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THE ROCK IGUANA, *CYCLURA PINGUIS*,
ON ANEGADA, BRITISH VIRGIN ISLANDS,
WITH NOTES ON *CYCLURA RICORDI* AND *CYCLURA CORNUTA*
ON HISPANIOLA

W. MICHAEL CAREY



UNIVERSITY OF FLORIDA

GAINESVILLE

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THE ROCK IGUANA, *CYCLURA PINGUIS*,
ON ANEGADA, BRITISH VIRGIN ISLANDS,
WITH NOTES ON *CYCLURA RICORDI* AND *CYCLURA CORNUTA*
ON HISPANIOLA

W. MICHAEL CAREY¹

SYNOPSIS: A field study of the ethoecology of the rock iguana, *Cyclura pinguis*, on Anegada, British Virgin Islands was conducted from 27 March to 5 May 1968. The sympatric Hispaniolan species, *C. ricordi* and *C. cornuta*, were observed from 12 to 16 May 1968. The results of these studies and all known ethoecological literature on the genus are discussed.

Cyclura pinguis inhabits primarily xeric limestone areas, is heliothermic, and exhibits behavioral thermoregulation. Retreats nearly always consist of natural cavities in the limestone or beneath boulders. *C. ricordi* and *C. cornuta* are primarily burrowers. Adult of all three species are principally herbivorous, although some animal matter is taken. Probably all *Cyclura* juveniles are primarily insectivorous. Parasitism from ticks and nematodes is a common occurrence in *Cyclura*. Five adult males on the main study plot ranged from 522 to 545 mm ($\bar{x}=534.60 \pm 3.88$ mm) in snout-vent length and from 5.95 to 7.17 kg ($\bar{x}=6.72 \pm 0.21$ kg) in body weight; five adult females ranged from 426 to 487 mm ($\bar{x}=468.00 \pm 10.87$ mm) in snout-vent length and from 4.31 to 5.13 kg ($\bar{x}=4.75 \pm 0.13$ kg) in body weight. The five males occupied home ranges from 116.06 to 985.11 m² ($\bar{x}=546.61 \pm 160.46$ m²) in area; home ranges of the five females measured from 155.47 to 412.31 m² ($\bar{x}=276.28 \pm 41.62$ m²). Extensive unutilized zones existed between home ranges of iguanas of the same sex. Aside from food, available shelter seems to be the most important factor governing selection of home range locale. *Cyclura pinguis* exhibited a density of 2.03 iguanas/hectare (0.82/acre), the lowest density figure

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of any lizard for which data are documented. The sex ratio was equal. Evidence suggests monogamy. Three adult females had 12, 14, and 16 yolked ovarian follicles. Adulthood appears to be attained between 7 and 9 years of age and between 350 and 400 mm snout-vent length. The reproductive cycle in *C. pinguis* suggests synchronization with the two rainfall maxima in the Virgin Islands. Adult iguanas far outnumbered juveniles (87.5% vs. 12.5%) suggesting decline of the population. This disproportionate age structure seems to be the result of interactions (competition/predation) with domestic livestock. With the resultant loss in fecundity, relatively few adults now exist to continue the population. A conservation program is outlined whereby the population might be restored. This program might be applicable to other decimated *Cyclura* populations as well.

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INTRODUCTION

Rock, or ground, iguanas (genus *Cyclura* Harlan) are large, primarily herbivorous lizards endemic to the Bahamas, Greater Antilles, Cayman Islands, and Virgin Islands. The current distribution of extant species is spotty, but Pleistocene and Recent fossil remains have been found on several islands no longer supporting populations: e.g., St. Thomas (Miller 1918), Puerto Rico (Barbour 1919), Great Exuma (Allen 1937), New Providence (Etheridge 1966), Navassa (Patton 1967), and possibly Barbuda (Etheridge 1964). These remains clarify several distributional patterns.

Only Hispaniola supports sympatric forms. *Cyclura ricordi* and the rhinoceros iguana, *C. cornuta*, occur in portions of the Cul-de-Sac-Valle de Neiba plains of the Dominican Republic and in scattered areas farther south on the Barahona Peninsula. These are xeric salt plains that were once part of a Pleistocene waterway separating the then north and south islands (*sensu* Williams 1961) of Hispaniola. This apparently comprises the total range of *C. ricordi*, whereas *C. cornuta* ranges over much of Hispaniola and several of its satellite islands.

Cyclura belongs in the iguane line of the family Iguanidae (Savage 1958, Avery and Tanner 1971), but intrageneric relationships are poorly understood. Hence nomenclature in this paper essentially follows that of the last systematic treatment of the group (Barbour and Noble 1916) and subsequent species descriptions. A study of the evolutionary relationships among the species is in progress (Schwartz and Carey, in preparation).

No previous detailed studies on the ecology and behavior of any *Cyclura* species have been done, though several short papers describe various aspects of their activity. Gosse (1848) first reported habits of the Jamaican *C. lophoma* (= *C. collei*). Nearly a century later Grant (1940a) and Lewis (1944, 1946) noted the apparent impending extinction of this species on Jamaica and Goat Island. Short works on *C. cornuta* (Noble 1923, Klingel 1929) and reports dealing with the Bahamian forms *C. rileyi* (Stejneger 1903), *C. figginsi* (Bailey 1925), and *C. carinata bartschi* and *C. nuchalis* (Cochran 1934) also have appeared. Activity of the Cuban *C. macleayi macleayi* has been reported by Buide (1951), Street (1952), Sutcliffe (1952), Hardy (1956), and Cooper (1958). The forms on Cayman Brac and Little Cayman (*C. macleayi caymanensis*) and Grand Cayman (*C. macleayi lewisi*) were studied by Grant (1940b) and Carey (1966). Grant (1944) also studied *C. stejnegeri* on Isla Mona, off the western coast of Puerto Rico.

In addition to the *Cyclura* species already extinct (*mattea*, *nigerrima*, *portoricensis*, and a few unnamed forms), several others may face similar fates, because they inhabit tiny islands and cays—a situation that keeps many populations, although dense, precariously small. On the Greater Antilles, where ecological diversity is greater, *Cyclura* occurs only in restricted xeric habitats, and their decline or extinction has been caused primarily by man's activities. Because of the generally precarious status of *Cyclura* species, all are listed in the International Union for the Conservation of Nature and Natural Resources (IUCN) RED DATA BOOK on endangered amphibians and reptiles (Honegger 1968).

The present report and that by Carey (1966) are parts of a projected series of studies concerning the ecology and behavior of West Indian rock iguanas. The results will provide means for interpreting ethoecological components of the generalized *Cyclura* niche in these discrete but roughly similar insular communities.

This report on the ethoecology of the rock iguana, *Cyclura pinguis* Barbour (Fig. 1), on Anegada, British Virgin Islands includes remarks regarding the sympatric Hispaniolan forms, *C. ricordi* (Duméril and Bibron) and *C. cornuta* (Bonnaterre) and reviews all known literature dealing with ethoecology of *Cyclura*.

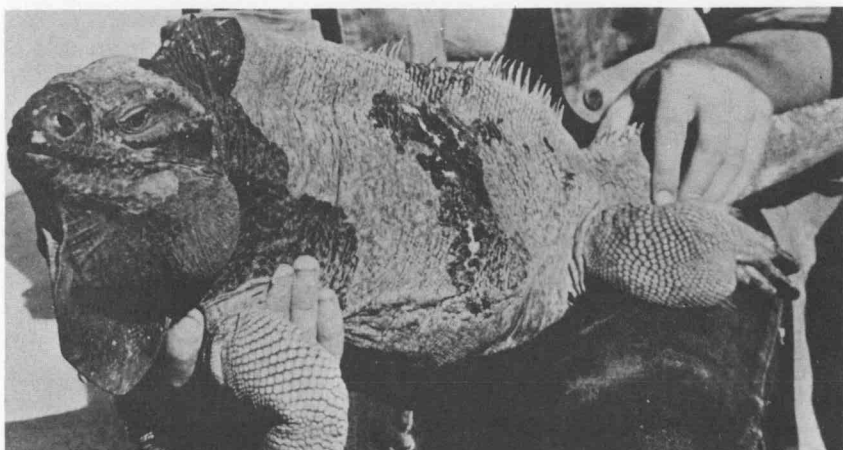


FIGURE 1.—Adult male *Cyclura pinguis* from Anegada, British Virgin Islands. Note the prominent dorsal ridge.

Literature on *C. pinguis* is scarce. Schomburgk (1832) first reported iguanas on Anegada when he mentioned having seen "*Iguana sapidissima*" on the island, but it was not until 1916 that the first specimen (an adult female) was collected by James L. Peters. Barbour (1917) subsequently described the species as new, and in later papers he (1917, 1919, 1930, 1935, 1937) mentioned, or implied, its extreme rarity. Today his comments seem unwarranted, although the species is not common. Grant (1937) gave a brief account of stomach contents of adults, and Underwood (1962) supplied brief notes on their habits.

ACKNOWLEDGMENTS

I wish especially to thank my faculty advisor, Roy W. McDiarmid, for his continued patience and interest in my research and for critically reviewing the manuscript. I also thank Derek G. Burch, Wade C. Sherbrooke, Richard Thomas, and Walter G. Whitford for their helpful suggestions concerning various sections. Albert Schwartz aided in many ways, primarily through providing contacts in the Dominican Republic.

I am indebted to several island residents for their aid during my stay on Anegada, especially the Levans family who provided my room and board. Aubrey Levans and "Brasso" Norman provided much companionship and help in the field. During my stay in the Dominican Republic, similar provisions were made by the family of Sixto Inchaustegui of Santo Domingo. In addition, they made possible my trip to the vicinity of Lago de Enriquillo.

James Feigl aided in preparation of the illustrations. The line drawing is by James Seagle.

A major part of the fieldwork for this study was made possible through a Grant-in-Aid of Research from the Society of the Sigma Xi. To this organization I extend my sincere thanks.

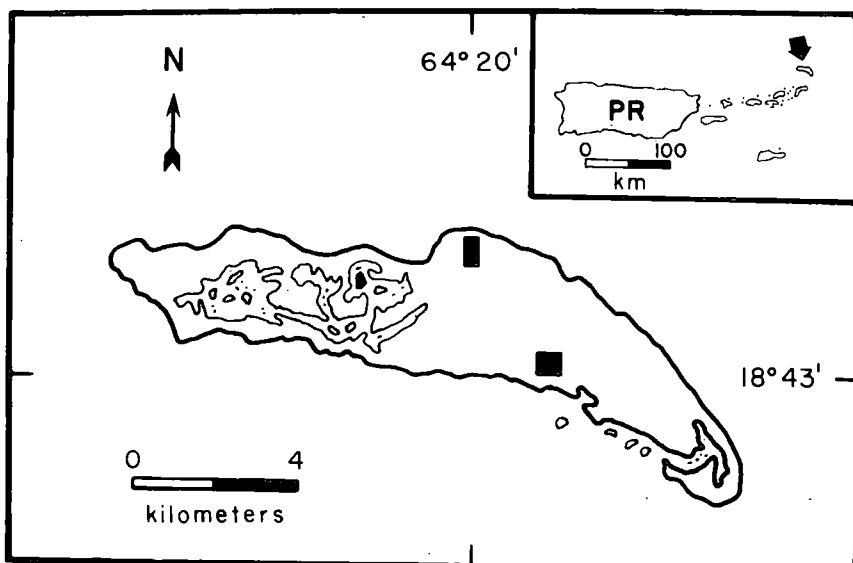


FIGURE 2.—Map of Anegada, British Virgin Islands showing ponds and study areas. Blackened areas are (from left) Windberg Key, Citron Bush, and The Settlement. Inset shows location of Anegada (arrow) in relation to Puerto Rico (PR) and other islands on Puerto Rican Island shelf.

DESCRIPTION OF THE ISLAND AND STUDY SITES

Anegada lies on the Puerto Rican Island Shelf, which consists primarily of Puerto Rico, Vieques, Culebra, and the Virgin Islands (Heatwole and MacKenzie 1967). It is the northeasternmost island on the shelf (Fig. 2), lying about 24 km north of Virgin Gorda, and is about 15 km long and 3 km wide at its widest point.

Although lying on the same bank as the other Virgin Islands, which are volcanic in composition and remarkably hilly, Anegada is composed almost entirely of limestone, is essentially without relief, and has a maximum elevation of about 9 m. Most of the western end is a sandy plain or salt flat with many highly saline ponds that often inundate the area during rainy periods. The eastern and central portions are largely eroded limestone plains, honey-combed with cavities leading beneath the surface.

A total of 40 days (27 March-5 May 1968) was spent on Anegada, and preliminary investigations for a later intensified study were carried out on the two sympatric forms, *C. ricordi* and *C. cornuta*. This represents about 215 hours of actual field time. Five days (12-16 May 1968) were spent in the Dominican Republic in the vicinity of Lago de Enriquillo, just east of Jimaní near the Haitian border. This desolate portion of the Cul de Sac is some 40 m below sea level.

The main study area on Anegada was located about 3.5 km northwest of The Settlement (Fig. 2), a point where sandy and rocky areas meet. This plot will be referred to as the "Citron Bush," a local name applied to the general area of which the study site was a part. This area is roughly rectangular and encompasses about 4.93 ha (ca 12.19 acres). Boundaries are natural and may somewhat restrict movements of iguanas to and from the area. To the south and west are large, nearly denuded sandy areas, to the north mostly sandy beach and the Atlantic Ocean, and to the east an extremely dense thicket. Only adult iguanas inhabit the Citron Bush. The substrate consists almost entirely of weathered limestone projections, soil-filled pockets, and countless natural cavities leading to caverns beneath the

limestone. In the southwestern portion of the study plot is a small sandy area with numerous scattered limestone boulders. The ground cover is mostly dead vegetation; e.g. leaves, cacti, logs, and brush.

The second study area was located about 2.5 km west of the Citron Bush. This plot is known locally as Windberg Key and is a tiny, egg-shaped islet lying about 100 m off the western shore of Red Pond on the main island (Fig. 2). This islet is 90 m long and 50 m wide at its widest point and about 0.28 ha (ca 0.69 acres). Windberg Key was inhabited only by juvenile iguanas. The substrate is heavily eroded and cracked aeolian limestone with few natural cavities and little sand. Limestone boulders are scattered over much of the key. Except during the dry season when Red Pond dries up considerably, the isolation of Windberg Key is nearly complete.

Additional observations were made at other localities whenever the opportunity arose; the principal ones being Cedar Well Key, Low Key, and much of eastern Anegada. The first two areas are actually peninsulas jutting into the north and south sides of Flamingo Pond, just west of Red Pond. Each key is about 150 m long and 100 m wide. The substrate on each is eroded limestone with many boulders.

In the Dominican Republic, observations were made along roads at localities that appeared suitable. This was done on a day to day basis to obtain general ideas regarding the ethoecology of *C. ricordi* and *C. cornuta*.

METHODS AND MATERIALS

An analysis of plant composition in the Citron Bush was obtained by randomly selecting ten points in the area and counting the numerical abundance of each species within a ten meter radius of each point; frequency, relative abundance, and cover were determined. On Windberg Key this was done for every plant.

An entire day was usually spent at the plots, observations being made between 0700 and 1800 hours (roughly the diel activity period of *C. pinguis*). Investigations of lizard population structure, density, biomass, and home range usually employ mark and recapture techniques or at least some means of individual recognition. Past experience with adult *Cyclura* species, however, argues against mark and recapture because the initial capture frightens an individual so much it may abandon the area. On Cayman Brac, on two separate occasions, adult male *C. macleayi caymanensis* were captured for inspection; upon release they fled and were not seen again. A similar experience at the beginning of my study occurred at the east end of Anegada. Fortunately, these lizards usually exhibit several distinctive features (scars, missing digits, color pattern, etc.) making recognition simple, even from a distance of several meters. Most juveniles on Windberg Key were not distinctly featured; hence marking was essential. Various designs were painted at the base of their tails for recognition.

Iguanas and their main retreats were assigned a number. Characterizing features, sex, age class, approximate snout-vent length (SVL) and weight (juveniles were measured and weighed), air and substrate temperatures, position in relation to the "center of activity" (to be discussed below), time of day, and date were recorded.

Adult *C. pinguis* were secured only with some difficulty. The easiest way was to chase them into their holes and (if the holes were short) either noose them or annoy them until they surged from the hole and could be grabbed. Pulling iguanas from holes often required the assistance of a native. *Cyclura*, as do *Conolophus* in the Galápagos Islands (Carpenter 1969), often entangle their legs among roots on the sides of the holes. This, in addition to inflation of the body, makes them difficult to extricate. *C. pinguis* adults could never be approached close enough in the open to be caught by hand or noose. Juveniles were collected by any of the above methods or by hand as they hid beneath rocks.

All measurements were recorded to the nearest millimeter, weight to the nearest

0.10 of a pound and converted to kilograms. These data were secured for adults in the Citron Bush at the conclusion of the study.

All temperatures were measured in the shade with a Schultheis quick-recording thermometer. Body temperatures of the lizards were taken cloacally and externally on the flank. Substrate temperatures were measured at the point occupied by the observed iguana; air temperatures about 200 mm above that point. Water temperatures were taken at a depth of 150 mm.

Humidity data were gathered with a standard meteorological sling-psychrometer. Readings were taken four times daily at a central point on the main study plot.

Food preferences were determined by analysis of stomach contents and fecal droppings. Plants seen being consumed by *C. pinguis* were identified.

Unless otherwise indicated, ranges are followed by means in parentheses. Preserved material from Anegada and the Dominican Republic is deposited in the collection of Albert Schwartz.

Sample sizes in this study were small. For example, only five animals were examined for stomach contents. As inadequate as this might appear, it is absolutely essential when investigating most *Cyclura* populations because of low population numbers. Many populations are dense but very small because of specialized habitat preferences. Sampling to the extent that most biologists would consider satisfactory would obliterate some populations (e.g., *C. macleayi lewisi* on Grand Cayman or any of the tiny-island populations in the Bahamas).

ENVIRONMENTAL CONDITIONS

CLIMATE.—In general, the climate of the Virgin Islands is tropical, with insolation reaching its greatest intensity in the spring (Stone 1942). The mean annual rainfall varies greatly, ranging from 88.9 to 177.8 cm

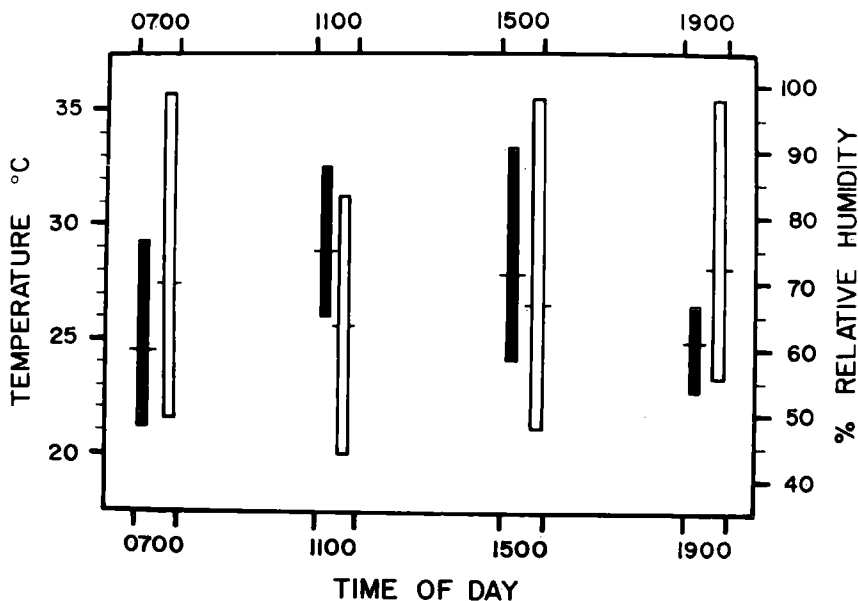


FIGURE 3.—Diel ranges and means of air temperature (black bars) and relative humidity (white bars) in the Citron Bush, Anegada, British Virgin Islands, 27 March-5 May 1968.

at the various stations. Two rainfall maxima occur annually, a small one in May or June and a larger one in October.

During this study, shade temperatures were taken in the Citron Bush at least four times daily at 0700, 1100, 1500, and 1900 hours and were incidental to studies of activity cycles of *C. pinguis*. The maximum temperature recorded during the period of observation was 33.4°C on several occasions; the minimum was 21.1°C during three late-March mornings. Ranges, means, and humidity data are given in Fig. 3. In the Dominican Republic, temperatures in the shade ranged from lows of 29.4°C to 31.1°C at the beginning of *Cyclura* activity (around 0700 hours) to highs of 37.4°C to 41.0°C between 1300 and 1600 hours.

Rainfall was not measured, but showers were frequent during the first week of the study. After 3 April it rained only five more times. The entire West Indian region had been suffering under drought conditions for some time prior to the study.



FIGURE 4.—Typical xerophytic thorn forest habitat of *Cyclura* in the West Indies. Photo taken 10 February 1965 on Cayman Brac, British West Indies.

VEGETATION.—The vegetation on Anegada is typical Antillean xerophytic thorn forest or scrub formation (Fig. 4). The beach around most of the island supports either shore scrub and pioneer vegetation or mangrove, *Rhizophora mangle*. Vegetation on the sandy plain to the west is rather dense and coppice-like in some areas. The loblolly tree

(*Pisonia rotundata*), boxwood (*Bumelia obovata*), and seagrape (*Coccoloba uvifera*) are common. Because of its porosity, the eastern rocky plain is more arid. Principal plants are seagrape, agave (*Agave* sp.), cacti (*Melocactus intortus* and *Pilosocereus royenii*) and poiknerboy (*Pithecolobium bahamense*). Epiphytes such as *Tillandsia utriculata* are common on trees all over the island.

The greatest concentrations of *C. pinguis* were in the xeric limestone regions. Iguanas were relatively rare on the sandy plain, except on the numerous limestone outcroppings forming peninsulas or islets in the salt ponds. Rocky areas were possibly inhabited in preference to sandy ones because of the abundance and diversity of refuges.

The Citron Bush is an ecotone between the sandy and rocky plains. A composition analysis of its vegetation and that of Windberg Key appears in Table 1. The vegetations of Cedar Well Key and Low Key are similar to that of Windberg Key.

VERTEBRATE ASSOCIATES.—Few other vertebrates inhabit Anegada. Apparently there are no naturally occurring predators or competitors to adult *C. pinguis*. However, introduced domestic animals have become

TABLE 1.—PERCENT RELATIVE ABUNDANCE, FREQUENCY, AND COVER OF VEGETATION ON THE TWO STUDY PLOTS ON ANEGADA, BRITISH VIRGIN ISLANDS, 27 MARCH-5 MAY 1968.

Species	Citron Bush		Windberg Key
	Percent Relative Abundance	Percent Frequency	Percent Relative Abundance
<i>Conocarpus erectus</i>	2.7	30	62.4
<i>Cassine xylocarpa</i>	1.4	50	
<i>Colubrina arborescens</i>	9.1	100	
<i>Lantana reticulata</i>	11.6	70	
<i>Tabebuia heterophylla</i>	3.5	60	
<i>Plueria alba</i>	6.3	80	
<i>Crossopetalum rhacoma</i>	6.0	80	
<i>Strumphia maritima</i>	2.9	50	
<i>Coccoloba uvifera</i>	1.8	50	
<i>Pithecolobium bahamense</i>	12.8	100	24.8
<i>Pisonia rotundata</i>	3.4	30	
<i>Vallesia antillana</i>	0.1	10	
<i>Croton discolor</i>	8.8	50	
<i>Randia aculeata</i>	2.4	40	
<i>Amyris diatrypa</i>	5.2	60	
<i>Ziziphus rignoni</i>	1.4	70	
<i>Eugenia procera</i>	0.1	10	
<i>Reynosa uncinata</i>	0.3	10	
<i>Zanthoxylum flavum</i>	0.7	40	0.8
<i>Agave</i> sp.	4.9	70	
<i>Bursera simarouba</i>	0.2	20	0.8
<i>Bumelia obovata</i>	0.2	20	11.2
<i>Melocactus intortus</i>	5.4	90	
<i>Opuntia</i> sp.	1.8	30	
<i>Pilosocereus royenii</i>	12.8	100	
Percent cover		46	61

TABLE 2.—VERTEBRATE ASSOCIATES OF *Cyclura pinguis* IN THE CITRON BUSH, ANEGADA, BRITISH VIRGIN ISLANDS, AND THEIR KNOWN OR POSSIBLE INTERRELATIONSHIPS.

Possible or Known Competitors	Possible or Known Predators	Relationships Unknown
Mammals		
<i>Bos taurus</i>	<i>Homo sapiens</i>	<i>Artibeus jamaicensis</i>
<i>Sus scrofa</i>	<i>Sus scrofa</i>	<i>Mus musculus</i>
<i>Equus asinus</i>	<i>Felis catus</i>	
<i>Capra hircus</i>	<i>Canis familiaris</i>	
<i>Ovis aries</i>	<i>Rattus norvegicus</i>	
Birds		
<i>Falco sparverius</i>	<i>Falco peregrinus</i>	<i>Zenaida asiatica</i>
<i>Mimus polyglottos</i>	<i>Falco sparverius</i>	<i>Zenaida macroura</i>
<i>Tyrannus dominicensis</i>	<i>Buteo jamaicensis</i>	<i>Columbigallina passerina</i>
	<i>Crotaphaga ani</i>	<i>Anthrocothorax dominicus</i>
	<i>Fregata magnificens</i>	<i>Coereba flaveola</i>
	<i>Mimus polyglottos</i>	<i>Dendroica petechia</i>
Snakes		
<i>Alsophis portoricensis</i>	<i>Alsophis portoricensis</i>	<i>Typhlops richardi</i>
Lizards		
<i>Anolis cristatellus</i>	<i>Ameiva exsul</i>	<i>Sphaerodactylus macrolepis</i>
<i>Anolis pulchellus</i>		
<i>Ameiva exsul</i>		
<i>Mabuya mabouya</i>		
Frogs		
<i>Leptodactylus albilabris</i>		

increasingly important in these respects (Table 2). Under pristine conditions *C. pinguis*, at present omnivorous (albeit primarily herbivorous), probably occupied several trophic levels concurrently. Juveniles and eggs were probably subjected to some natural predation just as they are today. The colubrid snake, *Alsophis portoricensis anegadae*, was commonly reported by natives to feed on juveniles, as was *A. cantherigerus* on the Caymans (Carey 1966). *Alsophis portoricensis* also has been reported to feed on other lizards similar in size to juvenile *Cyclura* (Schmidt 1920, Grant 1932). Predatory birds such as *Falco sparverius* and *Buteo jamaicensis* are almost certainly a constant threat to juveniles. Hawks, owls, gulls, and herons feed on young marine iguanas, *Amblyrhynchus cristatus*, in the Galápagos (Carpenter 1966). Hatchling *Cyclura* on tiny islands in the Bahamas are almost certainly vulnerable to such predators, especially gulls and herons.

The teiid lizard, *Ameiva exsul* (Wolcott 1924), and several resident passerines (e.g., *Mimus*) are occasional lizard-egg feeders and possibly prey on eggs of *C. pinguis*. Mockingbirds (*Mimus*) feed on *Amblyrhynchus* eggs in the Galápagos (Carpenter 1966).

Important natural competitors of *C. pinguis* were presumably few and essentially the same as those today (Table 2). Seemingly, only herbivorous birds and insects could have competed with adult *C. pinguis*

for food, and these were probably of minor influence. Juvenile iguanas were probably subjected to considerably more competition since they were insectivorous as well as herbivorous. They would have been sensitive not only to the feeding activities of adults and their competitors, but also to the numerous resident insectivores (Table 2), including birds, several lizards, and possibly a frog.

About 300 years ago the ancestors of the present native human colony (which now numbers about 200, all living in The Settlement) arrived on Anegada and brought dogs, cats, goats, cattle, donkeys, pigs, and sheep with them. Although most of these animals abound on the island today, it is impossible to detect what effect they may have had on the relationships of *C. pinguis* with the natural fauna. Iguanas continue to occupy the same consumer levels, but apparently now lead a more competitive existence.

Natives say that dogs feed on both the eggs and juveniles of *C. pinguis* and occasionally will run down and kill adults. I witnessed this on one occasion on Anegada. Dogs and domestic pigs are known to prey on eggs and juveniles of other large iguanines (Hirth 1963a, Carpenter 1965, 1966, Rand 1968). Cats probably affect only juveniles.

Herds of goats and cattle overlap considerably with the greatest concentrations of iguanas, feeding on brushy undergrowth and possibly increasing exposure of juvenile iguanas to predators. In addition, elimination of this brush may increase the difficulty of food procurement for the young iguanas directly and through resulting decreases in insect density.

Windberg Key apparently supports very little vertebrate life other than *C. pinguis*. Only *Anolis cristatellus wileyae*, *Sphaerodactylus macrolepis macrolepis*, *Alsophis portoricensis anegadae* and the Antillean mango, *Anthracothorax dominicus* were in evidence. No mammals were seen. As no domestic animals inhabit Windberg Key, it seems probable that resident iguanas lead a more natural life than their main-island counterparts. If the domestic animals invaded Windberg Key, *C. pinguis* would very likely be eliminated.

On 13 April, I observed the morning activity of a female in the Citron Bush. She faced southwest about 20 m from her retreat. A bananaquit, *Coereba flaveola*, flitting about had no apparent influence on the iguana until it emitted a shrill whistle. The iguana immediately turned 180°, fled to its retreat, and entered after hesitating for a moment at the entrance.

A blind snake, *Typhlops richardi catapontus*, was collected about 80 mm below the surface just inside a cavity occupied by a male iguana. In the Dominican Republic I frequently encountered curly-tailed lizards,

Leiocephalus schreibersi, about 2 m inside iguana burrows, generally during the heat of the day or at night.

PARASITES.—No dissections were made for endoparasites in *C. pinguis*, but other forms of *Cyclura* (*carinata* [Dosse 1938], *macleayi caymanensis* and *macleayi lewisi* [Grant 1940b], and *macleayi macleayi* [Barus *et al.* 1969]), host several nematode species. *Cyclura ricordi* and *C. cornuta*, autopsied upon return from the Dominican Republic, also hosted several nematodes. Those in *C. cornuta* were identified as *Atractis cruciata* (John Lewis, pers. comm.).

I have observed ticks of various species on all of the above iguanas, as well as on *C. rileyi*, *C. figginsi*, and *C. stejnegeri*. Several are discussed by Robinson (1926). A series of 59 ticks taken from *C. pinguis* represented a new species, *Amblyomma antillorum* (Kohls 1969). About 20-30 ticks per lizard were found only on adult *C. pinguis*, most frequently in the area of the femoral pores and in the thoracic region.

No ticks were found on 17 *C. ricordi* examined. *C. cornuta* (N=10) was infested by *Amblyomma albopictum* in the same areas as described for *C. pinguis*.

GENERAL FEATURES OF THE LIZARDS

Cyclura pinguis is one of the largest members of the genus. There was a highly significant difference ($t=5.772$; $P<.01$) in SVL between adult males and females in the Citron Bush (Table 4), and for all adults for which data were obtained ($t=4.359$; $P<.017$ [data extracted from Fig. 5]). Adult males in the Citron Bush averaged 534.50 ± 3.88 mm SVL; adult females 468.00 ± 10.87 mm.

There also was a highly significant difference ($t=8.000$; $P<.01$) in body weight between adult males and females in the Citron Bush (Table 4), and for all adults for which data was obtained ($t=6.621$; $P<.01$ [data extracted from Fig. 5]). Adult males in the Citron Bush averaged 6.72 ± 0.21 kg in body weight, adult females 4.75 ± 0.13 kg.

Adults of both sexes are dull, olive-gray above with columns of turquoise (sometimes green) dots (ca 2 mm in diameter) extending downward from the dorsal crest to the lateral fold. Beginning at or below the fold are reticulations of turquoise and brown, fading on the belly to blue-cream. The head is olive-brown, the throat and gular pouch lighter. The tail is blue dorsally, fading to dull brown posteriorly. Limbs are blue above, each scale bordered in black, and tan to cream below. Spines of the dorsal crest vary considerably from shades of blue to black.

Aside from being larger (Fig. 5), males have proportionally much larger heads, with the temporal region and jowls obviously being more "swollen." Both sexes possess a prominent, fatty dorsal ridge (Figs. 1,

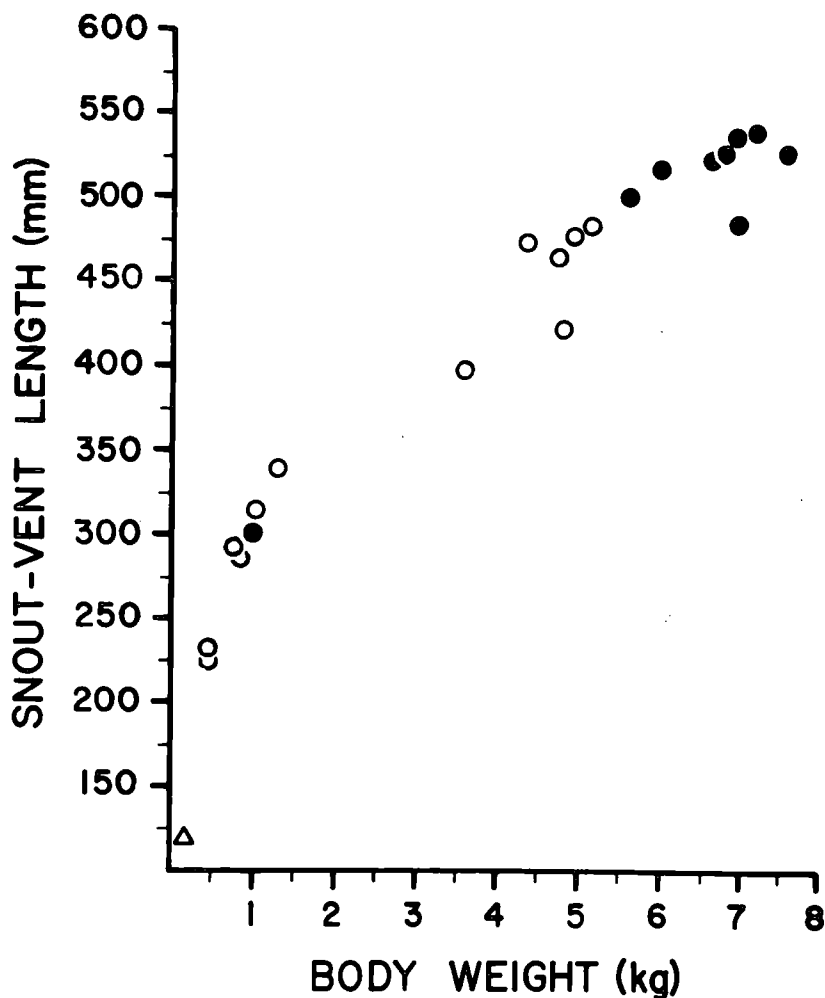


FIGURE 5.—Length-weight relationship for *Cyclura pinguis* (N=22), Anegada, British Virgin Islands. Black dots, males; white dots, females; triangle, sex unknown.

7), although in males the ridge is somewhat higher than in females. The above characters permit immediate recognition of sexes. In addition, the longest spines of the dorsal crest are usually about 18 mm in males, whereas they are about 10 mm in females. Also, the tail base of males is more laterally compressed than in females.

Cyclura ricordi is somewhat smaller than *C. pinguis*; the adult males range from 315 to 400 mm (\bar{x} =355 mm, N=4) SVL, and adult females range from 308 to 365 mm (\bar{x} =340 mm, N=3).

Cyclura ricordi is powder blue to tan above, darker to black below.

There are four to five white bands on the flanks that are bordered in black and end on the belly. The arms are black above, lighter below; the legs olive-blue. The spines of the dorsal crest are blue or black and about 15 mm high. Juveniles are generally somewhat darker than adults.

Cyclura cornuta is the same general size as *C. pinguis*. Adults range from uniform gray-brown to nearly black dorsally and lighter ventrally. The juvenile pattern (tawny bands interspersed with cream dots) is obscured in adults. The limbs are usually olive, the head rusty in juveniles and dark brown in adults.

Rhinoceros iguanas are unique in that the sclerotic coats of the eyes are light metallic brown rather than some shade of red as in all other known extant *Cyclura* species. Individuals of both this and the preceding species are difficult to sex externally.

The local name of all three of these lizards is "guana;" this term apparently is uniform for all *Cyclura* populations throughout the West

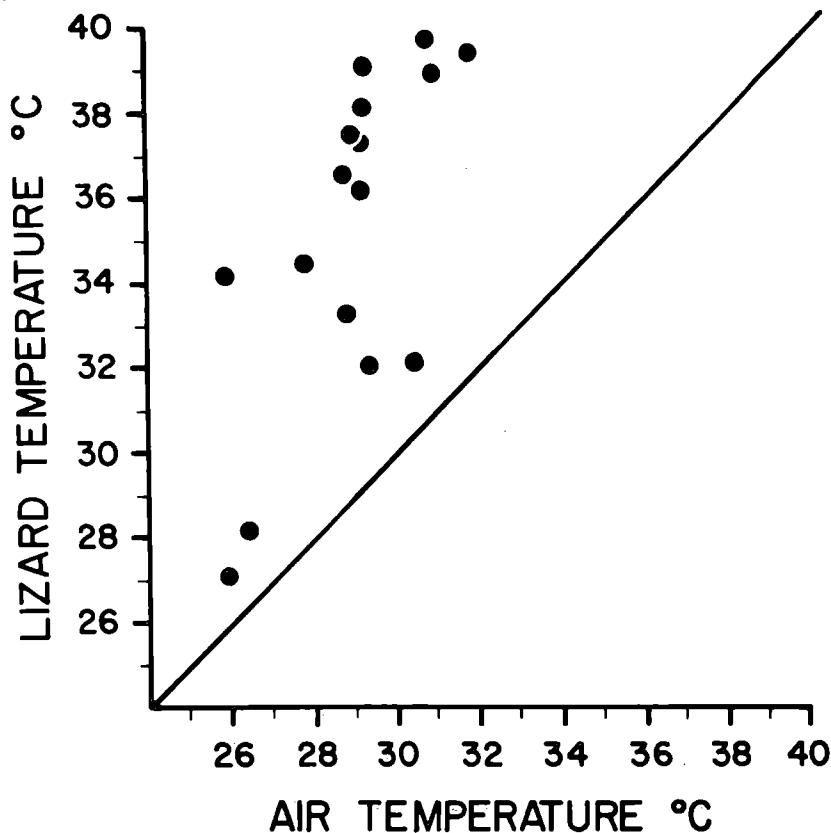


FIGURE 6.—Relation of ambient and body temperature at time of capture for active *Cyclura pinguis* ($N=16$), Anegada, British Virgin Islands.

Indies, regardless of the country. On Anegada juveniles are called "four o'clocks."

THERMAL RELATIONSHIPS

FIELD WORK.—Because of the relatively few iguanas on Anegada and my reluctance to upset their daily routines, temperature data for only 16 animals were obtained. These data were procured on sunny days, usually after 1100 hours, so the lizards had ample opportunity to reach desired activity temperatures. The distinct differential between ambient and cloacal temperatures (Fig. 6) clearly indicates that *C. pinguis* is a heliothermic lizard. In the strict sense, heliothermy merely implies that heat gain in an ectothermic animal is obtained principally through solar energy (Cowles 1940). It does not necessarily suggest that some form of *behavioral* thermoregulation occurs, although that possibility is not ruled out. Heath (1964) pointed out that even though many reptiles are fully capable of regulating their body temperatures behaviorally, they can also attain and retain equable temperatures without need of active regulation. Perhaps the most striking of the several examples of behavioral thermoregulation described for lizards is that of the marine iguana on the Galápagos. In this species "prostrate" or "elevated" basking postures are assumed in accordance with time of day, intensity of solar radiation, and body temperature (Bartholomew 1966).

Behavioral thermoregulation can be seen in the daily activity pattern of *C. pinguis*, which agrees closely with that seen in *C. macleayi caymanensis* (Grant 1940b, Carey 1966). *Cyclura pinguis* usually appears each day shortly after 0700 hours, when ambient temperatures average around 25°C. Upon emergence they walk to the nearest patch of sunlight and assume a prostrate basking posture similar to that described for *Amblyrhynchus*. Prostrate basking in *C. pinguis* consists of lying flat on the belly with the limbs extended in "spread eagle" fashion (Fig. 7).

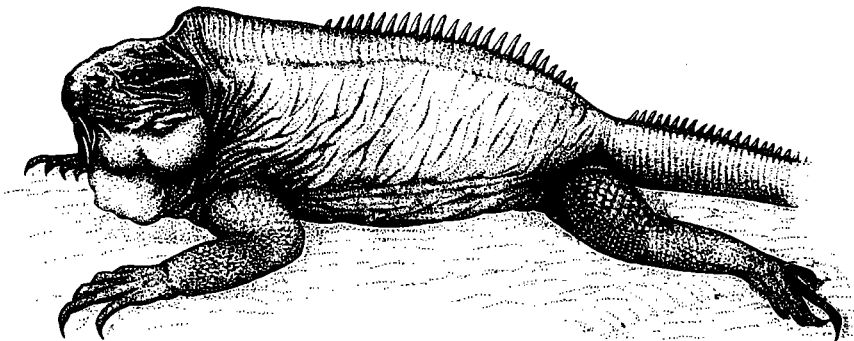


FIGURE 7.—Adult male *Cyclura pinguis* in typical prostrate basking posture. Note extension of limbs.

In *Amblyrhynchus* the head and neck are laid flat; in *C. pinguis* the head is elevated.

About 1 hour later, apparently after reaching a desired body temperature, they rise on their arms to a semielevated position. At this time (ambient temperature ca 27°C) they begin to move about in search of food, stopping every few steps to taste bits of material around them. Basking continues after feeding, rarely in full sun but in a sun-and-shade mosaic among bushes, similar to that utilized by the green iguana, *Iguana iguana*, at San Blas, Nayarit, México (McGinnis and Brown 1966). Throughout most midafternoons, when ambient temperatures hovered around 30°C, *Cyclura pinguis* was seen in partial or full shade. In later afternoons, from 1500 to 1800 when temperatures generally dropped below 30°C, *C. pinguis* again came out into exposed places, usually near a retreat. No iguanas were seen after this time, when temperatures usually fell below 26°C. Coolest ambient temperatures at night (usually after 0100) averaged 22°C. Iguanas observed after sunset were always in their holes and presumed sleeping.

Elevated basking was not observed in *C. pinguis*, and probably would be of little use to a form able to utilize the shade and filtered insolation of brushy areas. On the other hand, *Amblyrhynchus* spends the entire day on the barren lava coasts of the Galápagos Islands, with no shady retreats available. Elevated postures allow them to maintain body temperatures below the lethal threshold while in direct sunlight (Bartholomew 1966).

Insufficient data for reliable determination of eccritic temperatures were obtained. Cloacal temperatures secured from 16 active animals ranged from 27.1°C to 39.8°C (35.29°C); 56% of the records were greater than 36°C, and 25% ranged from 39°C to 39.8°C. This contrasts with mean activity temperatures of 31.98°C for *Conolophus subcristatus*, 35.13°C for *C. pallidus* (Carpenter 1969), and 36.1°C for green iguanas, *Iguana iguana* (McGinnis and Brown 1966). Means slightly greater than 34°C were observed by Carpenter (1966) for marine iguanas on several islands. Bartholomew (1966) indicated a preferred temperature range of 35° to 37°C for these lizards.

The first several days of the study (late March) were characterized by cool, blustery weather that had no profound effect on *C. pinguis*. Midmorning temperatures at that time averaged in the low 20's, and it was windy and overcast. Though air temperature may have an indirect effect on daily activity of these iguanas, it may not be the main influencing factor. Milstead (1957a, b) found that light intensity and/or soil temperature governed *Cnemidophorus* activity in southwestern Texas, and this may also be true of *C. pinguis*.

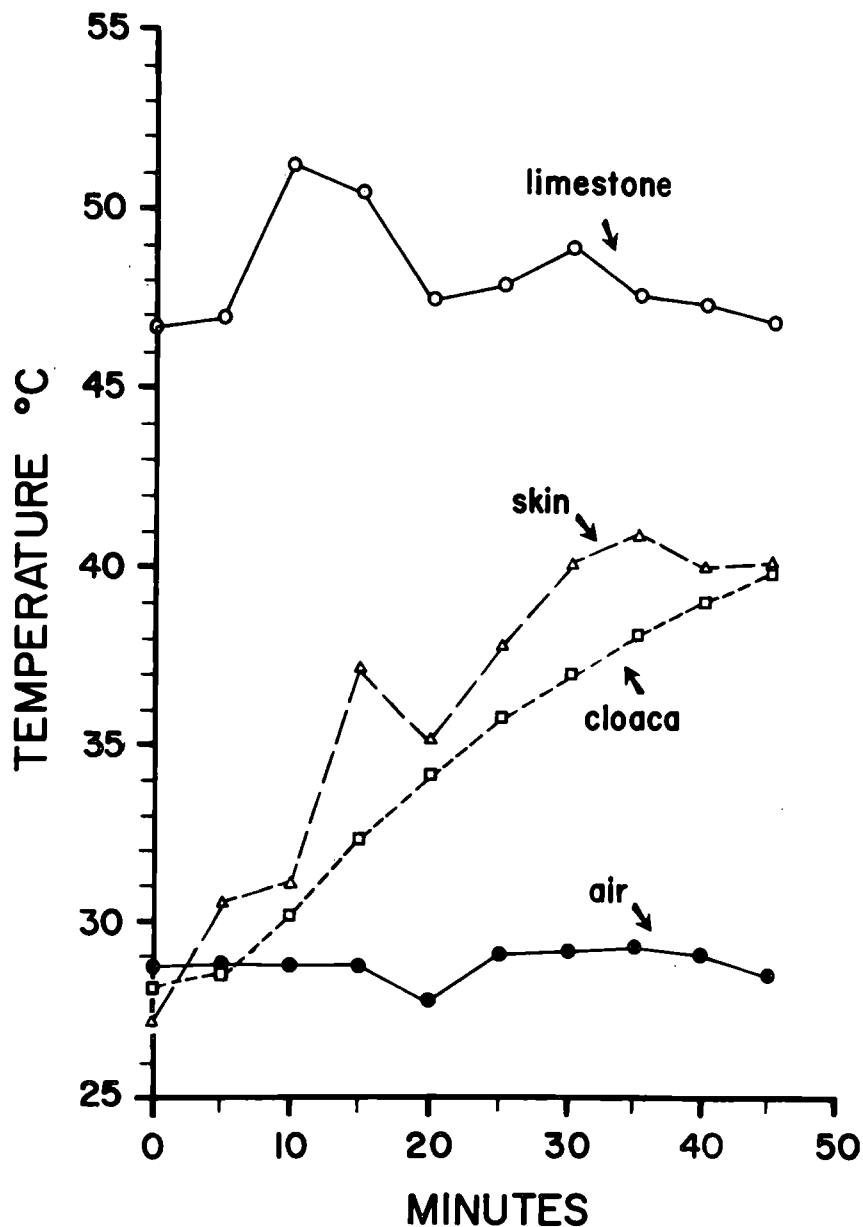


FIGURE 8.—Relation of skin and cloacal temperatures to environmental temperatures in a juvenile *Cyclura pinguis* (772 g), Anegada, British Virgin Islands. Lizard was placed in full sunlight at 1400 hr, 2 April 1968. Thin cloud cover lasting 6 min began at T_{17} ; maximum wind velocity about 12 km/hr.

Although torrential rains drove *Cyclura pinguis* into their burrows, light steady rainfalls were apparently not annoying. Light rain may have a desirable cooling effect, as adults were seen in the open during several steady downpours. I have kept many *Cyclura* species in outdoor enclosures in southern New Mexico, where ambient temperatures usually exceeded 35°C by noon each summer day. Adults usually basked most of the morning. Often as I sprayed the iguanas with a garden hose, they followed the spray around the pen for about 10 minutes and then were wary of it. On several occasions they raised up on their toes, apparently

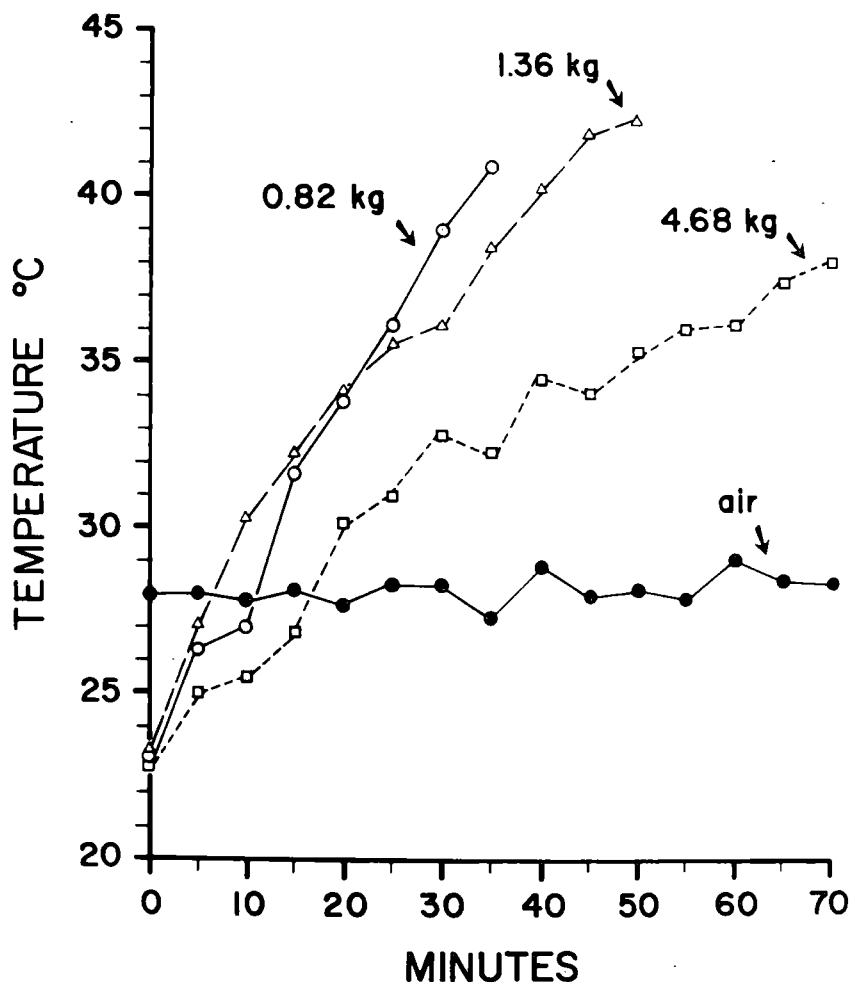


FIGURE 9.—Relation of heating rate to body size in *Cyclura pinguis* (N=3) on Anegada, British Virgin Islands. Lizards were placed together in full sunlight at 1000 hr, 20 April 1968; maximum wind velocity about 8 km/hr.

to avoid contact with the hot, sandy surface, which averaged 60°C during the hottest part of the day.

EXPERIMENTAL WORK.—Bartholomew (1966) indicated a need for additional experimental work on the thermal relations of large lizards. Although a comprehensive coverage of the thermal relations of *Cyclura* is beyond the scope of this paper, limited data on the heating rates of various sized *C. pinguis* in relation to environmental temperatures are useful (Figs. 8, 9). In both experiments, animals were tied at the waist and placed in full, midmorning sunlight. The method gave them free movement and allowed them to thermoregulate. Dorsal skin, air, and substrate temperatures were measured at 5-minute intervals until panting began, usually around 40°C. Panting apparently enables the animals to remain longer within their range of thermal tolerance. The rapid flow of air over the blood engorged tongue permits dissipation of slightly more heat than is produced metabolically (Kour and Hutchison 1970). Data for marine iguanas closely agree with this figure (Bartholomew 1966), but green iguanas begin panting at a slightly higher temperature (ca 42°C) (McGinnis and Brown 1966). Frantic efforts to escape usually accompanied panting in *C. pinguis*, and they were then quickly placed in the shade.

A juvenile weighing 772 g was used to determine the relation of skin and cloacal temperatures to air and substrate temperatures. Primary sources of heat gain (insolation and conduction from substrate) caused panting in forty-five minutes, at a temperature of 39.8°C. Although skin and body temperatures remained close throughout (skin was always at least 1° higher), they had nearly equalized when panting began (Fig. 8). These data are in agreement with that obtained by Kour and Hutchison (1970) for other lizards.

An indication of body size-heating rate relationships was obtained by tethering three animals of different weights (0.82, 1.36, and 4.68 kg) simultaneously. As in marine iguanas (Bartholomew 1966), rates of heating were related inversely to body weights (Fig. 9).

RETREATS

Little has been recorded concerning retreats of *Cyclura*. Gosse (1848) did not mention holes as retreats of *C. lophoma* (= *C. collei*) on Jamaica, but stated (upon another's observations) that they lived in trees. Lewis (1944) observed *C. lophoma* in trees (at least 3 m above ground) and *C. macleayi caymanensis* commonly basking on *Conocarpus* branches. This and the Grand Cayman form, *C. macleayi lewisi*, usually favor natural cavities as retreats (Grant 1940b, Carey 1966). Climbing has also been documented for *C. rileyi* on San Salvador (= Watlings

Island) in the Bahamas (Stejneger 1903, Paulson 1966) and *C. macleayi* on Cuba (Cooper 1958), but they too retreat into holes among the rocks. *Cyclura cornuta* on Ile de la Petite Gonâve lives in the crevices in coral rock (Klingel 1929). I saw this lizard in the hills bordering Lago de Enriquillo in the Dominican Republic, but found that there they dig burrows in the sand as well as in the fossil coral cliffs as earlier reported by Noble (1923). *Cyclura ricordi* also burrowed in the hills bordering the lake. On Isla Cabritos, they lived only among crevices in rocks. Several Bahaman forms (i.e. *C. nuchalis* and *C. carinata bartschi* [Cochran 1934], *C. figginsi* [Bailey 1925, Wayne King, field notes, Tony Granés, pers. comm.], *C. inornata* [Rabb and Hayden 1957, Wayne King, field notes], and *C. baeolopha* [Wayne King, field notes]) prefer natural cavities. Sutcliffe (1952) and Hardy (1956) observed both burrowing and retreating to limestone cavities in *C. macleayi macleayi* in Cuba and adjacent islands. Burrows extended to nearly 3 m in length and had no enlarged chambers. Burrows of *C. ricordi* and *C. cornuta* were much longer (ca 10 m) and also lacked chambers.

In the Citron Bush, *C. pinguis* used burrows or natural cavities in the limestone, excavations beneath large limestone slabs, or cavities formed under large overlapping slabs that were raised slightly by the root system of a loblolly tree (*Pisonia rotundata*) as refuges. Only one adult male was observed outside of a limestone area. His retreat was a burrow, presumably self-excavated.

Immatures on Windberg Key used only slabs as retreats. A single slab often harbored as many as five iguanas beneath it. A very young individual in The Settlement lived in a pile of debris in an abandoned hut, and I never observed it more than a few meters from the debris.

Refuge entrance sizes ranged from holes just large enough for an adult to squeeze through to some much larger than an iguana. Refuges ran parallel to the surface, usually not more than 1 m deep, and varied in length from a minimum of about 2 m to an indeterminate maximum far into the limestone. Refuges contained moist soil and forest litter in the immediate interiors, with swarms of mosquitos at the entrances and in the moist interiors.

Excavations in limestone slabs probably offer considerably less security because of the short distance between entrance and terminal chamber (often less than 2 m), but still provided sufficient concealment. A typical slab was about 4 m² and about .25 m thick.

Cavities formed by roots of loblolly trees seem to offer much more security. The roots grew beneath and onto the slabs, forming extremely sturdy refuges. The cavities were not deep, but wound around wherever roots were growing, to form a maze.

Cyclura macleayi macleayi (Buide 1951) and *C. macleayi caymanensis* (Carey 1966) flee from intruders in short spurts, repeatedly stopping to bob and hiss, while *Cyclura pinguis* rushes directly to the hole, rarely hesitating at the entrance. Both *C. ricordi* and *C. cornuta* retreat in spurts before finally entering their burrows, as does *Conolophus* in the Galápagos Islands (Carpenter 1969).

Once *C. pinguis* individuals enter their holes, they may not come out for a surprisingly long time. When I approached the Citron Bush at 0900 on 14 April, an adult female entered her refuge and stayed there. At 1345 I found her still lying in the terminal chamber. On 19 April an adult male reemerged 2 hours and 47 minutes after having taken refuge.

It is well known that marine iguanas enter the sea for feeding purposes, but they will not willingly enter the sea for escape unless their body temperatures are approximately that of the water (Bartholomew 1966). An iguana just leaving the sea will quickly drop back if approached, but a basking individual cannot be induced to retreat to the water.

Only *C. cornuta* (Noble 1923) and *C. macleayi macleayi* (Hardy 1956, Lando and Williams 1969) are known to retreat to water. Gosse (1848) stated that his captive *C. lophoma* (= *C. collei*) readily took to water, but not necessarily as a retreat. An adult male *C. pinguis* on Cistern Well Key often entered the water when disturbed. Temperature seemed to have little influence on his behavior. On 7 April, after recording his cloacal temperature, I placed him on the ground, and he immediately took flight into Red Pond. At that time his cloacal temperature was 40.2°C and the water was 27.5°C. He tried to dive, but the water was too shallow. On the morning of 12 April, his temperature was 37.0°C and the water was 27.9°C. Upon release his behavior was identical to that described above. On four subsequent occasions he entered the water upon my approach. I assume, therefore, that *Cyclura*, unlike *Amblyrhynchus*, can and will use water as a retreat regardless of the difference between body and water temperature.

FOOD AND FEEDING BEHAVIOR

In nearly all *Cyclura* studies vegetation was recorded as the primary food in the wild. *Cyclura lophoma* (= *C. collei*) was observed feeding on the "guinea-hen weed" (*Petiveria* sp., Gosse 1848). On Cayo de la Piedra *C. macleayi macleayi* reportedly feeds principally on *Opuntia* buds, but eats crabs also (Sutcliffe 1952). On Little Cayman, *C. macleayi caymanensis* has been observed feeding on bay vine (*Ipomoea pes-caprae*), broad leaf (*Cordia caymanensis*), and guana berry (*Erno-*

dea littoralis) (Grant 1940b). On Cayman Brac they often raid cultivated areas, feeding on potato vine, plums, mangoes, and fallen pawpaws (Grant 1940b, Carey 1966). *Cyclura stejnegeri* on Isla Mona was observed feeding on *Tribulus cistoides* (Martin 1966). The literature is extensive regarding the herbivorous habits of other iguanine genera.

Examination of stomach contents of five animals revealed that vegetation composed a major part of the diet of adult *C. pinguis* (Table 3). Grasses and leaves were the most common items. Analysis of scat composition supplemented this analysis, although most of the plant material was unidentifiable. One adult female (400 mm SVL) contained four lepidopteran larvae, each about 75 mm long and 12 mm in diameter. Grant (1937) found seagrape leaves, cactus fruit, and "wild nutmegs" in the stomachs of two adults. Underwood (1962) suggested that *C. pinguis* fed on cactus shoots, fruits, and seagrasses.

TABLE 3.—STOMACH CONTENTS OF ADULT *Cyclura pinguis* (N=5), ANEGADA, BRITISH VIRGIN ISLANDS, INDICATING FREQUENCY AND VOLUME PERCENTS.

Food	Percent Frequency	Percent Volume
Plants		
<i>Conocarpus erectus</i>	60	19
<i>Coccoloba uvifera</i>	20	12
<i>Lantana reticulata</i>	20	4
<i>Reynosa uncinata</i>	40	20
<i>Erithalis fruticosa</i>	40	6
Grasses	20	10
Unidentified	100	14
Insects		
Lepidoptera larvae	20	15

Stomachs of juvenile *C. pinguis* were not examined. It is quite possible that insects form the major food item. Juveniles of several *Cyclura* species (*cornuta*, *figginsi*, *inornata*, *macleayi*, *pinguis*, *ricordi*) kept in the laboratory at various times have shown a marked preference for insects (esp. crickets, grasshoppers, and mealworms) over plant material. Insects are a major food source for *Ctenosaura similis* juveniles in Guanacaste Province, Costa Rica (Roy W. McDiarmid and Dennis R. Paulson, unpubl. data). In addition to most fruits and vegetables, captive *C. pinguis* adults feed on canned dog food and laboratory mice and rats.

Cyclura pinguis is an active forager. Following basking in the morning they move quickly about an area, hesitating every few steps to taste particular objects (pebbles, plants, etc.) in their path. They feed in typical iguanine fashion, snapping off leaves and flowers with a twist of the head or by the jaws alone, often using their forefeet to pull a food item closer. They occasionally climb into low bushes to feed. I saw them actively feeding on the leaves of *Conocarpus erectus*, *Coccoloba uvifera*, and *Pisonia rotundata*.

Stomachs of *C. ricordi* and *C. cornuta* contained exclusively fruits of unidentified cacti. None were observed feeding in the field. In captivity, feeding is identical to that of *C. pinguis*.

"Sneezing" fluid from the nostrils in the form of a fine salt spray was common in each of these rock iguana species. As in other iguanines (Templeton 1964, 1967), this probably is an extrarenal mechanism for ridding the body of excess salt.

HOME RANGE

SELECTION OF HOME RANGES.—Natural cavities (Fig. 10) and loblolly trees occurred in nearly all home ranges of adult iguanas, and because both form refuges it appears that shelter is an important factor in home range selection. In addition, iguanas were occasionally observed resting on the lower (2-3 m high) branches of these trees, as well as in the shade beneath the trees. Though loblolly leaves were never found in stomachs, an adult male was once seen nibbling them.

Selection of mates may also influence the choice of home range sites. An area must be chosen that has sufficient available food as well as

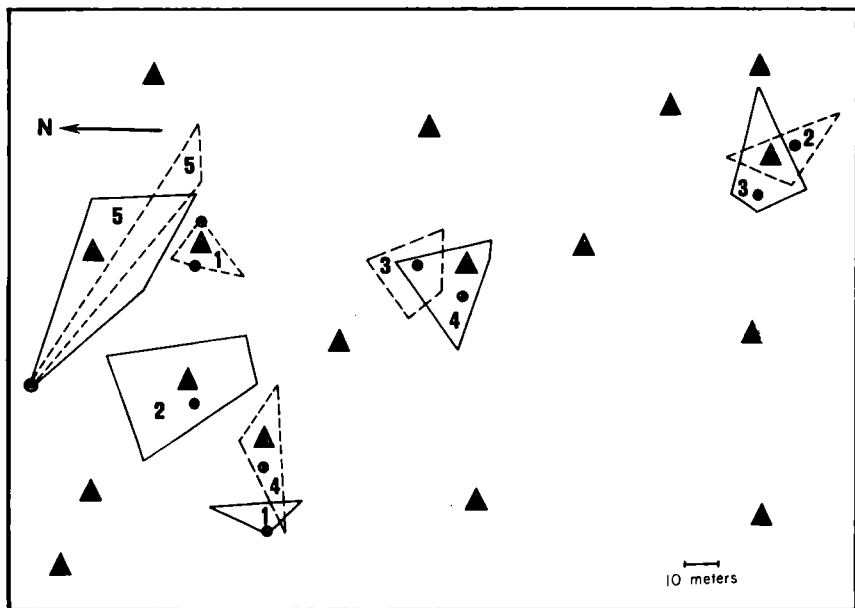


FIGURE 10.—Major segment of Citron Bush showing home ranges of male (solid lines) and female (broken lines) *Cyclura pinguis*. Natural cavities within home ranges are indicated by black dots; other symbols represent loblolly trees, *Pisonia rotundata*.

refuges, because pairs usually occupy overlapping home ranges. All observed pairs on Anegada had refuges 23 m or less apart. One pair (male 5 and female 5) occupied the same retreat.

It has been documented previously (Fitch 1940, Stebbins 1944, Blair 1960, Hirth 1963b, Tinkle 1967) that within the home range of some lizards all daily movements are made from a center of activity. It may serve as a feeding site, place of refuge, or simply as a basking site. The center of activity is not necessarily the geometric center of the home range, though, with one exception, that of *C. pinguis* in the Citron Bush was approximately so. The center of activity of adult iguanas in the Citron Bush was their place of refuge; the trees, the cavities, or both. All travels were made from these refuges and, upon disturbance, the animals immediately returned. Feeding and basking took place at almost any site within the home range, but there seemed to be preferred sites for these activities also.

Several workers (Blair 1960, Tinkle *et al.* 1962, Carpenter 1966) have seen females of some lizards laying their eggs outside of their normal activity area. The first authors suggested that this behavior might be instrumental in the dispersal of hatchlings throughout the population. It is likely that the same behavior will be demonstrated for *C. pinguis*, although it was never directly observed. Home ranges of immatures never overlapped those of adults. In fact no young of any age were observed closer than several hundred meters to the nearest known adults. One immature (probably a hatchling from the previous year) lived in The Settlement, at least 3 km from the nearest known adult. On Cayman Brac, juvenile *C. macleayi caymanensis* were found only in the settlement of West End, about 5 km from the adult population (Carey 1966). C. Rhea Warren (pers. comm.) collected juvenile iguanas at the airport on Cayman Brac, about 5.5 km from the nearest known adults. Natives on both Anegada and Cayman Brac report that females lay eggs in the sandy periphery of each village. I saw a juvenile *C. macleayi lewisi* on Grand Cayman living in a stone fence near native houses, over 4 km from the adults. According to natives, females lay eggs in sandy areas inland from the rocky beach, more than 5 km from any known adults. The attraction to settlements is probably the increased density of insects. In the Dominican Republic, juveniles of *C. ricordi* were seen at the same localities as adults, who apparently have no individual territories.

Each year scores of female green iguanas (*Iguana iguana*) on Barro Colorado Island, Canal Zone, migrate to the tiny island of Slothia in Gatun Lake to lay their eggs (Rand 1968). Rand suggested that this communal nesting results from lack of desirable sites on Barro Colorado

as a result of high population density. Also, migration to the islet serves to decrease predation, which is great on Barro Colorado.

Because some *Cyclura* females may travel substantial distances to lay their eggs, it is possible that *C. pinguis* on Windberg Key hatched there rather than colonizing the islet. There is no evidence for aggregate nesting. However, such nesting habits have been observed in *Amblyrhynchus cristatus* in the Galapagos (Carpenter 1966), *C. cornuta* on Isla Beata, off the southwestern tip of the Dominican Republic (Noble 1923), and *C. stejnegeri* on Isla Mona (Richard Thomas, pers. comm.). All of these are high-density populations.

The principal reasons suggested for nesting on Slothia presently do not hold for iguanas on Anegada. There are many seemingly desirable laying areas other than Windberg Key, and predation on females or eggs other than by such unnatural predators as dogs must be of low magnitude.

The north, south, and east shores of Windberg Key, though very rocky, are a tangle of buttonwood (*Conocarpus erectus*). Activity of the young iguanas is almost completely confined to this protective mass of vegetation. The large slab under which these lizards usually take refuge is located on the east shore amongst the buttonwood. They were occasionally seen basking on the grassy interior of the island. The center of activity would be difficult to designate since the entire tangle of buttonwood was used, with few excursions from it. The only suitable laying site was the sandy area on the west shore.

A juvenile in The Settlement lived in a debris pile inside an abandoned hut. This hut was clearly its center of activity, because it ventured only a few meters away from it each day to feed and bask and fled back to it at the slightest disturbance.

ADULT HOME RANGES.—Home range estimates for adults were obtained using a slightly modified minimum convex polygon method (Tinkle *et al.* 1962). This method entails connecting the outermost points of recapture on graph paper to form a convex polygon, then estimating the minimum home range by computing the enclosed area by any of several techniques. In this study, sightings were used instead of recaptures, and home range areas (Fig. 10) were determined by the extrapolation technique first used for lizards by Jenssen (1970). Home ranges were plotted on graph paper of tested weight consistency (5 pieces of equal size within 0.003 g of each other on a Mettler balance). The plotted home ranges were then cut and weighed on the balance against a piece from the same paper scaled to a known area (334.45 m²). The results closely agree with those obtained by employing a planimeter.

Although territoriality was not directly observed in this study, aggres-

sive behavior is common in iguanids and spacing (members of the same sex separated and those of opposite sex overlapped [Fig. 10]) implies such intraspecific interactions. All iguanas observed in the Citron Bush remained on their home ranges throughout the study. Hence permanent residency in the area during the period of study was assumed.

Males occupied home ranges from 116.06 to 985.11 m² (546.61 ± 160.46 m²; N=5); female ranges were from 155.47 to 412.31 m² (276.48 ± 41.62 m²; N=5) (Table 4). The difference was not significant nor was the product-moment correlation coefficient r value between the log_e of the body weights versus the log_e of home range areas (males and females treated both separately and together). This is difficult to explain biologically, because males were significantly longer and heavier than females. It has been shown that home ranges of birds (Armstrong 1965, Schoener 1968), mammals (McNab 1963), and reptiles (Turner, Jennrich, and Weintraub 1969) are most always related to body weight. As males in all of these classes usually are larger than females, males should occupy larger home ranges. This has been demonstrated already in several lizards (see literature reviews in Tinkle 1967 and Turner *et al.* 1969; Jenssen 1970).

TABLE 4.—HOME RANGE AND LIZARD SIZES FOR ALL ADULT *Cyclura pinguis* IN THE CITRON BUSH, ANEGADA, BRITISH VIRGIN ISLANDS.

Individual	Snout-Vent Length (mm)	Weight (kg)	Number Observations	Home Range Area (m ²)
MALES				
2	545	7.17	6	846.34
1	539	6.95	7	116.06
5	536	6.81	4	985.11
4	531	6.72	3	401.46
3	522	5.95	3	384.09
\bar{X}	=	534.60	4.60	546.61
FEMALES				
4	487	5.13	4	241.98
1	481	4.86	10	155.47
3	426	4.77	4	295.42
5	470	4.68	3	412.31
2	476	4.31	3	277.21
\bar{X}	=	468.00	4.80	276.48

The lack of significant size difference in *C. pinguis* is probably the result of the small sample sizes (five for each sex), leading to extremely high variances. The number of recaptures (sightings in this case) in each sample is quite low also (Table 4). One disadvantage of the minimum convex polygon method of determining home range area is that estimates of home range size tend to increase as the recapture numbers increase (Jennrich and Turner 1969). However in this study, the highest number of sightings within each sample yielded the smallest home

range estimates! In the above paper, Jennrich and Turner provided a correction factor for estimates based on the minimum polygon method, but with few observations. I applied this correction factor to my data but found that the new estimates, when added together, were 16 percent larger than the entire study area (bear in mind boundaries are natural). I concluded that my original home range estimates are likely minimum. However, the fact that low estimates persist as the number of sightings increases all but negates the probability that the estimates would increase significantly with additional sightings. If energy needs control home range size (see below for discussion), herbivory as seen in these iguanas might preclude any need for movements outside the rather small areas shown. It seems that the correction factor of Jennrich and Turner takes into account only the correlation of low home range estimates with few observations, and not the biology of the occupants of those home ranges.

At a reduced probability level the difference in home range area between males and females is significant ($t' = 1.630$; $P < .20$) (the value t' is calculated when sample variances are heterogenous [Steel and Torrie 1960: 81]). I suspect that if sample sizes were larger (in this case only 5 males and 5 females were observed), males would be shown to occupy significantly larger home ranges than females. Also, since some (probably all) females in the Citron Bush proved to be gravid, this may have temporarily forced them into additional areas because of increased energy demands.

The t - and t' - tests for body weight and home range area indicate that males occupy larger home ranges simply because they are larger than females and need more area for energy harvest. Correlation coefficients for the \log_e of body weight versus the \log_e of home range area are low, indicating that body weight may not be a principal factor (although again this could be a product of low sample sizes), but that other parameters may contribute to males having larger home ranges than females.

Male lizards usually are more active than females, especially during the breeding season, but this may be true only for polygamous species. In animals that mate for life (which may be the case here) this would less frequently be a factor, and in territorial forms, males would be apt to patrol more.

Still, the most important factor governing home range or territory size appears to be energy needs. Within the vertebrates, it has been shown that carnivores require more room for food gathering than herbivores or omnivores due to the usually higher relative density of food for the latter (St. Girons and St. Girons 1959, McNab 1963, Schoener 1968, Turner *et al.* 1969). McNab found that carnivorous mammals of a particular weight required home ranges about four times that of herbivorous mammals of the same body weight.

As most lizard studies have been conducted on small insectivorous species, comparisons with *C. pinguis* are difficult. Almost all of these small insectivores (e.g., *Cnemidophorus*, *Eumeces*, *Sceloporus*, *Uta*, etc. [Turner *et al.* 1969]) occupy home ranges markedly larger than that of *C. pinguis*. The only herbivore with available data is the chuckwalla, *Sauromalus obesus* (Johnson 1965). Males of this species are about 1/32 the body weight of *C. pinguis* males and occupy home ranges averaging nearly 10 times those of male *C. pinguis*. This difference likely reflects the much denser vegetation in the study area of the iguana. The desert monitor, *Varanus griseus*, a carnivorous lizard intermediate in weight between the two forms discussed above, occupies home ranges varying from 2 to 5 km² (data converted from Turner *et al.* 1969), nearly 10,000 times the home range size of male *C. pinguis*.

Between home ranges occupied by iguanas of the same sex, there are "neutral zones," or undefended areas apparently used by residents of adjacent territories primarily for feeding (Gordon 1943). In lizards, utilization of neutral zones has been reported for *Agama agama* (Harris 1964) and *Sceloporus merriami* (Milstead 1970). Three *S. merriami* males foraged in a neutral area with no antagonistic encounters; when territorial boundaries were crossed away from the area, antagonistic encounters occurred. Milstead attributed the lack of antagonism to the fact that the three males were outside their territories and thus not defensive. In this paper the phrase "unutilized zone" will be used in place of neutral zone, because I have not proven that territoriality exists in *C. pinguis* and thus cannot unequivocally state that the zones are undefended.

Although my home range data indicate that much of the Citron Bush is unutilized (Fig. 10), I once saw these zones occupied. On 30 April, an adult male and female I had not seen previously were feeding several meters from the east boundary of the home range of adult male No. 5. Upon disturbance they fled the area and were not seen again.

JUVENILES HOME RANGES.—On Windberg Key the study of home range behavior in juveniles was conducted as described for adults, but juvenile home ranges broadly overlapped. In fact, all inhabitants of Windberg Key used the same limestone slab for retreat! Subsequently, I concluded that each iguana was utilizing the entire islet as its home range.

POPULATION DENSITY AND BIOMASS

Relatively low population numbers and the large size of these lizards permitted use of the total count method to estimate population density. Individual features were used in recognition.

Population density did not seem to fluctuate in the Citron Bush during the observation period. Two transients were seen in the unutilized zones, but apparently neither took up residence there. The presence in the Citron Bush and much of Anegada of seemingly suitable but unoccupied habitat must be due to low density of the lizards.

The area of the Citron Bush study site was 4.93 hectares (ha) (ca 12.19 acres) and for Windberg Key 0.28 ha (ca 0.69 acres). The Citron Bush had 10 adult iguanas, or 2.03/ha (0.82/acre); Windberg Key had 7 juvenile iguanas, or 25.00/ha (10.14/acre).

Biomass was determined at the completion of the study by capturing and weighing each animal. The Citron Bush supported 57.35 kg of adult iguanas or 11.63 kg/ha (4.70 kg/acre) and Windberg Key 5.90 kg of immatures or 21.07 kg/ha (8.55 kg/acre).

Tinkle (1967) recently summarized the literature on lizard population density. *Cyclura pinguis* has the lowest density of the few lizards for which data are available. Data on lizard biomass are scarce in the literature. *Cyclura pinguis* biomass/acre is about 10 times greater than that of a Kansas population of *Eumeces fasciatus* (ca 454 g/acre, Fitch 1954), and *Anolis nebulosus* from Nayarit, México (ca 488 g/acre, Jenssen 1970). However food selection and size of the animals must be considered in the comparison.

One might expect that the relatively low population density of *C. pinguis* in comparison to much smaller lizards is due to their great size. Since the *C. pinguis* population is apparently below the carrying capacity, the density figures are somewhat misleading. Should population density increase, unutilized zones probably would disappear. Continued increase could result in reduced home range size. According to Tinkle (1967) and Hunsaker and Burrage (1969), at this point territorial behavior might shift to a social hierarchy. Hunsaker and Burrage suggest that a continuum exists between these two social systems. Hierarchies in iguanines have been observed in *Amblyrhynchus cristatus* (Schmidt 1935, Carpenter 1966) under natural circumstances, and in *Ctenosaura pectinata* (Evans 1951), which shifted from a territorial system in response to increased population density resulting from a rapid increase in food (domestic crop). Hunsaker and Burrage (1969) reported an intergeneric social hierarchy amongst several penned iguanines in the San Diego Zoo. These authors postulated that a continuum would be advantageous, because a species could react rapidly to environmental constraints or sudden increases in space and available food. Social hierarchies apparently also serve to prevent density increase by restricting breeding to dominant animals (Tinkle 1967). Perhaps the groups of iguanas observed on Ile de la Petite Gonave, Haiti (8 *C. cornuta*)

(Klingel 1929) and Cayo de la Piedra, Cuba (4 *C. macleayi macleayi*) (Sutcliffe 1952) represent social hierarchies. Studies of *C. ricordi* in the Dominican Republic suggest some sort of gregarious social structure. Though animals were not seen in groups, their burrows were numerous and less than one meter apart in some places. Juvenile *C. ricordi* commonly were seen in the area, indicating a population structure different from *C. pinguis*.

Possibly some form of hierarchy existed on Windberg Key, even though the residents were immature. Limited access to and from Windberg Key restricted the movements of hatchlings. Distribution of the vegetation and other resources, following division of the habitat into home ranges or territories, might preclude the availability of sufficient resources for every resident. An hierarchial system would permit grazing over the entire key, alleviating the problem, but there were still indications that the two largest inhabitants (314 and 344 mm SVL) were undernourished. Both were lean and bony, with heads proportionally larger than their bodies. Iguanas of equivalent size on the main island were of normal proportions. The skeleton of another iguana of this size class was found on Windberg. The cause of death could not be determined; possibly it died of starvation.

I observed no antagonistic encounters on Windberg Key, but I did observe such behavior in the laboratory. Three *Cyclura* were kept in a pen 2.25 m². A large *C. macleayi macleayi* (female, 325 mm SVL) usually displaced the smaller *C. pinguis* (female, 240 mm SVL) and *C. cornuta* (sex ?, 243 SVL) at the feeding pan and basking sites by bobbing and nipping. *Cyclura pinguis* displaced *C. cornuta* in the same way. These data suggest that *C. pinguis* could develop an hierarchial system, given the necessary circumstances.

POPULATION STRUCTURE AND REPRODUCTION

BREEDING STRUCTURE.—The sex ratio of adult iguanas in the Citron Bush (and at other localities periodically checked) remained a constant 1:1 (5 males, 5 females) throughout the study. In most cases (80%—Citron Bush; 82.4%—Combined sites), a female was seen in company with, or at least in close proximity to, a male. Each case of suspected pairing in the Citron Bush was confirmed by overlapping activity areas (Fig. 10). On 29 March and 25 April, I watched the lone pair on Cedar Well Key feeding side by side. Each time they were disturbed they fled to their respective retreats (located only a few meters apart). On 30 April, I observed a male and female on Low Key walking together

across an area of sparse vegetation. The male trailed the female by about 2 m.

These observations suggest monogamy. This type of breeding system may be a result of intrasexual antagonism, as in *Uta stansburiana* (Tinkle 1967). The layout of home ranges in the Citron Bush suggests intrasexual antagonism and secondary monogamy in *C. pinguis*, but this kind of nonobligatory monogamy should be more common in populations approaching maximum density. In depleted populations, such as those of *C. pinguis*, pressure is lessened and residents have more choice in mate selection since more area could be covered uncontested. Nevertheless, abnormally low population numbers might retain monogamy at the facultative level, since the number of unpaired animals would be limited.

Nothing is known about duration of pairing in *C. pinguis*. Barring disturbances refuges utilized by pairs were usually permanently occupied.

Females usually outnumber males in populations of adult lizards (Blair 1960, Hirth 1963b, Harris 1964, Tinkle 1967), but only one unpaired *C. pinguis* female was seen in the Citron Bush and an unpaired male was present in the same general area (Fig. 10). All unpaired adults observed elsewhere on Anegada were males. Except in one case, the large sizes and general appearance of the females indicated advanced ages. Mortality may affect females more severely than it does males because of increased exposure of females to predators during egg-laying trips. Females distended with eggs would be hampered in their movements, and may also be less wary during this time. Carpenter (1966) observed the laying behavior of female marine iguanas by tunneling into egg-laying burrows from the side without being noticed by the females. Female desert iguanas, *Dipsosaurus dorsalis*, remain underground while carrying eggs (Norris 1953).

Female deaths from cave-in of the burrows have been reported for marine and green iguanas (Carpenter 1966, Rand 1968). The burrowing behavior of captive female *Cyclura macleayi macleayi* is similar to that of marine and green iguanas (Shaw 1954), all digging tunnels about 1 m long. *C. cornuta* on Isla Beata (Noble 1923) and *C. figginsii* on Guana Cay, Bahamas (Chris Coenen, unpubl. data) excavate egg burrows about 0.6 m long. Haast (1969) reported that a female *C. cornuta* deposited her clutch in a tunnel 0.4 m long.

REPRODUCTION.—Three female *C. pinguis* (476, 426, 400 mm SVL) contained enlarged, yolk-filled ovarian follicles, whereas three females measuring less than 400 mm SVL were reproductively inactive. Although the sample was too small to determine accurately the size at which females become reproductive, all observed females exceeding 400 mm SVL were considered adults. Because of considerable hiatus be-

tween the largest individuals (314-344 mm SVL) without yolk-filled follicles and the smallest individual (400 mm SVL) with such follicles, sexual maturity must be attained between 350 and 400 mm. Males of equivalent size or larger were considered adults.

Lack (1967) stated that female size and clutch size are correlated in many species of animals. This holds both intra- and interspecifically for all species of lizards for which reproductive data are available (Tinkle *et al.* 1970). My limited *C. pinguis* data also tend to support this relationship. In three adults examined, the largest female contained 16 yolked follicles, the intermediate 14, and the smallest 12. These ova ranged from 23 to 34 mm (31.53 mm) by 25 to 29 mm (27.23 mm), 30 to 34 mm (32.54 mm) by 24 to 29 mm (27.26 mm), and 31 to 34 mm (32.67 mm) by 23 to 29 mm (26.92 mm), respectively.

Stejneger (1903) reported five eggs in a female *C. rileyi* collected 13 July 1903 on San Salvador, Bahamas. Female *C. macleayi caymanensis* lay 8 - 20 eggs in May or June (Grant 1940b). Grant suggested a similar laying period for *C. macleayi lewisi*. *Cyclura collei* females lay about 20 eggs in April or May (Lewis 1944, 1946). Street (1952) reported 16 eggs laid by a *C. macleayi macleayi* on Cuba. On 10 July 1953, a female of the same species in the San Diego Zoo laid 17 eggs averaging 65.6 mm by 44.5 mm. This female and another were bred to captive males in June of the previous year; oviposition of an unstated number of eggs occurred about a month later (Shaw 1954). *Cyclura cornuta* females lay about 17 eggs each on Isla Beata (Noble 1923). Captives of this species laid clutches of 16 (\bar{x} =70.20 by 45.30 mm), 11 (\bar{x} =66.72 by 45.21 mm), 23 (\bar{x} =68.35 by 46.67 mm), and 20 eggs in July and August in the San Diego Zoo and the Miami Serpenterium (Haast 1969, Shaw 1969). A nest of *C. stejnegeri* investigated by Richard Thomas on Isla Mona on 14 July 1965 contained 12 eggs, one of which measured 78 by 47 mm. A female *C. figginsi* (290 mm SVL) collected on 3 February 1967 on an unnamed Exuman cay about 5 km northeast of Great Exuma, Bahamas, contained 7 enlarged follicles. Clutch sizes of *C. figginsi* on Guana Cay numbered 3 to 4 eggs; oviposition occurred in early to mid-June (1970) (Chris Coenen, pers. comm.). Three female *C. ricordi* (365, 347, and 308 mm SVL) collected on or about 14 May 1968 in the Dominican Republic contained 6, 4, and 4 yolk-filled ovarian follicles, respectively.

All females of *C. figginsi*, *C. pinguis*, and *C. ricordi* examined for reproductive condition contained, in addition to maturing ova, a nearly equal complement of follicles about one quarter the size of the maturing ones. Determination of the significance of these smaller follicles is difficult. They may represent a second clutch for that year, or the next season's clutch. However, Tinkle *et al.* (1970) showed that late-maturing

lizards usually are not multiple-brooded. Compensation for fecundity loss in *C. pinguis* is another possibility, but populations of *C. figginsi* and *C. ricordi* are not known to be disturbed, yet they too possess a second group of maturing eggs. Insular lizards, which apparently live to rather advanced ages with little or no natural predation on adults (hence low adult mortality rate), seemingly would have little need for more than one clutch per year. It is possible that natural juvenile mortality may be greater than suspected. Further study is needed to satisfactorily solve this problem.

A clutch of 16 *C. macleayi macleayi* eggs in Cuba required 93 days to hatch (Street 1952). The clutch of 17 eggs from a captive *C. macleayi macleayi* began hatching after 119 days (Shaw 1954). Noble (1923) postulated 9 weeks for hatching in *C. cornuta* on Isla Beata. The clutches of 16, 11, and 23 eggs of *C. cornuta* in the San Diego Zoo began hatching after 106, 111, and 115 days (Shaw 1969). In the Miami Serpenterium a clutch of 20 eggs required 125 days to hatch (Haast 1969).

Judging from the size of ova in *C. pinguis*, the eggs may have been near ovulation. Oviposition probably occurs in April, May, or June, and, allowing 90-120 days for incubation, hatching would then occur in August or September.

Fitch (1970) stated that the giant iguanas inhabiting the drier parts of the tropics synchronize their yearly breeding seasons with the time of maximum rainfall. *Ctenosaura* and *Iguana* generally lay their eggs during the dry season to take advantage of maximum incubation temperatures (Davis and Smith 1953, Alvarez del Toro 1960, Hirth 1963a, Rand 1968). The young hatch during the early rainy season, a period of denser vegetation and more abundant insect food. A similar laying schedule is followed by *Basiliscus vittatus* (Alvarez del Toro 1960, Hirth 1963b). In *Amblyrhynchus*, oviposition occurs toward the end of the rainy season (January or February) (Carpenter 1966). Carpenter suggested that the breeding cycle is timed to avoid the *garúa* season, a four month period of heavy mist and cool temperatures beginning in June. Similar timing may be operating in *Conolophus pallidus* on Barrington Island, Galápagos; females contain leathery-shelled oviducal eggs in December (Slevin 1935).

Cyclura also seems to lay in synchronization with periods of maximum rainfall, but in a somewhat different pattern than that documented for other tropical iguanas. Captive *C. macleayi macleayi* and *C. cornuta* lay in mid to late summer, about the time of maximum rainfall on their native islands. *Cyclura figginsi* on Guana Cay excavate burrows in early June, several days prior to the beginning of the rainy season (Chris

Coenen, pers. comm.). The females remain by the nests until the first rains, then oviposit and bury the eggs.

Cyclura pinguis females apparently oviposit at the beginning of the rainy season (April or May) with hatching occurring 3 to 4 months later. In general, rainfall in the Virgin Islands is at its heaviest from May to November, with the lower of two maxima occurring in May and June and the higher in October (Stone 1942). The increased moisture may prevent dessication of the eggs during incubation, as well as increasing plant growth and insect abundance, to assure an adequate food supply when the hatchlings appear.

ADDITIONAL NOTES ON NESTING.—Nest guarding by *Cyclura* females in the San Diego Zoo has been recorded. *Cyclura macleayi macleayi* females attempted to drive off would-be nest molesters (other large lizards and humans) with vigorous bobbing and open-mouthed charging (Shaw 1954). Under similar circumstances, *C. cornuta* females repeatedly approached molesters but did not attack (Shaw 1969). Similar behavior has been reported for marine and green iguanas (Carpenter 1966, Rand 1968). *Cyclura figginsii* females on Guana Cay reportedly guarded a previously excavated burrow from other females while waiting for the rains to begin (Chris Coenen, unpubl. data). It is not known whether they guarded the nest after oviposition.

AGE AT MATURITY AND REPRODUCTIVE POTENTIAL.—Sexual maturity probably is not reached for several years following hatching. Fitch (1970) postulated 3 years as the minimum breeding age for *Ctenosaura similis*, an iguanine species smaller than *C. pinguis*. He based this estimate on the fact that young thought to be 9 months old were still less than half grown and coexisted with young seemingly belonging to the next oldest age group. Mayhew (1971) postulated a 5 or 6 year maturation period for *Dipsosaurus dorsalis*, smallest of the iguanines, based on the average growth rate of captive and wild juveniles and a known SVL upon attaining maturity. Employing this method, a minimum maturing period of 7 to 9 years can be speculated for *C. pinguis*. Two subadult specimens were maintained in captivity for 10 months on an 8 hour per day photoperiod and food *ad libitum*. Mean growth rates were 1.17 and 2.97 mm per month; a maximum growth rate of 3 mm per month for *C. pinguis* (of this age-group) in the wild was then assumed. The SVL of *C. pinguis* hatchlings is unknown. The lone main island juvenile measured (ca 6 months old if presumed date of hatching is correct) was 117 mm SVL, suggesting a SVL of about 100 mm at hatching. Hatchlings of *C. macleayi macleayi* and *C. cornuta* (iguanas equivalent in adult size to *C. pinguis*) in the San Diego Zoo ranged from 95 to 100 mm SVL (Shaw 1954, 1969). As it appears that maturity in *C. pinguis*

is attained at or around 400 mm SVL, 7-9 years would be required to reach this size at a growth rate of 3 mm per month.

As all examined *C. pinguis* females exceeding 400 mm SVL were reproductively mature and paired, it seems that all pairs on Anegada were potential producers of offspring. Reproductive potential was determined on the basis of the number of enlarged yolk-filled follicles. This potential is influenced by size and age of the females, age at initial reproduction, number of clutches, and the number of reproductive females in the population. There is no reliable method for aging iguanas, so reproductive potential can be crudely estimated only for adult females. Three adult females in the Citron Bush had an average of 14 enlarged ovarian follicles. If only one clutch per year is deposited, potential reproduction of the five females in the Citron Bush was roughly 70 offspring for 1968.

Considering the low density of *C. pinguis* in the Citron Bush and probable slow rate of adult turnover, environmental resistance against that potential production appears great. The differential between potential production and the actual number of offspring reaching sexual maturity can probably be attributed to predation. In addition, parasitism might also affect iguana eggs on Anegada; such a condition was described for marine iguana eggs on the Galápagos (Carpenter 1966).

Miscellaneous egg and juvenile mortality factors reported in other species of *Cyclura* could be the same for *C. pinguis*. All but one of the 17 eggs laid by captive *C. macleayi macleayi* hatched, but five of the hatchlings died within 75 days (Shaw 1954). Death was attributed to failure of the juveniles to assimilate the yolk mass in the abdominal cavity. Artificial incubation was attempted on 45 of 50 eggs laid in the San Diego Zoo by *C. cornuta* females (Shaw 1969); 26% hatched and 28.8% contained dead embryos or young that died within the egg after having slit the shell with the egg tooth. The percentage of fertile eggs was not determined. All 20 eggs laid in the Miami Serpenterium by a *C. cornuta* hatched (Haast 1969), although two of the hatchlings died of unknown causes soon afterward.

AGE STRUCTURE.—Iguanas on Anegada (including the Citron Bush, but excluding Windberg Key) were grouped as juveniles, subadults, young adults, and older adults on the basis of size and appearance. These age structures (Fig. 11) are meaningful only for March and April 1968 (5-7 months after presumed hatching). Figure 11 may be confusing unless one remembers that adults and juveniles did not mix. Thus the Citron Bush was 100% adults (10% young adults, 90% older adults), and a cross section of many colonies shows percentages of all age classes.

The age structure of *C. pinguis* suggests a low annual turnover of

adults. On Anegada adult iguanas comprised over 87 percent of the population six months after presumed hatching. This suggests that other than established adults few individuals survive each year. This contrasts with *Uta stansburiana* (Tinkle 1967), which exhibits nearly complete annual turnover, multiple breeding, and early maturation and live only a year or two, whereas *C. pinguis* probably attains an advanced age for a lizard. An experienced "woodsman" on Anegada told me of several iguanas that had lived on the same retreats since he had been a child (recognition was based on individual markings). The man was in his sixties at the time of my research.

Animals in the wild usually die before their potential life span is attained, often during or before their reproductive prime (Lack 1967), but island species frequently have fewer competitors and/or predators than their mainland counterparts. This decrease in competitive interaction often results in decreased mortality. Adult *C. pinguis* on faunistically impoverished Anegada could realize their potential life span. This may be true for West Indian rock iguanas in general. A comparison of *Lacerta sicula* populations on the Italian mainland (where predators are numerous) and adjacent islands (where predators are few) (Kramer 1946) showed the average ages for male lizards to be 1.9 years and 4.4 years respectively. Annual adult mortality averaged 40% on the mainland and 20% on the islands.

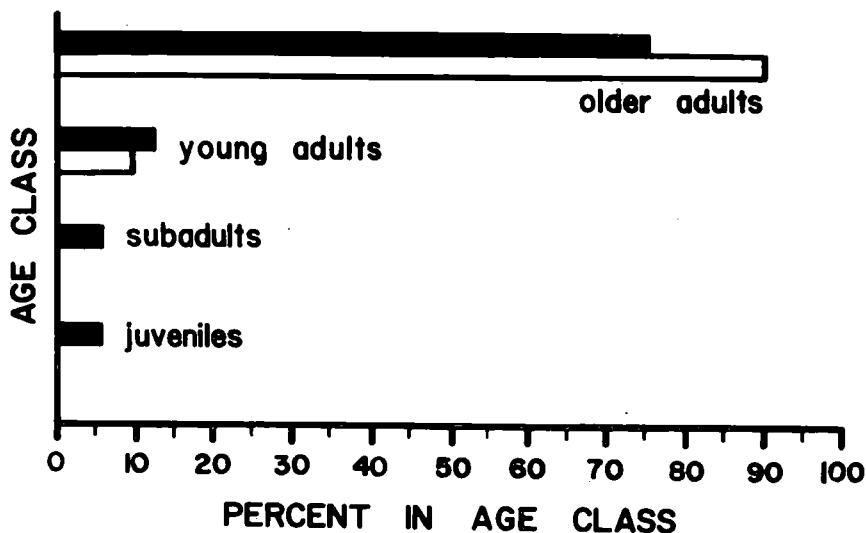


FIGURE 11.—Age distribution of *Cyclura pinguis* population on Anegada, British Virgin Islands, 27 March-5 May 1968. Black bars, all of Anegada; white bars, Citron Bush.

The population age structure of *C. pinguis* on Anegada suggests that juveniles are subject to high mortality before they grow large enough to fend off predators. Approximately six months after the presumed hatching period, juveniles and subadults made up only 12.5 percent of the population, young adults and older adults 87.5 per cent (Fig. 11). The differential mortality indicated by this disproportionate age structure suggests decreasing predator pressure on larger lizards. Once large size has been attained, fewer mortality factors operate. Death of adults apparently results only from hazards during egg-laying, occasional predation by dogs and man, old age, and environmental catastrophies. *Sceloporus olivaceus* (Blair 1960) and *Uta stansburiana* (Tinkle 1967) usually migrate only a few meters from their home ranges to lay, while *C. pinguis* females may travel great distances. The greatest mortality of juveniles probably occurs during the period of occupancy of areas peripheral to the areas occupied by adults. Their small size, coupled with the relatively recent increase in predators, probably subjects the young lizards to increased pressure in these areas.

DISCUSSION

A population consisting of a large proportion of old individuals is frequently thought to be senile or declining, whereas those with a high proportion of young individuals are regarded as thriving. For example, in the Galápagos the land iguana, *Conolophus subcristatus*, is thriving (large proportion of young) on some islands and declining on others (only old individuals) (Dowling 1964, Hillaby 1964). No *C. pallidus* juveniles were seen on Barrington Island, also suggesting decline, and land iguanas no longer exist on some islands, such as Baltra and Santiago, where they were recorded previously. Their extinction on these islands coincides with the introduction of goats, which are believed to compete with the lizards (particularly juveniles) for food. Only large adult land iguanas presently persist on Barrington and Santa Cruz islands, where goats have been established for some time. Goats feed on vegetation at the same heights as juvenile iguanas, as well as much higher up than juveniles can reach, thus easily out-competing them for the vegetative part of their diet. The goats also clear the area of protective undergrowth, exposing juveniles to predators, especially hawks (Dowling 1964). On goatless Fernandina and South Plaza, land iguanas flourish.

Insufficient evidence is available to predict the future of *C. pinguis* on Anegada; but the population seems to be operating at a density level below that of the past, making extinction a distinct possibility. This conclusion is based on: (1) the presence of suitable, but unoccupied habitat;

(2) the apparent lack of communal nesting that characterizes several high density iguanine populations, including at least two species of *Cyclura*; and (3) the disproportionately high percentage of old individuals. Similar properties probably were characteristic of the *C. collei* populations on Jamaica and its satellite, Goat Island. This species had been considered extinct on Jamaica since the early 1940's but recent evidence suggests that at least a few individuals persist in the Hellshire Hills of southeastern Jamaica (Woodley 1971). On Goat Island, they definitely are gone. Lewis (1944) saw no juveniles during six months of intermittent collecting on the island. The 22 animals collected during that period for transplant to the mainland, definitely were old adults. The principal factor leading to extinction on Goat Island and almost total decimation on Jamaica was the mongoose. These animals prey heavily on juveniles and eggs.

It is probable that ancestral *C. pinguis* colonized Anegada via Greater Puerto Rico, from which the former island was separated (became a discrete land mass) about 8,000 years ago. However, island hopping remains a possibility (Heatwole and MacKenzie 1967). Osseous remains have been found on Puerto Rico (Barbour 1919) and St. Thomas (Miller 1918), and were described as *C. portoricensis* and *C. mattea* respectively.

Ancestral *C. pinguis* were probably herbivorous and entered an environment essentially free of competitors and predators. The present decline of the iguana population on Anegada is a phenomenon that may be attributed to competition and/or predation from an introduced domestic fauna (especially grazing animals), as well as the advanced age at initial reproduction. West Indian *Cyclura* occupy feeding niches roughly equivalent to those of grazing animals elsewhere, as do Galapagoan *Conolophus* (Stebbins 1966).

The reduction in density has created a secondary deleterious situation, irreversible unless the primary sources of population regression are eliminated. Removal of females from the *Cyclura* population is much more acute in these late-maturing animals. Tinkle *et al.* (1970) stated that during the evolution of late-maturing species, these must have been compensations for fecundity loss. The principal compensation would be the larger size of the female at maturity, allowing for larger clutch size and production of larger eggs. The larger body size also might eliminate some predation, thus increasing adult life expectancy and providing additional opportunities for reproduction. In addition, late-maturing lizards with long life expectancies often exhibit postovipositional parental care, which should increase juvenile survivorship (Tinkle 1969). Postovipositional parental care of the nest has been observed in *Cyclura*, as well

as in other tropical iguanines. This and the additional breeding opportunities through longer life expectancy would defray the reproduction cost of delayed maturity (Tinkle *et al.* 1970).

As *C. pinguis* seems to possess all of the required characteristics for an intimate evolutionary bond to delayed maturity, any disruption of that bond could lead to reproductive catastrophe. Cole (1954) emphasized that population stability in animals with delayed maturity requires the balance of several factors, such as degree of parental care, clutch size and frequency, and adult life expectancy. Although fecundity of *C. pinguis* probably was sufficient under natural conditions, only a tiny percentage of offspring currently attain adulthood. If potential production (initially reduced for island life via K [carrying capacity] selection) per adult female is at a physiological maximum for *previous* conditions on Anegada, then there are simply not enough reproductive females in the present population to supply the number of offspring required to return to the potential value of K . This might be accomplished by any factor that increases the rate of population growth. Slobodkin (1961) stated: "physiological properties of each species are intimately related to its r [intrinsic rate of increase] value and any evolutionary change in r implies changes in litter size, age at initial reproduction, or longevity, or some combination of these." He further pointed out that selection for an increasing r will be expected to result in an earlier onset of initial reproduction in species with small clutches. Cole (1954) stressed the importance of age at initial reproduction, *not* litter or clutch size, as the principal factor in population growth.

Delayed maturity in birds such as raptors and swifts is characterized by single broods per season, high annual adult survivorships, and long developmental periods (Tinkle *et al.* 1970), again roughly the conditions found in *Cyclura*. An evolutionary increase in r can best be accomplished by lowering the age of initial reproduction, thus producing a substantial increase in offspring per female-lifetime. An increase in offspring might assure an ultimate return to K .

The discussion of population decimation in *C. pinguis* probably can be applied to the recent extinction or depletion of *C. collei* on Jamaica and Goat Island and *C. nigerrima* on Navassa. The Jamaican populations consisted only of a few very old adults (Lewis 1944). There simply were not enough females, even if they did reproduce, to overcome the tremendous pressure against the juveniles.

The circumstances surrounding the apparent extinction of *C. nigerrima* on Navassa are unknown. The five specimens in museum collections were taken in the late 1800's. Neither Thomas (1966) nor Patton (1967) saw living iguanas during their brief visits to Navassa, although

the latter reported finding fossil material. Thomas stated that the island presently is uninhabited, but previously was occupied by the Navassa Phosphate Company (1864 to 1898), by three families of lighthouse keepers (1917 to 1929), and by the U.S. military during World Wars I and II. As a result of these human agencies, Navassa now has an introduced fauna of rats, cats, and goats—seemingly major offenders in the decimation of land iguana populations.

The Grand Cayman population, *C. macleayi lewisi*, currently is meager, although the causes are unclear. Grant (1940b) thought that the population consisted of about a dozen individuals; the animals were so scarce that many of the natives were unaware that iguanas even existed on Grand Cayman! It recently has come to my attention (Wayne King, pers. comm.) that within the past few years a pair of young *C. macleayi caymanensis* from Little Cayman were released on Grand Cayman. This is indeed alarming since these animals apparently have survived and reproduced, thus threatening through competition and/or intergradation the already highly precarious existence of *C. macleayi lewisi*. Dr. King has informed me that action will be initiated to remove these alien iguanas from Grand Cayman as soon as possible.

CONSERVATION

At this writing, the Caribbean Research Institute of the College of the Virgin Islands is attempting to save *C. pinguis*. This project is being funded by the New York Zoological Society and the World Wildlife Fund. Unfortunately, recent efforts to breed the species in large enclosures have failed (Edward Towle, pers. comm.). The ideal solution would be the removal of all domestic animals from Anegada. However, since livestock is an integral component of the food supply of the native population of Anegada, attempts to eliminate these animals undoubtedly would meet insurmountable opposition.

Whatever the methods, steps must be taken now to ensure the continued existence of *C. pinguis* on Anegada. In fact, a general statement to this effect should be made in regard to the entire genus. Although many species actually are not endangered *presently*, all are listed as depleted in the IUCN's RED DATA BOOK on endangered amphibians and reptiles (Honegger 1968). They occupy such restricted or specialized habitats that little environmental disruption would be required to dangerously upset the populations.

The allocation of setting aside iguana preserves with resident wardens as advocated by the IUCN is only part of the answer. I feel that a more

productive solution would be the education of the native islanders about the importance of their own natural fauna. If the steady and devastating advances of tourism cannot be halted, then extensive national parks or preserves (both desirable to, and usually respected by, tourists) should be set aside wherever *Cyclura* species occur. Iguanas, though repulsive in appearance to many, are still great curiosities to the general public. This could be coupled with rigid protection measures enforced by the natives.

On human-inhabited islands, livestock should be excluded from the preserves, not necessarily from the entire island. On small uninhabited islands (such as in the Bahamas) there is no domestic livestock. Here collecting and needless slaughter for "sport" provide potential danger. All collecting should be deemed illegal, unless for breeding purposes in approved zoos or similar scientific institutions. Success in breeding *Cyclura* under proper captive conditions is becoming well known (Shaw 1954, 1969, Haast 1969, Murphy 1969, Burchfield 1973). Breeding programs in zoos could perform dual functions: (1) for trading purposes with other zoos, thus relaxing collecting pressure on natural populations; and (2) for recycling fit juveniles back into natural populations after principal decimating factors have been removed. Employment of the latter function has been successful in the Galápagos Islands with several races of the Galápagos tortoise, *Geochelone elephantopus* (Perry 1970, Pritchard 1971).

I believe that this program would enhance greatly the survival chances of the *Cyclura* population on Anegada, at least, and possibly wherever other populations exist. Also, wherever such programs are in operation, comprehensive surveillance at regular intervals should be maintained on the populations. Further investigation of the status of all other *Cyclura* populations (especially on human-inhabited islands) is needed to determine the applicability of protective measures similar to those outlined above. At this writing, a Cornell University graduate student, Thomas A. Wiewandt, had just begun an ethoecological study of *C. stejnegeri* on Isla Mona.

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