

ECOLOGY, BEHAVIOR, AND MANAGEMENT OF THE MONA ISLAND GROUND IGUANA,
CYCLURA STEJNEGERI

A Thesis

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by

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CYCLURA STEJNEGERI

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Cornell University, 1977

The giant West Indian ground iguana unique to Mona I., P.R., was studied in the field for three years. Mona is a flat, cavernous, 5,500-ha island of limestone and dolomite with a subtropical-dry climate. The iguana population is sparse and distributed island-wide, with talus slopes and sinkhole depressions being preferred habitats. Year-round these diurnal lizards pass most of the day resting motionless, conserving energy and water. Activity is sporadic, possibly optimizing foraging efficiency while minimizing intraspecific strife. Iguanas eat chiefly fruits, flowers, large slow-moving insects and non-resinous, non-aromatic leaves. Factors promoting herbivory in juvenile Cyclura and other "small" lizards are discussed.

The iguana's communication system is primarily visual, consisting of stereotyped postural attitudes and head movements. Unlike most iguanid lizards, this species shows no identifiable species-typical bobbing display pattern; use of display elements is clearly graded in form. Disputes between males are resolved through ritualistic face-to-face pushing matches; females rely mainly on escalated displays in dispute settlement. The display repertoire, and published accounts for other species, suggest that bobbing displays in lizards evolved from intention movements, representing ambivalence between upright, alert, flight-preparatory or assertion postures and low postural attitudes associated with remaining inconspicuous or being submissive.

The mating season is extremely brief, and males compete aggressively for control over sites containing retreats attractive to females. A male's mating success depends chiefly upon the frequency with which he encounters females and upon his ability to catch a female quickly when she is receptive, mate without interference from competing males, and keep her from contacting other males between insemination and fertilization. Females appear to seek multiple insemination and mate with one or more males. From the standpoint of time/energy optimization, the only male reproductive strategy effective for monopolizing structurally complex areas that attract many females is short-term defense of a small territory. In contrast, where both retreats and females are relatively few, territorial behavior is less costly and fitness is improved through extended courtship and defense of a comparatively large area year-round. The older, more dominant males make the long-term investment and obtain most copulations.

Because Mona's surface area is predominantly rock, females must migrate to the scarce soil deposits offering conditions favorable for nesting. The onset of the two-week, mid-summer nesting season is apparently cued by photoperiod. Females typically nest in aggregations and individuals patrol completed nests for 3-4 days against gravid females searching for loosened soil. Evidence is given that nest-guarding neighbors recognize each other as individuals. Origins and evolutionary consequences of communal nesting in iguanine lizards are discussed and a model developed to illustrate how intense competition selects for late, synchronous nesting, nest-guarding, delayed maturity, and reduced sexual dimorphism.

Clutches are relatively small, with 5-19 uniformly large eggs, among the largest known for the family. Large egg and hatchling size offers several adaptive advantages: reduced susceptibility to desiccation and entrapment during emergence, increased food availability for hatchlings, and a shortened period of vulnerability to predators. In-nest mortality is low, and hatchling survivorship appears dependent upon Mona's uncertain rainfall pattern. Birds are the only significant native iguana predators, and they affect only the small, slow-growing juveniles.

The outlook for the future of cycluran iguanas throughout the West Indies is bleak; the animals' life history requirements are incompatible with man's present and expanding land-use practices. Introduced free-ranging mammals, especially pigs, goats, cats, dogs, and mongooses, have had a devastating impact. Pigs, for example, eat an average of 25% of the Mona Iguana's eggs annually. Detailed conservation guidelines applicable to Mona and many other Caribbean islands are presented.

BIOGRAPHICAL SKETCH

Thomas A. Wiewandt was born in Fremont, Ohio, on 28 September 1945, and spent most of his childhood in Los Alamos, New Mexico. He obtained a Bachelor of Science degree at Marietta College, Marietta, Ohio, where he was awarded the Beta Beta Beta and Eggleston-Ruby Prizes for outstanding achievement in biology and was elected to Omicron Delta Kappa, Who's Who Among Students in American Colleges and Universities, and Phi Beta Kappa.

Having spent two summers under the guidance of Richard G. Zweifel and Wesley E. Lanyon participating in a co-sponsored NSF - American Museum of Natural History undergraduate research program at the Kalbfleisch Field Station on Long Island, Wiewandt decided to embark on graduate studies in zoology. He received a Master of Science degree at the University of Arizona under the direction of Charles H. Lowe. He has worked as a teaching assistant in introductory biology, ecology, and vertebrate zoology, and spent one summer teaching algebra and sociology to American G.I.'s in Germany. His publications have been primarily in the field of herpetology, and he has assisted with research projects in nuclear chemistry, environmental physiology, and the population dynamics of reptiles, amphibians, and Saguaro cacti. While employed by the Puerto Rican Department of Natural Resources as resident ecologist of Mona Island, he helped formulate a comprehensive management plan for the island.

Wiewandt is seeking a career that will enable him to combine his interests in behavioral ecology, conservation, and photography. His photographs have appeared in Audubon and Natural History, and he is

currently working on the completion of a film documentary about the wild-life of Mona Island, emphasizing the life history of the Mona Iguana.

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Research in a wilderness setting can easily lapse into preoccupation with the task of day-to-day survival. Had it not been for 1.5 years of dependable logistic assistance and concern from the U.S. Coast Guard and the Zorniak Flight Academy, much of the study would have been more difficult, if not impossible. The University of Puerto Rico Department of Marine Sciences, members of the Natural History Society of Puerto Rico, the staff of DNR's research vessel "Jean A," the Mona police, the Mona fishermen from SW Puerto Rico, and a host of other friends and visitors also gave a helping hand. Oliverio Serrano of the Marine Resources Development Foundation aided in the repair of a tempermental telemetry system. Kentwood Wells and Herbert Raffaele played a major role in making my exit from modern society possible without jeopardizing my credit rating and career interests in the process. During my periodic sojourns to San Juan, David and Nonnie Humphrey, Miguel and Nanda Frontera, Oris and Neeley George, and Mitch and Kay Fram gave me shelter, warm hospitality, and intimate friendship I shall never forget.

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In spirit, the practical aspects of this study have been most strongly influenced by Frank H. Wadsworth, Director of the Institute of Tropical Forestry, whose long-standing devotion to the conservation of Mona's natural and historical resources has made an immense contribution in the interests of future generations. Several biologists professionally involved with programs for the management of introduced mammals have helped appreciably by providing advice and relevant literature: James K. Baker, Research Biologist, Hawaii Volcanoes National Park, U.S.D.I.; Reginald H. Barrett, Research Biologist, C.S.I.R.O. Division of Wildlife Research, Australia; Susan P. Bratton, Research Biologist, Great Smoky Mountains National Park, U.S.D.I.; Craig G. MacFarland, Director, Charles Darwin Research Station, Galápagos Islands; Glenn A. Hood, Director,

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PROLOGUE

La Iguana de Mona--no lizard, large or small, has ever left such a vivid first impression in my mind: Before me on Mona's desolate plateau in the mid-day heat of May 1972 must have been some mythical composite beast of Egyptian design. His head and body were enormous, legs stocky, and tail uncommonly short. The two peculiar bulges crowning his head and the giant sagging jowl muscles seemed most improbable indeed. That intricately wrinkled skin and massive head ornamented with prominent ridges, enlarged spines, and horn on the snout gave the animal a rather ferocious and appropriately prehistoric appearance. He tossed his head upwards and it rolled in an uncoordinated fashion. I had maneuvered to within touching distance and the iguana just stood there poised at the edge of a crevice, tense and defiant, holding his tail up off the ground, straight and stiff to the tip in a ridiculous pose. His fore-quarters swayed back and forth slowly, as though he were caught in ambivalence between staying to observe me a bit longer or retreating to the security of the hole. The penetrating stare I received was interrupted only by the flash of an opaque white nictitating membrane crossing the surface of his deeply set eyes. Meeting this remarkable beast on his terms in his domain--a hostile terrain of sharply weathered limestone with a host of unfriendly plants, intense heat, glare, stark silence, and the delicately blended aromas of sea, frangipani blossoms, and pungent shrubbery--was a humbling, primordial experience.

INTRODUCTION

Iguanas of the genus Cyclura, also known as ground or rock iguanas, form a group of large, robust, and often colorful lizards indigenous to islands of the Greater Antilles and the Bahamas. All species frequent rocky habitats of eroded limestone in subtropical dry climates. They are a striking part of West Indian natural heritage, primarily owing to their conspicuousness, their prehistoric countenance, and their former abundance. Some attain lengths of 1.5 m or more, only about half of which is tail, making them the largest native land vertebrates to have survived in the Greater Antillean faunal region and among the largest lizards in the Western Hemisphere.

Ground iguanas appear to have originated as an early offshoot from an ancestral line that eventually led to modern spiny-tailed iguanas, Ctenosaura, of continental Latin America (Avery & Tanner, 1971). Few fossil remains have been found, and our understanding of the group's paleohistory is consequently weak. In addition, neither geologists nor biogeographers have agreed on how land and sea of the Caribbean region have changed through the ages. It is generally agreed, however, that the origin of much of the West Indian biota dates to the Late Tertiary (Rosen, 1975), i.e., roughly 2-25 million years ago.

Dispersal over land-bridges from the continental mainland, trans-oceanic dispersal from continental centers of origin, and fragmentation of parent populations effected by continental drift have all been offered to explain how plants and animals first reached the Caribbean

islands. Simpson (1956) provided a comprehensive review of the "land-bridge" vs. "over-sea" hypotheses and developed a convincing case favoring waif dispersal via windstorms or rafting. The present strength of the Gulf Stream would hinder rafting from Central America, but in pre-Pliocene times, there were considerable differences in oceanic circulation in the Caribbean-Gulf area, largely due to the absence of the Central American isthmus (Emiliani et al., 1972). As noted by Darlington (1938), the sea was probably also smoother then due to lighter prevailing winds before the differentiation of polar and equatorial climates. In a more recent review of the subject, Rosen (1975) has championed the idea that zoogeographic patterns in the West Indies are best explained by the drifting apart of an already populated early lower Central American archipelago, spreading northeastward to form the Antillean island chain. Rosen's approach is particularly attractive in that it offers a feasible explanation for heretofore problematical disjunct distributions of some monophyletic groups.

Regardless of how iguanas were originally transported to the Antilles, subsequent island-to-island dispersal was influenced by the combined effects of ocean currents, wind, tectonic movements, and eustatic sea-level fluctuations, all of which were significant factors operating during Plio-Pleistocene times. Most of the smaller islands and cays with extinct or living forms of Cyclura (including Mona, Anegada, the Bahamas, Turks, and Caicos islands) were under water during all or part of the Pliocene and early Pleistocene (Horsfield, 1975; H. K. Brooks, pers. comm.) and consequently received their populations no earlier than the Pleistocene. Sea-level minima which accompanied glacial episodes of the Pleistocene (see Donn & Ewing, 1962) facilitated

rapid dispersal by completely removing water barriers between islands in some cases and in others by significantly decreasing the distance separating them. Present submarine profiles of island banks in the Greater Antillean region suggest that most gaps which persisted through periods of low sea-level and had to be crossed to account for the modern distribution of Cyclura were narrow, about 20-75 km wide. Horsfield (1975) has recently shown that island uplift, subsidence, and tilting have also occurred in the Greater Antilles during the Quaternary Period. However, precisely how these different geological phenomena interacted to alter the position, size, and configuration of islands and island groups has remained an unsolved puzzle of considerable scientific interest.

It is by no means remarkable that iguanas have dispersed so successfully among islands in the West Indies when evolutionary trends within the family are considered. The center of origin for the Iguanidae appears to be Gondwanaland (Estes & Price, 1973), the pre-Cretaceous supercontinent which fractured to form South America, Africa, Southern India, Madagascar, Australia, and Antarctica; and an important early stock of New World iguanine lizards was presumably partially aquatic, much like modern lizards of the genus Iguana ("gallina del palo") are today. These animals commonly rest and feed in trees along river courses, characteristically diving into the water and surfacing under plant cover when pursued. In some parts of Panama I. iguana also swim to off-shore islands for nesting (Rand, 1968). Alvarez del Toro (1972) even reported seeing tight aggregations of this species that had apparently spent the night submerged among mangrove roots beneath 0.5 m

of water. A strong propensity towards amphibious habits well developed early in the group's history is further suggested by the existence of the Galápagos Marine Iguana, Amblyrhynchus cristatus, which has the distinction of being the world's most seaworthy lizard. This species lives on exposed lava reef rock at the edge of the ocean, feeds on seaweeds at depths up to 12 m, and will voluntarily stay submerged for over 30 minutes at a time (Hobson, 1969).

Even though cycluran iguanas are specialized for life in dry, rocky habitats, they still exhibit aquatic tendencies. Early in the century, Noble (1923) recognized that these animals are preadapted for dispersal across water gaps. He observed a Hispaniolan Rhinoceros Iguana (C. cornuta) plunge into a lake to escape, diving beyond view and then surfacing after about five minutes. Flight into calm water as a means of escape has also been observed in C. pinguis on Anegada (Carey, 1975) and in juvenile and adult C. n. nubila on Cuba (Hardy, 1956; Lando & Williams, 1969), yet it appears that Cyclura typically avoid running to water when alternative cover is nearby (Gosse, 1848; Carey, 1966; T. Wiewandt, pers. obser.). Of particular interest is Buide's (1951) report from fishermen who have seen Cuban Iguanas at sea "moving from key to key, crossing narrows of more than 200 yards in width by swimming on the surface with the tail employed in the manner of a sculling oar." Most of the dispersal of West Indian ground iguanas must have taken place before the arrival of man in the Greater Antilles, dated at approximately 5,000 years B.C. (Cruxent and Rouse, 1969).

Nineteen named, morphologically distinct forms of Cyclura are

presently recognized: three are extinct and another possibly so, two are endangered, five are threatened, and eight are fragmented into tiny populations of variable status (Table 1). Those which have survived to this decade have been grouped into eight species by Schwartz & Carey (MS: 1977). Only C. cornuta and C. ricordi inhabit the same island (Hispaniola). Present trends, historical records, and a growing collection of paleontological remains indicate that Cyclura populations are rapidly declining with respect to both density and range. Man has clearly been the prime cause of the group's demise, either directly through hunting or indirectly by giving domestic animals free range, importing exotic predators, or otherwise modifying critical aspects of the lizards' natural habitat.

The extinct Puerto Rican Iguana (C. portoricensis) was in Barbour's (1919) estimation the largest member of the entire genus and shared distinctive skeletal traits with C. stejnegeri of Mona and the late C. mattea of St. Thomas. Remains of the former were found on the floor of a cave near Ciales, and the species was probably exterminated by the sizable Indian population on Puerto Rico before the Spanish Conquest, for in 1919 neither living inhabitants nor the literature revealed any hint of its existence. Bones of C. mattea, also of Recent age and recovered from a kitchen midden in St. Thomas (Miller, 1918), suggest these lizards were exploited there as food by Pre-Columbian Indians, as we know they were in the Bahamas Archipelago (Auffenberg, 1975), in Cuba (Morison, 1942, p. 449), and in Jamaica (Woodley, 1971).

While ground iguanas were once commonly hunted for food in parts of

Table 1.--Known extinct and living forms of cycluran iguanas.

Species*	Distribution	Status	Explanation for		Outlook for		Source
			Status	Status	Future	Future	
<u>C. mattea</u>	St. Thomas, V.I.	Extinct--Recent	Overhunting by pre-Columbian Indians suspected.				Miller, 1918; Barbour, 1919
<u>C. portoricensis</u>	Puerto Rico	Extinct--Recent	Overhunting by pre-Columbian Indians suspected				Barbour, 1919
<u>C. cornuta onchiopsis</u> (<u>C. nigerrima</u>)	Navassa I., Haiti	Extinct--Recent	Unknown--man, cats, and goats are suspect				Thomas, 1966; Patton, 1967
Unnamed	Great Exuma, Bahamas	Extinct	Unknown				Allen, 1937
Unnamed	New Providence, Bahamas	Extinct--Pleistocene	Unknown				Etheridge, 1966
Unnamed (possibly a <u>Cyclura</u>)	Barbuda, Lesser Antilles	Extinct--Late Pleistocene	Unknown				Etheridge, 1964
<u>C. collei</u>	Jamaica and Coat Island	Possibly Extinct	Overhunting by man since 1700; predation from introduced mongoose; development by U.S. Navy		Very poor--last individual seen in 1969; no subsequent signs of survivors		Lewis, 1944; Woodley, 1971; Lewis, pers. comm. 1976
<u>C. nubila levisi</u> (<u>C. macleayi levisi</u>)	Grand Cayman	Endangered	Population sparse and juveniles extremely rare in 1937-1938; numbers reduced by hunting		Poor, though apparently still surviving; may be in competition with introduced iguanas		Grant, 1940; Lewis, 1944; Carey, 1975; C.B. Lewis, pers. comm. 1976
<u>C. n. caymanensis</u> (<u>C. m. caymanensis</u>)	Little Cayman and Cayman Brac	Declining	Dogs, cats, and hunting apparently responsible on Cayman Brac; feral cats pose a threat to juveniles, which are now rare, on Little Cayman		Unfavorable on Cayman Brac; much better on Little Cayman		Grant, 1940; Carey, 1966; M.V. Haunsome, pers. comm. **, C.B. Lewis, pers. comm. 1976

Table 1 (Continued)

Species	Distribution	Status	Explanation for		Outlook for		Source
			Status	Future			
<u>C. n. nubila</u> (<u>C. m. macleani</u>)	Cuba, Isle of Pines, and small nearby keys	Declining	Formerly widespread--suffered initial decline from hunting; range still rapidly shrinking (cause unstudied)	Unknown			Barbour, 1919; Auffenberg, 1975
<u>C. c. cornuta</u> (<u>C. cornuta</u>)	Hispaniola and peripheral islands	Common, but threatened	Widespread in Haiti and Dominican Republic but faced with accelerating habitat alteration by man, goats, and burros, plus predation from dogs, cats, pigs, and mongooses	Appears good in some areas, bad in others; depends largely upon control of domestic and feral animals plus the nature of human population growth and development			Haiti: P. Meylan, pers. comm.***; D.R.: Wiewandt and Cicca, pers. observ.***
<u>C. c. stejnegeri</u> (<u>C. stejnegeri</u>)	Mona I., Puerto Rico	Common, but threatened	Limited natural habitat is being decimated by goats and considered for development; pigs are preying on eggs and cats probably taking juveniles	Good if human use is carefully regulated, feral animals brought under control, and nesting areas given special protection			Wiewandt (see text)
<u>C. ricordi</u>	S.W. Dominican Republic	Common, but threatened	Populations are highly localized; small natural range of species being disturbed by man, goats, burros, dogs, and/or cats	Good only if domestic and feral animals are controlled and an active conservation program accompanies development			Wiewandt and Cicca, pers. observ.***
<u>C. pinguis</u>	Anegada, V.I.	Endangered	Habitat destruction by livestock especially goats and cattle; predation from dogs and possibly cats and pigs	Presently small and senescent population may might recover if domestic animals are controlled and development projects deferred; extinction highly possible			Carey, 1975

Table 1 (Continued)

Species	Distribution	Status	Explanation for		Outlook for	
			Status	Status	Future	Source
<u>C. c. carinata</u>	Turks and Caicos Is. (on 15-20 cays and islands)					
<u>C. c. bartschi</u>	Bahama Bank (Booby Cay)					
<u>C. r. rileyi</u> (<u>C. rileyi</u>)	Bahamas (San Salvador and vicinity)					
<u>C. r. nuchalis</u> (<u>C. nuchalis</u>)	Bahamas (Acklins Bight)	Locally endangered to common, but vulnerable	Throughout the Bahamas Archipelago, all forms are hunted for food, "sport," or the pet trade. Most populations are confined to tiny cays, thus while some are still relatively dense, all are precariously small. Those cohabiting islands with man are also declining from habitat modification or predation by dogs and cats. Historical and paleontological records suggest many populations have already been extirpated or severely reduced in size.		Highly variable, from poor to good, depending largely upon effectiveness of government sponsored conservation programs	Barbour and Noble, 1916; Auffenberg, 1975, 1976; Carey, 1975, 1976; Carey, pers. comm.; Iverson, pers. comm.***
<u>C. r. cristata</u> (<u>C. cristata</u>)	Exuma Chain (White Cay)					
<u>C. cycchlura figginsii</u> (<u>C. figginsii</u>)	Exumas (on several cays and islands around Great Exuma)					
<u>C. c. inornata</u> (<u>C. inornata</u>)	Exumas (Leaf Cay and SW Islands Cay)					
<u>C. c. cycchlura</u> (<u>C. baolophia</u>)	Bahamas (Andros Is.)					

* As denoted by Schwartz and Carey (in 1977); formerly accepted names appear in parentheses.

** 1975 Royal Society/Cayman Island Government Expedition.

*** Research sponsored by New York Zoological Society, through a grant to Walter Auffenberg (1975-1976).

the West Indies, even to the extent that ships in the Bahamas were cargoes with them for export to the U.S. (Barbour & Noble, 1916), this factor appears to be of relatively minor importance in most areas today. This is probably best explained by the amount of work involved in catching them at their presently low densities. Shooting them for "sport" or collecting for the pet trade, are, however, nuances of hunting that have been on the rise (Auffenberg, 1975). At present the accelerating rate of human expansion and development coupled with extensive habitat modification (including the important effects of feral mammals, livestock, and free-running pets) clearly pose the most serious problems for these lizards.

Carey (1975) has reviewed the scientific literature pertaining to Cyclura. Nearly all former accounts have been either taxonomic descriptions or notes pertaining to miscellaneous aspects of their distribution, ecology, and behavior. The field study of C. pinguis by Carey (1975) is the first in-depth consideration of the habits and ecological relationships for any species of Cyclura. Published reports on the biology of the Mona Iguana are limited to a note on collecting (Grant, 1944), an incidental note on diet (Martin, 1966), and taxonomic diagnoses (Stejneger, 1904; Barbour & Noble, 1916). Concurrent with my investigation on Mona, Walter Auffenberg and two of his University of Florida graduate students, John Iverson and David Auth, conducted an extensive ecological study of C. carinata in the Caicos Islands.

I have undertaken a broad-based study of the behavioral ecology of the Mona Iguana. Emphasis is on determinants of life history attributes,

especially the type and relative availability of critical resources (shelter, food, mates, and nest sites). Unfortunately, herpetological investigations permitting comparative analysis are few. Many of the hypotheses presented are necessarily speculative and are offered to stimulate thought and further investigation. Another important aim of this study was to examine the habits and requirements of the Mona Iguana for the development of a conservation program. There is an immediate need for such a program on Mona and almost everywhere cycluran iguanas still occur (see Table 1). A detailed discussion of problems posed by introduced mammals and man, along with proposed solutions to these problems, is available upon request from the author. The key points of this proposal are presented in abbreviated form in the concluding chapter.

In this paper, the Mona Iguana is designated as Cyclura stejnegeri, even though Schwartz & Carey (MS: 1977) favor the trinomen C. cornuta stejnegeri, which emphasizes its relationship to the Hispaniolan Rhinoceros Iguana, C. cornuta. All authors past and present agree that these two forms are closely related, but how far they have diverged in evolutionary time, presumably at least 10,000 years, is still an open academic question. Because I believe that more is to be gained in terms of conservation if the Mona Iguana is treated as a distinct species, I favor the retention of Cyclura stejnegeri Barbour & Noble until its position can be discussed in less speculative terms.

ENVIRONMENTAL CONDITIONS

The seuenth day, we arriued at Mona: where wee watered: which we stood in great need of, seeing that our water did smell so vildly that none of our men was able to indure it.

Whilst some of the Saylers were a filling the Caskes with water, the Captaine and the rest of the Gentlemen, and other Soldiers, marched vp in the Ile sixe myles; thinking to find some other prouision to maintaine our victualling. As we marched, we killed two wild Bores; and saw a huge wild Bull, his hornes was an ell betweene the two tops. We also killed Guanans, in fashion of a Serpent, and speckled like a Toade vnder the belly.

These wayes that wee went, being so troublesome and vilde, going vpon the sharpe Rockes, that many of our men fainted in the march: but, by good fortune, wee lost none but one Edward Brookes Gentleman; whose fat melted within him, by the great heate and drought of the Countrey. We were not able to relieue him nor our selues; so he died in that great extremitie.

7 April 1607
Rev. Samuel Purchas
(Arber, 1910)

Mona is the second largest and the most remote of Puerto Rico's off-shore islands. It is roughly 11 km x 7 km in size, 5,500 ha (13,600 acres) in area, and is situated 68 km west of the Puerto Rican mainland in the middle of the Mona Channel, a key passageway between the Atlantic and Caribbean (Fig. 1). The only land mass in close proximity is Monito, a 16-ha island located some 5 km northwest of Mona. In general appearance, Mona resembles a vast flat-topped iceberg of low profile. Almost 95% of the island's surface area is a slightly domed and undulating plateau, limited around the windward, northern perimeter by sheer cliffs dropping 4585 m into the sea. The cliffs of the south side are steep, but break away in many places as talus slopes that descend to a narrow coastal terrace mostly 3-4 m in elevation.

Mona is formed of carbonaceous rock of sedimentary origin. The

Isla de Mona

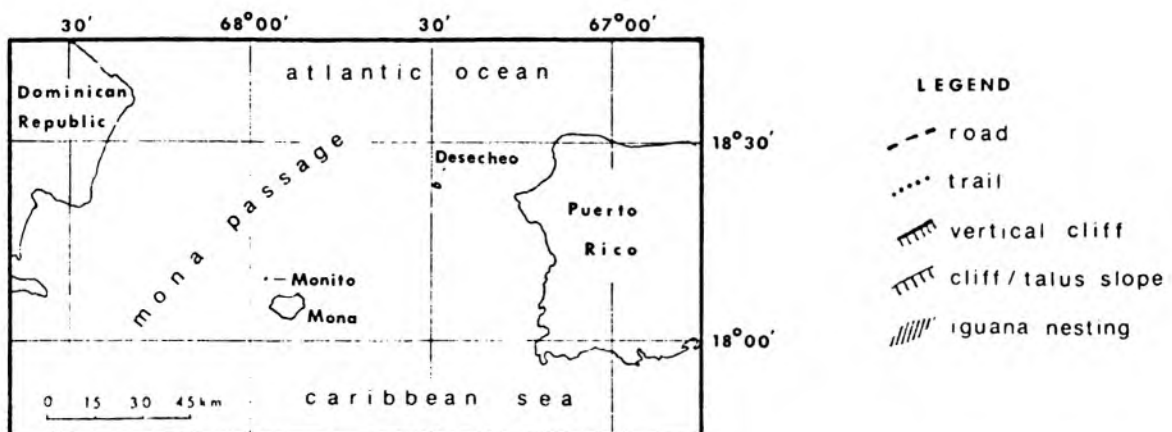
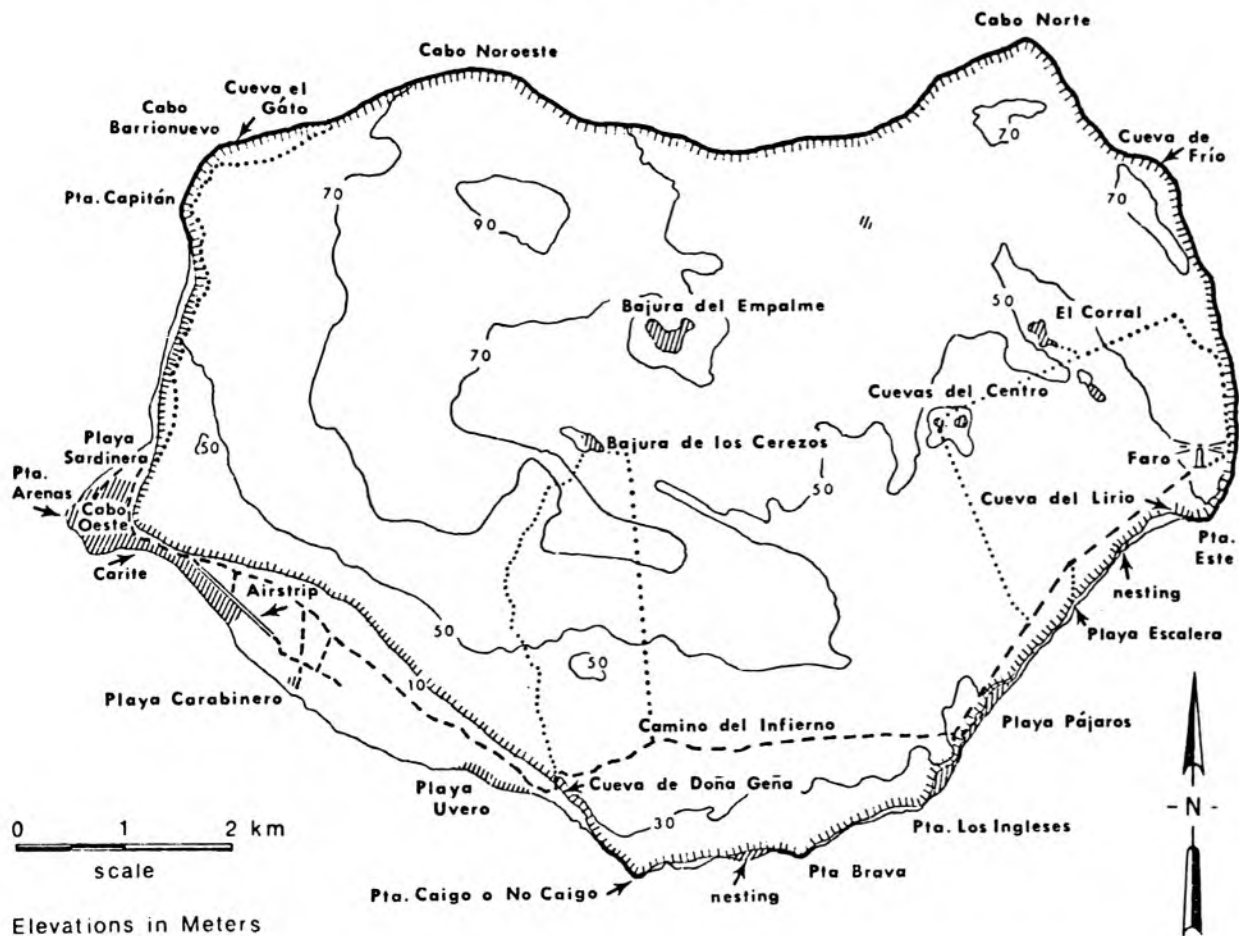


Fig. 1.--Topography, place names, and principal iguana nesting habitat of Mona Island, Puerto Rico. Topographic features based on Briggs & Seiders (1972).



LEGEND














PLANT COMMUNITY	
	PLATEAU FOREST
	DEPRESSION FOREST
	PLATEAU SHRUB
	CACTUS/LOW SHRUB
	CACTUS FOREST
	COASTAL FOREST (CLOSED CANOPY TYPE)
	COASTAL FOREST (OPEN CANOPY TYPE)
	MANGROVE
	CLIFFSIDE
	MARITIME SHRUB
	PLANTATION- MAHOGANY
	PLANTATION- CASUARINA
	DISTURBED/ SUCCESSIONAL

Fig. 2.--Plant communities of Mona Island, P. R. Map from Rogers (1975) courtesy of B. Cintrón and L. Rogers, Puerto Rican Department of Natural Resources.

island's foundation of dolomite was deposited during early-middle Miocene times (about 18-25 million years ago), and was subsequently capped by a thin layer of pure limestone (now 0-15 m in thickness), presumably of Pliocene - early Pleistocene age (Kaye, 1959). Later, this tableland emerged and has remained elevated above sea level for at least one million years. Also during the Pleistocene, the low, raised-reef deposits forming the coastal terrace were added around the southern perimeter of the island. It is likely that Mona's shores once corresponded in dimension to the present submarine bank that surrounds Mona and Monito, yet there is no evidence of a more extensive former connection with either Puerto Rico or the Dominican Republic (Kaye, 1959).

The island, complete with an array of ecological conditions peculiar to such areas, presents a fine example of karst topography. The entire upland surface is weathered into a micro-relief of solution pits and unyielding points. Caves are conspicuous and numerous in the cliffs, but most are relatively shallow and underlie only 12% of this tableland. The scarce accumulations of soil on the plateau are largely confined to small shallow potholes and sinkhole depressions, the latter feature representing about 3% of the upland surface area. The coastal plain is mantled with a thin, spotty layer of sandy soil, reaching its greatest depth and purity in narrow coastal strips paralleling beach deposits, and including much of Cabo Oeste (see Rivera, 1973). Because of Mona's highly permeable limestone substrate and the general lack of soil to retain water, the island has no watershed; not even dry channels carry intermittent flow following rainstorms (Jordan, 1973). Surface

depressions in the rock, a few of which exceed a meter in diameter, catch and hold rainwater for periods ranging from hours to months. Brackish ground water exists in the coastal lowlands, in evidence today by several shallow wells and a small pond with an adjacent land-locked mangrove. Water also collects at least seasonally behind rimstone dams in some of the caves.

Being at a subtropical latitude and receiving an average annual precipitation of 810 mm (31.9 inches), Mona falls within Holdridge's "subtropical-dry" life zone category (Ewel and Whitmore, 1973). Calvesbert (1973) and Wadsworth (1973a, p. 37) have evaluated and discussed the island's climate. Thirty years of rainfall records kept by U.S. Coast Guard personnel at the Mona Island Light Station were averaged to give representative baseline precipitation data (Fig. 3). Mona has a pronounced dry season from January to April. Mean monthly rainfall peaks in October, with the greatest minimum expected rainfall (3.3 cm when $p=0.9$) occurring in October and November. Most of the rain is received as brief, patchy afternoon or evening showers (personal observations). "Prolonged rainless or nearly rainless periods can be expected. At one time there were 66 days without rain and at another 103 days with no daily rainfall of more than 0.25 inch. During one period of four months the rainfall was 1.08 inch and during six months 3.01 inches. Of the days in which rain falls on one end of the island three out of four produce no rain on the other end" (Wadsworth, 1973a).

The temperature regime was inferred by Calvesbert from records kept at three climatological stations in comparable environments, i.e., the

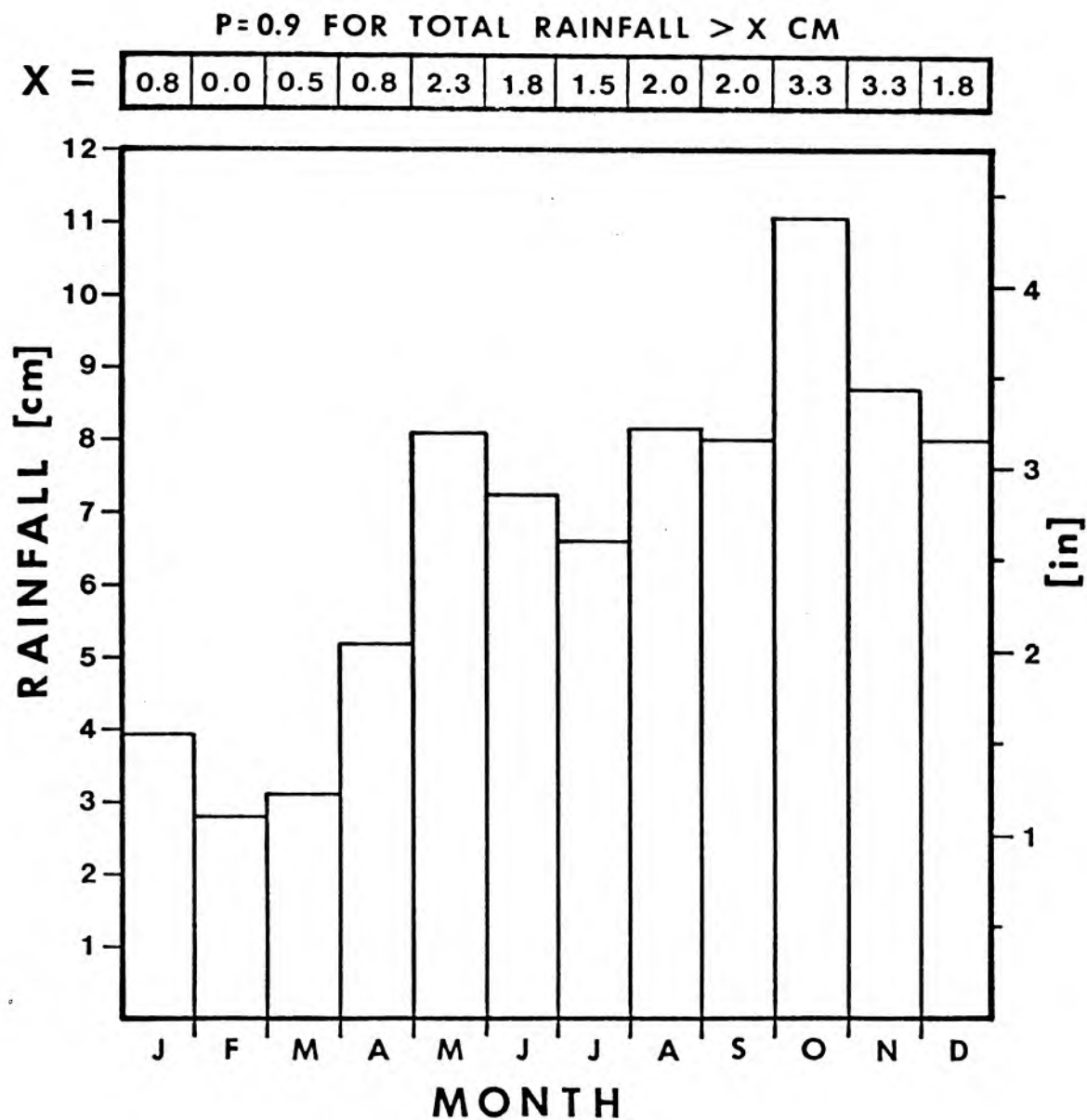


Fig. 3.--Histogram of mean monthly precipitation with tabulated monthly minima expected when $p = 0.9$, based on records from a 30-year period on Mona I., P. R., as reported by Calvesbert (1973).

extreme southeast coast of the Dominican Republic, the south coast of Puerto Rico, and Vieques Island, P.R. (Fig. 4). Deviation between these estimated long-term monthly means and actual values for Mona is not expected to exceed 1°C . Extremes of temperature, both seasonal and diurnal, are well tempered by the surrounding ocean, producing a mild thermal environment year-round. Comparisons between source data drawn upon by Calvesbert and recent temperature data from Mona (Table 2), indicate that monthly minima and maxima fall within the $17\text{--}35^{\circ}\text{C}$ range. The normal scope of temperature change throughout the day is $11\text{--}14^{\circ}\text{C}$.

Mona's climate is humid. Sample humidity profiles show that diurnal fluctuations in relative humidity are notably constant, typically ranging from daytime lows of 40–64% to nighttime highs of 89–100% (Table 3).

Because of the island's small land mass, there is no land-sea breeze pattern superimposed over the trade winds, which, on an annual basis, blow about 80% of the time from an easterly direction. Extreme wind speeds of hurricane force (>74 mph, 119 kmph) occur on Mona about once every eight years, and tropical cyclones affect the island on the average of once every five years. Fully developed hurricanes cross the island about once every 17 years (Calvesbert, 1973).

Mona's vascular flora exceeds 400 species (Roy Woodbury, pers. comm.); 74 are native trees and large shrubs, most of which are broadly distributed in the West Indies (Little, 1955). In mapping the island's vegetation, Cintrón and Rogers (1974) recognized 10 plant associations (Fig. 2; for lists of dominant species in each, see Appendix I). For

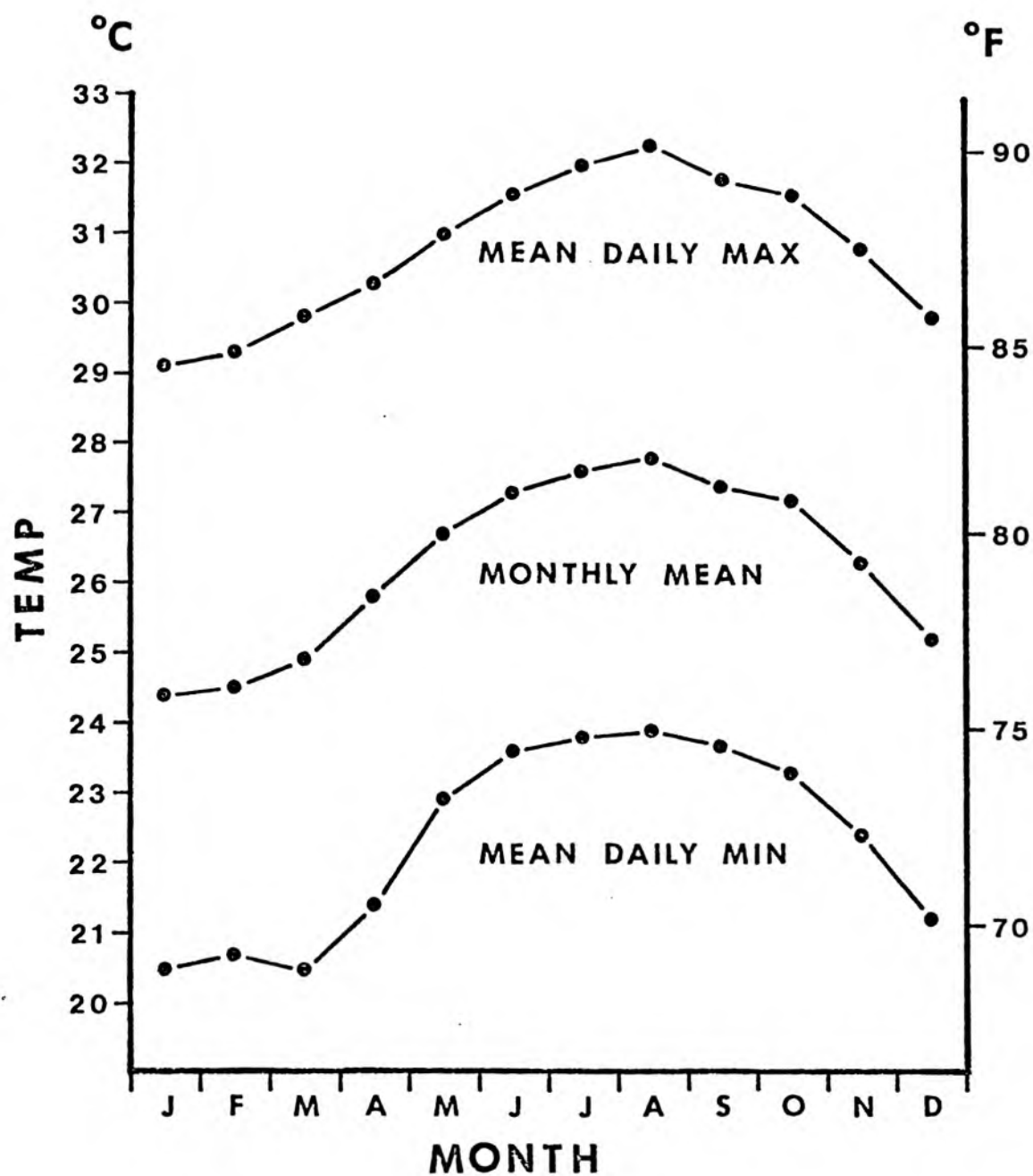


Fig. 4.--Temperature regime for Mona I., P. R., estimated by Calvesbert (1973) from climatological data taken at other coastal sites in Puerto Rico and the extreme southeast coast of the Dominican Republic.

Table 2.-- Summary of daily maximum-minimum temperature data recorded during 1975 on Mona Island, P.R., at a standard U.S. Weather Bureau substation situated upon the plateau near Sardinera.

Time Period	No. of Days Sampled	Mean Max.	Max.	Mean Min.	Min.
26-31 March	6	89.3°F (31.8°C)	91°F (32.8°C)	69.8°F (21.0°C)	66°F (18.9°C)
2-15 April	12	90.3°F (32.4°C)	93°F (33.9°C)	68.6°F (20.3°C)	64°F (17.8°C)
3-25 May	21	90.5°F (32.5°C)	93°F (33.9°C)	69.8°F (21.0°C)	66°F (18.9°C)
18-20 June	3	93.0°F (33.9°C)	94°F (34.4°C)	71.7°F (22.1°C)	70°F (21.1°C)
4-16 July	12	92.9°F (33.8°C)	95°F (35.0°C)	71.1°F (21.7°C)	69°F (20.6°C)

Table 3.-- Range of variation in relative humidity sampled during 1975 on Mona Island, P.R., at a standard U.S. Weather Bureau substation situated upon the plateau near Sardinera. Measurements made on a continuous-recording hygrograph (Weather Measure Corp.).

Month	No. of Observation Days	Daily Maxima	Daily Minima
April	16	90-100%	40-63%
May	14	89- 98%	50-62%
Late June	6	90- 95%	43-64%
July	13	95- 98%	50-60%
Late August	7	91- 97%	45-55%
September	6	90- 97%	50-60%

the most part, these differ chiefly in structure, rather than composition. Covering 86% of Mona's plateau is an open-canopy forest of short, slow-growing trees (generally less than 5 m in height) with dense shrubby undergrowth rooted entirely within the small soil-filled pot-holes and solution cavities that penetrate the limestone. Present in profusion are several species of epiphytic bromeliads, an endemic orchid, and a ground-cover of tenacious cholla cactus. In upland areas highly stressed by wind and salt spray, the canopy thins and disappears with assemblages of cacti and shrubs predominating. As one would expect, the island's forest is best developed (attaining maximum heights of 12-20 m) in areas offering greatest physical protection and soil depth, i.e., on the coastal plain and within sinkhole depressions that dot the plateau (Cintrón and Rogers, 1974).

Vegetation covering the plateau has never been greatly modified by man (Wadsworth and Gilormini, 1945), although browsing by feral goats has clearly altered its character. Because of its accessibility, the coastal lowland forest (represented only on the southwestern coastal plain) was, on the other hand, extensively cleared and selectively cut during the past to exploit the area for charcoal, fence posts, agriculture, and grazing (Wadsworth, 1973b). A portion of the cleared land was later reforested in Australian Pine (Casuarina) and Mahogany, both of which are now well established.

Mona's terrestrial fauna has been inventoried and discussed in detail elsewhere (in Isla Mona, 1973--see Wadsworth, 1973). Among the arthropods, 526 insect species, 52 spiders, 4 centipedes, 2 scorpions,

1 tailless whipscorpion, and 4 land crabs have been reported. Twenty-one species of terrestrial molluscs were recently collected and identified by F. Thompson (pers. comm.). Native vertebrates include a single amphibian, 3 species of snakes, 6 species of lizards, 22 species of resident birds (9 of them sea birds), and 4 species of bats. In addition, fossil remains of a very unusual giant tortoise have been found; sea turtles (primarily Hawksbill) regularly nest on the island's 7.2 km of beaches; and roughly 80 species of presently non-resident birds have been observed on Mona. Introduced mammals include pigs, goats, cats, rats, and mice.

As in other remote and relatively undisturbed small-island ecosystems, the unusual character of Mona's wildlife rather than species diversity makes it of special interest to man. The island has a high proportion of endemic forms (more in fact than all of Puerto Rico's other offshore islands combined, including Vieques and Culebra--Raffaele, 1973) and supports substantial populations of other animals that have become rare and endangered on the Puerto Rican mainland. Seventy percent of Mona's terrestrial herpetofauna, for example, is endemic, and Mona is the only place in the Commonwealth (and one of the few in the Caribbean) where the endangered Hawksbill Turtle still nests in significant numbers (Thurston & Wiewandt, 1977).

Facilities on Mona today are limited to an unmanned lighthouse on Cabo Este (kept in operation by the U.S. Coast Guard) and associated buildings (now vacated), a dirt landing strip for small planes on the coastal plain, and an assemblage of six cabanas, two wood and four

concrete, at Sardinera. The facilities at Sardinera are tended by police officers and P.R. Dept. of Natural Resources (DNR) management personnel on rotating duty from the mainland. A single road crosses the island from Sardinera to the Lighthouse (Fig. 1), and for the past two years, two semi-operative government vehicles have been in use there.

PROCEDURE

Field work covered a period of three years (May 1972-April 1975), approximately two-thirds of which was spent in residence on Mona. Trips to San Juan were usually made once every 5-8 weeks. Some continuity in observations was maintained during my absence through part-time assistance from other employees of DNR. The only extended break in the investigation occurred from September through December 1974.

The first six months were largely spent exploring the island to gain familiarity with the environment as a whole and to select representative, conveniently located study areas. Thereafter I concentrated my endeavors at a number of sites in three areas: 1) the southwestern coastal plain between Sardinera and Carabinero, 2) the eastern cliffside and coastal terrace in the vicinity of Cueva del Lirio, and 3) the inland chain of "bajuras" which includes El Corral (Fig. 1). At the first locality, only nesting was studied, and a census route was established through the area. At the second, I examined seasonal variation in iguana density as a function of fruit availability and from two blinds observed the behavior of four juveniles and six adults residing at the cliff edge. At the third, daily activities of adults, including territorial and breeding behavior, nesting, and feeding habits, were of principal concern. Most observations were aided with 8 x 30 binoculars; in some cases a 15-60x spotting scope was used.

Special care was taken not to alter the normal behavior of the field animals under observation. None were artificially manipulated

through food offerings, and to minimize trauma associated with being handled, few were captured. All study animals without distinctive scars or other features that would permit instant individual recognition were marked with paint, mostly by shooting them with rubber-tipped darts to which balls of cotton were glued and dipped in Pactra quick-drying day-glo paint. Metallic silver paint also proved conspicuous and durable. Iguanas sleeping or hiding but partially exposed were sometimes easy to mark with a small brush tied to the end of a pole. Such identification spots persisted for six to nine months in most cases, but those applied shortly after molting rubbed off within weeks. To minimize the possibility of harming the animals physically or modifying their social behavior, neither head nor neck was marked.

Iguanas captured for weights and measurements were usually noosed with a loop of insulated braided wire at the end of a 6-m telescoping fiberglass fishing pole. This technique worked well on approachable individuals, but had the disadvantage that the animals usually bite their tongues in the process of being captured. Because Mona Iguanas are sometimes careless about leaving their tails partly exposed after dashing to cover, it was occasionally possible to take them by hand with a firm grip and sudden yank on the tail. Also, I captured two individuals at night while they were sleeping outside their retreats. When held, the iguanas often relax and then unexpectedly thrash about to get free. Adults are incredibly strong and bite without hesitation. Cloacal temperatures were taken with a quick-recording Bacharach thin-bulb mercury thermometer (code no. 12-0177), and body weight was measured with a Chatillon 0-12 kg spring-tension scale.

Captive adults can be sexed by examining the femoral pores, which are generally enlarged in males, vestigial in females. From a distance, however, this species is extremely difficult to sex--elderly females and young males were especially problematical. There are no striking field marks in color or body form; nevertheless, several more subtle differences proved useful: Typically, the head and jowl muscles are proportionately larger in males, and their facial spines are more often blunt, probably due to excessive wear from fighting. Fewer females have regenerated tails, and the sacral gap in the row of mid-dorsal spines is often broader and more flattened dorsally. Females also sometimes bear mating scars on the nuchal crest. Enlarged nuchal spines or sex-related differences in the length of mid-dorsal spines are absent in C. stejnegeri (and apparently C. cornuta). Where an individual's morphological traits left doubt, its behavioral responses toward other iguanas of known sex aided identification.

Because of Mona's dense undergrowth, few iguanas could be observed from distances exceeding 20 m. Blinds proved impractical except at the cliff edge and at nesting areas, where they were indispensable since individuals in more exposed situations are generally wary. Four "permanent" blinds were constructed, and temporary blinds were made when and where needed by simply tacking burlap cloth draped to the ground between trees.

Through continued observations at one inland depression (hereafter referred to as La Bajurita), iguanas living there became accustomed to my presence, permitting me to document their habits without needing a

blind. I was treated with nearly total indifference by males, but females remained relatively timid, most keeping a safe distance of at least 7 m from me. During the 1973 breeding season, females avoided courtship in my presence and no copulation was seen. In 1974, however, after a full year of regular appearances in the area, I observed courtship and mating. I also installed a blind for observation of any particularly wary individuals that might have otherwise remained in hiding, but this measure proved to be of no special value. This depression was mapped in detail (Figs. 5 & 6) so that daily movements and social interactions could be charted.

Microenvironments of importance to iguanas at La Bajurita were sampled. Relative humidity was measured with a Bacharach sling psychrometer (code no. 12-7011), a portable 24-hour Serdex hygrothermograph (Bacharach code no. 22-7042), and a Weather-Measure seven-day hygrograph (model #H321). The latter two instruments, purchased by DNR, were available for use in conjunction with this project during March 1975 for six and two field days, respectively. Maximum and minimum temperature values were measured with Taylor self-registering max-min thermometers (code no. 5450).

Obtaining data on home range, activity periods, and migratory movements can be profitably approached on Mona through remote tracking with radio-telemetry equipment. Because of operational difficulties, however, only two iguanas were monitored using this technique. After one false start, preassembled transmitter collars were purchased from AVM Instrument Company (Champaign, Illinois 61820): Type D collar

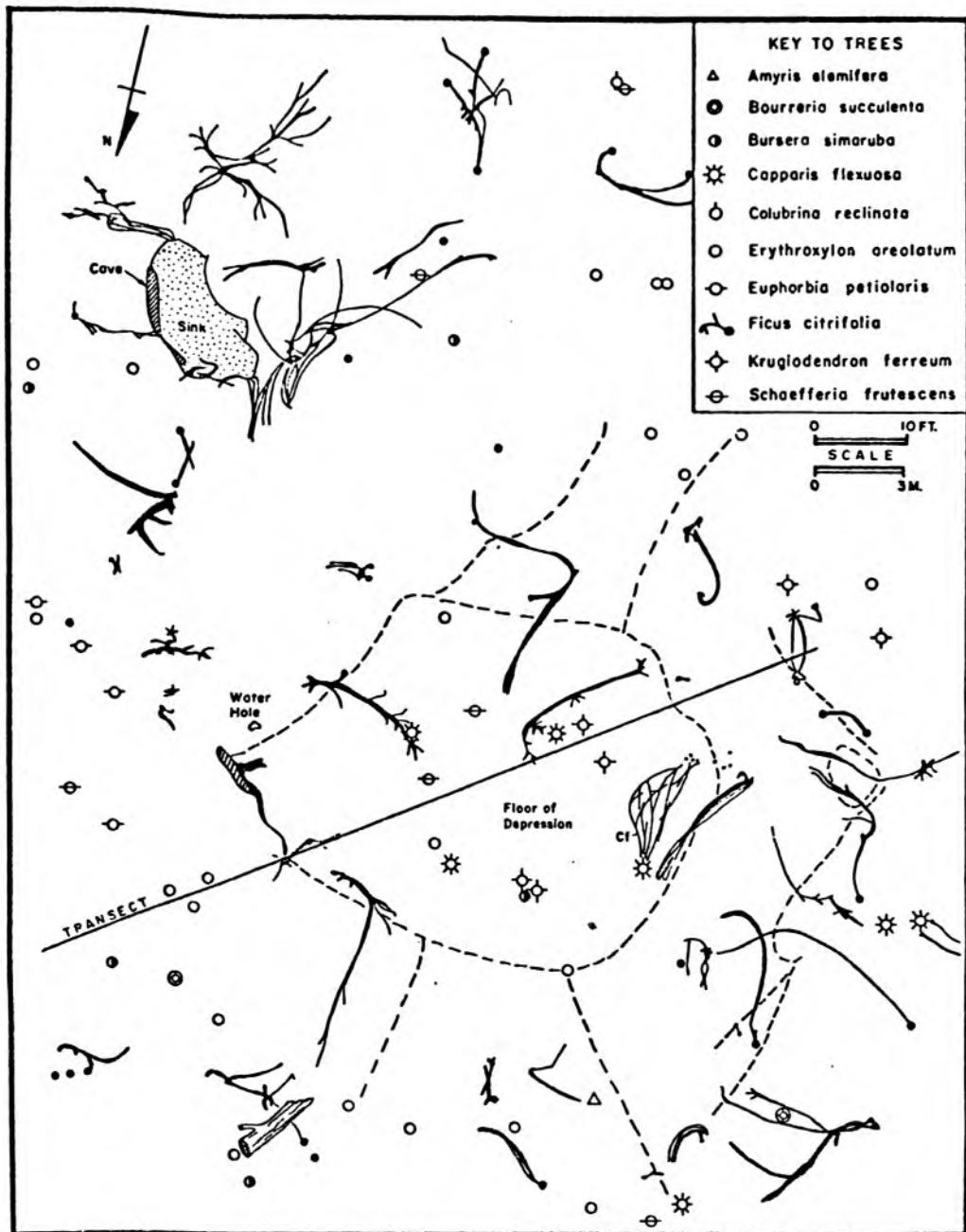


Fig. 5.--Map of a rocky inland depression study area, La Bajurita, on Mona I., P. R. Symbols for trees are not drawn to scale, except for the sprawling lines that represent *Ficus* trunks/roots. Broken lines indicate natural boundaries of geological features. See Fig. 6 for profile through transect.

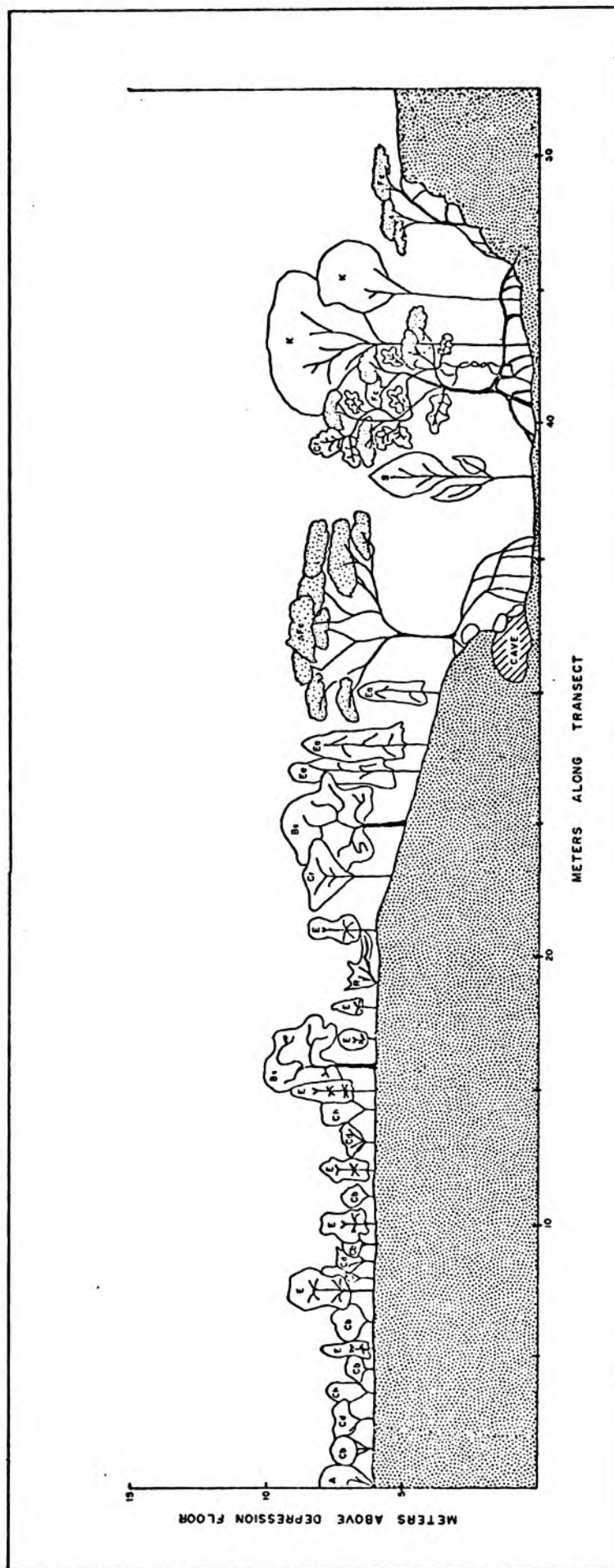


Fig. 6.--Profile of transect through the rocky inland depression La Bajurita, indicated in Fig. 5, on Mona Island, P. R. Key to trees and shrubs: A = *Antirrhoea acutata*; Bs = *Bursera simaruba*; Cb = *Croton betulinus*; Cd = *Croton discolor*; Cf = *Capparis flexuosa*; Ch = *Corchorus hirsutus*; Cr = *Colubrina reclinata*; E = *Euphorbia petiolaris*; Ea = *Erythroxylon areolatum*; Fc = *Ficus citrifolia*; Kf = *Krugiodendron ferreum*; R = *Reynosa uncinata*; S = *Schaefferia frutescens*. Sampling and illustration courtesy of B. Cintrón.

containing a brass loop antenna and transmitter SB2 with a frequency output in the 148.0-148.5 MHz range and powered by a 2.7V Power Conversion Model 400 lithium battery. Each collar weighed 65 g, and iguanas wearing them showed no signs of annoyance or skin abrasion. Collars are ideally suited for use on these lizards since the head musculature is exceptionally well developed, so the fit need not be tight to prevent it from slipping over the animal's head. Unfortunately, the batteries, with a four-month life expectancy, died after one month's operation.

The telemetry reception system consisted of a Drake SPR-4 Communications Receiver secured to a pack frame--total weight with batteries was 12.2 kg--and a two-element hand-held Yagi antenna for direction finding. Iguanas within a crevice could be located from a distance of 0.4 km through plateau forest, while those on the surface were detectable at 1.0 km.

Diet was evaluated by direct observation of iguanas foraging in the field, by analysis of 128 fecal samples, and by examining the stomach contents of three dead animals. Only fresh (moist) feces were collected, and these were immediately preserved in alcohol or formalin to kill detritivores in the sample. While some particularly soft food items like flower petals and fungi would be altered beyond recognition during digestion, iguanas do not masticate their food, and most items could be identified. Because some flower parts like the calyx, peduncle, and stamens are relatively resistant to digestion, even tiny flowers were often recognizable. Species represented in each sample were taped in a plant-press notebook of heavy drawing paper for future

reference and identification. When practical, the number of each item found was counted in totality; relative abundance was otherwise expressed as a subjective estimate of volume. Because samples were no more than a day or two old at the time of collection, seasonal changes in feeding habits could be evaluated as well. I developed a reference collection of fruits and seeds from the more common woody species and kept notes on their phenological patterns during the three years I was on Mona (Appendix II). Regrettably, much of the phenological data cannot be properly interpreted because of incomplete rainfall records; after the departure of regular Coast Guard personnel in August 1973 when the Mona light was automated, it was no longer possible to monitor rainfall on a continuous basis, particularly after the theft of the rain gauge.

To investigate nesting behavior, incubation conditions, hatching, and emergence of young, I focused my observations on one large nesting aggregation (S-14), monitored natural nest temperatures during incubation, excavated nests during and after emergence, and incubated several eggs artificially.

At study area S-14 on Cabo Oeste, I monitored nesting activities continuously throughout the duration of the 1973 season. Two blinds were constructed at the site, one of which was suspended from the trunk of a large Casuarina tree 3 m above the ground, providing a vantage point with a clear view of every nest in the vicinity. Daily observations were begun at 0830 hours (08h30), just before the iguanas moved

into the area to commence digging, and were terminated at dusk when they returned to retreats for the night. On several occasions, I left the blind for a short period in the afternoon when a prominent lull in activity occurred during the midday heat. Notes were dictated into a tape recorder and transcribed each evening.

Every new nest hole was flagged and numbered nightly so that covered nests could later be relocated. Stake markers positioned and angled near hole entrances indicated the location and direction of each nest tunnel. Thermistors on wire leads 1-3 m in length were tied to wooden stakes and planted in the egg chambers of four nests. Nests were opened and closed via the same passageway excavated by the female. Temperature readings were monitored on a homemade single-channel tele-thermometer. Thermistors and meter were calibrated together against a standard mercury thermometer in a water bath, and measurements are accurate to at least $\pm 0.5^{\circ}\text{C}$. Ambient substrate temperatures were measured in the top 1 cm of soil over the nest and air temperatures in the shade 1 m above.

In the field, hatching success was determined in three ways:

- 1) marked nests were excavated during or shortly after the hatching season; 2) escape holes dug by hatchlings were traced back to the nest chamber retaining egg shells, undeveloped eggs, and suffocated hatchlings and contents were counted; and 3) well preserved remains in old nests encountered while digging for new ones were examined. Nests one year or more old were often fresh-looking, but their age was evident from a growth of plant root fibers over the inner membrane of the egg shells.

While excavating marked nests, I encountered several that contained hatchlings digging their way out. These animals could be aged to the day of hatching in most cases by noting the extent to which the umbilical scar had closed. Freshly hatched young show a gaping umbilical scar which requires approximately three days to close (pers. obser.). Eggs and hatchlings were weighed with an Ohaus 0-250g spring-tension scale. Hatchlings and other juveniles captured during the course of the study were tagged with colored plastic button fasteners lodged under the skin on the neck (one on each side) with a "Buttoneer," a technique devised by Pough (1970) for use on snakes. Tags were found securely in place on one tagged juvenile recaptured nine months later.

Nine eggs were removed from nests in the field for observation and photographing during incubation and hatching. The first two, placed on slightly dampened sand in inflated plastic bags, developed mold within three weeks. The other seven, all incubated in a 5-gallon glass terrarium, survived and hatched successfully. I had placed these on a bed of clean (but not sterile) sand that felt dry (1-2% water, calculated as weight lost by drying/wet sample weight). Moisture was introduced by periodically wetting the upper surface of a sandstone slab supported several centimeters above the eggs. Sand was filled in around the stone, taking care not to bury the eggs, and where the straight edge of the stone rested against the glass, the eggs could be viewed. The top of the terrarium was then covered with aluminum foil. Temperature was maintained at 23-30°C.

All major aspects of the life history of the Mona Iguana were documented through 16mm motion picture (at 24 frames per second) and 35mm still photography. I shot 6700 ft. of movie footage (with a Beaulieu R-16 electric camera) of behavioral interactions during territorial defense, courtship, mating, and nesting. Displays were reviewed and analyzed with the aid of a Selecta-frame Stop Motion Projector (Traid Corporation, Glendale, Calif.), which permitted film study at variable speeds from 0-24 frames per second. Also, an official set of black-and-white aerial photos was available for reference to aid in the interpretation and evaluation of topographic features, distances, and areas.

In addition to the Mona study, I made short-term comparative observations on three other species of cycluran iguanas: C. n. nubila, an introduced population of Cuban Iguanas on Isla Magueyes, P.R., and C. cornuta and C. ricordi in the Dominican Republic. Two weeks were spent on Isla Magueyes (6-14 May 1972, 26-30 April 1974), with facilities provided by the University of Puerto Rico Department of Marine Sciences. The trip to the Dominican Republic (24 July - 13 August 1975) was sponsored by a grant from the New York Zoological Society to Walter Auffenberg. Measurements taken on field-caught C. cornuta were supplemented with data from iguanas housed at the National Zoological Park in Santo Domingo, courtesy of Jude Duvz1. Iguana specimens collected in the Dominican Republic were deposited in the herpetological collection at the Florida State Museum, while those from Mona were given to the American Museum of Natural History and Cornell University.

POPULATION DISTRIBUTION, SIZE, AND COMPOSITION

Distribution and Retreats:

Crossing Mona on foot, one can expect to encounter iguanas singly, at a rate approximating one animal per 1-2 km traversed. Because 90% of the island's surface area is a conspicuously homogeneous plateau environment dominated by short-tree forest (81%) and shrub (9%) communities (see Fig. 2 and Appendix I), it was possible to obtain census counts that I feel are representative for the iguana population as a whole. The most practical means found for indexing relative abundance was making direct counts while walking routes of known distance. About 63 km of roads, trails (shown in Fig. 1), and cross-country routes on the plateau (including its entire periphery) were censused in 1972-1973, many stretches of which were covered several times and the counts averaged to strengthen the data. Census counts were taken at all hours of the day when iguanas were active, during all seasons (except mid-July - mid-August when nesting was in progress), and included all size classes. No spatial segregation between juveniles and adults or between males and females was evident.

Sighting frequency on the plateau averaged 0.8 iguanas/km, except on routes along major escarpments and cliffside talus slopes, where iguanas were three to four times more common. In these areas (<5% of Mona's surface), conditions are more mesic, there is a greater abundance and diversity of retreats, and individuals living in these ecotone zones

benefit by having a wide variety of food plants to choose from in a small home range.

In contrast, iguanas were rare on much of the southwestern coastal plain, presumably because natural shelter is scarce and roughly half of the area has been cleared and reforested in trees of no value to the iguanas, i.e., they shade-out most understory vegetation and bear inedible fruits. Iguana density rose dramatically there, however, during the nesting season when many females migrated to unshaded, sandy portions of this wide coastal terrace to nest (see Nesting Biology).

To estimate overall population size and density, I have assumed that 1) my census figures are representative for the island as a whole and 2) a walking observer can, on the average, sight iguanas within a 10-14 m radius. This gives a mean density of 0.33 iguanas/ha (0.132 iguanas/acre) and a total population size of approximately 2000. Because activity patterns are to a great extent asynchronous in this species (see Daily and Seasonal Activities), the population could conceivably number twice this size. I therefore consider 2000 a conservative estimate and 4000 liberal, placing the density at about 1 iguana/2 ha.

Natural cavities or crevices in the limestone are utilized as retreats. Many are occupied by individuals while others are shared communally. Most appear to permit the occupant(s) to lie in a nearly horizontal position on bare rock 1-2 m inside the entrance, which is often little wider than the animal itself. Iguanas never dig their own retreats on Mona, though some enlarge existing crevices by clearing away

soil accumulated beneath boulders or limestone outcrops. These lizards often roam the twilight zone of the island's large caves but apparently do not venture into total darkness. Iguanas frequenting caves typically retire to shelter within sinkhole rubble or under stalagmites. Though I once observed a juvenile climb about 4 m up a large, dead, hollow Erythroxylon areolatum tree to bask on a limb in the late afternoon sun, I have never seen a tree hole serving as a retreat on Mona.

Because most Mona Iguanas apparently spend a significant portion of their lives underground, this microenvironment deserves special consideration. Caves and crevices on the island are not equally attractive to iguanas, so I examined the living conditions in one cave-crevice system (Fig. 7) that could be conveniently studied and was heavily utilized by several iguanas year-round. The cave is crescent-shaped, 3-4 m deep, 21 m long, and has enlarged openings at both ends (see Fig. 5). The associated network of overhead cavities used as retreats is well drained and apparently better ventilated than most crevices. Iguanas always chose resting sites within 1.5 m of the surface.

The site had the special advantage of having a lower passageway large enough to permit me to monitor the microclimate of the lizards' retreat from below. During three days of continuous recording of relative humidity and air temperature next to a sleeping iguana in mid-March 1975 (Point A in Fig. 7), the humidity fluctuated between 76% and 91%, while temperature remained nearly constant, ranging from 22.8°C to 23.3°C. Throughout the following three days (under similar weather conditions, i.e., clear mornings and partly cloudy afternoons) the

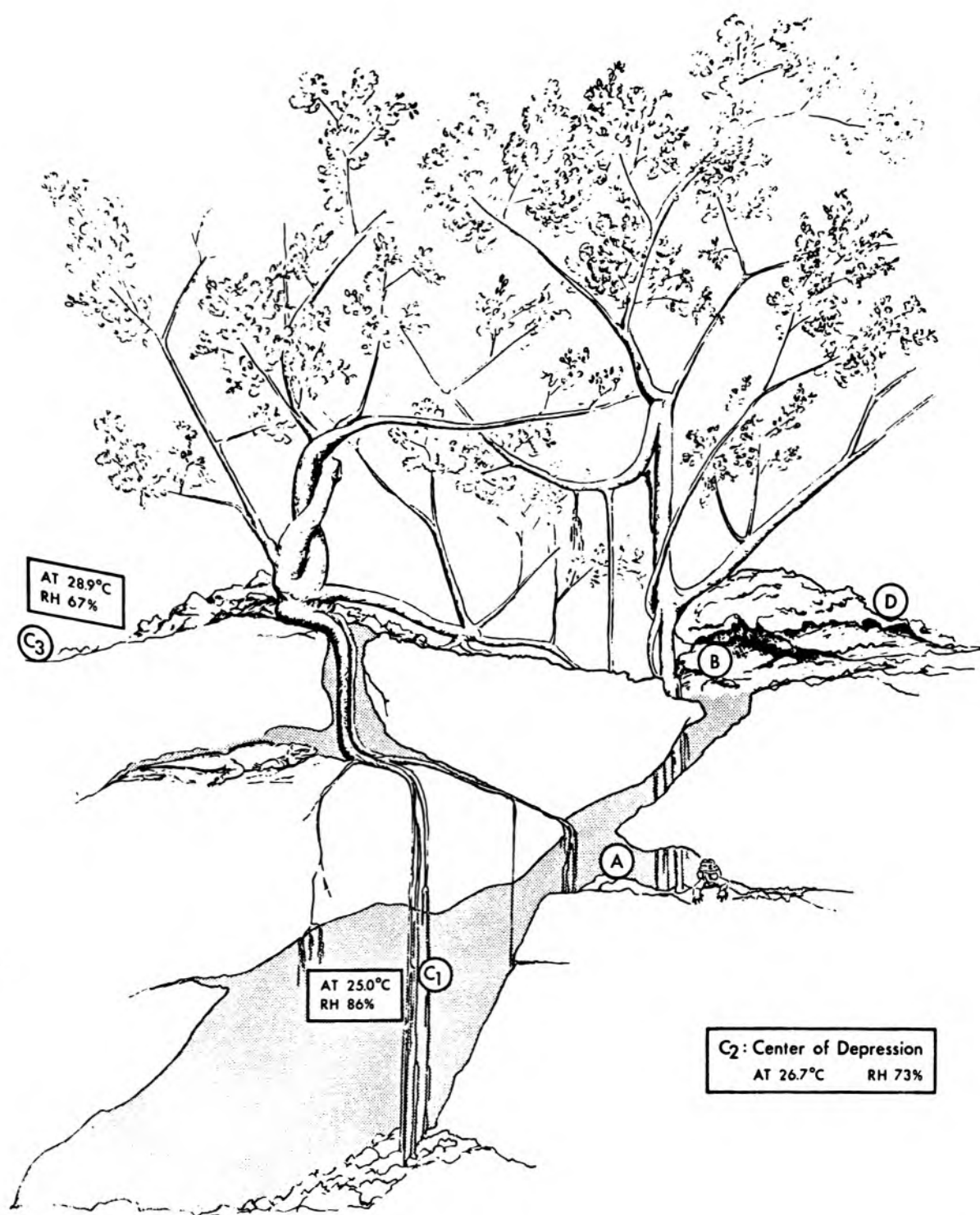


Fig. 7.--Cross-section through the Fig Row retreat complex at La Bajurita study area, Mona I., P. R. Ambient conditions were monitored at points A-D (see text). Representative mid-afternoon shaded air temperatures and relative humidity readings taken only minutes apart at three sites on 1 April 1975 are shown at points C₁, C₂, and C₃.

Table 4.-- Maximum-minimum temperature readings taken over a 10-month period in a cave retreat heavily utilized by iguanas at La Bajurita study area, Mona Island, P.R. Measurements are accurate to the nearest 0.5° C.

Time Period	Max	Min	ΔT (Max-Min)
30 May 1974 - 17 June 1974	27.5	26.0	1.5
17 June 1974 - 26 June 1974	28.0	25.5	2.5
26 June 1974 - 5 July 1974	29.0	26.5	2.5
5 July 1974 - 2 August 1974	29.0	26.0	3.0
2 August 1974 - 1 February 1975	30.0	23.0	7.0
1 February 1975 - 9 March 1975	26.0	23.5	2.5
9 March 1975 - 1 April 1975	25.5	23.0	2.5

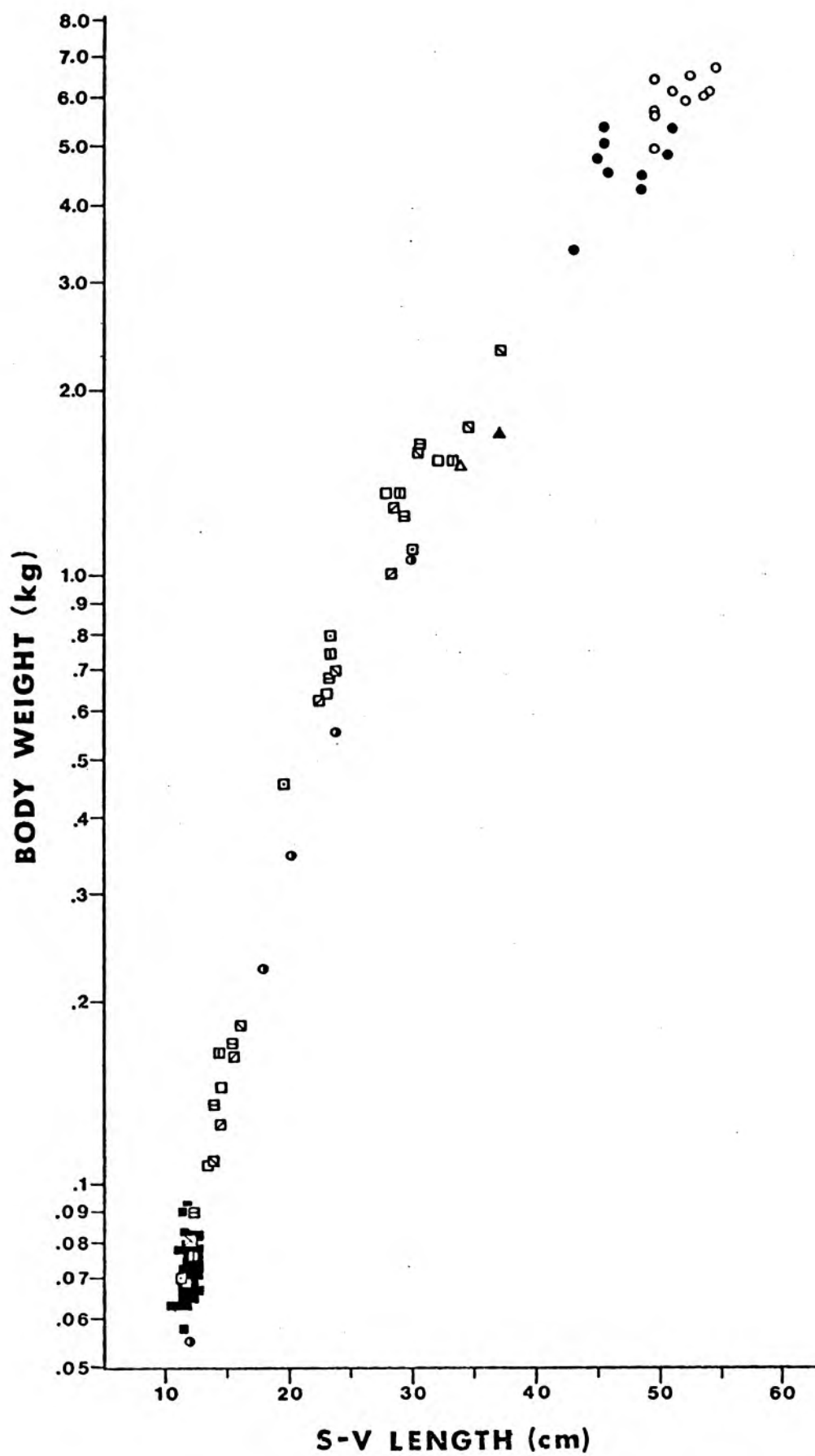
hygrothermograph was positioned on a rock outside the retreat (Point B in Fig. 7). Here, the range in relative humidity remained the same as within the cavity; temperature, however, fluctuated between 21.1°C and 25.6°C . A set of representative mid-afternoon measurements taken only minutes apart at different sites (C_1 , C_2 , and C_3) on 1 April 1975 are also given in Fig. 7. All measurements except those at C_1 were taken in the shade at "iguana-level," i.e., about 15 cm above the substrate.

A maximum-minimum thermometer tied to the Ficus roots at Point C_1 was left underground for 10 consecutive months, including those when annual high and low temperatures would normally occur (Table 4). Cave temperature varied through a 7.0°C range (23.0°C – 30.0°C), approximately half the expected annual fluctuation in ambient temperature. A second max-min thermometer, located outside the cave at Point D, was left in a shaded location 15 cm above ground for five weeks (30 May – 5 July 1974). It registered a 7.5°C variation between high and low readings, while during the same period the cave environment fluctuated only 3.5°C , 3.0°C below the ambient high of 32.0°C and 1.0°C above the ambient low of 24.5°C .

Growth and Population Structure:

Size and growth data were obtained from animals taken in the field or maintained in captivity (Figs. 8, 9 and 10). Only four juveniles at least three months of age were captured, the largest of which was recaptured nine months later. Because egg predation by feral pigs was unusually low in 1972, hatching success was high, and 54 hatchlings from nine different marked nests were intercepted before they had escaped

Fig. 8.--Scatter diagram for body length (snout-vent) and weight of iguanas from Mona I., P. R. Circles represent field-caught adult males (open circles), adult females (solid circles), and juveniles (semi-solid circles). Measurements for 52 hatchlings taken from nine different nests fall within the cluster of squares in the lower left corner. Six of the hatchlings (open squares with individualized marks) are being reared in captivity at the San Diego Zoo. An immature female (solid triangle) and a male (open triangle) C. cornuta from the Dominican Republic are included.



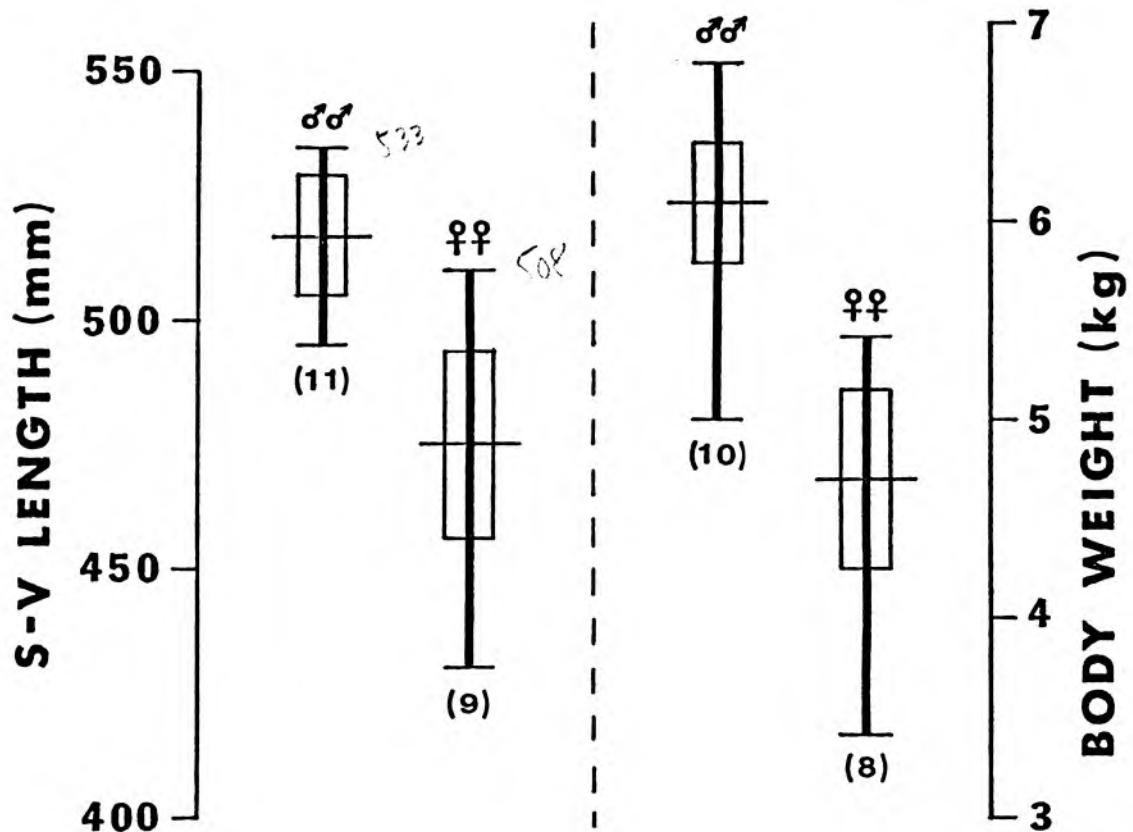


Fig. 9.--Body length and weight comparisons for adult male and female iguanas captured on Mona I., P. R. Sample size (in parentheses), range, mean, and twice the standard error on either side of the mean (bar) are shown.

from the nest chamber. Five more "nestlings" were taken the following year, and seven eggs were successfully hatched in a terrarium. Forty-four were tagged and all released except two hatchlings kept in captivity on Mona and eight donated to the San Diego Zoological Park on the condition that the animals be regularly weighed and measured to facilitate comparisons with field-caught juveniles.

At the time of this writing, six of the eight hatchlings at the SDZ were still alive, all apparently in excellent physical condition. The two deaths occurred 3.4 and 4.2 months after hatching. For the first 18 months the iguanas were maintained indoors in an elevated cage on wheels that could be rolled into the patio of the reptile house on warm days to give the animals sunshine. The indoor relative humidity remained at approximately 70% and the temperature 26-29°C, 24 hours a day. In May 1974, they were moved to an open outdoor enclosure and since then have been kept outside between May and October and indoors between November and May (T. Schultz, pers. comm.). Their usual diet of a mixed fruit and vegetable salad offered three times per week has been supplemented once weekly with mice. The iguanas have been fed mice ever since their arrival at the zoo, with the size of the mice provided increased as they grow. Thus far no vitamin supplementation has been given, however, bone meal is sprinkled over their salad tray regularly (J. Bacon, pers. comm.).

The SDZ juveniles, now in their fifth year, have not yet begun nesting, although one mating was seen last summer (July 1976, J. Bacon, pers. comm.). This observation suggests that at least one of the males

has already reached sexual maturity but that the females are still immature. This mating may have been forced, the recipient not having an escape route under captive conditions. Social interactions of these iguanas are now being studied by Susan L. Keller, a graduate student at San Diego State College.

Like the Anegada Ground Iguana (C. pinguis), female Mona Iguanas apparently attain sexual maturity between 35 and 40 cm snout-vent length (SVL)--see Fig. 8 and Carey, 1975. The species are similar in adult body size and weight. Although no C. stejnegeri in the 30-43 cm SVL range were captured on Mona, of more than 100 gravid females observed at nesting areas, the smallest was filmed and estimated through subsequent size comparisons to have been between 38 and 40 cm SVL. This young female laid only six eggs, with a five-egg clutch being the smallest found among 42 clutches examined. Two Rhinoceros Iguanas (C. cornuta, another species with adult size comparable to C. stejnegeri) captured in the Dominican Republic, fell in the 34-37 cm size range. The larger of the two, a female (FSM 33650) was immature; femoral pores of the male were clearly enlarged and secreting, but this individual was not dissected and its reproductive condition undetermined. Three of the six SDZ juveniles had already acquired enlarged, secreting femoral pores by the end of their third year, at 27.9-31.1 cm SVL, the first sign of their sexual differentiation (J. Bacon, pers. comm.). Femoral pores began enlarging in a fourth, the smallest of the six at the onset of its fifth year, at 28.5 cm SVL (J. Bacon, pers. comm.).

A growth rate for C. stejnegeri in the wild is estimated from

comparisons between the growth curves of captive iguanas and size measurements of field animals (Fig. 10). Included are the six SDZ hatchlings, the two captives kept on Mona (one of which escaped during its fourth month), and the six field animals at least six months in age but measuring less than 31 cm SVL. In approximating the age of field animals, I have made two assumptions: 1) that all hatched in October or early November, a proposition supported by three years of personal observations (1972-1974) plus knowledge of nesting times for 1976 (pers. obser.), 1975 (Lee Rogers, pers. comm.), and 1962-1965 (L.A. "Chin" Ramirez, personal field notes); and 2) that size at hatching was close to 11.9 cm SVL ($N=65$, range = 10.5-12.7 cm, $s=0.5$ cm).

Initial growth of Mona Iguanas is slow during their first year of life. Young are well supplied with yolk at hatching and show little interest in plant or animal food during their first month. Four iguanas observed in the field and presumed to be 4-6 mos. old all appeared similar in size to newly emerged hatchlings, suggesting that little, if any, growth occurs at this time. In 1974, a hatchling 6-7 months of age was captured near the talus slope adjacent to the airstrip--this animal was very thin but alert, was only 12.0 cm SVL, and weighed 57 g, less than any of the 65 "nestlings" measured. Similar results were obtained from the hatchlings kept on Mona, which were fed a variety of native fruits, flowers, and insects. The zoo records also showed a trend towards slow growth during the first year. Though these data from field and captive situations are consistent, different causes may have produced the same effect. On the one hand, the iguanas may have had

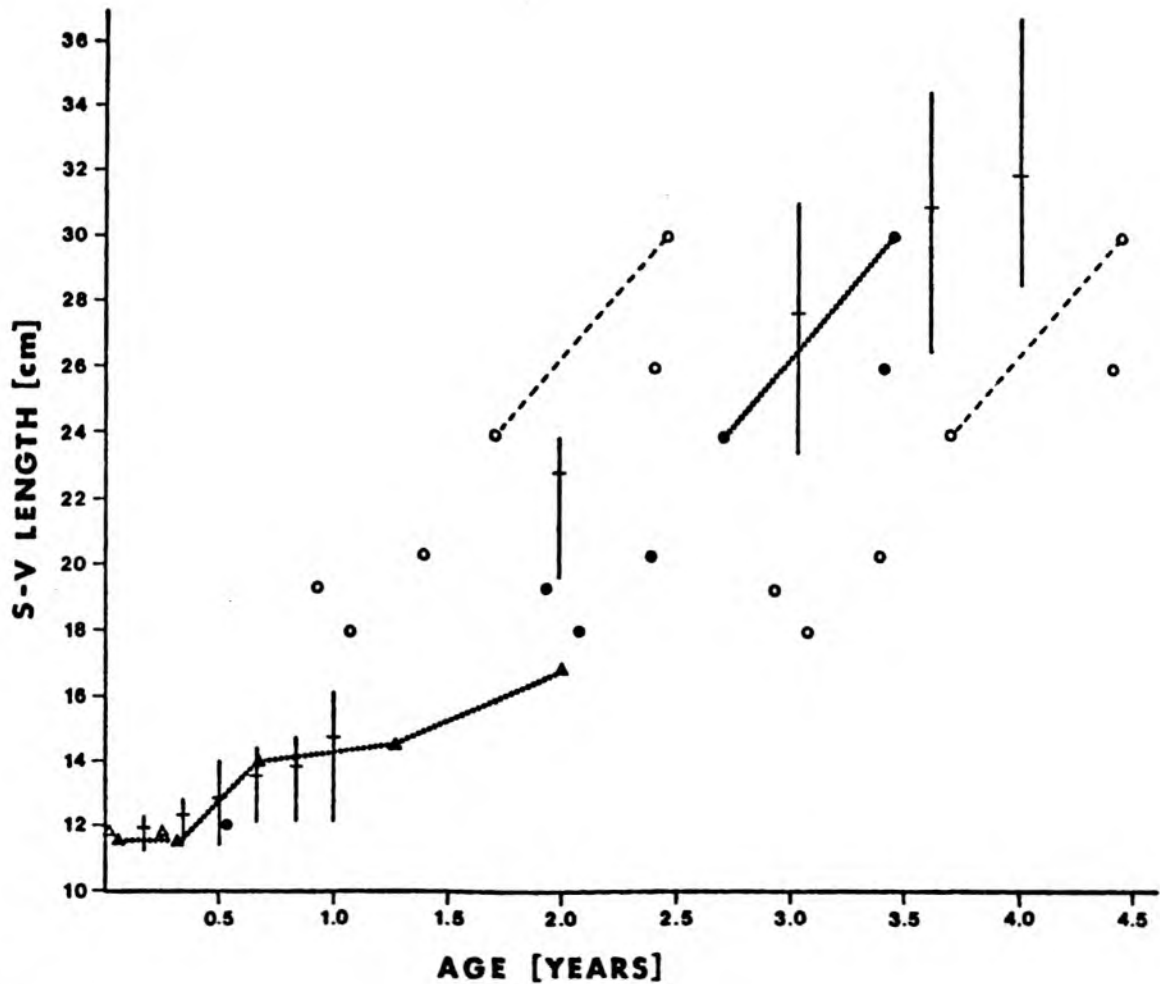


Fig. 10.--Growth curves for Mona Iguanas reared in captivity relative to growth potential suggested by measurements of field-caught juveniles older than six months in age. Vertical bars represent the size ranges of six juveniles in the same cohort at the San Diego Zoo, the crosses indicating mean values. Triangles are animals maintained in captivity on Mona. Circles are field animals of unknown age; each is plotted three times to represent the different age classes to which they might belong, the most probable distribution shown as solid circles. The two connected dots represent the only recapture.

difficulty adjusting to some aspect of captivity; while on the other, their predominantly herbivorous habits and apparently erratic activity patterns (to be discussed), combined with the fact that these lizards must endure the spring dry season roughly two months after emerging from the nest, are factors that could influence growth significantly in the field.

Deriving a realistic estimate of growth rate in a wild lizard population from records for captives can be problematical. One would expect growth spurts to characterize the development pattern in field animals, with rapid growth occurring during times when forage is optimal and little or no growth occurring when conditions favor inactivity. The zoo animals, on the other hand, should be growing at a rapid and relatively steady rate, for they have been provided a high-protein diet and maintained in a thermal and social environment that favors daily activity. Illustrating the effect that a change in diet can make, Mayhew (1963) found a three-fold increase in growth rate when a juvenile chuckwalla, Sauromalus obesus, switched from flowers to Tenebrio larvae. Regal (1971) has clearly demonstrated that dominant lizards caged together with conspecifics maintain (through behavioral thermoregulation) higher activity temperatures than they do under isolated conditions. An overall increase in metabolic rate, a greater demand for food, and accelerated growth would be anticipated in situations where a lizard that is normally asocial in habit is kept in a close social group. Growth inhibition in subdominant individuals would also be expected. It is noteworthy that at the onset of its fourth year, the smallest of the

six zoo animals, though robust and healthy, had fallen a full year behind the growth attained by the largest member of the group (see Fig. 10).

At the end of three years in captivity, the SDZ juveniles had grown at an average rate of 52.3 mm/year, which appears to be a close approximation of the maximum growth rate in the wild population. In plotting the six data points in Fig. 10 for field animals between 18-30 cm SVL, I have represented each at 12-month intervals in the three most probable age classes. Growth achieved in nine months by the one individual which was recaptured indicates a natural growth rate nearly identical to the most rapid growth of captive animals. This is in all likelihood a growth spurt, for during that nine-month period, caterpillars of the Sphingid moth Pseudosphinx tetrio underwent a population explosion (see Foraging Behavior & Diet). These larvae are eagerly sought when available; and when initially captured, this juvenile had been feeding on them. Under normal field conditions, Mona Iguanas probably develop at an overall rate not exceeding that suggested by the middle set of points (dots) in Fig. 10.

Assuming that maturity is attained at a body size of approximately 38 cm, female Mona iguanas would not enter the breeding population before their fifth summer. Allowing for periods unfavorable for growth, six or seven prereproductive years is presumably a more realistic estimate. Growth determinations by Fitch (1973a) for Ctenosaura similis and by Berry (1974) for Sauromalus obesus suggest that a wide range of individual variation would also be expected.

During three years of field work, I encountered only 30 different juveniles three months old or more but smaller than about 90 cm overall length. Four of these juveniles were captured for measuring and weighing. Two others were measured in the field by noting reference points on the rock substrate where the animals were lying and later measuring those distances. When necessary, size was subjectively estimated, and all 30 juveniles were assigned to one of four classes: A) 32-38 cm (N=8), B) 38-48 cm (N=7), C) 48-65 cm (N=6), and D) 65-90 cm (N=9) in overall length. Each group was scaled to correct for inequalities in the size ranges represented, yielding a relative frequency distribution of 1 : 0.7 : 0.4 : 0.4. These data suggest heavy losses from the two smallest size classes, as expected; nevertheless, no meaningful inferences concerning survivorship can be drawn, since the annual recruitment of hatchlings into the population fluctuates considerably because of differential egg loss to predation by pigs (see Associations with Man & Other Animals).

Census counts indicate that immature iguanas constitute 5-10% of the Mona population. Two island-wide censuses taken in 1972 and 1973 (both from mid-May to mid-October) over established trails and cross-country and coastal routes produced flush counts of 80 and 106 iguanas, respectively, 10% and 6% of which were juveniles. Of 37 iguanas positively identified as different individuals at La Bajurita during a total of 521 hours of observation time at that locality (mostly spent quietly sitting and watching), only two animals sighted (5%) were small enough to be considered immature.

Males were sighted more frequently than females on Mona, but this may largely be due to the fact that females are the more wary sex and are consequently less evident. Whenever a pair was encountered, the female was invariably the first to retreat. Even at night, in cases when I have found male and female sleeping under the stars side by side, the female was the first to awaken and flee for cover. During 70 observation periods in the non-nesting season at La Bajurita, an average of 6.06 males (49%), 3.50 females (28%), and 2.75 unidentified individuals (22%) were sighted (Table 5). In nine of the 70 census samples, the number of females equalled or exceeded the number of males seen. Those in the "unidentified" lot were largely timid animals; therefore, most were probably females, so the sex ratio may actually be nearly equal in that area.

Tail length relative to overall length changes ontogenetically in C. stejnegeri. In hatchlings, 60-65% of the animal's total length is tail (N=61), and the proportion drops to 50-58% in adults (N=15, without broken or regenerated tails: seven males, range 50-56%; eight females, range 53-58%). The incidence of broken, regenerating tails was more than three times greater in males than females sampled (12 of 24 = 50% vs. 6 of 42 = 14%). Most tail-breaks in this population presumably come from agonistic encounters (see Territoriality, Courtship, & Mating), suggesting that today competitive strife is considerably more intense among males than females.

Records from 19 paint-marked iguanas watched between June 1973 and July 1974 suggest that one complete molt per year is the norm for adult

Table 5.-- Summary of iguana sightings at La Bajurita study area on Mona Island, P.R., made between 9 November 1973 and 7 July 1974.

Month	No. of Observation Periods	Mean No. of Iguanas Sighted			Total
		Males	Females	Unidentified	
Nov.	6	5.17	2.0	2.83	10.0
Dec.	2	7.0	2.5	2.0	11.5
Jan.	4	6.25	2.0	2.0	10.25
Feb.	4	5.25	3.75	3.75	12.75
Mar.	4	7.0	5.25	5.5	17.75
Apr.	8	6.63	3.75	2.37	12.75
May	14	6.64	3.71	2.0	12.36
June	24	7.58	4.08	2.08	13.75
July	4	3.0	4.5	2.25	9.75
Total		54.52	31.54	24.78	110.86
Overall \bar{x}		6.06	3.50	2.75	12.31

$\chi^2 = 3.97$, $.1 < \beta < .2$ (monthly mean totals compared);

$\chi^2 = 1.39$, $\beta < .01$ (same as above but less values for 7 and 9 March--see text)

iguanas on Mona. Although some molting was observed at all times throughout the year, most occurred in September to October, within the period of highest annual rainfall and food availability.

Discussion:

Retreat Utilization.--West Indian ground iguanas are somewhat opportunistic and utilize a variety of retreat possibilities, varying with the ecological and geological setting. I noted in the Dominican Republic, for example, that in regions where the terrain is well mantled with sandy soil and natural cavities and crevices are few, C. cornuta live in self-excavated burrows, especially along arroyo banks. In poorly drained flatlands in Haiti (disturbed and seemingly marginal habitat today), C. cornuta seek shelter off the ground among closely grouped arms of giant columnar cacti (P. Meylan, pers. comm.). In the Dominican Republic, C. ricordi inhabit self-dug burrows, limestone cavities, and tree holes (Wiewandt & Gicca, pers. obser.); most apparently dig burrows, possibly the outcome of interspecific competition with C. cornuta, for in areas of sympatry, the latter species was found in the more rocky subhabitats. Reduced risk of being trapped within a collapsed burrow is one obvious factor that could select for preferential use of rock crevices and tree holes when available. Gosse (1848) found a number of adult and juvenile C. collei in Jamaica sheltering communally in hollow trees (though juveniles were apparently segregated from adults) but did not state whether alternative retreats were available in the area. Similarly, Grant (1940) reported finding some C. nubila caymanensis in tree cavities.

A retreat offers an iguana three important potential benefits: 1) physical protection from predators, 2) escape from pursuit by conspecifics, and 3) an option to avoid environmental extremes. Because of their small size, juvenile Mona Iguanas are especially vulnerable to predators and may profit from the protective cover provided by retreats; mature individuals, on the other hand, are not subject to natural predation. Man's presence on Mona has been a threat to adult iguanas, yet assuredly of minor significance to animals inhabiting the more remote portions of the island. I assume then, that "retreat-seeking" behavior in adults is primarily an adaptive response to the animals' social and/or physiological needs, a contention supported by the fact that adults often pass the night sleeping on the ground in exposed locations. (The role of retreats in the social behavior of the Mona Iguana is discussed later as it relates to interactions between conspecifics.)

Status of the Mona Population.--Two lines of demographic evidence suggest that the present density of iguanas on Mona is unnaturally low and may be decreasing. First, though it appears unlikely that any of the extant populations of cycluran iguanas are in a state of natural equilibrium today, biomass levels of other Cyclura which have been studied recently are unquestionably higher than that of C. stejnegeri. Most of these data have been tabulated by Iverson (1977) and show that the biomass of Mona's population is approximately one order of magnitude below what might be expected. All species live under similar ecological conditions. To cite one specific comparison, drawn from a population of C. cornuta (having adult body size similar to C. stejnegeri), P. Meylan

(pers. comm.) observed a solitary adult under every clump of vegetation on tiny Ile Petite Gonâve, Haiti, giving a minimum density figure of 13 adults/ha, about 26 times greater than what I found on Mona. Petite Gonâve is evidently one of the few locations in Haiti where iguanas have not been harassed by man through regular hunting or deforestation, although domestic pigs and goats now have unrestricted range on the island and no juvenile iguanas were sighted.

Second, the Mona Iguana population has an apparent relative scarcity of immature animals, a feature that suggests senescence and declining density. Because of their smaller size and greater propensity for climbing, one would expect juvenile iguanas to be under-represented in any census sample. Nevertheless, for a number of reasons, I feel that my infrequent sightings of prereproductive animals reflect more than sampling error: Like adults, juveniles are active during daylight hours when they can be most easily seen. Five juveniles which I observed at length spent most of their time on the ground, and those seen climbing or feeding in shrubs or trees were conspicuous when doing so. Also, only hatchlings tend to be noticeably more wary than adults.

There are sound historical reasons for believing that Mona's iguanas have been adversely affected by man, dating back to land-use practices of Pre-Columbian Indians and continuing to the present. The animal's life cycle has been seriously disrupted during nesting and incubation. This and related problems are presented in detail in the last chapter.

Longevity.--Though we presently have no meaningful longevity records or

reliable techniques for determining age, Mona Iguanas and perhaps all species of Cyclura are probably among the longest lived lizards in the world. Due to the impoverished nature of insular faunas, the intensity of predation (excluding alterations by man) is unquestionably less than in nearby mainland areas. While juveniles have remained subject to predation from birds or snakes, all the larger species of cycluran iguanas, including C. stejnegeri, have no native predators to fear as adults. The physical environment is also a moderate one. Such ecological conditions not only optimize a lizard's chances to realize its potential life expectancy but also permit the slow life-style and relatively slow growth characteristic of the Mona Iguana. These features are strongly correlated with increased longevity in animals (see Comfort, 1961). Carey (1975) met an experienced Anegada "woodsman" in his sixties who was acquainted with several individually recognizable Cyclura pinguis that had occupied the same retreats for at least 40-50 years. I suspect that mature iguanas on Mona often exceed 40 years in life span and perhaps sometimes reach twice that age.

FORAGING BEHAVIOR AND DIET

Miscellaneous notes in the literature suggest that all cycluran iguanas are omnivorous herbivores (see Carey, 1975). No one, however, has taken a close look at what these lizards eat and when they eat it, relative to the food resources available in a particular habitat. Many aspects of an animal's behavioral biology and demography can only be appreciated through a knowledge of food habits, also basic to any management program. I have therefore examined seasonal, geographic, and ontogenetic variables as determinants of diet in Mona's iguanas. These considerations were broadened in scope and aided tremendously by a simultaneous field project conducted by Barbara Cintrón and Lee Rogers (1974) to survey and map the island's plant communities.

In addition to many observations of foraging in the field, 118 fresh scats from adult iguanas and the contents of two stomachs were analyzed. The scat samples were not collected island-wide; most came from Mona's eastern side, where all of the island's natural plant communities occur in relatively close proximity. Thirty-five samples were collected at one depression, La Bajurita, over a 12-month period. The others came from a variety of plant associations and geographic areas: Cliffside/Coastal Lowland Forest of the southeastern terrace. between Cueva del Lirio and Cueva de la Escalera (N=23) and of the southwestern terrace in the vicinity of Uvero (N=7); Plateau Shrub/Cactus, Low Shrub near the eastern and northeastern cliffside (N=32); Plateau Forest/Depression Forest on El Camino del Infierno (N=18) and within and around El Corral de los Indios (N=10). The dominant flora encountered

in transects through each of these plant associations is given in Appendix I, with notations of which species and which vegetative parts were eaten by iguanas. For the complete floral analyses of transects including density and frequency data, the reader should consult Cintrón & Rogers (1974).

A total of 71 plant species (Table 6) and less than a dozen animal species (Table 8) were found in the adult iguanas' diet. Of the plant material, grasses, sedges, and cacti were poorly represented, as were the leaves of most abundant shrubs and trees. Only three leaf-types appeared consistently in samples from all areas throughout the year: Capparis flexuosa, a sprawling woody liana/shrub with moderately large, heavy and rather brittle non-aromatic leaves; and two legumes, Centrosema virginiana and Galactia dubia, both herbaceous vines with thin leaves. Of the 12 species eaten in greatest quantity and regularity, i.e., ranks L_1 - L_3 in Table 6, seven (58%) fall in the grass, herb, or succulent categories.

The number of plant species per sample ranged from one to 12. Excluding scats containing animal matter or a significant percentage of flowers, 28 samples were predominantly leaves and 47 were predominantly fruits, with the mean number of species per sample 5.2 and 1.6, respectively. No difference in size was evident between fruit- and leaf-containing scats. Because fecal droppings were collected "at random," i.e., whenever there was an opportunity to get fresh samples, regardless of season or locality, the relative importance of fruit in the diet of these animals is clearly great. When fruits were readily available, they were taken to the near exclusion of leaves.

Table 6.-- Plants in the diet of adult Mona Iguanas, determined through analysis of 118 scats and 2 stomachs, plus field observations.

Species	Family	Growth Form ¹
LEAVES:		
L ₁ Species: Frequently represented as >1/3 of leaves in sample		
<u>Capparis flexuosa</u>	Capparidaceae	WV/AS
<u>Centrosema virginiana</u>	Fabaceae	H
<u>Galactia dubia</u>	Fabaceae	H
L ₂ Species: Represented as >1/3 of leaves in 1-3 samples and a common item in lesser amounts in other samples		
<u>Coccoloba microstachya</u>	Polygonaceae	T
<u>Commelina virginica</u>	Commelinaceae	H
<u>Desmodium mollis</u>	Fabaceae	H
<u>Paspalum glabrum</u>	Poaceae	G
<u>Plumeria obtusa</u>	Apocynaceae	AS
<u>Portulaca</u> spp.	Portulacaceae	SuH
<u>Tephrosia cinerea</u>	Fabaceae	H
L ₃ Species: Frequently represented as >1/3 of leaves in sample but seasonal or localized in occurrence		
<u>Corchorus hirsutus</u> (seasonal)	Tiliaceae	S
<u>Jacquinia arborea</u> (localized)	Theophrastaceae	AS
L ₄ Species: Represented as >1/3 of leaves in one sample, but not found in more than two other samples		
<u>Capparis cynophallophora</u>	Capparidaceae	T
<u>Chamaesyce prostrata</u>	Euphorbiaceae	H
<u>Hippomane mancinella</u>	Euphorbiaceae	T
<u>Rauwolfia tetraphylla</u>	Apocynaceae	T
<u>Tabebuia heterophylla</u>	Bignoniaceae	T

Table 6 (Continued)

Species	Family	Growth Form ¹
L ₅ Species: Often represented in small amounts, but never found in quantities >1/3 of leaves in sample		
<u>Antirrhea acutata</u>	Rubiaceae	S
<u>Coccoloba diversifolia</u>	Polygonaceae	T
<u>Croton discolor</u>	Euphorbiaceae	S
<u>Eupatorium corymbosum</u>	Compositae	SuS
<u>Gyminda latifolia</u>	Celastraceae	T
<u>Krugiodendron ferreum</u>	Rhamnaceae	T
<u>Reynosa uncinata</u>	Rhamnaceae	S
<u>Stigmaphyllon periplocifolium</u>	Malpighiaceae	WV
<u>Stylosanthes hamata</u> (localized)	Fabaceae	H
<u>Sarcomphalus taylori</u>	Rhamnaceae	T
L ₆ Species: Represented, though not in quantity or with regularity		
<u>Bourreria succulenta</u>	Boraginaceae	T
<u>Croton humilis</u>	Euphorbiaceae	S
<u>Erithalis fruticosa</u>	Rubiaceae	AS
<u>Erythroxylon areolatum</u>	Erythroxylaceae	T
<u>Eugenia maleolens</u>	Myrtaceae	T
<u>Euphorbia petiolaris</u>	Euphorbiaceae	T
<u>Gayoides crispum</u>	Malvaceae	H
<u>Hypelate trifoliata</u>	Sapindaceae	T
<u>Indigophora suffruticosa</u>	Fabaceae	S
<u>Jacquemontia pentantha</u>	Convolvulaceae	H
<u>Lantana involucrata</u>	Verbenaceae	S
<u>Cynanchium lineare</u>	Asclepiadaceae	H
<u>Cynanchium monensis</u>	Asclepiadaceae	H
<u>Panicum maximum</u>	Poaceae	G
<u>Paspalum cespitosum</u>	Poaceae	G
<u>Pisonia albida</u>	Nyctaginaceae	T

Table 6 (Continued)

Species	Family	Growth Form ¹
L ₆ Species (Continued)		
<u>Schaefferia frutescens</u>	Celastraceae	T
<u>Sida acuminata</u>	Malvaceae	H
<u>Sida glabra</u>	Malvaceae	H
<u>Stachytarpheta jamaicensis</u>	Verbenaceae	S
<u>Torrubia discolor</u>	Nyctaginaceae	T
<u>Tournefortia microphylla</u>	Boraginaceae	S
L ₇ Species: Represented by field observations only		
<u>Argythamnia candicans</u>	Euphorbiaceae	S
<u>Boerhaavia diffusa</u>	Nyctaginaceae	H
<u>Boerhaavia erecta</u> (localized)	Nyctaginaceae	H
<u>Callisia repens</u>	Commelinaceae	H
<u>Capraria biflora</u>	Scrophulariaceae	H
<u>Croton betulinus</u>	Euphorbiaceae	S
<u>Ipomoea triloba</u> (localized)	Convolvulaceae	H
<u>Opuntia dillenii</u>	Cactaceae	C
<u>Rivinia humilis</u> (localized)	Phytolaccaceae	H
FLOWERS:		
<u>Antirrhea acutata</u>	Rubiaceae	S
<u>Caesalpineia divergens</u>	Fabaceae	S
<u>Capparis flexuosa</u>	Capparidaceae	WV
<u>Erythroxylon areolatum</u>	Erythroxylaceae	T
<u>Plumeria obtusa</u>	Apocynaceae	AS
<u>Portulaca</u> spp.	Portulacaceae	SuH
<u>Schaefferia frutescens</u>	Celastraceae	T
<u>Stigmaphyllon periplocifolium</u>	Malpighiaceae	WV
<u>Tephrosia cinerea</u>	Fabaceae	H
<u>Tribulus cistoides</u>	Zygophyllaceae	H

Table 6 (Continued)

Species	Family	Growth Form ¹
FRUITS:		
<u>Amyris elemifera</u>	Rutaceae	T
<u>Ayenia pusilla</u> (nonfleshy fruit)	Sterculiaceae	H
<u>Bourreria succulenta</u>	Boraginaceae	T
<u>Capparis flexuosa</u>	Capparidaceae	WV
<u>Cissus caustica</u>	Vitaceae	SuV
<u>Coccoloba diversifolia</u>	Polygonaceae	T
<u>Coccoloba microstachya</u>	Polygonaceae	T
<u>Coccoloba uvifera</u>	Polygonaceae	T
<u>Corchorus hirsutus</u> (nonfleshy fruit)	Tiliaceae	S
<u>Crossopetalum rhacoma</u>	Celastraceae	T
<u>Erythroxylon areolatum</u>	Erythroxylaceae	T
<u>Ficus citrifolia</u>	Moraceae	T
<u>Ficus crassinervia</u> (localized)	Moraceae	T
<u>Galactia dubia</u> (pods)	Fabaceae	H
<u>Gyminda latifolia</u>	Celastraceae	T
<u>Harrisia portoricensis</u>	Cactaceae	CC
<u>Hypelate trifoliata</u>	Sapindaceae	T
<u>Jatropha multifida</u>	Euphorbiaceae	AS
<u>Krugiodendron ferreum</u>	Rhamnaceae	T
<u>Metopium toxiferum</u>	Anacardiaceae	T
<u>Portulaca</u> spp. (capsules)	Portulacaceae	SuH
<u>Rauwolfia tetraphylla</u>	Apocynaceae	T
<u>Reynosia uncinata</u>	Rhamnaceae	S
<u>Sarcomphalus taylori</u>	Rhamnaceae	T
<u>Tephrosia cinerea</u> (pods)	Fabaceae	H
<u>Torrubia discolor</u>	Nyctaginaceae	T

¹ Key to abbreviations: AS, Arborescent Shrub; C, Cactus; CC, Columnar Cactus; G, Grass; H, Herb; S, Shrub; Su, Succulent; T, Tree; WV, Woody Vine.

Like all herbivorous lizards, Mona Iguanas do not masticate their food. They tear off leaves with a bite and twist of the head and then swallow them whole. Large items are usually shifted around in the mouth and bitten once or twice before being swallowed. The tongue is used to retrieve small fruits and even tiny flowers that have fallen to the ground from trees overhead. Only rarely do adult iguanas climb while foraging, though I have seen them in low shrubs and in two instances 2-3 m up in trees, places that could be reached easily by climbing a tangle of low branches. Leaves from the canopy brought down by wind, rain, or dry weather are usually of little interest to the iguanas (an important exception being Capparis flexuosa)--this also held true when I provided a spread of fresh cuttings to iguanas.

There is considerable variability in digestive efficiency evident between samples containing the same species, between different species in the same sample, and between plant parts. Leaves of most trees and shrubs were least altered physically, while those of tender or succulent herbs were usually digested more completely. The two most commonly eaten herbs, Centrosema virginiana and Galactia dubia, both legumes, appeared in some samples as though the leaflets had just been plucked from the vine, while in others everything had been digested except the skeletal network of veins. The pubescent leaves of the shrub Corchorus hirsutus are degraded to formless masses of fuzz, with the stems and seeds relatively untouched by digestion. Leaves of a few herbs, most notably Callisia repens and Boerhaavia spp., never appeared in fecal samples even though I have observed iguanas feeding on these common

plants and found Boerhaavea represented in a stomach sample--possibly these leaves are totally macerated during digestion. Plant parts that usually appear to be well assimilated are fruits and flower petals. Most fruits are reduced to little more than naked seeds, pits, or cores, plus stems. In some cases the fruit's skin passes through intact while in others it is digested away. Fruits of the abundant Depression Forest tree Ficus citrifolia are among those least successfully digested, probably owing to their fibrous, pulpy texture.

Mona Iguanas are opportunistic in their feeding behavior, thus their diet varies with geographic and seasonal differences in the character of the island's plant communities. The most pronounced seasonal changes in samples collected at La Bajurita reflect the availability of flowers, fruits, and caterpillars (Table 7). The flowers of the trees Erythroxylon areolatum and Schaefferia frutescens are tiny (ca. 3 mm in diameter), but when the ground is littered with thousands of fallen flowers, iguanas can eat them profitably. In general, flowers are eagerly taken by the iguanas, but those of most species are sparse or relatively inaccessible and are therefore infrequently represented in scats.

The shrub Corchorus hirsutus holds the distinction of being the only plateau species with aromatic leaves eaten in quantity by iguanas and this appears to be a seasonal preference. For two consecutive years I noticed that Corchorus began appearing in the iguanas' diet only when the plant's seeds were mature. Seeds and leaves were then taken together, but the seeds passed through intact. The fruits of Corchorus have

Table 7.-- Principal food items in diet of iguanas residing at a rocky inland depression on Mona Island, P.R.

Time of Collection	No. Samples Analyzed	Species (leaves unless otherwise specified) ¹
22 June 1973	1	<u>Plumeria obtusa</u> <u>Capparis flexuosa</u> <u>Reynosia uncinata</u> <u>Ficus citrifolia</u> --fruits
10-19 July 1973	4	<u>Erythroxylon areolatum</u> --tiny flowers <u>Schaefferia frutescens</u> --tiny flowers <u>Capparis flexuosa</u> --leaves and flowers <u>Reynosia uncinata</u> <u>Galactia dubia</u> <u>Krugiodendron ferreum</u> <u>Commelina virginica</u> <u>Schaefferia frutescens</u>
25 September- 3 October 1973	4	<u>Pseudosphinx</u> --caterpillars, pupae, and an adult <u>Ficus citrifolia</u> --fruits <u>Antirrhea acutata</u> --fruits and flowers <u>Centrosema virginiana</u> <u>Reynosia uncinata</u> --fruits <u>Bourreria succulenta</u> --fruits
9-21 November 1973	3	<u>Centrosema virginiana</u> <u>Pseudosphinx</u> --caterpillars <u>Bourreria succulenta</u> --fruits <u>Capparis flexuosa</u>

Table 7 (Continued)

Time of Collection	No. Samples Analyzed	Species (leaves unless otherwise specified) ¹
28 February- 10 March 1974	4	<u>Capparis flexuosa</u> <u>Pseudosphinx</u> --caterpillars <u>Commelina virginica</u> <u>Corchorus hirsutus</u> <u>Centrosema virginiana</u>
12-19 April 1974	4	<u>Capparis flexuosa</u> <u>Corchorus hirsutus</u> <u>Centrosema virginiana</u> <u>Galactia dubia</u> <u>Pseudosphinx</u> --caterpillars
20-31 May 1974	8	<u>Pseudosphinx</u> --caterpillars <u>Centrosema virginiana</u> <u>Galactia dubia</u> <u>Capparis flexuosa</u> <u>Reynosia uncinata</u> <u>Krugiodendron ferreum</u>
9-10 June 1974	2	<u>Pseudosphinx</u> --caterpillars <u>Capparis flexuosa</u> <u>Ficus citrifolia</u> --fruits <u>Reynosia uncinata</u> --fruits and leaves
19-29 June 1974	3	<u>Reynosia uncinata</u> --fruits and leaves <u>Capparis flexuosa</u> <u>Pseudosphinx</u> --caterpillars

¹ In descending order of abundance.

a tough, woody exterior, so it is unlikely that eating them is the iguanas' main objective. Possibly seed maturity in this shrub is accompanied by a drop in the concentration of defensive chemicals in the plant's juices, evolved to encourage such predation to promote seed dispersal.

From May 1972 to April 1975, peak fruiting periods were noted for 17 of Mona's common trees and shrubs that bore fruits of particular interest to the iguanas (Fig. 11). Most fruiting (59%) occurred during the period August to November, the wettest four-month period of the year. A high degree of intraspecific fruiting synchrony was evident among trees of most species, a notable exception being Ficus citrifolia. Of these 17 fruit types, most were purple to black in color and less than 15 mm in diameter.

In some cases, seasonal fruit availability affects the distribution and density of iguanas on Mona. A favorite food of the iguanas is the fruit of the large coastal tree Hippomane mancinella or "manzanillo" (Manchineel). The ripe fruits are green, about 3 cm in diameter, and are extremely poisonous to man and other mammals (see Little & Wadsworth, 1964, for details). This tree is common on Mona's coastal terrace below Cueva del Lirio, where it produces impressive summer crops of fruit that fall to the ground at maturity. The aroma is intense and sweet, a temptation to man and iguanas alike; this odor may be a cue to iguanas that the fruit is available. These little "apples" are so plentiful that most turn yellow and rot on the ground before they can be eaten; iguanas will not eat the fruit after it has yellowed. During a

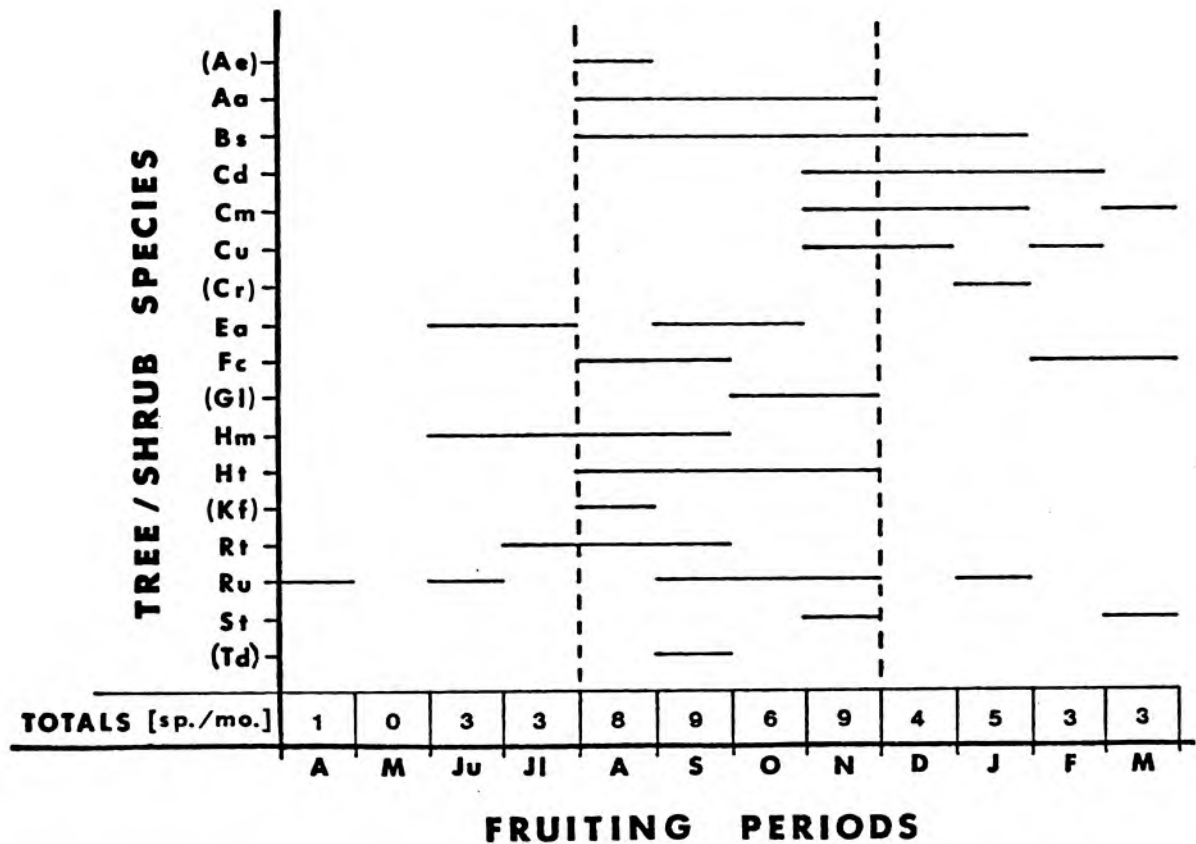


Fig. 11.--Distribution of principal fruiting periods observed on Mona I. between 1972 and 1975 for common trees and shrubs that bear fruit known to be of major importance in the diet of iguanas there. Species in parentheses are those for which only one peak fruiting period was observed during the three-year period. Key to species: (Ae, Amyris elemifera); Aa, Antirrhea acutata; Bs, Bourreria succulenta; Cd, Coccoloba diversifolia; Cm, C. microstachya; Cu, C. uvifera; (Cr, Crossopetalum rhacoma); Ea, Erythroxylon areolatum; Fc, Ficus citrifolia; (Gl, Gyminda latifolia); Hm, Hippomane mancinella; Ht, Hypelate trifoliata; (Kf, Krugiodendron ferreum); Rt, Rauwolfia tetraphylla; Ru, Reynosia uncinata; St, Sarcomphalus taylori; (Td, Torrubia discolor).

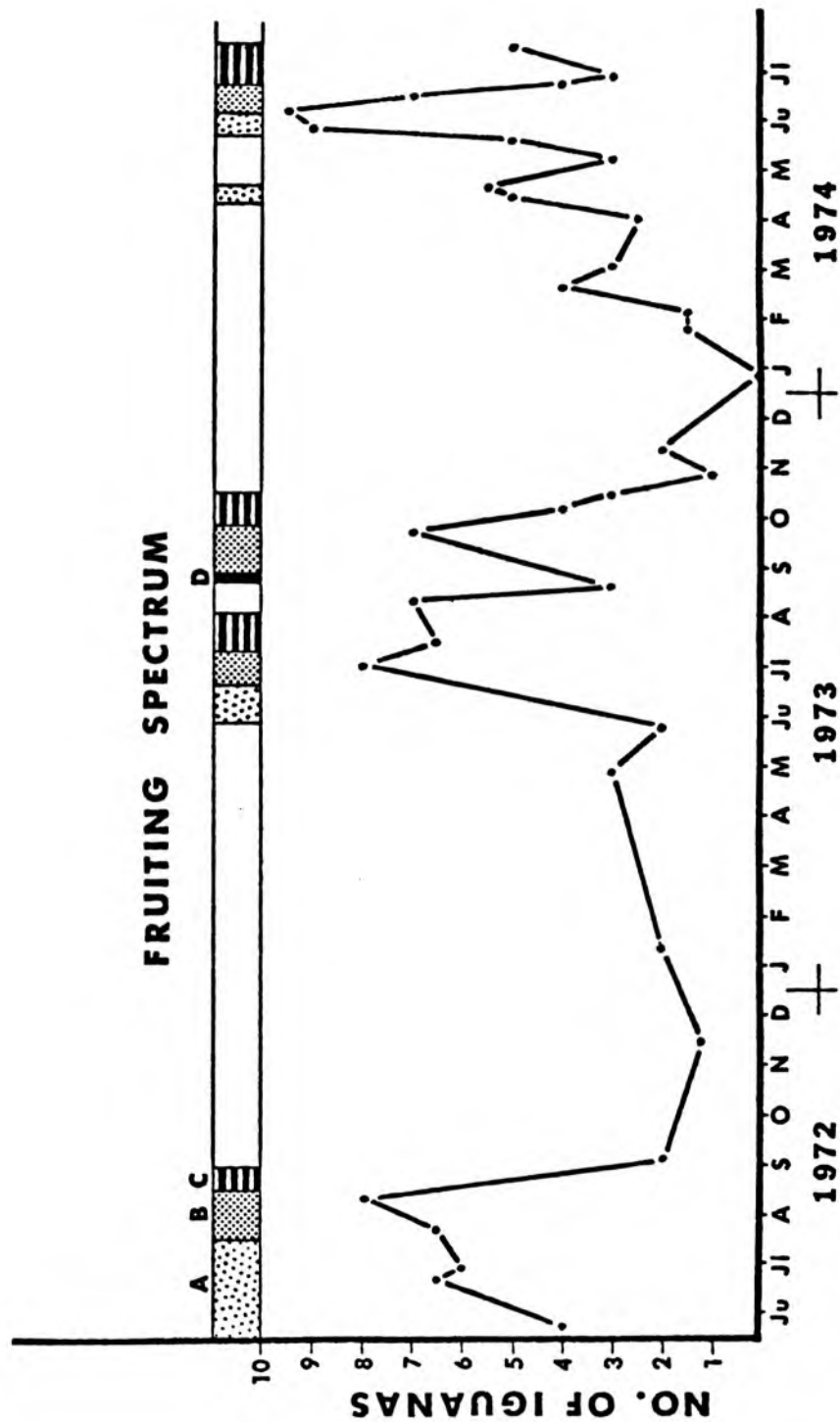


Fig. 12.--Number of iguanas sighted during 54 census counts in Lirio Terrace Study Area compared with the relative availability of Manzanillo (*Hippomane mancinella*) fruits. Fractional numbers represent the averages of two or three counts made during the same week. Fruiting spectrum: A. Trees loaded with mature, green-colored fruit, beginning to fall; B. Peak occurrence of green fruit on ground; C. Fruits on ground yellowing and beginning to rot; D. Second major fruit-fall, initiated by heavy rain.

26-month census period, the average number of iguanas sighted along a 0.4-km route through this forest roughly tripled during the Manchineel fruiting season (Fig 12). Only one iguana resided in the area year-round; the others took up temporary residency in retreats normally vacant during the off-season. It is likely that these seasonal immigrants usually inhabit adjacent cliffside areas. The fruit's popularity was further evident in the iguanas' fecal droppings, which contained up to 13 cores per scat (the cores are woody and nearly as large as the whole fruit). In only one instance were leaves (Capparis flexuosa) seen in combination with Manchineel cores.

To photograph an iguana eating Manchineel "apples," on 10 July 1973, I offered three iguanas some fruits, at a site about 0.5 km from the nearest Manchineel trees. The female investigated and flicked her tongue at the fruit but would not eat it. The males, both approachable individuals, accepted it, but with noticeable hesitation and little interest. Surprised by their response to the fruit, I returned the following day to repeat the offer. Again, the female (gravid and near term) refused to try the fruit, but the two males responded with "run-to-it" enthusiasm, snapping them up as soon as they hit the ground, though neither would eat more than five (perhaps they were filled to capacity). The occasion was, to my knowledge, the last they saw of Manchineel fruits that summer, and only then did it really occur to me that perhaps these particular individuals may have never before tasted these delectable fruits.

One year later, when Manchineel fruits were just coming into season, I again offered them to one of the same males. Upon arriving

at the site (on 27 May 1974), I found him lying about 4 m from me and pulled the clear plastic bag containing the fruits from my pack. The iguana eyed it for a moment and then instantly walked straight to me. I started to walk away, and he followed. Nothing like that had ever happened before, a clear testament to the learning ability of these remarkable lizards!

Mona Iguanas devote little time and energy to foraging and the only animal foods eaten are those as easy to catch as a fallen leaf. Three items listed in Table 8--the weevil, the snail, and the feathers--were probably taken inadvertently while feeding on something else. The two feathers came from fecal samples collected in Mona's booby rookery on the NE coast, where the ground is littered with feathers. The island has a sizable population of Rolita Doves (Columbina passerina) that frequently nest on or within 1 m of the ground on Mona; this is an animal whose eggs and chicks would seemingly fall easy prey to iguanas, but I have seen no indication that this occurs. Should an iguana come dangerously close, perhaps the dove's convincing broken-wing act is enough to lure it away from the nest. An injured bird of adult Rolita size might well be an attractive morsel. Miguel C. Frontera, an avid outdoorsman who has been visiting Mona for many years, told me that he once stepped into the brush to retrieve a dove he had shot and all he found was a contented-looking iguana with feathers scattered about. I have never seen iguanas feeding on carrion, and I regularly came across the remains of hunter-killed goats in the field.

Land crabs are exceedingly common on Mona but are apparently rarely

Table 8.-- Animal matter consumed by adult Mona Iguanas as determined from analysis of fresh feces (N=118), stomach contents (N=2), and field observations.

Species	Number of Samples (No./Sample)
CRUSTACEA:	
<u>Gecarcinus</u> sp.	
legs only	3 (1-3)
complete crab	1 (field observation)
(<u>G. lateralis</u>)	
INSECTA:	
Coleoptera	
Curculionidae	1 (1)
Scarabaeidae (Subfamilies:	3 (1-3)
Dynastinae, probably genus	
<u>Strategus</u> , and Melolothinae) ¹	
Lepidoptera	
Sphingidae: <u>Pseudosphinx tetrio</u>	
eggs	2
larvae	20+ (1-8/sample, plus many field observations)
pupae	2 (3, 6)
adults	1 (1)
Pieridae: <u>Ascia monuste</u>	1 (field observation)
(a mating pair)	
MOLLUSCA:	
Terrestrial Gastropod	1 (1)
(immature <u>Drymaeus elongatus</u>	
<u>beattyi</u>)	

Table 8 (Continued)

Species	Number of Samples (No./Sample)
MISCELLANEOUS:	
Iguana skin	2
Feathers	1 (2)

¹Identified by E. Richard Hoebeke, Department of Entomology, Cornell University.

eaten by iguanas. Once I observed a nesting female pick up and bite a small crab (probably Gecarcinus lateralis), after which she shook her head violently, tossing the crab about two meters. This was either an attempt to subdue the animal or a response to being pinched. She then walked over to where it landed, picked it up again and ate it.

Animal foods of apparently greatest significance to the iguanas are large, slow-moving insects that can be found on the ground and undergo periodic population explosions, rendering them exceptionally abundant at times. The scarab beetle parts found in iguana scats all appeared in samples collected during the first week of October 1973 from widely separated localities upon the plateau. These beetles are presumably leaf-litter inhabitants, and their relative abundance in the field passed unnoticed. By far the most marked cycles observed were those of the large sphingid moth Pseudosphinx tetrio, whose larvae are host-specific on Mona to the arborescent shrub Plumeria obtusa, also known as frangipani or "alelf," a species that abounds island-wide.

During my first year on Mona (May 1972-May 1973), the alelf were lush and bloomed profusely with no Pseudosphinx to be seen. This is not a caterpillar that can be overlooked easily, for its appetite is devastating to the appearance of its host plant, it has brilliant aposomatic coloration of red, orange, and chartreuse in contrast against black, and it typically reaches about 15 cm in length before pupation. I first saw one of these giant caterpillars on 3 June 1973, and within 13 weeks, a population had developed that spread like a wave of disaster across Mona's landscape, stripping nearly every leaf, fruit, and flower from

the alElf. Everywhere caterpillars were dispersing and dying on the ground in their search for more food, and iguanas were gorging themselves. At such times caterpillars became the iguanas' principal food item, and scats turned into puddles of gray-green ooze. Every iguana seen, large or small, had a blackened face from dried caterpillar juice. Pseudosphinx pupate in leaf litter, and the iguanas were also feasting upon these giant pupae. The inevitable population crash followed in late September and early October. Caterpillars were rare during the winter months, reaching a low in January 1974, as the alElf sprouted new leaves. A minor resurgence occurred in mid-February, and a second major population peak developed in early July. This happened around the lighthouse; population phenology differed in other parts of the island.

As of August 1976, Plumeria caterpillars were still present on Mona, but I suspect that one prolonged dry season may finish off this moth population. Miguel Frontera told me that about 13 years ago he helped the Coast Guard personnel sweep up Pseudosphinx tetrio caterpillars around the Mona lighthouse, enough to fill a wastebasket. That population apparently died off sometime during the following decade, and the 1973 population probably originated from an adult that flew (blew?) in from Puerto Rico or the Dominican Republic; the species occurs in both places (pers. obser.).

Also during the summer and fall months of 1973, accompanying the spread of the Plumeria Sphinx Moth, several other large lepidopteran larvae were building in numbers, none of which were seen the previous year. Though more sparsely represented or more localized in distribution, some of these species undoubtedly contributed to the diet of

iguanas in parts of the island not studied. Larvae of one cryptically colored sphingid that fed on the coastal vine Ipomoea tuba were eagerly eaten by my wild-caught pig, who nosed but refused to eat Plumeria caterpillars. The arborescent shrub Plumeria obtusa has a milky sap reputed to be poisonous (Little & Wadsworth, 1964), and caterpillars feeding on the plant presumably carry the toxin(s) in their tissues, giving them protection from predatory birds and mammals and explaining the origin of their warning coloration. Iguanas may thus be the only native vertebrate predators capable of exploiting Pseudosphinx caterpillars.

The diet of juvenile Mona Iguanas is very similar to that of adults, except for expected differences in the size of food items eaten and the preponderance of herbaceous plants (Table 9). During spring and early summer months when small fruits were scarce, chiefly foliage and flowers were taken; later in the year, fruits became the prominent items. Eight of the nine genera of plants whose leafy parts were eaten are herbaceous (4 legumes, 2 portulacas, 1 euphorb, and 1 grass), and the ninth is a succulent shrub (Eupatorium corymbosum, Compositae). Three species not also found in the diet of adults are Chamaesyce anegadensis, Pilea microphylla, and Gossypium barbadense (flowers), all of which are uncommon or highly localized in distribution. The only animal material represented was two small mature insects, several tiny land snails in one sample, and small Pseudosphinx caterpillars.

Discussion:

Plants and Plant Parts Eaten.--Ostrom (1963) noted that while the diets

Table 9.-- Analysis of diet of juvenile iguanas on Mona Island, P.R.

Location and Date	Iguana	Food Item	Quantity (no. of bites taken)
FIELD OBSERVATIONS OF FORAGING			
<u>East Cliffside:</u>			
10 March 1973	Rusty (1st yr. juv.)	<u>Portulaca quadrifolia</u>	(6)
13 March 1973	Peaches (1st yr. juv.)	<u>Chamaesyce anegadensis</u>	?
20 March 1973	Rusty	<u>Eupatorium corymbosum</u>	?
21 March 1973	Rusty	<u>Portulaca quadrifolia</u>	(5)
		<u>Galactia dubia</u>	(2)
		Tenebrionid beetle	(1)
3 April 1973	Rusty	<u>Portulaca quadrifolia</u>	(8)
		<u>Eupatorium corymbosum</u>	(3)
9 April 1973	Rusty	<u>Portulaca quadrifolia</u>	(28)
		<u>Eupatorium corymbosum</u>	(9)
29 May 1973	Hatch C (1st yr. juv.)	<u>Portulaca quadrifolia</u>	(33)
		<u>Eupatorium corymbosum</u>	(33)
		flowers and buds	
		<u>Antirrhea acutata</u>	(17)
		immature fruit	
<u>Inland Depression:</u>			
7 October 1973	Green Specks (19.3 cm SVL, 33.0 cm tail)	<u>Erythroxylon areolatum</u> fallen fruits	?
9 October 1973	Green Specks	<u>Antirrhea acutata</u> climbed shrub for ripe fruits	(4)

Table 9 (Continued)

Location and Date	Iguana	Food Item	Quantity (no. of bites taken)
STOMACH CONTENT ANALYSIS			
<u>SW Coastal Plain:</u>			
November 1972	Hatchling	<u>Rivinia humilis</u> fruits	8
		Small land snails (<u>Lucidella umbonata</u>)	11
ANALYSIS OF FECES			
<u>East Cliffside:</u>			
March 1973	?	<u>Galactia dubia</u>	7 leaves
		<u>Portulaca oleracea</u>	4 pieces
		Parts of one insect	2
		Cactus spine	1
20 June 1973	Hatch C	<u>Galactia dubia</u>	31 leaves
		<u>Chamaesyce prostrata</u>	18 sprigs
		<u>Ayenia pusilla</u> fruits	8 complete
		<u>Panicum maximum</u> seeds	7
		<u>Desmodium mollis</u> seeds	2
30 June 1973	23.9 cm SVL, 38.3 cm tail	<u>Pseudosphinx</u> caterpillars	5
		<u>Tephrosia cinerea</u>	75+ leaves
		Grass	2-3 blades
		<u>Pilea microphylla</u>	ca. 25 leaves
		Unidentified fruit	1
4 April 1973	30.0 cm SVL,	<u>Tephrosia cinerea</u>	125+ sprigs
		<u>Portulaca</u> fruit capsules	33
		<u>Portulaca quadrifolia</u>	ca. 20 leaves
		<u>Portulaca</u> flowers	6
		<u>Galactia dubia</u>	9 leaves

Table 9 (Continued)

Location and Date	Iguana	Food Item	Quantity (no. of bites taken)
		<u>Paspalum glabrum</u>	1 blade
		<u>Centrosema virginiana</u>	1 leaf
		<u>Ayenia pusilla</u>	1 fruit
<u>N End of Faro Road:</u>			
8 March 1974	20.3 cm SVL, 34.0 cm tail	<u>Gossypium barbadense</u>	1-2 flowers
		<u>Ayenia pusilla</u>	5 seeds
		<u>Galactia dubia</u>	2 leaves
20 April 1974	1st or 2nd yr. juv.	<u>Stylosanthes hamata</u>	ca. 75%
		<u>Centrosema virginiana</u>	16 leaves
		<u>Galactia dubia</u>	4 leaves
		<u>Commelina virginica</u>	3 leaves
<u>Inland Depression:</u>			
25 September 1973	Green Specks	<u>Ficus citrifolia</u> fruits	1
28 February 1974	Subadult	<u>Centrosema virginiana</u>	ca. 40%
		<u>Commelina virginica</u>	ca. 30%
		<u>Galactia dubia</u>	ca. 10%
		<u>Ficus citrifolia</u>	ca. 5%
		fruit	
		<u>Pseudosphinx</u>	2-3
		caterpillars	
<u>Inland Trail, E Mona:</u>			
2 October 1973	?	<u>Antirrhea acutata</u>	73
		fruits	
		<u>Reynosia uncinata</u>	6 leaves
			1 fruit
		<u>Bourreria succulenta</u>	1 fruit
		<u>Pseudosphinx</u>	1
		caterpillar	

Table 9 (Continued)

Location and Date	Iguana	Food Item	Quantity (no. of bites taken)
<u>SW Cliffside, Uvero:</u>			
16 November 1973	18.0 cm SVL,	<u>Bourreria succulenta</u>	13 fruits
	30.0 cm tail	Unidentified tiny seeds	18

of herbivorous lizards differ, "in nearly every case the preferred plant substances seem to be soft, even pulpy tissues." Low-fiber items are the parts that are best digested; assimilation efficiencies (calories ingested less calories egested/calories ingested) for low-fiber plant parts run high, e.g., 75% for clover leaves fed to the Australian skink Egernia cunninghami (Shine, 1971--MS, cited by Wilson & Lee, 1974) and 86.3% for sweet potato tuber fed to Ctenosaura pectinata (Throckmorton, 1973). These values are similar to those for animal foods (see Pough, 1973). Yet overall, plant foods have relatively low caloric values (see Table 10), are low in protein content (see Watt & Merrill, 1975), and often contain secondary compounds (especially in aromatic or resinous foliage) requiring detoxification, a process that can be costly to the consumer (see Freeland & Janzen, 1974). Seeds are comparatively nutrient-rich, but are usually protected by a coat impervious to digestion.

While fruits and leaves appear similar in caloric value (Table 10), they are very different as foods. This is well exemplified in Morton's (1973) comments on the evolutionary implications of fruit-eating: Most important, the plant as well as the consumer has something to gain from the relationship, namely seed dispersal. Fruit-eating, then, promotes adaptations by the plant (e.g., improvements in digestibility and food value) to attract fruit predators, while leaf-eating (like insect-eating) promotes adaptations that oppose predation, e.g., increases in protective chemicals or spines. When fruit is available it is usually easy to obtain and is often exceedingly abundant; thus, the effort needed to collect it is minimal.

Table 10.-- Average caloric values for assorted plant parts and animals.

Item	Number of Species (Samples)	Average Value (g cal/g dry wt)	Source
<u>PLANTS:</u>			
Leaves (Subtropical- dry scrub, Caicos Is.)	9 (9)	4412	Auffenberg, unpubl.
Leaves (mixed)	57- [(260) (82) (51) (22)	4229	Golley, 1961
Litter (mixed)		4298	Golley, 1961
Stems and branches (mixed)		4267	Golley, 1961
Seeds		5065	Golley, 1961
Fruits (Subtropical- dry scrub, Caicos Is.)	9 (9)	4594	Auffenberg, unpubl.
<u>ANIMALS:</u>			
Insects			
Orthoptera	(12)	5386	Cummins, 1967
Coleoptera	(5)	5668	Cummins, 1967
Décapod Crustaceans	(10)	2516	Cummins, 1967
Molluscs (Gastropoda)	(3)	4600	Cummins, 1967
Vertebrates	(40)	6274	Cummins, 1967

Flowers, like leaves are not really "meant" to be eaten, but must be designed to attract pollinators. While flowers are not significantly different from stems, leaves, and roots in caloric content (Golley, 1969), flower nectars may contain essential amino acids in addition to carbohydrates (Baker & Baker, 1973). Flowers may also offer pollen, which is particularly rich in protein, but its utilization requires specialized conditions in the gastrointestinal tract that permit the grains to "germinate," rendering the nutritious cellular contents available for digestion (Howell, 1974); whether iguanas can do this is unknown.

In spite of their seasonality, fruits predominate in importance to the Mona iguana population and are assuredly the principal plant foods contributing towards growth, reproduction, and fat reserves. Mona Iguanas are clearly not haphazard in their selection of plant foods--their diet strongly favors items that are relatively low in cellulose, low in aromatic compounds, and easily obtained. On theoretical grounds, these are the food types that would be expected if they were to harvest what is available for a maximum net energy gain. A persisting puzzle however, is why leaves of Capparis flexuosa, which are never well digested, are so attractive to these animals--perhaps they are taken primarily for their water or mineral content. It would also be of great interest to find out how these lizards cope with the strong alkaloids in fruits and leaves of Hippomane mancinella.

Comments on the Occurrence and Evolution of Herbivory in Lizards.--

Carey (1975) speculated that all cycluran iguanas are primarily insectivorous as juveniles. It has been suggested that large herbivorous

lizards must be insectivorous as juveniles because of greater metabolic demands imposed by their small size, with a consequent need for energy-rich animal foods (Pough, 1973); and it is true that some lizards herbivorous as adults are insectivorous as juveniles (e.g., Basiliscus basiliscus, Fleet and Fitch, 1974). However, my field data for C. stejnegeri (a large species with hatchlings that average 74g) and Iverson's (1977) field data for C. carinata, one of the smallest members of the genus (hatchlings average 14.6g), show that neither species takes insect food at any age unless it is exceptionally easy to obtain. Quite possibly this is the case for all Cyclura.

Evidence from a number of sources suggests that there has been keen competition on Mona for insect foods, promoting obligate herbivory in the iguanas at all ages. Support for this hypothesis comes from 1) current theory of community structure and evolution, 2) a gross evaluation of potential competitors present on Mona, and 3) data on insect and lizard populations of other Caribbean islands relative to those of the Central American mainland.

Ecological theory suggests a history of community evolution on Mona dominated by intense inter- and intraspecific competition. Mainland-island comparisons have demonstrated that insular ecosystems are characteristically depauperate in species composition and have relatively few, if any, high-order carnivores (Carlquist, 1974). Vertebrate animals that are present, however, often show high population densities and expanded activities (e.g., see Soulé, 1966; MacArthur, 1972; Andrews, 1976), indicating communities which are effectively saturated with

individuals (Pianka, 1974). In addition, many island habitats are structurally simple and relatively unproductive; karst formations, like Mona, are excellent examples (see LeGrand, 1973). All of these features point to competition as an ecological force that has predominated over predation in community organization (see Pianka, 1974; Menge & Sutherland, 1976).

Spiders, lizards, and birds are significant potential competitors for insect food on Mona. Several species of orb-weaver spiders are incredibly abundant, a distinctive feature of the island's fauna. Mona has three species of moderate-sized diurnal insectivorous lizards, Anolis monensis, Ameiva alboguttata, and Mabuya sloanii, all of which are common island-wide. The activities of all three are concentrated on or near the ground and each occupies a different feeding niche (pers. obser.). The most common resident insectivorous birds are the Pearly-eyed Thrasher (Tyrannus dominicensis), the Mangrove Cuckoo (Coccyzus minor), and the Yellow-shouldered Blackbird (Agelaius xanthomus). Both the thrasher and the blackbird take considerably more than insect food (pers. obser.): The Yellow-shouldered Blackbird appears to be primarily a foliage-gleaner, but frequently feeds on small fruits and is a nectar-feeder as well. The thrasher will attack and dismember small reptiles and large insects (like anoles, baby sea turtles, carpenter bees, and sphinx moths) and eats a wide variety of fruits; visitors report they also prey upon eggs and chicks of other birds.

Supporting the idea that insects constitute a limited food resource on Mona are data from sweep samples taken from secondary vegetation on

several Caribbean islands and the mainland of Central America. Janzen (1973) found that the island insect faunae not only have fewer species of insects, but also exhibit a dramatic reduction in insect numbers during both dry and wet seasons and a relatively small proportion of large insects. Furthermore, Allan et al. (1973) found that the proportion of predatory arthropods (mostly spiders) in Puerto Rican samples was exceptionally high, both in species composition and numerical abundance, relative to equivalent samples from continental Latin America. Samples from Guánica, P.R., where climatic conditions are similar to Mona's, were 49% predators. These data indicate that predatory invertebrates may be contributing substantially toward reducing island insect faunae and maintaining them at relatively low levels.

Perhaps the most convincing evidence that insects constitute a limited food resource for many insectivorous vertebrates on West Indian islands comes from studies of Anolis populations. Virtually every island in the Caribbean has one or more species in this lizard complex, and representatives abound on the mainland as well. During the past 15 years, a number of authors have reported an impressive array of ways in which insect foods are partitioned by island anoles, an evolutionary outcome of interspecific competition unmatched by anoles on the continent (see Andrews, 1976, and citations therein). Through comparisons of growth patterns in mainland and island lizards, Andrews (1976) discovered that island anoles spend more time searching for food and grow appreciably more slowly. Island forms also have the capacity to respond to conditions of artificially high food abundance with an increased

growth rate, something those on the mainland cannot do, suggesting that mainland populations are already getting sufficient food to permit growth at physiologically maximum rates (Andrews, 1976).

Janzen (1973) noted a shift towards herbivory in Ameiva and Cnemidophorus (two genera of teiid lizards generally known for their insectivorous habits) on Isla Providencia and speculated that the Providencia populations have successfully moved towards herbivory by being able to bask more and thereby process plant matter faster in this "predator-free" island environment. Certainly as animal foods become scarce, should the consumer have to expend more energy in obtaining a particular food item than it will yield in return, then the best investment would be to broaden the diet to include abundant, easily obtained items with lower energy values (e.g., see Schoener, 1971). However, the proposition that these lizards must be able to bask longer (and presumably maintain higher body temperatures) to become herbivorous is unlikely. Dawson's (1967) data and my own field observations of Ameiva and Cnemidophorus indicate that many of these lizards normally operate at high body temperatures, irrespective of diet. Furthermore, herbivory in lizards ranges through a spectrum of diurnal desert-dwelling forms active during the hottest hours of the day (see DeWitt, 1967) to a cave-dwelling xantusiid that feeds by day and night and apparently has little or no need to bask (Mautz, 1976). Unfortunately virtually nothing is known about the relationship between temperature and digestive function in lizards, and we cannot assume that activity temperatures after basking correspond to optimal temperatures for digestion or that eating

plant matter creates special thermoregulatory needs (see Dawson, 1967).

Ecological conditions promoting and permitting the shift from insectivory to herbivory in lizards appear closely tied to a scarcity of insect prey and relatively low natural mortality. In a recent discussion of herbivory in lizards, Rand (1977) noted that herbivorous lizards occur most frequently in areas of low productivity. Such environments are theoretically characterized by a reduced role played by high-order predators in community organization (see Pianka, 1974; Menge & Sutherland, 1976). In the absence of significant pressure from predation, lizard populations are consequently apt to expand to the limits of the food supply (see Soulé, 1966; Janzen, 1971; Andrews, 1976). This sets the stage for intense inter- and intraspecific competition, circumstances that might well lead to broadening the diet, at least seasonally, to include plant matter.

Herbivorous habits may in turn impose constraints on demographic flexibility. Pointing out that plant food is digested with greater difficulty and at lower efficiency than animal food, largely because recent reptiles lack any specialized grinding devices, Szarski (1962) suggested two important conditions accompanying herbivory in lizards: 1) a low metabolic rate, and 2) slowed reproductive output. Both factors would render plant-eating lizards more vulnerable to predation. Herbivorous forms that have succeeded in areas where predation is relatively great may have done so by being able to retain insectivorous habits as juveniles during at least part of the year (e.g., Ctenosaura similis, Montanucci, 1968; Basiliscus basiliscus, Fleet & Fitch, 1974),

thereby offsetting mortality by making relatively early maturity and larger or more frequent clutches possible (see Evolution of Female Reproductive Strategy).

I suggest that Cyclura habitats offer both juveniles and adults few dietary alternatives to herbivory and that slow growth is a consequence of an energetically poor diet and inefficient food processing; this consequence can be tolerated only in environments where predation is relatively light. On Mona, only small juveniles are vulnerable to predation (see Associations with Man & Other Animals--Native Species), therefore, natural selection would be expected to favor diets promoting rapid growth early in life. Cyclura are highly selective in the plants and plant parts eaten, in a way optimizing net energy gain. In addition, these iguanas have remained opportunistic predators, and I suggest that if juveniles could regularly find suitable insect prey in sufficient quantity, they would indeed utilize this food type preferentially, as do captive individuals (see Carey, 1975). Herbivory versus insectivory in lizards should be viewed as a continuum, with the position of each species ultimately determined by the historical availability of different food types, their net energy values, and predation intensity.

DAILY AND SEASONAL ACTIVITIES (ASOCIAL)

Activity Patterns:

Two features of the Mona Iguana life-style which stand out above all others are its variability and its extremely slow pace, the latter broken only during the breeding and nesting seasons. Much of the individual, daily, and seasonal variation in the activities of these lizards is discussed later as it relates to their social behavior (see Territoriality, Courtship, & Mating). A representative example of the behavioral variability seen among 12 individuals in the same place during the same hours is presented in Table 11. It is noteworthy that all degrees of activity occurred, ranging from total immobility in some animals (N=4: three underground and one on the surface) to basking (4) and foraging (4) in others. Mobility and foraging did not in all cases (2) accompany basking.

Observing an iguana's "daily routine" throughout 10 months of the year (outside breeding and nesting seasons) is generally uneventful. In a minute-by-minute analysis of the activities of seven iguanas in April 1974 (Table 12) representing observations of 13 activity periods spanning morning and afternoon hours and averaging 4.5 hours in duration, I found that in 11 of the observation periods the animal spent over 94% (\bar{x} = 98.4%) of its time lying or sitting (this category includes basking). In the other two cases, foraging occupied 19% and 25% of the iguana's time, only a tiny fraction of which was spent actually eating.

Table 11.--Summary of the activities of 12 adult iguanas observed at an inland sinkhole depression (La Bajurita) on Mona Island, Puerto Rico, on 1 March 1974, an example of daily activities recorded in the area during the non-breeding season. Weather was sunny with scattered clouds.

Iguana	Observation Period	Where Sighted	Time of Emergence	Distance Moved	Number of Movements	Interval(s) of Active Basking	Amount of		Courtship/Agonistic Responses
							Foraging	Responses	
MALES:									
Four-toed Freddie	1005-1730	Lying in crevice with Trixie and Fannie	Inactive	----	None	None	None	None	
Bulbtail	1313-1409	Emerging from crevice in ♂ Silversides' territory	1313 (temporary activity)	< 2 m	Chased back into crevice	None	None	None	Encounter and fight with Silversides; final retreat to crevice after being bitten at 1409 ³⁰
Rolo	1005-1730	On rock foyer in front of retreat in his territory	? - at 1005, lying out where he usually sleeps	----	None	None	None	None	
Left Cold	1005-1700	Within his territory on sink floor	Before 1005	45-50 m	11	Several short ones throughout day	Ate 12 Capparis leaves	Intention movement to chase Silversides	
Big Billy Blue	1005-1730	In and on fringe of his territory--spent most of afternoon lying in shade of shrub	? - at 1005, lying out where he usually sleeps	9 m	3	1154-1205	None	None	
Randy Redtail	1005-1730	Within his territory; entire afternoon spent in one spot	? - usually sleeps out	7 m	3	1118-1158	None	Trotted 3 m towards approaching ♀ - she departed	
Silversides	1005-1550	Within and off territory	Before 1005	65-70 m	15	None from 1005-1550	Ate 11 Capparis leaves; moved to foraging area beyond view at 1550	Fight (on territory) with Bulbtail ³⁰	

Table 11 (Continued)

Iguana	Observation Period	Where Sighted	Time of Emergence	Distance Moved	Number of Movements	Interval(s) of		Amount of Foraging	Courtship/Agonistic Responses
						Active Basking			
FEMALES:									
Tricolored Trixie	1005-1730	Lying in crevice with Freddie and Fannie	Inactive	----	None	None	None	None	None
Pink-Flanked Fannie	1005-1730	Lying in crevice with Freddie and Trixie	Inactive	----	None	None	None	None	None
Redflanks	1149-1245	Emerged from crevice and moved beyond view at 1245	1149	30-35 m	5	1203-1245	Moved to foraging area beyond view at 1245	Departed as Randy approached	
Silvia	1645-1730	Beyond view between 1005 and 1645; returned to vicinity of her retreat at 1645	Before 1005	?	?	?	Unknown, but she was in foraging area most of the day		?
Unmarked and unidentified	1005-1015	Retreated to crevice and did not re-emerge**	Before 1005	?	?	?			?

* Fights between males are unusual during the non-breeding season.

** This female may have been frightened by my presence.

Table 12.-- Activity analysis for several iguanas observed at an inland depression on Mona Island, P.R., a sample taken two months prior to the onset of breeding in 1974. Weather was sunny with scattered clouds during all observation periods, except for 18 April which was overcast in the afternoon.

Iguana	Date Observed (Hours)	Activity (in %)		
		Sitting/Lying	Foraging	Other
MALES:				
Left Gold	16 Apr. (0930-1345)	97	0	3
	18 Apr. (1320-1905)	99	0	< 1
	19 Apr. (1122-1835)	100	0	< 1
	20 Apr. (1550-1850)	100	0	< 1
Rolo	18 Apr. (1400-1700)	81	19	< 1
Big Billy Blue	22 Apr. (0640-1230)	97	3	< 1
		(27 basking)		
Silersides	16 Apr. (0957-1345)	94	0	6
	19 Apr. (1122-1515)	75	25	< 1
	22 Apr. (0646-1230)	98	2	< 1
		(28 basking)		
FEMALES:				
Silvia	16 Apr. (0930-1345)	100	0	< 1
	18 Apr. (1320-1750)	100	0	< 1
Tricolored				
Trixie	16 Apr. (0930-1337)	97	0	3
Green Jeanie	20 Apr. (1550-1850)	100	0	< 1

Table 13.-- Activity analysis (in %) for three territorial male iguanas observed at an inland depression on Mona Island, P.R., a sample taken during the breeding season in 1974. Weather was sunny with scattered clouds throughout all three observations periods.

	<u>Left Gold</u>	<u>Randy Redtail</u>	<u>Twin Green</u>
Date	19 June	26 June	20 June
Hours Observed	0800-1445	0742-1301	0810-1541
ACTIVITY:			
Sitting/Lying (Basking)	82.5 (20)	88.4 (21)	82.4 (7)
Foraging	1.3	0.2	1.4
Patrol/Female-Seeking	12.4	10.9	11.2
Agonistic Encounters with Other ♂♂	1.3	0.0	1.9
Courtship Advances/Mating	2.5	0.5	3.1

Walking about but not foraging, overt social interactions, and defecation occupied the remaining 0 - 5.7% of the time. In all cases, overt social interaction comprised less than 1%. Even with the marked increase in activity observed during the breeding season, the vast majority of a territorial male's time is spent sitting or lying (Table 13).

¶ Similarly, Wilson & Lee (1974) found that the most conspicuous feature of a large herbivorous skink they studied in the field (Egernia cunninghami), was the short total period spent in activity. The skink's activity (foraging plus thermoregulatory movements) averaged 25.2 minutes per day on days when foraging was observed, and feeding apparently occurs on only one day in every two suitable basking days. Their estimate of food-gathering effectiveness, the percentage of metabolized energy used for requirements other than food-gathering, is between 91 and 95%. In neither iguana nor skink does availability of plant foods appear to be a limiting factor today.

I have here referred to "active" animals as those seen above ground and awake. It is not always clear whether an iguana should be considered active or inactive. An individual, for example, that passed the night sleeping on the surface may be found the following morning lying in the same position, awake and aware of what is happening around him and ready to respond if necessary, even though the usual signs of arousal (emergence and basking) have not occurred. Therefore, in evaluating activity times and temperatures in this section, I have avoided such ambiguity by using ^{only} sightings of animals moving to or from crevices, independent of any obvious social interactions.

Iguanas could be expected to emerge from nighttime retreats at any time during morning or early afternoon hours after surface air temperatures had reached at least 26°C ; they generally retired 1-2 hours before dark. The importance of temperature in limiting the onset of activity was particularly apparent on unusually cool, sunny mornings following nighttime rain: in such cases, arousal began late in the morning, only after the air had warmed to temperatures normally attained earlier in the day. Typically there was no noticeable change in activity during the hottest hours of the day or under windy or cloudy conditions; and, outside the breeding season, no sex or age related differences in activity periods were evident. Cloacal temperatures of two adult females, one that had been sleeping halfway inside a crevice and one that had just emerged from a retreat were 25.6°C and 26.7°C , respectively. Both readings were taken at mid-day when ambient air temperatures were 28.9°C , on 31 January and 1 February 1975.

The movement of iguanas back to sinkhole retreats for the night was the most synchronous of all daily activities observed (Fig. 13). Increasing daylength shifted the retirement period to later in the afternoon, as would be expected, and late afternoon rainfall promoted somewhat earlier movement back to the sink. Recurrent sightings of two females (of approximately equal size) showed a trend in one (Tricolored Trixie) to return relatively early, while the other (Green Jeanie) was clearly inconsistent in this respect.

Eleven iguanas were observed during rain showers varying from a sprinkle to a downpour. One female twice retreated at the onset of

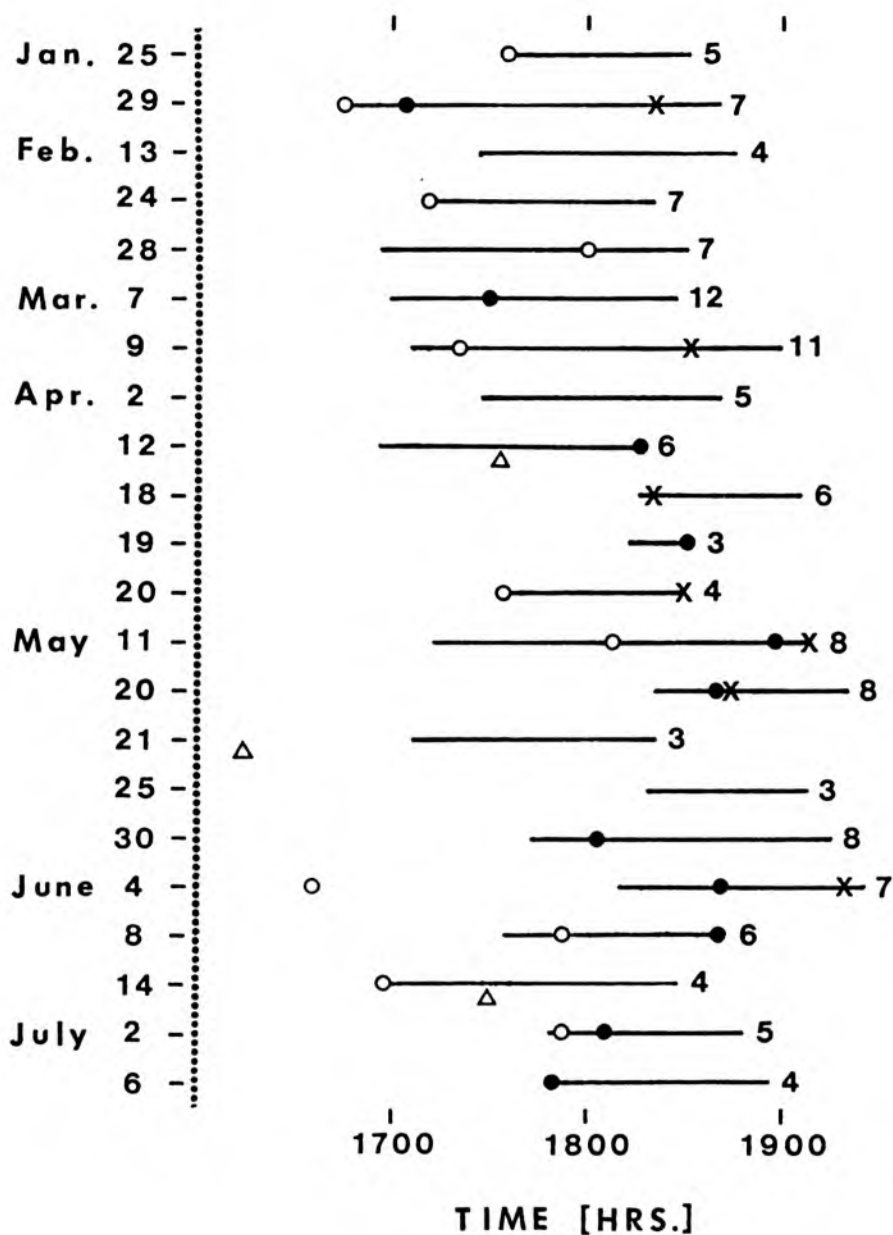


Fig. 13.--Periods during which three or more iguanas were observed retreating to nighttime retreats at an inland depression on Mona I., P. R., in 1974. The number of iguanas seen entering crevices is given at the end of each line. Recurrent records for three individuals are shown: Tricolored Trixie, open circles; Green Jeanie, solid circles; Four-toed Freddie, "X's". Triangles below a line indicate onset of rainfall.

light rains. The other animals appeared to welcome rainfall; they remained active throughout and most drank. To cite one example, on 16 July 1973, two males present at a sinkhole depression when a mid-afternoon downpour began started drinking as water collected in small solution pits in the rock. One drank four times and then began rubbing his left side against rocks and a tree trunk. The other drank nine times, each 30-60 seconds in duration, and rested for intervals of about two minutes between drinks. He, too, walked about afterwards, rubbing the sides of his body and tail against rocks and trees. He lay down, rose 20 minutes later to scratch his right jowl muscle against a rock, and finally reclined in the wet leaves again. When rainfall is insufficient to permit drinking from puddles, iguanas may lick water from the rocks. Nesting females paused to drink from rain puddles and carried on with nesting activities in the rain. On three occasions I also noted that one of the females fitted with a radio-transmitter collar slept out during nighttime showers, the heaviest amounting to 1.0 cm between 21h00-23h30, during which time the air temperature dropped from 26.5°C to 22.6°C.

Nights are spent sleeping underground or on the surface near a retreat. The only individuals known to sleep above ground habitually were four males at La Bajurita, all of which held territories there year-round. Non-territorial males at that site invariably retired to crevices for the night. One female who was also territorial often spent the night sleeping out, the others doing so only occasionally, if ever--in most such instances, exposed females were lying partially

protected under rock ledges. Males in particular are sound sleepers: When I marked one using a rubber-tipped dart at close range, the dart struck his side with a hollow "thump" and bounced off, but he never opened an eye or altered his breathing. The usual sleeping posture is prone with one or both arms tucked backwards alongside the body. Nesting females seek shelter for the night near nesting areas, but when none is available, they sleep on the ground amid plant cover. Gravid females which have nearly completed a nest burrow often pass the night within it, and on occasions they continue digging after dark.

I observed no significant seasonal changes in abundance of iguanas at La Bajurita (see Table 5) or seasonal shifts in basking behavior. Activity was, however, greatest on days following appreciable rainfall ending prolonged dry spells. This was most striking at La Bajurita in early March 1974 after the area received nearly 4.5 cm of rain between 28 February and 3 March, immediately following the year's driest month. The number of iguanas seen there rose to all-time highs of 22 and 24 animals (55% and 63% of which were marked individuals) on 7 and 9 March, roughly twice the overall daily average (Table 5). Similarly, on 19 May 20 iguanas (80% having I.D. marks) were seen active after the close of a 16-day rainless period. In both cases, all rain fell during the night; and curiously, the increase in activity occurred not the day after the first appreciable rainfall (>1 cm) breaking the dry spell, but rather six days later, only after additional rain (>1 cm) had fallen.

The above observations suggest that a segment of the Mona iguana population is usually underground, even during weather conditions normal

for activity. This contention is supported by two other lines of evidence: First, individuals were often seen resting all day in crevices or in shade on the surface when other iguanas were up and about. Three such animals I am certain never left their retreats for at least two consecutive days. It was a rare occasion that I did not find one or more iguanas totally inactive throughout each observation period. Second, crevice-seeking is the principal manner in which both males and females avoid or terminate aggression from conspecifics (see Territoriality, Courtship, & Mating).

As pointed out by Cowles and Bogert (1944) and elaborated upon by many others since that time, a reptile can readily adjust its body temperature by changing its position, orientation, posture, or color. Although no color modifications were noticed in Mona Iguanas, several behavioral traits associated with acquiring heat were observed. These lizards typically begin the day with a warm-up session. The iguana may walk straight from its hole to a patch of sunlight, but most first spend a few minutes to an hour sitting in the shade by the retreat entrance. The basking posture and orientation most commonly assumed by iguanas just beginning to warm up is unchanged year-round and highly stereotyped: hind legs widely spaced and flat on the ground; front legs fairly straight, elevating the forequarters; the head held high, with eyes sometimes closed; and the body presented broadside to the sun. On unusually windy, cool, cloudy mornings, iguanas were seen basking flattened against the rock substrate. This prostrate posture was frequently used by individuals basking on leaf-litter in sinkhole depressions later

in the day. Lying flat would enable the animal to receive heat from a relatively warm substrate in addition to that gained from direct solar radiation. On clear, sunny days, uninterrupted periods of basking lasted for 20-80 minutes. Residents of the sink either move to sunnier areas around the periphery of the depression to bask where the canopy thins or keep moving from one shifting patch of sunlight to another or do both. For example, during a 6.6-hr. morning to early afternoon observation period at La Bajurita, the male occupying the floor of the depression spent 10 short intervals (2-14 minutes each) basking, a total of 65 minutes basking time. "Passive basking" was also noted, the animal just resting in one place and catching whatever sunlight happens to cross that spot as the day progresses.

Basking is not a prerequisite to feeding, defecation, courtship, or aggressive behavior. Although most foraging occurs later in the day, a brief foraging interval, often accompanied by defecation, commonly precedes initial morning basking. On one occasion I observed an iguana consume 14 Capparis flexuosa leaves during a 7-minute circuitous walk from his retreat to a basking site--this represents a respectable-sized meal. Pre-basking courtship displays were often seen. Twice I witnessed early morning chases initiated by males that had emerged from their retreats 8 and 24 minutes before, the intervals spent sitting in total shade ($AT=27.0^{\circ}C$ and $28.0^{\circ}C$). In these two instances I was certain that no basking in either full or partial sun had preceded the encounters.

Cloacal temperatures of seven adult iguanas were measured immediately after capture. As already mentioned temperatures of two

females, one that was sleeping halfway inside a crevice and one that had just emerged from her retreat, were 25.6°C and 26.7°C , respectively, when ambient mid-day air temperatures were 28.9°C . Two territorial males captured when air temperatures were 30.6°C and 31.1°C , and nearby rock substrata in the sun measured 38.3°C and 40.0°C , had cloacal temperatures of 37.8°C and 36.2°C , respectively. Three others taken in late afternoon hours were 35.8°C ($\text{AT}=29.5^{\circ}\text{C}$), 37.3°C , and 36.8°C , the last from a gravid female at a nesting area. These sample temperatures fall within the normal activity range reported by Carey (1975) for the Anegada Ground Iguana Cyclura pinguis.

Movements and Home Range:

Daily activities normally begin and end in close proximity to retreats, and social activity is centralized there. Movements into peripheral areas apparently relate principally to the acquisition of food, which as mentioned above, varies in quantity and quality throughout the year (see Foraging Behavior and Diet). While the density and diversity of inland retreats are highest around sinks, the understory in depression forests is thin and food is relatively scarce, a situation caused or at least aggravated by the presence of feral goats and pigs (see Associations with Man & Other Animals). Few iguanas leaving La Bajurita could be followed into the scrubby undergrowth without alarming them. Marked resident iguanas that were occasionally sighted in peripheral areas were all within 100 m of the sinkhole depression.

Individuals occupying the same retreat or retreat complex consistently exited and entered from the same general direction (see

Figs. 21 and 22), yet there is no evidence that any were defending territories in feeding areas beyond the sink. Although no encounters between iguanas in the shrub thicket were seen, the unlikelihood of territoriality in these peripheral areas can be inferred from the near absence of chases heard there--an iguana crashing through the brush in hot pursuit of another would be difficult to miss.

The movements of two females captured at La Bajurita were monitored by radio-telemetry for one month in February 1975, during the non-breeding season. One, Tricolored Trixie, was a local resident I had observed for a year; the other, younger and unknown to me, had a distinctive appearance (she was missing one toe and four others were deformed. Trixie remained hidden in a crevice during the first five days after being captured and released. I suspect this was in response to the trauma of being noosed and handled. Thereafter she resumed what appeared to be normal activity during daylight hours, moving from a crevice in the morning and heading northward into the shrub thicket. On two occasions I located her lying alone approximately 30 and 50 m from the depression: once in a grove of Ficus trees and once in a field dominated by Croton discolor, Plumeria obtusa, and Reynosia uncinata shrubs. Five times I sighted her returning to the sink between 15h25 and 17h30, at air temperatures ranging from 26°C to 29°C (see Fig. 13 for 11 additional records from 1974). She utilized two different retreats about 15 m apart; and on two of eight tracking days (subsequent to the initial five), she had remained inactive or had retired early. On those occasions she was found underground in mid-afternoon, once on a

cloudy day ($AT=28^{\circ}C$) and once on a clear, sunny day ($AT=27.8^{\circ}C$).

The second female (LR3), presumed to have been a transient individual at the site of capture, was followed more closely. She passed the first two days hiding underground and two days later was tracked to a site in the cactus forest 0.4 km from the sink. During the subsequent three weeks, she remained relatively sedentary, having limited her activities to an area not exceeding 1400 m^2 in size. The area was also occupied by a male and contained two retreats 23 m apart. LR3 shuttled back and forth between retreats every 2-3 days, and consistently (checked on 11 occasions) spent the night sleeping on the surface in the vicinity of one hole or the other. On one occasion, I was able to determine that she had spent the entire day within a crevice and then emerged sometime between 16h05 ($AT=27^{\circ}C$) and 21h20 ($AT=24^{\circ}C$) to sleep on the surface that night. The transmitter died on 27 February, and to remove the collar, I recaptured her at night on 1 April at one of the sites where she often slept.

Female LR3's 0.4-km movement made shortly after being transmitter-tagged deserves special consideration. Being handled may have motivated this long-distance move, but her subsequent behavior suggests that she had returned to an area with which she was already quite familiar. So what, then, was she doing at the sink in the first place?

Possibly exploratory forays afield are not unusual. Retreats, nest sites, and many favorite food sources (especially fruiting trees) are patchy in distribution on Mona, and familiarity with a large area acquired through experience over many years would appear highly adaptive.

Although about one-third of the marked iguanas studied at La Bajurita were seen there regularly year-round (apart from the nesting season), often the whereabouts of the others remained open to question. While a segment of the population is presumed to be normally underground and inactive, some individuals reappear with sufficient irregularity to suggest that they may be oscillating between residency there and elsewhere (see examples--the short-term strategists--in Fig. 27). Data already presented from a study area on the southeastern coastal terrace indicate that such seasonal shifts in residency do, in fact, occur: retreats normally vacant in the manchineel forest are occupied when fruit is available (see Fig. 12).

Both males and females are proficient long-distance "navigators" (in the broad sense of the term). After removing a male from his territory for studies of social readjustments among the remaining iguanas in his absence, I discovered the animal's capacity for homing. He was captured at night, carried in a nylon sack to the lighthouse, and kept indoors for seven weeks. I released him at noon 0.4 km from his home site. When visiting the area two weeks later, I found he had returned. Having been preoccupied with studies elsewhere during that two-week period, I do not know how many days the iguana had spent in transit.

Year after year females journey to what appear to be traditional nesting grounds. By capturing two nesting females and giving them collars equipped with radio transmitters to permit studies of their post-nesting movements, I had hoped to learn where these animals travel to reach nesting areas. Both females, one gravid and one spent, were

radio-tagged near Punta Arenas on 23 July 1974. The spent female (green collar) was Frieda Flagtail, an iguana that had nested in the same area the three successive years of my investigation. She remained hidden in a pile of debris for two-and-one-half days after the capture and then departed. The gravid female (orange collar) passed one day in hiding and then resumed nesting activities. She disappeared the morning of the third day.

Because the equipment performed poorly, neither female could be radio-tracked once they had left the nesting area on the southwestern coastal plain, but two resightings were reported since then. Orange Collar was seen at close range by a visiting student on 26 March 1975, upon the plateau at the cliffside in the vicinity of Punta Capitán, a distance of approximately 3.5 km from the nesting area. On 15 November 1975, a DNR biologist, Elizabeth Litovitch, sighted one of the collared iguanas about halfway across El Camino del Infierno, a straight-line distance of 6.5 km from Punta Arenas. Since the second sighting was in the opposite direction from the first, it is likely that this was Frieda. Also, it is certain that all females nesting near Punta Arenas migrate at least the 0.5-km distance across Cabo Oeste (see Fig. 1); this part of the island has a natural scarcity of retreats, receives heavy human use, and is seldom travelled by iguanas during the non-nesting season.

Discussion:

Sporadic Activity as an Adaptive Strategy.--In recent years it has become increasingly apparent that behavioral thermoregulation in lizards

is a phenomenon sensitive to a wide array of ecological variables. A number of authors--most notably Regal (1967, 1968) and Case (1976)--have found that lizards can undergo daily and seasonal shifts in thermal preferenda under laboratory conditions. Regal (1971) also demonstrated through ingenious laboratory experiments that social relationships can affect thermal activity. Huey (1974) found that in open habitats the tropical Puerto Rican lizard Anolis cristatellus carefully regulates its body temperature by shuttling back and forth between sun and shade, but in an adjacent forest, where basking sites were few and distant, the species passively tolerates lower and more variable temperatures. Huey speculates that this behavioral/physiological difference is due to higher costs associated with achieving and maintaining a high body temperature in forested habitats; costs can involve time, energy, or physical risk inherent in shuttling behavior. The above investigators have helped to show that a lizard's behavioral adjustments of body temperature can be viewed as an adaptive strategy, molded by both endogenous and exogenous factors. Following this line of thought, I postulate that the irregularities and inconsistencies in the activity regimen of Mona's iguanas are socioecological adaptations geared to minimizing metabolic expenditures.

Since Mona Iguanas are not active every day, we can speculate on theoretical grounds that costs associated with initiating activity and maintaining a high body temperature sometimes outweigh the benefits. What might these costs be? Time and effort demanded by basking appear negligible. For most individuals, suitable basking sites are no more

than 10 m from retreats, and weather is generally favorable throughout the year for achieving normal activity temperatures. Furthermore, the iguanas are obviously not time-limited. Another potential cost of significance to many lizards is increased vulnerability to predation--this, too, can be eliminated from consideration here. Two factors remain that might act to discourage consistent activity: 1) social pressure, and 2) the periodicity with which water and preferred foods become available.

Social pressure from conspecifics is undoubtedly an important determinant of activity in some individuals. During the breeding season there was intense aggressive pressure from territorial males on females and subordinate males to remain within crevices (see Territoriality, Courtship, & Mating). Though aggression from dominant animals is generally less intense outside the breeding season, other members of a social group may be able to minimize confrontations through staggered activity times.

Social factors, however, cannot alone explain the consistently sporadic nature of basking and foraging. It is noteworthy that all individuals observed with regularity, regardless of sex or social rank, spent days of nearly total inactivity even though conditions were warm and sunny and others were moving about. Where iguanas remained inactive differed, however. Individuals that would benefit most by remaining conspicuous, i.e., dominant animals, spent most periods of rest, including nights, at the surface. Less dominant animals were seen less frequently above ground and characteristically retired to crevices at night.

The temporal distribution of food resources is a critical factor in determining activity patterns of many animals and may be of central importance to the Mona Iguana. While some plant foods are always available, items of greatest significance in the iguana's diet (fruits and large, slow-moving insects) tend to be ephemeral and are to a great extent unpredictable in occurrence (see Foraging Behavior & Diet). What foraging strategy would permit the iguana to minimize energy expenditures yet capitalize upon transient food crops of special nutritional value? Since the animal has no daily foraging requirement, occasional forays afield to monitor the current status of food resources available within its home range would appear to be the most economical approach. As particularly desirable items come into season, the iguana might be expected to shift temporarily to a retreat closer to the supply or to keep returning until the resource is exhausted or spoiled. (Such changes in residency accompanying periods of localized fruit availability were documented in one study area--see Fig. 12.) Reserves so acquired could sustain the animal during lean intervening periods and provide the major input for growth and reproduction. Some intense radio-telemetry work over a period of several months is needed to test this hypothesis.

One of the smallest representatives of the genus Cyclura, the Caicos Island Iguana, Cyclura carinata, affords a striking contrast to the Mona Iguana in activity pattern. Weather permitting, Caicos Iguanas are active every day, consistently accompanied by one or more foraging periods (D. Auth, pers. comm.; Iverson, 1977) averaging 108 minutes

each (W. Auffenberg, unpubl. data). Although diet is qualitatively very similar in both species (W. Auffenberg, unpubl. data for C. carinata), C. carinata is under significantly different physiological and ecological constraints that would appear to account for this behavioral difference. Situated further north and on smaller islands with lower structural and biotic diversity, the Caicos populations examined occupy a thermally more variable environment, with activity largely reduced during winter months (D. Auth, pers. comm.), and presumably have fewer feeding options. Furthermore, with the small body size of C. carinata, a higher metabolic rate is to be expected during activity, and this iguana's ability to withstand desiccation and periods of food shortage is undoubtedly less than that of C. stejnegeri. Food availability and accessibility appears to be a limiting factor for the C. carinata population on Pine Cay (Iverson, 1977). Whether the activity regimen of Mona's iguanas was different before man's arrival, when iguana density was assuredly greater than it is today, is unknown. I doubt, though, that food would have reached a critical level before nest-site availability became limiting to the Mona population (see Nesting Biology).

Nesting Migrations.--Long-range movements would appear to be a normal occurrence on Mona and in other comparable Cyclura habitats where surface soils are thin and suitable nest sites are few (see Nesting Biology). Thus far, however, the only other well documented evidence of long-distance nesting migrations in lizards is for the Green Iguana, Iguana iguana, on Barro Colorado Island in the Panama Canal Zone.

Montgomery et al. (1973) followed the post-nesting movements of four I.

iguana that swam to nest on Slothia, an islet adjacent to Barro Colorado, and found that upon returning to Barro Colorado, the four females continued travelling for distances of 300 m, 950 m, 2.15 km, and 3.0 km into the depths of the monsoon forest. In this ecological setting the availability of favorable nest sites appears limited by the presence of nest predators native to Barro Colorado and by "shading-out" from the dense tropical understory and canopy vegetation (Rand, 1968a). Even on Mona where the canopy is comparatively thin, sites receiving shade much of the day are not used for nesting. Both iguana populations nest in aggregations (see Nesting Biology), and as noted by Rand, group nest-digging tills the soil and effectively keeps clearings open by destroying new plant growth. This action has been intensified on Mona through overbrowsing by feral goats and rooting by pigs.

How and when do female iguanas learn where suitable nest sites are located? During the nesting season, there is conspicuous and widespread trial-and-error digging on Mona's plateau, suggesting that females acquire a migration pattern through experience. Once a female has encountered a site that "looks" and "feels" right, the best strategy to adopt would be to return to that spot the next year and continue doing so as long as conditions remain favorable there. If such finds occur largely by chance, one would expect that a female might not necessarily encounter equally attractive sites that are nearer to her normal activity area. My observations agree with those of Montgomery et al. (1973), who puzzled over the finding that some females travel considerably greater distances to nest than would appear "necessary,"

assuming each did indeed migrate from and to a single home area. We cannot assume that female iguanas have a working knowledge of all parts of their home island, and choice of a migration route is probably limited by individual experience. The possibility of a genetically or experientially acquired (through imprinting) ability to return to nest at the site where the female was born merits investigation.

A recent study of the migratory movements of the snake Coluber constrictor to and from winter hibernacula revealed that a formative period may exist during which dispersal distance and direction, as well as the home range occupied, become "fixed" behavioral attributes in many members of the population (Brown & Parker, 1976). I suspect that such an ontogenetic process may be operative in iguanas, and that further radio-telemetry work would be most profitably spent examining movement patterns of newly matured females throughout two or more full years in succession.

FORM AND FUNCTION OF DISPLAYS

Visual displays involving stereotyped body movements and postures play the primary role in communication systems among iguanid and agamid lizards. Such displays are commonly accompanied by exhibition of colors or color patterns that facilitate species or sex recognition (e.g., Harris, 1964; Ferguson, 1966; Williams & Rand, 1977). Sexual dimorphism is often striking, and where it occurs, males are characteristically the larger and more ornamented sex, showing not only more brilliant coloration but also accessory structures like enlarged mid-dorsal crests and extensible throat fans (dewlaps). As already mentioned, Cyclura stejnegeri is a curious exception--males and females show no dimorphism in color, pattern, cephalic horns, crest development, or dewlap size, and there is relatively little difference in adult body form and size. Even among cycluran iguanas, such extreme monomorphism is unusual. Evolutionary factors that have promoted this male/female convergence in appearance will be considered in a later section. Focus here is on body movements and postures employed by these animals during social encounters, with emphasis on context and display intensity.

There are two fundamental differences in the head display movements of the Mona Iguana from those of all other iguanid lizards that have been described: 1) most displays are three-dimensional, i.e., the head is elevated and tilted or rolled simultaneously; and 2) they are very loosely structured, the form of the display being particularly variable and context-dependent.

Quantifying three-dimensional display movements can be done properly only with the aid of two cameras running simultaneously. The displays need to be filmed from both frontal and lateral views to provide information on head rotation and amplitude attained during the display; this was done, but necessarily on different occasions since I had only one camera. Instead of employing a linear measurement as is usually done, I have expressed "amplitude" in degrees through which the head swings upward between the onset and peak of the display and "tilt" in degrees rotated on its axis. By using this approach, it was possible to make comparative measurements from movie footage taken in the field without having to cope with discrepancies in subject size and camera-subject distance. Only display sequences filmed directly head-on or lateral to the animal were quantified, though many others were studied in slow motion for gross evaluation. In all "bobbing" (used here in the broadest sense), movement occurs in the head and forequarters only and does not involve "push-ups."

The iguanas' head-bobbing displays fall into three main classes: shallow bobs, tosses, and rolls. Characteristics of each are depicted in Fig. 14. Frame-by-frame analysis of 158 displays from nine individuals helped strengthen my overall impression that display types are highly graded in use (see Table 14). Display intensity and the manner in which display units (e.g., one unit = one head toss) are arranged into sequences are, however, sufficiently animal- and situation-dependent to preclude precise analyses from such fragmentary data. Whether tosses or rolls are given does not appear to relate to the

Fig. 14.--Characteristics of head movements in displays of the Mona Iguana. Amplitude is the arc described between the onset and peak of the display as viewed laterally; tilt is the extent to which the head is rotated on its axis during the course of the display, as viewed frontally. Numbers indicate sample size, the mean value being shown as a solid line within dashed lines representing the limits of the range. "Bobs" are single display units from the "multibob" performance (Bob duration = 0.21 sec., N=2). Tosses ("R") given in combination with the female "head-up, tail-up" rejection posture (Toss duration = 0.25 sec., N=6) are grouped separately from those ("C") observed in all other contexts (\bar{x} = 0.39 sec., Range 0.21-0.58, N=76). Rolls are treated as full-cycle displays, i.e., ending in roughly the same position as they began (\bar{x} = 0.46 sec., Range 0.37-0.58, N=17).

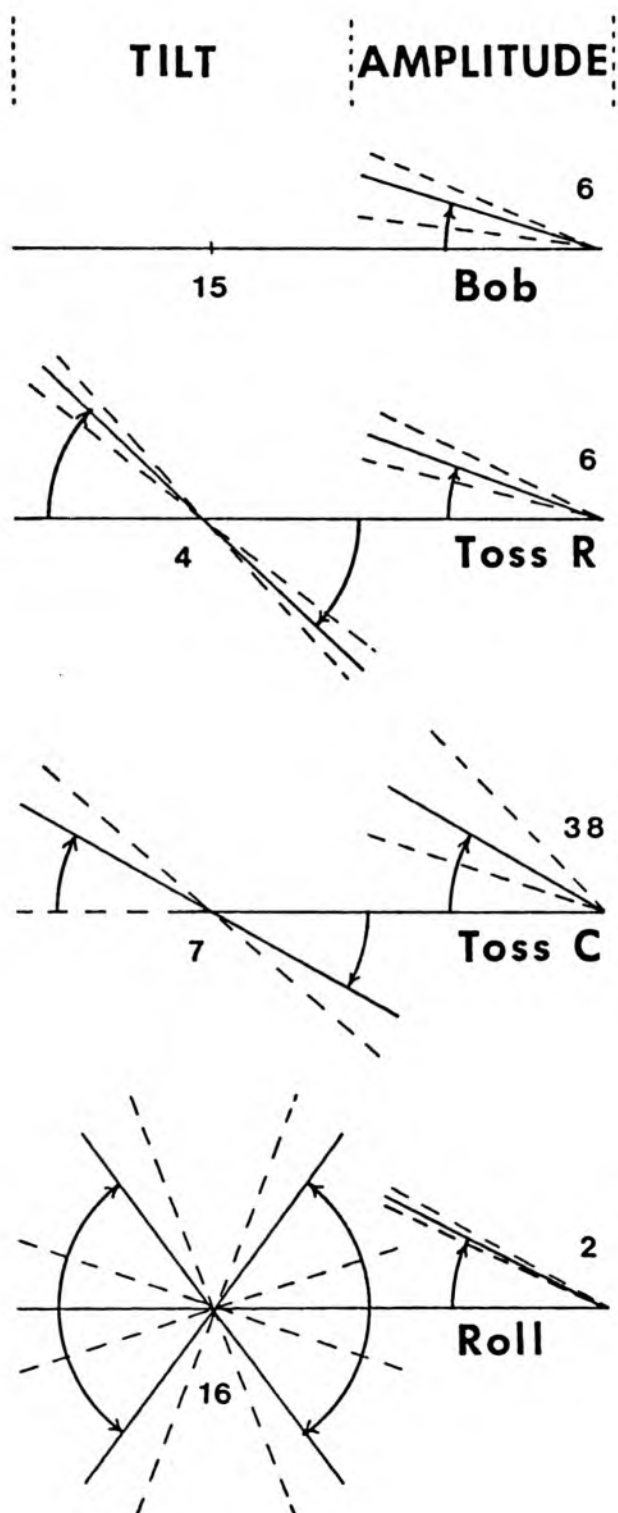


Table 14.--Repertoire of head displays of the Mona Iguana.

Head Display Form	Function and Context
<p>MULTIBOB:</p> <ul style="list-style-type: none"> - shallow vertical head jerks, typically in series of 2-5 - mouth closed <p>I° TOSSES OR ROLLS:</p> <ul style="list-style-type: none"> - given singly or in sets, usually < 8 display units/set - display form smoother and amplitude usually higher than multibob - tosses and rolls seldom combined in a single display set - mouth closed - those given by females rejecting a male's advances appear relatively shallow and rhythmical <p>II° TOSSES OR ROLLS:</p> <ul style="list-style-type: none"> - typically given in sets of 5-20 display units/set - rolls usually given in a discrete series of 4-10 at onset or between tosses - display set occasionally includes toss-rolls - successive tosses usually separated by latency intervals of 0.8-2.0 sec. - mouth partially open during rolls and closed to wide open during tosses <p>TOSS-ROLLS (HEAD BOUNCING):</p> <ul style="list-style-type: none"> - erratic combination of toss and roll displays--the two merge completely with no apparent sequencing - latency intervals extremely short (< 0.5 sec) or absent altogether - mouth open, often wide open, throughout - tongue engorged with blood 	<p>EXPRESSION OF UNEASINESS:</p> <ul style="list-style-type: none"> - commonly given by young animals in midst of larger individuals and by iguanas confronted with strange objects or situations <p>ADVERTISEMENT/MODERATE ASSERTION:</p> <ul style="list-style-type: none"> - typical response of large males near safety of a retreat when approached slowly by man - given by non-territorial males attempting to establish territory on fringe of another's territory - commonly seen during male-female encounters and during female-female encounters - used by females in combination with courtship rejection posture, i.e. head and rump high, chest low, tail arched <p>STRONG ASSERTION/COURTSHIP:</p> <ul style="list-style-type: none"> - response of territorial female to intruding female, often followed by chase - frequent exchanges between females in close proximity (1-3 m apart) at nesting areas - courtship displays given by males during and outside breeding season <p>COURTSHIP/ULTRA-HIGH LEVEL OF EXCITEMENT:</p> <ul style="list-style-type: none"> - juveniles defending a retreat entrance from within against other juveniles of comparable size - females defending a deep nest hole while stationed in its entrance - courting males, especially during breeding season

DISPLAY
INTENSITY

relative orientations of displayer and the displayee. Structurally the two display forms merge indistinguishably into toss-rolls, which superficially look more like head bouncing than either tossing or rolling. Functionally, rolls generally suggest a higher level of excitement or a greater degree of assertion than tosses, while bounces, their structural intermediate, indicate maximal arousal. Displays given with the mouth open are always of relatively high intensity. On three occasions, I noticed that resident female iguanas confronted by intruding females displayed with low intensity head rolls, while the intruder responded with shallow, vertical head bobs. Such bobs usually appear in sets, i.e., multibob patterns, and are given by animals under circumstances demanding caution. The name "multibob" I have borrowed from Stamps & Barlow's (1973) paper on Anolis aeneus, for the term is an appropriate description of the display act and its occurrence matches contextually (see Table 14). This display has been unambiguously described for several other species of iguanid lizards, yet there has been confusion over its functional significance, accompanied by the introduction of differing terminology for it, e.g., "assertion" display. Stamps & Barlow have reviewed this issue.

Another display that has been cited by a number of authors and ascribed different functions is given by females (and sometimes males) in response to a courting male (see references in Carpenter, 1967). The female rises on all four legs and presents herself caudally or caudo-laterally to the approaching male, arching her tail. Cyclura stejnegeri females also hold their heads at an elevated angle of about 23° (Range

19-33⁰, N=5) above the horizontal plane, accompanied by shallow, often rhythmical head tosses or rolls (see Figs. 14 & 17B). The female may sidle away from the male or simply retreat slowly to a nearby crevice. Sometimes a female remains stationary, holding this "head-up, tail-up" posture, in which case the male moves in for close investigation of her cloacal area, checking it with tongue flicks. This suggests to me that there may be a sex- or season-specific olfactory cue, enhanced by a posture that superficially appears to be a sexual offering. Often, however, when the male noses in close, she strikes his head with the side of her tail, thereby discouraging his interest. In no instance did I see a female give the "head-up, tail-up" display during the mating season. My observations indicate that this is clearly a rejection display, agreeing with Carpenter's (1967) evaluation. Incidentally, several other authors (cited by Carpenter, 1967) have suggested that this display serves an "enticement" function. It is easy to see how such a posture could be misinterpreted, but the possibility remains that in some species the display signals sexual readiness.

Activities of two gravid females filmed simultaneously while nesting illustrate the way in which display form, patterning, and intensity relate to motivation. Debbie Drytail, a medium-size female, was actively digging in hole #9, when a medium-large female, Frieda Flagtail, ambled over to investigate. Frieda paused, gave a series of six toss-rolls with mouth partially open and then moved closer. Standing at the edge of the hole, peering at the tail of the busy occupant within, Frieda, with mouth open again, displayed a set of four head rolls immediately followed by three tosses towards her right shoulder and then two

towards her left (her mouth almost closed during the last two). Debbie backed out of the hole, and a confrontation immediately erupted with a violent exchange of bites; this was the third such dispute to have arisen between these females over rights to hole 9 in the course of an hour. Frieda ended up next to the nest hole, with Debbie about 1.5 m away. The exchange of displays that followed is shown in Fig. 15. The victor, Frieda, gave an exhibition of emphatic gestures, varying in pattern and intensity as a function of Debbie's responses: both toss amplitude and the latent period between successive tosses were clearly related to the timing of Debbie's toss displays. The appearance of toss-rolls, as already mentioned, suggests a higher level of excitement, even though amplitude of the display units is relatively low. Frieda's mouth-opening and closing was unexpectedly erratic and was sometimes accompanied by jaw-licking, indicating she had probably hurt her jaw or tongue during the fight. Debbie turned away, moving off to the shaded periphery of the nesting area, and Frieda then began digging in hole 9. For no apparent reason, Frieda found the hole unsuitable, abandoned it only a couple of minutes later, and started a new hole (#24). Debbie made a dash for the vacated hole and resumed digging. After 13 minutes, Frieda vacated hole 24, returned to the proximity of hole 9, and began head roll displays. Debbie responded from the entrance with emphatic head bounces (toss-rolls), tongue engorged with blood and mouth wide open. Frieda then moved on to dig in hole #7. During the subsequent hour, Debbie finished excavating hole 9 and began egg laying.

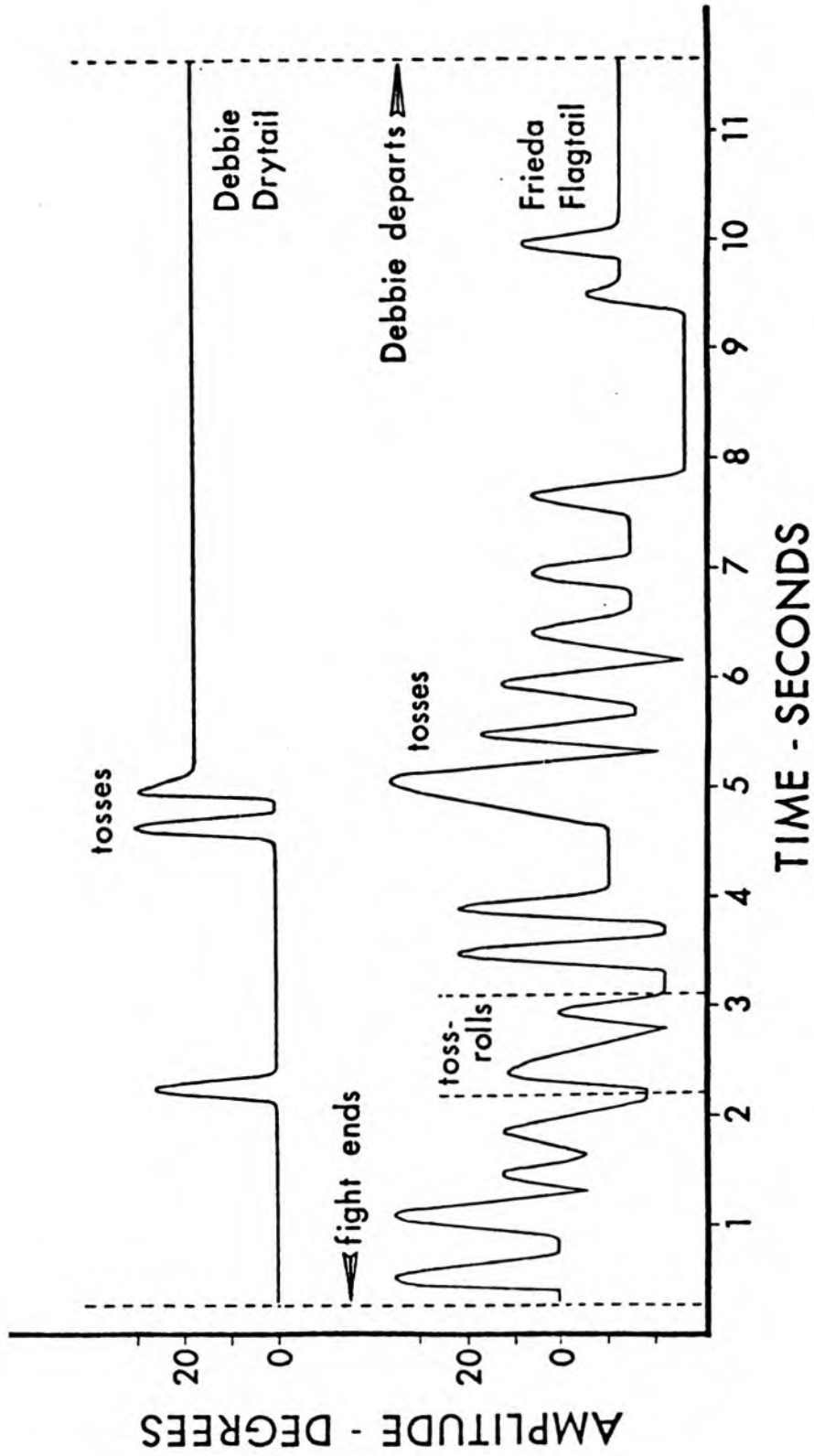


Fig. 15.--Exchange of displays between two gravid female iguanas following a fight over a nest burrow at coastal nesting area S-14a, Mona I., P. R. Amplitude is the arc described between the onset and peak of the head movement as viewed laterally.

Decoy Experiments:

Fifteen experimental trials were conducted with a stuffed Cyclura cornuta having the body size and appearance of an adult C. stejnegeri; this specimen (Fig. 16) was part of an old diorama at the American Museum of Natural History, a loan from the Dept. of Herpetology. The dummy was presented to 12 different individuals (seven adult males, four adult females, and one small juvenile). In all instances it was either placed in a spot where I expected an iguana to discover it while moving about or was positioned in the animal's presence, concealed under a burlap cover and later unveiled by pulling a string several meters away.

Two female iguanas completely ignored the decoy, the other nine adults were attracted by it, and the juvenile avoided it. One female (on 15 May) approached head on, rose up in a broadside challenge posture, stumbled, fell off balance, and after regaining her composure, sat by the decoy, yawned, tossed her head a few times, and departed. Three males also expressed relatively little interest in the dummy (on 16 and 23 April). In one case it was placed about 1 m from the retreat of Peter Pinktail, who customarily defended that area from intruding males. Peter walked over to it, giving it a casual inspection, tossed his head high a couple of times, and then just sat in front of it, doing nothing. In another instance, the decoy was uncovered about 2 m from a basking male, Four-toed Freddie, who noticed it immediately but did not investigate until a few minutes later. He circled it once, giving no displays. Suddenly male Silversides appeared and chased Freddie into a crevice several meters away, practically running over the dummy in the

Fig. 16.--Cyclura cornuta decoy used in experimental field response trials on Mona I., P. R. Top: Adult territorial male (left) courts the unaltered dummy. Bottom: Decoy with plaster caps on its jowl muscles, which evoked attack by a territorial male.



process. Silversides then returned to the decoy but expressed no further interest in it.

One female, Silvia, encountered the decoy on four occasions (19 and 22 April, 11 and 19 May). She shared a retreat in the NW side of La Bajurita with male Rolo and actively defended the vicinity of the hole (within a radius of about 4 m) from other females; intruders were chased from the area, or, more typically, driven into hiding underground. In all four experimental trials the decoy was placed out of view about 2 m from Silvia's retreat, along the route she and Rolo often followed when foraging. On her first encounter, while returning home from the shrub thicket adjacent to the sink, she sighted it about 3 m away, responded with high and low amplitude head tosses, walked closer, paused, and displayed; she continued doing so for seven minutes until standing face-to-face with it. Silvia gave some high amplitude tosses, interjecting a few shallow tosses, and then rose into a full challenge display (see Fig. 18B): body arched and laterally compressed, crest and tail stiff, chin up and throat bloated--all accompanied by a prance back and forth in front of the decoy. She paused near its head, tossing her head high with mouth partially open, displays that continued off and on for three minutes. Finally she lashed the dummy severely with her tail and within a minute seemed calmer, lying down beside it. Eight minutes later she was up and circling again with renewed threat gestures terminating in a quick "body-snap," delivering a bite to its back and a simultaneous tail-lash to its head (see Fig. 18J). Her response three days later never advanced beyond assertive head tosses and rolls, but

three weeks later she repeated the same escalated sequence with one addition: just before assuming the challenge posture, she paused and huffed loudly a few centimeters from the decoy's face. The fourth trial, eight days after the third, yielded a lower intensity response than the second: Silvia approached with head-tossing and then reclined in the leaves about 1 m away, giving occasional shallow tosses from that position. Her drop in responsiveness on trials 2 and 4 suggest habituation since both occurred relatively soon after trials 1 and 3, another indication that these lizards can learn rapidly.

Some of Silvia's head-tossing display sequences towards the decoy were filmed and analyzed, revealing more information that relates to the interpretation of Fig. 15. In the presence of an unchanging stimulus (the decoy), all intra-individual differences in display, except for a certain amount of structural variation that would be expected even if the same performance were repeated time after time, are presumably due to changes in motivation. The variation found in Silvia's reaction to the decoy clearly exceeds anything yet reported for iguanid lizards (e.g., see Jenssen, 1971; Stamps & Barlow, 1973; Berry, 1974). Tosses occurred singly or in series with as many as eight in a sequence. In one sequence, for example, Silvia gave a discrete series of eight tosses with time intervals of 0.08/0.08/0.21/0.58/ 1.21/1.50/2.21 seconds between consecutive tosses; in another instance, she began with four full head roll cycles lapsing immediately into a series of 13 tosses spaced by intervals of 0.08/0.42/0.33/0.83/1.04/ 2.87/0.33/0.13/1.37/ 0.21/0.54/0.96 sec. I suspect, however, from the nature of this latter

progression that it is really two toss sequences separated by a 2.87-sec. time interval. Earlier displays in each sequence also tend to have greater amplitudes. It therefore appears that Frieda's display pattern in Fig. 15 represents three run-on display sequences, the second and third triggered by Debbie's tosses, thereby truncating the first and second. Had Debbie not displayed at all, Frieda's displays during the first two seconds would have probably been succeeded by several low amplitude tosses somewhat similar to those seen in the 6.5- to 10.5-second part of the time scale. Thus, the sequencing of display units and the cadence of each display performance are loosely organized and highly motivation/stimulus dependent. The same characteristics are evident in male displays. While there is a possibility that cues used for individual recognition are somehow encoded in the iguanas' variable display repertoires (see Nesting Biology), no individual-specific "signature displays" (see Berry, 1974) were found.

In contrast to Silvia's aggressive behavior towards the decoy iguana, three males responded with courtship gestures, each differing in form. Silvia's mate, Rolo, encountered the dummy on 19 May near their home crevice. He trotted forward, giving two low-amplitude head tosses in transit, and when about 1.5 m away began a charge, with mouth open and head held low, nearly touching the ground (see Fig. 17B). He paused about 0.3 m from it, raised his head, gave six exuberant toss-rolls (see Fig. 17C) and then advanced to nudge it gently beneath the jowl muscle. This was followed by three tosses. His interest was short-lived, however, for only two minutes later he walked away and stopped to rest in a



Fig. 17.--Displays and behavioral attitudes associated with courtship and mating preliminaries in Mona Iguanas. In "A" a male gives a head toss from a rock outcrop above a female and begins his courtship approach. Approaching male pauses to give a series of head tosses and rolls in "B," and makes a courtship dash towards female, who assumes the head-up, tail-up rejection posture accompanied by bobs and/or rolls of head. Immediately after approaching a receptive female, the male in "C" pauses to give high-intensity toss-roll displays and bites the nape of her neck (D) while moving astraddle her. A, C, and D are renderings from single frames of motion picture film; B is a composite based on three frames.

patch of sunlight, facing the opposite direction.

The decoy elicited a more intense response from male Yellowfoot on 5 June. At 08h25 he emerged from his nighttime retreat and began basking at 08h40. Thirty-one minutes later, following a traditional route along the cliff edge and sighting the decoy about 5 m away, Yellowfoot advertised his presence with a series of seven head tosses. After a brief pause he moved a couple of meters closer, displayed nine toss-rolls, and charged with head low and mouth open, ending with a nudge on the dummy's neck behind its jawl. Four tosses followed, he advanced a little to a neck-to-neck position, gave five more tosses, paused, and gave two tosses. Yellowfoot walked around the decoy, tasting it with flicks of his tongue, continued with periodic head displays, and finally lost interest after about 10 minutes. A third male, Pozo, tested on 8 June, exhibited the same approach, display, and investigative behaviors but with a curious addition: after getting no response from the decoy, he walked a couple of meters away from it and repeated his head-low, mouth-open charge--this occurred three times within 15 minutes.

Both males and females consistently reacted to the decoy as though it were a female, the females responding with indifference or aggression and the males with indifference or courtship. How do these lizards, which show little sexual dimorphism in appearance, identify the sex of a strange iguana? A number of authors have suggested that in some species sex recognition is in part based on behavioral responses to the advances of another lizard, most clearly demonstrated by Ferguson (1966). Where

females closely resemble males in appearance and are the more quiescent sex when approached by other adults, one might expect an inanimate model to be treated as a female. Therefore, the observed responses towards the stuffed Cyclura are not surprising.

While no sex-related color differences occur in the Mona Iguana, there are differences in physique, subtle as they may be, that could function as sex cues. The most obvious are the greatly distended abdomens of gravid females during the breeding season and the relative size of the animal's jowl musculature, which is often larger in adult males than females. The decoy has a shrunken abdomen and female-like jowl development. To test the effect of jowl size, I added gray plaster caps to each bulge, thereby enlarging them to a size somewhat greater than that normally seen in males (see Fig. 16). This experimental trial occurred on 5 August 1976 during a brief return trip to Mona. Unfortunately, I saw only one iguana whose identity I was sure of, Left Gold, a male I had observed extensively but had not tested with the decoy on a previous occasion. The decoy was placed about 3 m from his retreat and well within the limits of his territory. Gold was basking in a patch of sunlight roughly 5 m from the spot where I unveiled the newcomer with a "face-job." He sat eyeing it for 1-2 minutes and then walked slowly over to it, giving no head displays. Suddenly Gold rose into a full lateral challenge display, prancing back and forth in a semi-circle in front of it, promptly followed by a "body-snap" attack (bite in the side with a simultaneous tail-lash delivered to the head). This must have been a powerful blow, for the decoy, which is plaster-filled, was knocked over on its side.

Left Gold's response was decisive and entirely characteristic of male/male interactions seen under similar circumstances--of special note was the absence of head displays from beginning to end, highly atypical in male/female or female/female interactions. This trial occurred approximately one month after the close of the breeding season, a time when neither courtship nor territorial defense are intense; Gold is a dominant male who has consistently maintained a territory and courted females year-round. Despite the shortcoming of having only one experimental trial to compare with the other 14, I believe the outcome is strongly suggestive that jaw size is used by these lizards as a cue in sex recognition.

Juvenile iguanas were never seen in close association with adults (though not segregated from them), and a hatchling observed encountering the decoy avoided it. The hatchling, Peaches, scaled a nearly-vertical face of rock at the cliff edge and, upon reaching the top (10h49), spotted the decoy about 1 m away. Peaches stopped abruptly and gave nine multibob displays, advanced a few centimeters, repeated the performance of nine displays, then turned around, retreated about 10 cm, and ended with seven more sets of multibobs before moving into a crevice (10h58). At 11h07, Peaches emerged from hiding and headed back down the cliff face, keeping an eye on an adult male basking on a ledge about 2 m below. Peaches remained on the rock wall near a crevice for 13 minutes, then turned around and once more began climbing, only to change direction again upon finding the decoy still present. After 26 additional minutes of resting and moving about on the wall, Peaches climbed back up

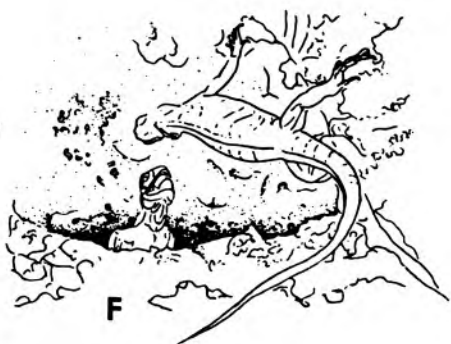
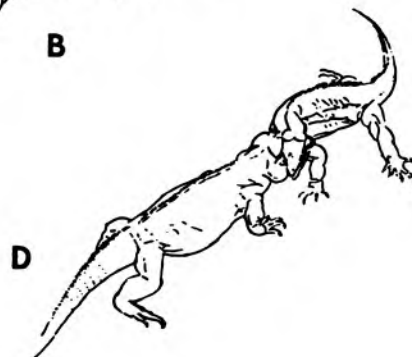
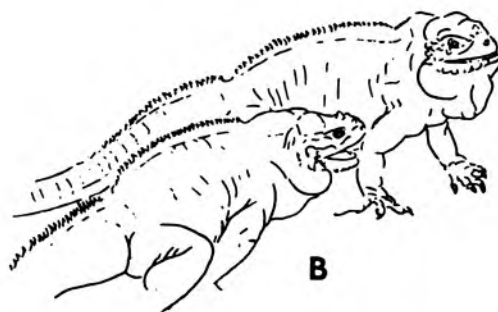
to the cliff edge; then, exercising great caution and using a circuitous route, Peaches ventured onward, first beneath a shrub off to one side and then around the decoy. Lizards sometimes eat young of their own kind (e.g., see Hirth, 1963a; Alvarez del Toro, 1972; Iverson, 1977) and avoidance of individuals that are appreciably larger is not surprising. If Mona was once densely populated with iguanas, cannibalism of small juveniles by adults might have been much more likely than it appears today.

Fighting Between Males:

Defending a piece of real estate attractive to females, i.e., a territory, is the usual prerequisite to breeding in male Mona Iguanas (elaborated upon in the upcoming chapter), and serious challenges regarding ownership are resolved through fighting. Fights among adult males are highly formalized tests of strength, face-to-face pushing matches, mouths stretched wide open, and noses usually pointed in opposite directions (Fig. 18DE). The deliberate, stylized manner in which most fights begin suggests that, in early stages of the battle, attack is secondary to defense through out-pushing the other animal. When the two iguanas are jockeying for new positions, sometimes a rock or tree trunk gets in the way, and one male ends up pushing for 10-20 sec. against the object while his opponent pauses, watching, resuming the match when the former corrects his error. Most clashes are less than 15 minutes in duration and end without violence when one or both iguanas back slowly away in retreat.

The usual outcome of an encounter between two males is retreat by

Fig. 18.--Aggressive interactions between male, female, and juvenile Mona Iguanas. A) Medium-large female and a young female in her first or second nesting season exchange head toss displays. The veteran female had destroyed the younger ones nest while digging her own, and a pig rooted out the remaining eggs of both. The two females were attempting to refill the hole left by the pig. B) A male crouches and huffs while his adversary circles, prancing in full challenge display. C) Momentary stand-off between females disputing ownership of a nest site. D) Face-to-face pushing match between a gravid female and a spent female who is attempting to defend her nest site. E) Face-to-face pushing match between males fighting over a breeding territory. F) Hatchling within retreat hissing and tossing his head (tongue engorged with blood), defending the site from a challenger who displays while clinging to rock wall and circles around the resident. G) Gravid female threatening another with toss-roll displays from entrance of a nearly completed nest hole. H-J) Female digging a nest burrow is challenged by a persistent, gravid female attempting to displace her (H); occupant lunges to bite intruder on the neck (I), who responds with a "body-snap" attack, delivering a bite and tail lash simultaneously. All of the above renderings were taken from slides or single frames of motion picture film.



one or both or a chase ending in escape of the individual being pursued. None of the 262 chases seen were initiated with the forewarning of head displays, though many potential chases are prevented by intention movements of the aggressor, e.g., getting up from a prostrate position in preparation to chase an intruder. A fleeing animal will sometimes run into the forest, but more typically he will dive into a nearby crevice, ending the chase abruptly. Rarely does an aggressor enter a crevice after the other animal. Occasionally, a chase crossing the territory of a third iguana will prompt his joining the race in pursuit of the others.

If the pursued is strongly motivated to challenge his pursuer, a fight may erupt, with or without close-range display preliminaries. Bluffing displays, i.e., a broadside challenge or huffing from a crouched position (Fig. 18BC), do not discourage fighting except in disputes originating on the border of a male's territory--in such cases one or two rounds of threat exchange are often followed by mutual retreat. Crouching and huffing by one or both competing males is a typical prelude to fighting; and because this prostrate posture was never accompanied by reduced aggression from the opponent in any of the 47 fights witnessed, it should be regarded as a defensive, and not a submissive, attitude.

Two special evasive tactics are used by some males put on the defensive, allowing them to assert themselves and to evaluate another's persistence short of actual combat. One method is to use a tree trunk or similar obstruction, as a shield against the opponent's attacks. The

other is to lead the aggressor on an exhausting chase by running in circles through his territory. The longest such chase observed was sustained without interruption for approximately 140 m, at which point both animals slowed to a walk. This tactic was twice seen to accompany successful encroachment on another's territory, though ending in a take-over only after fighting.

The longest fight observed lasted for nearly an hour, a dispute between Silversides (SS) and Bulbtail (BT) over the territory SS was holding. Prolonged encounters occurred most frequently just before and during the early part of the breeding season, and were among the most variable and brutal. The confrontation of SS vs. BT consisted of five rounds, 2, 6, 12, 10, and 25 min. in duration, spaced by brief pauses of less than one minute. Rounds 1-4 were quite conventional, marked by much pushing and some gnawing on the side of the opponent's face, drawing a little blood; two brief departures in style were bouts of cheek-to-cheek pushing with noses pointed in the same direction. During Round 5, SS clamped onto BT's snout (including lower jaw) and made three downward chomps. BT freed himself and succeeded in biting his opponent's jowl muscle. After another bout of intense pushing, the two locked jaws, BT with SS's lower jaw in his mouth, but not biting. When SS chomped down on BT's snout, his opponent exploded into a thrash-about, flipping SS over on his back and breaking the hold--I could hear much gnashing and crunching of teeth and bones (?). The fight resumed, but within two minutes the encounter ended. Bulbtail quietly retired to a nearby retreat in the territory formerly held by his adversary, as

Silversides walked slowly away, having made his last stand for the season. Silversides was seen on three subsequent occasions (in mid-June) and appeared uninjured by the ordeal.

Mona Iguanas have extremely tough skin; even vicious biting seldom draws blood, and battle scars on body and limbs are consequently rare. Minor facial lacerations that heal within a few days, incurred during all serious confrontations, were useful indicators of recent fights not seen. Most bleeding comes from within the contestants' mouths. Veteran fighters, particularly large males, have very worn facial spines; this is less evident in females. And as already mentioned, the incidence of broken, regenerating tails is significantly greater in males than in females. No animals were seen with extremely short or freshly broken tails.

Aggression by Juveniles:

After dispersing from nest sites as hatchlings, juvenile Mona Iguanas take up residence in rocky areas and like adults, apparently acquire site attachment to a particular area. This is indicated not only by recurrent (though infrequent) sightings of six juveniles in the same areas over periods of 9 months or more, but also by observations (one in the field and two in captivity) of retreat-centered territorial behavior directed against others of similar size. In a 10- to 15-min. dispute between two hatchlings, the resident, perched at the entrance to his retreat, confronted the intruder with hissing, emphatic head-tossing (mouth wide open, tongue engorged), and occasional lunges, as his

adversary circled in a broadside challenge posture while clinging to a vertical rock wall (Fig. 18F). I also observed a similar encounter between free-ranging juvenile Cuban Iguanas, Cyclura nubila, on Magueyes Island, P.R.

Discussion:

In communication systems, signals are often classed as "discrete" or "graded." Discrete signals tend to be invariable and "all-or-none" in occurrence, while the intensity of a graded signal is dependent upon motivation and context (see Brown, 1975). The two categories are not mutually exclusive, and in fact elements of both are usually found together in an animal's display repertoire.

The various push-up and bobbing displays of iguanid lizards typically contain highly stereotyped "Display Action Patterns" (Carpenter, 1967a) that are decidedly discrete in form. Several investigators (most notably Ferguson, 1971; Jenssen, 1971; and Stamps & Barlow, 1973) have meticulously analyzed these patterns for a few species on individual and population levels. Their results suggest that while advertising its presence and sexual condition, a lizard may also be communicating information about its population identity, individual identity, and level of arousal. The portion of the display containing the action pattern characteristic of the population, Jenssen (1977) has termed the "core display" and the display units appended to it "display modifiers."

Modifiers showing little intra-individual variation, i.e., those

patterns that are discrete at the individual level, could convey information facilitating individual recognition, while those that are graded (e.g., extent to which a throat fan is extended, Stamps & Barlow, 1973) can indicate the animal's level of arousal (Jenssen, 1977). It should be added that species identity is evidently reinforced by coloration, ornamentation and body form, and display site in some cases (Rand, 1961; Ferguson, 1966; Rand & Williams, 1970; Webster & Burns, 1973; Williams & Rand, 1977). One would expect a lizard's displays to include prominent discrete signal elements and patterns wherever a number of closely related species live sympatrically, thereby minimizing the chance for mismating. Where there is geographic isolation and no possibility for ambiguity in species recognition, one would anticipate greater display variability within the population (as in bird song, e.g., Marler, 1960, and Mirsky, 1976). The point appears well illustrated by the display repertoire of the Mona Iguana, for I could identify no core display pattern.

Largely because of their graded character, Mona Iguana displays show a high degree of intra-individual variability. Display units are employed (all contexts considered) in what appears to be a continuum of display form and intensity. Displays are tailor-made to match context and mood of the individual.

Threat gestures in visually oriented lizards, as apparently in most other animals, tend to be relatively generalized and graded in form. The displayer strives to appear as large and as formidable as possible,

through a sequence of escalated overtures. How far the display is carried depends largely on the motivation of the displaying animal, usually inseparable from the response of the one being displayed to. This is nicely illustrated by Brattstrom's diagram of sequential "defense" (threat) behaviors in the Bearded Dragon, Amphibolurus barbatus (1971, fig. 5). The display is dependent on the proximity of the stimulus and the sex of displayer. These lizards were observed to challenge a human hand, and a slowly advancing finger would cause a male to go through a progressive sequence of eight postures. With a slow withdrawal of the stimulus, the sequential elements would drop out in reverse order but could be made to reappear at any point by advancing toward the lizard again. The female, lacking the male's showy "beard," uses an abbreviated pattern of display, usually involving escape behavior after an initial open-mouth posture. This example of behavioral sequencing in response to changing stimulus intensity (proximity) is an interesting analogue to the response by Silvia in the presence of the dummy iguana, where stimulus intensity was fixed and the escalation of threat gestures was totally self-motivated.

Use of a graded threat-display repertoire to minimize energy expenditures and to reduce risk of injury would appear highly adaptive; nevertheless, male Mona Iguanas skip the low-intensity threat preliminaries (head displays), moving quickly into the chase or lateral challenge and attack phases. Why this is so is not altogether clear, but theoretically, low-intensity displays are likely to diminish in importance where they are ineffective in discouraging another's trespassing,

i.e., where a challenger has the potential for greatly improving his fitness by testing the resident's motivational and physical strength directly. This might be expected where male/male competition for breeding territories is especially keen, as is apparently the case on Mona (see Territoriality, Courtship, and Mating). Also, because animals are often most vulnerable to predation while fighting, less emphasis on display might be expected only in environments with light pressure from predation. Females, on the other hand, having to carry nearly all of the reproductive burden, may be subject to greater long-term loss in fitness through physical risks associated with fighting and must presumably be more frugal in their energy expenditures, perhaps accounting for their well-graded series of head displays characteristically given as a prelude to the broadside challenge.

Several of the Mona Iguana's structural attributes appear related to display and aggression. The enlarged, mid-dorsal spines that decorate the trunk and tail of both males and females are absent on the neck, where they are longest in most male iguanine lizards. Although nuchal spines are tiny in this species, they are born on a prominent fleshy flap (possibly analagous to a row of enlarged spines) distinct from the mid-dorsal crest. The Mona Iguana's dewlap, an enlarged, permanently "erect" fold of skin, is equally well developed in both sexes. Such structures enhance the animal's apparent size and ferocity, and their adaptive value to females of the Mona population appears related to intrasexual competition for favorable nest sites (see Fig. 18 DHIJ and Nesting Biology).

Particularly striking are the unusual enlarged horns, spines, and bulges on the iguana's massive head, all present in males and large females. Confrontations seen involving one male clamped onto another's snout suggest to me that the distinctive horns on the snout of Cyclura stejnegeri (like those of C. cornuta) may function as defensive weapons to help disengage an opponent's hold. With jaws interlocked, contesting heavy-bodied lizards risk serious injury, a risk that might favor this "ornamentation." The lizard's lateral facial spines afford added protection during combat, and, like the nasal horns, could also act as armor protective against the sharp limestone rock, a function that appears well served by the conspicuous parietal bulges crowning the animal's head. These bulges are cushion-like in construction: adhering to the skin is a layer of tough fibrous connective tissue and beneath that a thick pad of fatty tissue overlying the musculature in the skull's supratemporal fenestrae (pers. obser.). In contrast are the animal's sagging jowls, which are solid muscle masses (pers. obser.) that function in adducting the lower jaw (see Oelrich, 1956). The hypertrophied appearance of these features is accentuated by head-roll display movements viewed frontally, suggesting that their extreme development may be display-related, most likely an advertisement of fighting "ability."

A fighting style like that of the Mona Iguana occurs in at least one related species, Cyclura nubila (Street, 1952), but it has not been reported for any other iguanid lizard. Analogous pushing contests occur, however, in C. carinata and in the Galápagos Marine Iguana, Amblyrhynchus cristatus. In the former species, the characteristic

fight position is shoulder-to-shoulder (Iverson, 1977), while in the latter, combating males meet head-on, butting and shoving with the tops of their heads (Carpenter, 1966). Many iguanids utilize tail-lashing interspersed with lunges and attempts to bite (Carpenter, 1967), which appears to be a comparatively primitive technique. Jaw interlocking (termed "jaw fencing" by some authors) is another common fighting position, seen in Anolis lineatopus (Rand, 1967a), A. monensis (pers. obser.), Conolophus subcristatus (Root, 1967), and Chalarodon madagascariensis (Blanc & Carpenter, 1969), among others. These classes of fighting behavior are clearly not mutually exclusive, and the more ritualistic tests of strength, such as those exhibited by Cyclura and Amblyrhynchus, sometimes lapse into tail-lashing and biting as well.

Some lizards limit aggression through the use of submissive postures or special displays (reviewed by Brattstrom, 1974). No behaviors of this kind were evident in Mona Iguanas. Adult male trespassers were invariably chased or confronted with a full challenge unless the intruder chose to retreat promptly.

An ontogenetic form of submission occurs in young males, however. In many if not most lizards, young males bear a striking resemblance to females of the same species, and reports of adult males courting and even mating with younger males occasionally appear in the herpetological literature (e.g., Evans, 1940; Trivers, 1976). Homosexual matings are probably more common than is generally recognized simply because determining the sex of the subordinate requires its capture and often its dissection. On Mona, prior to the iguana breeding season, I saw one

young animal, Penciltip, being restrained by a large adult, Randy Redtail, who held the former with a grip near the base of the tail. Unfortunately I missed seeing whether the encounter began with courtship displays. Penciltip remained quite passive, much more so than some of the females I have seen under similar circumstances. While Randy was attempting to secure a hold further forward, as is usually done during mating preliminaries, he wriggled free and into the safety of a crevice. During the breeding season, Penciltip joined in on normal male activities (unsuccessfully), confirming his identity as a male. Furthermore, in the group of Mona Iguanas being observed during their fifth year of life at the San Diego Zoo, S.L. Keller (pers. comm.) has witnessed female-type rejection displays given by the smallest male in response to courtship gestures by a larger male. Carpenter (1967) has reported seeing similar display behavior in males of other iguanid lizards.

Such behavior is probably not unusual in this species and may be widespread among lizards, strongly suggested by its apparent adaptive value to young males: Although a young male pursued by the courtship advances of other males would presumably be able to escape by running away, he might thus reveal his sex (see Ferguson, 1966), thereby risking pursuit and harm from the larger animal. On the other hand, if he were to remain passive and give rejection displays, even with the "risk" of occasional rape, his presence would be accepted until he had gained the stature necessary to compete effectively for females. Also, a subordinate male of a long-lived species presumably has a great deal to gain by maintaining a close affiliation with a social group. He could, for

example, monitor the activities of others in the group and might be able to breed opportunistically. Though I have no data for opportunism of this nature, the phenomenon is well documented for a number of other vertebrates (e.g., in fish, Morris, 1952; Barlow, 1967; Constanz, 1975; in amphibians, Fellers, 1975; and in mammals, LeBoeuf, 1974).

Delaying the onset of chemical (in addition to physical and behavioral) dimorphism may be yet another means for young males to conceal their sexual identity. As in most iguanid lizards, adult male Cyclura have well-developed femoral pores, and while the function of the exudate of these glands on the undersurface of the thigh has remained a mystery (see review by Cole, 1966), it is a logical candidate for limited chemical communication; evidence to this effect was reported (though apparently never published) by Hunsaker (1962). This waxy secretion rubs off on the substrate and is produced most copiously during the breeding season, even to the point of forming a set of comb-like tines protruding from the thigh (in C. stejnegeri, pers. obser.). It is interesting that in some cases males attain sexual maturity before the femoral glands become active. A young specimen of C. cornuta (MCZ 33410, SVL 38.5 cm) from Beata Island, Dominican Republic, was found to be both a reproductively mature male and entirely female in external appearance, including reduced femoral pores.* In the Caicos Iguana (C. carinata) population on Pine Cay, from which a large series of specimens was collected, males characteristically mature well before femoral pore secretions develop,

*Histological preparation of one testis courtesy of Dr. Emil L. Mantini, Alachua General Hospital, Gainesville, FL.

and newly matured males are also virtually indistinguishable from females (Iverson, pers. comm.). Young Caicos males wander throughout the territories of older males, much as do females, without apparent persecution by residents (Iverson, pers. comm.). While there are alternative explanations for these observations, I suspect that social effects can influence femoral pore development and activity, a consideration that deserves further attention. It would be of special interest, for example, to examine the social organization of C. ricordi in the Dominican Republic, a species in which both adult males and females (at least in some cases) have secreting femoral pores (Wiewandt & Gicca, unpubl. data).

Mona Iguanas lack the courtship nod, a series of rapid shallow nodding movements performed by males during the "courtship charge" with head lowered. To my knowledge the iguanid lizards Sauromalus obesus (Berry, 1974) and Chalarodon madagascariensis (Blanc & Carpenter, 1969) are the only other representatives of the family studied to date that do not possess this primitive display. The consistency with which the courtship nod appears in iguanid lizards as a group (see Carpenter, 1967) indicates that it serves a basic function that has retained its importance to the courtship process throughout the history of the family. This is in line with speculation by Stamps & Barlow (1973) that courtship nodding is subordinant (appeasement) behavior (derived from "multibob" signals), a maneuver allowing the male to approach within copulating distance without frightening the female. Accordingly, the disappearance of nodding from the Mona Iguana's display repertoire,

together with the fact that the mouth is kept open throughout the courtship approach (a threatening gesture not reported in the courtship advances of other iguanids), could be explained by two compensating attributes that might serve to lessen the female's fear of a male's advances: 1) greatly reduced sexual dimorphism in adult body size, and 2) long-term male/female associations. Some males give continued attention to females year-round, sometimes accompanied by much body contact during the breeding and prebreeding seasons and by abbreviated precopulatory display (see next chapter). S. obesus is also relatively monomorphic in size, it is sedentary in habit and presumably long-lived, and male/female associations involve frequent physical contact (Berry, 1974). Less is known about Chalarodon; from Blanc & Carpenter's (1969) brief account, it is evident that sexual dimorphism is much better developed in this species, but no details are given on how the sexes relate to each other throughout the year.

Data available on the display repertoires of two other cycluran iguanas indicate that these peculiarities found in the Mona Iguana are by no means characteristic of the genus. Two weeks spent on Isla Magueyes, P.R., observing an introduced population of Cuban Iguanas, C. nubila nubila, revealed several striking differences (pers. obser.): Bobbing displays are considerably more shallow and rapid, appear more stereotyped, and have a predominantly vertical motion (I did see occasional bobs with a twist, but none that approached a roll). Furthermore, head-nodding accompanies the males' courtship charge, in which the head is held low but the mouth is kept closed. These features (with the

exception of the occasional head tilt) are also characteristic of C. carinata displays (Iverson, 1977). Displays of the Rhinoceros Iguana, C. cornuta, are three-dimensional and have the same uncoordinated appearance as those of C. stejnegeri (pers. obser.), but without the opportunity to observe the former in social contexts, I could draw no meaningful comparisons between these closely related forms. C. cornuta (from which C. stejnegeri is probably derived) is the only living species known to exist sympatrically with a congener (C. ricordi), an association that may have promoted much of the uniqueness evident in displays of C. cornuta and C. stejnegeri today.

Three ideas have been advanced concerning the evolutionary origin of bobbing and push-up movements in iguanid lizards: Noble & Bradley (1933) suggested they might be adaptations to enhance depth perception (yet bobbing rarely accompanies foraging); Smith (1946) proposed that they constitute a residual habit from a time when throat fans were more highly developed than today (not known to be the case); and Carpenter (1967) argued that they have always functioned as aggressive actions. As Carpenter (1967, pp. 101-102, 151) noted, and I concur, while the first two hypotheses are possible, neither appears very tenable. I also believe it is unlikely that both push-ups and bobbing began as aggressive acts. Intimidation postures, e.g., lateral flattening, crest raising, and dew-lapping, are clearly complemented by a movement elevating the body off the ground--thus a push-up. I would not, however, propose a similar route for the evolution of head-bobbing, which, incidentally, is known to occur in four other lizard families: Agamidae (e.g., A. agama,

Harris, 1964; Hydrosaurus pustulosus, Gonzalez, 1974); Chamaleonidae (Kästle, 1967); Scincidae (Mabuya sloanii, pers. obser.); and Gekkonidae (Hemidactylus flaviviridis, Prashad, 1916; Phelsuma chloroscelis, Kästle, 1964). Assuming that the simplest bobbing movements generally represented in display repertoires of modern iguanids, i.e., multibob and courtship bob, are the most primitive, then we should scrutinize the utility of these displays in our search for the origin of head-bobbing.

Lizards performing "multibobs" appear to be making intention movements to flee, a motion I see as comparable to tail-flicking in birds, a flight-preparatory movement that Daanje (1950) noted is a common component of avian displays. It is significant that this bobbing performance (I hesitate to call it a display) is characteristically given in situations (often non-social) in which the lizard is either retreating or might be expected to make a rapid exit. Also, the frequency with which bobbing occurs appears to be closely correlated with the imminence of danger, especially evident in the exploratory behavior of recently matured females at nesting areas and in the responses of timid animals towards my presence (i.e., the closer I was, the more the lizard bobbed before departing). In non-social contexts, the up and down bobbing motion is probably an expression of ambivalence between upright, alert, flight-preparatory postures and low postural attitudes associated with remaining inconspicuous.

The multibob performance, I would judge, is the most primitive bobbing movement in iguanid lizards. In a social context, multibobs signal uneasiness and can serve to identify a subordinate individual.

Derived activities such as submission displays, courtship nodding, or assertion displays may evolve through ritualization, i.e., specialization of the behavior to serve a communicative function (see Tinbergen, 1952). Submissive posturing accompanied by shallow head nods occurs in males of the iguanid Chalarodon madagascariensis (Blanc & Carpenter, 1969); given by subordinates, this display promptly stops aggression by dominant individuals. It is easy to visualize the transfer in function to courtship as suggested by Stamps & Barlow (1973). Furthermore, in the Mona Iguana, low intensity head tosses, which can occur singly or in series and function as assertion displays, appear to be no more than an intensified and smoothed-out multibob performance. Possibly a close evolutionary tie between the two in iguanid lizards accounts for some of the persistent confusion that now exists in the literature over what should be called an "assertion" display (see discussion in Stamps & Barlow, 1973, pp. 84-85). A careful examination of how ontogeny affects display structure and function might clarify this issue.

It should be emphasized that the above hypothesis is in keeping with ethological concepts concerning the origin and elaboration of display movements in other vertebrate classes, especially birds, that have been meticulously developed during the past 30 years. Additional ideas on the evolution of bobbing and push-up displays in lizards, complementary to my own and formulated independently, are currently in press (Barlow, 1977, and Greenberg, 1977--cited by Jenssen, 1977).

TERRITORIALITY, COURTSHIP, AND MATING

Among the most widespread behavioral phenomena in wild populations of vertebrate animals is territoriality. The term, used here in the traditional sense, denotes defense of a fixed area from others of the same species by means of advertisement, threat, or attack (see Brown, 1975). Functionally, territories are structured around any one or a combination of critical requirements: mates, food, and access to special abiotic resources, e.g., shelter and basking sites. Viewed as a product of natural selection, territoriality is likely to evolve and be maintained only under circumstances where the risk or energy costs associated with the defense of a particular resource are low relative to the benefits so derived, an important theoretical argument developed by Brown (1964) and later elaborated by Rand (1967b) as it relates to lizard ecology, nicely supported by Simon's (1975) study. One could predict, for example, that Mona Iguanas should not maintain feeding territories since foods of greatest significance in the animal's diet tend to be patchy in time and space and locally abundant when available (see Foraging Behavior and Diet), a resource that would be impractical to defend. These lizards do most of their foraging off-territory, as expected.

Three discrete classes of territorial behavior occur in the Mona Iguana, each centered on a different resource: 1) mating sites, retreat-focused and defended by males against males in competition for

access to females; 2) retreats, defended year-round by juveniles and females against others of their own size/sex; and 3) nest sites, defended by females against females during the nesting season while guarding holes or completed nests (treated separately under Nesting Biology). Within these first two classes, there are appreciable individual differences. The variations found vividly illustrate how territorial behavior as a time-investment strategy relates to variables in the physical environment, to intrasexual competition, and to fitness, forming the theme of this chapter.

Territories and Mating, Rights & Rites:

In June 1973, shortly after beginning studies of the iguanas at the inland depression at La Bajurita, I noted a sharp rise in the incidence of chasing and fighting among males (see Fig. 19). This was clearly the onset of the breeding season, the males striving to obtain or hold a territory. Aggressive encounters centered on the SE slope of the depression, an area that was soon parcelled into three mini-territories (two controlled by distinctive males I dubbed Bulbtail and Four-toed Freddie). During the ensuing two weeks, fights and chases continued erupting, and several changes in the position and ownership of these small territories occurred. The females were timid, and no mating was seen. In early July, efforts to defend territories on the SE slope suddenly terminated. Elsewhere however, around and within the depression, four males, each in control of relatively large, fixed areas, remained territorial. These behavioral differences were unexpected and

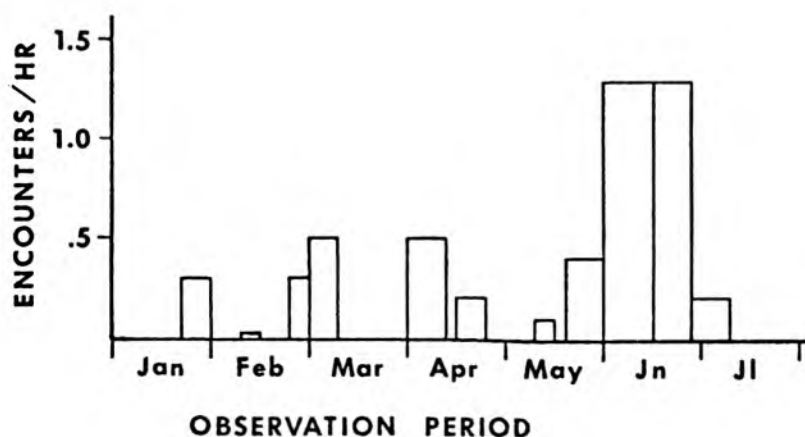


Fig. 19.--Histogram of agonistic encounters (fights + chases) between male Mona Iguanas per hour observation time at La Bajurita study area in 1974. Each bar marks the mean number of encounters seen during the group of observation days indicated.

intriguing, and I spent the remainder of 1973 and half of 1974 making periodic visits to the site to examine the group's social relationships in greater detail.

Plots of the movements of iguanas residing at La Bajurita were charted on maps of the area (Fig. 5) between January and July 1974, during 62 observation days, a total of 315 hours observation time. Understory vegetation was sparse in and around the sink, often permitting a clear view from one position of three or more individuals. All activities in the area could be monitored from three observation posts; because these lizards were accustomed to my presence, are slow, and tend to be noisy when moving about through the leaf litter, I was able to record almost every movement and social interaction that took place. The mapped area (approximately 1350m^2) included only a small portion of each animal's home range, but because retreats were centered there, so was most social activity. This was especially evident during the breeding season.

The activity plots were combined on 21 sheets (14 for males, 7 for females), each page being a compilation of 9-70 hours observation time, and each "spaghetti pattern" for movements of individual iguanas was color coded. These data are too complex to present in their entirety (but are available from the author) so I have extracted examples illustrative of each trend or point discussed and have simplified the format for figures in most cases. Of particular interest were considerations of territory ownership, location, size, period held, and the costs and benefits associated with owning it.

Distribution and Utilization of Retreats in the Study Area.--A knowledge of the structure of the physical environment at La Bajurita is of utmost importance in interpreting the social behavior of iguanas living there. The distribution of crevices suitable for retreats (as indicated by at least intermittent use) is shown in Fig. 20. Note the conspicuous cluster of retreats in the zone between the "water hole" and the "sink." As was already mentioned and diagrammed in Fig. 7, this rocky SE slope is undermined by a cave large and deep enough to permit a person to walk underground from the sink to the eastern edge of the depression. Many of the overhead crevices are interconnected, forming a retreat complex I shall hereafter call Fig Row. These retreats consistently received heavy use year-round by both males and females. Of iguanas sighted most regularly in the vicinity of La Bajurita, 77% (10/13) of the females and 58% (7/12) of the males occupied Fig Row predominantly. The attractiveness of Fig Row as living quarters may simply be a function of its size; however, I suspect that the multiplicity of entrances, the apparently good drainage, "flow-through" ventilation, and many horizontal resting places are important additional advantages. Since males compete with each other for access to females, the presence of numerous females in Fig Row may in itself be a special attraction to males.

Iguanas entering or leaving the study area consistently headed in the same general direction on each occasion. Routes chosen by different females overlapped broadly and strongly reflected the location of the retreat(s) occupied (Fig. 21): females residing in crevices on the southeastern edge of the depression (Lower Fig Row) characteristically

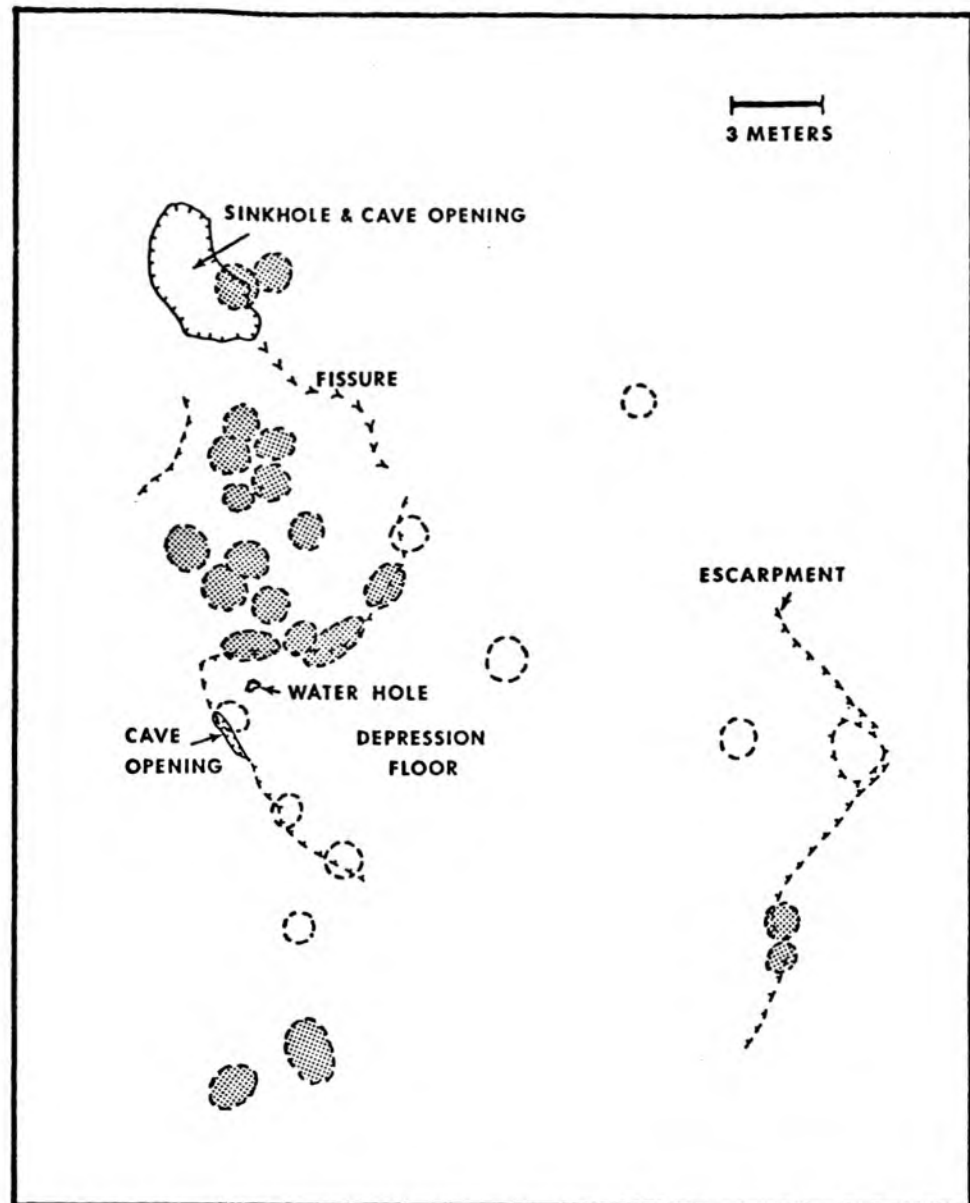


Fig. 20.--Distribution of retreats utilized by female Mona Iguanas at La Bajurita study area. Each circle encompasses a retreat entrance, some of which may share underground connections; those stippled received the heaviest use.

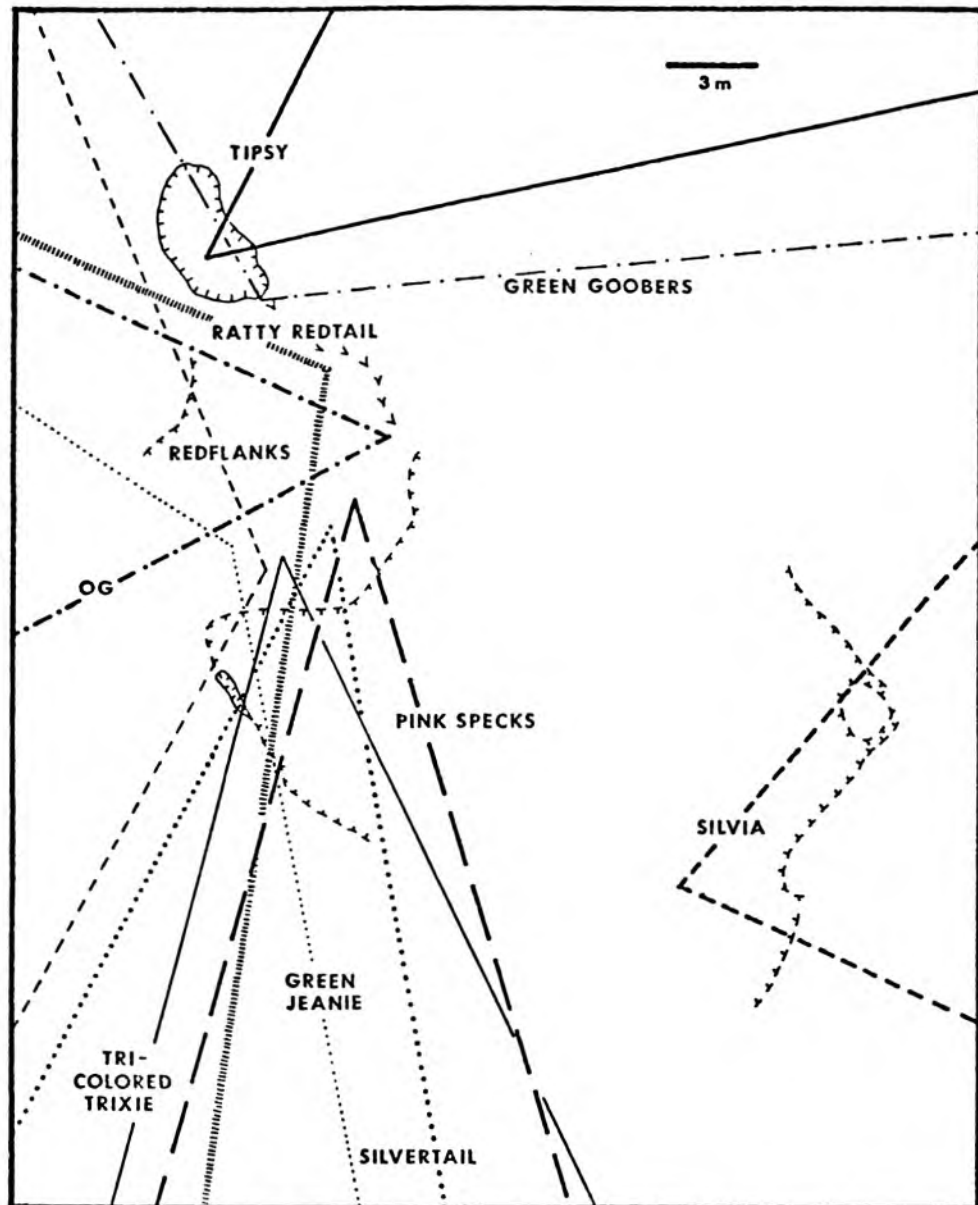


Fig. 21.--Spatial relationships among 10 female Mona Iguanas resident at La Bajurita. Sites where a female can be expected to seek shelter lie near the apex of each pair of converging lines. Distally the lines subtend a zone through which she moves en route to or from outlying areas; of 111 such observations ($\bar{x} = 11.1/\text{female}$, range 3-33), only one failed to conform to this pattern.

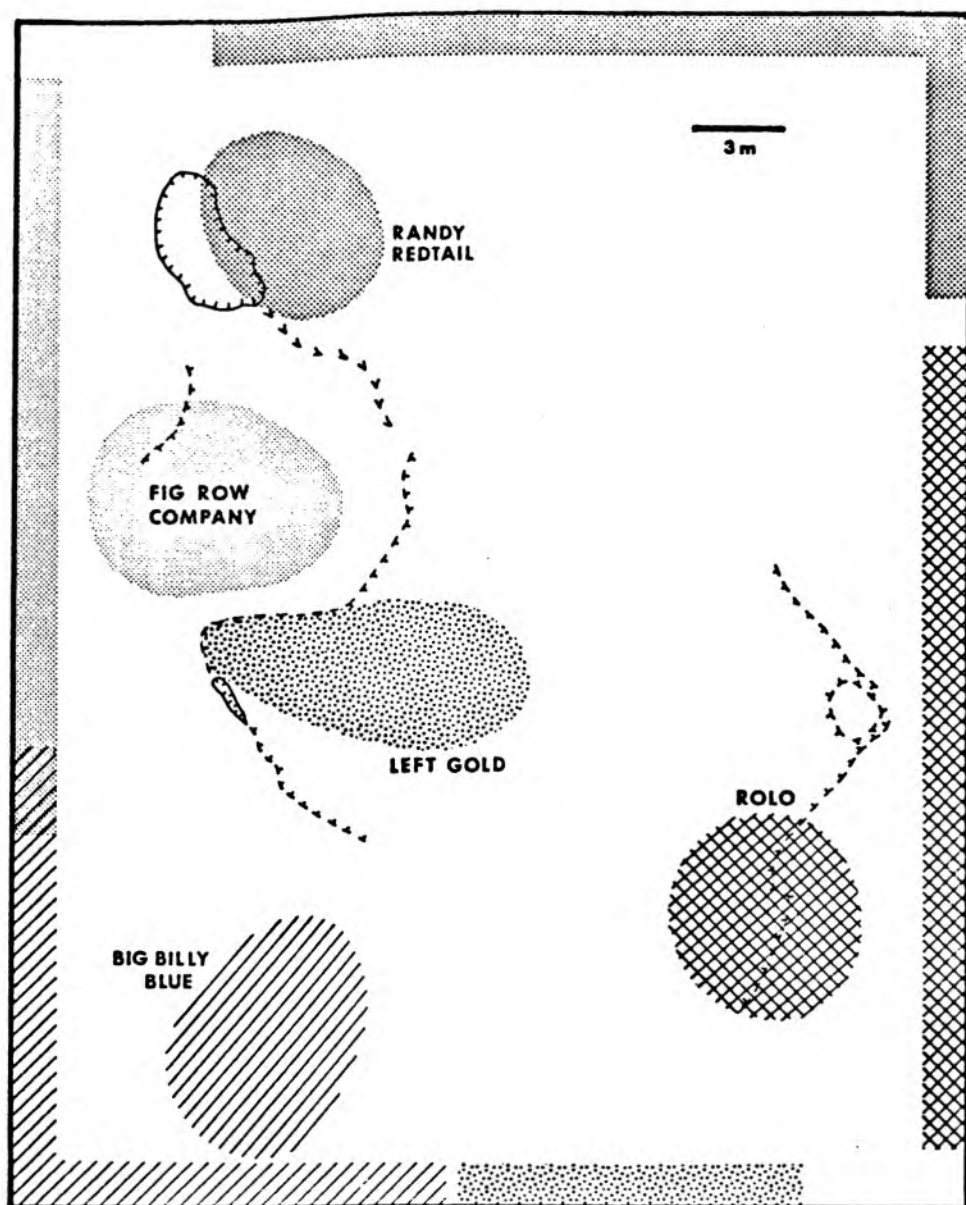


Fig. 22.--Spatial relationships among male Mona Iguanas resident at La Bajurita. Inner, patterned patches indicate core activity areas within the study area. Marginal strips indicate the zone through which the male(s) pass en route to or from out-lying areas; of 212 such observations only two failed to conform to this pattern.

crossed the depression floor, exiting up the northern slope, while the residents of Middle and Upper Fig Row followed a more easterly course, and the three females living apart from the Fig Row commune took south-westerly routes. Two of these three females defended territories around the proximity of their retreats, but in all female/female confrontations seen, the aggressive intent of the resident and persistence of intruder were conspicuously lax in comparison with male/male interactions. Only two encounters observed developed into chases. No aggression was found among females inhabiting the Fig Row complex.

The organization of males at La Bajurita was much more tightly ordered (Fig. 22). Four of the largest individuals, Randy Redtail, Rolo, Left Gold, and Big Billy Blue, monopolized approximately 85% of the area. These four males maintained retreat-focussed territories year-round, intensifying their effort during the breeding season. Seven other males shared the remaining 15%, which included all crevices in Middle and Upper Fig Row--Left Gold dominated Lower Fig Row. One to three "floating" males, i.e., those seen in many different places, commonly being chased by residents, were often present at La Bajurita as well. Iguanas dispersing from the area to forage in peripheral zones invariably took a route offering the least social resistance, and there was consequently little overlap in directions taken. Left Gold, who defended the floor of the depression, was sandwiched in among the territories of other males. Upon leaving the depression to forage elsewhere, he consistently used a narrow corridor between the territories of Big Billy Blue and Rolo (see Fig. 24A), and was occasionally challenged

while doing so. Males of Upper and Middle Fig Row all exited and entered from northeasterly to southeasterly directions.

Breeding Territories, Large and Small.--The striking behavioral contrasts noted in 1973 between males residing in Fig Row and the four big landowners, hereafter referred to as the Fig Row Company and the Big Four, respectively, reappeared in 1974. By 12 November 1973, one Fig Row male, Silversides, had established himself as proprietor of Middle and Upper Fig Row, chasing all other males who entered or exited from the retreat complex. To my knowledge he was never challenged until six months later, 19 May 1974, when Four-toed Freddie staked out a claim in Middle Fig Row. Silversides then concentrated on defending Upper Fig Row. Within the next two weeks several other iguanas expressed an active interest in acquiring a piece of Fig Row, and on 30 May, Silversides lost out altogether after the long, brutal battle (described in the previous chapter) with another challenger, Bulbtail.

Three serious contenders for Fig Row remained at the onset of breeding on 16 June: Bulbtail in Upper Fig Row, Four-toed Freddie in Middle Fig Row, and Twin Green, a persistent male who had been hanging out on the fringe of the other two territories and leading the residents, especially Freddie, on frequent looping chases. In a fight lasting 32 min., Green fought valiantly against Freddie, who delivered some nasty bites. The contest ended when Freddie backed away and retreated to a crevice, a victory for Green that enabled him to hold a position in Middle Fig Row, cinched by an additional battle three days later (19 June) that forced Freddie into Lower Fig Row. After a third

fight with Green, Freddie lost all claim to a territory in Fig Row, and moved to a vacant hole on the south side of the depression, leaving Bulbtail and Twin Green to dominate through the end of breeding activities. Four key stages in the changing structure and ownership of Fig Row territories during the prebreeding and breeding seasons in 1974 are illustrated in Fig. 23.

Lower Fig Row had been opened to occupancy because Left Gold relinquished claim to that area when I experimentally removed one of the Big Four, Rolo, from his territory on 30 May. Left Gold first investigated the vacant territory four days later and fought to defend it on 9 June. The take-over was gradual (Fig. 24), and Gold continued defending the depression bottom until 22 June. Thereafter, most of the floor of the depression remained open as a neutral zone. During all breeding activities there, however, Gold retained dominance over other males, so it became, in effect, an annex to his new territory. Left Gold met two persistent challengers to his new acquisition, both outsiders who came from and departed to the west. A fight with each ensued (21- and 6-min. durations) as did many exhausting circular chases, the last of which occurred on 17 June.

In switching territories, Left Gold gave up rights to the water hole, from which he frequently drank, the only one in the area that usually contained a little rainwater, and gave up a retreat shared regularly by no less than three females. Situated on the upper rim of the depression, the new territory offered a better vantage point, more sunshine, easier access to peripheral foraging areas, and Rolo's ever-

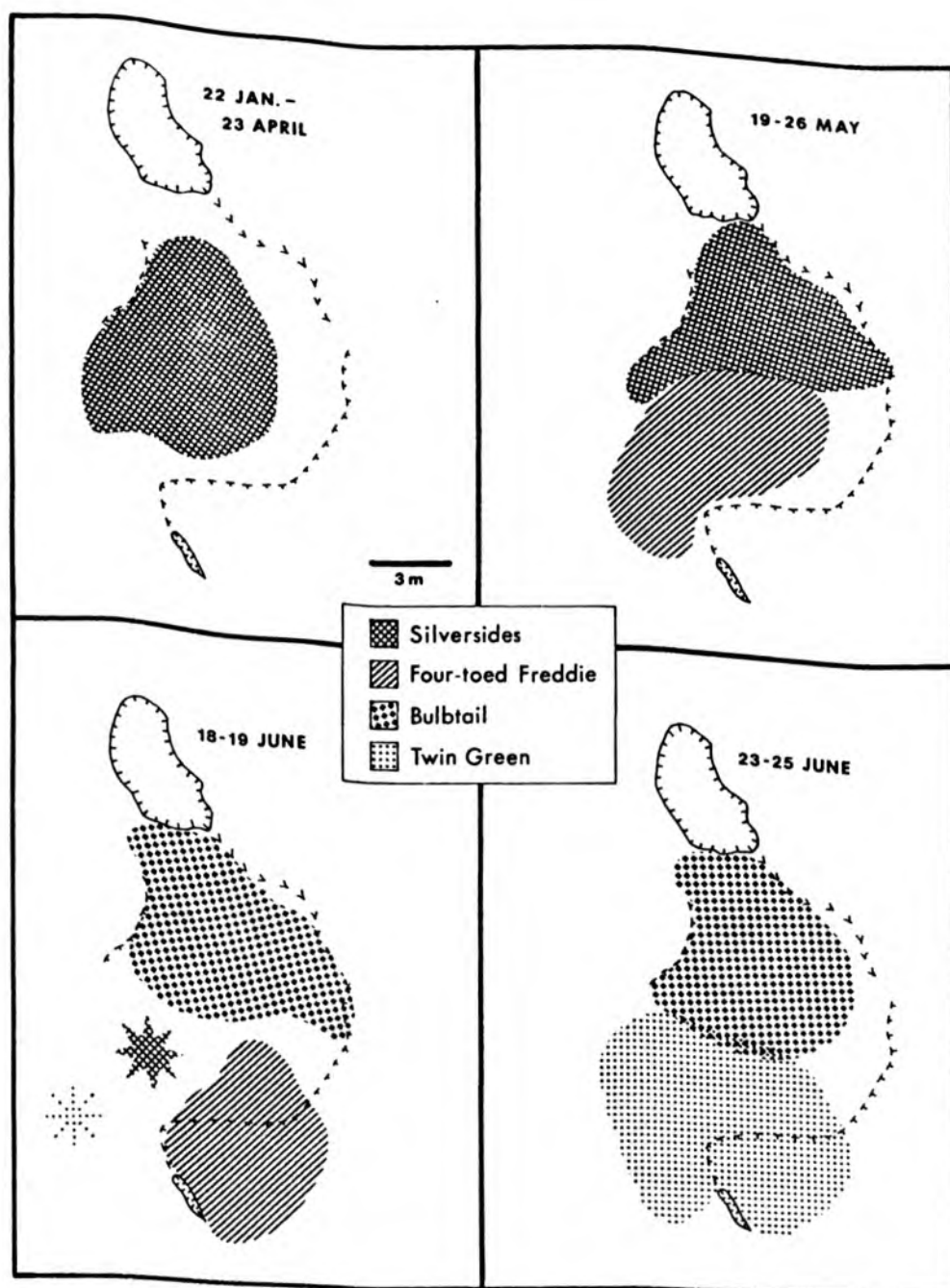


Fig. 23.--Changes in territory ownership and location that occurred among male Mona Iguanas residing in Fig Row from January to July 1974. Dotted star in lower left marks the site (above ground) where Twin Green frequently rested, while attempting to establish a position between existing territories. Cross-hatched star indicates Silversides' last appearance during the mating season, his defense limited to the proximity of a retreat.

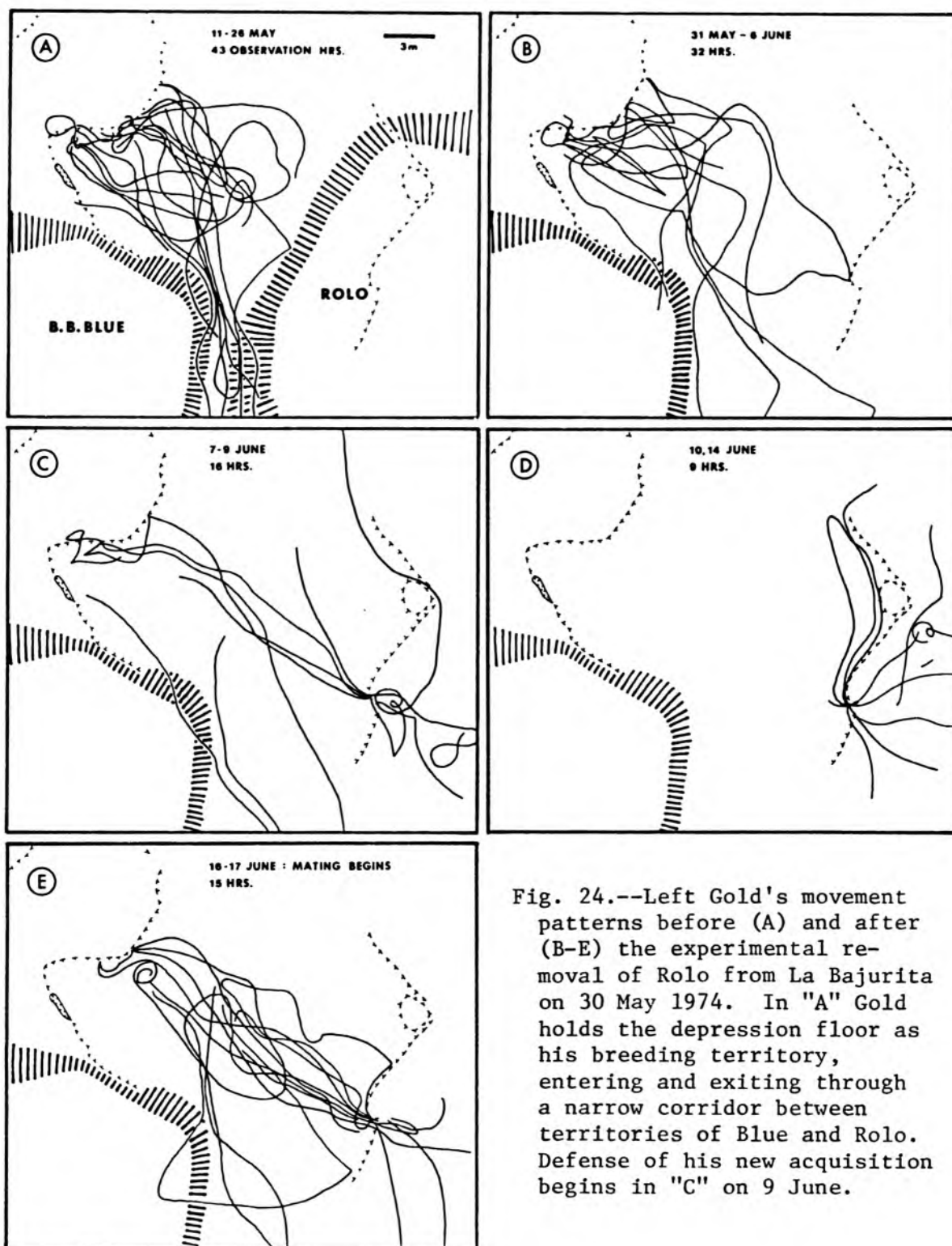


Fig. 24.--Left Gold's movement patterns before (A) and after (B-E) the experimental removal of Rolo from La Bajurita on 30 May 1974. In "A" Gold holds the depression floor as his breeding territory, entering and exiting through a narrow corridor between territories of Blue and Rolo. Defense of his new acquisition begins in "C" on 9 June.

present retreat-mate, Silvia. Of all females observed, Silvia was among the least timid, showed the greatest antagonism toward other females around her retreat, and remained extraordinarily faithful to that particular site--only once did I see her venture down to the depression floor. One reason I chose to remove Rolo from his territory was to examine what effect, if any, the change would make in Silvia's behavior. There were no noticeable effects.

On 19 July, well after all mating activity had passed, Rolo was released 0.4 km from La Bajurita, as already mentioned, and within two weeks he had found his way home and reclaimed his old territory. Unfortunately, I was engaged in studies of nesting activity and was unable to document the exact date of his return or to observe his confrontation(s) with Left Gold.

Territory Patrol and Mating.--Mating commenced on 16 June 1974, and continued for 13 days. Observations were made daily and averaged 8.5 hrs./day. During this period, there were conspicuous changes in the activities of both males and females. Territorial males were nearly always surveillant over their territories, alert to intrusions by other males and to the presence of any females in the area. Only during this month were resident males seen making routine checks of every retreat occasionally or regularly used by females (e.g., see Fig. 25). Non-territorial males ventured more frequently into established territories--most such incursions were centered, however, in Fig Row. Males and females alike abandoned normal foraging excursions, though some locally available items like fallen Capparis leaves were taken when

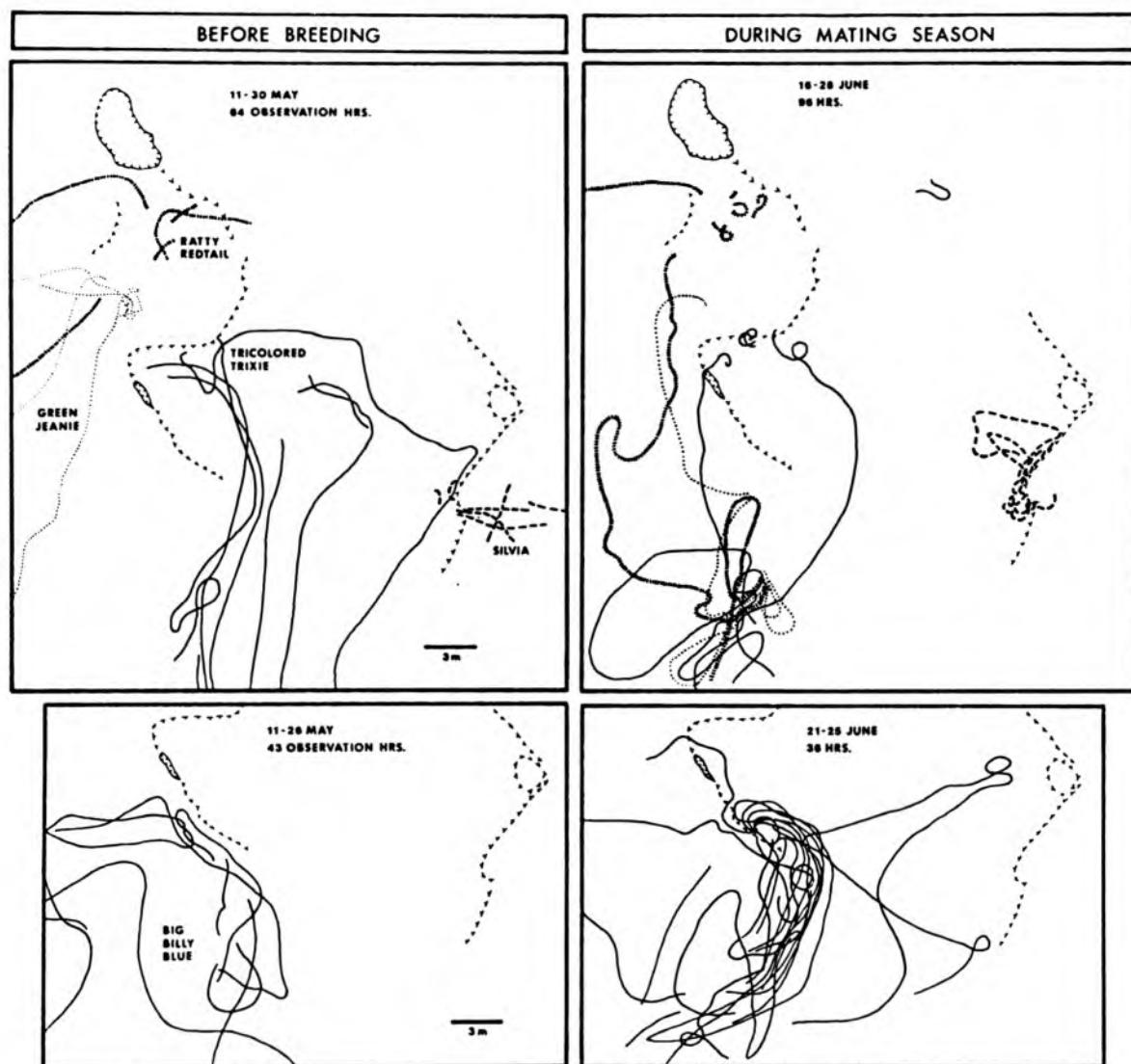


Fig. 25.--Comparisons of movement patterns of four female Mona Iguanas (top) and one territorial male (bottom) before and during the 1974 mating season at La Bajurita.

found. Fresh scats were rare and unusually small during this period. Females maintained an extraordinarily low activity profile and seldom ventured more than a few meters from the safety of a crevice.

Sexually receptive females varied considerably in their behavior. Silvia, for example, was not seen more than 4 m from her retreat during the entire 13-day period, and was serviced by one male, Left Gold, on six different occasions, never accepting him more than once on any given day. In contrast, Tricolored Trixie and Lora each traversed the territories of four different males and mated with three. Immediately after mating with Gold on the floor of the depression, Trixie moved up the slope into Billy's territory and submitted to him; two days later I saw her in copulation with Randy Redtail in his territory. Lora was mated three times in prompt succession, twice in the depression and once in Billy's territory. The more timid females were seen copulating only once, as was the case with seven of the 11 females observed breeding (Table 15). However, two sources of bias may have affected this outcome: 1) my presence may have contributed to their unwillingness to emerge on other occasions; and 2) I may have missed seeing other matings. I am therefore inclined to believe that multiple inseminations may be more common than not. Date and location for each of the 21 matings observed are given in Fig. 26.

Some females, like Trixie, were receptive to copulation upon the male's first courtship advance, but more typically, females required repeated precopulatory stimulation before they would submit. Randy Redtail, for example, spent several days making advances at Green

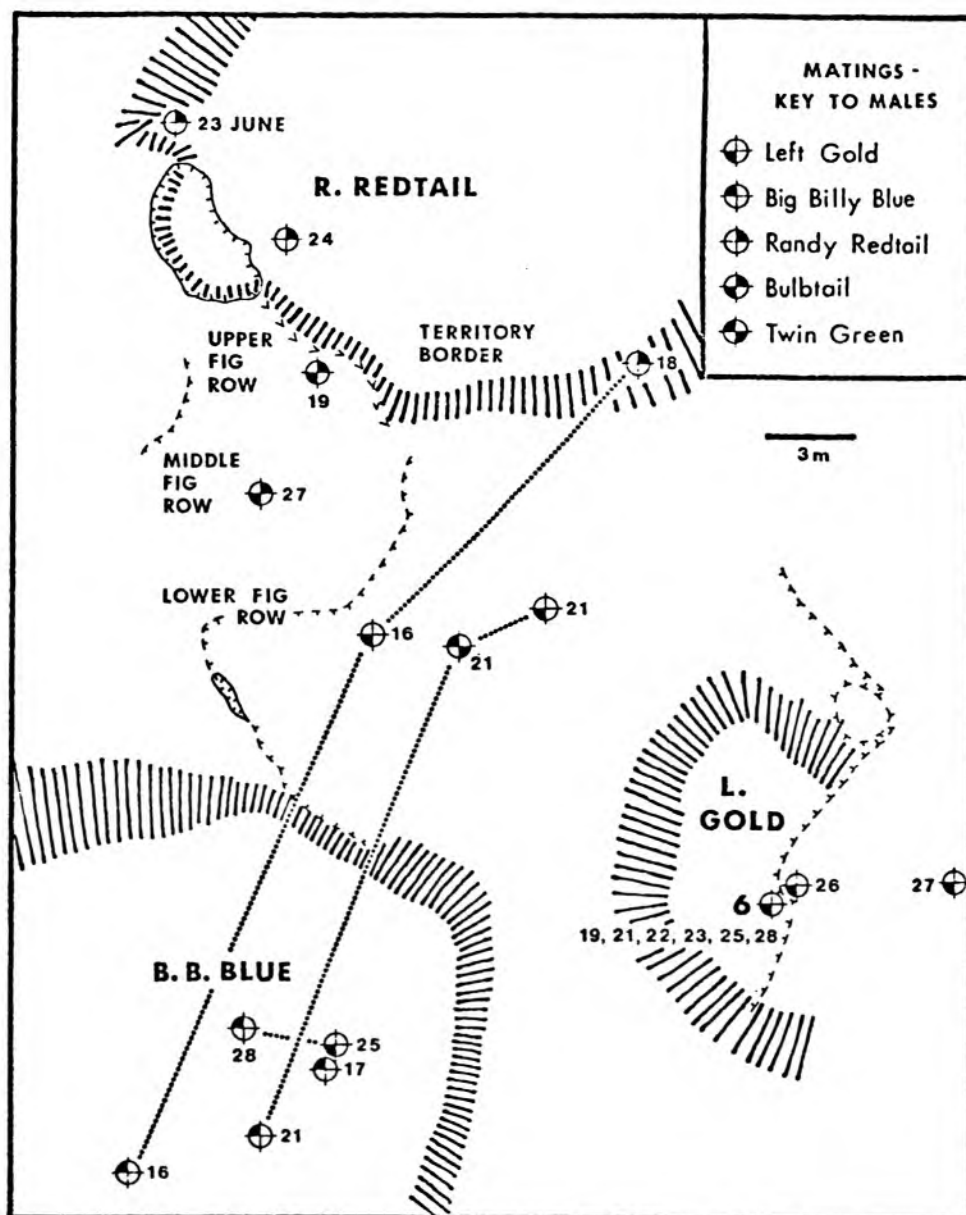


Fig. 26.--Location and date of copulations among Mona Iguanas observed during the 1974 mating season at La Bajurita. Territory limits for the three long-term strategists have been sketched in. Register marks indicate the site of each mating, six of which (Left Gold x Silvia) occurred in approximately the same place. Small numbers tell the day of the mating, in June. Dotted-line connections indicate multiple insemination of the same female by different males.

Goobers and Topsy Green before they became receptive. In such instances, the courting male would typically wait 2-3 m from the female's retreat and, upon her appearance, display a series of toss-rolls with mouth open, promptly followed by a dash to her, head lowered. A pause for another round of head displays often preceded his attempt to seize her. Securing a hold on the female's fleshy nuchal crest is characteristic, but before this can be accomplished, the male usually must first grab something else, often her tail or loose skin on her flank, to restrain her while getting in a better position, a neck-hold and straddle over her. At this stage an unwilling female may turn to bite or, more commonly, struggle into a crevice, dislodging the male in the process. The male may follow her into the hole to investigate, but typically he backs off to await her re-emergence. Big Billy Blue spent an entire morning pursuing, pinning, and losing Green Jeanie in this manner. She never remained in hiding for long, however. Every 10 minutes or so, Jeanie would re-emerge to face another assault from Billy. As the morning progressed, her stays in the crevice became shorter. By noon her nuchal crest was raw and bleeding, and she accepted him shortly thereafter.

Such changes in female responsiveness to male advances appear closely tied to his aggressive acts. This is further suggested by the behavior of males in the act of subduing a female. Many other iguanid lizards simply hold on to the nape of the female's neck and proceed with intromission. In contrast, male Mona Iguanas often let go, bite, and pull repeatedly at the crest, as though providing added stimulation to

the area. The effect appears to be pacifying, and the female usually goes limp before copulation is attempted. Sometimes the female is also dragged about a bit, and her forequarters tossed to and fro during the preliminaries.

Numerous variations were observed in the precopulatory style of courting males. As noted by Berry (1974) in her study of the chuckwalla Sauromalus obesus, some males handle the task with great "patience" and "finesse" while others appear overanxious and clumsy. It was amusing to see one Mona Island male rush up to a female and nab her gently by the skin of her cheek, while another male (Freddie) charged at his prospective mate (Lora), never pausing to display, and grabbed her by the head, as though to engulf her. Lora was intimidated by Freddie's tactics, and she fled for cover. Freddie had several similar opportunities to court Lora that same afternoon and the following morning in the same place; however, on these occasions he approached her so meekly that he was totally ineffective. He sat watching her and displaying to her repeatedly and even walked around and over her, but he never again attempted to seize her. Later that second day, three males mated with Lora in succession, and Freddie lost out altogether. It thus appears that individual experience may play an important role in the development of behavior patterns in these lizards, a quality that would be of particularly great value to a long-lived species.

Left Gold was successful in using abbreviated preliminaries to mounting Silvia. She was relatively unafraid of his presence, and most mounting attempts began casually and at close range, typically initiated

with such gestures as cheek-nipping. He regularly greeted her with head toss and/or roll displays (as the now-captive Rolo had done year-round), and during the breeding season, the two were mutually responsive to body contact. I filmed one meeting in which Silvia rose to her feet as Gold approached, displaying. She walked towards him, and, upon meeting, both leaned into the other's body, Silvia nearly poking Gold in the eye with her long, sharp facial spines. I observed a different pair at night (one was a female equipped with a radio-transmitter collar) sleeping together, the male lying upon her tail with his chin resting on her sacrum--this occurred in February, well removed from the breeding season. Tactile communication of this sort is probably normal in pairs sharing the same or adjacent retreats, especially during the breeding season.

To accomplish intromission, the male twists his tail under and perpendicular to her tail, gives two or three pelvic thrusts to snug up to her cloaca, and inserts the nearest hemipenis. Males maintain their hold on the female's neck through^{out} copulation. The briefest copulation seen lasted approximately 15 seconds, the longest 2 min. 15 sec. None were interrupted, and all appeared successful. The 15-sec. mating was delivered by Gold to Silvertail in the center of Billy's territory (he was nowhere in sight at the time). Gold had mated with Silvia earlier that same day (a 55-sec. union), perhaps explaining the brevity of the second mating, which might also have reflected anticipation of Billy's return.

Gold accomplished 11 of the 21 copulations observed at La Bajurita

in 1974, and these decreased in duration as the season progressed. Each of his first four matings (16-21 June) exceeded 1.5 min. (\bar{x} = 1.8 min.); and a sharp fall-off occurred thereafter (22-28 June)--unions observed from beginning to end during this period (N=5) all lasted less than 1 min. (\bar{x} = 39 sec.).

Mating apparently occurs infrequently at odd times throughout the year. The Mona Police reported seeing pairs in copula on 4 October 1973 and 6 February 1974. I saw none out of season but did witness contact preliminaries at La Bajurita on three occasions, advances made by Big Billy, Randy Redtail, and Left Gold; only once was a neck grip achieved.

Postcopulatory behavior was of consistent form. After uncoupling, the male staggers for about half a minute, walking slowly and stiffly, the cloaca is scraped briefly on the ground during retraction of the partially extruded hemipenis, and at least one courtship display is given. The female moves away slowly, pausing to reply with shallow head rolls/bobs, sometimes seeking a retreat promptly. If the female attempts to leave the male's territory, he invariably pursues her and may, time permitting, circle around in front to intercept her. Bulbtail, for example, overtook Ratty Redtail as she was departing from his territory after mating and stopped right in front of and perpendicular to her, displaying emphatically. Then he crawled over her back three times, pausing each time with rear legs or tail resting upon her. She nevertheless continued on her way at a leisurely pace; he finally gave up, returning to his territory 34 min. later. I interpret this behavior as "postcopulatory guarding" (reviewed by Parker, 1974), a male's attempt

to prevent immediate inseminations of the same female by other males.

Reproductive Strategies of Males, an Evaluation of Costs and Benefits:

Only male iguanas that held territories during all or part of the 1974 breeding season were successful at courtship and mating at La Bajurita. Several challengers drifted in from outside areas, but none were able to displace residents or gain access to females. All territory shifts and take-overs (excluding the one induced by my iguana-removal experiment) came from residents of the Fig Row retreat complex.

Most noteworthy, two temporally different systems of territorial behavior centered on a single critical resource (females) occur together in the same localized breeding population (at La Bajurita). Some males employ a "long-term" strategy, defending year-round, while others do so on a "short-term" basis, for a month or less, maintaining a low social profile throughout the rest of the year. The former strategy is exemplified by activities of the Big Four (the Big Three, after Rolo's removal) and the latter by the Fig Row Company (see Fig. 27).

These two classes of males were compared with respect to agonistic encounters (Tables 16 & 17) and mating success (Table 15) during 25 observation days between 30 May and 29 June 1974. These data are summarized in Table 18. The differences are striking: males making the long-term investment engaged in roughly half as many chases and one-fourth as many fights, and their combined mating success was four times as great. Two-thirds of the encounters met by the Big Three were from outsiders, whereas 81% of those met by the Fig Row Company were among themselves. It is interesting too that, in spite of his changing

Fig. 27.--Histograms comparing the activity of eight territorial males at La Bajurita study area. The basic profile repeated in each histogram represents the total number of observation days spent at the study area during time periods averaging six days each from January to July 1974. The extent to which columns are filled-in indicates the proportion of days the iguana was sighted. Solid bars mean the male was territorial at the time, stippled bars non-territorial.

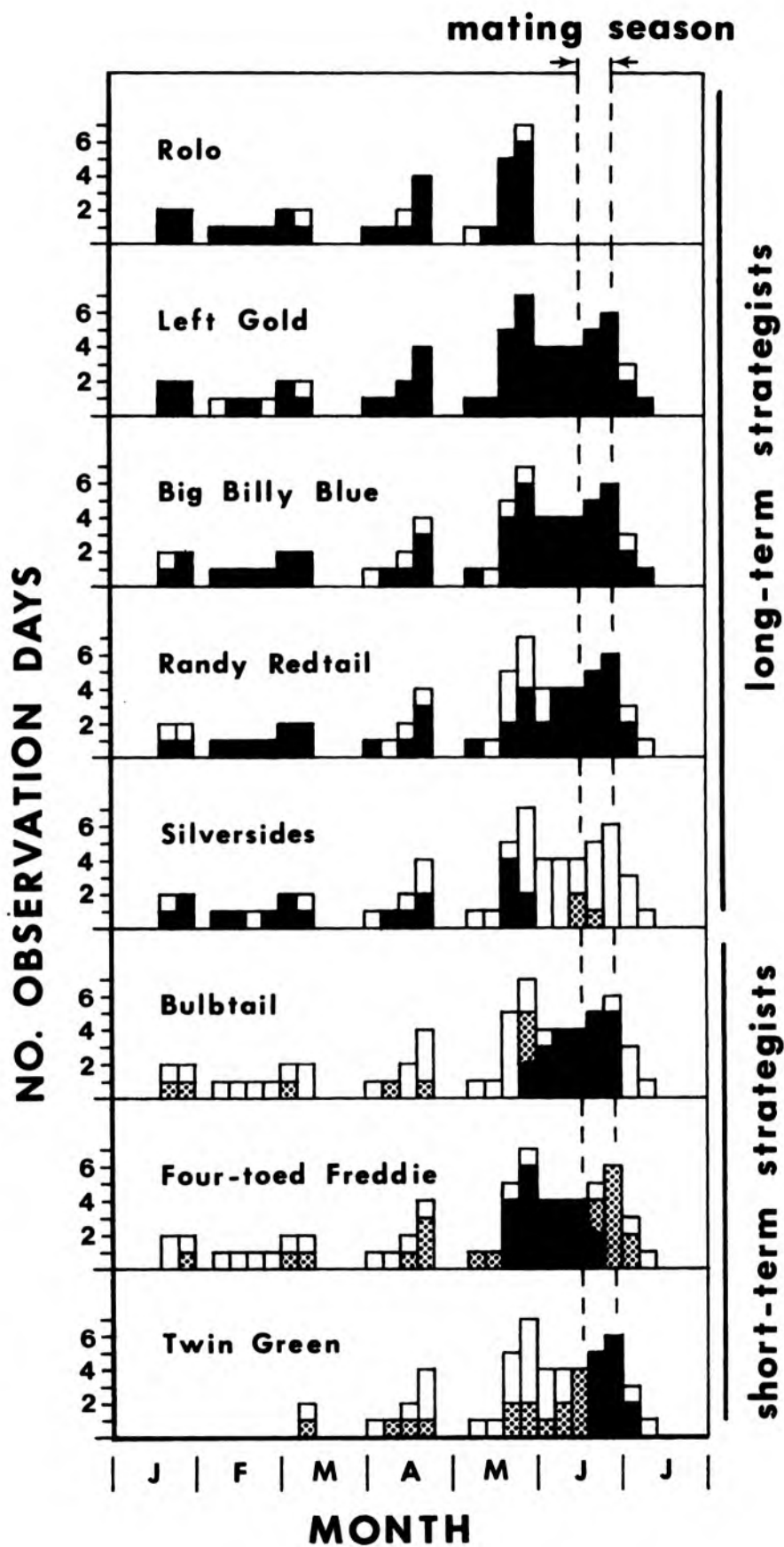


Table 16.-- Dominance matrix for chases by male Mona Iguanas during the 1974 breeding season at La Bajurita.

Aggressor	Intruder							Total Times as Chaser
	Big Billy Blue	Left Gold	Randy Redtail	Bulbtail	Four-toed Freddie	Twin Green	Silversides	Outsiders
Big Billy Blue	-	1	1	1	1	5	1	14
Left Gold	1	-	0	0	2	2	0	19
Randy Redtail	0	0	-	2	0	4	0	20
Bulbtail	1	0	1	-	22	13	1	13
Four-toed Freddie	0	2	0	0	-	9	1	12
Twin Green	0	0	1	0	2	-	0	6
Silversides	0	0	0	0	0	1	-	0
Outsiders	0	0	0	0	0	0	0	-
Total Times Chased	2	3	3	3	27	34	3	84
								159

Table 17.--- Dominance matrix of the outcome of fights among male Mona Iguanas contesting territories during the 1974 breeding season at La Bajurita.

Apparent Winner	Apparent Loser							Total Wins
	Big Billy Blue	Left Gold	Randy Redtail	Bulbtail	Four-toed Freddie	Twin Green	Silversides	
Big Billy Blue	-	0	0	0	0	1	0	1
Left Gold	0	-	0	0	0	0	0	3
Randy Redtail	0	0	-	1	0	0	0	4
Bulbtail	0	0	0	-	0	2	1	3
Four-toed Freddie	0	0	0	0	-	4	0	8
Twin Green	0	0	0	0	5	-	3	8
Silversides	0	0	0	0	0	1	-	1
Outsiders	0	0	0	0	0	0	0	0
Total Losses	0	0	0	1	5	8	4	28

Table 18.-- Comparative summary of characteristics of male reproductive strategies based on territorial behavior in Mona Iguanas at La Bajurita.

	Long-term Strategists ¹	Short-term Strategists ²
FEATURES:		
Territory structure	Large size ($\bar{x} = 205 \text{ m}^2$; range 121-252) Physically simple, few retreats	Small size ($\bar{x} = 46 \text{ m}^2$; range 33-60) Complex network of retreats throughout
Defensibility of Territory	Relatively easy	Difficult
Duration of Territorial Behavior	Year-round	$\bar{x} = 26$ days (range 17-34)
No. Females Residing in Territory	3 (all territories combined)	10 (in Fig Row)
COSTS DURING BREEDING SEASON (30 May-29 June: 162 hrs. over 25 days):		
Chases/male	$\bar{x} = 27$ (range 26-29)	$\bar{x} = 49$ (range 43-54)
Fights/male	$\bar{x} = 2.7$ (range 1-4)	$\bar{x} = 11$ (range 4-16)
Chase:Fight Ratio	10:1	4.5:1
Interference during Precopulatory Activity	None (when on territory)	Common
BENEFITS:		
Mating Success in Females/Male	$\bar{x} = 4$ (range 3-5)	$\bar{x} = 1$ (range 0-2)

¹ Big Billy Blue, Randy Redtail, Left Gold

² Bulbtail, Twin Green, Four-toed Freddie

territories after my removal of Rolo, Left Gold was not challenged more frequently than the other two males (Billy and Randy) whose territories remained stable throughout (see Tables 16 & 17).

Comparison was also made of body size, which is presumably a reasonable indicator of relative age and experience, with territory size (Table 19). While I chose not to traumatize my study animals by capturing them for measurements, I did rank the males by apparent size. The male I removed from the lot, Rolo, was a 6.8 kg animal, one of the largest among them, and the smallest was assuredly greater than 5 kg in weight (an assessment based on weights of adults captured elsewhere). The three males in Class A all adopted the long-term strategy, while two of the three smallest residents, Class C, used the short-term strategy. The other member of Class C, Silversides, is a noteworthy intermediate; he was badly defeated in his attempt to compete using a long-term strategy in Fig Row. Among the non-territorial males identified at La Bajurita, only one, Penciltip, could be placed in a size class distinctly smaller than Class C. This small roving male was never seen challenging the others to a fight and was frequently chased from one territory to another. All individuals appeared to be in good physical condition throughout the study, and none showed depletion of reserves in the tail.

There were broad differences and a clear dichotomy in territory size. The Fig Row males all held territories that were, at the largest, only half the area of the smallest held by males holding permanent territories. Shifts in territory position and shape that occurred

Table 19.-- Comparisons between body size and territory of male iguanas at an inland sinkhole depression, Mona Island, P.R.

Body Size		Territory	
Male	Class	Approx. Size (in m ²)	When Held
The Big Four	Rolo	170	Year-round
	Big Billy Blue	241	Year-round
	Randy Redtail	252	Year-round
	Left Gold	121	Year-round
The Fig Row Company	Bulbtail	43-46	30 May-26 June 1974
	Twin Green	60	19 June-5 July 1974
	Four-toed Freddie	32-34	19 May-21 June 1974
	Silversides	41-47	12 Nov. 1973-30 May 1974

during the course of the breeding season were not, however, accompanied by significant changes in territory size. Four such comparisons were made: 1) Silversides, 47 m^2 vs. 41 m^2 (a 13% loss); 2) Four-toed Freddie, 34 m^2 vs. 32 m^2 (a 6% loss); 3) Bulbtail, 43 m^2 vs. 46 m^2 (a 7% gain); and 4) Left Gold, 121 m^2 vs. 121 m^2 (before vs. after he moved into Rolo's vacant territory). Curiously, in this last case, Left Gold's new territory never exceeded 71% of Rolo's former territory, even though core areas were identical. It appears that territories held by the Fig Row Company were near the absolute minimum in which any mating could be accomplished without interference from neighboring males. Owners of these mini-territories spent most of their time near its geometric center, the territory's average radius being approximately twice the animal's individual distance (minimum personal space, which was about 1.2 m between males throughout the year).

Mating success of the Fig Row Company was limited not so much by small territory size as by in-group interference during mating preliminaries. Several potential copulations were lost by Fig Row males in this manner, especially well illustrated by the interactions of four males competing for access to two receptive females during a 1.4-hour period on the third day of the breeding season (paraphrased from field notes):

Female Orange Blotch emerged from a crevice in Middle Fig Row and was promptly courted by Twin Green. She accepted his advances, but no sooner had Green mounted her, Silversides (who had lost his territory) crawled from a hole in Middle Fig Row. Green responded by releasing his hold on Blotch, who was frightened by the encounter and prepared to dive into the crevice from

which Silversides had come. Silversides pounced on Blotch, securing a grip on her nuchal crest, and began tossing her forequarters from side to side. Green walked over to the pair and bit his adversary on the flank. Silversides immediately released his partner and entered a fight with Green, Blotch fleeing to a hole. Seven minutes later she re-emerged while the fighting males had reached a standoff. Four-toed Freddie then rushed from his territory in Lower Fig Row and began fighting Green, as Silversides lay nearby, prostrate and huffing. Again, Blotch retreated. Silversides cut in and continued fighting Green; Freddie backed off and returned to Lower Fig Row. The fight continued for another seven minutes with Silversides getting in a nasty bite to the middle of Green's back, but ended as Silversides was forced down into the crevice from which he had come.

Later in the morning Ratty Redtail emerged in Upper Fig Row, Bulbtail's territory. He courted her, nipping and tugging at her mid-dorsal spines, gradually working his way up to her neck. Ratty pulled away, entered a crevice, and Bulbtail followed. After a few seconds he reappeared, as did she six minutes later, whereupon he displayed, rushed over to her, and continued his nipping. After a short round of courtship, he withdrew a little and sat nearby, intently watching her. Just then Green made a courtship dash for Ratty, who ducked into a hole as Bulbtail chased the intruder back to his territory in Middle Fig Row. Later that afternoon Bulbtail succeeded in mating with Ratty.

In contrast to the encounters described above and to similar episodes seen at other times, neighboring males never intervened in foreplay activities of the Big Three ($N=25+$ observations) unless the female being courted was within another's territory or in a neutral zone.

After Left Gold had given up defending the floor of the depression, social encounters occurring in that neutral zone revealed that mating is occasionally completed off-territory in the midst of one or two competing males ($N=2$ cases, described below). Dominance relationships were evident under these circumstances, but with little respect paid to the "rights" of the dominant, i.e., the larger or more aggressive individuals were not immune to attack from subordinates during mating preliminaries.

I therefore hesitate to apply the term "hierarchy" here. This social structure was clearly illustrated by the interactions of three males competing for Rola on the depression floor:

Rola emerged from her retreat on the edge of the depression and moved towards the spot where Four-toed Freddie was basking. Bulbtail, who was in his territory in Upper Fig Row, spotted her, descended the rocky slope, and made a dash to grab her by the neck, whereupon Freddie backed off momentarily. A few seconds later Freddie attempted to cut in. Bulbtail released Rola, chased Freddie for about 3 m, and continued courting. Again Freddie interfered, with the same consequence, but this time Rola retreated to her hole. Bulbtail investigated and then returned to Upper Fig Row.

Five minutes later Rola reappeared and moved to the center of the depression. Twin Green left Middle Fig Row to court her. As Green approached, Freddie edged towards Rola, but Green charged in and seized her by the neck. Freddie backed off. Green moved astraddle Rola and achieved intromission. Freddie walked over to the pair, gave Green a quick bite on the neck, moved away a bit, and sat by, watching. Green did not respond to the attack and continued with copulation (1.4 min.) as though nothing had happened. Left Gold then spotted the activity below, moved down from his new territory, chased both of the Fig Row males away from Rola, and promptly mounted her, grabbing the nape of her neck. She struggled to get free as Gold pulled her to and fro. Green approached and bit his successor; Gold responded with a quick turn, snapping. Green backed off, Gold resecured his position, and a 1.75-min. mating followed uninterrupted.

Comparisons made outside the breeding season (22 January - 30 May) revealed five to nine times fewer chases and fights among adult males per hour of observation time, while agonistic encounters remained about three to four times more frequent within the Fig Row Company than in the Big Four group (Table 20). Most (75%) of the competitive strife among Fig Row males stemmed from aggression by Silversides, who was attempting to defend Middle and Upper Fig Row from resident males leaving and entering the retreat complex. Because activity patterns differ

Table 20.-- Comparison of confrontation rates among male Mona Iguanas at La Bajurita during nonbreeding vs. breeding seasons.

		Confrontations/Individual/100 Hours Observation Time					
		22 January-30 May (T = 134 hrs. over 33 days)			30 May-29 June (T = 162 hrs. over 25 days)		
		Fights	Chases	Fight:Chase Ratio	Fights	Chases	Fight:Chase Ratio
<u>Long-term Strategists</u>							
The Big Four		0.19	2.05	1:10.8	-----	-----	-----
The Big Three		-----	-----	-----	1.67	16.67	1:10
<u>Short-term Strategists</u>							
The Fig Row Co. (excluding Silversides)		0.75	5.97	1:8	67.9	30.25	1:4.5
<u>Silversides</u>		1.49	11.94	1:8	-----	-----	-----

considerably between the breeding and nonbreeding seasons (see sighting-frequency data in Fig. 26), the off-season data are unavoidably more speculative and conservative, since the Fig Row males were seen less commonly in the study area than the Big Four were. Although systematic records of competitive interactions were not begun until January 1974, 23 observation days were spent at this study area during the nonbreeding season between 7 July and 6 December 1973 (including every month except August) and no significant departures from the January-May activity patterns were noted.

Courtship persistence and vigilance for intruders are potential costs associated with year-round territoriality. The Big Four routinely slept in exposed locations at the focal point of activity within each territory, and so were able to monitor their immediate environment to a maximum extent. The cost of such behavior in terms of a presumed increase in metabolic expenditure is unknown, but it is probably of minor importance since temperature and humidity conditions at a retreat entrance are very similar to those within. Attentiveness to females outside the breeding season is relatively low-key, an apparently inexpensive activity. It thus appears that the Big Four long-term territory holders maintained the less costly reproductive strategy on a full-year basis.

Discussion:

Adaptive Significance of Twin Breeding Strategies.--A territory is the normal prerequisite for breeding by male Mona Iguanas. A male's mating success depends chiefly upon the frequency with which he encounters

females and upon his ability to nab a female quickly when she is receptive, mate with her without interference from competing males, and keep her from contacting other males between insemination and fertilization. A territory serves as the buffer zone in which these objectives can be accomplished, varying with respect to two interdependent factors: 1) the density and behavior of females within that area, and 2) the extent to which other males respect the occupant's interests in the site.

A male's competitive ability will depend upon his size, strength, experience, persistence, and the energetic feasibility of his efforts. Because this is an exceptionally long-lived species endowed with a good memory, experience is surely of much greater significance than in most lizards.

In selecting a place of residence, females appear to respond primarily to the quality of available retreats, while males respond mainly to the density and distribution of potential mates. It is important to recall that most mating occurs near retreats selected by females, in areas they frequent throughout the year. Territory quality is therefore highly variable in this respect. A site such as Fig Row that is structurally complex and attracts many females is clearly more difficult to defend than a physically simple one occupied by few females, e.g., the territories of the Big Three. Fig Row territories must necessarily be small to be effectively guarded, thereby decreasing the likelihood of uninterrupted courtship and mating and increasing the overall cost/benefit ratio. Incidentally, the difficulty of defending such territories may explain why the Fig Row females were cohabiting without any apparent antagonism towards each other.

Assuming that territorial behavior by males and the associated mating systems here observed are derived from intense male/male competition and optimization of time/energy investments, I propose that the only strategy that will work in Fig Row is a short-term effort concentrated in a small territory. Where bluffing and extending defense to times beyond the breeding season are unlikely to discourage challengers when females become receptive, it is, in effect, a waste of energy to adopt a long-term strategy. The ease with which Silversides was dethroned just prior to breeding, despite his vigorous fighting and six-month vested interest in Fig Row, illustrates the point. Furthermore, the returns in terms of mating success were marginal in Fig Row for two apparent reasons: 1) the territories were unusually small, with interference from competing males correspondingly great; and 2) the resident females avoided competitive strife between males and generally attempted to move into contiguous areas for mating. Thus, even though the probability of encountering a female at Fig Row remained high, a male's chances for completing copulation there were relatively low. This would explain why the largest and presumably the most experienced males staked out territories elsewhere.

In areas that are often traversed by females but offer relatively few retreats, competition between males is less intense and territorial behavior becomes more feasible and less costly. Under these circumstances, a male may improve his fitness by maintaining a relatively large territory year-round and extending the courtship period. The longer and more regularly such territories are defended, the less likely

it is that trespassing will occur during the breeding season. Furthermore, a male who continues throughout the year to court potential mates walking through or residing within his territory is in a better position to monopolize them when the critical time arrives (evidence for this is suggested by comparison of Figs. 21 & 25 & Table 15). The stronger the "pair bond" developed, the more likely the female is to seek or stay within his domain when she becomes receptive, and to accept his advances without hesitation. Implied, of course, is that the female also benefits from the relationship by being able to mate smoothly and without interference. The short duration of copulation is presumably another adaptation to facilitate mating under highly competitive circumstances.

Long- and short-term reproductive investments do not appear to be mutually exclusive behavior patterns. Young males probably begin as "floaters" until they can acquire the strength and experience to hold a breeding territory. Thereafter, the strategy employed probably hinges primarily on the defensibility of available territories, with the older and more dominant males securing those territories permitting both access to females and year-round defense. I would judge that, as social conditions change over the years and vacancies appear, individuals may shift from one system of territorial behavior to the other. Because one would expect males to advance from a less efficient to a more efficient system with respect to mating success, the usual direction of change, if or when it can occur, is probably from a short-term towards a long-term strategy. That such changes can occur in field populations of lizards is suggested by observations that some species undergo shifts from

territoriality to a dominance hierarchy where local density is high (Ctenosaura pectinata, Evans, 1951; Sceloporus occidentalis, Fitch, 1940; Anolis lineatopus, Rand, 1967a; and Uta stansburiana, Ferguson, 1971). Furthermore, in a study of female Anolis aeneus, Stamps (1973) found territoriality in some habitats and dominance hierarchies in others; nevertheless, she was unable to account for the observed differences through determinations of density and distance to nearest neighbor. This would hardly be surprising if the elasticity between social systems is viewed not as a product of density per se but rather of density relative to the availability and defensibility of critical resources.

Postcopulatory Guarding.--Parker (1974) noted two theoretical considerations that are necessary for the evolution of postcopulatory guarding behavior: 1) an overlap period during which sperm from ejaculates of different males can compete for fertilization of a female's ova, and 2) a high male/female encounter rate relative to the duration of the overlap period. Without knowing when fertilization occurs, however, it is impossible to specify the overlap period. A female's ability to store sperm contributes to the likelihood that multiple insemination will result in sperm competition, and sperm storage is characteristic of many, if not most, reptiles (see Porter, 1972). Good genetic evidence that sperm competition does occur in at least some reptiles was found in the garter snake Thamnophis sirtalis by Gibson & Falls (1975). Furthermore, copulatory plugs discovered in the cloacas of recently mated female snakes presumably represent an evolutionary consequence of sperm

competition (Devine, 1975). By obstructing further mating, the copulatory plug appears to be one means by which a male can enforce the chastity of his mate. If a lengthy duration in copula is required for the addition of a mating plug, as suggested by Gibson & Falls (1975), it is highly unlikely that they exist in Cyclura stejnegeri.

Another significant aspect of postcopulatory guarding is that female Mona Iguanas do not show coition-induced inhibition to sexual receptivity. This is in sharp contrast to the situation in female Anolis carolinensis, which develop sexual inhibition within 1 min. after copulation (Crews, 1973). Similarly, field observations by Trivers (1976) suggest that Anolis garmani typically mate only once during each ovulatory cycle. Both lizards lay only a single egg per cycle. Receptivity extending beyond the first copulation or two per batch of eggs is unusual among animals (see Trivers, 1972) and may be interpreted in three ways: First, if a female must risk more than she would gain by avoiding males after copulation, e.g., having to suspend feeding and basking, it may simply be less disadvantageous for her to tolerate multiple matings. This adaptive option, suggested by Parker (1974) does not appear to fit the case in point. Second, the female may be attempting to insure adequate fertilization, an important possibility discussed later. And third, perhaps a female can benefit by enhancing the genetic variability of her offspring through multiple insemination before fertilization. It is often assumed that a female is capable of making an accurate assessment of a male's fitness and should limit herself to the services of a single male (see Trivers, 1972), but I

believe this need not always be so. Females would be expected to mate preferentially with dominant males, but not necessarily with only one each. A female could conceivably do better by diversifying her reproductive investment where clutches are sizable, paternal investment in the offspring ends with insemination, and population size is small.

Retreat Defense by Juveniles and Females.--It is not immediately evident why juveniles or females should defend retreats on Mona, for there appears to be an abundance of rock crevices available. I believe this behavior can be attributed to two factors: First, many crevices are not inhabitable for one reason or another, and perhaps only a relatively small percentage offer comfortable quarters. Second, an iguana having occasion to seek safety from aerial predators or conspecifics would benefit from close familiarity with escape routes within its home range and might be expected to maintain clear access to suitable hiding places. Retreat defense may have thus been more common before exotic mammals were introduced, when the iguana population was assuredly more dense than it is today.

A third possible value of retreat defense, one that applies specifically to mature females, relates to their reproductive fitness. An aggregation of females at one site is a special attraction to males, an attraction that can be expected to increase with greater numbers of females present. This situation leads to intensified competitive strife among males, especially during the breeding season, which in turn greatly increases the probability of intervention during mating. A female caught in the midst of quarreling males might suffer bodily harm

or inadequate insemination, and a preponderance of male/male aggression may inhibit or greatly reduce her secretion of gonadotropic hormones and result in her laying inviable eggs, a possible social effect first and nicely demonstrated in a lizard by Crews (1975). Furthermore, the promiscuous behavior of males, the decreasing copulation times (possibly reflecting lowered virility)* observed in the most sexually active male, and the apparent willingness with which females submit to multiple insemination, together suggest that the female may drive other females away from the male's territory as a security deposit against inadequate insemination by a temporarily overspent mate. Such behavior appears comparable to that of a dominant female preventing subordinate females from mating until she has mated (e.g., Robel, 1970). It is significant in this regard that Silvia, who showed the most consistent aggression towards other females near her retreat, was monogamous yet mated with her partner on six different occasions. Similarly, a visitor reported seeing elsewhere on Mona five matings by a single pair during the course of one afternoon.

Mating System Terminology.--Selecting an appropriate term to describe the Mona Iguana's mating system is problematical. Individuals differ with respect to breeding habits, and traditional terminology is inadequate. Some females mate with only one male, whereas others accept (or seek) more than one, and males take as many mates as possible, with or

*A number of authors have shown that in some birds and insects the concentration of spermatozoa drops during successive ejaculations, and copulation time may be shortened as well (see citations in Trivers, 1972, p. 167).

without having established a "pair bond" beforehand. It would thus be misleading to define the iguana's mating system as polygamous (either polyandrous or polygynous), promiscuous (implying the absence of pair bond relationships), or monogamous (see usage in Brown, 1975).

In a new ecological and evolutionary scheme for classifying avian mating systems, Emlen & Oring (1977) present nine categories based on the manner of and environmental potential for mate monopolization. Their only category applicable to Mona's iguanas is Resource Defense Polygyny, defined as a system whereby males acquire multiple mates indirectly by defending resources essential to females. Male iguanas defend retreats attractive to females, and the degree to which individual males are able to control this resource is apparently a chief determinant of mating success. While the Emlen & Oring classification has great heuristic value, there is an obvious complication in applying it here. Using a term to describe what males are doing says nothing about mate selection by females, and, as already shown, female Mona Iguanas are not simply passive occupants of a male's territory, for their movements affect both where and with whom mating occurs. In short, there is no satisfactory terminology for systems of this complexity.

NESTING BIOLOGY

Phenology:

Two of Mona's geological features permitted island-wide assessment of the iguana's nesting habits and precise evaluation of nesting patterns. The island's surface area is predominantly rock, and less than 1% of it is suitable for nesting (see *Iguanas & the Activities of Man*); nesting locations are therefore very limited and predictable. In addition, all soil deposits upon the plateau are lateritic clay, dyeing the iguanas reddish-orange from head to tail as they dig; nesting animals are thus seasonally conspicuous and easily identifiable.

The nesting season is extremely short, a period of two weeks beginning in mid-July. Its onset and decline are accordingly abrupt, and most egg-laying occurs within one week (Fig. 28 and Table 21). The season is the same island-wide, though activity peaks were a few days apart in nesting areas studied simultaneously on different sides of the island.

Not only is nesting highly synchronous throughout the population, but its timing from year to year differs no more than one week, regardless of variations in weather. This conclusion is based on nine years of nesting records (this study; L.A. "Chin" Ramirez, field notes; and Lee Rogers, pers. comm.). The onset of nesting is not triggered by rainfall. Rainfall data for April - July show striking variations in precipitation pattern during 1972, 1973, and 1974 (see Fig. 34). The

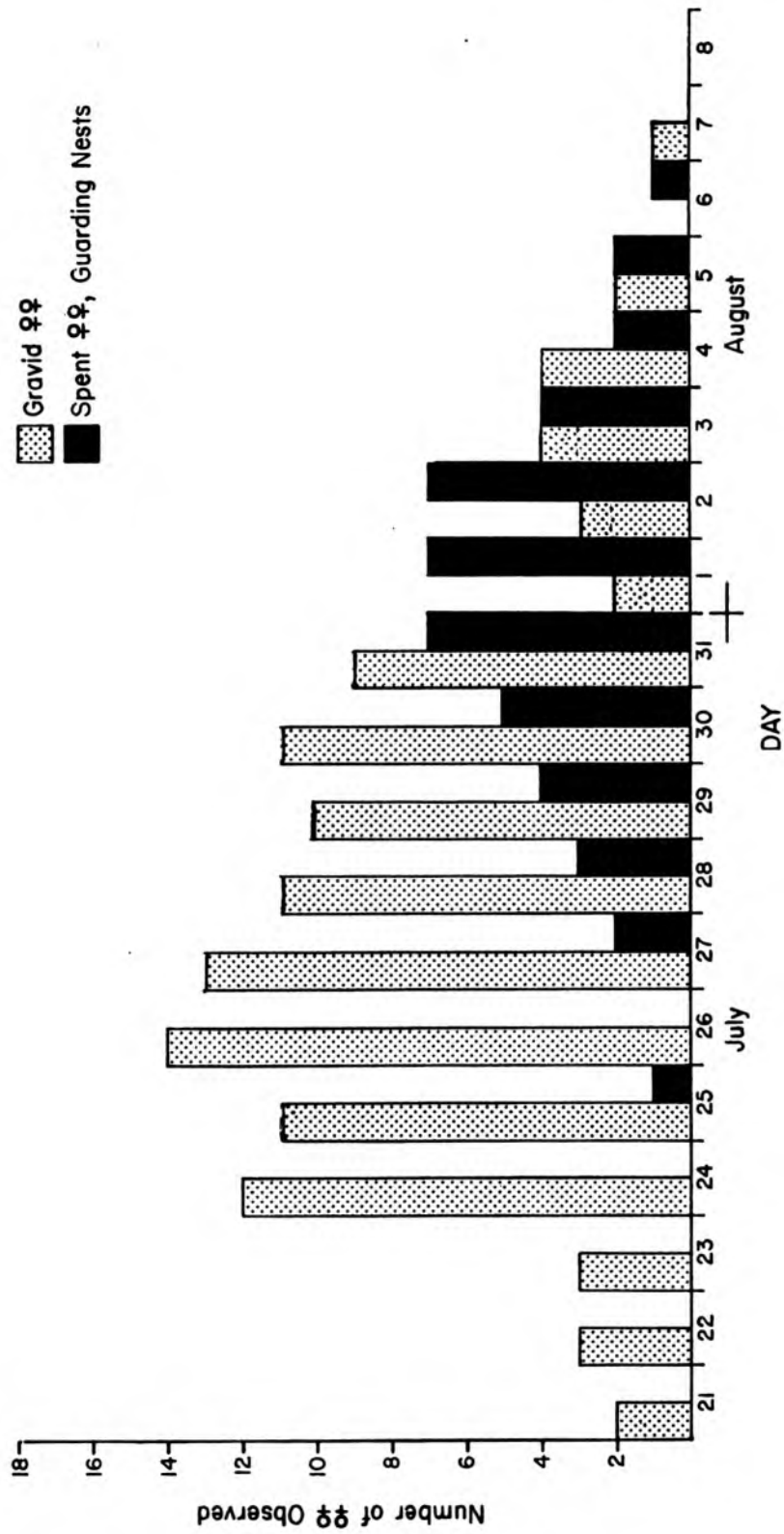


Fig. 28.--Frequency distribution of female iguanas observed throughout the 1973 nesting season at study area S-14a on the southwestern coastal plain of Mona I., P. R.

Table 21.-- Gravid female Mona Iguanas observed at nesting area S-14a for the year 1973. The number of gravid females seen each day is subdivided into three classes representing different degrees of involvement in nesting activities.

Date	Degree of Involvement		
	I ¹	II ²	III ³
21 July	0	0	2
22 July	2	0	1
23 July	0	1	2
24 July	5	4	3
25 July	4	3	4
26 July	5	4	5
27 July	3	2	8
28 July	1	3	7
29 July	3	4	3
30 July	4	5	2
31 July	2	3	4
1 August	0	1	1
2 August	0	2	1
3 August	1	2	1
4 August	1	3	0
5 August	0	2	0
6 August	0	0	0
7 August	0	1	0
8 August	0	0	0

¹ = Animals that wander through nesting area, often investigating existing holes, but do not dig.

² = Activities include investigation of existing holes and digging for brief periods.

³ = Activities marked by digging much of day or by oviposition.

length and severity of the spring dry season differed appreciably, and more than four times as much rain fell during this period in 1972 as in 1973. Gorman & Licht (1974) found that ovarian cycles in several species of anoline lizards in Puerto Rico correlate poorly with rainfall patterns but appear closely related to temperature and possibly photoperiod. Although temperature was not monitored, it seems improbable that Mona's temperature regime was sufficiently uniform from year to year to produce the observed uniformity in nesting phenology.

Daylength thus appears to be the predominant candidate for the cue synchronizing the Mona Iguana's reproductive cycle. This is not to say, however, that other environmental effects are unimportant in determining the timing and duration of the nesting season. Intraspecific competition for nest sites, rainfall, and food availability for hatchlings are factors that I believe interacted to create the distinct seasonality in nesting seen today. These relationships are discussed in detail under Evolution of Female Reproductive Strategy.

Females apparently nest each year. Those studied at La Bajurita were all noticeably swollen with eggs during the mating season, and one distinctive female, Frieda Flagtail, came to nest at the same coastal locality during all three years of the study.

Behavior of Nesting Females:

As already mentioned, gravid females may migrate appreciable distances on Mona to reach favorable nesting areas, or if conditions permit, they may nest near their usual place of residence. This species characteristically nests in aggregations of two or more in areas offering

suitable soil, a sunny exposure, and security from man. Some females nest singly in soil-filled potholes on the plateau, but most such efforts are abandoned because of insufficient soil. The soil must be deep and stable enough to support excavation of a nest burrow that will accommodate the female. Nest tunnels average 1.1 m in length (N=7, range 0.6-1.5 m) and approximately 21 x 15 cm in width x height. Eggs are deposited in a terminal nest chamber just large enough to permit the female to turn around underground, i.e., about 26 cm wide (N=7), and at an average depth of 54 cm (N=31, range 30-76 cm).

Most of the females resident at La Bajurita probably nest in the immediate vicinity, and this may be a key attraction of the area. While La Bajurita is too rocky and shady to permit nesting, another small depression about 50 m away supports a nesting aggregation. Two marked females from La Bajurita were seen nesting there; others were probably present but could not be identified because their paint marks were masked by a coat of red soil. On one occasion nine females were seen competing for nest space in the sunny clearing (about 16 m²) within the depression. There was also much trial digging in the larger potholes around the periphery of these depressions, but no deep excavations were seen.

Nesting aggregations are most numerous on Mona's coastal terraces in places where limestone is well mantled with stabilized, sandy soil. Very few iguanas frequent these areas during the off-season, undoubtedly because of a natural scarcity of retreats, so the vast majority of females nesting there are migrants. Area S-14, site of one of the

largest coastal nesting aggregations (studied from a blind throughout the 1973 nesting season), was inspected or used by 37 females given paint identification marks or having other distinctive features. I recorded an additional 35 sightings there but cannot be sure how many different individuals were represented. It appears safe to assume that about 50 iguanas examined nesting possibilities at S-14 in the 1973 season, and about half stayed to complete nests there, 16 at S-14a (Fig. 29) and approximately nine at the smaller peripheral areas S-14b-d.

Nest construction and social behavior of two other species of iguanas known to nest communally, the Common Green Iguana, I. iguana, and the Galápagos Marine Iguana, Amblyrhynchus cristatus, have been described by Rand (1968a) and Rand & Rand (1976), and by Carpenter (1966) and Eibl-Eibesfeldt (1966), respectively. In most respects, the nesting pattern of I. iguana closely resembles that of Cyclura stejnegeri. Rand (1968a) divided the process into four phases: 1) exploration, 2) digging, 3) egg laying, and 4) filling. I shall add a fifth, nest guarding, represented in some iguana populations, including Mona's, as a discrete phase that follows filling. The mechanics of how nest holes are dug and refilled, as described in detail by Rand (1968a) for I. iguana, appear identical to behavior I noted for the Mona Iguana and will therefore not be repeated here.

Exploration, Digging, and Hole Defense.--The first females to arrive at a nesting area begin by examining existing pits and depressions in the ground, most left from the previous summer's activity. A little trial

digging usually accompanies the inspection of each hole. This pattern continues throughout the nesting season, with newcomers attracted by both unoccupied and occupied holes. The deeper holes receive the most attention. At S-14a, many holes proved unsuitable and were consistently abandoned; only 41% (16/39) of the holes started had been used for nesting by the end of the season. Should a burrow collapse or the digging become too difficult, the site is deserted.

Most females concentrated their efforts on one or two excavations, though some dug vigorously in several holes. Eight of the 16 iguanas that oviposited at S-14a settled on a single hole shortly after arriving there; seven of these used holes begun by other females, and six completed nests during their first day of digging. The remaining iguanas each worked on 2-12 different holes ($\bar{x} = 6.3$) and devoted 2-5 days ($\bar{x} = 3.0$) to digging before nesting. One hole (#7) was actively worked on by seven females during the nesting season, yet it remained unused even though two different tunnels were dug, one of which was deep enough for an iguana to hide in overnight.

Other than difficulties incurred while digging, competition between females was the primary cause for changes in hole ownership. Often a hole is necessarily vacated for a spell because of intolerably hot conditions. The soil temperature in nesting areas may exceed 50°C at the surface, and to avoid overheating, the iguanas must periodically retreat to shade. Nesting females were frequently seen panting at the entrance to their burrows, but this method of dissipating heat is of limited effectiveness. Most digging occurred during the cooler hours of

the day, 09h00-11h30 and 16h00-19h00. In one female's absence, a cooler female may move in and take over the abandoned hole. As might be expected from a lizard near its upper thermal limit, gravid females cooling off do not rush in to attack intruders, but accept such takeovers passively. I also noted that during agonistic encounters, small females are more easily displaced than large females, and residents in deep holes appear to hold a logistic advantage that increases with increasing hole depth, i.e., deep holes can be more effectively guarded than shallow ones because the former offer greater physical protection from attack and provide more shade and a better heat sink (soil temperatures at normal nest depth are extremely stable and fall within the 30-33°C range).

Nesting activities usually terminate at dusk, but occasionally females continue digging after dark. Nocturnal nesting is probably a response to intense competition encountered during the day and may reflect temperature stress or a developing need to oviposit without delay. Three such cases were noted: Two were in the S-14 nesting area, and eggs were laid before morning. The third iguana had excavated a hole in the Casuarina woods beneath a large tree, a site that was unusual and apparently unfavorable in that it was heavily shaded throughout the day. This last female was captured at 21h00 while digging, was measured, and was immediately returned to her hole, which she abandoned that night and never completed.

Competition between females in nesting aggregations appears to influence the way a female allocates her digging/resting time. A female

observed digging alone at a small nesting area on Mona was compared with a female in the S-14 aggregation (Table 22). The two iguanas were of similar size, neither was interrupted by a dispute during the observation period, both were working on "hip-deep" holes, and both were seen panting while nesting. While there is little difference in the percentage of time the females devoted to digging (28% vs. 35%) during each observation period, differences in the number, duration, and progression of digging intervals are striking. This suggests that both females were putting as much effort into digging as was physiologically feasible but that the effort was divided in two very different ways. The aggregate nester, which had the most apparent need to remain watchful for intruders, subdivided her digging time into numerous, short spurts, while the solitary animal came to the surface fewer times, but rested longer after each, and progressively increased the duration of digging efforts.

Oviposition and Filling.--After preparing a nest hole, the gravid female retires underground to lay her eggs (\bar{x} oviposition time 66 min., range 50-90 min., N=9). Eggs are spread in a single layer over the floor of the nest chamber, usually with a little sand separating them. They resemble chicken eggs in shape, but are larger (Table 23) and have a tough, pliable shell. A little sand often adheres to the moist surface of freshly laid eggs, but the substrate remains dry to the touch, giving no indication that females wet the sand as they lay. The eggs do, however, acquire moisture and gain weight as incubation progresses (see Table 23). Clutch size averages 12.0 (Fig. 30). The smallest female seen nesting at S-14a, one that was probably in her first laying season, deposited

Table 22.-- Nest digging contrasted for a female Mona Iguana nesting alone in a small nesting area vs. one nesting in the S-14 aggregation. The S-14 female had been challenged by another female two minutes prior to the observation period.

	Solitary Female	Female in S-14 Aggregation
Observation time	60 min (09h45-10h45)	20 min (10h15-10h35)
Percent of time spent digging	28	35
No. of digging intervals	10	15
No. of digging intervals per 10-min observation time	1.7	7.5
\bar{x} duration of each digging effort (range)	1.7 min (0.54-4.28)	0.40 min (0.12-0.75)
Time progression for digging efforts	0.54/0.53/0.66/0.77/1.59/1.62/2.36/ 2.39/2.20/4.28 min	0.75/0.12/0.33/0.75/0.33/ 0.50/0.42/0.25/0.17/0.42/ 0.67/0.25/0.42/0.25/0.33 min

Table 23.-- Size and weight of iguana eggs from Sardinera District of Mona's southwestern coastal terrace

Nest No.	Age of Clutch	N	Mean Max. Length x Width in mm (range)	Mean Weight in Grams (Range)
S-14(1), 72	< 2 hrs.	13	78(76-79) x 48(45-51)	--
S(37), 73	3-5 hrs.	13	77(73-82) x 48(45-52)	85(82-88)
S-13, 72	< 1 day	13	81(75-83) x 50(48-54)	--
S-14, 76	< 1 day	18	73(74-82) x 51(46-56)	88(82-93)
S-9(B), 72	< 1 week	6	82(79-83) x 49(48-51)	--
S-14(29A), 73	17 days	6	89(85-94) x 49(48-40)	103(101-112)
S-14(10), 72	33 days	13	79(76-86) x 51(48-53)	102(89-108)
S-14(21), 72	60 days	5	89(76-83) x 57(53-58)	126(111-140)
S-15, 72	61 days	13	85(70-95) x 57(56-61)	140(130-159)

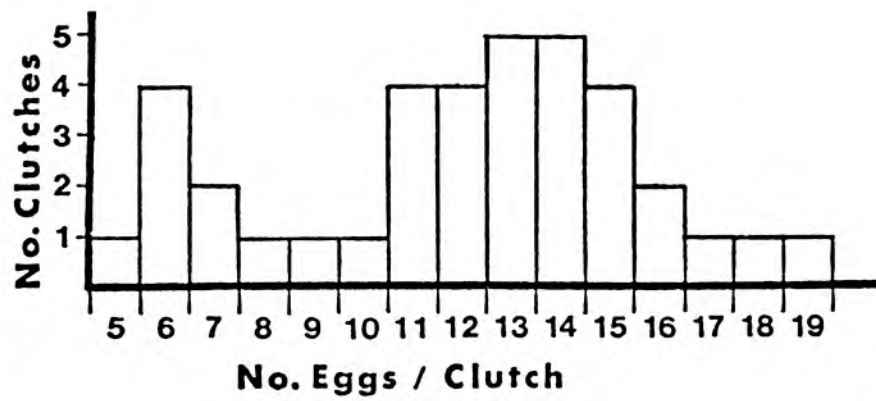


Fig. 30.--Frequency distribution for clutch size in Mona Iguanas.

six eggs; as the animal grows, clutch size undoubtedly increases, a characteristic of most large reptiles. Nineteen eggs/clutch ($N=37$) is the maximum found in Mona's iguana population.

I observed one temporary nest-hole take-over by a second female while the first was underground ovipositing. Debbie Drytail investigated hole #3 four times while Right Scar was laying her eggs; on each occasion Debbie backed out, responding with a head roll. With her fifth entry she began digging and paused periodically at the burrow's entrance, sitting guard and resting in normal fashion, half in and half out of the hole, but giving head roll displays even though no other females were in view. Debbie continued digging actively for 47 min., probably working on a side branch to the occupied tunnel. After laying, Right Scar evicted the intruder.

Sides sunken and prune-like, spent females emerge and promptly begin filling the passage to the nest chamber, taking care not to cover the eggs, leaving an air space over them. In most cases the filling operation requires about three hours to complete. All signs of the nest entrance are obliterated, and any holes within a 1-2 m radius of it are filled.

Little feeding occurs during the mating season by adults of either sex, and gravid females eat little during nesting, perhaps owing to a lack of space for food in an abdominal cavity filled with eggs. I observed feeding during nesting activities at S-14a on 21 occasions, six involving five gravid females and 15 involving nine spent females. Overall, more gravid than spent animals were sighted, so after correcting for these differences in observation probability, the ratio of

relative feeding frequency in gravid vs. spent iguanas is reduced to 1:6.4.

Nesting Mona Iguanas do not, for the most part, appear to be under physical stress from such seasonal reduction in food intake. Activity is presumably sustained largely through reserves stored as fat bodies. In contrast, I. iguana typically have shrunken muscle masses at the base of the tail and the animals' pelvic bones show dorsally during nesting, suggesting that they have been forced to metabolize protein in addition to fat for energy (Rand & Rand, 1976). Shrunken tail musculature is a trait that was seen in only four females nesting on Mona.

Nest Guarding.--Where there is a high probability of one female destroying another's nest while preparing her own, as occurs in iguanas with communal nesting, defense of the site beyond digging, laying, and covering operations might be expected to evolve. Guarding behavior of this nature does indeed occur in Mona's population. Thirteen of 16 females that completed nests at S-14a in 1973 returned to patrol the sites for at least one day after laying (\bar{x} = 3.4 days, maximum 10 days). Nesting activity dropped off sharply on 31 July and 1 August, at which time the number of spent females guarding nests had climbed to the season's high of seven (see Fig. 28 and Table 21).

Extended guarding behavior undoubtedly prevents much of the egg mortality that would otherwise occur through intraspecific competition, but does not eliminate it all. I estimate that 10-15% of completed nests are disturbed by subsequent nesting, with partial or total egg loss in each clutch (see Table 24). Females digging into unattended nests

ignore eggs encountered, kicking them out as if they were stones. Sometimes a second female will add her eggs to the clutch of the first, typically puncturing several of the other's eggs in the process.

Spent females guarding their nest sites are extremely aggressive towards intruders, but in cases where the resident is appreciably smaller than a persistent, gravid challenger, she may be unable to prevent intrusion. Defense tactics include circling, huffing, biting, tail-lashing, and delivering sand (by pushing with front feet and kicking with front and rear feet) back into the hole and on the rival. A relatively small resident chased away from her nest site during the course of a dispute always returns promptly to resume the harassment. Formalized tests of strength, i.e., face-to-face pushing matches (see Fig. 18D), are an element of fighting witnessed on six occasions between spent and gravid females and once between contesting gravid females (N=100+ encounters with chasing or biting, approximately half gravid vs. gravid and half spent vs. gravid). The longest and most dramatic dispute seen occurred between a medium-sized resident and a medium-large intruder: The fight began late one afternoon, ended at dusk, resumed at 09h55 the following morning, and continued throughout the day until dark. The persistent newcomer made little progress in digging due to the harassment she received, and whenever she retired to the shade to avoid overheating, the resident refilled her hole. By the end of the afternoon, the two appeared to have reached a stalemate. "Persistent," noticeably fatigued and her right eye caked with dirt, had only a shallow hole to show for her effort; but she continued digging after dark

and succeeded in completing a suitable nest burrow before morning, one, incidentally, that did not intercept the eggs of the other female.

I have the impression that temporary dominance relationships are occasionally established between females nesting concurrently in the same area and have found evidence that iguanas have the discriminatory ability to recognize each other as individuals. The owners of nest #9, Debbie Drytail, and nest #20B, Agatha Redankle, permitted their nearest defending neighbors (owners of nests 16 and 25, respectively) to sit or lie directly upon their nest sites, but would not allow any other iguanas ($N=6$), gravid or spent, large or small, in the vicinity. In both cases the behavior appeared on the second day after the neighbor had completed her nest; before that, neither tolerated the presence of the other. The owner of nest #16 passed an entire morning lying atop Debbie's nest, while she was resting about 2 m away. Debbie and Agatha spent a total of 10 and 5 days, respectively, patrolling their nest sites, and these non-agonistic encounters were noted on their sixth and third days of defense. To my knowledge, this is the first report of a reptile exhibiting the "dear enemy" phenomenon, well known for birds and some mammals holding adjacent territories (see review in Wilson, 1975).

Incubation, Hatching, Emergence, and Dispersal:

After the nesting season, females presumably return to their usual home ranges, leaving their eggs and young unattended. The temperature of the nest chamber remains stable, typically fluctuating no more than $1-2^{\circ}\text{C}$ per day and probably never varying more than $5-6^{\circ}\text{C}$ throughout the incubation period, even though surface temperatures often soared well

over 40°C during the day and settled to 23-27°C at night. Six of 13 nest/air/surface temperature curves recorded on 9, 11, & 14 August and 13 October 1972 are presented in Fig. 31; the others show nothing different and are therefore omitted. In contrast to findings by Carr & Hirth (1961) for Green Turtle nests, there were no perceptable rises in nest temperature from beginning to end of incubation. Maximum-minimum thermometers placed in two other nests and left there throughout the last month before hatching gave a minimum reading of 29°C and a maximum of 31°C.

Mona Iguana eggs hatch approximately 83 days after laying (N=8 nests, range 78-89), during the latter half of October. Hatching success in nests undisturbed by man, pigs, or other iguanas runs high on the island's southwestern coastal plain: 86% of 295 eggs (25 clutches) examined hatched successfully (Table 24).

The effect of naturally occurring differences in soil type, temperature, and moisture content on hatching success remains undetermined, thanks largely to the feral pigs that rooted up my study areas in 1973. The iguanas are very exacting in their selection of nest sites, being particularly careful to avoid shaded areas. We can therefore infer that embryonic development is significantly slower or mortality significantly higher in sites receiving relatively little sun. To characterize this set of environmental differences, on 6-7 August I made comparisons of temperature and soil moisture for two adjacent sites, one in a nesting area and the other beneath the Casuarina canopy in a place that is heavily shaded much of the day. Soil temperatures taken at two-hour

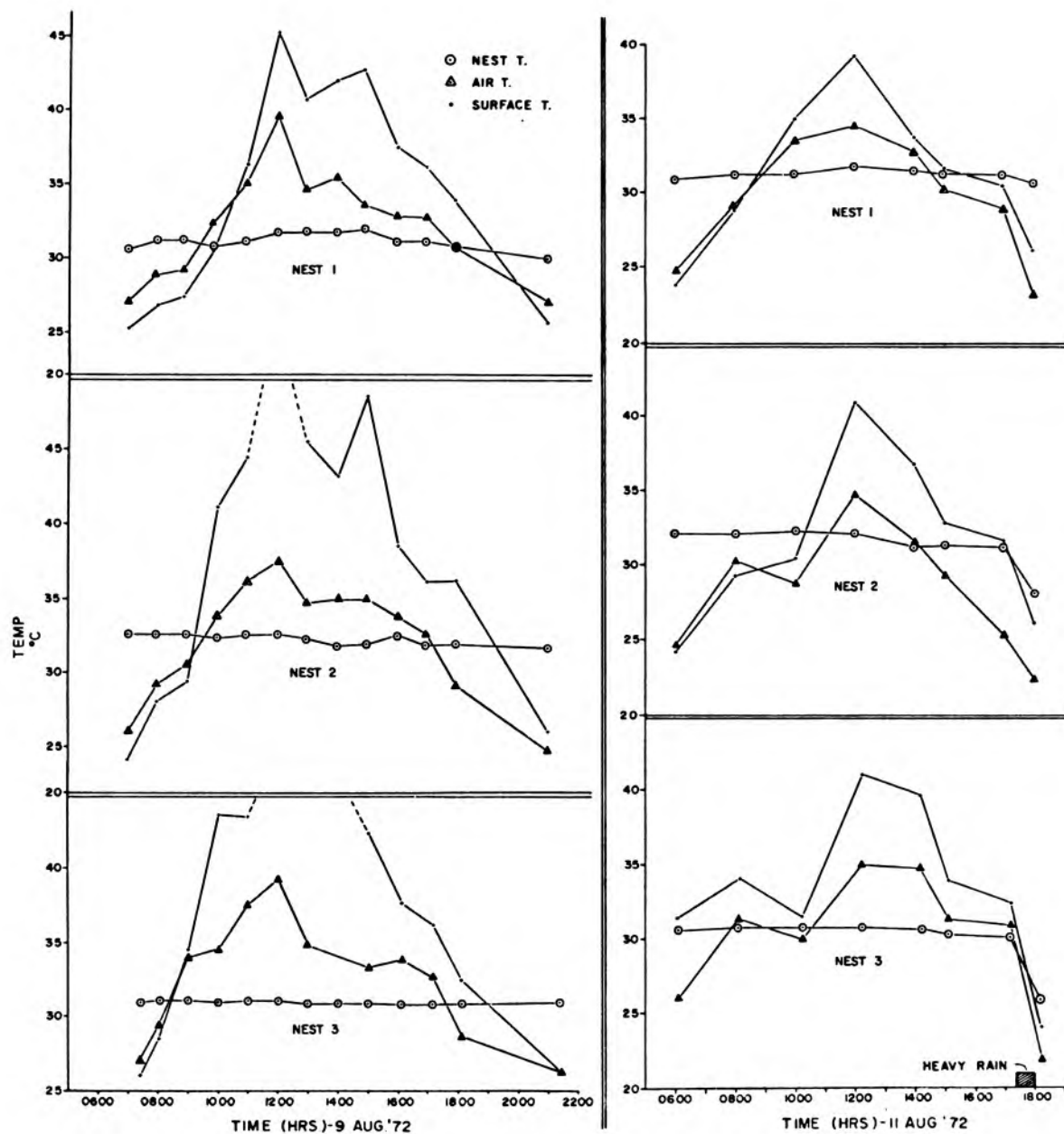


Fig. 31.--Representative temperature curves for three iguana nests on the southwestern coastal plain of Mona I., P. R.

Table 24.-- Hatching success of iguana eggs in nests examined on Mona's southwestern coastal terrace. Predation by feral pigs has been omitted from this tally.

No. and Status of Nests	No. of Un- developed Eggs	Died in Hatching	Hatched Success- fully	Total
21 single clutches, 1972	37(15%)	2(1%)	209(84%)	248(100%)
4 single clutches, 1973	2(4%)	0	45(96%)	47(100%)
5 old (before 1972) single clutches	4(7%)	?	50(93%)	54(100%)
3 multiple clutches (of two or more females), 1972	28(34%)	3(4%)	50(62%)	81(100%)
2 clutches completely destroyed by subsequent nesting, 1972	21(100%)	--	--	21(100%)
Total	92(20%)	5(1%)	354(79%)	451(100%)

intervals at a depth of 47 cm differed by 2.2-3.1°C day and night (\bar{x} = 2.8°C), and soil moisture content at 47 cm was 3.2 times greater (4.1% vs. 1.3% by weight) in the shade. The last measurable rainfall occurred 16 days prior to these determinations. Heavy rain, of course, would depress nest temperatures. A nest temperature consistently two to three degrees below the optimum seems minor, but findings by Licht & Moberly (1965) show that eggs of I. iguana have remarkably stringent thermal requirements, with high mortality at temperatures only a few degrees above and below 30°C. Furthermore, if time of hatching is critical for ecological reasons, as I believe it is (see Evolution of Female Reproductive Strategy), retarded development could appreciably lower the hatchlings' fitness.

The eggs of each clutch hatch in synchrony, and as in sea turtles (Carr & Hirth, 1961), emergence from the nest is a team effort. In general, all eggs in a given nest begin hatching within a 24-hour period, and the young spend 1-2 days freeing themselves from the egg shell. The hatchlings must then dig from their underground prison, through packed sandy soil and a superficial mat of roots. Their escape holes rarely correspond with the original tunnel dug and refilled by the female. The young dig as a group, and those last to hatch are sometimes buried alive by their siblings, accounting for about 1% of the in-nest mortality. I have observed them surfacing at midday, and at the S-14 study area I noticed that most emergence occurred after heavy rains. Before leaving the site, hatchlings bask in the sun next to the hole, and if frightened, will either flee or retreat back into the nest.

Snout-vent lengths of 65 hatchlings taken from nests in the field averaged 11.9 cm (range 10.5-12.7, $s=0.5$ cm); weights of 66 hatchlings less than one week old averaged 74 g (range 60-92).

The effort to escape from the nest chamber may typically require from a couple of days to a week or more, as estimated from the stage of closure of the umbilical scar and the general condition of the young upon emergence. While digging in one nesting area on 15 November 1972, I found a group of five hatchlings that had apparently been trapped underground for 2-3 weeks. All were bright-eyed and active, though relatively thin (58-70 g in weight), their yolk reserves totally spent. Without cooperative digging and periodic rain to soften the ground, it is likely that many hatchlings would die underground; the generous endowment of yolk carried by each at hatching is presumably an adaptation to insure the animal's survival during this critical stage. It is noteworthy in this regard that the greatest probability of rainfall on Mona occurs during the months of October and November (see Fig. 3), providing hatchlings with the best conditions for escaping from the nest and a generous food supply before the onset of the dry season.

During the first half of November in 1972, after most of the eggs had hatched, at least two or three hatchlings were sighted daily, either adjacent to the beach or on the road. On 11 December, when the area was next checked, I was surprised to see that most of the young had seemingly vanished. I suspect that the majority moved inland from the flat coastal nesting areas to the rocky cliff margins, but none of the 44 hatchlings tagged were ever seen again. The few juveniles sighted

thereafter were situated primarily along the rocky talus slopes of the island's coastal terraces. These areas probably provide the greatest diversity of plant and animal foods, as well as virtually unlimited cover.

Evolution of the Female Reproductive Strategy, A Discussion:

The five most definitive adaptations found in the nesting biology of Mona's iguana population are 1) communal nesting and associated migrations; 2) abbreviated nesting/hatching seasons; 3) delayed maturity, large female body size, and long life-expectancy; 4) extended parental care; and 5) clutches with relatively few but uniformly large eggs. This section focuses on the role played by social and environmental factors (pre-dating man's arrival) in the evolution of these attributes. While I make repeated reference to the adaptive value and evolution of these life history characters in Mona's environment, most are suited equally well to ecological conditions elsewhere in the Caribbean where Cyclura are established and may, in fact, have had their origins elsewhere.

Communal Nesting, Origins and Consequences.--The natural scarcity of suitable nest sites on Mona has been a selective force of paramount importance to the iguana population. It is evident that seasonal migrations and communal nesting were once an adaptive necessity, and in most parts of the island it is still clear that iguanas are forced to compete aggressively for the limited available nest space. Similarly, iguana nesting aggregations found in the wet tropical lowlands of Central

America occur where well drained sites warmed by sunlight are in short supply (see Rand, 1968a; Fitch, 1973a), and in the Galápagos, where accumulations of soil are sparse (see Carpenter, 1966; Eibl-Eibesfeldt, 1966). In all three cases, the eggs require favorable incubation conditions for about three months of the year, and hatching must be timed to get the young off to a good start. Egg-laying is thus seasonal, apparently offering little evolutionary opportunity for iguanas to avoid competitive interference by nesting during different parts of the year.

While physical constraints on when and where successful nesting can occur are assuredly fundamental to the formation of aggregations in some ecological settings, it is quite possible that natural selection may favor communal nesting for other reasons. A female choosing a site already worked by other iguanas would usually find easier digging, ^{and} may be able to usurp another's hole, ^{she may also} or may lower the risk of predation to herself and/or her emergent hatchlings by nesting in synchrony with a group. On the other hand, costs associated with aggressive interactions and the risk of losing a clutch to females nesting subsequently may be considerable; it is possible, too, that an assemblage of nests might be more attractive to potential egg-predators than a solitary nest. In Guanacaste Province, Costa Rica, female Ctenosaura similis, also known to nest communally, utilize a network of subterranean passages, several females ovipositing in the same connecting burrow system, with individual clutches laid in separate chambers (Hackforth-Jones, MS: 1976). In this case, no shortage of potential nest sites was evident in that geographic region, so communal nesting presumably evolved in response to

or has been maintained by other selective pressures, predation and time/energy savings being the most likely (Hackforth-Jones, MS: 1976). Whether Ctenosaura utilize the same sites in successive years is unknown.

There is evidence that traditional use of the same localities year after year may actually improve conditions for nesting and thus enhance the attractiveness of such sites. Rand (1968a) noted that group nest-digging by I. iguana over the years effectively maintained a clearing in the forest. While excavating nests in study area S-14 on Mona, I discovered that approximately half of the nest tunnels were forked, one passage leading to the fresh clutch from that season and the other often going to an old clutch of empty shells. Such old passages though sand-filled, were still identifiable by their looser soil. It is of interest that, with the low density of iguanas on Mona today, many seemingly favorable sites for nesting on the island's southwestern coastal plain remain unused, and a locally clumped nesting pattern predominates. Recall that gravid females seen digging at the onset of nesting are strongly attracted to even shallow depressions left from the previous season.

On Mona the spring dry season usually breaks by May, iguanas nest in late July and early August, and hatching is coincident with the annual October-November "wet" season. This pattern places incubation at a time when the eggs are not apt to desiccate, and hatching occurs during the period optimal for emergence and foraging on fruits and ephemeral herbs (see Foraging Behavior & Diet). The iguana's ovarian cycle is thus timed to match seasonal conditions most favorable for the

survival of eggs and hatchlings. In my estimation, however, Mona's climatic regime is not sufficiently limiting or predictable from year to year to explain why nesting activities are crowded into a two-week period.

I believe that competition between females for favorable nest sites can act as a nesting synchronizer. In Fig. 32, three hypothetical stages are outlined for the evolution of an abbreviated nesting pattern derived from a less restrictive seasonal pattern with limits imposed only by climate and associated variables, such as food availability for hatchlings. I am attempting to illustrate a concept structured from my observations on Mona but do not wish to imply that the whole evolutionary process took place there or that its utility is limited to the case in point. Two assumptions have been made: 1) that extended nest guarding is an advanced form of parental care in iguanine lizards and is derived from nest-hole defense that characteristically accompanies burrow digging and filling operations; and 2) that the island's climatic regime limits successful nesting to a period of two months, mid-June to mid-August, an intentional simplification.

In Stage 1, accompanying the expansion of the founder population, the genetic contributions of two classes of females would be strongly selected against: those nesting outside the June-August season and those nesting early within the season. Early females run a high risk of losing their eggs to disturbance by the late-comers. Clearly, the outcome would be pronounced directional selection.

As directional selection proceeds, in Stage 2, a greater proportion of the population would be expected to nest later in the season and

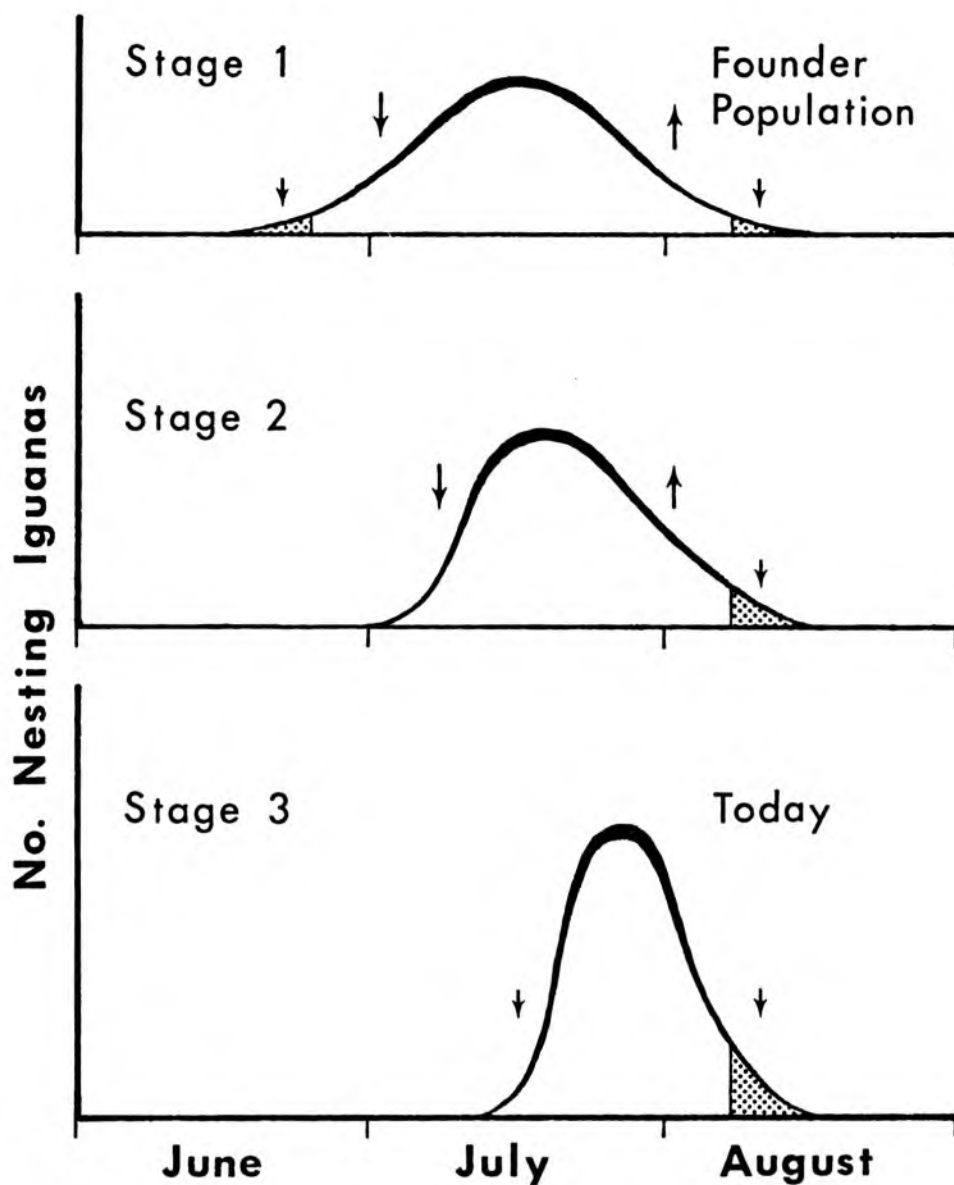


Fig. 32.--Model for the evolution of a late, abbreviated iguana nesting season where competition among females for suitable nest sites is keen. Stippled areas represent nesting efforts under environmental conditions marginal for incubation, hatching, and/or survival of first-year young. Arrows indicate the action of selection. The curve is driven to the right by egg-loss in females that nest early to those nesting later and is kept to the left by limitations from the physical environment.

concurrently, resulting in intensified competitive strife. This would be accompanied by increased nesting at marginal times near the close of the season and in places with more difficult digging and less favorable incubation conditions. Late nesting would probably take a heavy toll on hatchlings that miss optimum periods for emergence, dispersal, feeding, and getting established at a retreat before the sudden onset of the dry season in January. Furthermore, tendencies towards extended nest guarding would be favored in females that nest relatively early.

Stability is attained, in Stage 3, when selection against late nesting balances that against early nesting. In addition to the limitations imposed by climate, females arriving relatively late in the season may have difficulty finding suitable unoccupied sites once nest-guarding behavior is established in the population. Nesting early is advantageous only if a female is able to protect her investment until most other females have departed from the nesting area.

In the context of intense female/female competition for nest sites, large body size and delayed maturity should also be favored by selection where mature females have no natural predators (as on Mona, see Associations with Man & Other Animals) and can benefit from long life expectancy. Large females are clearly able to intrude and defend their interests more effectively than small individuals. The highest pay-off, in terms of adult survivorship and reproductive success, should therefore go to females that postpone breeding until reaching an age and stature at which costs associated with competition are lowered. I suspect that the evolutionary consequences of male/male competition for

mates and female/female competition for nest sites are sufficiently similar to explain much of the male/female convergence in appearance found in Mona's iguana population.

Reproductive Effort and Environmental Certainty.--We can predict from theoretical considerations (see Wilbur et al., 1974) that maintaining reproductive effort ("that proportion of the total energy budget of an organism that is devoted to reproductive processes"--Hirshfield & Tinkle, 1975) at a conservative level and nesting annually after the first breeding season would be the Mona Iguana's optimal reproductive strategy. Such a strategy should enable a female to compete more effectively each year and presumably extend her life expectancy as a breeding adult. Because mature females suffer no risk from predation and apparently face few other environmental hazards, the opportunity to reproduce again the following year is nearly certain. Where competition for nest space is intense (perhaps once augmented by the nesting habits of Mona's extinct land tortoise--see Associations with Man & Other Animals), egg survivorship may have been particularly low, providing strong selective pressure for long adult life, iteroparity (repeated reproduction), and extended nest guarding. Furthermore, in Mona's semi-arid environment with its variable and unpredictable rainfall pattern (see Environmental Conditions), I suspect there may be considerable year to year disparity in survivorship among hatchlings during their first nine months of life. It is obvious that a female has no way of knowing several months to a year ahead of time exactly what conditions her progeny will encounter after hatching and cannot, therefore, maximize reproductive output

during the good years. Such environmental uncertainty would favor year to year uniformity in reproductive effort. On the other hand, should nesting females acquire a significant competitive advantage as they grow and gain experience, one would predict an increase in reproductive effort.

As yet we have no reliable way to measure reproductive effort so that such predictions can be tested (see Hirshfield & Tinkle, 1975), but I believe that some instructive interspecific comparisons can be drawn. Since my analysis has focused to a great extent on the evolutionary consequences of female/female competition during nesting, I believe the most intriguing and meaningful contrast possible at this time is with the Panamanian population of Green Iguanas, I. iguana, studied by Rand (1968a), Montgomery et al. (1973), Sexton (1975), Rand & Rand (1976), and Burghardt et al. (1977), on Barro Colorado Island and adjacent islets. Nesting Iguana are presumably influenced by a social environment as competitive as that on Mona (see Rand, 1968; Rand & Rand, 1976), but predation on both juveniles and adults appears to have been an overriding ecological challenge during the evolutionary history of this mainland population. Iguana have an annual reproductive cycle and migrate to nesting areas (Montgomery et al., 1973), sometimes swimming to islets where terrestrial predators are few (see Sexton, 1975). Compared to Mona Iguanas, females mature in roughly half the time (Rand, 1977) and mean clutch size is approximately three times as large (Rand, 1968a). Upon emerging from the nest, Iguana hatchlings usually depart from the area in clusters of 2-12 (Burghardt et al., 1977). Certain individuals

were found together for several days, and the grouping tendency is quite strong for at least the first six months of life (Burghardt, pers. comm.). Such behavior does not occur in Mona Iguanas and is assuredly an adaptive response to heavy predation. Although no figures are available for the Panamanian population, I. iguana in Columbia seldom live more than 10 years (Müller, 1972), which is an extremely short life expectancy for a large iguanine lizard.

Viewed together, these life history features indicate that female Iguana should be investing appreciably more in reproductive effort than Mona females. In light of the recent conclusion by Tinkle & Hadley (1975) that clutch weight/body weight ratios cannot provide meaningful estimates of reproductive effort, no such comparisons will be made here (this approach has been pursued by Iverson, 1977, for the subfamily Iguaninae). Instead, I would like to call special attention to observations of the physical condition of females during the nesting season, an attribute that should reflect the relative proportion of available energy spent for reproduction. Recall the contrast drawn earlier in the physical appearance of nesting I. iguana and C. stejnegeri: females in the Panamanian Iguana aggregation were comparatively emaciated, suggesting that at that time of year they operate near the limit of their energy reserves (see Rand & Rand, 1976). Another mainland iguana widespread in Central America, Ctenosaura similis, shares many life history attributes with I. iguana (see Fitch, 1973a,b; Henderson, 1973; Fitch & Henderson, MS: 1976), and females of this species seen nesting were also notably thin and emaciated (Hackforth-Jones, MS: 1976). On the

other hand, like the Mona Iguana, the Cyclura carinata population studied by Iverson (pers. comm.) appears to be budgeting more conservatively, for females maintain a robust appearance throughout the reproductive season.

Nest Guarding--Guarding behavior after nest-covering has been reported for three populations of iguanine lizards besides Mona's: I. iguana in Chiapas, Mexico (Alvarez del Toro, 1972); Amblyrhynchus cristatus on Hood I., Galápagos Is. (Eibl-Eibesfeldt, 1966); and Cyclura carinata on Pine Cay, Caicos Is. (Iverson, 1977). The absence of such nest-guarding behavior has been specifically reported in two other populations: I. iguana in Panama (Rand, 1968a) and A. cristatus on Narborough I. (Carpenter, 1966; Eibl-Eibesfeldt, 1966). While Rand (1968a) found no extended guarding behavior associated with the Iguana nesting aggregation studied in Panama, Alvarez del Toro (1972) reported different behavior for the same species in Mexico, stating that "a few of them visit the nest daily during the first 15 days [after refilling the hole] and pile more sand and debris upon it, repairing it if for some reason it appears open or disarranged." In Mexico, the females observed were apparently not assembled in aggregations and may have nested within their normal home ranges; no mention was made of the duration of such visits or where the female passed intervening hours. The fact that the Panamanian Iguana depart from the nesting area soon after laying and presumably migrate back to their normal home ranges (see Montgomery et al., 1973; Rand, 1968a) suggests not that they would have little to gain by tending their nest sites for even a few extra days, but rather

that they cannot afford the additional expenditures associated with extended intraspecific conflict and being away from optimal food resources or protective cover.

Descriptions of nesting activities in two insular races of Galápagos Marine Iguanas (A. c. cristatus on Narborough I. and A. c. venustissimus on Hood I.) show how local differences in ecology can affect nesting behavior. From positions on nearby rocks, female iguanas on Hood I. keep watch over their egg-laying sites for a few days after filling the nest burrow, occasionally descending to check the spot with tongue flicks and to scrape more dirt over the egg cache (Eibl-Eibesfeldt, 1966). Neither Eibl-Eibesfeldt nor Carpenter (1966) found such guarding behavior on Narborough, and females there are not as prone to fighting over burrows as are the Hood iguanas (Eibl-Eibesfeldt, 1966). These authors make it clear that both populations are faced with a natural scarcity of suitable digging sites and are forced to nest in aggregations. Nevertheless, one important ecological difference between the two islands is evident: In contrast to the open nesting beaches of Narborough, the area used by Amblyrhynchus on Hood I. offers very little loose sand above the high tide line; females must dig their burrows in small patches of hard, gravelly soil upon the plateau, and many burrows are abandoned because of lava blocking the way to further digging (Carpenter, 1966).

With respect to nesting opportunities, the situation on Hood I. is a close parallel to that on Mona. Presumably difficult digging encourages females to exploit the efforts of their neighbors, before and after

filling. In both cases this pressure has been countered by extended nest-guarding behavior and may have led to the reduction in male/female sexual dimorphism. Eibl-Eibesfeldt (1966) noted that, unlike the other races of the Marine Iguana, the Hood females assume a bright, male-like coloration during the egg-laying season. The fact that the Hood population nests approximately one month later than the Narborough iguanas (Carpenter, 1966) might be explainable in terms of my evolutionary model presented in Fig. 32. Further data are needed, however, before making such an evaluation is possible.

Caicos Iguanas, C. carinata, defend completed nests for several days to a month or more after oviposition (Iverson, 1977). Eggs are laid in a terminal portion of burrows normally used as retreats and are consequently apt to need protection not only against other females seeking nest burrows, but also against subadults and males seeking shelter after the nesting season. Guarding females are consequently aggressive towards all conspecifics. By reducing their daily home range, spent females can resume foraging and guard their nest sites simultaneously, typically watching for intruders while perched in nearby food plants (Iverson, 1977). Owing to the geological and ecological similarities in Cyclura habitats throughout the range of this group, I would expect nest-guarding behavior to be common to most, if not all, West Indian ground iguanas.

Clutch, Egg, and Hatchling Sizes.--Iguana populations on oceanic islands, where natural enemies are few, can afford to produce smaller clutches, with eggs of larger size, than would be possible in most

mainland ecosystems. At the extreme is the Galápagos Marine Iguana (Amblyrhynchus), which lays a two- to three-egg clutch (Carpenter, 1966). A 27-cm (SVL) Amblyrhynchus can be expected to lay only two, relatively giant eggs, whereas Costa Rican Ctenosaura similis of similar size produce approximately 35 tiny eggs (see Hackforth-Jones, MS: 1976); hatchlings of the former species are roughly thirty times the weight of the latter (see Fitch & Henderson, MS: 1976; Bartholomew et al., 1976). Eggs of Amblyrhynchus are the largest known for any iguanid lizard, and those of the Mona Iguana run a close second, with hatchling length essentially identical in the two species (compare bar in Fig. 33 with data in Bartholomew et al., 1976). Female C. stejnegeri, however, mature at a body size near the maximum recorded by Carpenter (1966) for adult female Galápagos Marine Iguanas; the Mona iguanas start with clutches of five or six eggs and attain maxima of 18-19 in older individuals.

What I find most remarkable in the above comparison between Amblyrhynchus and C. stejnegeri is the consistently tiny clutch size of the Marine Iguana. Why has selection not favored slightly larger females capable of 1) gaining a competitive edge during disputes over nest sites, 2) laying more eggs, and 3) avoiding all risk of predation by Galápagos Hawks? A number of observations made by Carpenter (1966) suggest (though not stated in his discussion) that limits on clutch/body size are imposed by special problems associated with nesting in loose beach sand. Nesting Mona Iguanas select stabilized soil or sand deposits, the upper 20 cm of which are typically supported by a mat of plant

roots. Consequently, burrows seldom collapse as females dig, but the weight of a man walking over a nest can readily capsize the underground air space in the egg chamber, vital for proper development and emergence of the young. In contrast, Carpenter noted that stamping heavily on the sand above a known Amblyrhynchus nest had no such effect, to be expected since sea-lions frequent the same beaches during nesting (Carpenter, 1966; Eibl-Eibesfeldt, 1966). Clearly, larger nest chambers, expected with increasing clutch volume, are more likely to collapse under the weight of a heavy animal on the surface. Since the diameter of a nest tunnel presumably reflects the size of the iguana digging it, selection probably also opposes large body size in female Amblyrhynchus (females average 80% of the males' S-V length and 50% of their weight--see Carpenter, 1966--compared to 92% and 76% in Mona's iguanas). Carpenter found females fatally trapped in burrows that had collapsed around them, and wider burrows would appear to amplify such a risk.

Evidence available at this point suggests that the Mona Iguana has a reproductive strategy significantly different from its closest living relative, C. cornuta, in Hispaniola and the Cuban Iguana, C. n. nubila. All three are among the largest species represented in the genus today. Measurements of 16 adult Dominican C. cornuta (Wiewandt & Gicca, unpublished data), nine males ($\bar{x}_{SVL} = 522$ mm, range 499-545) and seven females ($\bar{x} = 476$ mm, range 442-510), coincide almost exactly in mean and range with adults sampled on Mona (see Fig. 9). Male C. n. nubila may attain 60 inches (1524 mm) overall length (Buide, 1951), exceeding the length of the other two species though not as massive in body form

(pers. obser.). My experience with an introduced population of C. n. nubila on Isla Magueyes, P.R., suggests that although males may reach great length, females remain dramatically smaller and probably rarely, if ever, exceed the size of female C. stejnegeri.

Both C. cornuta and C. n. nubila appear to be laying slightly larger clutches with smaller eggs than are C. stejnegeri. Clutch size in C. cornuta determined from four females that laid in captivity (see Shaw, 1969; Haast, 1969), from a natural nest found in the midst of hatching (see Noble, 1923), and from dissection of a gravid specimen (collected by Wiewandt & Gicca) averaged 16.7 eggs, compared with Mona's 12.0. A wild female C. n. nubila observed in Cuba by Street (1952) and a captive individual at the San Diego Zoo (see Shaw, 1954) laid 16 and 17 eggs, respectively. Hatchlings from Mona's population, contrasted with sizes of field-caught and zoo-hatched Hispaniolan and Cuban iguanas, show consistent and appreciable differences (Fig. 33). The C. cornuta sample includes 1) one juvenile from Haiti (MCZ 3597), with a snout-vent length of 80 mm (A. Schwartz, pers. comm.); 2) 20 hatchlings taken by Noble (1923)--AMNH nos. 40832-37, 40851-61, 41019-21--on Isla Beata, D.R. (\bar{x}_{SVL} = 105 mm, range 94-115); and 3) 12 zoo hatchlings reported by Shaw (1969) (\bar{x}_{SVL} = 102 mm, range 95-108). In addition to the 15 C. n. nubila indicated in Fig. 33, which were hatched in captivity by Shaw (1954), 16 Cuban Iguana eggs measured by Street (1952) in the field were at the lower end of the size range for freshly laid C. stejnegeri eggs (see Table 23), and hatchling C. n. nubila that I observed in the field on Isla Magueyes, P.R., were noticeably smaller than

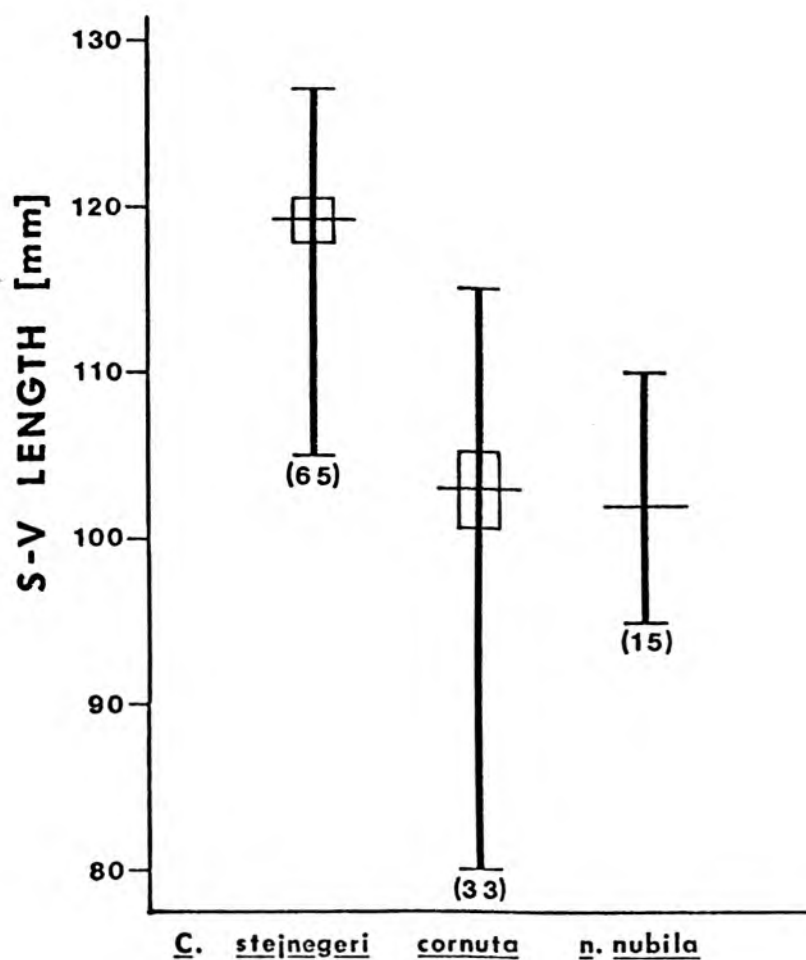


Fig. 33.--Comparisons of body length for hatchlings of three species of large-bodied cycluran iguanas. Range, mean, and sample size are indicated, with rectangles representing twice the standard error on either side of the mean. Data for C. n. nubila, as reported by Shaw (1954), include only sample range and mean.

those of the Mona Iguana. Because higher diversity of potential iguana predators would be expected on relatively large islands and on small islands close to large islands (see MacArthur, 1972), survivorship is presumably somewhat lower in Hispaniolan and Cuban populations, selective pressure that would favor somewhat larger egg clutches.

Ecological factors that encourage a stepped-up investment in individual progeny are undoubtedly diverse, varying with respect to both local conditions and the lizard's habits. Large egg and hatchling size in Mona Iguanas would appear to offer several important adaptive advantages: First, by virtue of their lower surface-to-volume ratio, relatively large eggs and hatchlings are less susceptible to desiccation. Rand (1968b) has established that an iguana's soft-shelled eggs dehydrate much faster than hard-shelled crocodile and bird eggs. In semi-arid habitats with uncertain rainfall patterns, as on Mona, even a slight reduction in desiccation rate might prove critical in some years. Second, large hatchlings are less likely to be trapped underground after hatching than are small individuals, for they have both physical and metabolic advantages associated with larger body size. Third, because juveniles, like adults, are predominantly herbivorous (see Foraging Behavior & Diet), smaller hatchlings would be at a physiological disadvantage in their ability to utilize plant foods (see Pough, 1973; Wilson & Lee, 1974). Fourth, large hatchlings would have a greater variety of food types at their disposal, a factor that is probably very important since fruits of several trees widespread on Mona are near the size limit for consumption by hatchlings. And fifth, any increase in

body size helps to shorten the time period during which juveniles are exposed to predation, particularly important on Mona since hatchlings are near the upper prey size limit for two species of snakes, the only known non-avian predators native to the island (see Associations with Man & Other Animals). I would not attempt to single out one factor as being more critical than the others, for clearly all are interrelated. Perhaps the remarkable uniformity in size among Mona hatchlings (see Fig. 33, standard deviation 5 mm) reflects the force with which smaller hatchlings are selected against in Mona's environment.

ASSOCIATIONS WITH MAN AND OTHER ANIMALS

Native Species:

The low species diversity, relative simplicity, and isolation of communities on oceanic islands permit evaluation of relationships, past and present, to a degree that would be impossible in most mainland ecosystems. Through an inventory of present faunal associates and a look at the fossil record on Mona, I have identified a number of native species whose presence may have been significant to the iguana population. Such considerations, necessarily speculative, help provide an interpretive framework for discussing ways the iguana has adapted to its biological environment. The recent impact of man and introduced mammals is treated separately in sections that follow.

Predators and Competitors.--Considering the size at which Mona Iguanas reach maturity, their size at hatching, their nesting behavior (see Nesting Biology), and the habits of other native animals in the ecosystem, I believe that predation normally affects only the smaller juveniles. I found no evidence of nests being raided by egg-eating birds (e.g., Pearly-eyed Thrashers, Margarops fuscatus) or arthropods. Nest burrows are deep, and females refill the passage immediately after laying. Because their nests are never situated on Mona's beaches, competition between sea turtles and iguanas for nest space does not occur (Thurston & Wiewandt, MS: 1977), and loss of emergent hatchlings

to coastal predators like gulls and frigatebirds is presumably insignificant. The Yellow-crowned Night Heron or "Yaboa" (Nyctanassa violacea), a predator well equipped to kill young iguanas, is a nesting resident that ranges island-wide. However, this species is crepuscular to nocturnal in habit, and is a crab/crayfish specialist (Martin et al., 1951), with no shortage of such food on Mona (Wiewandt, MS: 1977).

Falcons and hawks have probably long been important iguana predators. This contention is supported by two lines of evidence: First, juvenile Mona Iguanas are behaviorally attuned to avian predators. Hatchlings observed moving about on a cliff face kept close to crevices, attentive to anything happening above or below them. One hatchling basking on a rock when an airplane flew overhead suddenly cocked his head upward and immediately dashed into a crevice, re-emerging a few minutes later. Another individual fled for cover when surprised by the sudden flash of an innocuous White-tailed Tropicbird making a "touch-and-go" landing at a cave opening about 3 m above. A yearling observed near a sinkhole depression moved very cautiously, walking when close to vegetative cover and running when crossing clearings. Second, hatchling iguanas are strongly banded, and this disruptive coloration fades out during the animal's third year, after the stage of high vulnerability to avian predators is past.

Five species of raptors have been recorded on Mona. Mona's most abundant and only known nesting resident bird of prey is the Sparrow Hawk, Falco sparverius. Its diet is known to vary considerably according to season and locality and includes insects, birds, small

mammals, reptiles, and amphibians (Bent, 1938). This small falcon will hunt large lizards the size of hatchling iguanas. Elsewhere in Puerto Rico, Raffaele (pers. comm.) observed one capturing a large Ameiva exul, and Prieto and Sorenson (1975) found that Sparrow Hawks occasionally prey upon the Arizona Chuckwalla, Sauromalus obesus tumidus. Nevertheless, the occurrence of this bird on Mona might not pre-date the twentieth century: it was first reported in 1935 and possibly blew in from Hispaniola during a hurricane in 1926 (Raffaele, 1973). Alternatively, the bird's recent appearance could represent a reinvasion subsequent to a prior local extinction. Because of the ease with which most birds can cross water gaps, invasion/extinction/reinvasion cycles are probably relatively common in this group, a possibility that must be kept in mind when considering former relationships.

Four larger raptors, the Peregrine Falcon (Falco peregrinus), Osprey (Pandion haliaetus), Sharp-shinned Hawk (Accipiter striatus), and Red-tailed Hawk (Buteo jamaicensis), have all been sighted on Mona (Raffaele, 1973; Red-tailed Hawk--Wiewandt, pers. obser.). Three of these species have feeding habits (see Bent, 1937, 1938) which pose little threat to iguanas. The Peregrine Falcon and Sharp-shinned Hawk prefer bird prey, though the latter occasionally takes small mammals, reptiles, frogs, and insects. For the Osprey, fish is almost the exclusive food, though in Baja California, Van Denburgh (1922) observed many dead chuckwallas, Sauromalus hispidus, in Osprey nests. The fourth species, the Red-tailed Hawk, rarely includes other birds in its diet and feeds almost exclusively upon rodents (Bent, 1937); in the absence

of rodent prey, young iguanas probably make a good substitute.

At what size do iguanas cease to be acceptable prey for raptors? Typically, prey animals are relatively small, of a size which can be not only killed but carried, normally weighing half the bird's own weight or less (Brown and Amadon, 1968). Thus, a hatchling Mona Iguana is near the prey size-limit for a Sparrow Hawk, and a large hawk (e.g., a Red-tailed weighing 1100-1200 g) would be likely to prey only upon juveniles under 25 cm snout-vent length, i.e., those less than three years in age (see Figs. 8 and 10). Interestingly, this is the same age at which the iguana's banded body pattern begins to disappear.

Two of the island's three species of snakes, Alsophis portoricensis variegatus and the boa Epicrates monensis, are known to feed on lizards. The Alsophis, a diurnal ground-dwelling snake and the most common on Mona, was seen eating an Ameiva in the field and will readily take Anolis in captivity (pers. obser.). Schmidt (1928) found an Anolis in the stomach of a Mona Boa. This boa is a nocturnal, arboreal animal that may feed largely on Anolis monensis, which often sleep in exposed locations on the tips of branches. I know of three instances in which these boas were found crawling about on branches at night, presumably in search of food; juvenile iguanas pass the night sleeping in rock crevices. Anolis and Ameiva abound island-wide, and because both the Mona Alsophis and Epicrates are characterized by slender body form and small adult body size (Schwartz, 1966; Sheplan & Schwartz, 1974), one would not expect iguanas to be a significant item in the diet of either species.

Two extinct land vertebrates were uncovered in Mona's fossil record: a unique giant tortoise, Geochelone (Monachelys) monensis (Williams, 1952), and a large hystricomorph rodent, Isolobodon portoricensis (H. W. Anthony, MS: seen by Williams, 1952, and Auffenberg, pers. comm.). These remains, Pleistocene to sub-Recent in age (Williams, 1952; Auffenberg, pers. comm.), suggest relatively recent extinctions, quite possibly from the hand of man. The rodent was a common item in the diet of the Pre-Columbian Indians (Anthony, 1926). Both species were probably important members of Mona's ecosystem during the iguana's evolutionary history and therefore deserve special consideration as potential competitors.

Isolobodon is one of six West Indian genera (three are extinct) in the family Capromyidae (Simpson, 1956). The Bahamian Hutia, Geocapromys ingrahami, is a living relict species native to Cyclura habitat and may well exemplify the life-style of hutias known from Mona. The natural history of this rodent was examined in detail by Clough (1972, 1974) on East Plana Cay. This animal resembles a small (about 630-g) porcupine in body form and gait. Active primarily by night, they spend the day within crevices and cracks in the limestone and exhibit no inclination to dig or burrow. Bahamian Hutias eat leaves, small twigs, bark, and fruit. Six among 31 plant species identified on East Plana Cay by Clough & Fulk (1971) were found to be food plants; five of the six genera and four of the six species also occur on Mona, and none are important items in the iguana's diet. Three of these have a very limited distribution on Mona, but two, Phyllanthus and Croton, are

shrubs abundantly represented island-wide and are generally avoided by iguanas and goats alike. Both are euphorbs--the former is tough and leafless, while the latter is oily and aromatic. Furthermore, Mona's iguanas select soft plant parts, not bark or twigs. Thus hutias might be expected to interfere little with the activities and requirements of the iguana population.

Living land tortoises of the genus Geochelone are grazing/browsing animals capable of considerable habitat modification at high densities (see Merton et al., 1976; Hnatiuk et al., 1976). In Mona's environment, they would be expected to nest in places similar to those utilized by iguanas (see MacFarland et al., 1974a). I suspect, then, that the ecological requirements of G. monensis and Cyclura stejnegeri overlapped broadly and the two species may have been in competition for some food items and possibly nest space. The tortoise may well have had a reproductive strategy differing from that of the iguana, however, especially with regard to time and frequency of nesting. Galápagos Giant Tortoises (G. elephantopus), for example, have a laying period that extends over seven months and often deposit more than one egg clutch per year (MacFarland et al., 1974a).

Iguanas and other native vertebrates may have once been in competition with each other for fruits from many of Mona's trees and shrubs, the most important food type in the iguana's diet. The extinct tortoise must have fed on fruit to some extent, as do many resident and migrant passerine birds. The fruit bat Artibeus jamaicensis occurs on Mona in small numbers (pers. obser.), along with several common nesting species

of doves and pigeons. Upon visiting the island today, one would have difficulty imagining competition for food between Mona's "gamebirds" and iguanas. Yet numbers of both have most assuredly been one to two orders of magnitude greater in the past. Just 25-50 years ago, White-crowned Pigeons nested on Mona's plateau by the thousands, and individual flocks numbered as high as 500; since then, the breeding population has fallen to several hundred (Raffaele, 1973). A clear correlation between this decline and public hunting is revealed in unpublished P.R. Fish & Wildlife census records. The iguana population must have experienced a considerably more gradual drop, probably beginning in the Taino Indian period (see Iguanas and the Activities of Man). Introduced mammals, discussed in the next section, now play a devastating role in the island's ecosystem.

Competition between juvenile iguanas and other animals on Mona for insect foods was discussed separately, under Foraging Behavior & Diet.

Parasites and Symbionts.--Most large terrestrial reptiles host ticks and/or mites; C. stejnegeri has both. The four juveniles captured appeared free from external parasites, while most adults carried some ticks, usually fewer than 20. One underweight male was heavily infested with ticks--I removed 96 and scraped away some of the hundreds of tiny instars that remained. Ticks collect primarily on the animal's underparts, around the legs, and along the middorsal crest. I noticed mites on only one iguana, a female: hundreds were present; they were orange and occurred in combination with a few ticks. The ticks were identified by Barry M. O'Connor, Cornell Dept. of Entomology, as Amblyomma

cruciferum. A different species, A. albopictum, was found on C. cornuta (Carey, 1975) and its sympatric congener C. ricordi (collected in the Dominican Republic by Wiewandt and Gicca in 1975; identified by Dr. Nixon Wilson, Univ. of North Iowa).

Mona Iguanas exhibited conspicuous unrest and physical discomfort during daylight hours when pursued by at least three types of flies (Calliphoridae, Sarcophagidae, and Tabanidae). The "blow-flies" and "flesh flies" are attracted to the iguanas' moist eyes and to bloody scrapes incurred in fighting. At times, as many as 20-30 flies swarmed over a lizard's head, the iguana responding with blinks, twitches, head rolls, and scratching with a rear leg. Some appeared to try ridding themselves of the pests by retreating to crevices, usually with continued scratching and head shaking accompanied by audible "klunks" of head against rock. In what appears to be a mutualistic relationship, Anolis monensis often jump on iguanas to feed upon flies gathered there. Not once did I see an iguana snap at one of these small lizards, even when the anole was perched on the side of the iguana's mouth.

Particularly annoying to the iguanas was a brown, clear-winged species of "deer fly," (collected by Wiewandt and identified as Stenotabanus stigma by Dr. L.L. Pechuman, Cornell Dept. of Entomology), a bloodsucking tabanid that reached annual population peaks during summer months. Typically only one or two would attack an iguana at the same time, but the moment one would alight anywhere on the animal's body, a concerted effort was made to dislodge it. After a few minutes of leg-flipping and spasmodic jumping and twisting about, the iguana

would usually get up, move a few feet, lie down, and attempt to relax again. These flies may be host-specific, for I was never bitten. Conversely, during damp periods mosquitoes were particularly bothersome to me yet appeared to show no interest in iguanas, in contrast to Henderson's (1974) observation that sleeping I. iguana host numerous mosquitoes.

No extensive search for endoparasites was made; however, gut contents of two healthy adult C. stejnegeri that I examined and another seen by Juan A. Rivero (pers. comm.) contained masses of nematodes in the colon. This is probably the normal condition for members of the genus, for the four other species examined thus far have each been host to one or more prolific nematode species (Bowie and Franz, 1974; Carey, 1975; Iverson, 1977; personal observations). In the Mona material, two different nematodes were found: a viviparous species belonging to the Family Atractidae (J.R. Georgi, Cornell Veterinary College, pers. comm.) and an unidentified oviparous species. The possibility exists, as suggested by Dubuis et al. (1971) for the herbivorous agamid lizard Uromastix acanthinurus, that these worms facilitate the lizard's assimilation of plant foods (and are not really parasites in the true sense of the word), a proposition that should be investigated further.

On Mona, within minutes or hours after an iguana defecates, the terrestrial hermit crabs (Coenobita clypeatus) begin picking apart the feces for food (Wiewandt, MS: 1977). Nowhere on the island will one find persisting accumulations of iguana feces except in a few particularly open, hot, and dry locations. Similarly, Grubb (1971) found that

Coenobita rugosus is dependent upon feces of the Giant Aldabra Tortoise. Walter Auffenberg (unpublished data) has recently provided experimental evidence for what makes the feces of these herbivorous reptiles so attractive: The caloric content of the Cyclura carinata feces he analyzed was surprisingly high relative to the caloric values of plant foods ingested; thus, the iguana's digestive efficiency is presumably low and an energy-rich, partially degraded, and perhaps detoxified food resource is left behind for the detritivores. No one, to my knowledge, has observed Cyclura eating their own feces.

Introduced Mammals:

During the colonial period early explorers from Europe introduced large mammals (primarily goats and pigs) to many of the islands of the New World to provide food for subsequent voyages or for shipwrecked sailors who might end up stranded on a remote, uninhabited island. Both intentional and non-intentional introductions of foreign animals and plants into insular environments have persisted throughout man's history, but only in recent years have we begun to realize the devastating effects that many exotic species are having upon native floras and faunas.

Insular ecosystems are exceptionally fragile (see Carlquist, 1974) and to predict how native and exotic forms will interrelate one must have a thorough understanding of the habits and requirements of both. Through careless management, more typically than not the actual or potential impact of a non-native species is considered only after it has become established and ecological side-effects begin to appear. The problem must be communicated to the layman as well, for it is often he who is responsible for bringing in the exotic, be it a pet, a hitchhiking pest, a source of food, or simply a "nice" addition to the landscape.

Mammals that most frequently accompany man have been among the worst offenders, i.e., dogs, cats, pigs, goats, cattle, burros, rabbits, rats, and mice. All are usually successful in establishing themselves without human encouragement. They typically compete with native animal species, prey upon them, or degrade the environment upon which native wildlife depends. Of the nine common exotics listed, all have been at

least temporarily established on Mona in the past. The rabbits, dogs, cattle, and burros have died off, but the others have persisted and are abundant today. Ranked in the order of the threat these survivors pose to the island's environment as a whole are: 1) goats, 2) pigs, 3) cats, 4) rats, and 5) mice.

Another familiar exotic, the mongoose, is a voracious, virtually uncontrollable predator that has been unwisely introduced into many Caribbean islands to kill rats and snakes. Though established on the mainland of Puerto Rico and Vieques, it is fortunately absent on Mona. This indiscriminate carnivore was clearly instrumental in the decimation of the Jamaican Ground Iguana (Cyclura collei), its decline documented by Lewis (1944).

The problem of controlling the introduced populations of goats and pigs on Mona has been underestimated both in importance and difficulty by persons responsible for the island's management. The literature concerning islands and parklands around the world emphasizes several significant facts: 1) these animals are capable of completely ruining a natural terrestrial ecosystem before any equilibrium can be attained; 2) the problem is worldwide and is particularly severe on islands; 3) programs necessary to bring these animals under control require careful organization, trained manpower, and money; and 4) the animals can rarely be completely eliminated so an active program for their control and scientific evaluation must be a sustained effort. In Mona's case the expense of such a program is well justified because, although environmental degradation is clearly evident, studies elsewhere indicate

that at this stage the trend is largely reversible through proper management. At stake is a remnant of Puerto Rico's, and the world's, most precious natural heritage.

In the subsections that follow, I present a resumé of problems posed by introduced mammals on Mona, together with historical perspectives for each population and a set of guidelines for their control. Although focusing on the conservation of iguanas, I have endeavored to use an ecosystem approach (especially regarding goats) to emphasize the magnitude of the problems and the importance of prompt corrective management. Such considerations deserve attention elsewhere in the Caribbean. What follows is a condensed version of a supplement to this work available upon request from the author. The supplement includes a literature review, additional background material and data, methodological details, and recommendations pertaining specifically to Monito.

Mice and Rats.--House mice (Mus musculus) are occasionally seen in the Mona lighthouse and in buildings at Sardinera. They were reported present on Mona in Hübener's (1898) account. I have never seen them in the field away from areas of human habitation, and although they may occur island-wide, it appears unlikely that they are abundant enough at this time to pose any special threat to the environment.

"Roof" or "Black" Rats (Rattus rattus) range throughout Mona. They are omnivorous--I have observed them climbing an Agave stalk for the plant's fruit, sorting through iguana fecal droppings for seeds, plundering a nest containing five Pearly-eyed Thrasher chicks, and hoarding an assortment of seeds, insects, and crabs. Though primarily nocturnal

in habit, these rats are sometimes active during daylight hours. At dusk they can frequently be seen running about in treetops within the inland sinkhole depressions. Nests appear to be most common within holes and crevices in the limestone. Their density over most of Mona appears to be moderate at this time, and no harmful effects to the iguanas have been noticed, although in human dwellings and in areas of high visitor use, rats have become a serious pest to man.

Cats and Dogs.--Domestic cats that had gone wild, i.e. become feral, were present on Mona as early as 1898 (Hübener, 1898). As free-ranging carnivores, cats are today quite common throughout the island. They are most numerous in the southeastern and southwestern parts of Mona, the island's only areas of human habitation. As a rough estimate, based on personal sightings in the field, population size appears to be between 100-200.

Department of Natural Resources management personnel helped trap eight cats for stomach content analysis using size #3 Hav-a-Hart traps. All were baited with fish. Three were captured in the vicinity of the lighthouse and five on the southwestern coastal plain. The results are summarized in Table 25. The sample is small and needs to be expanded, but the following things are apparent from the data: 1) cats from the southwestern coastal plain tended to be in a better state of health than those taken near the lighthouse; 2) reptiles and a few species of invertebrates constituted the principal food items; and 3) rodents were not represented in their diet.

The extent of predation upon Mona's juvenile iguanas is nearly impossible to assess with any degree of accuracy because they are so

Table 25.-- Stomach content analyses of feral cats trapped on Mona Island, P. R.

Date	Cat No., Sex and Color	Site of Capture	Physical Condition	Stomach Contents	Parasites in Stomach ¹
9 Feb. '74	#1, M, grey tabby	Faro	Young and lean	6 <u>Scolopendra centipedes</u>	Gorged with pinworms, many of the Genus <u>Atractis</u> (from the <u>Ameiva</u>)
23 Feb. '74	#2, F, brown tabby	Sardinera	Very healthy pregnant embryos 5 mm. long	Human garbage 1 <u>Scolopendra</u> 1 <u>Grasshopper</u> Parts of 1 unidentified insect	None visible
7 Mar. '74	#3, M, tabby	Just south of Faro Helipoint	Adult, healthy	1 <u>Scolopendra</u> 1 <u>Grasshopper</u> 1 Large beetle 1 Ball of downy, grey feathers	Ca. 50 roundworms, hooked to stomach lining (Genus <u>Physaloptera</u>)
5 Apr. '74	#4, F, tabby	Sardinera	Adult, healthy non-pregnant	2 <u>Ameiva</u> 2 <u>Grasshoppers</u> 1 Cricket	None visible
15 May '74	#5, M, tabby	near Faro	Young, scrawny carrying many cactus spines	5 <u>Scolopendra</u> 1 <u>Ameiva</u> 1 Fur ball (apparently its own)	Many <u>Physaloptera</u> sp.

Table 25 (Continued)

Date	Cat No., Sex and Color	Site of Capture	Physical Condition	Stomach Contents	Parasites in Stomach
3 Feb. '75	#6, M, tabby	by Airstrip	Adult, healthy	Feathers and parts of a Rolita Dove	3 <u>Physaloptera</u> sp.
3 Feb. '75	#7, M, tabby	Carabinero Dump	Large adult, excellent health, much internal fat	1 <u>Ameiva</u> 1 <u>Anolis</u> 1 <u>Mabuya</u> 1 <u>Alsophis</u> Hair, apparently its own	None visible
9 Feb. '75	#8, M, tabby	Carabinero	Young, healthy	1 Grasshopper	A few <u>Physaloptera</u> sp.

¹ Identified by J. R. Georgi, Professor of Veterinary Parasitology, Cornell Univ.

sparsely represented at this time. Pressures that do exist are undoubtedly buffered somewhat by the abundance of alternative prey species on the island; however, for the first two to three years after hatching, young iguanas are small enough to be taken by cats.

Convincing evidence that cats and dogs can have a devastating impact on a thriving population of ground iguanas (i.e., Cyclura carinata) comes from a recent study by Iverson (1977 and pers. comm.) on Pine Cay in the Caicos Island Bank. Pine Cay, which had no human residents before 1968, is small (750 acres=304 ha), and is both physiographically and biologically considerably less complex than Mona. The island therefore offers a valuable opportunity to examine cause-effect relationships within a natural ecosystem.

Human use of Pine Cay is confined to a small unimproved landing strip and a coastal plot approximately 15 acres (6.1 ha) in size. Before 1974, the only building on the island was a guest house with 10 people in residence. Cats and dogs that accompanied these people have been ranging freely over the entire island. Between September 1973 and September 1974 a work force of about 20 men settled there to construct a hotel complex near the lodge. During this time the dog population averaged between two and three and the cats began multiplying rapidly. Upon completing the hotel in September 1974, the work crew departed, leaving the cats and dogs to fend for themselves. Cats have been actively preying upon juvenile and adult iguanas, and dogs have been killing adults (adult C. carinata are relatively small, 40-76 cm overall length; of those taken by the cats, the largest recorded was 51.5 cm).

Between June 1974 and August 1975, Iverson documented a 71% reduction in the iguana population, and a year later, he found the number of iguanas on Pine Cay near zero.

Although dogs do not reside on Mona today, they stand among the most destructive and elusive exotic predators and are being brought to the island by visitors and personnel stationed there. Uncontrolled dogs are creating a growing threat to the welfare of wildlife (primarily deer, waterfowl, and other ground-nesting birds) and livestock throughout the United States--these problems have been documented and thoroughly reviewed by Denney (1974). Reports of turtle and iguana nests being plundered by dogs are not unusual (e.g., Hirth, 1963b; Carr, 1973; MacFarland et al., 1974a). In the Galápagos, dogs prey heavily upon sea lions, land iguanas, marine iguanas, and young giant tortoises (Kramer, 1973; MacFarland et al., 1974a). Dogs were once used extensively for hunting ground iguanas throughout the West Indies and are still employed for this purpose on some islands today, including the Bahamas (Auffenberg, 1975) and Hispaniola. A clever and exceptionally knowledgeable "iguanero" who I met in the Dominican Republic regards both dogs and cats as serious threats to iguanas there. He has seen feral cats kill juveniles and eat them completely. Cats, he says, are no threat to the eggs and adults, but dogs are; not infrequently he finds the remains of dog kills and has seen them digging up nests. Similar anecdotal accounts that incriminate free-running dogs in the decline of Cyclura in the Cayman Islands and on Anegada were reported by Grant (1940) and Carey (1975), respectively.

Pigs.--Feral pigs (Sus scrofa L.) range throughout many temperate, subtropical and tropical parts of the world. These introduced populations are usually traceable back to stock that originated from continental Europe, where the pig still abounds in some areas as a wild animal. Pigs have been feral on Mona for at least 384 years (Hakluyt, 1904, in Wadsworth, 1973b). I estimated that the Mona population numbered 300-700 in 1975 and feel that it probably reached the environment's carrying capacity long ago.

Although preferring the more mesic habitats, Mona pigs range island-wide. They root in almost any patch of soil large enough to accommodate their noses, and the scarcer the food supply, the further they are likely to wander in search of food. When available, fruits assume primary importance in the diet of these animals; second in importance are roots and stalks (Tillandsia to a large extent), and third are grasses and herbaceous plants. Carrion is readily eaten and may represent a significant part of the diet of pigs in some sectors of the island during the hunting season. Invertebrate animals are taken regularly though apparently in small quantities. The pigs occasionally eat cacti and fungi as well.

Feral pig populations have been shown to be destructive to native plant communities wherever they have been studied (e.g., in the Great Smoky Mountains, Bratton, 1974b; in the Galápagos Islands, Eckhardt, 1972, Hamann, 1975; in New Zealand, Moore & Cranwell, 1934, Wodziki,

1950; in Hawaii, Spatz & Mueller-Dombois, 1972). And amphibians, reptiles, and birds frequently suffer from the effects of feral pigs through predation and/or habitat alteration (see, e.g., Wodziki, 1950; Sablina, 1955, cited in Bratton, MS: 1974a; Carr, 1973; MacFarland et al., 1974a).

The pigs of Mona prey upon iguana eggs to a considerable extent. Unlike feral cats, signs of the activity of feral pigs are not subtle and are usually unmistakable. In study areas on the southwestern coastal plain, iguana nest destruction by feral pigs ranged from 0 - 5%, 65 - 100%, and 25 - 55% of the estimated total completed during the summers of 1972, 1973, and 1974, respectively (see Table 26). The relative degree of nest predation in any given year has been directly correlated with the rainfall pattern throughout the 3-4 month period before nesting (Fig. 34). Little predation occurred during the unusually moist year 1972, whereas the prolonged spring dry season of 1973 resulted in a sharp rise in pig mortality and particularly severe nest destruction. The amount of herbaceous ground cover, grass, and mature fruit available during May and June, just prior to the nesting season, appears to be a useful indicator of how much predation can be expected. From these data I would predict that during a "normal" year approximately one-fourth of the iguana nests on the SW coastal plain are lost to pigs.

The annual nest toll is apparently even higher within inland sink-hole depressions. Though few in number and small in size, many of these

Table 26.-- Census data for predation by feral pigs on iguana nests in Mona's southwestern coastal plain

		Number of Nests Found Destroyed by Pigs (% of observed or estimated total)				
		Carabinero District	Airport District	Sardinera District (less S-14)	S-14 Study Area	Yearly Mean For All Areas
1972	Nesting through Hatching	0 (<5%)	0 (<5%)	0 (<5%)	1 ? (<5%)	<5%
1973	1-11 August	4 } (100%)	13 }	35 }	2 }	
	12 August	1 }	6 } (80%)	8 } (65%)	3-4 } (65%)	70%
	16-18 August		1 }	1 }	7 }	
1974	4-13 August				3 }	
	14-17 August				8 }	
	4-23 August	2 (50%)	8 (32%)	17 (25%)		32%

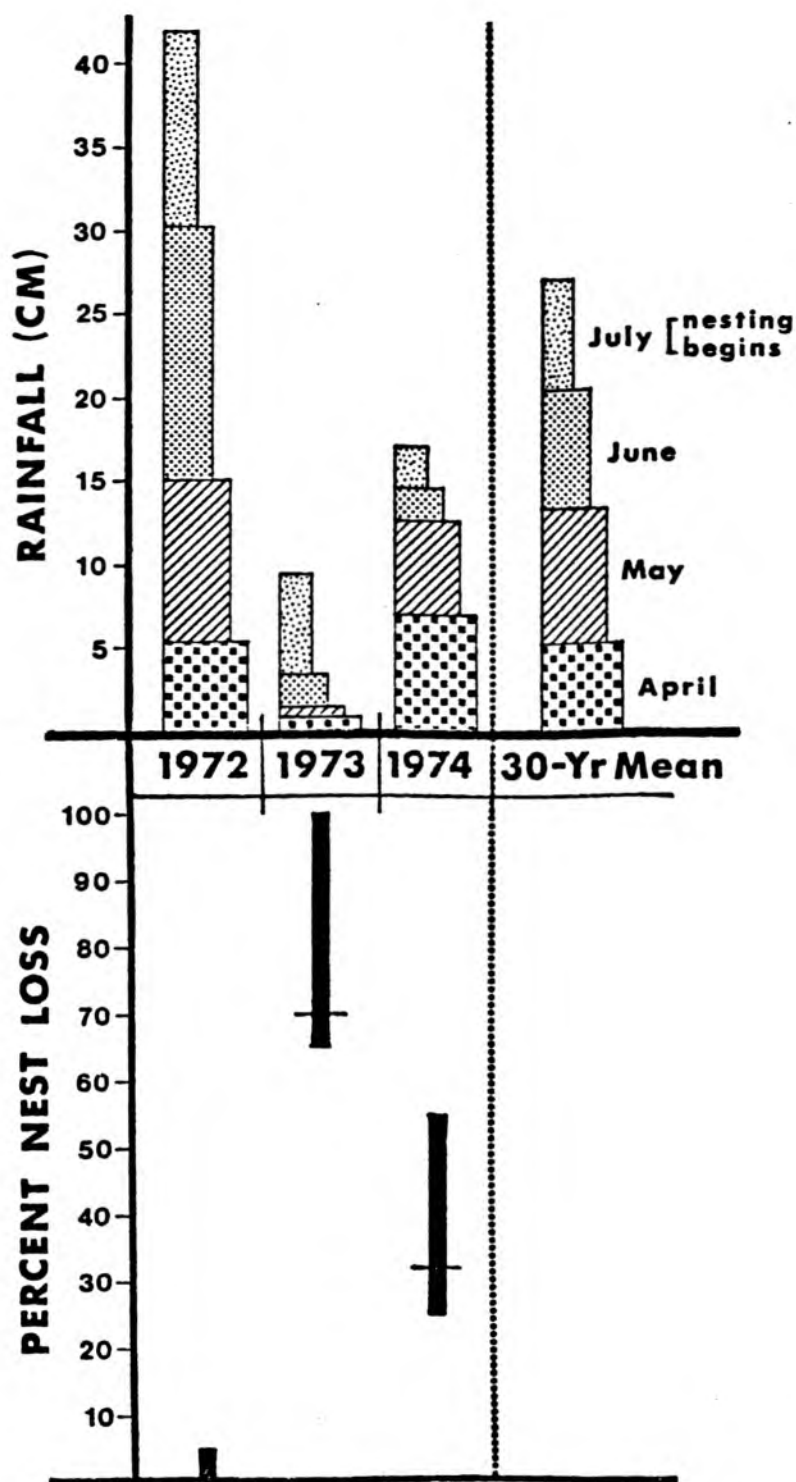


Fig. 34.--Annual loss of iguana nests to predation by feral pigs on the SW coastal plain of Mona I., P. R., relative to rainfall prior to the nesting season. Each solid black bar indicates the range of variability in nest loss for different districts studied, relative to the observed or estimated number of nests completed in each district. Means for overall loss each year, from the total of 168 completed nests, are shown as a cross on the bar.

depressions are important nesting areas for iguanas. They often contain open accumulations of soil, represent the most mesic habitat areas of the limestone plateau, and thus receive heavy use by pigs as one might expect from a highly water-dependent animal with rooting habits.

A pig observed (from a blind) in the act of plundering an iguana nest approached a female iguana that had just finished covering her nest late one afternoon. The female fled from the site and watched from a distance of about 15 meters as the pig promptly laid the nest open by rooting out a pit about 0.6 m deep with its snout. The pig then ate every egg, shell included. The following morning the iguana returned to re-fill with soil the hole left by the pig (for this reason, counts of nests destroyed by pigs may be lower than actual). She also defended the site against other females searching for a place to dig. The iguanas' inability to cope with the ways of this introduced predator is obvious.

Mona's pig population has persisted since the colonial era, and that the iguanas still exist today appears due to a combination of fortuitous factors. Survival of the iguana population can be attributed to the fact that the nest toll fluctuates widely from one year to the next; that pigs are not 100% efficient in their search for iguana eggs; and that expansion of the pig population has been limited by periodic droughts with accompanying shortages of food and water. Hübener (1898) makes specific reference to the fact that although he found pig bones in some of the caves, the pigs appeared to be extinct. This seems highly unlikely however, since Winslow (MS: 1909) reported just 11 years later

that local fishermen, using dogs and shotguns, often brought boars with long curved tusks in for food. Hübener's statement does however suggest that the pig population was quite small at the time and may represent an ebb in numbers due to drought, intensive hunting during the Mining Period, or other causes.

Goats.--Still native to mountainous regions of southern Europe, Asia Minor, and the Himalayas, goats (Capra hircus L.) are today among the most cosmopolitan mammals in the world owing to their success as a hardy domesticate with the ability to colonize terrain unsuitable to most other livestock commonly transported by man. Few islands have escaped their introduction, and they have proliferated in a feral state regardless of differences in climate and available food. Early historical records for Mona give no mention of goats until approximately 100 years ago (Wadsworth, 1973b). They have penetrated all parts of the island and are flourishing today. In 1973, I estimated the size of the Mona population at 7,000-10,000, and expanding.

As a synthesis of trends evident from the literature, a predictable sequence of events occurs following the introduction of goats into a "naive" island ecosystem. Accompanying the invasion and expansion of the goat population, the particularly palatable herbaceous species are eaten and the tender accessible parts of the tastier woody species are consumed and browsed back as new growth appears. When these favored items become scarce, goats continue removing any new growth or seedlings within reach and begin working on the less palatable species, i.e., types and parts of plants are attacked that were once left untouched or

eaten only in small quantities; at this stage one can expect browsing on a broader spectrum of species, bark-stripping, and overturning and consumption of moderately protected plants like some cacti. The population continues expanding until food resources become scarce enough to begin limiting its growth; by the time this stage has been reached, the entire ecosystem has undergone drastic modification. The few elements of the flora that happen to be particularly goat-resistant due to possession of toxins, spines, etc., spread and become dominants, and the loss of palatable native forms opens the path for the establishment of resistant exotic species. Because mature palatable trees and arborescent shrubs are partially inaccessible to browsing pressure, these species continue to be represented until the last of their numbers die of old age and the last of their seedlings are consumed. Goats generally eat the plants down to ground level and often uproot the entire plant while foraging. As a result, the mulch layer is steadily depleted, preventing the build-up of topsoil required for water-retention, aeration, and nutrient accumulation; hence productivity declines and erosion increases. In most cases the effects of trampling and increased erosion hasten the degradation process.

In essence, then, the major problem with goats on islands lies in their phenomenal capacity for degrading native plant communities, thereby depleting resources of ultimate importance to the welfare of native animal life. Plants which have had no need to evolve or maintain a system for defense against goats are apt to be as vulnerable to such herbivores as "prey" animal species that have never experienced the

devices of a predator. Insular life forms whose identity has been molded over millenia in the absence of selective pressures of this sort are usually ill-equipped for such a challenge. The world-wide impact of feral goats on island floras illustrates the point well (e.g., on St. Helena, Wallace, 1975, Darwin, 1889; on Guadalupe I., Carlquist, 1965, Moran, 1967; in New Zealand, Turbott, 1963, Atkinson, 1964, Beever et al., 1969, Beever & Beever, 1969, Parris, 1969, Sykes, 1969; in the Galápagos Is., Weber, 1971, Eckhardt, 1972; in the Hawaiian Is., Yocom, 1967, Baker & Reeser, 1972, Mueller-Dombois & Spatz, 1972, Spatz & Mueller-Dombois, 1973; on Santa Catalina I., Coblentz, 1974). Studies made in the Galápagos Islands exemplify two ways in which destruction of natural vegetation might harm reptile populations: MacFarland et al. (1974a) found that goats have created a near absence of food for young tortoises, and Dowling (1964) determined that juvenile land iguanas, Conolophus spp., are unnaturally vulnerable to predation by hawks due to the present scarcity of protective vegetative cover on islands over-browsed by goats.

A more speculative and intriguing consideration is that goats are also capable of inducing regional climatic desertification. Otterman (1974) reported that substrates with high reflectivity denuded by over-grazing are cooler than adjacent regions covered by natural vegetation, thereby producing a "thermal depression" effect which, on theoretical grounds, should result in a decreased lifting of air necessary for cloud formation and an appreciable drop in precipitation. The light-colored limestone substrata of many islands of sedimentary origin, e.g., Mona,

would appear no less susceptible to this effect than the bright sandy soils of the Mediterranean area considered by Otterman.

On Mona it is clear that some of the island's plant communities are in serious trouble from overbrowsing by feral goats. The most apparent and alarming signs of browsing damage are in the areas where goats tend to congregate for nighttime shelter and daytime shade from the heat, i.e., sinkholes at cave entrances and rocky inland depressions characterized by Depression Forest vegetation. The Depression Forest associations are among the most limited in area (covering only about 3% of the island's surface - Cintrón & Rogers, MS: 1974) and represent some of Mona's most important habitat for native wildlife. These areas support a relatively dense forest of tall trees, often 10-12 m in height, showing a considerable variety of species with many co-dominants (Cintrón & Rogers, MS: 1974). Here and in some of the coastal forests, browse lines are clear, and many of the native tree species are not replacing themselves naturally. Within the inland sink El Corral de los Indios, for example, the only species that now appear to be propagating are Euphorbia petiolaris (a tree with highly caustic sap), Consolea rubescens (a tree-sized cactus), Jatropha multifida (a toxic introduced species), and Phyllanthus epiphyllanthus (a tough, fibrous shrub). Ficus citrifolia, a tree which appears capable of sustaining itself vegetatively by sending down hanging roots that eventually anchor and enlarge, is prevalent here, as it is in sinks and depressions island-wide. This species is not, however, reproducing from seed. An inspection by Cintron and Rogers (MS: 1974) of the forest floor in the "batey" district of El Corral revealed no seedlings of any canopy trees there.

From a recent survey of other depressions on Mona, Rogers (pers. comm.) has found similar damage: Canella winterana and Capparis cynophallophora are reproducing freely, with seedlings and saplings present in all sizes; both leaves and woody parts of these species are highly seasoned. Species of Eugenia (another highly aromatic group), including E. axillaris, E. fetida, and E. fragrans, and Pisonia albida also appear to be reproducing moderately well. Coccoloba microstachya seems to be propagating quite successfully in the depressions, possibly representing a goat-facilitated invasion of the depressions by a primarily plateau species. All other species (except for the Euphorbia, Jatropha, Consolea, and Phyllanthus mentioned above) are almost never found as saplings or seedlings above 10 cm tall. During periods of increased precipitation I have observed sprouts below the forest browse lines and an abundance of tree seedlings not normally represented--these typically disappear within a few weeks however.

Signs of browsing damage and altered successional patterns are also evident in Mona's plateau forest and scrub communities. Some shrubs such as Strumpfia maritima seen along the trail to La Bajura de los Cerezos have been browsed back to tiny balls of twigs and leaves incapable of flowering and fruiting (Roy Woodbury, pers. comm.). The trunks and lower branches of many columnar cacti of the genera Lemaireocereus and Cephalocereus bear scars from being gnawed down to their woody inner skeleton, and Mammillaria and Melocactus are often found open with the interior scooped out or overturned with the roots chewed off. I have observed a goat attacking a Snowball Cactus (Mammillaria nivosa) by

curling back its lips and penetrating the flesh by biting through and removing the layer of spines with its long curved incisors. Most over-turned cacti are probably the result of pig rooting, though goats are also capable of dislodging the smaller species by pawing with their hoofs. Wadsworth (pers. comm.) believes that the cactus "forest" association, unique to a small area around the lighthouse, probably represents a successional stage which has been maintained by heavy goat browsing in the area.

Areas upon the plateau that have been bulldozed clear or burned within the past 40 years are now supporting secondary growth of the type which I would expect to appear and be maintained under browsing stress (see Cintrón & Rogers, MS: 1974). Panicum maximum, a grass introduced a century ago for pasture, is the most common early invader of burned areas, and cosmopolitan weeds abound. In some of the older successional areas one can find almost pure stands of the very unpalatable shrubs Croton discolor and Croton humilis. Corchorus hirsutus, Croton betulinus, Reynosia uncinata, Antirrhea acutata, and Plumeria obtusa are also frequently represented; Reynosia has tough and spiny leaves, Plumeria has mildly toxic sap, and the others are highly aromatic shrubs. The only tree species represented as a dominant invader is the noxious tree Euphorbia petiolaris, one of the few species that has been propagating successfully within the depression forests.

As goats reduce or eliminate the more palatable plant species, causing an increase in the relative proportion of plants containing high concentrations of toxic secondary compounds, the nutritional welfare of

less adaptable generalist herbivores sharing that environment, e.g., the iguanas on Mona, can be expected to suffer (see Freeland & Janzen, 1974). The diets of Mona's goats and iguanas overlap broadly, with food plants selected by iguanas nearly all belonging to a subset of those taken by goats (see Appendix I). In fact, I have found only one plant species in the iguanas' diet that is strictly avoided by goats:

Hippomane mancinella (Manchineel), a poisonous coastal species the fruit and leaves of which iguanas can eat and digest in limited quantities. Fifty-three percent of all plant species known to be taken by goats are also eaten by iguanas, and of those known food species represented among dominants in Mona's 10 principal plant communities (see Cintrón & Rogers, MS: 1974), 63% are in common with the iguanas' diet.

The goats also browse more generally than iguanas on most food plants, i.e., goats eat leaves, flowers, fruits, stems, and sometimes bark and roots, whereas the iguanas often eat only the plant's flowers and/or fruits. Coccoloba microstachya, Bourreria succulenta, Amyris elemifera, Antirrhea acutata, and Reynosia uncinata are, for example, five dominant trees and shrubs within the extensive Plateau Forest vegetation type, and while the iguanas relish only the fruits of these species, the goats eat both the foliage and fruits, though the fruits of the shrubs Antirrhea and Reynosia are clearly preferred to the plants' leaves. Also noteworthy is the fact that except for Ficus, all of the Depression Forest species with fruits known to be important in the iguanas' diet are now unable to propagate successfully because of the goats.

There are no signs at this time that Mona's presently small iguana population is under nutritional duress because of the presence of feral goats; however, if these mammals are permitted to continue flourishing at the expense of the island's native trees and shrubs, serious indirect competition will unquestionably develop.

A look at the history of human occupation of Mona suggests that the goat population has not always expanded freely as it does today (see Table 27). In 1868 when goats were first mentioned in historical records, they were already numerous enough to sustain hunting (Wadsworth, 1973b), a population level that could have been reached within 10 years after their liberation (see Eckhardt, 1972). Throughout a major portion of the Mining Period, goats undoubtedly served as an important food supply for the sizable human settlement on Mona. Near the turn of the century Hübener reported that three men were used to hunt goats continuously (Wadsworth, 1973b). It seems reasonable to infer, then, that the goat population was severely trimmed back and/or maintained at a relatively low level by intensive hunting pressure during that period. As the interest in guano mining dropped off soon after the turn of the century, the population was free to expand again, and in the years 1917, 1919, 1925, and 1927, goats were reported as being abundant (Wadsworth, 1973b).

During the thirties intensified use of Mona accompanied the removal of wood, charcoal production, and later the establishment of a Civilian Conservation Corps program (Wadsworth, 1973b). The goats were probably once again hunted regularly and intensively. Large tracts of native

Table 27.-- History of human occupation of Mona Island, P.R. (compiled from Wadsworth, 1973).

Historical Period	Duration	Human Population	Comment
Taino Period			
Pre-Columbian	?-1494	> 150	Taino culture thriving
Post-Columbian	1494-1543	> 150-50	Indian population dwindles. Many ships stopping for provisions from Tainos.
	1543-1578	50-ca. 20	Indian civilization ends
Period of Abandon (i.e., "officially" abandoned)	1578-1762	< 50	Used by fishermen and a few settlers and as stop-off for pirates
	1762	"well-peopled"	
	1763-1847	?	Intermittent use by fishermen
Mining Period	1847-1877	?	Coastal cutting/export of wood
			Intermittent unofficial phosphates extraction
	1877-1889	30-100	First official mining enterprise
	1890-1896	300-400	Intensive phosphate mining--second episode
			Construction of first lighthouse
	1897-1899	4 ⁺ (in 1898)	End of German mining operation

Table 27 (Continued)

Historical Period	Duration	Human Population	Comment
Mining Period (Cont.)	1900-1903	?	Re-location of light-house
	1904-1921	?	Third mining episode
	1922-1927	46 settlers + mining and lighthouse crews	Coastal farming Coastguard construction/maintenance operations
Recent	1927-1937	ca. 30-50	Coastguard construction/maintenance operations Settlers engaged in fishing, agriculture, wood removal, and charcoal production
	1937-1942	ca. 150	CCC Camp Cofresi
	1943-1946	ca. 50	P.R. Agricultural Co. commercial fishing project
	1946-1953	?	
	1953-1962	?	U.S.A.F. occupation
	1962-1972	4-40 *	No residents; recreational development under P.R. Dept. of Agriculture
			Addition of police detachment

Table 27 (Continued)

Historical Period	Duration	Human Population	Comment
Recent (Cont.)	1973-1975	2-170 *	Departure of Coast- guard crew
			Rapidly intensifying recreational use
			No residents

* Based on visitor records from Dept. of Natural Resources and personal observations.

forest near Uvero that had been selectively cut for stakes, burned for charcoal, or cleared for agriculture were able to regenerate successfully, indicating that at least in this part of Mona, browsing pressure was significantly less than it is today. That some browsing in the area did exist, however, is suggested by the relatively low diversity of species and predominance of goat-resistant species (Rogers, pers. comm.).

Goats were reported as abundant in 1950 (Unpublished P. R. Fish & Wildlife records - see Table 28), just three years before Mona was leased to the U.S. military. During the following decade under the Federal Government a support team on Mona assisted with aerial bombardment exercises on Monito, a new airstrip was constructed, bulldozers utilized in training exercises cut a grid of trackways over much of the island's plateau (Wadsworth, 1973b), and an ecological research program associated with the Air Force Division of Chemical and Biological Warfare was underway (comparative data from these environmental studies could prove extremely valuable, but the results were never publicized and have apparently been lost or intentionally destroyed). How these activities and hunting at the time affected the goat population remains unknown, but it is curious that the census in 1960 showed a relatively sharp drop in numbers since 1950 (Table 28). Inconsistencies in censusing techniques may be involved, but I suspect that at least part of the difference reported is due to a localized response by the goats to regular disturbance along the more accessible routes where census counts were taken.

Table 28.-- Relative abundance of feral goats encountered during cross-island censuses on Mona Island, P. R.

Census Period	Distance Covered	Goats Sighted/Km	Billy:Nanny:Kid Ratio
*24 Nov.-14 Dec. 1950	145 km	4.2	100:175:22
*June 1960	84 km	1.3	100:70:55
*Fiscal Yr. 1964	338 km	1.9	100:96:24
*Fiscal Yr. 1965	764 km	2.1	100:98:25
May-July 1973	106 km	2.5	100:83:61

*Data from unpublished P. R. Fish and Wildlife records

During the past 15 years the only reduction in the Mona goat population by man has come through poaching and public hunting, representing less than 10% of the population per year, and quite possibly the lowest toll from any 15-year period in the history of goats on the island.

If goats were first brought to Mona during the early part of the Mining Period and were intensively hunted then as suggested, they would have had little time to modify the island's original flora prior to Britton's 1915 botanical survey. Unfortunately Britton's collection was very ~~in~~ⁿcomplete (including only about half of Mona's flora as known today), and his report gave no information concerning relative abundance. Few meaningful comparisons can be drawn between past and present, yet it is noteworthy that of the 62 native species of large shrubs and trees identified by Britton, all still occur on the island today (Little, 1955; R. Woodbury, pers. comm.).

In addition to inadvertent goat control that may have been operative intermittently during Mona's past, three natural factors have apparently helped slow the degradation of the island's plant communities: First, the arborescent flora of Mona contains no endemic species and is, for the most part, of broad geographic distribution in the West Indies, with 46% of its species occurring in continental Latin America as well (Little, 1955). Consequently, the evolution of a large percentage of Mona's woody species has been shaped by associations with extant and extinct browsers native to the West Indian area, including cycluran iguanas. One would expect, therefore, a greater degree of browse resistance in Mona's flora than would be found on islands with a high percentage of endemics and no history of native browsers, e.g., the Hawaiian Islands. Second, also

acting in Mona's favor is the island's karst topography, eliminating the problem of goat-induced erosion and minimizing the extent of trampling in most areas. And third, even under intense browsing pressure, long-lived species such as those characterizing Mona's forest will continue to be represented in the canopy for many years, disappearing only after mature individuals have died of old age. All of these factors indicate that the prospects for restoring a natural equilibrium to the island's upland forest communities are excellent at this time if appropriate action is taken in the near future.

Control Measures and Recommendations.--If Mona's terrestrial ecosystem is to be given the protection it deserves, the introduced populations of cats, pigs, and goats must be brought under strict control. Because the cats are small, elusive, and relatively solitary in habit, I suspect that little can be done to lessen their numbers besides continued live-trapping and shooting them on sight. Cooperation from all hunters going to Mona could be enlisted (perhaps aided by the incentive of a bounty). Controlling goat and pig populations presents a wider array of management possibilities, the topic to be discussed in the remainder of this section.

Much of the frustration and expense associated with pig and goat control programs arises from the task of keeping ahead of the reproductive capacity of these animals. At latitudes where the climate is mild and seasonal variations are not great, females of both species can be expected to mature in their first year and breed continuously thereafter, often twice annually (Rudge, 1969; Barrett, 1971, MS: 1973).

Number of surviving young per litter is typically one or two in goats and one to five in feral pigs. Observations by myself and M. Marcial (in Lawson, 1967) indicate that the reproductive potential of the Mona populations is similarly high, and as in most island environments, there are no pig or goat predators on Mona to help limit population expansion. Periodic droughts take a toll on Mona's pigs, but the goats can endure such times without serious consequences.

Maintaining population size at ecologically tolerable levels requires intensive and sustained management. Once a population is reduced to below the environment's carrying capacity, food becomes less important in limiting numbers, thereby favoring increased reproduction. This, in turn, means that a greater percentage of the remaining population must be cropped annually to establish effective control. In one representative goat population that has been hunted for many years by both government and private shooters, Rudge & Smit (1970) calculated that goat numbers will more than double every two years, using a minimum observed birth rate and a maximum estimated death rate. Attempts that have been made world-wide to reduce or eliminate feral pig and goat populations (e.g., see Baker & Reeser, 1972; Barrett, MS: 1973; Kramer, 1973; Bratton, MS: 1974a, and citations therein; MacFarland et al., 1974b) clearly show that 50-70% of each population must be removed annually to effect any control. The magnitude of the task should be obvious.

A program for controlling the feral mammals populating Mona Island has never existed. Recreational hunting in its present form is useless

to scientifically based management. During three recent hunting seasons on record, an average of only 184 goats and fewer than 20 pigs were taken each year. This toll is no doubt matched or even exceeded somewhat by those taken by poachers and employees, but no matter how liberal the estimate, one can be certain that less than 10% of the population is killed annually. An absurd bag limit of one pig or goat per hunter per day has been traditional since the time the Fish & Wildlife Program was begun on Mona in 1950. Yet even if this limit were to be lifted, I am certain that the change would be of little consequence. The fact is that most hunters find the island's remoteness and inhospitable terrain too intimidating, and the vast majority of hunters I have personally encountered come to Mona primarily to drink and party on the beachfront. Few demonstrate experience in handling firearms, and fewer show any understanding of the natural environment there.

Possible approaches to feral mammal control include schemes for 1) completely eliminating the population, 2) reducing population size and keeping it at a low level, and 3) minimizing damage by limiting access. The most ecologically and economically desirable long-term solution to Mona's pig and goat problems would be removal of both populations entirely. Unfortunately the island is too large, remote, cavernous, and densely vegetated to permit total extermination through an intensive shoot-out campaign. Aerial shooting from helicopters has proven efficient for the deployment of goats in New Zealand, but this technique is effective only in habitats with wide open spaces (Williams et al., 1974).

Use of disease as a method for eliminating Mona's feral pigs merits consideration. Hog cholera is a virus that has been extensively studied (reviewed by Dunne, 1970) and is known to be highly specific to pigs, highly contagious, generally lethal, and world-wide in distribution. Despite intensive U.S.D.A. efforts in recent years to eradicate this disease, outbreaks still occur occasionally in some areas, including the Puerto Rican mainland. Introducing infected pork to Mona or innoculating one resident pig with the virus would probably be sufficient to kill all or most of the population. Populations long isolated such as the one on Mona are likely to be most severely affected. An outbreak of hog cholera on an off-shore island in California completely eradicated that population of feral pigs (L. W. Locke, Histopathologist of the Patuxent Wildlife Research Center, pers. comm.). Nevertheless, if a follow-up hunting program to shoot any survivors proved necessary this would be problematical in Mona's environment and surviving individuals could repopulate the entire island within a few years. In short, the effectiveness of the disease could not be ascertained without actually trying it, and risk to hogs on the mainland of Puerto Rico could be great if proper precautions were not taken. Obtaining the virus for such a program would require a detailed and convincing proposal for evaluation by officials from both Puerto Rican and Federal divisions of the U.S.D.A. (L. W. Locke, pers. comm.).

Because of its effectiveness and economical virtues, poisoning as a means of population reduction is being developed and used in New Zealand in places where there is no risk to native species (Howard, 1966; Rudge,

MS: 1973). Poisoned carcasses and leaves are left as bait for pigs and goats, respectively. Since poisons can be a serious hazard to non-target species, this approach should not be attempted on Mona.

To successfully manage Mona's goat and pig populations, professional hunters are required. Following is a list of suggestions for ways in which the greatest overall returns from both hired and visiting hunters could be achieved:

1. Hire a team of experienced hunters to bring the populations down to a manageable level during the first year, and staff at least two professional hunters and two biologists to work together such that at least one of each is always in residence on the island.
2. Direct control at the nanny/sow segment of the population.
3. Spread the hunting pressure island-wide to minimize responsive shifts in range and activity patterns.
4. Concentrate control efforts in the more remote areas where recreational hunters are less likely to venture.
5. Employ the "Judas" goat technique of J. K. Baker to assist hunters in finding herds: Adult nannies are captured, given leather collars with a sheep bell, and released at widely scattered localities. The tinkle tells hunters where to find the goat herd each nanny has joined. Goats with a bell are never shot. This method has proven particularly successful in thickly forested areas of Hawaii Volcanoes National Park (Baker, pers. comm.).

6. Because cave and sinkhole habitats are heavily utilized by both goats and pigs, these areas should be intensively hunted, especially during twilight hours.
7. Prepare informative handouts to help direct visiting hunters in a manner best suited to the needs of the control program.
8. Encourage public participation in organized hunts and drives, an effort that could perhaps be arranged through local sportsmen's clubs.
9. Whenever practical, the meat should be saved and possibly sold for a nominal fee to help defray the cost of the program.
10. In relatively remote areas, carcasses should be disposed of with discretion to avoid conflicts between management staff and visitors who might be angered by chancing across offensive remains.

Well trained dogs used to track and capture pigs and goats can be a tremendous asset to improving hunting efficiency (see Saywell, 1943, cited in Wodziki, 1950; Giffin, MS: 1970; Baker & Reeser, 1972). In fact, dogs were once used successfully on Mona for pig hunting (Winslow, MS: 1909). It would appear that while of great value in some parts of Mona, especially on the coastal terraces, this approach may be severely limited by the harsh terrain and cacti characterizing the island's vast plateau. If dogs are brought to Mona for this purpose in the future, they should be males and/or spayed females, trained not to kill native wildlife, and kept on a leash when not actively hunting.

In habitats difficult to traverse, trapping as a method for taking pigs is often more productive than hunting (Barrett, pers. comm.; P. L. Smith, pers. comm.). The mobility patterns of pigs and the conspicuous signs of their activity permit one to place traps in strategic locations. Because they often travel in small groups (on Mona, I have observed bands with as many as nine pigs, three adults and six young), multiple captures are a common occurrence, given an appropriate trap design and attractive bait. Despite the initial cost for constructing traps, savings in time and manpower can be expected if the trapping program is carefully planned and executed. Some experimentation with trap designs and baiting, together with a knowledge of where and when to set traps, are required.

As one would expect, trapping success is greatest when pigs are actively seeking a resource in short supply (Barrett, pers. comm.; Bratton, MS: 1974a). Mona's dry season provides a perfect opportunity to capitalize on the nutritional stress the feral pigs must endure there. Semi-permanent corral-type traps installed around or adjacent to major iguana nesting areas and all accessible water supplies would unquestionably be productive at the appropriate time of the year. Maximum effort should be directed toward pig control in dry years when the pigs are most vulnerable.

Simultaneous to developing a program for feral mammal control through direct reduction in numbers by means of shooting and trapping, sections of the island of greatest accessibility and ecological importance to native species should be progressively fenced-off into

management units and then cleared of goats and pigs. Such a fence must obviously have a mesh large enough to allow iguanas to pass through freely, yet small enough to exclude weanling pigs and goats. This approach offers the following advantages: 1) a permanent solution to the problems created by both pigs and goats within critical management areas is provided (assuming that fences are carefully installed and regularly checked for damage); 2) seed reserves for segments of the forest are given complete protection from these mammals; 3) the fences help delimit hunting and non-hunting forms of activity; and 4) the progress being made can be readily observed and the recovery phase studied and compared with unprotected areas.

The fence-and-clear strategy should be initiated on Mona's southwestern coastal plain, this being the most critical area at this time primarily because of damage from pigs. I recommend that the project be accomplished in four stages (see Fig. 35), ranked in order of relative ease and importance. Emergence of approximately 1500 hatchling iguanas and at least 9,000 hatchling Hawksbill turtles can be expected annually if this coastal zone is fenced-off and is also given proper protection from visitors.

Although representing only a partial solution to the problems posed by feral pigs, localized use of repellents or strong attractants might aid in protecting iguana nests in areas where use of fencing is impractical. No effective pig repellents are presently known, but broadcasting nesting areas with a strong attractant such as blood meal might mask the scent of iguana eggs and prevent pigs from finding them. This

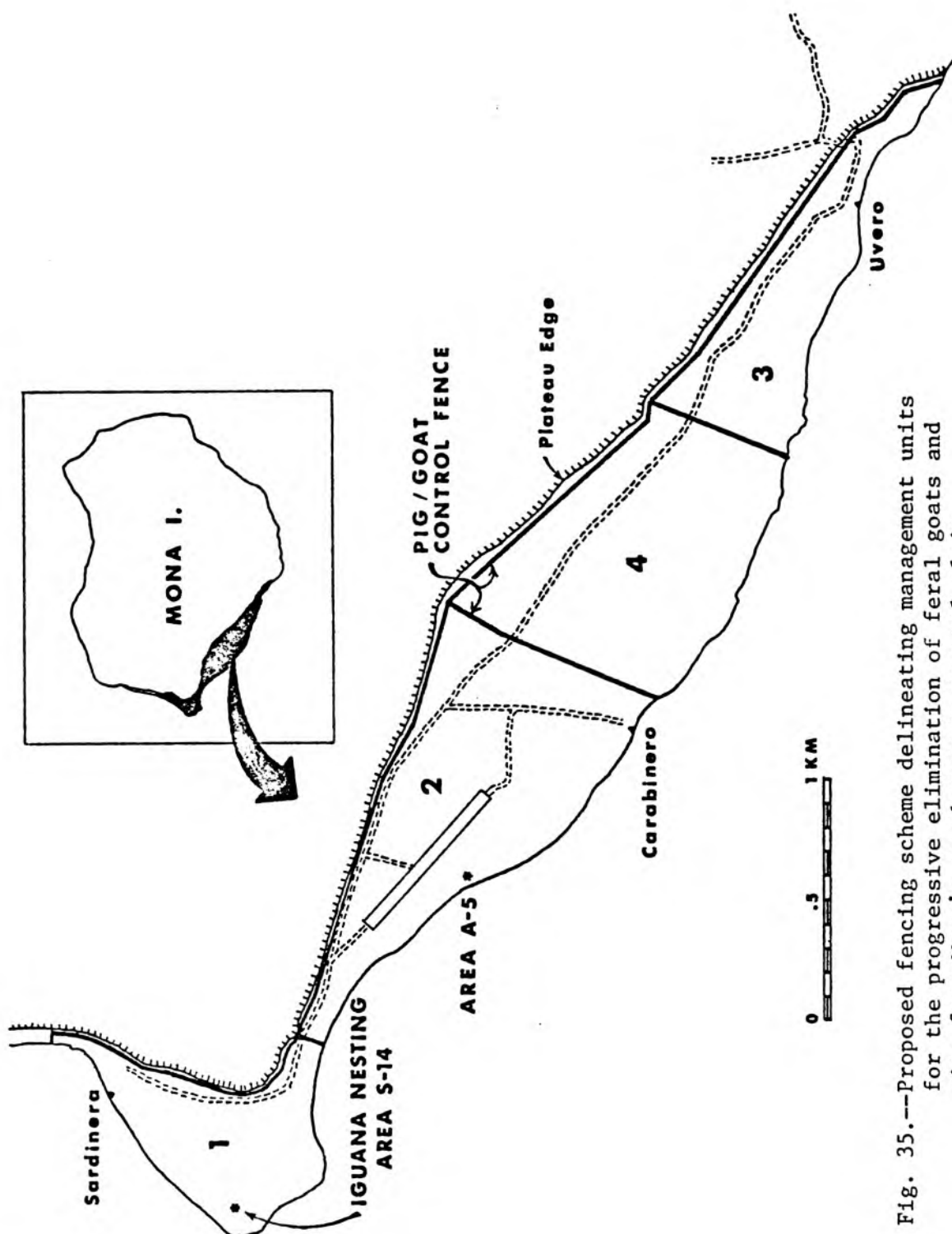


Fig. 35.--Proposed fencing scheme delineating management units for the progressive elimination of feral goats and pigs from Mona's southwestern coastal plain.

technique would require little manpower, would be inexpensive, and deserves testing in the immediate future.

The only way to ascertain the effectiveness of feral mammal control efforts is through faithful bookkeeping, consistent and carefully executed censusing techniques, and continued evaluation of areas and species receiving greatest disturbance. Kill data must be collected to document how control efforts are being distributed and to determine to what extent the populations are under control. Weather records (especially rainfall) and notes on food availability each month (especially ephemeral types) are essential, for few trends can be meaningfully interpreted without this information. Gathering these data will require close cooperation (unheard of in the past) between the island's managers, biologists, and hunters. Since computer facilities are available in the P. R. Department of Natural Resources, it would be especially wise to program and store all data of this nature right from the beginning.

Control efforts should also be accompanied by studies of plant communities under browsing, rooting, and trampling pressure. Since Depression Forest associations appear to be among Mona's most sensitive indicators of overbrowsing, these areas are well suited for assessing recovery or persisting damage. Fenced plots from which pigs and goats are completely excluded are necessary to provide a measure of changes that can be expected in the total absence of such pressure. These need be installed at the onset of the program, as it will undoubtedly be a number of years before a representative set of management units can be

fenced-off and cleared of these mammals. One such enclosure was recently completed and surveyed (along with an adjacent open plot) within a small carefully selected inland depression (see Cintrón, MS: 1976). The plot relieved of stress from feral mammals has already responded dramatically with respect to understory shoots, seedlings, and leaf litter accumulation. Establishing enclosures for similar studies within a variety of other vegetation types on the plateau should be given high priority in the near future, as it is important to determine the regeneration characteristics and capacities for each major class of vegetation; such enclosures require little labor or expense. In these areas, artificially cleared plots should accompany open and fenced plots.

To summarize, once free in insular ecosystems, goats and pigs represent a major alien, disruptive force demanding stringent control, lest all natural interrelationships between land, flora, and fauna be sacrificed. This problem must be viewed in a global context to gain a full appreciation of its nature and magnitude. The road to effective control, as a management objective, is well marked by Baker & Reeser (1972):

. . . a basic philosophy considered by New Zealanders stresses the importance of over-control rather than risk irreparable damage by return of the same old problems through practicing under-control. Emphasis on total eradication is based upon a fundamental principle that success is not measured in numbers of animals killed but in how few, if any, are left to start over again.

The lessons to be learned from our own misadventures are: (1) there must be a plan; (2) it must receive uninterrupted review and implementation; and (3) it must be programmed for sufficient funds and manpower to achieve its objectives.

I urge that a full-scale program for the control of feral mammals be implemented on Mona as soon as possible using the fourfold approach developed in this section: 1) begin an intense overall shooting campaign, followed up with continued cropping as necessary to hold the population at a low level; 2) progressively fence off critical sections of the island into management units from which all goats and pigs are cleared; 3) build up a computerized bank of meaningful population data from kill and census records; and 4) maintain a vegetation damage/recovery inventory to measure the program's effectiveness.

Perhaps someday we will have better control techniques at our disposal as more is learned about the behavior and physiology of these mammals; but for now we must approach the problem using techniques that have proven successful elsewhere. It is not easy for me to prescribe the slaying of thousands of animals that I have lived with for three years. The goats I now regard as admirable and even majestic creatures in a wild state, yet I feel it is essential that man intervene once again, this time to correct a severe injustice that was unfortunately bestowed upon the island by our naive predecessors.

Iguanas and the Activities of Man:

Past, Present, and Future Relationships.--The Mona Iguana, like probably all Cyclura, possesses a combination of demographic traits which reflect the group's insular origin and extreme vulnerability. The iguana is long-lived, females nest no more than once each year, clutch size is small, and juveniles are slow-growing and late-maturing. Aside from man, iguanas on Mona have no predators as adults and are consequently more likely to realize their potential life span than mainland counterparts. One can therefore expect an unusually long time lapse between generations and a larger proportion of post-reproductive animals in the population (Cole, 1954). All of these features are characteristic of species adapted to exist near the environment's carrying capacity (K), influenced by an array of selection pressures (K-selection) different from those of species which frequently experience periods of population depletion and expansion (r-selection). Such correlations between population phenomena and ecological conditions have received a great deal of attention in recent years (e.g., see MacArthur, 1972; Pianka, 1974; Wilbur et al, 1974; Hirshfield & Tinkle, 1975; Wilson, 1975).

These demographic data contain highly significant implications for management of the Mona Iguana and other species sharing these characteristics. Such populations are particularly susceptible to disturbance, and recovery will be inherently slow. Management measures must therefore be implemented before the population declines to a dangerously small size. The smaller the population, the more likely the

total reproductive output by adult females will be insufficient to overcome the sum of environmental resistance (from natural and unnatural sources) against eggs and juveniles. Juveniles, because of their slow growth, will be exposed to predation from small introduced carnivores like house cats for a prolonged period of time. Furthermore, reproductive patterns and behaviors that are finely tuned to the specific ecological conditions of the island where the population evolved may not be suitable for long-term survival elsewhere. Thus management is most likely to be successful if directed at restoring natural conditions to the iguana's native island, unless, of course, the habitat has been irreparably damaged. Attempts to translocate the species to other islands are likely to fail, and failure may require more than a century to express itself.

On Mona, man-induced mortality of adults does not appear to be a significant decimating factor at this time; nevertheless, intensified human use compounded by careless planning and management could quickly change the status quo. During the course of this investigation, 12 Mona iguanas were found dead or dying (Table 29), 10 of these being in areas heavily used by visitors. At least half of these deaths are definitely attributable to man. Two additional animals were injured by vehicles (only two of which were then in operation on the island), possibly resulting in their deaths as well. The iguanas are no match for a speeding truck or a frustrated hunter.

I attribute Mona's low iguana density and seemingly inadequate representation of juveniles to the combined effects of predation from

Table 29.--- Summary of casualties to Mona Iguanas recorded between May 1972 and August 1974.

Class	Nature of Casualty	Locality	Date
Adult male	Killed by vehicle	Paved track to lighthouse	16 Sept. 1972
Adult male	Killed by vehicle	Paved track to lighthouse	6 Feb. 1973
?	Injured by vehicle---fate unknown	Paved track to lighthouse	18 July 1973
?	Injured by vehicle---fate unknown	El Camino del Diablo	20 May 1973
?	Shot in the head	Bajura de los Cerezos	29 Dec. 1973
?	Drowned	In old concrete trough at Playa de Pájaros	23 Sept. 1972
Adult male	Found dying with deep body lacerations	Playa de Pájaros	19 May 1972
Adult male	Found dying with deep body lacerations	Playa de Pájaros	July 1974
Gravid female	Unknown---found rotten	Punta Arenas	August 1973
?	Unknown---found rotten	By trail behind lighthouse	1 June 1972
Adult male	Unknown---found rotten	On coastal terrace between Cueva Escalera and Cueva del Lirio	10 Aug. 1972
Adult male	Unknown---no external wounds	Below Cueva del Lirio	July 1974

Table 29 (Continued)

Class	Nature of Casualty	Locality	Date
Adult male	Seen alive but weak, with one eye out; later found dead	Sardinera	25 June 1973
Hatchling	Apparently poisoned--found dying near bar of soap and "frothing at the mouth"	Pozo Portugués	16 Nov. 1972

introduced mammals and a history of disturbance to the few significant nesting areas. Because of the island's paucity of soil, less than 1% of its surface area is suitable for nesting. From the standpoint of human comfort, access to the sea, and agricultural possibilities, pre- and post-Columbian settlers (see Table 27) necessarily concentrated their development along the coastal terraces and within the larger sinkhole depressions, exactly where iguanas migrate for nesting. In addition, the coastal "Jaucas" sand deposits (see Rivera, 1973) between Sardinera and the airstrip, which may well have represented the largest nesting ground on the island at one time, is now forested with shade trees (Casuarina and Mahogany) planted by the Civilian Conservation Corps in the 1930's. Mona's enchanting upland "bajuras" (sinks) and southern beachfront zones have continued to attract visitors to the iguana's prime nesting areas. This conflict of interests between man and iguanas can be successfully resolved only through thoughtful planning and careful management.

When nesting, females of this species seek accumulations of stable but non-rocky soil with a sunny exposure and nearby cover (this last requirement has probably become important only since the coming of man). Unlike the common Green Iguana, Iguana iguana (see Hirth, 1963b), and the Marine Iguana, Amblyrhynchus cristatus (see Carpenter, 1966), the Mona Iguana will not nest on beaches. Most nesting occurs in clearings within the larger sinkholes and particularly in scrubby or grassy areas adjacent to beaches or woods along the southwestern and southeastern coasts (see Fig. 1). Of those upland nesting areas within the large

sinkhole depressions, the most heavily used is Los Corrales de los Indios (a collective reference to El Corral proper plus the smaller bajuras which border the same escarpment). Because much of the soil in La Bajura de los Cerezos is apparently too rocky or heavily shaded to suit the iguanas, relatively little nesting occurs there--of all the larger bajuras, this is the least valuable in terms of iguana nesting and is fortunately the one most accessible to visitors. The coastal terraces hold the island's most extensive deposits of workable soil, much of which is compacted sand, but this, too, is confined to a few areas. On the SW coastal plain, apparently the largest single expanse of land edaphically suitable for nesting extends from the beachside area adjacent to the airstrip north to Sardinera, much of which, as already stated, is now forest plantation. Even today, nesting is concentrated in this portion of the island. Subsequent sightings on the plateau of two nesting females tagged near Punta Arenas suggest that these animals migrate considerable distances to reach favorable nesting areas (see Daily & Seasonal Activities--Asocial).

Karstified limestone terrain characteristically has little surface soil (LeGrand, 1973); this is the principal habitat type of cycluran iguanas, suggesting that populations other than Mona's share similar limitations. Comments by Lewis (1944) indicate such similarities for three other West Indian iguanas: C. collei of Jamaica, C. nubila lewisi of Grand Cayman, and C. n. caymanensis of Cayman Brac and Little Cayman.

This early French naturalist [duTertre] relates that Cyclura come down from the mountains during May to lay 13 to 25 eggs in a heap in the sand on the sea-shore. C. caymanensis was found to

conform to those observations....On Grand Cayman, Cyclura macleayi lewisi [=C. nubila lewisi] is said to have been common in former years along the north coast... where there is a wide sandy coastal shelf. The people hunted the species for food, and in one way or another the population has been greatly reduced. According to the evidence of our searches in 1938, the species no longer frequents the coast,--not even during the breeding season--but digs nests in the earth [red phosphatic clay] in the more or less secure uninhabited east central portion of Grand Cayman.

Lewis stated further that the only evidence of past nesting by C. collei on Great Goat Island was found in the "red earth" near the island's coastal mangrove swamp. The critical question which persists above all is how many, if any, of the iguanas surviving in the rugged interiors of these islands have continued to nest successfully. Migration in itself indicates the important role these soil-rich coastal areas have played in the populations's evolutionary history. On a portion of Andros I., Bahamas, where iguanas (C. cychlura) have no soil available, eggs are laid in the large termite nests there (Auffenberg, pers. comm.). Females on Mona commonly dig in soil-filled potholes on the plateau to attempt nesting, but the majority of those efforts are abandoned. The only nest I uncovered that was completed in this type of a situation suffered total mortality from an apparently natural cause, probably overheating or desiccation.

Privacy from man is of utmost importance to the nesting females. Compared to males, female C. stejnegeri are extremely shy, and the nesting process is easily disrupted. During the searching and digging phases, an iguana unable to find seclusion in an otherwise choice

location can be expected to move on and settle for a less desirable site. Persons walking through nesting areas may inadvertently cause casualties to females in the act of laying by causing burrows to collapse; deaths due to entrapment of this nature have been recorded for both Marine and Green Iguanas (Carpenter, 1966; Rand, 1968a). Even a single disturbance to a female in the act of filling her hole or guarding the site may result in complete abandonment of the nest. An unfilled passage would leave the eggs vulnerable to desiccation, overheating, and predation by animals such as birds, crabs, rats, or insects, that would normally be no problem. An undefended nest gives egg-laden females nesting subsequently at the same site the opportunity for easy digging in already loosened ground, an energy saving for the newcomer that is likely to result in total or partial damage to the first female's eggs.

As the nesting season draws to a close, females disperse from nesting areas and the eggs must incubate for about three months without parental care. Aside from the presently sizable losses of eggs to predation by pigs, nest cave-ins due to trampling pose a serious threat. Females refill the passage leading to the egg chamber, but they never cover the eggs with soil. The weight of a person or large animal over the nest will collapse this underground air space, which is vital to the proper development, hatching, and emergence of the young. It is probable that goats have been causing physical damage of this sort to nests within the bajuras on the plateau.

Captive breeding is not a viable alternative to protecting and improving natural nesting possibilities on Mona; nevertheless, such

endeavors should be encouraged to help minimize collecting from the wild population. These iguanas are of great public and scientific interest within and beyond Puerto Rico, and well designed small-scale breeding programs can, if successful, provide a supply of animals for exhibition in zoos and additional opportunities for research. We have a great deal to learn about captive breeding of reptiles. The San Diego Zoological Garden has maintained and bred Rhinoceros Iguanas, C. cornuta, for a number of years, yet despite their considerable experience in reptile-keeping, only 12 of 50 eggs laid survived through hatching (Shaw, 1969). Haast (1969) reported high hatching success for one of several clutches laid at the Miami Serpentarium but gave no information concerning methodology. For exhibition purposes, Cyclura are usually housed with other large lizards, including egg-predators, a policy clearly counter-productive to propagation in captivity. Furthermore, attempts to maintain Cyclura in captivity typically result in premature death; the maximum zoo longevity records published for the genus are 6 to 7.5 years (for C. cornuta in all cases--Carey, 1973). Weaknesses in our present understanding of the requirements of these unusual animals are evident.

It has become increasingly clear that the future well-being of mankind will depend largely upon how skillfully and harmoniously we can merge with our natural environments. The real challenge is to develop and apply scientific understanding rapidly enough to keep ahead of the losses. In this race against time, we have thus far made a very poor showing in the conservation of West Indian iguanas and the ecosystems of which they are an integral part. In general, scientific understanding of

Caribbean ecosystems, as densely populated as they are, is pathetically weak, and public understanding is consequently nonexistent. This is a particularly dangerous combination, for although people usually agree that the essence of conservation, i.e., saving something for the future, is intrinsically good, few can be readily converted to live by this ethic if something must in the process be sacrificed today. For this reason adjunct programs for environmental education and enforcement of regulations are essential. Time has remained the critical factor; thus the only practical approach to many conservation problems is to establish strictly managed wildlife sanctuaries in areas that are still relatively undisturbed, where it is possible to restore or preserve a complete ecosystem.

Mona Island offers just such an opportunity, and none could be more appropriate. Compared with other islands of its kind, Mona shows an impressive biological wealth, both terrestrial and marine, in an exceptionally pollution-free and manageable environment. In addition to the large representation of endemic species, many plants and animals rare, endangered, or absent on the Puerto Rican mainland are abundant on Mona. The iguana population is still sufficiently large and viable that complete recovery can be anticipated under careful management, and ecological degradation from introduced mammals has not yet progressed to a point of no return. Mona is also small enough and distant enough from its neighbors to give it the relative biological simplicity desirable for studies of structural and functional inter-relationships. It clearly has the potential to support a wide range of long-term environmental

research from which guidelines for the management and ecological rehabilitation of other Caribbean islands could be derived. The island is of additional geological, historical, and recreational attraction. It is aesthetically magnificent. Furthermore, Mona is entirely government owned, has no permanent residents, and access can be easily controlled due to the island's unusual physiography. Monito, Mona's tiny sister sea-bird island, is a valuable extension of the Mona ecosystem, and the two should be considered an inseparable whole.

Mona has reached a critical point in its history: it must be whole-heartedly saved now or its special character and intrinsic values will be lost forever. Aside from repeated threats from government-generated land-use proposals, weekend and holiday visitation has reached proportions which are alarming in the face of a laissez faire management policy. Visitor numbers have more than quadrupled over the past eight years. In 1974, 100-125 visitors typically flocked to the island on short holiday weekends, and during Holy Week, I estimated a total of 350, with use highly concentrated in beachside areas. Almost all visitors are Puerto Ricans, Puerto Ricans who share a growing desire to venture away from their overcrowded industrializing homeland, even for a few brief hours or days each year. The relative proportion of those coming to hunt for sport has dropped considerably, while the representation of high school and college students coming for camping, swimming, and hiking in an unspoiled natural setting has risen sharply. Unfortunately the wildlife (including reef communities), the cave formations, and the archaeological treasures are particularly vulnerable to human

abuse and already show signs of unnecessary wear. It is to be hoped that a stable administrative framework will soon be found to provide Mona with adequate protection and maintenance as a unique natural area for future educational, scientific, and recreational pursuits.

Recommendations.--

1. Nesting and incubation phases of the Mona Iguana's life cycle are extremely susceptible to direct interference from man.

Accordingly, I recommend that:

- A. No new facilities should be constructed in or near important nesting areas.
- B. No camping should be permitted in or near these areas between 7 July and 15 November; (in particular, the following camping areas now receiving heavy to moderate visitor use should be closed during this period: the entire Cabo Oeste area, including Punta Arenas and Carite; Carabinero; the zone adjacent to Playa Uvero; and El Corral de los Indios).
- C. Visitor distribution should be regulated by limiting camping on the coastal terraces to sites officially approved by management staff (this could perhaps be achieved in an unobtrusive manner by providing fireplaces and other primitive camping facilities only in places where the impact will be minimal).
- D. No fences should be erected that might hamper movement of females to coastal or sinkhole areas during nesting migrations.

- E. Research projects, e.g., archaeological digs, in or near nesting areas should be deferred to the nonreproductive season.
 - F. All types of cross-country vehicles should be prohibited.
 - G. If the services of trail animals like horses or mules find a place in the management program, they should be kept away from nest sites to prevent trampling.
 - H. No pets should be permitted on Mona.
2. The Casuarina and Mahogany plantation zone between the beach and the road extending from the airstrip to Sardinera should not be reforested when the present trees die or are harvested. Clearing away small patches of forest rather than overall thinning would benefit iguana nesting the most. Open clearings will probably be avoided by iguanas until protective cover from secondary growth has developed. For this reason accumulated debris that could offer shelter to nesting females should not be burned or removed.
 3. All collecting of iguanas should be rigidly controlled. Capturing and removing iguanas from Mona should continue on a permit-only basis, with preference to organizations with approved facilities for a breeding program.
 4. To minimize road casualties, trails should be emphasized, improved roads limited, and speed limits set very low; no private vehicles should be allowed.
 5. Visitors and especially all persons working or living on

Mona should be well informed about the habits, requirements, and uniqueness of these iguanas. This could be facilitated through informative handouts, but environmental education must begin in the elementary schools.

6. Control of introduced mammals is crucial and should be undertaken in the immediate future.

LITERATURE CITED

- Allan, J.D., L.W. Barnthouse, R.A. Prestbye, and D.R. Strong. 1973. On foliage arthropod communities of Puerto Rican second growth vegetation. *Ecology* 54:628-632.
- Allen, G.M. 1937. Geocapromys remains from Exuma Island. *J. Mamm.* 18:369-370.
- Alvarez del Toro, M. 1972. Los Reptiles de Chiapas. Gobierno del Estado Chiapas, Tuxtla Gutierrez, Mexico. 179 p.
- Andrews, R.M. 1976. Growth rate in island and mainland anoline lizards. *Copeia* 1976(3):477-482.
- Anthony, H.W. 1926. Mammals of Porto Rico, living and extinct--Rodentia and Edentata. N.Y. Acad. Sci., Scient. Surv. Porto Rico and Virgin Islands 9:24-29.
- Arber, Edward. 1910. Travels and Works of Captain John Smith, President of Virginia, and Admiral of New England, 1580-1631. John Grant, Edinburgh. 984 p.
- Atkinson, I.A.E. 1964. Relations between feral goats and vegetation in New Zealand. *Proc. N.Z. Ecol. Soc.* 11:39-44.
- Auffenberg, W. 1975. The dragon isles: West Indian rock iguanas. *Bahamas Naturalist* 1:2-7.
- _____. 1976. Rock iguanas, Part II. *Bahamas Naturalist* 2:9-16.
- Avery, D.F., and W.W. Tanner. 1971. Evolution of the iguanine lizards (Sauria, Iguanidae) as determined by osteological and myological characters. *Brigham Young Univ. Sci. Bull., Biol. Ser.*, 12:1-79.

- Baker, H.G., and I. Baker. 1973. Amino-acids in nectar and their evolutionary significance. *Nature* 241:543-545.
- Baker, J.K. and D.W. Reeser. 1972. Goat management problems in Hawaii Volcanoes National Park; a history, analysis, and management plan. U.S.D.I. Nat. Resour. Rept. No. 2, 22 p.
- Barbour, T. 1919. A new rock iguana from Porto Rico. *Proc. Biol. Soc. Wash.* 32:145-148.
- _____, and G.K. Noble. 1916. A revision of the lizards of the genus Cyclura. *Bull. Mus. Comp. Zool.* 60:139-164.
- Barlow, G.W. 1967. Social behavior of a South American leaf fish, Polycentrus schomburgkii, with an account of recurring pseudofemale behavior. *Amer. Midl. Natur.* 78:215-234.
- Barrett, R.H. 1971. Ecology of the Feral Hog in Tehama County, California. Ph.D. Dissertation. Univ. California, Berkeley. 345 p.
- _____. 1973. Current research on feral pigs in northern Australia. Unpubl. report, C.S.I.R.O. Div. Wildlife Res., Australia. 4 p.
- Bartholomew, G.A., A.F. Bennett, and W.R. Dawson. 1976. Swimming, diving and lactate production of the Marine Iguana, Amblyrhynchus cristatus. *Copeia* 1976(4):709-720.
- Beever, R.E., and J.E. Beever. 1969. Studies on the vegetation of Cuvier Island, II. Structure of the forest. *Tane* 15:69-74.
- _____, B.S. Parris, and J.E. Beever. 1969. Studies on the vegetation of Cuvier Island, I. The plant communities and a vascular plant species list. *Tane* 15:53-68.
- Bent, A.C. 1937. Life histories of North American birds of prey (Part 1). *Bull. U.S. Nat. Mus.* 167:1-409.

- _____. 1938. Life histories of North American birds of prey (Part 2). Bull. U.S. Nat. Mus. 170:1-482.
- Berry, K.H. 1974. The ecology and social behavior of the chuckwalla, Sauromalus obesus obesus Baird. Univ. Calif. Publ. Zool. 101:1-60.
- Blanc, C.P., and C.C. Carpenter. 1969. Studies on the Iguanidae of Madagascar III. Social and reproductive behavior of Chalarodon madagascariensis. J. Herpetol. 3:125-134.
- Bowie, A., and R. Franz. 1974. Cyrtosomum mega sp. n. (Nematoda: Oxyuroidea) from the lizard, Cyclura carinata. J. Parasitol. 60: 628-631.
- Bratton, S.P. 1974a. An integrated ecological approach to the management of the European Wild Boar (Sus scrofa) in Great Smoky Mountains National Park. Unpubl. Rept. Natl. Park Serv. 42 p.
- _____. 1974b. The effect of the European Wild Boar (Sus scrofa) on the high-elevation vernal flora in Great Smoky Mountains National Park. Bull. Torrey Bot. Club 101:198-206.
- Brattstrom, B.H. 1971. Social and thermoregulatory behavior of the Bearded Dragon, Amphibolurus barbatus. Copeia 1971(3):484-497.
- _____. 1974. The evolution of reptilian social behavior. Amer. Zool. 14:35-49.
- Briggs, R.P., and V.M. Seiders. 1972. Geologic map of the Isla de Mona quadrangle, Puerto Rico. Misc. Geol. Invest., U.S.G.S., Map I-718.
- Britton, N.L. 1915. The vegetation of Mona Island. Mo. Bot. Gard. Ann. 2:33-56.

- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-169.
- _____. 1975. *The Evolution of Behavior*. W.W. Norton and Co., Inc., New York. 761 p.
- Brown, L., and D. Amadon. 1968. *Eagles, Hawks, and Falcons of the World*. Vols. I and II. McGraw-Hill Book Co., New York. 945 p.
- Brown, W.S., and W.S. Parker. 1976. Movement ecology of Coluber constrictor near communal hibernacula. *Copeia* 1976(2):225-242.
- Buide, M.S. 1951. Observations on the habits of the Cuban iguana. *Herpetologica* 7:124.
- Burghardt, G., H.W. Greene, and A.S. Rand. 1977. Social behavior in hatchling Green Iguanas: Life at a reptile rookery. *Science* 195:689-691.
- Calvesbert, R.J. 1973. The climate of Mona Island, Appendix A. In: *Isla Mona*, Vol. II. Environ. Qual. Bd., San Juan, P.R.
- Constantz, G.D. 1975. Behavioral ecology of mating in the male Gila Topminnow, Poeciliopsis occidentalis (Cyprinodontiformes: Poeciliidae). *Ecology* 56:966-973.
- Carey, W.M. 1966. Observations on the ground iguana Cyclura macleayi caymanensis on Cayman Brac, British West Indies. *Herpetologica* 22:265-268.
- _____. 1973. Some notable longevity records for captive iguanas. *Int. Zoo Yearbook* 13:154-156.
- _____. 1975. The rock iguana, Cyclura pinguis, on Anegada, British Virgin Islands, with notes on Cyclura ricordi and Cyclura

- cornuta on Hispaniola. Bull. Fla. State Mus., Biol. Sci. 19(4): 189-233.
- _____. 1976. Iguanas of the Exumas. Wildlife (Feb.):59-61.
- Carlquist, Sherwin. 1965. Island Life. Natural History Press, Garden City, N.Y. 451 p.
- _____. 1974. Island Biology. Columbia Univ. Press, N.Y. 660 p.
- Carpenter, C.C. 1966. The marine iguana of the Galápagos Islands, its behavior and ecology. Proc. Calif. Acad. Sci. 34:329-376.
- _____. 1967. Aggression and social structure in iguanid lizards, pp. 87-105. In: Lizard Ecology, a Symposium. W.W. Milstead (ed.). Univ. Missouri Press, Columbia.
- Carr, Archie. 1973. So Excellent a Fishe. Anchor Press/Doubleday, Garden City, N.Y. 266 p.
- _____, and H. Hirth. 1961. Social facilitation in Green Turtle siblings. Anim. Behav. 9:68-70.
- Case, T.J. 1976. Seasonal aspects of thermoregulatory behavior in the chuckwalla, Sauromalus obesus (Reptilia, Lacertilia, Iguanidae). J. Herpetol. 10(2):85-95.
- Cintrón, B. 1976. Some effects of goat browsing on the natural vegetation of Mona Island. In: Tercer Simposio sobre los Recursos Naturales de Puerto Rico. P.R. Dept. of Natural Resources, San Juan. In Preparation.
- _____, and Lee Rogers. 1974. Plant communities of Mona Island. Unpubl. final rept., U.S.D.I. Bur. Sport Fish. Wildl. Proj. W-8-17, Study III, Job 1, Atlanta, Ga. 54p.

- Clough, G.C. 1972. Biology of the Bahaman Hutia, Geocapromys ingrahami. J. Mammal. 53:807-823.
- _____. 1974. Additional notes on the biology of the Bahamian Hutia. J. Mammal. 55:670-672.
- _____, and G. Fulk. 1971. The vertebrate fauna and the vegetation of East Plana Cay, Bahama Islands. Atoll Res. Bull. (138):1-17.
- Coblentz, B.E. 1974. Ecology, Behavior, and Range Relationships of the Feral Goat. Ph.D. Dissertation. Univ. Michigan, Ann Arbor. 274 p.
- Cole, C.J. 1966. Femoral glands in lizards: a review. Herpetologica 22:199-206.
- Cole, L.C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29:103-137.
- Comfort, A. 1961. The life span of animals. Scient. Amer. 205:108-119.
- Cowles, R.B., and C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. 83: 261-296.
- Crews, D. 1973. Coition-induced inhibition of sexual receptivity in female lizards (Anolis carolinensis). Physiol. Behav. 11:463-468.
- _____. 1975. Psychobiology of reptilian reproduction. Science 189:1059-1065.
- Cruxent, J.M., and I. Rouse. 1969. Early man in the West Indies. Sci. Amer. 221(5):42-52.
- Cummins, K.W. 1967. Calorific equivalents for studies in ecological energetics. Mimeo from Pymatuning Laboratory of Ecology, Univ. Pittsburgh. 51 p.

- Daanje, A. 1950. On locomotory movements in birds and the intention movements derived from them. *Behaviour* 3:48-98.
- Darlington, P.J. 1938. The origin of the fauna of the Greater Antilles with discussion of dispersal of animals over water and through air. *Quart. Rev. Biol.* 13:274-300.
- Darwin, C. 1889. *A Naturalist's Voyage*. John Murray, London. 615 p.
- Dawson, W.R. 1967. Interspecific variation in physiological responses of lizards to temperature, pp. 230-257. *In: Lizard Ecology, A Symposium*. W.W. Milstead (ed.). Univ. Missouri Press, Columbia.
- Denney, R.N. 1974. The impact of uncontrolled dogs on wildlife and livestock, pp. 257-291. *In: Trans. 39th N. Amer. Wildl. and Nat. Resour. Conf. Wildlife Mgmt. Inst., Washington, D.C.*
- Devine, M.C. 1975. Copulatory plugs in snakes: enforced chastity. *Science*:844-845.
- Dewitt, C.B. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana, Dipsosaurus dorsalis. *Physiol. Zool.* 40:49-66.
- Donn, W.L., W.R. Farrand, and M. Ewing. 1962. Pleistocene ice volumes and sea-level lowering. *J. Geol.* 70:206-214.
- Dowling, H.G. 1964. Goats and hawks--a new theory of predation on the land iguana. *Animal Kingdom* 67:51-56.
- Dubuis, A., L. Faurel, C. Grenot, and R. Vernet. 1971. Sur le regime alimentaire du lezard saharien Uromastix acanthinurus Bell. *C.R. Acad. Sci. (Paris) Ser. D*, 273:500-503.
- Dunne, H.W. 1970. Hog cholera, p. 177-239. *In: Diseases of Swine* (3rd Ed.). H.W. Dunne (ed.). Iowa State Univ. Press, Ames.

- Eckhardt, R.C. 1972. Introduced plants and animals in the Galápagos Islands. *BioScience* 22(10):585-590.
- Eibl-Eibesfeldt, I. 1966. Das Verteidigen der Eiablageplätze bei der Hood-Meerechse (Amblyrhynchus cristatus venustissimus). *Z. Tierpsychol.* 27:127-131.
- Emiliani, C., S. Gartner, and B. Lidz. 1972. Neogene sedimentation on the Blake Plateau and the emergence of the Central American isthmus. *Palaeogeog., Paleoclim., Palaeoecol.* 11:1-10.
- Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- Estes, R., and L.I. Price. 1973. Iguanid lizard from the Upper Cretaceous of Brazil. *Science* 180:748-751.
- Etheridge, R. 1964. Late Pleistocene lizards from Barbuda, British West Indies. *Bull. Fla. State Mus., Biol. Sci.* 9(2):43-75.
- _____. 1966. Pleistocene lizards from New Providence. *Quart. J. Fla. Acad. Sci.* 28:349-358.
- Evans, L.T. 1951. Field study of the social behavior of the black lizard, Ctenosaura pectinata. *Amer. Mus. Novitates* (1493):1-26.
- Ewel, J.J., and J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. *U.S.D.A. For. Serv. Res. Pap.* ITF-18:1-72.
- Fellers, G.M. 1975. Behavioral interactions in North American treefrogs (Hylidae). *Chesapeake Sci.* 16:218-219.
- Ferguson, G.W. 1966. Releasers of courtship and territorial behavior in the side-blotched lizard Uta stansburiana. *Anim. Behav.* 14:89-92.
- _____. 1971. Variation and evolution of the push-up displays

- of the side-blotched lizard genus Uta (Iguanidae). Syst. Zool. 20:79-101.
- Fitch, H.S. 1940. A field study of the growth and behavior of the fence lizard. Univ. Calif. Publ. Zool. 44:151-172.
- _____. 1973a. A field study of Costa Rican lizards. Univ. Kan. Sci. Bull. 50(2):39-126.
- _____. 1973b. Population structure and survivorship in some Costa Rican lizards. Occ. Pap. Mus. Nat. Hist. Univ. Kansas (18): 1-41.
- _____, and R.W. Henderson. 1976. Age and sex differences in the ctenosaur (Ctenosaura similis). Unpubl. manuscript. 14 p.
- Fleet, R.R., and H.S. Fitch. 1974. Food habits of Basiliscus basiliscus in Costa Rica. J. Herpetol. 8:260-262.
- Freeland, W.J., and D.H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Amer. Natur. 108:269-289.
- Gibson, A.R., and J.B. Falls. 1975. Evidence for multiple insemination in the common garter snake, Thamnophis sirtalis. Canadian J. Zool. 53:1362-1368.
- Giffin, J. 1970. Feral game mammal survey. Unpubl. job completion rept. P-R Proj. W-5-R-21 Job 46(21), Bur. Sport Fish. Wildl., U.S.D.I. 14 p.
- Golley, F.B. 1961. Energy values of ecological materials. Ecology 42: 581-584.
- _____. 1969. Caloric value of wet tropical forest vegetation. Ecology 50:517-519.

- Gonzales, R.B. 1974. Behavioral notes on captive Sail-tailed Lizards (Hydrosaurus pustulosus: Agamidae). Silliman J. 21:129-138.
- Gorman, G.C., and P. Licht. 1974. Seasonality in ovarian cycles among tropical Anolis lizards. Ecology 55:360-369.
- Gosse, P.H. 1848. On the habits of Cyclura lophoma, an iguaniform lizard. Proc. Zool. Soc. London 16:99-104.
- Grant, C. 1940. The herpetology of the Cayman Islands. Bull. Inst. Jamaica, Sci. Ser. 2:1-65.
- _____. 1944. Cyclura stejnegeri--A portrait. Herpetologica 2:139-140.
- Grubb, P. 1971. The growth, ecology, and population structure of giant tortoises on Aldabra. Phil. Trans. Roy. Soc. London B, 260:327-372.
- Haast, W.E. 1969. Hatching rhinoceros iguanas Cyclura cornuta at the Miami Serpenterium. Int. Zoo Yearbook 9:49.
- Hackforth-Jones, J. 1976. The egg deposition burrows of the ctenosaur, Ctenosaura similis. Unpubl. manuscript. 18 p.
- Hamann, Ole. 1975. Vegetational changes in the Galápagos Islands during the period 1966-73. Biol. Conser. 7:37-59.
- Hardy, J.D. 1956. Notes on the Cuban iguana. Herpetologica 12:323-324.
- Harris, V. 1964. The Life of the Rainbow Lizard. Hutchinson and Co., Ltd., London. 174 p.
- Henderson, R.W. 1973. Ethoecological observations of Ctenosaura similis (Sauria: Iguanidae) in British Honduras. J. Herpetol. 7(1):27-33.
- _____. 1974. Aspects of the ecology of the juvenile common iguana (Iguana iguana). Herpetologica 30:327-332.

- Hirshfield, M.F., and D.W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. *Proc. Nat. Acad. Sci., U.S.A.* 72:2227-2231.
- Hirth, H.F. 1963a. The ecology of two lizards on a tropical beach. *Ecol. Mon.* 33(2):83-112.
- _____. 1963b. Some aspects of the natural history of Iguana iguana on a tropical strand. *Ecology* 44:613-615.
- Hnatiuk, R.J., S.R.J. Woodell, and D.M. Bourn. 1976. Giant tortoise and vegetation interactions on Aldabra Atoll--Part II: Coastal. *Biol. Conser.* 9(4):305-316.
- Hobson, E.S. 1969. Remarks on aquatic habits of the Galápagos marine iguana, including submergence times, cleaning symbiosis, and the shark threat. *Copeia* 1969(2):401-402.
- Horsfield, W.T. 1975. Quaternary vertical movements in the Greater Antilles. *Bull. Geol. Soc. Amer.* 86:933-938.
- Howard, W.E. 1966. Control of introduced mammals in New Zealand. *N.Z. Dept. Sci. Industr. Res. Inf. Ser.* (45):1-96.
- Howell, D.J. 1974. Bats and pollen: physiological aspects of the syndrome of chiropterophily. *Comp. Biochem. Physiol.* 48A:263-276.
- Hübener, Dr. Th. 1898. Die Inseln Mona und Monito. *Globus* 74:368-372.
- Huey, R.B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184:1001-1002.
- Hunsaker, D., II. 1962. Ethological isolating mechanisms in the Sceloporus torquatus group of lizards. *Evolution* 16:62-74.
- Iverson, John. 1977. Behavior and Ecology of the Rock Iguana Cyclura

- carinata. Ph.D. Dissertation, Univ. Florida, Gainesville. 379 p.
- Janzen, D.H. 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2:465-492.
- _____. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687-708.
- Jenssen, T.A. 1971. Display analysis of Anolis nebulosus (Sauria, Iguanidae). *Copeia* 1971(2):197-209.
- _____. 1977. Evolution of anoline lizard display behavior. *Amer. Zool.* 17:203-215.
- Jordan, D.G. 1973. A summary of actual and potential water resources of Isla de Mona, Puerto Rico, Appendix D. In: Isla Mona, Vol. II. Environ. Qual. Bd., San Juan, P.R.
- Kästle, W. 1964. Verhaltenstudien an Taggeckonen der Gattungen Lygodactylus und Phelsuma. *Z. Tierpsychol.* 21(4):486-507.
- _____. 1967. Soziale Verhaltensweisen von Chamaleonen aus der pumilus- und bitaeniatus-Gruppe. *Z. Tierpsychol.* 24:313-341.
- Kaye, C.A. 1959. Geology of Isla Mona, Puerto Rico, and notes on the age of the Mona Passage. *U.S. Geol. Surv. Prof. Pap.* 317-C:141-178.
- Kramer, Peter. 1973. Wildlife conservation in the Galápagos Islands (Ecuador). *Nature and Resources* 9(4):3-10.
- Lando, R.V., and E.E. Williams. 1969. Notes on the herpetology of the U.S. Naval Base at Guantánamo Bay, Cuba. *Stud. Fauna Curacao and other Caribbean Is.* 31:159-201.
- Lawson, A.P. 1967. Ecology of feral goats and feral pigs of Mona

- Island, Puerto Rico. M.S. Thesis. Colorado State Univ., Ft. Collins. 62 p.
- LeBoeuf, B.J. 1974. Male-male competition and reproductive success in Elephant Seals. *Amer. Zool.* 14:163-176.
- LeGrand, H.E. 1973. Hydrological and ecological problems of karst regions. *Science* 179(4076):859-864.
- Lewis, C.B. 1944. Notes on Cyclura. *Herpetologica* 2:93-98.
- Licht, P., and W.R. Moberly. 1965. Thermal requirements for embryonic development in the tropical lizard Iguana iguana. *Copeia* 1965(4): 515-517.
- Little, E.L., Jr. 1955. Trees of Mona Island. *Caribbean For.* 16:36-53.
- _____, and F.H. Wadsworth. 1964. Common Trees of Puerto Rico and the Virgin Islands. U.S.D.A., Washington. 548 p.
- MacArthur, R.H. 1972. Geographical Ecology--Patterns in the Distribution of Species. Harper and Row, N.Y. 269 p.
- MacFarland, C.G., José Villa, and Basilio Toro. 1974a. The Galápagos giant tortoises (Geochelone elephantopus), Part I: status of the surviving populations. *Biol. Conserv.* 6(2):118-133.
- _____. 1974b. The Galápagos giant tortoises (Geochelone elephantopus), Part II: conservation methods. *Biol. Conserv.* 6(3):198-212.
- Marler, P. 1960. Bird songs and mate selection, pp. 348-367. In: *Animal Sounds and Communication*. W.E. Lanyon & W.N. Tavolga (eds.). Amer. Inst. Biol. Sci., Washington.
- Martin, A.C., H.S. Zim, and A.L. Nelson. 1951. *American Wildlife and*

- Plants: A Guide to Wildlife Food Habits. Dover Publications, Inc., New York. 500 p.
- Martin, F.W. 1966. Collecting the cacti of Mona Island. Cactus and Succulent J. 38:122-126.
- Mautz, W.J. 1976. Resource partitioning by lizards in a cave habitat, Abstract. Herp. Review 7:91.
- Mayhew, W.W. 1963. Some food preferences of captive Sauromalus obesus. Herpetologica 19:10-16.
- Menge, B.A., and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Amer. Natur. 110:351-369.
- Merton, L.F.H., D.M. Bourn, and R.J. Hnatiuk. 1976. Giant tortoise and vegetation interactions on Aldabra Atoll--Part I: Inland. Biol. Conserv. 9(4):293-304.
- Miller, G.S. 1918. Mammals and reptiles collected by Theodoor de Booy in the Virgin Islands. Proc. U.S. Nat. Mus. 54:507-511.
- Mirsky, E.N. 1976. Song divergence in hummingbird and junco populations on Guadalupe Island. Condor 78:230-235.
- Moberly, W.R. 1968. The metabolic responses of the common iguana, Iguana iguana, to activity under restraint. Comp. Biochem. Physiol. 27:1-20.
- Montanucci, R.R. 1968. Comparative dentition in four iguanid lizards. Herpetologica 24:305-315.
- Montgomery, G.G., A.S. Rand, and M.E. Sunquist. 1973. Post-nesting movements of iguanas from a nesting aggregation. Copeia 1973(3): 620-622.

- Moore, L.B., and L.M. Cranwell. 1934. Induced dominance of Microlaena avenacea (Raoul) Hook. f., in a New Zealand rain-forest area. Rec. Auckland Inst. Mus. 1:219-238.
- Moran, R. 1967. Discussions of the flora of Guadalupe Island, pp. 69-71. In: Proceedings of the Symposium on the Biology of the California Islands. R.N. Philbrick (ed.). Santa Barbara Bot. Gard., California.
- Morison, S.E. 1942. Admiral of the Ocean Sea - A Life of Christopher Columbus. Little, Brown, and Co., Boston.
- Morris, D. 1952. Homosexuality in the Ten-spined Stickleback (Pygosteus pungitius). Behaviour 4:233-261.
- Morton, E.S. 1972. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. Amer. Natur. 107:8-22.
- Mueller-Dombois, D., and G. Spatz. 1972. The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. Island Ecosys. IRP/U.S. Internatl. Biol. Prog. Tech. Rept. No. 13, 46 p.
- Müller, H. 1972. Ökologische und ethologische Studien an Iguana iguana L. (Reptilia: Iguanidae) in Kolumbien. Zool. Beit. Breslau 18: 109-131.
- Noble, G.K. 1923. Trailing the Rhinoceros Iguana. Nat. Hist. 23(6): 540-558.
- _____ and H.T. Bradley. 1933. The mating behavior of lizards; its bearing on the theory of sexual selection. Ann. New York Acad. Sci. 35:25-100.
- _____ and H.K. Teale. 1930. The courtship of some iguanid and teiid lizards. Copeia 1930(2):54-56.

- Oelrich, T.M. 1956. The anatomy of the head of Ctenosaura pectinata (Iguanidae). Misc. Publ. Mus. Zool. Univ. Mich. (94):1-122.
- Ostrom, J.H. 1963. Further comments on herbivorous lizards. Evolution 17:368-369.
- Otterman, J. 1974. Baring high-albedo soils by overgrazing: a hypothesized desertification mechanism. Science 186:531-533.
- Parker, G.A. 1974. Courtship persistence and female-guarding as male time investment strategies. Behaviour 48:157-184.
- Parris, B.S. 1969. Studies on the vegetation of Cuvier Island, III. The establishment of permanent vegetation quadrats. Tane 15:75-85.
- Patton, T.H. 1967. Fossil vertebrates from Navassa Island, W.I. Quart. J. Fla. Acad. Sci. 30:59-60.
- Pianka, E.R. 1970. On r- and K-selection. Amer. Natur. 104:592-597.
- _____. 1974. Evolutionary Ecology. Harper and Row, New York. 356 p.
- Porter, K.R. 1972. Herpetology. W.B. Saunders Co., Philadelphia. 524 p.
- Pough, F.H. 1970. A quick method for permanently marking snakes and turtles. Herpetologica 26:428-430.
- _____. 1973. Lizard energetics and diet. Ecology 54(4): 837-844.
- Prashad, B. 1916. Some observations on a common house-lizard (Hemidactylus flaviviridis) of India. J. Bombay Nat. Hist. Soc. 24:834-838.
- Prieto, A.A., and M.W. Sorenson. 1975. Predator-prey relationships of the Arizona Chuckwalla. Bull. New Jersey Acad. Sci. 20(1):12-13.

- Raffaele, H. 1973. Assessment of Mona Island avifauna, Appendix K.
In: Isla Mona. Vol. II. Envir. Qual. Bd., San Juan, P.R.
- Rand, A.S. 1961. A suggested function of the ornamentation of East African forest chameleons. *Copeia* 1961(4):411-414.
- _____. 1967a. Ecology and social organization in the iguanid lizard Anolis lineatopus. *Proc. U.S. Nat. Mus.* 122:1-79.
- _____. 1967b. The adaptive significance of territoriality in iguanid lizards, pp. 106-115. In: Lizard Ecology, A Symposium. W.W. Milstead (ed.). Univ. Missouri Press, Columbia.
- _____. 1968a. A nesting aggregation of iguanas. *Copeia* 1968(3): 552-561.
- _____. 1968b. Desiccation rates in crocodile and iguana eggs. *Herpetologica* 24:178-180.
- _____. 1977. Reptilian arboreal folivores. In: The Ecology of Arboreal Folivores. G.G. Montgomery (ed.). Smithsonian Institution Press, Washington, D.C. In press.
- _____, and E.E. Williams. 1970. An estimation of redundancy and information content of anole dewlaps. *Amer. Natur.* 104:99-103.
- Rand, W.M., and A.S. Rand. 1976. Agonistic behavior in nesting iguanas: a stochastic analysis of dispute settlement dominated by the minimization of energy cost. *Z. Tierpsychol.* 40:279-299.
- Regal, P.J. 1967. Voluntary hypothermia in reptiles. *Science* 155: 1551-1553.
- _____. 1968. An Analysis of Heat-seeking in a Lizard. Ph.D. Dissertation. Univ. Calif., Los Angeles. 139 p.

- _____. 1971. Long term studies with operant conditioning techniques of temperature regulation patterns in reptiles. J. Physiologie 63:403-406.
- Rivera, L.H. 1973. Soils of Mona Island, Appendix C. In: Isla Mona, Vol. II. Environmental Quality Board, San Juan, P.R.
- Robel, R.J. 1970. Possible role of behavior in regulating Greater Prairie Chicken populations. J. Wildl. Mgmt. 34:306-312.
- Rogers, L. 1975. The vegetation of Mona Island, pp. 41-45. In: Primer Simposio del Departamento de Recursos Naturales. Depto. Recursos Naturales, San Juan, P.R.
- Root, A. 1967. Fighting male Galápagos land iguanas, Conolophus subcristatus, on Plaza Island--a photograph, p. 560. In: The Galápagos, eerie cradle of new species. R.T. Peterson (author). Nat. Geogr. 131:541-585.
- Rosen, D.E. 1975. A vicariance model of Caribbean biogeography. Syst. Zool. 24:431-464.
- Rudge, M.R. 1969. Reproduction of feral goats Capra hircus L. near Wellington, New Zealand. N.Z.J. Sci. 12(4):817-827.
- _____. 1973. The goat extermination campaign on Raoul Island. Unpubl. rept. DSIR Ecol. Div., N.Z. 4 p.
- _____, and T.J. Smit. 1970. Expected rate of increase of hunted populations of feral goats (Capra hircus L.) in New Zealand. N.Z.J. Sci. 13(2):256-259.
- Schmidt, K.P. 1928. Amphibians and land reptiles of Porto Rico, with a list of those reported from the Virgin Islands. N.Y.

- Acad. Sci. Scient. Surv. Porto Rico and Virgin Islands 10(1):
1-160.
- Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol.
Syst. 2:369-404.
- Schwartz, A. 1966. Snakes of the genus Alsophis in Puerto Rico and
the Virgin Islands. Stud. Fauna Curacao and other Carib. Is. 23:
177-221.
- _____, and W.M. Carey. 1977. Systematics and evolution in the
West Indian iguanid genus Cyclura. In preparation.
- Sexton, O.J. 1975. Black vultures feeding on iguana eggs in Panama.
Amer. Midl. Natur. 93(2):463-468.
- Shaw, C.E. 1954. Captive-bred Cuban Iguanas, Cyclura macleayi macleayi.
Herpetologica 10:73-78.
- Shaw, C.E. 1969. Breeding the Rhinoceros Iguana Cyclura cornuta
cornuta at the San Diego Zoo. Int. Zoo Yearbook 9:45-48.
- Sheplan, B.R., and A. Schwartz. 1974. Hispaniolan boas of the genus
Epicrates (Serpentes, Boidae) and their Antillean relationships.
Ann. Carnegie Mus. Nat. Hist. 45:57-143.
- Simon, C.A. 1975. The influence of food abundance on territory size
in the iguanid lizard Sceloporus jarrovi. Ecology 56:993-998.
- Simpson, G.G. 1956. Zoogeography of West Indian land mammals. Amer.
Mus. Novitates (1759):1-28.
- Smith, H.M. 1946. Handbook of Lizards. Comstock Publ. Co., Ithaca,
N.Y. 557 p.
- Soulé, M. 1966. Trends in the insular radiation of a lizard. Amer.
Natur. 100:47-64.

- Spatz, G., and D. Mueller-Dombois. 1972. Succession patterns after pig digging in grasslands communities on Mauna Loa, Hawaii. Island Ecosys. IRP/U.S. Internatl. Biol. Prog. Tech. Rept. No. 15, 44 p.
- _____. 1973. The influence of feral goats on Koa Tree reproduction in Hawaii Volcanoes National Park. Ecology 54(4):870-876.
- Stamps, J.A. 1973. Displays and social organization in female Anolis aeneus. Copeia 1973(2):264-272.
- _____, and G.W. Barlow. 1973. Variation and stereotypy in the displays of Anolis aeneus (Sauria: Iguanidae). Behaviour 47:67-94.
- Stejneger, L. 1904. The herpetology of Porto Rico. Rept. U.S. Nat. Mus. 1902:549-724.
- Street, G.B. 1952. Recent observations on the iguanas at Xanadu, Cuba. Privately printed. 12 p.
- Sykes, W.R. 1969. The effect of goats on vegetation of the Kermadec Islands. Proc. N.Z. Ecol. Soc. 16:13-16.
- Szarski, H. 1962. Some remarks on herbivorous lizards. Evolution 16:529.
- Thomas, R. 1966. A reassessment of the herpetofauna of Navassa Island. J. Ohio Herp. Soc. 5:73-89.
- Throckmorton, G. 1973. Digestive efficiency in the herbivorous lizard Ctenosaura pectinata. Copeia 1973(3):431-435.
- Thurston, J., and T.A. Wiewandt. 1977. Management of sea turtles on Mona Island, Appendix I (17 p), Unit Plan for the Management of the

- Mona Island Forest Reserve. Depto. de Recursos Naturales, San Juan, P.R. Submitted for publication.
- Tinbergen, N. 1952. "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. *Quart. Rev. Biol.* 27:1-32.
- Tinkle, D.W., and N.F. Hadley. 1975. Lizard reproductive effort: caloric estimates and comments on its evolution. *Ecology* 56:427-434.
- Trivers, R.L. 1972. Parental investment and sexual selection, pp. 136-179. In: *Sexual Selection and the Descent of Man, 1871-1971*. B. Campbell (ed.). Aldine Publication Co., Chicago.
- _____. 1976. Sexual selection and resource-accruing abilities in Anolis garmani. *Evolution* 30:253-269.
- Turbott, E.G. 1963. Three Kings Islands, New Zealand, a study in modification and regeneration, pp. 485-498. In: *Pacific Basin Biogeography, A Symposium*. J.L. Gressitt (ed.). Bishop Museum Press, Honolulu, Hawaii.
- Van Denburgh, J. 1922. The reptiles of western North America, vol. 1: Lizards. *Occ. Pap. Calif. Acad. Sci.* 10:1-611.
- Van Devender, R.W. 1975. The Comparative Demography of Two Local Populations of the Tropical Lizard, Basiliscus basiliscus. Ph.D. Dissertation. Univ. Mich., Ann Arbor. 110 p.
- Wadsworth, F.H. 1973a. Summary of the assessment reports and related information, pp. 36-47. In: *Isla Mona, Vol. I. Environ. Qual. Bd., San Juan, P.R.*
- _____. 1973b. The historical resources of Mona Island, Appendix N. In: *Isla Mona. Vol. II. Envir. Qual. Bd., San Juan, P.R.*

- _____, and J.A. Gilormini. 1945. The potentialities of forestry on Mona Island. *Caribbean For.* 6:219-244.
- Wallace, A.R. 1975. *Island Life*. AMS Press, New York. 563 p.
- Watt, B.K., and A.L. Merrill. 1975. *Handbook of the Nutritional Contents of Foods*. Dover Publications, Inc., New York. 190 p.
- Weber, Daniel. 1971. Pinta, Galapagos: Une ile á sauver. *Biol. Conserv.* 4(1):8-12.
- Webster, T.P., and J.M. Burns. 1973. Dewlap color variation and electrophoretically detected sibling species in a Haitian lizard, *Anolis brevirostris*. *Evolution* 27:368-377.
- Wiewandt, T.A. 1977. Management of Mona Island land crabs, Appendix K. In: Unit Plan for the Management of the Mona Island Forest Reserve. P.R. Dept. Nat. Resources, San Juan, P.R. Submitted for publication.
- Wilbur, H.M., D.W. Tinkle, and J.P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Amer. Natur.* 108:805-817.
- Williams, E.E. 1952. A new fossil tortoise from Mona Island, West Indies, and a tentative arrangement of the tortoises of the New World. *Bull. Amer. Mus. Nat. Hist.* 99(9):545-560.
- _____, and A.S. Rand. 1977. Species recognition, dewlap function and faunal size. *Amer. Zool.* 17:261-270.
- Williams, J.H., A.W. Begg, T.K. Burke, and P.H. Gresham. 1974. Government caucus committee on noxious animals control and related matters. Rept. to Minister Forests, New Zealand. Mimeo, 76 p.

- Wilson, E.O. 1975. Sociobiology--The New Synthesis. Harvard Univ. Press, Cambridge, Mass. 697 p.
- Wilson, K.J., and A.K. Lee. 1974. Energy expenditure of a large herbivorous lizard. *Copeia* 1974(2):338-348.
- Winslow, S.S. 1909. Mona Island. Unpubl. rept., U.S. Coast Geod. Surv. 12 p.
- Wodziki, K.A. 1950. Introduced mammals of New Zealand. Hutcheson, Bowman, and Stewart, Wellington. 255 p.
- Woodley, J.D. 1971. The Jamaican ground iguana in Hellshire, pp. 127-133. In: Hellshire Hills Scientific Survey, 1970. J.D. Woodley (ed.). Univ. West Indies, Inst. Jamaica, Kingston.
- Yocom, C.F. 1967. Ecology of feral goats in Haleakala National Park, Maui, Hawaii. *Amer. Midl. Natur.* 77(2):418-451.

APPENDIX I

Dominant Species in Mona Island Plant Communities as Related to the Diets of Iguanas and Goats (Plant list from Cintrón & Rogers, 1974)

1. PLATEAU FOREST (Area = 4,271 ha = 10,554 acres)

<u>Dominants</u> (in order of decreasing relative density)	<u>Iguanas</u>	<u>Eaten by</u> <u>Goats</u>
Canopy:		
<u>Coccoloba microstachya</u>	L, <u>Fr</u>	x
<u>Bursera simaruba</u>	o	x
<u>Tabebuia heterophylla</u>	L	?
<u>Plumeria obtusa</u>	<u>L</u> , <u>Fl</u>	x
<u>Euphorbia petiolaris</u>	o	x
<u>Bourreria succulenta</u>	<u>Fr</u>	x
<u>Amyris elemifera</u>	<u>Fr</u>	x
Understory/Shrub:		
<u>Croton discolor</u>	L	x
<u>Croton humilis</u>	o	x
<u>Croton betulinus</u>	L	x
<u>Antirrhea acutata</u>	Fl, L, <u>Fr</u>	x
<u>Reynosa uncinata</u>	L, <u>Fr</u>	x
<u>Comocladia dodonea</u>	o	x
Herb:		
<u>Opuntia repens</u>	o	o
<u>Pilea margarettae</u>	?	?
<u>Panicum utowaneum</u>	?	?
<u>Callisia repens</u>	L	?
<u>Commelina virginica</u>	L	?
<u>Centrosema virginiana</u>	<u>L</u> , <u>Fr</u>	x
<u>Ayenia pusilla</u>	<u>Fr</u>	?

KEY TO SYMBOLS USED IN THIS APPENDIX:

L = Leaves	<u>Underscoring</u> indicates a favorite food item of iguanas
Fl = Flowers	
Fr = Fruits	
o = Not eaten	
x = Taken by goats (typically including leaves, fruits, and flowers)	
? = Undetermined	

APPENDIX I (CONTINUED)

2. DEPRESSION FOREST (Area = 148 ha = 365 acres)

<u>Dominants (in order of decreasing relative density)</u>	<u>Eaten by</u>	
	<u>Iguanas</u>	<u>Goats</u>
Canopy:		
<u>Pisonia albida</u>	?	?
<u>Ficus citrifolia</u>	<u>Fr</u>	x
<u>Schaefferia frutescens</u>	<u>Fl</u> , L	x
<u>Eugenia fragrans</u>	?	x
<u>Krugiodendron ferreum</u>	L, <u>Fr</u>	x
<u>Capparis cynophallophora</u>	L	x
<u>Eugenia rhombea</u>	?	x
<u>Clusia rosea</u>	o	?
<u>Amyris elemifera</u>	<u>Fr</u>	x
<u>Bursera simaruba</u>	o	x
<u>Eugenia foetida</u>	?	?
<u>Capparis flexuosa</u>	<u>L</u> , <u>Fr</u> , <u>Fl</u>	x
<u>Bourreria succulenta</u>	<u>Fr</u>	x
Understory/ Shrub:		
<u>Consolea rubescens</u>	o	o
<u>Phyllanthus epiphyllanthus</u>	o	x
<u>Euphorbia petiolaris</u>	o	x
<u>Lantana involucrata</u>	L	x
<u>Reynosia uncinata</u>	L, <u>Fr</u>	x
Herb:		
<u>Cyperus tenuis</u>	?	?
<u>Panicum utowaneum</u>	?	?
<u>Callisia repens</u>	L	?
<u>Peperomia humilis</u>	?	?

3. PLATEAU SHRUB (Area = 381 ha = 942 acres)

Canopy: (not present)

Understory/Shrub:

<u>Croton discolor</u>	L	x
<u>Croton betulinus</u>	L	x
<u>Corchorus hirsutus</u>	<u>L</u> , <u>Fr</u>	x
<u>Melochia tomentosa</u>	?	x

APPENDIX I (CONTINUED)

3. PLATEAU SHRUB (continued)

<u>Dominants (in order of decreasing relative density)</u>	<u>Eaten by</u> <u>Iguanas</u>	<u>Goats</u>
<u>Reynosa uncinata</u>	L, <u>Fr</u>	x
<u>Plumeria obtusa</u>	<u>L</u> , <u>Fl</u>	x
<u>Euphorbia petiolaris</u>	o	x
<u>Croton humilis</u>	o	x

Herb:

<u>Opuntia repens</u>	o	o
<u>Boerhaavea diffusa</u>	L	?
<u>Ayenia pusilla</u>	<u>Fr</u>	?
<u>Galactia dubia</u>	<u>L</u>	x
<u>Portulaca</u> spp.	<u>L</u> , <u>Fr</u> , <u>Fl</u>	x
<u>Eragrostis ciliaris</u>	?	?

4. CACTUS/LOW SHRUB (Area = 71 ha = 177 acres)

Canopy: (not present)

Understory/Shrub:

<u>Croton discolor</u>	L	x
<u>Corchorus hirsutus</u>	<u>L</u> , <u>Fr</u>	x
<u>Consolea rubescens</u>	o	o

Understory/Shrub (in Plate Rock area):

<u>Croton betulinus</u>	L	x
<u>Cassia granulata</u>	?	x
<u>Corchorus hirsutus</u>	<u>L</u> , <u>Fr</u>	x
<u>Croton discolor</u>	L	x

Herb:

<u>Portulaca caulerpoides</u>	?	?
<u>Tephrosia cinerea</u>	<u>L</u> , <u>Fr</u>	x
<u>Mammillaria nivosa</u>	o	x
<u>Opuntia repens</u>	o	o
<u>Sporobolus virginicus</u>	?	?

APPENDIX I (CONTINUED)

4. CACTUS/LOW SHRUB (continued)

<u>Dominants (in order of decreasing relative density)</u>	<u>Iguanas</u>	<u>Eaten by</u>	<u>Goats</u>
Herb (in Plate Rock area):			
<u>Galactia dubia</u>	<u>L</u>		x
<u>Mammillaria nivosa</u>	o		x
<u>Opuntia repens</u>	o		o
<u>Chloris inflata</u>	?		x
<u>Portulaca</u> spp.	<u>L</u> , <u>Fr</u> , <u>Fl</u>		x
<u>Sporobolus argustus</u>	?		?
<u>Chamaesyce anegadensis</u>	L		?

5. CACTUS FOREST (Area = 39 ha = 96 acres)

Canopy:

<u>Lemaireocereus hystrix</u>	o	x
<u>Harrisia portoricensis</u>	Fr	x
<u>Plumeria obtusa</u>	<u>L</u> , <u>Fl</u>	x

Understory/Shrub:

<u>Cordia globosa</u>	L	x
<u>Croton discolor</u>	L	x
<u>Croton betulinus</u>	L	x
<u>Reynosa uncinata</u>	L, <u>Fr</u>	x
<u>Corchorus hirsutus</u>	<u>L</u> , <u>Fr</u>	x

Herb:

<u>Opuntia repens</u>	o	o
<u>Mammillaria nivosa</u>	o	x
<u>Centrosema virginiana</u>	<u>L</u> , <u>Fr</u>	x
<u>Commelina virginica</u>	L	?
<u>Galactia striata</u>	?	?
<u>Cissus caustica</u>	L	x

APPENDIX I (CONTINUED)

6. COASTAL LOWLAND FOREST (Area = 113 ha = 280 acres)

<u>Dominants (in order of decreasing relative density)</u>	<u>Iguanas</u>	<u>Eaten by</u>	<u>Goats</u>
A. Closed Canopy Type			
Canopy:			
<u>Guaiacum sanctum</u>	?		?
<u>Amyris elemifera</u>	<u>Fr</u>		x
<u>Bouyeria succulenta</u>	<u>Fr</u>		x
<u>Exostema caribaeum</u>	?		x
<u>Gymnanthes lucida</u>	?		x
<u>Eugenia foetida</u>	?		?
<u>Eugenia fragrans</u>	?		x
<u>Pithecellobium unguis-cati</u>	?		x
Understory/Shrub:			
<u>Croton humilis</u>	o		x
<u>Consolea rubescens</u>	o		o
<u>Croton betulinus</u>	L		x
<u>Reynosia uncinata</u>	L, <u>Fr</u>		x
Herb:			
<u>Panicum utowaneum</u>	?		?
<u>Justicia periplocifolia</u>	?		?
<u>Centrosema virginiana</u>	<u>L</u> , <u>Fr</u>		x
B. Open Canopy Type			
Canopy:			
<u>Coccoloba microstachya</u>	L, <u>Fr</u>		x
<u>Coccoloba diversifolia</u>	L, <u>Fr</u>		x
<u>Metopium toxiferum</u>	?		?
<u>Erithalis fruticosa</u>	L		?
<u>Gyminda latifolia</u>	L, <u>Fr</u>		x
Understory/Shrub:			
<u>Byrsonema lucida</u>	?		?
<u>Dodonea viscosa</u>	?		?
<u>Phyllanthus epiphyllanthus</u>	o		x

APPENDIX I (CONTINUED)

6. COASTAL LOWLAND FOREST (continued)

<u>Dominants (in order of decreasing relative density)</u>	<u>Iguanas</u>	<u>Eaten by</u> <u>Goats</u>
Herb:		
<u>Panicum utowaneum</u>	?	?
<u>Centrosema virginiana</u>	<u>L</u> , Fr	x

C. Mangrove

Canopy:

<u>Rhizophora mangle</u>	?	?
<u>Laguncularia racemosa</u>	?	?

7. COASTAL SHRUB (Area = 21 ha = 51 acres)

Canopy: (not present)

Understory/Shrub:

<u>Coccoloba uvifera</u>	<u>Fr</u>	x
<u>Suriana maritima</u>	?	?
<u>Strumpfia maritima</u>	?	x
<u>Conocarpus erectus</u>	?	x

Herb:

<u>Sporobolus virginicus</u>	?	?
<u>Cenchrus</u> spp.	?	?
<u>Sesuvium portulacastrum</u>	?	?
<u>Fimbristylus cymosa</u>	?	?

8. CLIFFSIDE (Area = 34 ha = 83 acres)

A. West-facing Cliffs

Canopy:

<u>Capparis cynophallophora</u>	L	x
<u>Coccoloba diversifolia</u>	L, <u>Fr</u>	x
<u>Eugenia axillaris</u>	?	?

APPENDIX I (CONTINUED)

8. CLIFFSIDE (continued)

<u>Dominants (in order of decreasing relative density)</u>	<u>Eaten by</u> <u>Iguanas</u>	<u>Goats</u>
<u>Pisonia albida</u>	?	?
<u>Erythroxylon areolatum</u>	<u>Fr, Fl</u>	x
<u>Bursera simaruba</u>	o	x
Understory/Shrub:		
<u>Capparis flexuosa</u>	<u>L, Fr, Fl</u>	x
<u>Antirrhea acutata</u>	<u>L, Fr, Fl</u>	x
<u>Trichostigma octandra</u>	?	?
Herb:		
<u>Paspalum laxum</u>	L	x
<u>Salvia serotina</u>	?	?
<u>Argythamnia candidans</u>	L	x
B. South-facing Cliffs		
Canopy:		
<u>Erythroxylon areolatum</u>	<u>Fr, Fl</u>	x
<u>Eugenia rhombea</u>	?	x
<u>Ficus citrifolia</u>	<u>Fr</u>	x
<u>Bursera simaruba</u>	o	x
<u>Tabebuia heterophylla</u>	L	?
<u>Capparis cynophyllophora</u>	L	x
Understory/Shrub:		
<u>Lantana involucrata</u>	L	x
<u>Capparis flexuosa</u>	<u>L, Fr, Fl</u>	x
<u>Tournefortia microphylla</u>	L	x
<u>Phyllanthus epiphyllanthus</u>	o	x
Herb:		
<u>Paspalum laxum</u>	L	x
<u>Opuntia dillenii</u>	?	?
<u>Tillandsia utriculata</u>	o	x
C. Manchineel Terraces		
Canopy: <u>Hippomane mancinella</u>	<u>L, Fr</u>	o

APPENDIX I (CONTINUED)

8. CLIFFSIDE (continued)

<u>Dominants (in order of decreasing relative density)</u>	<u>Iguanas</u>	<u>Eaten by</u>	<u>Goats</u>
Understory/Shrub:			
<u>Erythroxylon areolatum</u>	<u>Fr, Fl</u>		x
<u>Torrubia discolor</u>	<u>L, Fr</u>		x
Herb: <u>Opuntia repens</u>	o		o

9. PLANTATION (Area = 130 ha = 321 acres)

A. Mahogany

Canopy: <u>Swietenia mahagoni</u>	?		x
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Understory/Shrub:

<u>Coccoloba diversifolia</u>	<u>L, Fr</u>		x
<u>Gymnanthes lucida</u>	?		x
<u>Thrinax microcarpa</u>	?		?
<u>Metopium toxiferum</u>	Fr		?
<u>Canella winterana</u>	?		?
<u>Phyllanthus epiphyllanthus</u>	o		x
<u>Randia aculeata</u>	o		x
<u>Croton humilis</u>	o		x
<u>Argythamnia candicans</u>	L		x

Herb:

<u>Centrosema virginiana</u>	<u>L, Fr</u>		x
<u>Galactia striata</u>	?		?

B. Casuarina

Canopy: <u>Casuarina equisetifolia</u>	o		?
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Understory/Shrub:

<u>Eugenia foetida</u>	?		?
<u>Capparis flexuosa</u>	<u>L, Fr, Fl</u>		x
<u>Croton humilis</u>	o		x
<u>Argythamnia candicans</u>	L		x

APPENDIX I (CONTINUED)

9. PLANTATION (continued)

<u>Dominants (in order of decreasing relative density)</u>	<u>Iguanas</u>	<u>Eaten by</u> <u>Goats</u>
Herb:		
<u>Rivinia humilis</u>	L, Fr	?
<u>Lasiacis divaricatus</u>	?	?
<u>Opuntia repens</u>	o	o

APPENDIX II

Phenological Observations on Some Common Plants of Mona Island

Species		Observed Dates of:			
		Flowering		Fruiting	
(Common Name)	1973	1974	1975	1973	1974 1975
<u>Amyris elemifera</u> (Tea)	Nov.		Mar.	(1972-Aug.)	
<u>Antirrhoea acutata</u> (Quina)	July	Jan.-Aug. May (peak)	Mar.-?	Sept.-Nov.	Aug.-?
<u>Boussieria succulenta</u> (Palo de vaca)	Sept. Oct.	July-Dec.		late Oct.- Dec. (1972- Aug.-Sept.)	Dec.-Jan. '75
<u>Bursera simaruba</u> (Almácigo)	Mar.	late Mar.- Apr.	Mar.	Sept.-Oct.	
<u>Caesalpinia divergens</u>	Oct.	Jan.-Aug.	Jan.		Jan. May Dec. (black seeds only)
<u>Calyptanthus pallens</u> (Tapón blanco)		May June			

APPENDIX II (CONTINUED)

Species		Observed Dates of:			
		Flowering		Fruiting	
(Common Name)	1973	1974	1975	1973	1974 1975
<u>Capparis cynophallophora</u> (Bejuco Inglés)		mid-June			Feb. Mar.
<u>Capparis flexuosa</u> (Palinguán)	May June July	early July		May	
<u>Capraria biflora</u> (Té del país)		May			
<u>Cassia grammica</u> (Cañafistula)	July				
<u>Cassia granulata</u> (Cañafistula)		May			
<u>Casuarina equisetifolia</u> (Pino Australiano)		May			
<u>Coccoloba diversifolia</u> (Üvilla)		May		Nov. Jan.	Dec.-Feb. '75
<u>Coccoloba microstachya</u> (Üverillo)	Nov. Dec.	Jan. Aug.		Mar. Nov. Dec. (peak)	Jan.

APPENDIX II (CONTINUED)

Species		Observed Dates of:			
		Flowering		Fruiting	
(Common Name)	1973	1974	1975	1973	1974 1975
<u>Coccoloba uvifera</u> (Uva de playa)		early Mar. early Apr. late May		(1972-late Oct. and Dec.)	
<u>Colubrina reclinata</u> (Maví)	Nov.	May			Mar.
<u>Comocladia dodonea</u> (Carrasco)		mid-May	late Mar.		
<u>Corchoris hirsutus</u> (Malvavisco)		May		Jan.	Jan.
<u>Cordia globosa</u> (Capá)		May		Mar.	
<u>Crossopetalum rhacoma</u> (Coral)				Jan.	
<u>Croton discolor</u> (Lechecillo)	Sept.	Jan. Mar. early May Aug.	Mar.		
<u>Croton humilis</u> (Yerba bellaca)	July	Mar. May, July	Mar.		

APPENDIX II (CONTINUED)

Observed Dates of:							
Species		Flowering		Fruiting			
(Common Name)		1973	1974	1975	1973	1974	1975
<u>Dodonea viscosa</u> (Chamiso)			Jan.			Feb.-Mar.	
<u>Erithalis fruticosa</u>		July	May				
<u>Erythroxylon areolatum</u> (Indio)		early May July	Mar. May early July	Mar.	(1972-June peak) Apr.- Oct. (Sept. peak)	late June early July	
<u>Eugenia rhombea</u> (Hoja menuda)			May		Nov.-Dec.	Jan.	
<u>Eupatorium corymbosum</u>		(1972-June	late Apr. (starting to flower)				
<u>Euphorbia petiolaris</u> (Indio desnudo)		Mar. Apr. May Dec.	Jan.-May	Jan.-Mar.		Mar. Apr.	Mar. (peak)
<u>Exostema caribaeum</u> (Albarillo)		Sept.	Aug.				

APPENDIX II (CONTINUED)

Species		Observed Dates of:			
		Flowering		Fruiting	
(Common Name)		1973	1974	1975	1975
<u>Ficus citrifolia</u> (Jagüey blanco)					
				scattered thru year; peak-Mar. (1972-Aug.)	late Jan. Feb.-Mar.
<u>Ficus stahlili</u> (Jagüey)				(1972-June)	May
<u>Gossypium barbadense</u> (Algodón)	Nov.			early Mar. (peak)	late Jan. (peak)
					Jan.-Feb. (peak early Feb.)
<u>Guaiacum sanctum</u> (Guayacán blanco)	early May				
<u>Gymnanthes lucida</u> (Yaití)	July				
<u>Gyminda latifolia</u>				Oct.-Nov.	
<u>Harrisia portoricensis</u> (Higo chumbo)	May July	May Aug.		Mar. Oct. Nov. Dec. (1972-Sept. peak)	Jan. Feb. Mar. (Oct.-Nov. peak)
					Mar.

APPENDIX II (CONTINUED)

Species		Observed Dates of:			
		Flowering		Fruiting	
(Common Name)	1973	1974	1975	1973	1974 1975
<u>Hippomane mancinella</u> (Manzanillo)		Jan. Feb. Mar. early Apr.		May-Oct. (peaks early July, Sept.) (1972-May-Aug.; peak early Aug.)	May-June (peak mid- June)
<u>Hypelate trifoliata</u> (Melcocha, cigua)		July		Sept. Oct. Nov. (1972-Aug.)	
<u>Jacquinia arborea</u> (Barbasco)					Aug.
<u>Jatropha multifida</u> (Tártago emético)	Dec.	Jan. Feb. Mar. May	Mar.	Nov.	Mar. May
<u>Krugiodendron ferreum</u> (Bariaco)				(1972-Aug.)	
<u>Lantana involucrata</u> (Cariacillo Santa María)	(1972-June)	May July			

APPENDIX II (CONTINUED)

Species (Common Name)		Observed Dates of:				
		Flowering		Fruiting		
1973	1974	1975	1973	1974	1975	
<u>Lemaireocereus hystrix</u> (Dildo Español)	early May			late May- June	late Feb.- Mar.	
<u>Metopium toxiferum</u> (Papayo)	early Mar.	mid-Jan.- Mar.		June		
<u>Phyllanthus</u> <u>epiphyllanthus</u> (Bayoneta)	Mar. May	Mar.		June		
<u>Pithecellobium</u> <u>unguis-cati</u> (Uña de gato)	Apr.	Mar.		late Jan.	late Jan.	
<u>Plumiera obtusa</u> (Alelí blanco)	Apr. May (peak)					
<u>Randia aculeata</u> (Tintillo, escambrón)	Feb. Mar. May (peak) July					
	May June			early Mar.		
<u>Rauwolfia tetraphylla</u> (Palo amargo)	May (peak)		Aug. Sept. (1972-Sept.)	July		

APPENDIX II (CONTINUED)

Species (Common Name)	Observed Dates of:				
	Flowering		Fruiting		
	1973	1974	1975	1973	1974 1975
<u>Reynosia uncinata</u> (Chicharrón)		Mar.	Mar. (peak)	Jan. (peak) Sept. Oct. Nov.	Apr. June (no peak)
<u>Sarcomphalus taylorii</u>				Mar. Nov.	Mar.
<u>Schaefferia frutescens</u> (Jiba)	early July	early July			
<u>Stigmaphyllon</u> <u>periplocifolium</u> (Bejuco de paralejo)	July (peak)	Feb. Mar. May (peak)	mid-Mar.		
<u>Swietenia mahogani</u> (Caobo)	Mar.	June			Mar. Apr. (peak)
<u>Tabebuia heterophylla</u> (Roble blanco)	Mar. Apr. May (peak)	Apr. May (peak) June July (peak)	late Mar. Apr.		
<u>Tillandsia polystachya</u> (Piñón)	July	May			

APPENDIX II (CONTINUED)

Species		Observed Dates of:				
		Flowering		Fruiting		
(Common Name)	1973	1974	1975	1973	1974	1975
<u>Tillandsia recurvata</u> (Nidos de gungulén)						
<u>Tillandsia subluxa</u> (Piñón)					early June	Feb.
<u>Tillandsia utriculata</u> (Piñón)	late Mar. (peak)	June	Jan. (peak)			Apr.
<u>Torrubia discolor</u> (Barrehorno)	July			(1972-Sept.)		Feb.-Mar.
<u>Urechites lutea</u> (Babiero amarillo)	late May	May		May		
<u>Waltheria americana</u> (Malvavisco. Basora prieta)		May (peak)				

