Some recent studies of more complicated and more realistic models for biological populations (mainly insects) have denigrated the simple models as utterly unrealistic, while at the same time discussing their own numerical results in terms of the stable points, stable cycles and apparent chaos that would have been incomprehensible without the earlier studies of such simple models!

More generally, these explicitly mathematical studies supplement and enrich earlier verbal models, to help explain the great diversity of dynamical behavior exhibited by animal populations in the field and in the laboratory. In this Symposium, Jackson has already contrasted Lack's belief that natural populations fluctuate irregularly with Elton's belief in regularity; it now seems clear that an entire spectrum of behavior is possible and is to be expected. Such connections between the observed ranges of life history strategies and possible ranges of dynamical behavior have been discussed by many people (see, *e.g.*, Southwood, 1977, 1981 and Horn, 1978). The deliberately over-simplified metaphor of "r- and K-selection" (MacArthur and Wilson, 1967) borrows mathematical terminology to codify some general tendencies that many earlier authors, including Darwin, have discussed using "verbal models." This metaphor has been much used and abused: used sensibly, it helps us to see patterns among the records of success and failure in the control of insect pests, weeds or diseases, and it cautions against naive beliefs that any single strategy will be effective against all such nuisances (Conway, 1981); used foolishly, it generates fuzzy platitudes.

In detailed applications, single-species models have been successful in explaining observed data for particular field and laboratory populations. Broadly, the examples include laboratory populations of blowflies, daphnia, rotifers, weevils, collembola and other organisms exhibiting stable points or sustained cycles (and sometimes both, as a function of temperature), along with field populations exhibiting stable 4- or 10-year cycles. These applications of the theory are reviewed by May (1981, pp. 18–24; pp. 5–17 give a more full account of the work outlined earlier in this section).

INTERACTIONS BETWEEN SPECIES

From the time of Lotka and Volterra, mathematical models have contributed to our understanding of the interactions between species, as prey-predator, competitors or mutalists. Because of their greater complexity and greater number of parameters, fewer such two-species models make contact with data than do single-species models.

The generic heading of *"prey-predator"* covers many different kinds of pairwise interactions. Some aspects of theory and observations about plant-herbivore relations are discussed in this Symposium by Fox; for surveys of other aspects, see Caughley and Lawton (1981) and Lawton and McNeill (1979). As reviewed by Hassell (1978), arthropod prey-predator systems, especially host-parasitoid ones, offer some simplifying biological features that permit a degree of direct confrontation between mathematical models and data (at least in the laboratory). Vertebrate prey-predator interactions, however, seem to me to have so many behavioral and ecological complexities that simple mathematical models can usually do no more than indicate general trends (see, *e.g.*, Tanner, 1975).

A particularly interesting subclass of prey-predator relations are those between hosts and parasites, with parasite broadly construed to include viruses, bacteria, protozoans, fungi and helminths. The possibility that many natural populations may be regulated by their parasites has only recently received close scrutiny (*e.g.*, Crofton, 1971; Anderson and May, 1979; Price, 1980, goes further to include plants and gall-forming insects under this heading). Contemporary studies combine ingredients from conventional epidemiology (where the host population is assumed constant) with dynamic elements drawn from prey-predator theory, in pursuit of this possibility of regulation by parasitic infections. Most of the interaction parameters (disease-free birth and death rates in the host population, disease-induced mortality rates, recovery rates, rates of loss of immunity, and so on) can be estimated from data that are independent of the population data pertaining to the host abundance and the prevalence of infection. The resulting comparison between simple mathematical models and epidemiological data typically involves only one, or no, adjustable parameter. Examples where remarkably good agreement between theory and data have been achieved include: studies of laboratory mice populations regulated by infections with *Pasteurella muris* and with ectromelia pox virus (Anderson and May, 1979); possible regulation of forest insects in stable 5–12 year cycles by protozoan or viral infections (Anderson and May, 1980); prevalence and intensity of hookworm and other parasitic infections in human populations (Anderson, 1981); and the interaction between rabies virus and fox populations in Europe (Anderson *et al.*, 1981).

Verbal and mathematical models for the effects of *competition* upon the structure of natural communities have been reviewed

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in this Symposium by Grant and Brown. I do not take quite so gloomy a view as Brown; many very different approaches to the question of limiting similarity and niche overlap lead to qualitatively similar conclusions, although not to predictions that are quantitatively testable. That is, the theory suggests some general trends and patterns, but does not provide unambiguous quantitative relationships that are capable of crisp falsification by numerical data (and I admit this is justification enough for Brown's gloom). Two excellent reviews of the current state of competition theory are by Pianka (1981) and Roughgarden (1979).

Despite some recent theoretical work, and some interesting empirical work on particular associations, the study of *mutualistic* interactions is still in its formative stages (for a review, see May, 1981, pp. 94–100).

THEORETICAL ECOLOGY AND COMMUNITY PATTERNS

In theoretical studies of entire communities of interacting plants and animals, abstract mathematical models have been used to explore general questions (*e.g.*, the relation between "stability" and "complexity"), and more concrete models have been used to explore explicit patterns in community organization or trophic structure (*e.g.*, the relative abundance of the various species in different types of communities, or the relation between the number of species and the physical size of their constituent individuals, or the factors governing the remarkable constancy of only around 3 or 4 trophic levels in most food webs). In many instances, including all those just listed, such community-level models have been helpful in bringing the issues into sharp focus, sometimes overthrowing the conventional wisdom in the process. But many of these questions, again including all those just listed, still lack apodictic resolution. These matters are reviewed more fully in May (1981, pp. 197–227).

An excellent presentation of ideas about the structure of food webs has recently been given by Paine (1980). He points out that one school emphasizes patterns of energy flow (which can overlook vital links, such as pollinators or seed-dispersers, through which little energy may flow), while another school emphasizes the topological patterns of the web, as defined by direct associations between species (which can mislead by weighting strong and weak interactions equally). Paine believes we need, in general, to identify those food web links that are essential for the continued functioning of the community. These may, or may not, be given simply by energy flow or by topology. His paper is exemplary in the way it combines theoretical insights with knowledge of natural history, in order to suggest a coherent program of manipulative experiments.

THE ROLE OF THEORY

As stressed in the Introduction, there are many aspects, and many valid approaches, to ecological theory. Insofar as relatively simple mathematical models can be helpful, it is usually in clarifying what are (and what are not) the essential features in a complicated natural situation. An applied mathematician tries to identify these essential features, using what is often called "common sense" or "physical intuition"; they are then incorporated into a mathematical model, which makes qualitative or quantitative predictions. The predictions may be far from obvious, even in simple situations (vide the stable points, stable cycles, chaos discussed above). If the predictions accord with reality, our understanding is advanced; if not, we try to find what necessary ingredient was omitted. This credo is set out more lucidly and more fully in Levin's contribution to this Symposium, and it is shown in action in many of the examples sketched in the body of my paper.

Of course, ecological theory, in both verbal and mathematical forms, often runs ahead of observation. As Grant has observed, such theory delineates possibilities, from among which empirical studies discriminate the actualities.

Rather than further airing my opinions about the role of theory, I end by mentioning Darwin's.

Darwin's private correspondence reveals his views: "all observation must be for or against some view if it is to be of any service!"; "let theory guide your observations, but till your reputation is well established be sparing in publishing theory. It makes persons doubt your observations." (See Gruber and Barrett, 1974, p. 123.)

Publicly, however, Darwin consistently portrayed himself as adhering to the accepted scientific pieties of his day, namely the Baconian Method, in which one first marshals the facts and then sees what conclusions emerge. Thus on the first page of the *Origin*, Darwin claims to have "patiently accumlat[ed] and reflect[ed] on all sorts of facts which could possibly have any bearing on it. After five years' work I allowed myself to speculate on the subject, and drew up some short notes . . . ." Likewise, on the first page of *The Expression of the Emotions in Man and Animals*, he says "I arrived, however, at these three Principles only at the close of my observations." As Gruber and others have emphasized, Darwin's private notebooks tell a very different story, and one which is more familiar to a practicing scientist: "The pandemonium of Darwin's notebooks and his actual way of working, in which many different processes tumble over each other in untidy sequences—theorizing, experimenting, casual observing, cagey questioning, reading, etc.—would never have passed muster in a methodological court of inquiry . . . . He gave his work the time and energy necessary to permit this confusion to arise, at the same time persistently sorting it out, finding what order he could. It was an essential part of this 'method' that he worked at all times within the framework of a point of view which gave meaning and coherence to seemingly unrelated facts" (Gruber and Barrett, 1974, p. 122).

I think this is important. Naively simple formulations of The Way To Do Science—be they the Baconian Method of the Victorians or the extreme logical positivism of Popper today—are harmless in themselves, but have unfortunate consequences when they inspire doctrinaire vigilantes to ride the boundaries of a discipline, culling the sinners. The scrabbling, nonlinear way Darwin pursued his ends is typical of most good science. Writing about him, Ghiselin (1969, p. 236) says: "Viewed from without, science appears to be a body of answers; from within, it is a way of asking questions. . . . The 'predictionist thesis' and 'hypothetico-deductive' model seem a bit trivial as clues to what real scientists are trying to do." Although his avowedly anarchic, "anything goes," position is clearly too extreme, Feyerabend (1975) may be closer to the actuality than are his canonized colleagues, from Bacon to Popper. Indeed, I find it paradoxical that Popper's tenets are themselves unfalsifiable: Feyerabend would find it easier to explain their current vogue than would Popper himself.

More disciplined and professional remarks on some of these philosophical issues are given, in a broadly ecological context, by Hutchinson (1978), Halstead (1980), Wimsatt (1980) and McIntosh (1980). Much of this section is condensed from Bonner and May (1981).

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Problems in Distinguishing Historical from Ecological Factors in Biogeography[1]

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SYNOPSIS. The geographical distribution of animals is affected by both historical and present-day ecological factors. It is of great interest to distinguish between their effects. Unfortunately, both major classes of factors can yield similar biogeographic patterns, making it difficult to know which factor is more important. In addition, it is very important to examine all of the consequences of a particular hypothesis, as well as alternatives. Two examples are given: the Pleistocene forest refuge hypothesis and vicariance biogeography. The refuge hypothesis yields three predictions, but only one is upheld—concordance of centers of diversity; the distribution of positions and widths of contact zones is inconsistent with the hypothesis. The two alternative hypotheses, current ecology and current peripheral isolation, yield predictions which are upheld. The major prediction of vicariance biogeography, that concordant cladograms should indicate common vicariant sequences among the lineages, is rejected. Concordant cladograms can only result from common patterns of shared selection regimes and thus do not reflect vicariant patterns. More work needs to be done in distinguishing historical from ecological factors in species distributions.

INTRODUCTION

Biogeography attempts to explain the distributions of animals and plants. Whether or not a particular species survives in a particular place depends both upon its ecological requirements and on its history; all the ecological requirements for starlings and cattle egrets are present in the Americas, but owing to the vicissitudes of geological and climatic history, neither species lived there until recently. Because the relative magnitudes of ecological and historical factors are likely to be different for various organisms, there is a great diversity of explanations for the distributions of animals and plants.

In the past decade the field of biogeography has become divided into groups of workers specializing on either ecological or historical factors, often to the exclusion of alternative explanations (examples: MacArthur, 1972; Briggs, 1974; Nelson and Platnick, 1980*a*; Platnick and Nelson, 1978; Rosen, 1978). The questions have tended to be "Can we reject a particular hypothesis?" or "How well does a particular hypothesis fit the data?" (Ball, 1976). As a result, there has been virtually no attempt to enquire about the relative importance of history and ecology. It is the purpose of this paper to illustrate some problems in considering only one hypothesis, and also to show the dangers of not considering all of the predictions of a particular biogeographical model. I will present two examples, the Pleistocene forest refugia model, and the vicariance biogeography model.

PLEISTOCENE FOREST REFUGIA

In the lowland tropical forests of South America and Africa we see repeated and concordant geographic patterns. Diverse taxa exhibit broad geographic zones of relatively uniform morphology, separated by and embedded in areas where the characters are changing—character gradients, clines, and contact zones between subspecies, semispecies, and species. Maps of the zones of relative uniformity look very similar among various animal and plant phyla (Haffer, 1969; Simpson and Haffer, 1978).

The hypothesis is that, during the relatively cooler and drier Pleistocene, the formerly continuous tropical lowland forest fragmented and remained only in favorable areas. The forest-dwelling species

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were isolated in the forest refugia and differentiated independently of one another. When the climate became warmer and moister, the forest expanded and the formerly isolated populations came into secondary contact. The centers of high diversity and endemism are thought to be located at the sites of former refugia; not every species would have dispersed out of the former refugia since the Pleistocene, leaving higher diversity and endemism in the former refugia (Haffer, 1969, 1974; Simpson and Haffer, 1978; Prance, 1981). The observed distributions of tropical animals and plants of Africa and South America appear quite consistent with this hypothesis.

The full consequences of the Pleistocene forest refuge hypothesis have not been examined. There are actually three predictions of the refuge hypothesis: (1) there should be more species and more endemics in the sites of former refugia; (2) for those subspecies, semispecies, and species pairs showing secondary contact, the positions of the centers of the contact zones should be concentrated between the former refugia; and (3) the widths of contact zones should be broader for species with shorter generation times or faster dispersal rates. Only the first prediction has been investigated. Since the first prediction has been tested and discussed in detail elsewhere (Prance, 1981) I will discuss only the second two. I discussed the predictions in greater detail in another paper (Endler, 1981).

A contact zone can be defined as a zone or band where two subspecies, semispecies, or species meet, and where there may be intergradation (clines) or limited overlap. If contact zones result from secondary contact of formerly isolated populations, the positions of the centers of the contact zones should be concentrated between the former refugia. This is because, on average, the dispersal rates of closely related subspecies and species should be similar, and the advancing fronts of dispersing closely related species should meet midway between the former refugia. At the very least we would expect to find fewer contact zones in or close to the postulated former refuge sites; this would require great differences in dispersal rates among the vicariant species.

A study of the detailed maps of African passerine birds (Hall and Moreau, 1970) shows that in fact the contact zones are not clustered between the postulated refugia areas; quite the contrary. Fifty-two percent of the contact zones occur between forest species and species also found outside the forest, thirty-nine percent occur within postulated refuge areas, and only nine percent occur between the postulated refugia (Endler, 1981). The second prediction of the refuge hypothesis is not upheld.

The width of a contact zone can be defined as the distance (in kilometers, say) from a locality with gene frequency or hybrid index of 0.2 to another locality with 0.8. At the instant of secondary contact the width is zero. After secondary contact the width increases with the gene flow rate of the species concerned and the square-root of the number of generations since contact (Endler, 1977). Therefore the widths of contact zones should be broader for species with faster gene flow rates. The width of contact zones should also be broader for species with shorter generation times compared to those with long generation times because the time in years since the secondary contact of the forest will be the same for both groups.

A survey of gene flow rates showed that birds and neotropical butterflies have approximately the same gene flow rate per generation (Endler, 1981). Birds have a generation time of 1–4 yr, but many neotropical butterflies go through 6–10 generations per year. If the time since secondary contact is about 15,000 yr (last major climatic event), then birds have had 5,000 generations and butterflies have had 120,000 generations since secondary contact. Therefore we expect the contact zones to be narrower for birds than for butterflies. Data on contact zone widths of birds and butterflies show that not only does the prediction not work, but the pattern is actually the opposite. The contact zone widths for butterflies are almost always less than 50 km (usually less than 20 km) whereas the bird contact zone widths are almost all greater than 100 km, and many are greater than 1,000 km (Endler, 1981). Two out of three of the predictions of the Pleistocene forest refuge hypothesis are not borne out; therefore we seriously doubt the hypothesis.

An alternative hypothesis is that current ecological factors are largely responsible for present-day distributions of organisms in tropical forests, and history plays only a minor role. If this were true then it predicts that the areas of relative morphological uniformity, high diversity, and endemism should correspond to areas of relative uniformity in various environmental factors, and contact zones should be concentrated in areas where one or more environmental factors are changing.

If we superimpose maps of forest type, major rivers, climatic zones, geology, and soils, the result is a map showing areas where many of the environmental factors are changing, and also large areas where none of the factors change. For brevity I will call the zones of uniformity "conformities." For Africa the conformities correspond perfectly with the postulated refugia locations, and for South America the conformities correspond to virtually all of the postulated refugia (Endler, 1981). We thus have a serious competitor to the refuge hypothesis.

The two major postulated refuge areas in South America which do not correspond to environmental conformities are peripheral to the main body of tropical lowland forest. Both are in peninsulae of forest, and one in particular (Pará) is surrounded on three sides by sea and very unsuitable habitat for forest-dwelling species. Any species living in these areas can experience gene flow from only one direction, and therefore can differentiate parapatrically to a much greater extent than central populations (Endler, 1977, 1981). Thus all of the distributional phenomena in tropical lowland forests of Africa and South America can be explained entirely on the basis of present day ecological factors. This is not to say that historical factors are not important, but that they are not the only explanation. Much more work needs to be done to sort out the hypotheses. This problem has been discussed in greater detail elsewhere (Endler, 1981; Brown, 1982).

VICARIANCE BIOGEOGRAPHY

Vicariance biogeography is that branch of historical biogeography which attempts to explain all distributional phenomena on the basis of a model very similar to and more general than the Pleistocene forest refuge hypothesis. It postulates that species distributions are a result of the following process: (1) a species spreads over a large geographic range; (2) the range fragments several times into allopatric populations (each splitting is called a vicariance event; the fragmented populations are ecological vicars—Udvardy, 1969); (3) allopatric populations speciate; and (4) the new species may spread into the range of other species; sympatry indicates dispersal (after Rosen, 1978). This yields specific predictions about taxonomic relationships of the vicariant species: species resulting from recent vicariance events should be sister species, and species resulting from older vicariance events should be more distantly related. Relationships are worked out by means of cladistic methods (Nelson, 1979; Eldredge and Cracraft, 1980), which estimate only the order of branching of a phylogeny (Hull, 1979). An additional prediction is that because unrelated taxa experience a common history of vicariant events, there should be concordance in their estimated phylogenies (Rosen, 1975, 1978; Platnick and Nelson, 1978).

The major questions in vicariance biogeography are: (1) Is endemism geographically non-random? If so, what are the areas of endemism? (2) Are the interrelationships of the endemic taxa geographically non-random? If so, what is the pattern? (3) Does the pattern of the resulting cladograms correlate with geological history? (Nelson and Platnick, 1978). A very clear summary of the model and methods is found in Platnick and Nelson (1978) and other discussions are found in Nelson and Platnick (1978, 1980*a*), and Rosen (1978). The advantage of vicariance biogeography over the more classical ("dispersal") ap-

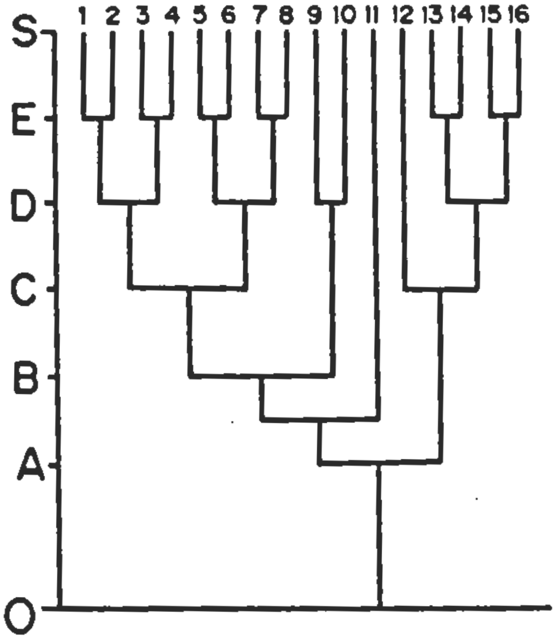

FIG. 1. The branching sequence of vicariant events in the simulations. Numbers 1–16 are the sixteen allopatric areas at the end of the simulations. Time is on the vertical axis. The first vicariant event occurs at time A, one occurs between A and B, and the subsequent events occur at times B through E. The areas were sampled at time S after the last vicariant event. Simulations varied in times A–E and E–S, holding other times proportional. If vicariance biogeography is correct, areas 1 and 2, 3 and 4, 5 and 6, and so forth, should contain sister species for most lineages examined; and the complete hierarchy of relationships should parallel this diagram.

proach is that it yields specific predictions which can then be tested.

Practitioners of vicariance biogeography and phylogenetic systematics (cladistics) are fond of talking about falsifiability and quoting Popper on the subject (for example Ball, 1976; Platnick and Nelson, 1978; Nelson and Platnick, 1978*a*, 1980*a*; Eldredge and Cracraft, 1980; Cracraft, 1982). Curiously enough, the methods of vicariance biogeography have not been subject to a direct test. Nelson and Platnick (1978) state that "Vicariance biogeography is inherently statistical," yet no one has attempted to estimate its errors and accuracy. This is equivalent to estimating a parameter by calculating a mean of a sample and not bothering with the standard error.

Some attempts have been made to estimate the errors of cladistic analysis, but these have not been applied to vicariance biogeography, and some have been limited to characters which are not normally used by systematists (Edwards and Cavalli-Sforza, 1964; Edwards, 1970; Felsenstein, 1973*a*, *b*, 1979; Harper, 1979). Simberloff *et al.* (1981) show how to test cladograms against null models and how to estimate the probability of obtaining concordance among cladograms by chance alone, but have not considered the effects of randomness on known vicariant sequences.

In order to test the methods of vicariance biogeography, and to estimate the errors of the resulting estimates of historical sequences, I carried out a series of computer simulations and analyses utilizing only the assumptions of vicariance biogeography and cladistic reconstruction of phylogenies. A similar approach was used by Camin and Sokal (1965) and Raup and Gould (1974).

The model worked as follows: A large area with many species was fragmented into smaller and smaller pieces in a series of steps. The splitting sequence of one set of simulations is shown in Figure 1. All of the species living in the area were therefore subject to the same series of vicariant events. After a given vicariant event, the allopatric populations of a given species speciated; *i.e.*, they became evolutionary independent entities (no gene flow). Each simulation started with ten species, each with *k* characters, all at state "0." In simulations with the vicariance pattern shown in Figure 1, each of the ten species gave rise to 16 by the end of the last vicariant event.

Evolution (changes in character states) was accomplished by allowing characters to change randomly from "0" to "1" with given probabilities over the course of the simulation. The probability of change of state was fixed during the simulations. The forward ("0" to "1") and backward ("1" to "0") rates were set at realistically very low values (10^{-8} per generation for the forward rate) and also set so that approximately one-half the characters were in state "1" at the end of the simulations. The choice results in character-state distributions similar to real data in the pages of *Systematic Zoology*. In some of the simulations backward rates were set at zero and the forward rates increased to yield similar character distributions. The dynamic properties of this model are similar to mutation in population genetics (for a discussion see Crow and Kimura, 1970). The results are the same for other combinations of rates and numbers of generations because the parameter of importance is the probability that a particular character will change during the time period studied; the probability of change per character is $P = 1 - (1 - u)^T$, where u is the rate and T is the number of generations. For example, if the forward change rate is 10^{-8} and the total number of generations is 10^{6}, the probability that a given character will change from "0" to "1" is 0.01. Simulations also varied in the number of generations since the last vicariant event in order to investigate the effects of sampling time.

Many simulations were run using various parameter values and vicariance sequences. For brevity I will report only on a few of them here, and only those with the vicariance sequence of Figure 1. The results of other simulations are similar and will be given in a subsequent paper.

Three classes of simulations were run:

(I) no assumptions were made about the genetics of the characters: they merely could change from state "0" to state "1," and in some simulations from "1" back to "0." The species were analyzed at the end of the simulation by the Wagner algorithm (Kluge and Farris, 1969; Farris, 1969–1972) using Farris' WAGNER78 program (Farris, 1978). Other methods were also tried (using Felsenstein's 1980 programs) with similar results. Only the Wagner analysis will be reported here.

(II) quantitative genetic characters: each character is controlled by *L* loci which act additively to yield a quantitative character value. The gene frequencies drift each generation. At the end of the simulation the character values were coded as two-state characters as suggested by Kluge and Farris (1969) and analyzed by the Wagner method (Farris, 1978). Analysis was also done on uncoded data using Felsenstein's (1980) continuous character maximum-likelihood method.

(III) quantitative threshold characters: each character is controlled by *L* loci which act additively on an underlying variable. Thresholds of expression determine the character state of the observed character (Falconer, 1960, ch. 18). These were recoded to two-state characters as in Kluge and Farris (1969), and analyzed by the Wagner method.

Classes II and III are more realistic than class I in that they incorporate the genetics of characters into the simulations. Many measurement and count characters in both soft and hard parts are known to have genetic properties of class II, and many skeletal characters with only a few character states (such as number of vertebrae or number of digits) are known to have genetic properties of class III. Felsenstein (1973*b*), Edwards and Cavalli-Sforza (1964) and Edwards (1970) discuss the statistical properties of phylogenetic reconstruction using these classes of characters.

In this paper I will discuss *only* the results of class I (no genetic assumptions) for two reasons: (1) although class II and III genetic properties are shared by all higher organisms, the genetics of most taxonomic characters is not known. (2) the results of class II and III simulations are not qualitatively different from those of class I. More detailed results will be given in another paper. Harper (1979) also deals with class I characters.

The assumptions of the Wagner method for estimating phylogenies are (1) the characters evolve independently; (2) over evolutionary time changes of states "0" to "1" to "0" are improbable; (3) retention of a polymorphism for both character states is far less probable than changes of state; (4) inequality of segment lengths on the tree is not so extreme that two changes of

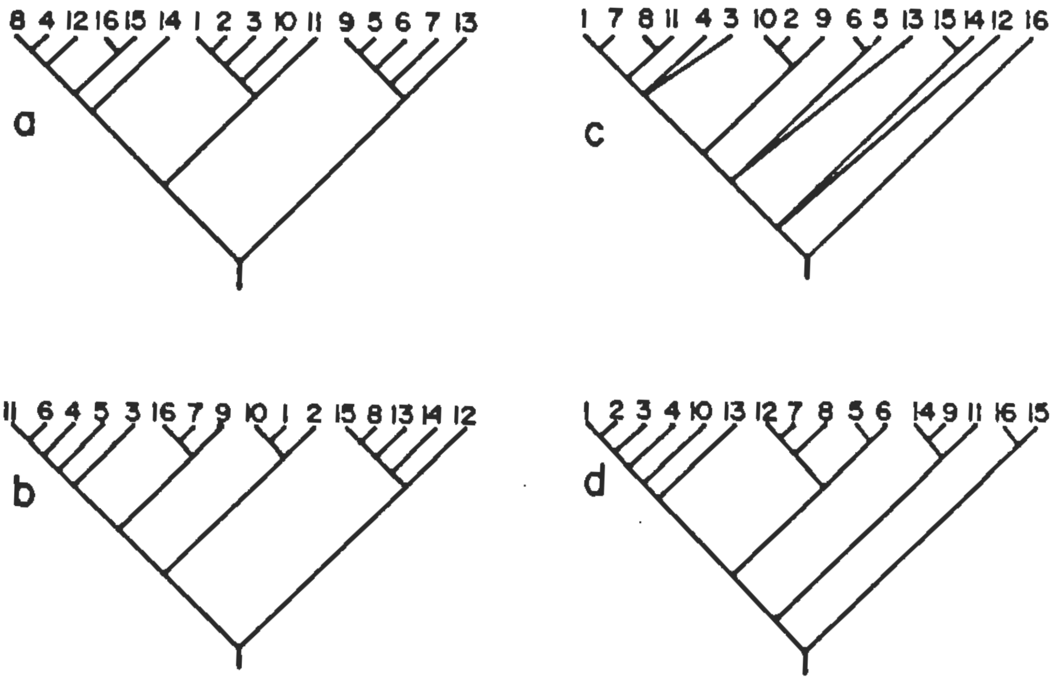

FIG. 2. The results of a typical single simulation of the vicariant sequence shown in Figure 1. The cladograms were constructed using the Wagner algorithm, and are rooted by the known primitive character states. Four out of the ten lineages in this simulation are shown; these are also the most similar lineages. Lineage *c* shows some trifurcations. There is only some resemblance to Figure 1. Note how the accuracy of the cladograms declines with more distant relationships.

state along a long segment are more probable than one change along a short segment (Felsenstein, 1973*a*, 1978–1980; Farris, 1969–1978). The simulations discussed here were run using these conditions. The Wagner method yields an unrooted tree, and the tree was rooted by including the primitive set of character types as an additional species in the Wagner calculations.

The basic question is: How well can the actual history be reconstructed on the basis of the cladistic relationships of the species at the end of each simulation? How concordant are the estimated phylogenies for all species experiencing the same vicariance sequence? The final results are biased in favor of the method because we know the primitive character states (all zero).

Figure 2 shows some typical results of the vicariance sequence of Figure 1. Other simulations yielded similar results. Counter to the predictions, various lineages sharing the same history do not yield concordant cladograms, and there is little resemblance between the branching sequence of Figure 1 and the cladograms of Figure 2. We need to know (1) how often does the estimated phylogeny reflect the actual vicariant sequence, and (2) how concordant will the cladograms of different lineages experiencing identical history be?

How often does the estimated phylogeny reflect the actual vicariant sequence? A quantitative estimate can be obtained by counting up the number of times a given degree of estimated relationship is the same as the relationships determined by the sequence of vicariant events. For example, we can ask how often species 1 and 2 are similar species (most closely related to nearest neighbors on the cladogram) and similarly for species 3–4, 5–6, 7–8, 9–10, 13–14, and 15–16. Similarly, we can ask how often species 1 and 2 are a sister group to 3 and 4 (second nearest neighbors) and so forth down the cladogram.

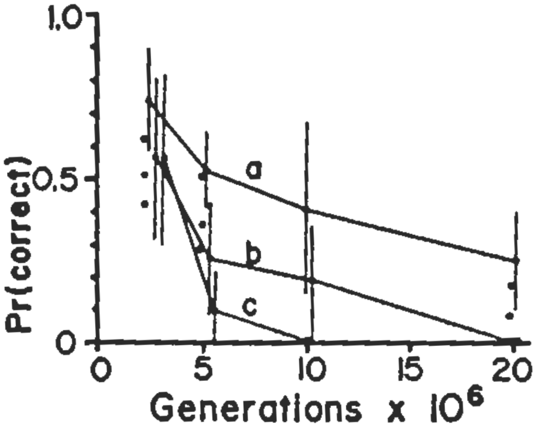

Fig. 3. The proportion of correct inferences of relationship in the simulations as a function of time since the last vicariant event (time E–S in Fig. 1). *a*, correctly designated as sister species (nearest neighbors in the cladogram). *b*, correctly designated as second nearest neighbors (for example species 1 and 2 should be a sister group of species 3 and 4). *c*, correctly designated third nearest neighbors. Solid dots and lines: forward and backward character change rates very low. Open circles: no backward rates. Vertical bars encompass two standard deviations of simulation results. For example, for nearest neighbors there is about a 75% chance of correctly deducing sister species 2.5 million generations after the event, but only about 40% about 10 million generations after the event. The curve actually bends down sharply near time zero because there is no phylogenetic information shortly after a vicariant event and before differentiation has started. The curves have the same shape for other combinations of character change rates and total generation times having the same probability of state change per character for the time period considered (see text).

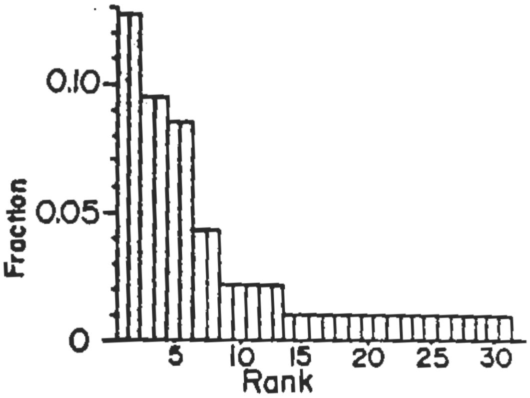

Fig. 4. Fraction of lineages with a given nearest neighbor on the cladograms *versus* rank abundance. Each bar represents a given nearest neighbor pair. The shaded bars mark correctly inferred nearest neighbors. The curve is much flatter and there are more bars for more distant neighbors. This is the combined results for two particularly concordant simulations using 40 characters per species.

Since some of the cladograms have "multifurcations" (non-dichotomous branching), a method similar to interpretation 2 of Nelson and Platnick (1980b) was followed: if it was possible to interpret a pair involved in a multifurcation as a nearest neighbor it was interpreted as such. This weights the results in favor of the method. The results are found in Figure 3. There are four major conclusions: (1) The overall accuracy (percentage correct inferences) declines with time since the last vicariant event. This was predicted on statistical grounds by Simberloff *et al.* (1981). (2) The accuracy is lower for older vicariant events. (3) There is no significant difference between simulations with backward rates (character state changes "1" to "0") and those with backward rates set to zero. (4) Unless the last vicariant event is fairly recent, the probability of a correct estimation of the branching sequence, hence the biogeographical events, is very low; the highest was about 75% and the average about 40%. Harper (1979) shows how the probability of obtaining a correct cladogram varies with the number of species and the number of layers in the actual branching sequence.

How concordant will the cladograms of various lineages experiencing common biogeographical history be? A quantitative estimate of concordance among cladograms is the frequency (among lineages) that a given nearest neighbor pair occurs, averaged over all observed pairs. If the cladograms of all lineages are identical, then the concordance value will be 100%, but if the cladograms are random the value will be small. For 20 characters per species the nearest neighbor concordance was 9.3 ± 12.4% and for 40 characters 15.2 ± 17.4%. The concordance remains quite low for increasing numbers of characters per species. Concordance is not significantly improved by disallowing backward rates, and decreases if we include more distant relatives in the counts. If we examine the most frequent nearest neighbors among all of the cladograms of all simulations, most of these are correct indications that these sister species experienced the most recent vicariant events (Fig. 4). Unfortunately, this is true only about half the time for single simulations of 10 lineages. Real data often contain fewer than five lineages, and the most common sister group pattern with that small sample size is only occasionally a reflection of the vicariance pattern. In addition, it would be difficult in practice to decide where to draw the line separating "most common" from less common (Fig. 4). A very large number of lineages would be needed to achieve the concordance necessary to give a reliable estimate of the vicariance pattern of the area.

Why should there be such poor concordance among cladograms of lineages with the same vicariant histories, and why should the cladograms be such poor estimators of the actual vicariance sequence? The problem is that the cladistic method is only an estimate of the pattern of shared derived patterns of the species. It cannot detect speciation events without the appearance of at least one unique derived character (Hull, 1979). Since cladistics estimates the order of appearance of characters, a fork in a cladogram can represent either a speciation event *or* merely the appearance of a new character without speciation (Hull, 1979). An additional clue is found in Figure 3: the decrease in accuracy with time since a vicariant event. Since the species evolve sets of character states independently of one another at any time after a given vicariance event, it is possible to get any combination of character states. The character state distributions a short time after a vicariance event are not necessarily the same as the distributions for the same species at some later time; the species have evolved since the event, and their patterns of shared derived characters will have changed. Therefore, the longer the time since a given vicariance event, the more difficult it will be to detect by a cladistic analysis. On average, a very large number of cladograms will replicate the pattern of vicariance events, but taking only a few at a time can yield quite spurious results. This is analogous to saying that the mean of a sample of 5 has a large standard error and is not a very good estimate of the "true" mean, though it is certainly the best estimate. As Felsenstein (1973*b*), Harper (1979), Hull (1979) and Simberloff *et al.* (1981) pointed out, a cladistic reconstruction must be viewed as a best guess in the face of uncertainty, not as an exercise in pure logic.

Although the simulations never yielded highly concordant cladograms, nevertheless there are excellent examples of concordance in nature (Rosen, 1975, 1978). It is of great interest to ask what could be responsible for the observed high levels of concordance in nature? One possibility is that the repeated patterns result from common environmental effects. Cladograms may be concordant because the patterns of shared derived characters reflect patterns of different shared environmental factors. For example, allopatric populations of forest-dwelling insects will share characters allowing them to live in various tree species and in varying forest microclimates. A whole community tends to differentiate from other vicariant communities, holding the coadaptations constant, hence the selection patterns and character distributions will be concordant.

In order to test the hypothesis that geographic variation in selection is the cause of concordant cladograms, the simulations were run again, but this time a given character was assigned either a high forward or a high backward character change rate at random ($P = 0.5$) until s out of k characters were chosen. Each lineage had the same pattern of character change rates. The characters of species 1 were allowed to vary at random. Two results will be presented: all characters under selection ($s = k$) and one-half of the characters under selection ($s = k/2$). Figures 5 and 6 show typical results for these cases. If some or all of the characters are selected the fraction of correct estimates of phylogeny is less than one percent, unless the selection pattern happens to match a vicariant pattern. This is the reason that taxonomists

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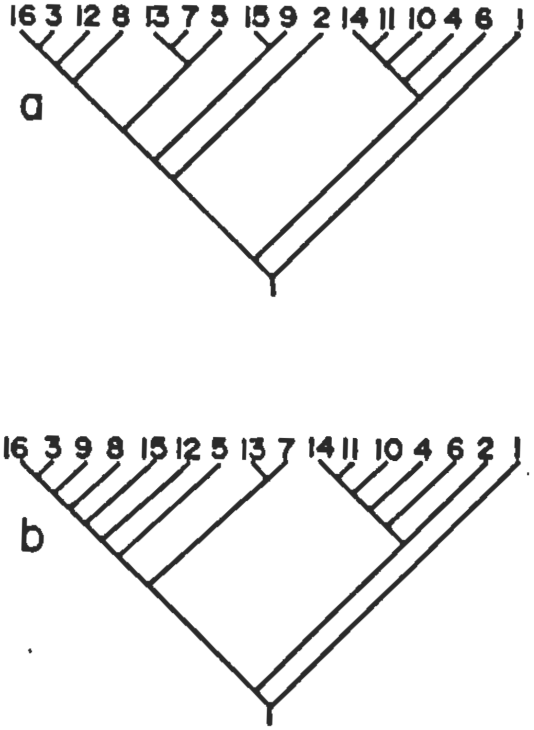

FIG. 5. Results of a single simulation with all characters selected for either character state "0" or "1," the direction per character determined at random with a 0.5 probability. Only species 1 was not subject to selection. Eight out of the ten lineages resulted in cladogram a. Cladogram b shows one of the two non-concordant lineages. There is no resemblance to Figure 1; the cladograms are determined by the patterns of shared selection regimes.

insist that the characters which they use are not subject to selection—selection violates the assumptions of the Wagner and other methods of deducing phylogenies. On the other hand selection does seem to explain concordance in cladograms: when all characters are subject to shared and different selection regimes the cladograms are 90 ± 14.1% concordant, and when 50% of the characters are selected the concordance is 55.2 ± 38.1%. In simulations where species 1 is also subject to selection the concordance rises to 100% when all characters are selected. Concordance appears to be a good measure of shared environmental effects and not history.

We therefore find that the method of vicariance biogeography is a poor indicator of the geographic history of a lineage, but it may be, in some cases, a good indicator of ecological relationships. A similar conclusion follows from Chernoff's paper in this symposium (1982); vicariance patterns will be false if the characters are influenced by selection. This is presumably the reason that many systematists wish to discredit the concept of natural selection (*e.g.*, Rosen and Buth, 1980). Note that these results do not invalidate the use of cladistic techniques to estimate taxonomic relationships, since cladistics is concerned with pattern, and not the processes determining the patterns (Eldredge and Cracraft, 1980; Cracraft, 1982). It is perfectly reasonable that species sharing the most selected characters should be taxonomically the most closely related, even if this does not reflect the vicariance pattern; the cladogram reflects both the phylogeny and the current ecology.

This result has an important implication for attempts to distinguish whether two species arose by allopatric or parapatric speciation. It is not possible to distinguish the biogeographic and genetic patterns resulting from the two modes of speciation (Endler, 1977). Recently Wiley (1981) and Cracraft (1982) have applied the methods of cladistic reconstruction and vicariance biogeography to the problem, and suggested that parapatric speciation should yield species which would be cladistically identified as sister species more often than allopatric speciation. They suggested that species forming by parapatric speciation would experience gene flow, leading to a greater frequency of shared derived characters than in allopatric speciation, where the speciating populations do not exchange genes.

The problem here is that, unlike allopatric speciation, parapatric speciation *requires* a selective difference between the speciating groups of populations, otherwise it will not work (Endler, 1977). In allopatric speciation, the isolated (allopatric) populations can diverge either by drift or by selection. Good taxonomic characters are supposed to drift, so they should reflect the "true" phylogenetic pattern if they

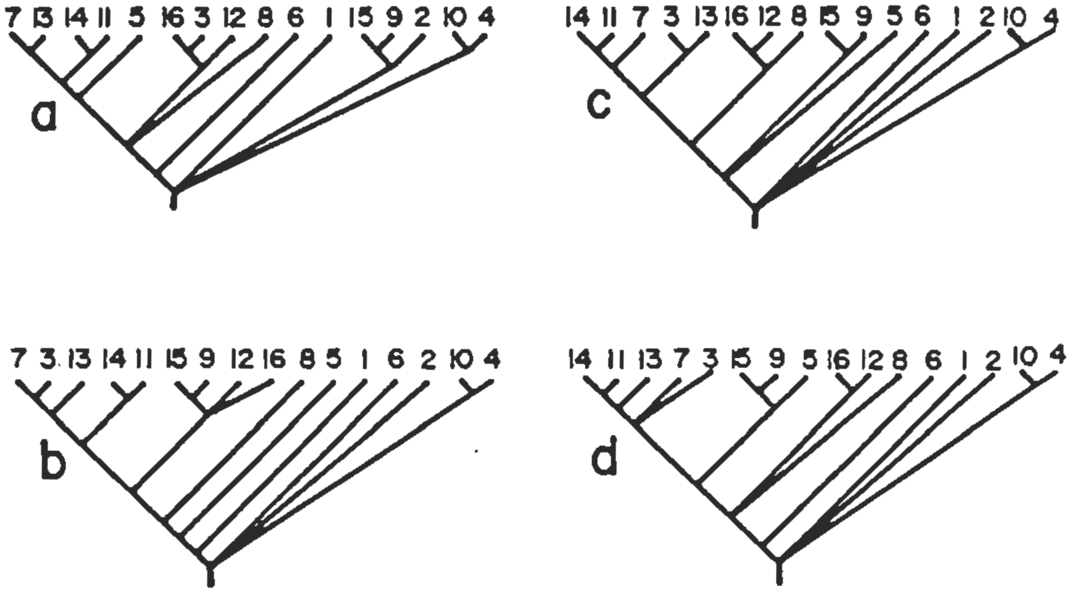

FIG. 6. The same as in Figure 5, but only 50% of the characters per species are subject to selection, the rest allowed to drift as in Figure 2. Four similar lineages are shown; the other six were more divergent. Once again there is no resemblance to Figure 1.

were not subject to selection. But a completely false picture of geographical history will be obtained if the characters are selected. In parapatric speciation, most of the characters will be selected in the different parts of the gradient causing the speciation, therefore it is very unlikely for parapatric speciation to ever give rise to species which would show as sister species by a cladistic analysis. They should actually be sister species to taxa on the same side of whatever gradient caused the speciation event. In Figure 6, species 11 and 14 of each lineage share a common selection pattern, yet they are actually quite distantly related in terms of the time since their gene flow was severed (Fig. 1). On the other hand species 5 and 6 experienced gene flow until recently (time E, Fig. 1), but share very few derived characters. Since sister groups can result from either (1) very recent divergence in allopatry of species whose systematics is based upon drifting characters or (2) shared selected characters in allopatry or parapatry, any pattern can result from allopatric or sympatric speciation. The distribution of sister species actually gives no information about the mode of speciation.

CONCLUSION

Organisms are subject to current ecology and history. The effects of the two can operate in various ways, sometimes yielding the same patterns. This makes it very difficult to distinguish between the two factors, and to estimate their relative importance. It is exceptionally important to consider several hypotheses, and test for all possible consequences of each hypothesis. The Pleistocene forest refuge hypothesis is a good example of a case where not all consequences were examined, and as a result, alternative hypotheses were ignored. The predictions of alternative hypotheses fit the data better than the refuge hypothesis. Vicariance biogeography suffers from not having all of its general predictions tested. Its major prediction, that concordant cladograms should result from concordant vicariance sequences, is rejected. Concordant cladograms can only result from shared geographic patterns of selection on the characters, and thus contain no information about their biogeographic history. Estimated vicariance patterns will be false if the characters are influenced by selection, and the degree of error is proportional to the time since the last vicariant event. An estimated vicariance pattern must be regarded as an example of statistical inference, with associated error, rather than as a logical deduction from the data.

Biogeography could profit by more attempts to examine the relative and joint effects of both history and ecology on distributions. One possible method would be to explore the ecological factors in sufficient detail so that these factors could be removed, leaving components of the distributions which presumably reflect historical events, but this is a formidable task. It is obvious that much work needs to be done in attempts to understand both historical and ecological factors in species distributions, without losing sight of the alternative hypotheses.

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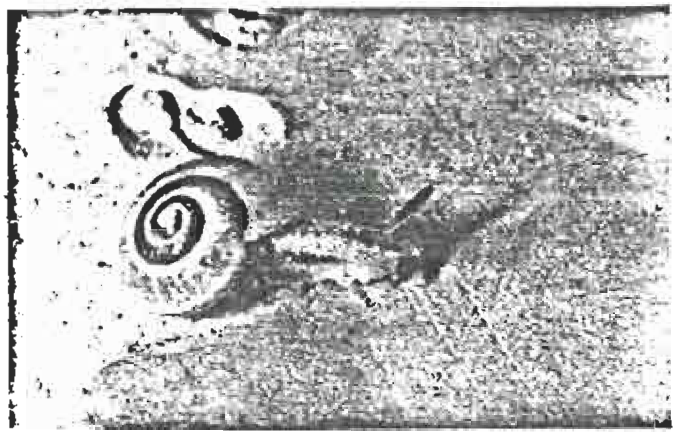

"For most endangered species, an inverse relationship exists between the size of the remaining population and the need for additional biological and ecological information."

Bernard Nietschmann, 1981
(Nat. Geog. Soc. Research Rep. 13:459-480).