BULLETIN

of the
FLORIDA STATE MUSEUM
Biological Sciences

Volume 24 1979 Number 3

BEHAVIOR AND ECOLOGY OF THE ROCK IGUANA *CYCLURA CARINATA*

JOHN B. IVERSON

UNIVERSITY OF FLORIDA GAINESVILLE

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

Communications concerning purchase or exchange of the publications and all manuscripts should be addressed to: Managing Editor, Bulletin; Florida State Museum; University of Florida; Gainesville, Florida 32611.

This public document was promulgated at an annual cost of $5,607.48, or $5.607 per copy. It makes available to libraries, scholars, and all interested persons the results of researches in the natural sciences, emphasizing the circum-Caribbean region.

Publication date: December 20, 1979 Price, $5.65

BEHAVIOR AND ECOLOGY OF THE ROCK IGUANA *CYCLURA CARINATA*

JOHN B. IVERSON[1]

SYNOPSIS: The natural history and social behavior of the rock iguana, *Cyclura carinata*, were studied during 25 weeks between September 1973 and June 1976 on several small cays in the Turks and Caicos Islands, British West Indies, and in captive enclosures in Gainesville, Florida.

Reproductive cycles were synchronized to climatic cycles. Testes sizes were maximal in April and May (the end of the dry season). Vitellogenesis began in January (onset of the dry season); ovulation and mating occurred in early May. Courtship was typical of most iguanid lizards; the mating system was probably one of serial polygyny with monogamy among some males.

A single annual clutch of 2 to 9 eggs was laid in early June in the terminal portion of the female's retreat burrow. Clutch size was positively correlated with female size. Clutch weight averaged about 25% of preoviposition weight. Females defended their nest burrows for several days to several weeks after nesting, but were not territorial during the remainder of the year. Hatching occurred after approximately 90 days. Neonates averaged 79.8 mm SVL and 14.6 gm. Juvenile growth rate averaged 19.2 mm SVL/year. Males reached sexual maturity at approximately 220 mm SVL and 375-475 gm and at an age of about 7 yr; females 185-200 mm, 200-300 gm at 6 to 7 yr. Adult males averaged 276 mm SVL and 935 gm, adult females 225 mm and 475 gm. The largest male measured 360 mm SVL and 1864 gm, largest female 292 mm and 1135 gm. Adults grew between 2 and 17 mm SVL/year.

Rock iguanas were primarily herbivorous at all ages and fed arboreally and terrestrially. Five partial septa partition the proximal colon region; this modification presumably increases digestive efficiency. Huge oxyurid nematode populations inhabited the colon, and their relationship with the iguana may be mutualistic rather than parasitic. Abdominal fat deposits were negatively correlated with gonadal activity.

Home range size was correlated with body size and habitat productivity, averaging 980 m^2 for females, 1260 m^2 for subdominant males, and 1590 m^2 for dominant males. Diurnal activity was bimodal during warmer months; high midday temperatures resulted in reduced activity. Winter activity was generally reduced and peaked at midday. Iguanas basked following emergence; most of the remainder of the day was spent feeding, interacting with other lizards, and shuttling in the sun-shade mosaic for thermoregulatory purposes. Basking preceded the termination of daily activity.

Rock iguanas performed ritualized "signature" displays or headbobs. Postural adjustments were among the modifiers producing variation in this display in different behavioral contexts. Displays were important to territory declaration, male challenging, and sex recognition. Males were territorial year-round in the field, but developed dominance hierarchies in captivity. Dominant males displayed less than subordinates. Male territorial defense probably evolved as a mechanism guaranteeing access to food resources and females for breeding.

The sex ratio was 1:1 in all age classes. Survivorship was positively correlated with body size. Juvenile densities reached 90.3/ha in optimum habitat, adults exceeded 31.1/ha. Biomass estimates were 5.15 kg/ha for juveniles and 17.01 kg/ha for adults. Life table data indicate replacement rate was near unity, and mean generation time was 14.0 years. In its life history strategy, *C. carinata* is a predominately K-selected species.

---

[1] The author is an Assistant Professor of Biology, Earlham College, Richmond, Indiana 47374, and an Adjunct Assistant Curator of Herpetology of the Florida State Museum, Gainesville, Florida 32611.

IVERSON, JOHN B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bull. Florida State Mus., Biol. Sci. Vol. 24(3):175-358.

TABLE OF CONTENTS

INTRODUCTION

PURPOSE

The genus *Cyclura* is one of the most poorly known lizard genera in North America, despite being one of the most conspicuous members of the West Indian fauna. Although a sizable literature exists regarding the genus, most of the references are faunal lists or general works and contain only anecdotal information; no thorough autecological study of any of the species has been made.

Few New World lizards have experienced as intimate a relationship with man, and suffered more from the interaction, than *Cyclura*. Major populations have been extirpated within historic times. Probably no presently existing population is entirely free from pressures induced by man and his animals. It is increasingly clear that a thorough knowledge of the habits and adaptations of our fauna is necessary if we are to be able to insure their survival in the face of continuing and increasing cohabitation with humans. It was for these reasons that study was begun on a still relatively common species: *Cyclura carinata*, the Turks Island iguana (Fig. 1). From September 1973 through June 1976 *C. carinata* was studied both in the field in the Turks and Caicos Islands and in the laboratory.

The goals of the study were: (1) to obtain data on the behavior, adaptations, life history, and community role of this species; (2) to determine what factors limit population size; (3) to discover methods by which the species might survive cohabitation with man, without threat of extinction; and (4) to provide an indepth charter study for extrapolation to similar investigations of other less common and more endangered species of *Cyclura* in the West Indies.

SYSTEMATIC RELATIONSHIPS AND DISTRIBUTION

The genus *Cyclura* is most closely related to the three largest herbivorous iguanine lizard genera inhabiting continental North and Central America: *Ctenosaura, Iguana,* and *Sauromalus*. On the basis of myology and osteology *Cyclura* is most similar to *Ctenosaura* and next most similar to *Iguana* (Avery and Tanner 1971). Endemic to the Antilles and Bahamas, *Cyclura* apparently evolved from a pre-*Ctenosaura* stock isolated in the islands. The genera *Amblyrhynchus, Brachylophus, Conolophus, Ctenosaura, Cyclura, Dipsosaurus, Enyaliosaurus, Iguana,* and *Sauromalus* constitute the subfamily Iguaninae (Avery and Tanner 1971).

Seven extant species constitute the genus *Cyclura*, distributed from the northern Bahamas through the Greater Antilles (Schwartz and Thomas 1975). Pleistocene remains are known from several islands within the present range (review in Carey 1975).

Cyclura carinata is closely allied to *C. rileyi* (San Salvador, Bahamas). The two species share a number of characters (lack of enlarged, tubercular, median frontal shields; presence of dorsal crest, with elongate spines, interrupted on shoulders and rump; maximum size less than 1 m, etc.) and are both distributed in the southern half of the Bahaman archipelago.

The relationship of *Cyclura ricordi* (Hispaniola) to *C. carinata* deserves additional study despite the larger size (commonly exceeding 1 m total length) of the former. The two species have similar dorsal crests and pigmentation patterns and are the only two species of *Cyclura* without enlarged supracephalic scales.

STUDY AREA

The Turks and Caicos Islands lie to the southeast of the Bahama Islands between latitude 21° and 22° N and longitude 71° and 72°31′ W (Fig. 2). Although politically distinct from the Bahama Islands, this

British Crown Colony is geologically part of the Bahaman archipelago. The islands are situated approximately 150 km north of Hispaniola and 890 km southeast of Miami, Florida. They consist of two groups of islands separated by a 35.5 km wide, deep water (> 2200 m) channel, the Turks Island Passage. The Turks Islands lie east of the passage, the Caicos to the west. The former consist of two inhabited islands (Grand Turk and Salt Cay), six uninhabited cays, and numerous emergent rocks.

The Caicos Islands lie along the perimeter of the Caicos Bank, a northwest-to-southeast-lying triangular shoal with a base and altitude of approximately 125 and 75 km, respectively. Depths frequently exceed 180 m within 2 km of the reefs surrounding the Turks and Caicos banks. Each of the banks is surrounded by depths of at least 1800 m. The highest elevation in the islands barely exceeds 85 m (on Providenciales). The present surface area of the islands, as calculated by the Turks and Caicos Survey Department, is approximately 500 km, with only 27 km^2 in the Turks Islands group. Recent evidence indicates that shoaling sand is filling many of the cuts, linking previously separated cays via sandy isthmuses (Noble and Klingel 1932).

Although these changes are usually not rapid, the effects of tropical storms can be. When Hurricane Donna passed directly over the Caicos Islands in 1960 the cut between Pine and Water cays was connected by a sand block. Shoaling since then has nearly filled the cut. These changes are now, and probably have been in the past, very important to the dispersal of fauna and flora between islands of the bank.

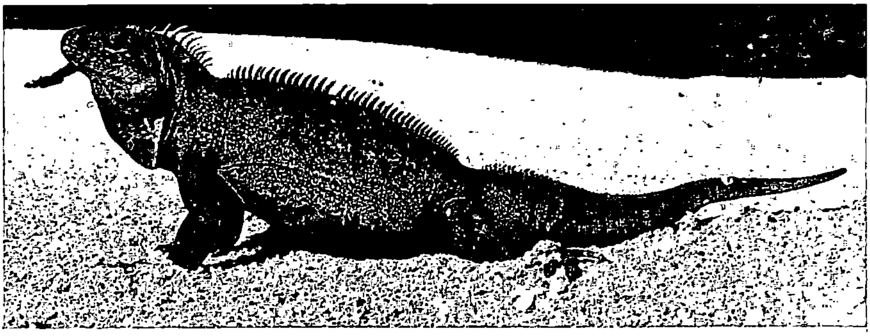

FIGURE 1.—Male *Cyclura carinata* basking on beach at Pine Cay, Turks and Caicos Islands.

My studies of *Cyclura carinata* in the Turks and Caicos Islands were predominately based in the West Caicos cays. The major islands comprising this group are, from north to south, Parrot, Dellis, Fort George, Pine, Water, and Little Water cays (see inset, Fig. 3). Studies reported here were confined to the latter four. These islands are phenetically very similar. Each has its leeward sandy beaches, windward rocky coasts and mangrove swamps, inland brackish water lakes, northeast-to-southeast-lying karst ridges paralleled by sandy dunes, maximum elevations of 8 m, vegetation increasing in luxuriance from west to east, and dense *Cyclura* populations.

Study was concentrated on Pine Cay, a privately owned island of nearly 350 ha (Fig. 3). The average elevation on Pine Cay is less than 3 m. Only three points on the island exceed 6 m; the highest point on the island barely exceeds 8 m. Extraordinary in the Bahama Archipelago, Pine Cay lies over an impermeable basin, preventing salt water intrusion. Maintained solely by rainfall, a freshwater lens sometimes exceeding 15 m in thickness occupies this basin. Average storage capacity has been estimated at over 510 million liters. The water table is exposed in seven inland lakes. This availability of fresh water is in part responsible for the presence on Pine Cay of an extensive stand of Caribbean pine (*Pinus caribaea*) found elsewhere in the Bahamas only on North Caicos, Grand Bahama, Abaco, Andros, and New Providence (Rabb and Hayden 1957). Vegetation on Pine Cay varies from sparse on the most recent westerly sand beach ridges to dense on the geologically older coral ridges to the east with better developed soils (see Vegetation).

During the summer of 1973, construction began on a private resort hotel, the Meridian Club, on Pine Cay. I was thus presented with an opportunity to study the consequences of increased human interference on theretofore relatively undisturbed iguana populations.

ZOOGEOGRAPHIC RELATIONSHIPS

The Turks and Caicos fauna is part of a larger southern Bahaman faunal group that includes the islands southeast of the Crooked Island passage, plus Rum Cay and Watling's Island farther north. At least 19 reptiles are endemic to the area, and although strongly divergent, most have a Greater Antillean ancestry (Schwartz 1968). This is despite the fact that the Bahaman platform has had its closest geological relationship with the North American tectonic plate since Triassic times (Freeland and Dietz 1971).

Among the amphibians, only *Hyla* naturally reaches into the southern Bahamas from the north and then only the Mayaguana passage. None is associated with *Cyclura carinata*. Over 115 species of

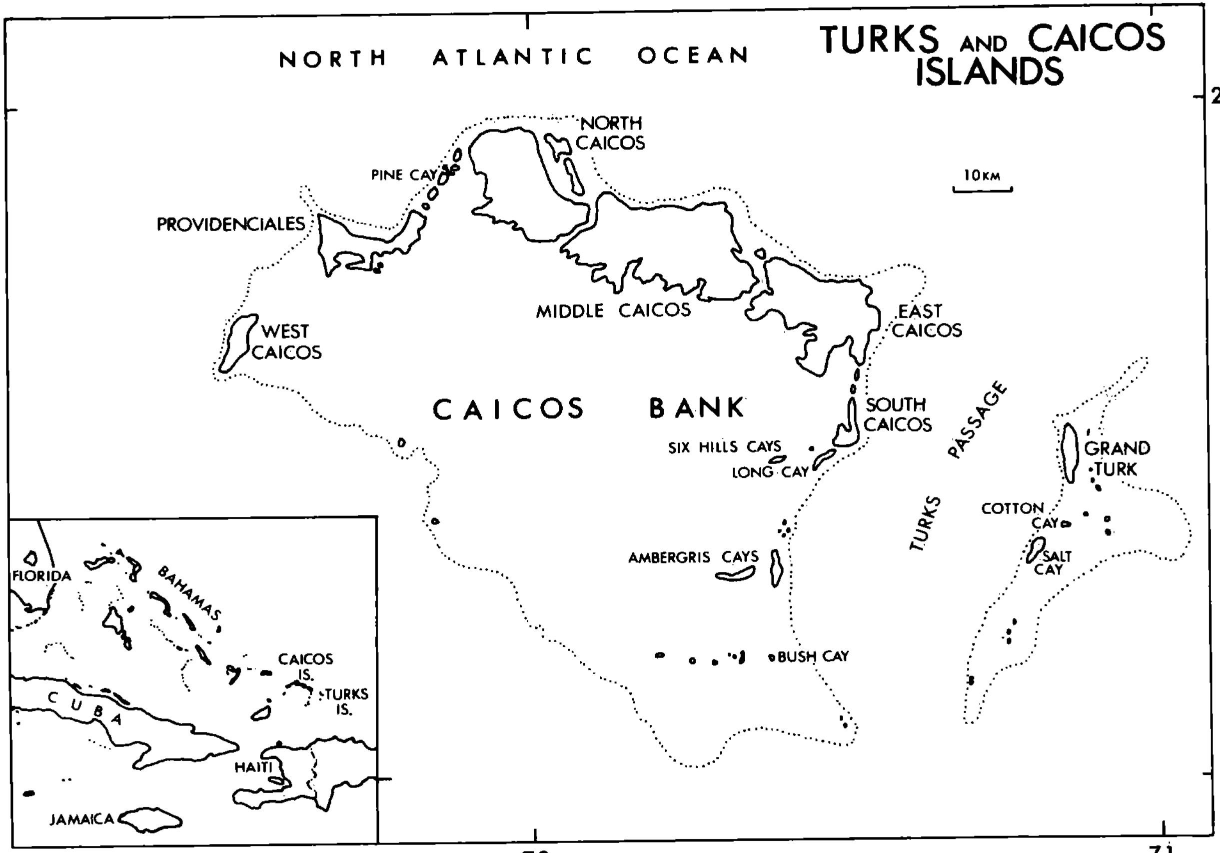

FIGURE 2.—Map of Turks and Caicos Islands in the British West Indies.

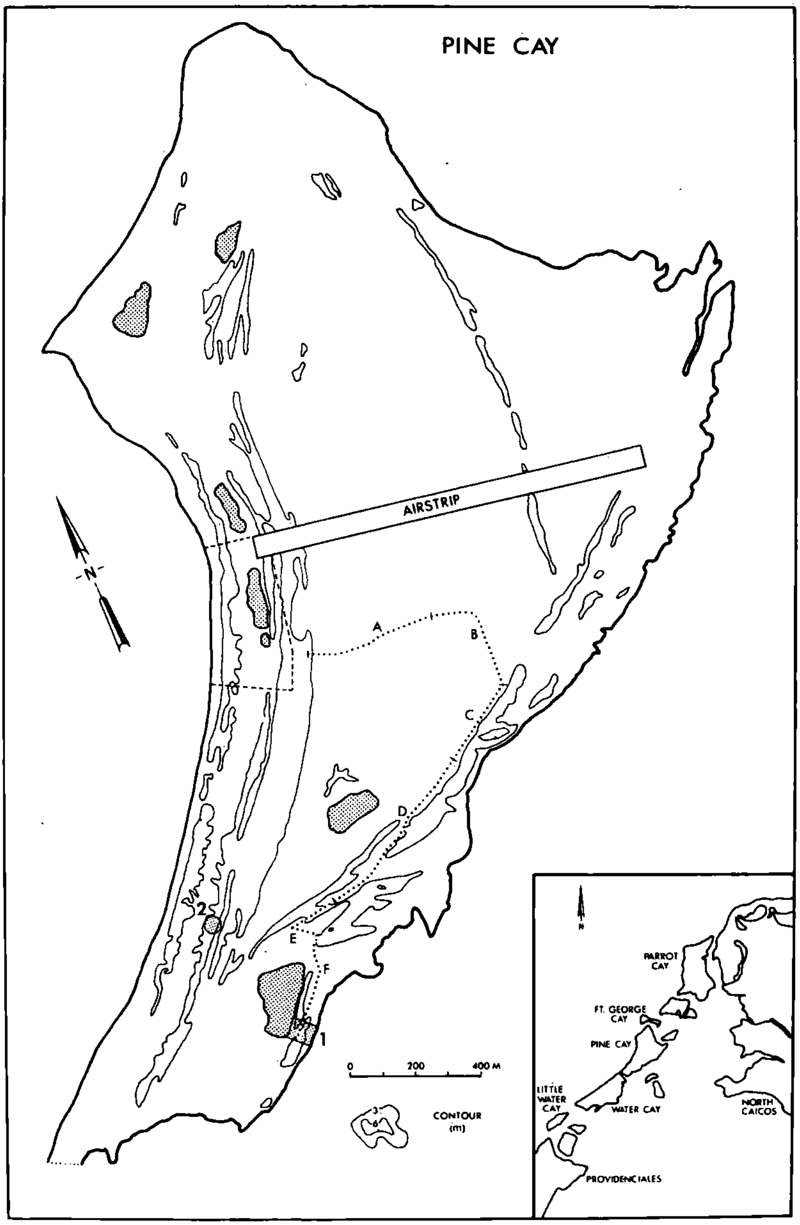

FIGURE 3.—Topographic map of Pine Cay, Caicos Islands, showing locations of principal study sites: (1) SW Blind, and (2) Ridge Area. Letters A through F indicate sectors of flush transect route (dotted line). Other trails and roads are not illustrated. Dashed line encloses limits of Hotel grounds. Unnumbered shaded areas indicate lakes.

birds have been identified on the Turks and Caicos Islands (Buden, pers. comm.). Differentiation of at least two of these has occurred within the southern Bahaman faunal region: *Columbina passerina* and *Calliphlox evelyane* (Bond 1961). The avian species most important to the biology of *Cyclura* will be discussed under sections concerning specific relationships (see INTERSPECIFIC COACTIONS and FOOD AND FEEDING). Of the depauperate mammalian fauna only the bat *Monophyllus redmani* has apparently diverged within the southern Bahamas (Buden 1975).

ACKNOWLEDGMENTS

I wish to express my sincere gratitude to Walter Auffenberg, chairman of my doctoral committee, for his constant aid and encouragement during this study. Thanks also are due to the other members of my committee: John Kaufmann, Frank Nordlie, Carter Gilbert, and Willard Payne.

I am particularly grateful to the New York Zoological Society for providing funds for the field work. Without its support the study would have been infeasible. Acknowledgment is also given to the University of Florida and the Florida State Museum for support and space for the duration of my studies.

Of the many people in the Caicos Islands who made this study possible, special recognition is due C. W. (Liam) Maguire and William and Ginny Cowles of the Meridian Club, Pine Cay, for their generosity in providing housing, innumerable meals, access to invaluable maps, and many other courtesies during the study period.

Special thanks are also due Francoise de Rouvray for breaking my monotonous bean, raisin, peanut butter, and cracker diet with incomparable French cuisine, and to Gaston Decker for extending every kindness to me while on Pine Cay. They enriched my visits to the islands more than any other two persons. For similar courtesies I also thank George and Marou Nipanich. I am also indebted to many other Turks and Caicos islanders for information and help throughout my study.

Donald Correll, Robert Anderson, and Walter Auffenberg supplemented my plant collections and identified most of the plants. Donald Buden supplied a list of birds recorded from the Turks and Caicos Islands. Arthropod identifications were made by Robert Woodruff (insects), and Martin Muma (solpugids and scorpions).

Walter Auffenberg and David Auth unselfishly allowed me access to their Caicos Islands field notes. Diderot Gicca and Thomas Wiewandt generously shared with me their field experiences with other species of *Cyclura*. Aerial photography of the study islands was made possible by William and Ginny Cowles. Numerous others have, in one way or another, added to the successful completion of this work; I apologize for my failure to acknowledge each one individually.

My wife, Sheila, typed the numerous manuscript drafts, endured my frequent absences from home, and supported me in many ways during all phases of the work. All illustrations are the work of the author.

MATERIALS AND METHODS

Preliminary evaluations of *Cyclura* populations in the Turks and Caicos Islands were made by Walter Auffenberg between 4 and 14 August 1973. Those investigations revealed Pine Cay in the West Caicos Islands to be the best island for study for several reasons, including the availability of water and adequate lodging, and the presence of an extremely dense *Cyclura* population. Specific study sites on Pine Cay were designated on my first visit in September 1973.

Eleven trips to the Caicos were made, with 163 days spent on Pine Cay and nearby islands (15-29 September, 8-22 December, 1973; 2-16 March, 1 June-20 July, 29 August-10 September, 26 November-6 December, 1974; 1-14 April, 29 July-16 August, 4-11 November, 1975; and 1-8 May, 8-15 June, 1976). Twelve additional days were spent observing and assessing *Cyclura* populations on numerous eastern islands of the Caicos Bank. Field notes from the Caicos islands were made available by Walter Auffenberg (48 study days from September 1973 through 1975) and David Auth (112 days from June 1974 through February 1976). Copies of all our field notes are filed in the Herpetological Library of the Florida State Museum.

A site of approximately 0.9 ha in the southwestern corner of Pine Cay was chosen as my major study area, which was to be used mainly for behavioral observations with as little interference and manipulation as possible on my part (Fig. 4). The area was initially chosen due to the abundance of lizard spoor and manure on open areas and the generally good visibility below the canopy.

An abundance of spoor typically reflects lizard density in the immediate area. Since *Cyclura carinata* on Pine Cay was extremely shy, it was necessary to construct a blind in this southwestern study site. Lizards generally ignored the blind after it had been in place for only one day. A total of 47 days (287 hr of actual observation) was spent in this blind during the study period. In order to quantify accurately observed lizard movements, yellow marker flags, spaced 6 m apart, were placed in a measured grid system around the blind. Each marker was assigned a letter N (north of the blind) or S (south), and a number (related to the distance from the blind). Thus a lizard at "N-5 West 3 m" was located 3 m west of marker number "N-5." This greatly increased the speed and accuracy of data recording and allowed me to tabulate precise lizard movements. During the course of field work, this entire study area was very thoroughly and accurately mapped. Surveyors' and topographic maps, prepared under the direction of Liam Maguire of the Meridian Club and based on numbered cement lot markers on Pine Cay, and aerial photos made possible precise mapping of lizard and landmark locations.

Field notes were recorded on a cassette tape recorder each day and transcribed in the field notebook at night. A Minolta SRT 101 35 mm camera, Sony AV 3400 portable video camera and recorder, and GAF ST/602 Super 8 movie camera were all employed to record lizard behavior. More than 1400 slides, 110 minutes of video, and 50 feet of movie film were taken. The utmost care was always taken at the southwestern blind to minimize interference with the natural system. Early in the study the resident population was marked without handling by means of a "Paint Rifle," a large plastic syringe firmly mounted on the end of a 1 m, 2 cm diameter, dowel. Maximum range exceeded 10 m, with accuracy possible from 6 to 7 m. Lizards were not at all bothered by this technique. By shooting various colors of paint on various parts of the body, I was able to recognize individuals. Index cards with outline drawings of the right and left sides of a lizard were used to record marking and color formation, as well as sex and natural external morphological features for each lizard. The cards were modified when parts of the paint pattern were shed and/or the lizards were remarked. Even after three-month absences, remnants of paint patterns, in conjunction with activity range and behavioral information, could be used to re-establish the identity of individual lizards.

As the study progressed, lizards were occasionally noosed from the blind for accurate measurement. In order to attract lizards to the blind for this purpose, as well as to induce lizard interaction, numerous substances were experimented with as "baits." Among the items tested were local fruits and flowers, soda and Ritz crackers, peanut butter, vanilla extract, crab parts, other vertebrate carrion, and sardines. The latter was the only substance that proved effective as bait, and its effect was striking: adult males would occasionally cross the territories of at least three other territorial males to

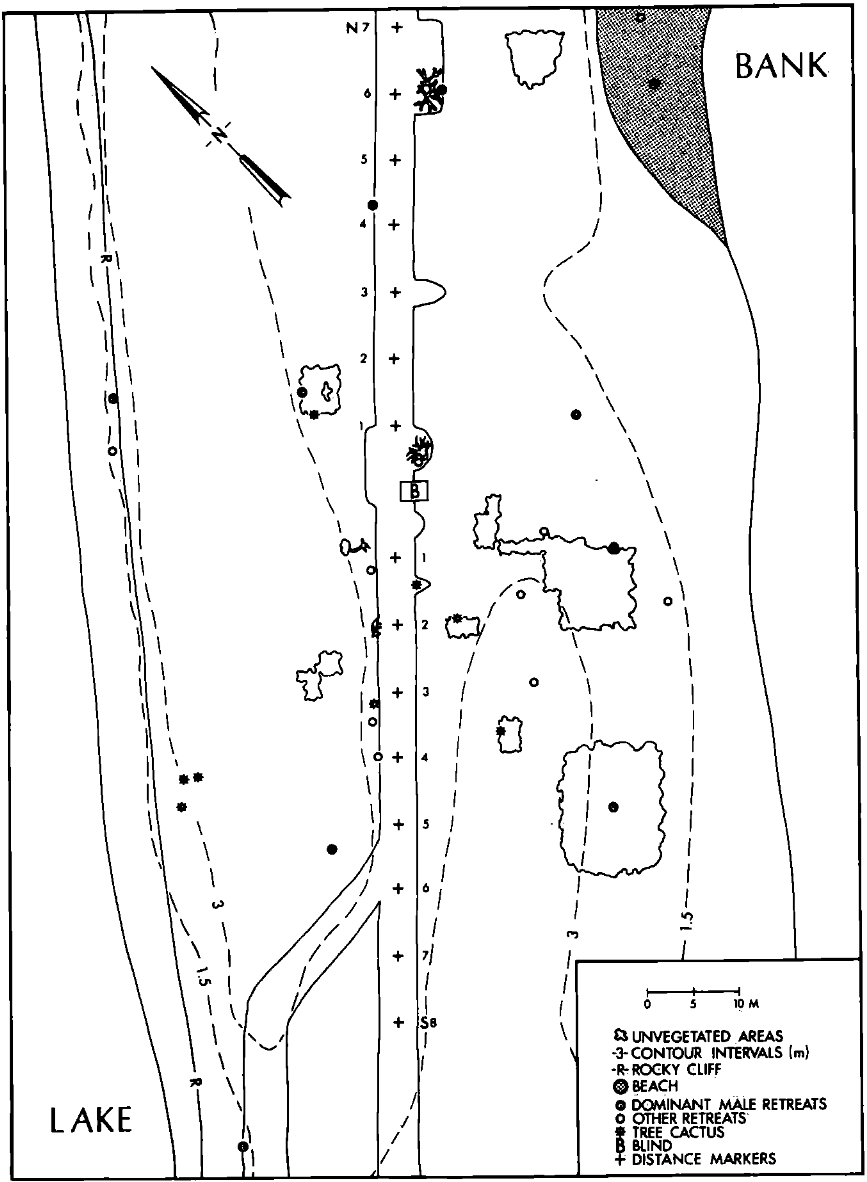

FIGURE 4.—SW Blind Study Area.

obtain the sardines. This bait was, however, less effective during the colder parts of the year and also when high winds rapidly dissipated the fishy odor. Lizards foreign to the study site were restrained in hardware cloth cages or on tethers and were sometimes introduced into the activity ranges of established lizards, and the resulting behavioral interactions recorded.

Because lizards on islands with even minimal human traffic were difficult to capture by noosing except from blinds, this technique was not frequently used on Pine Cay, except at the southwestern blind study site (hereafter referred to as the SW Blind). The technique was, however, fairly successful on islands rarely visited by humans. Juvenile lizards and occasional adults could be secured by chasing them under rocks or into hollow logs, from where they could be removed by hand. Noose snare traps and funnel traps at burrow mouths in areas of great activity were each experimented with, but met with only minimal success. Lizards were sometimes obtained by removing them from their burrows. Nests discovered in this process were either removed to the laboratory or marked for further observations. Numerous freshly killed or mortally wounded individuals were also secured from the mouths of local dogs and cats. In addition, the dried remains of many mammal-killed *Cyclura* were collected. An attempt was made to collect a sample of at least a few lizards in each season of the year to be used for dissection. Besides those lizards killed by dogs and cats, the bulk of this sample included lizards removed from the area on Pine Cay destined for occupation by a hotel and its adjoining beach cottages. Since most of these lizards would have been killed by bulldozer activity, this seemed the best source of material for dissection.

Specimens for dissection were weighed, measured, and preserved in formalin in the field. Transferred to isopropyl alcohol in the laboratory, preserved specimens were then autopsied for reproductive condition, gut content, fat bodies, and presence of parasites. Ovaries, testes, and fat bodies were excised, blotted, and weighed to the nearest 0.01 gm. In females, all yolked ovarian follicles, oviducal eggs, and corpora lutea were counted and measured to 0.1 mm with dial calipers. Testes volume was determined by water displacement.

In order to collect data on growth, lizards located in the area immediately adjacent to the site chosen for construction of the hotel were marked and released on the first visit to the study island. On each of four succeeding visits within a year no recaptures were made, despite a continued marking program all along the dunes parallel to the northwest coast. The disappearance rate in this habitat was obvious on my first return to the island in December 1973, when not a single iguana was seen in my original mark-recapture area. A second site was sought, one less disturbed and more densely populated. In July 1974, another mark and recapture program was initiated on an area of approximately 1.85 ha on the north end of nearby Little Water Cay (Fig. 5). Habitat and vegetation there are virtually identical to the areas of Open Scrub on Pine Cay (see HABITAT). Growth data were also collected on numerous juveniles maintained in the laboratory on lettuce, cat food, and bean sprouts.

Body length (snout to vent), tail length and condition, body weight (measured to the nearest five gm), sex (when possible), and any other obvious external morphological characters (especially in juveniles) were recorded for all lizards during the mark and recapture program. Maximum height (in mm) and number of annuli on dorsal spines of the neck, back, and proximal tail regions were also recorded for each adult. Each lizard was then marked with a unique combination of, at most, two clipped digits and released as soon as possible following capture (always within the hour). At the SW Blind "belts" of various colors modified from cat collars were secured around several lizards "waists" for later recognition.

In addition to lizard movements observed at the SW Blind, it was sometimes possible in sparsely vegetated sandy areas to map an individual lizard's activity range for a single day by his spoor. Since rain and wind quickly obliterate the tracks, this method is useful only if mapping is done late in the afternoon (following lizard retirement) on days lacking high winds or precipitation. A 15 m length of kite string was several times secured around a captured lizard's abdomen just anterior to his hind limbs. On release he would drag the string through the bush and a small portion of his movements could later be plotted. The success of this method varied, since the string occasionally became entangled in brush and was broken. A 3 m length string was similarly employed with success to locate a captured lizard's home burrows at the SW Blind. Following lizard submergence, known burrows were checked for string trailing into them.

Lizards were also tracked by radio-telemetry. This technique was used effectively in lizard displacement and homing experiments as well as for recording daily movements. All telemetry equipment was purchased from Mini-Mitter Co., Inc., Indianapolis, Indiana. Transmitters used were Model L Mini-Mitters operating at just over 27 Mhz. A 3-channel Lafayette HA 420 walkie-talkie fitted with a Mini-Mitter Beat Frequency Oscillator served as a receiver. A Mini-Mitter Model AF Directional Antenna was employed early in the study; however, technical problems precluded its use for most of the study. Triangulation by signal strength received from a whip antenna along right

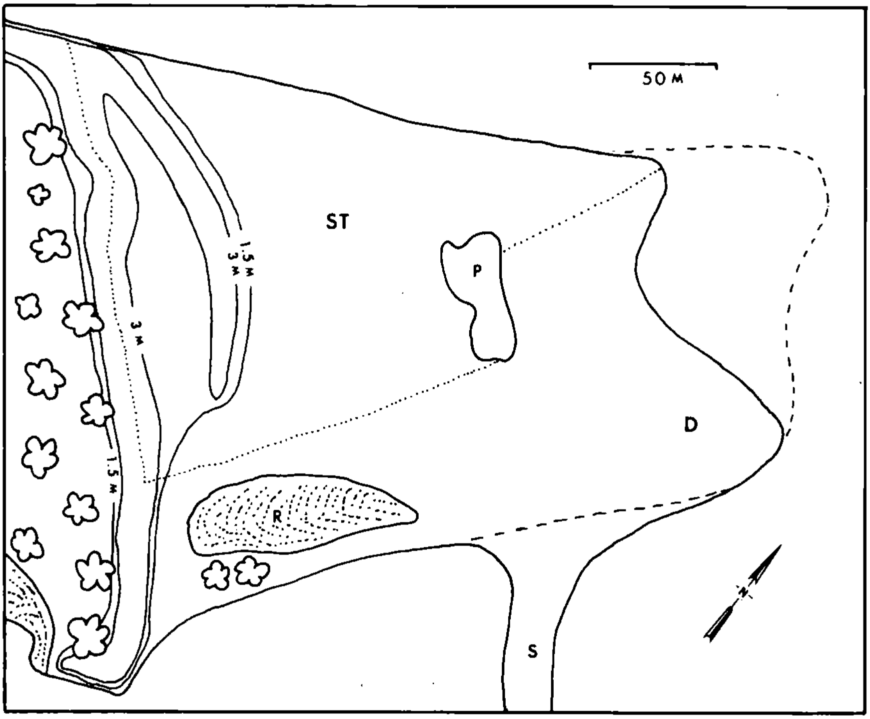

FIGURE 5.—Mark-recapture area on northeast point of Little Water Cay. Study area (ST) lies within dotted perimeter. Dashed line indicates island shape in 1967 based on 1:10,000 Turks and Caicos topographic series (Land Registration Department, Grand Turk). Sand from northernmost point has redeposited along a 950 m spit (s) on the Bank side of the island. Important physical features are included: approximate 1.5 m contour intervals, pond (P), dune region (D), and mud flats dominated by nearly pure stand of *Rachicallis* (R). Vegetation of the study area is typical Open Scrub.

angle transects proved much more effective, especially in areas of dense vegetation. The signal with this equipment varied from 100 m in sparsely vegetated dune areas to just over 50 m in thickly vegetated, rocky areas with greater relief. The range was entirely sufficient for successful use with this species.

Transmitters were secured to the previously described cat collar identification belts with electricians tape and strapped to the lizard's waist. A short length of twine was tied to the transmitter package atop the belt. Transmitter retrieval could then be accomplished by simply pulling the package from the lizard (leaving the belt in place for identification) as he lay in his burrow at night or early morning. In this way, a second disturbance of the monitored lizards was eliminated. The short trailing string did not seem to bother the lizards nor hamper their movements in any way.

Measures of lizard activity were made in three basic ways: (1) direct observation; (2) clocking mechanisms at burrow entrances; and (3) flush transects. To record lizard emergence and submergence times, an alarm clock was remodeled as a single-event recorder in a technique similar to that of Arlton (1936). A hole was drilled through the outer case of each of several inexpensive spring wind clocks directly above the timing wheel. The gravity-operated, tripper mechanism consisted of a small square of cardboard over which an elongate paper clip loop was suspended. A fine nylon thread attached to the cardboard square was stretched across the entrance of a lizard burrow. Disturbance of the thread removed the cardboard allowing the wire loop to drop through the timing wheel, stopping the clock.

A flush transect method similar to the 'King strip census' (see Giles 1971 for discussion) was also used for activity patterns as well as density estimates. The technique consisted of traversing a permanent census trail at different times throughout the day during each visit to the study island (Fig. 3). Distance along the transect route where each lizard was flushed and distance from trail to lizard (before being flushed) were recorded. A total of 103 transects was run during the course of the study. Data from the flush transects, coupled with direct data at the SW Blind study site provided the major basis for analysis of activity patterns and estimates of lizard density. In order to test and insure the accuracy of this transect method, the transect route passed through the SW Blind site, from which the most reliable density data were presumably available. The success of flush transects on Pine Cay was the result of the character of the island itself, as well as that of the lizard. *Cyclura* on the study island were wary and typically ran when humans approached. Although many lizards were seen during transects, the location of most was possible only after they bolted off over noisy leaf litter. This technique could therefore be successful only in areas where the vegetation was dense enough to prevent the lizard from seeing the observer until he (the observer) was within audible range of the noise of his flushing. Such was the case along the transect route I used.

Lizard burrow structure was investigated by digging up several burrows. Inactive burrows were usually chosen for excavation in order to minimize interference with lizard populations. However, several active adult burrows were unearthed in order to obtain the occupant and to correlate burrow structure with sex and size. Lizards so obtained were either displaced for homing experiments, brought to the laboratory for behavioral observation, preserved for dissection, or released into nearby inactive burrows after marking. The structure, including length, direction, depth, and substrate for all parts of each excavated burrow, was recorded. Eggs unearthed in nature, as well as clutches laid in captivity, were removed to the laboratory in Gainesville for incubation in moist sand under constant conditions. In an attempt to study turnover rates in burrow use, all burrows in a randomly chosen circular area (radius 26 m, area 0.22 ha) along the limestone ridges of the leeward side of southwestern Pine Cay were surveyed on six consecutive visits beginning in December 1973. This site was designated the Ridge Area (Fig. 3).

Before analysis of diet in this herbivorous lizard was possible, it was necessary to collect and identify the majority of the plant species on Pine Cay. Plant specimens were first collected on Pine Cay in September 1973 and recollected seasonally. From these various collections, a reference catalog of seeds, fruits, and leaves was assembled for use in identification of lizard food items.

Scat analysis based on 670 fecal pellets supplemented gut content analysis. Plant species and parts observed being eaten or bearing evidence of iguana feeding (i.e. tooth marks) were also recorded.

Microhabitat temperatures and precipitation were recorded only when an investigator was on Pine Cay. Climatic data from Grand Turk Auxillary Airfield, Grand Turk (21°26'N, 71°8'W; elevation 4 m) were also available.

A 3 x 8 x 1.25 m enclosure with attached observation blind was constructed in Gainesville, Florida, for captive observations. Artificial burrows, water, and an *ad libitum* supply of fruits, vegetables, pet food, and sardines were provided.

Several terms used herein require clarification. The "Study Islands" include Fort George, Pine, Water, and Little Water cays; the "Study Island" refers to only Pine Cay. The principal study sites on Pine Cay are designated as the SW Blind and Ridge Area (Fig. 3). Lizard body length or snout-vent length is abbreviated as SVL; tail length as TL. All references to lizards, rock iguanas, or iguanas, refer to *Cyclura carinata* unless otherwise qualified by a scientific name. All material collected incidental to this study, including other vertebrate and invertebrate specimens, has been placed in the collections of the Florida State Museum, University of Florida. Statistical methods are those of Steele and Torrie (1960) unless stated otherwise. Means are ordinarily given with ± one standard deviation. Definitions of behavioral terms appear in the text.

MORPHOLOGY

Cyclura carinata Harlan was described in 1825 from "Turk's Island." The location of Harlan's holotype is unknown. The species can be diagnosed as follows: nasals broadly in contact with the rostral; frontal, fronto-parietal, and occipital regions covered by small irregular, strongly keeled scales; circumorbital scales smaller than other supracephalic scales; 2 to 4 enlarged, vertically arranged canthal scales on each side; dorsal crest broadly interrupted on the shoulders and rump; nuchal section of the crest with 16 to 20 spines (up to 2 cm), which are longer than the 45 to 75 spines on the back; dorsal crest spines exceed 5 mm in height only in males; femoral pores average 21 on each leg (range 18-25); vertical rows on the tail strongly keeled, with four vertical scale rows between fifth and sixth rows; mid-dorsal tail scales enlarged and sharply keeled; males < 80 cm total length, females < 65 cm.

Two subspecies are recognized. The nominate subspecies can be distinguished by having the nasals separated by a large wedge-shaped scale; spinose, hexagonal scales on the outer tibial region, 3 or 4 of which equal the diameter of the tympanum; and fewer than 60 spines in the dorsal crest. *Cyclura c. bartschi*, described from Booby Cay, east of Mayaguana Island, Bahamas Island (Cochran 1931), is characterized by nasal scales usually in contact; 4 or more tibial scales equal to tympanic diameter, and usually more than 60 spines in the dorsal crest.

The following morphological descriptions are based only on specimens and data obtained in the Caicos Islands.

DENTITION.—Teeth heterodont, unicuspid at the symphysis and on premaxillary; remaining anterior teeth strongly tricuspid. Median and posterior teeth strongly compressed laterally and flared anteroposteriorly, with a multicuspid cutting edge; large median cusp flanked by 2-3 smaller anterior and 1-2 posterior cusps. Tooth formula: 0-10 pterygoid; 0 palatine; 4-10 premaxillary; 17-23 maxillary; and 19-28 dentary. Dentition similar to that of other iguanines (all primarily herbivorous) in both tooth counts (Table 1) and presence of increasing cuspidation from anterior to posterior along dentary and maxillary (see Avery and Tanner 1971 for comparisons). Nearly contiguous, laterally compressed, multicusped, pleurodont teeth forming continuous shearing surface, well-adapted for leaf chopping and shearing (Hotton 1955; Ray 1965; Montanucci 1968). Tooth positions increase ontogenetically (Fig. 6) as in *Ctenosaura*, *Iguana*, and *Anolis* (Ray 1965; Montanucci 1968). Maxillary and dentary counts positively correlated with skull length (r = 0.91 and r = 0.84 respectively).

SKELETON.—Basiphenoid wider than long, slightly to moderately constricted behind pterygoid processes; length/width ratio: 0.65-0.72. Five or more foramina on superficial surface of rostral part of premaxilla; parietal foramen small, pierced in frontal or fronto-parietal suture; parietal not produced posteriorly; angular and splenial elements present; splenial long, narrow; dorso-ventral borders of Meckel's groove fused anterior to splenial; antero-ventral alveolar foramen partially enclosed by border of splenial; coronoid with large process overlapping

TABLE 1.—TOOTH POSITION COUNTS IN *Cyclura carinata* FROM CAICOS ISLANDS, BRITISH WEST INDIES.

	Premaxilla	Right Maxillary	Left Maxillary	Right Dentary	Left Dentary	Pterygoid per side
Mean	6.9	19.3	19.3	21.9	21.7	—
Standard Deviation	± 1.4	± 1.2	± 1.2	± 1.5	± 1.6	—
Range	4 to 9	17 to 21	17 to 21	19 to 25	20 to 26	1 to 7
Sample Size	13	14	14	15	14	13

dentary; postero-ventral angular process pointed, elongate, directed antero-medially. Usually 24 presacral vertebrate, each with zygosphenes, zygantra, and zygopophyses. At least some autotomic caudal vertebrae with two pairs of transverse processes, fracture plane passing between them. Scapular and secondary coracoid fenestrae well-developed; clavicles simple or with posterior hook-like processes; interclavicle T-shaped or arrow-shaped; sternal fontanelle small or absent; 4 sternal and 2 xiphisternal ribs present. For description of hyoid apparatus see Avery and Tanner (1971).

HEMIPENIS.—Structure in the genus never illustrated, but that of *C. carinata* briefly described by Cope (1896). Hemipenis single-lobed, subcylindrical to clavate; sulcus spermaticus a broad open groove along the posterior surface of hemipenis; calyces cover distal half of hemipenis, proximal half covered with irregular creases; spines or spinose structures lacking; structure most similar to iguanine genera *Iguana* and *Amblyrhynchus* (Avery and Tanner 1971).

LEPIDOSIS.—Possess corneous subdigital combs on digits 2 and 3 (#4 = longest) of hind limbs (diagnostic of genus); subdigital lamellae multicarinate, not flattened, lacking mat of hair-like processes. Mid-dorsal crest spines exhibit considerable sexual size dimorphism (Fig. 7). Female neck spines never exceed 5 mm height (maximum recorded height, 3 mm). Male neck spines begin development (elongation) with onset of sexual maturity; thereafter, each time skin is shed, spine in-

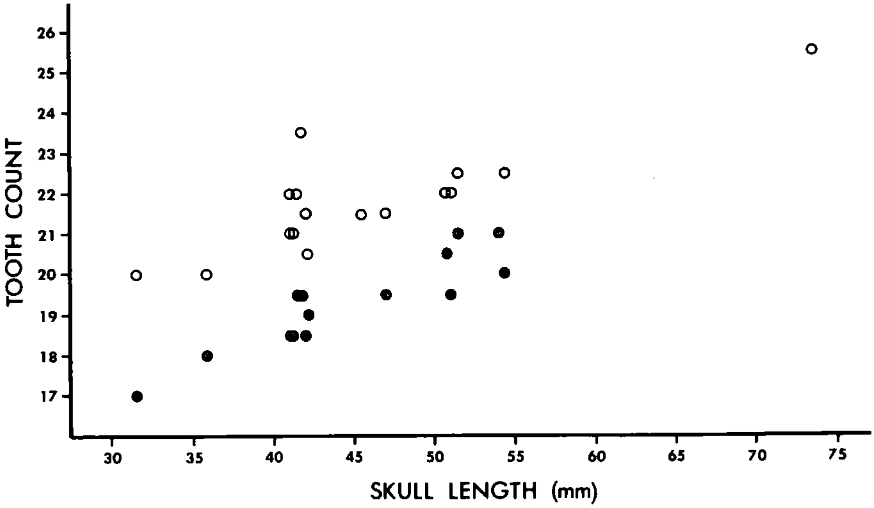

FIGURE 6.—Ontogenetic change in tooth numbers. Skull length measured from snout to occipital condyle. Maxillary (closed circles) and dentary (open circles) counts are averages of right and left sides.

FIGURE 7.—Adult male (A) and female (B) *Cyclura carinata.*

creases in length and an annular impression is formed around its base. After 2 (sometimes 3) skin sloughs, back spines begin development exactly as for neck spines; back spines are therefore shorter, with two fewer annuli than neck spines (most individuals). Relationship of spines to sexual recognition and annuli to growth and age discussed later. Back spines approach or even exceed neck spines in height in some old lizards; annuli become inconspicuous as the spines become smooth due to wear. Middorsal spines on anterior portion of the tail in males also elongate with age, albeit very slowly. Maximum middorsal scale height 18 mm in extremely old males. For other scale characters, see Schwartz and Carey (1977).

COLOR.—Exhibiting great individual and population color variability. Patterns tend to be darker (gray, brown, or green, depending on population) immediately following emergence and preceding submergence each day. Midday coloration typically light gray to bleached green (related to population). Changing albedo presumably is an adaptation to increase absorptive radiation in suboptimal ambient temperature regimes (Cowles and Bogert 1944). Color change most rapid during the morning basking period, timed at less than one hour. Relationships of changing albedo and skin reflectivity to thermoregulation under study (Auth, in preparation). Seasonal color changes related to hormonal levels (see Carpenter 1967; Ferguson 1976) not evident.

Interpopulation color differences on Caicos bank very pronounced. Lizards from eastern populations (Middleton and Long cays) drab gray dorsally and ventrally with only slight differences in darkness of gray. Fort George and Pine Cay lizards brownish to greenish-gray following emergence, nearly white-gray at midday; venter gray to blue-gray. Abrupt pigmentation change occurs between Pine Cay and Water Cay (to the south); lizards from Water and Little Water cays most brillantly colored of Caicos populations; basically dark gray-green on emergence, pale yellow-green during basking; typically lighter venter blue-gray, flushed with yellow. Yellow coloration extends over tail and on ventral surfaces of limbs and digits. Pine and Water cays have apparently been separated throughout historic time by a deep water channel, allowing the maintenance of very different color morphs.

Also exhibiting variable pattern of narrow vertical stripes on dorso-lateral body surface; stripes most obvious near anterior middorsal line, increasingly less apparent laterally and posteriorly; typically 9 or 10 stripes (i.e. areas where pigmentation simply lighter than adjacent regions). Pattern most obvious in hatchlings and juveniles; typically obscure in adults.

ANATOMY.—Thyroid gland morphology discussed by Lynn *et al.* (1966). Digestive tract anatomy discussed in Iverson (1980).

HABITAT

CLIMATE

The Turks and Caicos Islands experience a typical tropical maritime climate. East-southeasterly tradewinds predominate and average 25.9 km per hour throughout the year, and annual air temperature fluctuations are not great (Fig. 8). Recorded annual air temperature extremes between 1960 and 1968 on Grand Turk (110 km to the east of the study island) were 15.6 C and 36.0 C. However, microclimatic temperatures show much greater fluctuations both daily and seasonally. Temperatures on light coral sand substrates ranged from 12.5 C to 60.0 C on the study island; those on darker soils were considerable higher. Substrate temperature differentials between exposed and shaded areas were greatest during midday in July through August with a maximum recorded difference of 25 C (31-56 C). Twenty degree divergences are typical of summer days without midday precipitation. The maximum recorded winter (November-December) shaded-exposed substrate differential was 18.5 C.

To provide a general picture of the diurnal thermal environment, microclimatic temperature data from optimum days (unaffected by overcast or rainy conditions) on the study site were averaged by half hour for two periods, representing the longest and shortest days of the year (Fig. 9). Data from six days in late June 1974 and six in December 1973 were used. These differences in summer and winter temperatures are in part due to an annual fluctuation in day length (photoperiod) of nearly three hours. A more detailed analysis of the thermal environment and its relation to the biology of *Cyclura carinata* on Water Cay, Caicos Islands, is found in Auth (ms).

Since it was possible for me to monitor rainfall only while on the study island, data collected between 1900 and 1968 at the Grand Turk Auxillary Airfield (latitude 21°26′N, longitude 71°08′W; elevation 4 m) are presented here, unless otherwise indicated. A well-defined dry season exists from January through May with monthly rainfall averaging only 31.5 mm (Fig. 10). The wet season usually begins and ends rather abruptly in June and January, respectively, and rainfall averages 62.8 mm monthly. In addition to amount of rainfall, the percentage of days per month experiencing some rainfall also increases substantially during the wet season (Table 2). Average annual rainfall on Grand Turk is 597 mm. However, based on 458 mm recorded on Pine Cay in 194 days over three years, the annual estimate is approximately 862 mm, somewhat higher than on Grand Turk. Comparison of the vegetation, soil moisture, and general weather conditions across the bank on several occasions, in addition to information supplied by locals, indicate that rainfall is greater on the more western islands of the bank, but probably does not exceed 760 mm annually.

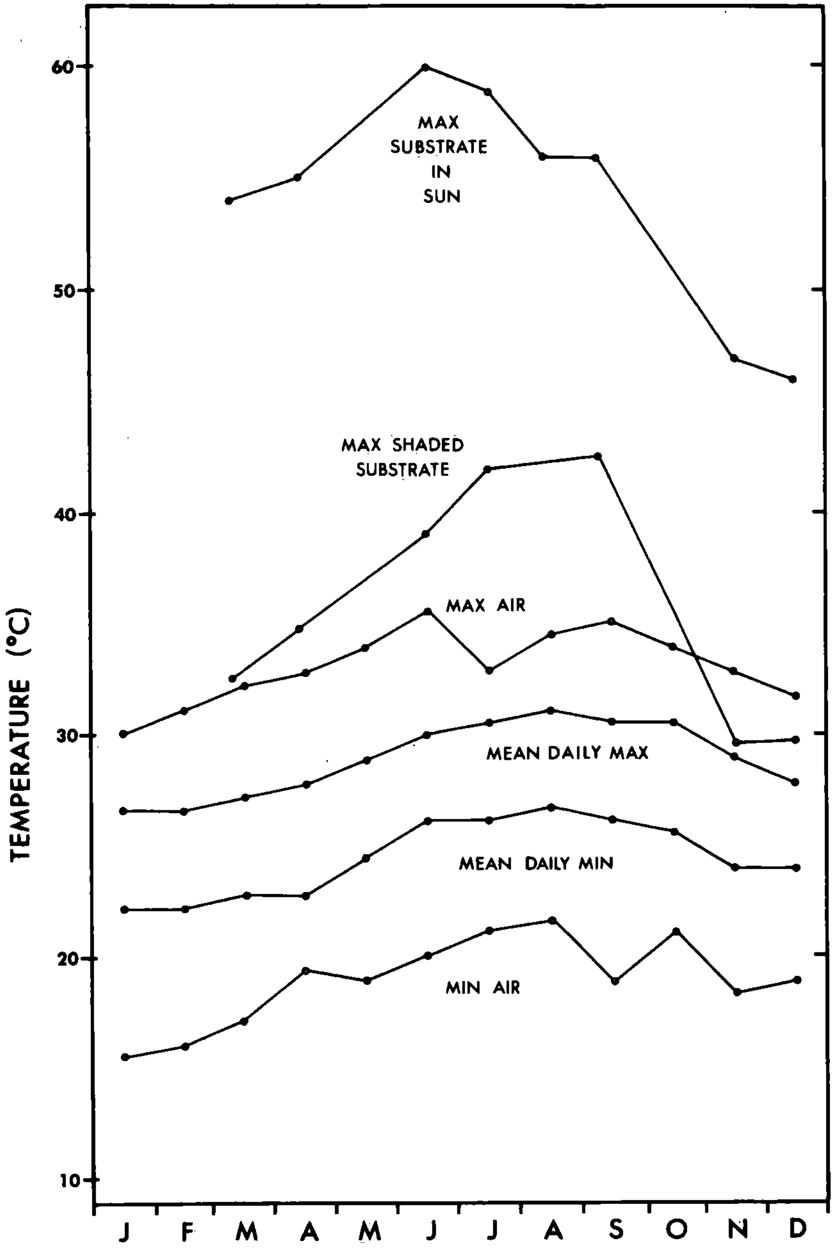

FIGURE 8.—Average monthly temperature regime in Turks and Caicos Islands. Substrate temperatures were recorded at SW Blind, Pine Cay, during study period; remaining temperatures collected between 1900 and 1968 at Grand Turk Airfield, Grand Turk.

TABLE 2.—MONTHLY FREQUENCY OF STUDY DAYS ON PINE CAY WITH PRECIPITATION.

	Jan	Feb	Mar	Apr	May	June
Percentage	0	--	17.6	0	25	37.8
Days Sampled	4	--	17	12	12	37

	July	Aug	Sept	Oct	Nov	Dec
Percentage	42.9	56.3	52.4	54.8	62.5	25
Days Sampled	28	16	21	31	16	20

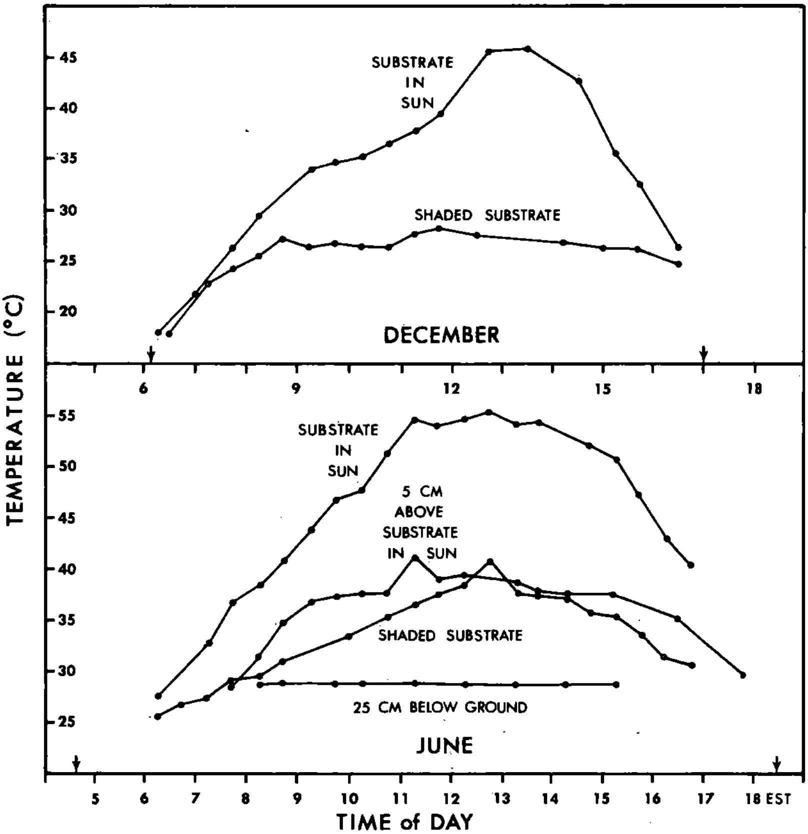

FIGURE 9.—Average diurnal microclimatic temperatures for June and December at SW Blind study site. Data averaged by half hour for six storm-free days in June, and four in December. Arrows indicate sunrise and sunset.

Changes in rainfall, temperature, and photoperiod are the major aspects of climatic seasonality. The effects of each of these are reflected in lizard activity. Days are often cool enough to curtail lizard activity in the winter, but almost never so in summer. The climate in the western cays of the Caicos Islands is one of a warm dry spring (March to May), followed by a hot, wet summer (June to October) which grades into an even wetter, but still warm autumn (September to December), and is followed by a cool, relatively dry winter (January to March). Abrupt changes in temperature and precipitation characterize the transition between the wet and dry seasons.

SOIL

Reflecting their reef origin, the Turks and Caicos Islands are characterized by honeycomb limestone formations usually covered with coral sand. The rocks are typically exposed along the windward shores, with broad sandy beaches along the leeward. Inland accumulations of humus provide a rich nutrient source and support more luxuriant vegetation (see Vegetation).

Iguanas frequent rocky and sandy areas as well as the more elevated humus areas, but generally avoid the lower areas with thicker

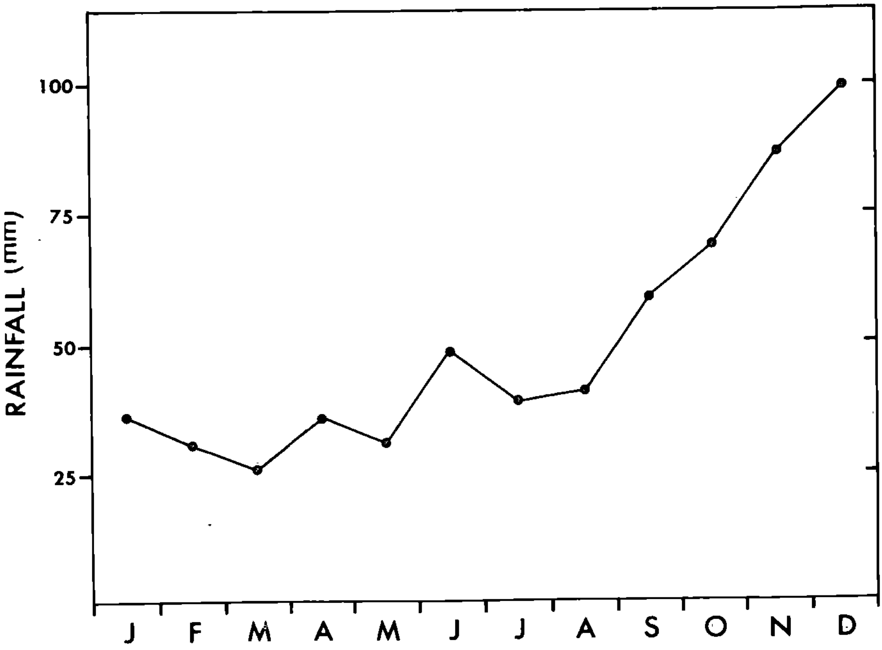

FIGURE 10.—Average monthly rainfall, 1900-1968, at Grand Turk Airfield, Turks Islands.

soils due to the proximity of the water table to the surface and their inability to dig through the root mass.

VEGETATION

The spatial relationships of the principal vegetation types on Pine Cay are illustrated in Figure 11 and listed in Table 3. Community distribution of most of the plants on Pine Cay is found in Auffenberg (ms). The vegetation on Pine Cay corresponds to the "Evergreen Bushland" of Beard (1949), and is physiognomically similar to that found on Anegada in the British Virgin Islands by D'Arcy (1975). The same genera (if not species) are represented in similar habitats on both islands. Although D'Arcy (1975) divided the flora of Anegada into only four primarily edaphic communities (shorelines, sandy plains, limestone plains, and vegetation near man), it seems justified on Pine Cay to distinguish additional plant communities within at least two of his provinces. A more thorough discussion of the components of the vegetation types on Pine Cay and their relationships appears in Auffenberg (ms).

Cyclura carinata inhabited all of Pine Cay's plant communities except the Marsh and portions of the Mixed Woodland vegetation types. These are areas where the proximity of the water table to the ground surface precluded the possibility of burrow construction and vegetation was too dense for movement. *Cyclura* reached its maximum adult abundance on Pine Cay in areas of Rocky Coppice (Fig. 12). Young lizards were more commonly observed in areas of Open (Fig. 13) and Dense Scrub.

BURROWS

Unless natural shelters in the form of abandoned land crab (*Cardisoma guanhumi*) burrows or honeycomb limestone or coral formations are available, *Cyclura carinata* digs its own burrows. Since natural retreats are not abundant on the study islands, most lizards dig their burrows. Large mounds of vegetation, dirt, and rocks piled up by bulldozers while clearing roads were often used for retreats by lizards on Pine Cay. These sites also offer excellent elevated basking sites.

Adult male iguanas exhibit relatively great attachment of specific burrows. This is reflected in the greater average length, depth, and complexity of burrows dug by males versus those dug by females. Mean burrow length for 8 females and 12 males from Pine and Water cays was 3.09 ± 0.96 m (range 1.83 to 5.02) and 4.39 ± 1.53 m (1.37 to 6.40), respectively. Mean burrow depth, measured to the top of the burrow terminus for these same lizards was 31.5 ± 25.3 cm (range 12.7 to 91.4) and 69.1 ± 42.9 cm (25.4 to 183.0 respectively). Sexual dif-

TABLE 3.—PRINCIPAL VEGETATION TYPES ON PINE CAY, CAICOS ISLANDS, BRITISH WEST INDIES.

Vegetation Type	Area (ha)	Percent of Total Area		Dominant Plants
Dense Scrub	119.94	34.41		*Casasia clusiaefolia* *Coccoloba uvifera* *Erithalis fruticosa* *Phialanthus myrtilloides* *Thrinax microcarpa*
Mixed Woodland	69.37	19.90		*Erithalis fruticosa* *Metopium toxiferum* *Pinus caribbaea* *Psidium longipes* *Reynosa septentrionalis*
Open Scrub	47.24	13.55		*Antirhea myrtifolia* *Coccoloba uvifera* *Ernodea millspaughii* *Psidium longipes* *Strumpfia maritima*
Beach or Rocky Coast	42.01	12.05	Beach	*Chamaesyce vaginulata* *Ernodea millspaughii* *Rachiallis americana* *Scaevola plumierii* *Strumpfia maritima*
			Rocky Coast	*Guapira obtusata* *Manilkara bahamensis* *Rachiallis americana* *Strumpfia maritima* *Zizyphus taylori*
Marsh and Lakes	26.33	7.55		*Conocarpus erectus* *Mariscus jamaicensis*
Airstrip and Hotel Development	17.85	5.12		--
Rocky Coppice	15.31	4.39		*Antirhea myrtifolia* *Coccoloba krugii* *Eugenia foetida* *Manilkara bahamensis* *Metopium toxiferum* *Pithecellobium guadelupense* *Reynosa septentrionalis* *Zizyphus taylori*
Mesic Coppice	10.53	3.02		*Byrsonema lucida* *Coccoloba uvifera* *Erithalis fruticosa* *Reynosa septentrionalis*
Total	348.58	99.99		

ferences in burrow depth are also due, in part, to the need for shallow incubating chambers for successful nesting in females; burrow length differences are also related to sexual dimorphism in size. Though adults of both sexes commonly use the same burrow, strongly territorial adult males never share them, unless as a retreat after having been frightened. Although territorial adult male lizards near the SW Blind maintained a single retreat, they were nevertheless aware of all burrows (and other potential retreats) both within their own territories and within those of adjacent males.

Even subadult lizards showed familiarity with burrows far outside their normal activity ranges. On 20 September 1973 near the Ridge Area on Pine Cay, a 178 mm SVL lizard was removed from its burrow. After marking, it was released at the site of its burrow. It ran directly and non-stop 16.1 m, where it entered another active burrow. The second burrow was found to contain the marked lizard, in addition to its resident male (SVL 229 mm). When released after marking, this resident immediately ran over the ridge and directly to the burrow first excavated. The lizards were clearly aware of the exact location of the other's burrow.

Blocking of a territorial male's primary burrow caused him to shift his retreat. Removal of the obstacle after one to three days was fol-

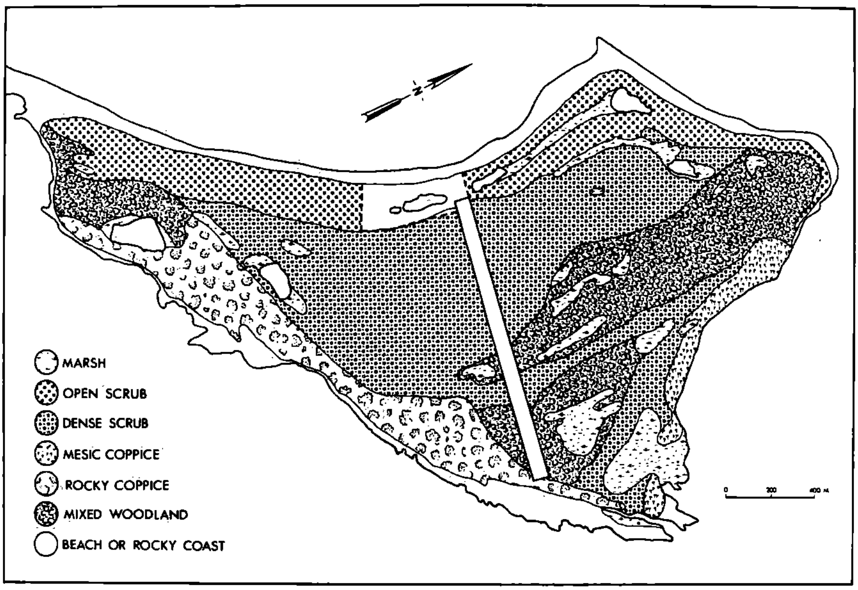

FIGURE 11.—Principal zones of vegetation on Pine Cay, Caicos Islands (after Auffenberg MS). Inland open areas represent lakes, airstrip, or hotel grounds (within dashed lines).

lowed by his return to the primary burrow. The effect of permanent destruction of the primary burrow was not determined. The short term blockage seemed to cause no change in activity range, but it is suspected that a shift may occur if the burrow is destroyed.

Juveniles and subadults frequently shift burrows. One subadult non-territorial male, in the SW Blind area, carrying a tranmitter, utilized three different burrows on three consecutive nights. However, in some areas the unavailability of auxiliary retreats necessitates the continual use of a single site. A hatchling took up residence in a small hollow tree limb in a brush pile on 1 September 1974 within only a few days of emergence. It still occupied the site in April 1975 when last observed. Thereafter it was not seen on the study site, and presumably had been killed.

The following patterns in burrow usage were observed in the Ridge Area. Large burrows active at the beginning of the study remained so throughout the study period, but there was considerable turnover of small burrows probably due to (1) predation on juveniles; (2) lack of burrow fidelity in juveniles; and (3) periodic excavation of burrows by terrestrial crabs. Since the burrow is central to all activity in *Cyclura carinata*, its importance cannot be overemphasized.

Not surprisingly, burrow excavation in all species of *Cyclura* seems to be related to the substrate conditions. In areas where sandy dune situations predominate, as on the typically small, low islands of the

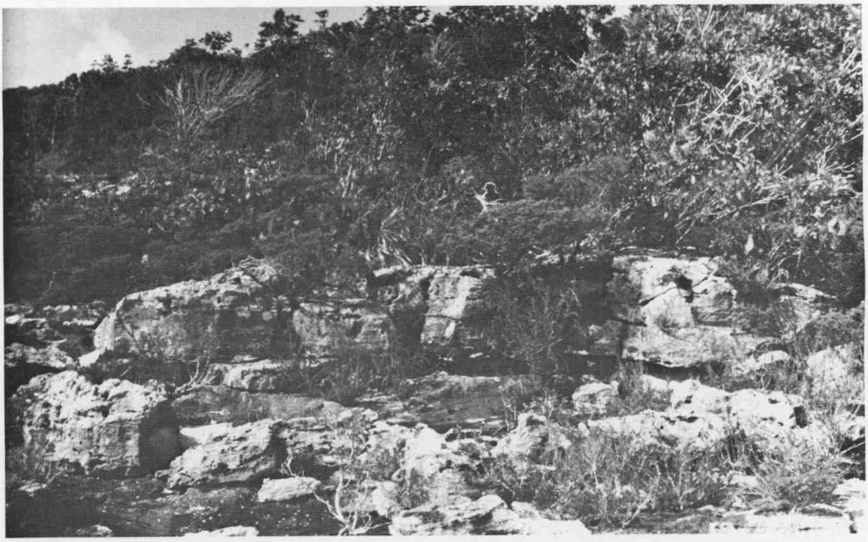

FIGURE 12.—Ecotone between typical Rocky Coppice (background) and Rocky Coast habitats on Pine Cay.

Bahaman archipelago, dug burrows are used. However, on islands dominated by cavernicolous limestone and coral exposures, where there is no possibility of burrow excavation by iguanas, natural retreats are employed (see Retreats under ACTIVITY AND MOVEMENTS).

The presence of at least some friable soil for nest construction appears to be a very important factor ultimately limiting distribution and numbers of *Cyclura* populations. In the species of *Cyclura* for which the nest site has been described (Noble 1923; Wiewandt 1977) a nest burrow was excavated in well-insolated soil areas, sometimes several km from the female's normal activity range (see Discussion under REPRODUCTION). In addition to protection, burrows could serve a thermoregulatory function; however, lizards do not use them as heat sinks, even under extreme conditions.

Adult *Cyclura* typically maintain their burrows by removing sand, leaves, and other debris during the middle of the day when general lizard activity is reduced due to high environmental temperatures. However, this is not a daily routine; a period of several days generally separates burrow cleaning activities. In removing debris, the lizard enters the burrow head first and kicks material backward as it moves further inside. Emerging from the burrow head first, it turns and repeats the procedure several times.

The complete excavation of a burrow was never observed; the time required is unknown. However, a young adult male completely ex-

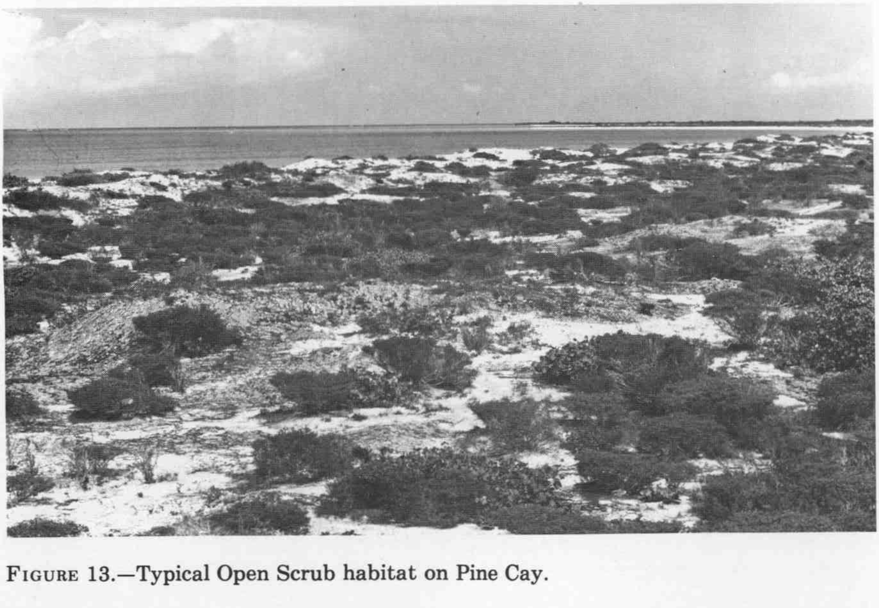

FIGURE 13.—Typical Open Scrub habitat on Pine Cay.

cavated a new burrow near the SW Blind during my absence between 20 July and 1 September 1974.

Neonate lizards usually use natural cavities or spaces cleared beneath rocks, roots, logs, etc., for retreats. In open sandy areas, they will excavate their own burrows. These burrows are usually shallow (< 15 cm deep) and short (< 50 cm), with diameters between 2.5 and 3 cm. Some have short side branches but these may be added by crabs.

Since many young lizards frequent more than one burrow and many small burrows are actively maintained by crabs, small burrows are not useful in estimating lizard density. Data concerning locations of large active burrows can, however, provide fairly accurate estimates of adult lizard density (see DENSITY AND DEMOGRAPHY).

Burrow dimensions and complexity are quite variable (Fig. 14), dependent in part on the surface and subsurface soil texture. The longest burrow excavated was in dune sand on Pine Cay and measured 6.4 m. It was occupied by both a female and a male when opened. One of the biggest burrows encountered was an active one which I could not completely excavate. The burrow was in an area of deep dune sand nearly devoid of vegetation. The 16 cm diameter of the burrow suggested that it had been dug by a male. Beyond 5.0 m of horizontal excavation, the burrow was 1.5 m below the sand surface. It continued downward with the same slope at least 1 m farther. Digging was suspended due to constant collapsing of the excavation pit.

Burrow orientation on Pine and Water cays (Fig. 15), appears to be related more to micro-topographic features than to intentional directional construction. More burrows generally open to the northwest and southeast on these two islands, because these retreats lie perpendicular to the generally northeast-to-southwest lying ridges (Figs. 3 and 14). *Cyclura* prefers digging under the limestone exposures in the sides of these ridges to digging in open flat sandy areas. In the latter areas, burrows are typically excavated into the sides of small hummocks formed by the accumulation of blown sand around the bases of clumps of vegetation. An obvious advantage in avoiding flat areas of open sand for burrow construction is the reduction of the possibility of entombment by burrow collapse.

As in the burrows of the Florida gopher tortoise *Gopherus polyphemus* (Young and Goff 1939), there are numerous arthropod inquilines in nearly every *Cyclura* burrow, many apparently obligatory. The most common and seemingly most obligatory were camel crickets (*Amphiacusta* sp.). Also found were solpugids (genus *Ammotrechella*), scorpionids, amblypygids (*Tarantula marginepennis*), nymphal cicadas (*Ollanta caicosensis*), and numerous unidentified spiders.

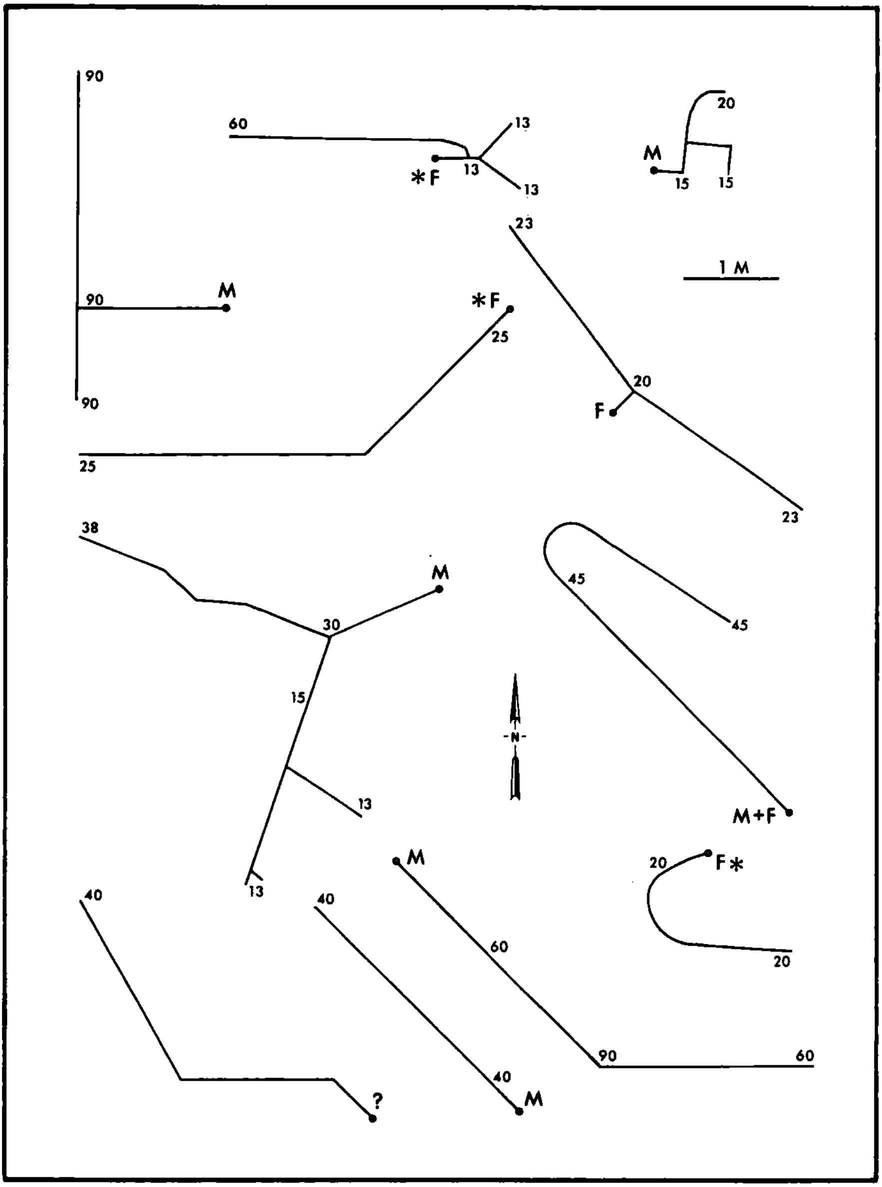

FIGURE 14.—Variation in burrow morphology and orientation in adult *Cyclura carinata.* Soil depth (in cm) to top of burrow is indicated; changes in depth are uniform between measurements. Letters adjacent to burrow entrance (solid circles) indicate sex of inhabitant. Asterisks mark burrows used for nesting in previous years.

REPRODUCTION

MALE SEXUAL CYCLE

The male testicular cycle closely parallels the female reproductive cycle. Since testes weight has been shown to be an accurate indicator of testicular activity in lizards (Hahn 1964; Marshall and Hook 1960; Ballinger 1973), no histological analysis was made. Testes reach maximum sizes in April and May, declining rapidly in June and July to maximum regression in early fall (Table 4). Testicular size maxima are coincident with breeding in *Cyclura carinata*. A similar cycle (early spring maxima and late summer minima) is typical of at least the iguanid lizards.

Sexual maturity in male *C. carinata* was determined by testicular enlargement between January and June, or actual observation of at

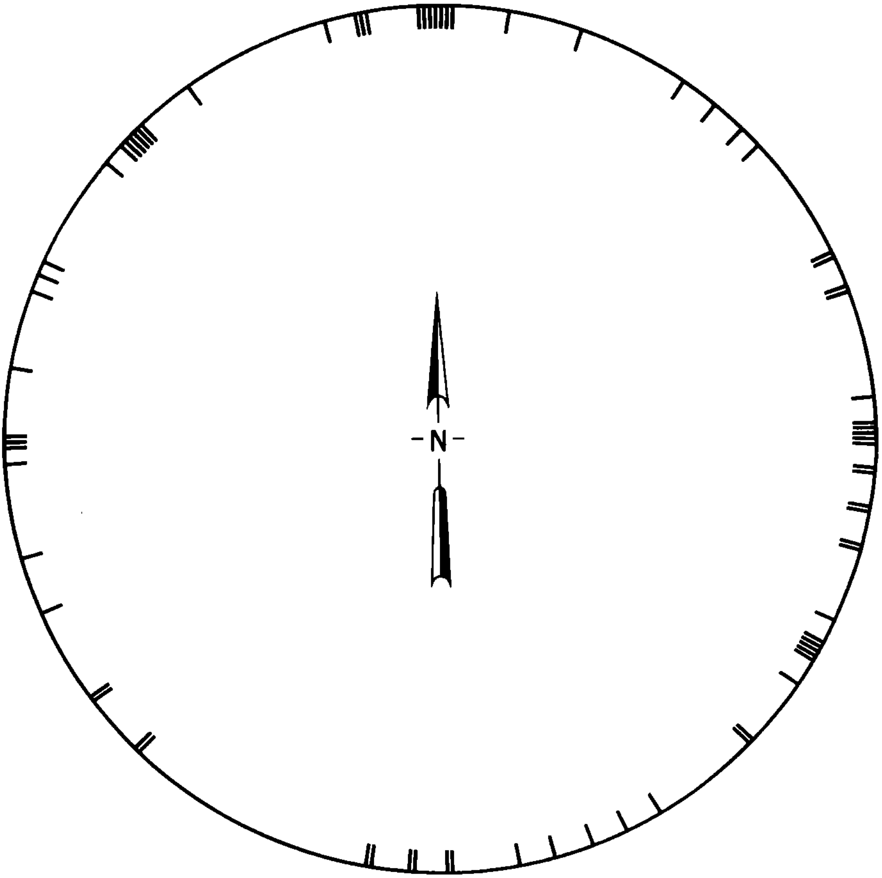

FIGURE 15.—Orientation of burrow entrances in *Cyclura carinata*, recorded as compass direction into burrow.

Table 4.—Seasonal Variation in Proportional Testes Weight (Testes Weight in gm x 10^{-5}/SVL in mm) in Male *Cyclura carinata* over 216 mm SVL.

Sample Date	N	$\overline{X}$ ± S.D.	Range
March 6	1	867	—
May 10	1	1358	—
June 30	7	178 ± 141.13	48-454
August 15	2	117	70-164
September 15	1	47	—
December 15	2	177	151-203
December 30	4	165.5 ± 115.37	62-305

tempted or successful matings in May. The smallest male with enlarged testes was 216 mm SVL (weight approximately 440 gm). The largest males without testicular enlargement were 222 mm SVL (435 gm live weight) and 210 mm SVL (365 gm). A 219 mm SVL captive male, which attempted copulations on numerous occasions during May 1975, was the smallest male observed to exhibit courtship behavior. These data indicate that sexual maturity in males is reached at approximately 220 mm SVL and a body weight of 375 to 475 gm. Growth data indicate this requires about seven years (see GROWTH). Adult males averaged 276.3 mm SVL (191-360) and 935.1 gm body weight (256-1864).

Female Sexual Cycle

Ovaries are difficult to distinguish from testes in lizards less than one year of age; however, the obvious presence of oviducts in females allows accurate sexing of even hatchlings. Immature ovaries contain numerous follicles up to 4 mm in diameter. Maximum follicular diameter in mature females between oviposition and spring recrudescence is also approximately 4 mm (Fig. 16). Yolking of follicles begins between 1 January and 1 March and continues until ovulation in early May. Maximum follicular diameters reach 30 mm at that time.

Seasonal combined ovarian weights reflect the same trends as follicular diameters (Fig. 17), with ovarian weight maxima (63.7 gm in a 248 mm SVL lizard with five enlarged follicles) in mature females occurring in early May and post-reproductive minima (generally less than 0.35 gm) from July through December. The maximum combined ovarian weight recorded in an immature (184 mm SVL) female was 0.275 gm in March. Immature weights were normally considerably less than this. Perhaps her ovaries were developing in preparation for breeding the following year when she would surely have been of adult size.

Oviducal eggs were not present before at least the last of April and were noted only as late as 9 June. Yolked follicles and oviducal eggs were never found in the same female and no yolked follicles (except an occasional atretic one) were found in post-ovipository females. Fresh corpora hemoragica averaged 6 mm in diameter, but regression was rapid and corpora lutea were usually unidentifiable by early September (Fig. 18).

Of only two females with oviducal eggs, one showed evidence of transuterine migration of ova. The right reproductive tract of that female included two corpora lutea in the ovary and three eggs in the oviduct; the left tract bore four corpora lutea and three oviducal eggs. Cuellar (1970) has previously discussed this phenomenon in lizards.

Minimum sizes for mature females (as indicated by the presence of yolked ovarian follicles, oviducal eggs or corpora lutea) were 184 mm SVL (250 gm; with enlarged yolked follicles), 190 mm SVL (280 gm;

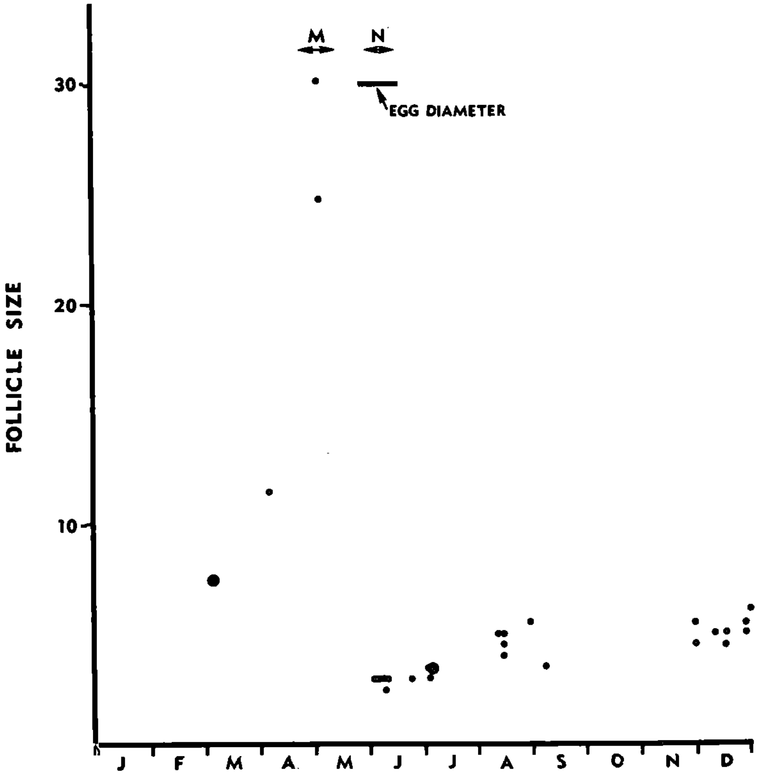

Figure 16.—Seasonal variation in maximum follicle diameter (mm) in ovaries of female *Cyclura carinata.* Small dots indicate individual females; large dots, two or more lizards. M and N mark mating and nesting seasons, respectively.

corpora lutea present), 194 mm SVL (live weight unknown; with corpora lutea), and 197 mm SVL (205 gm; with corpora lutea). Maturity of young adult and subadult females collected between September and January could not be accurately determined due to the regressed state of the ovaries even in obviously adult females. The largest immature females collected between January and August were 210 mm SVL (approximately 320 gm), 191 mm SVL (240 gm), and 184 mm SVL (weight

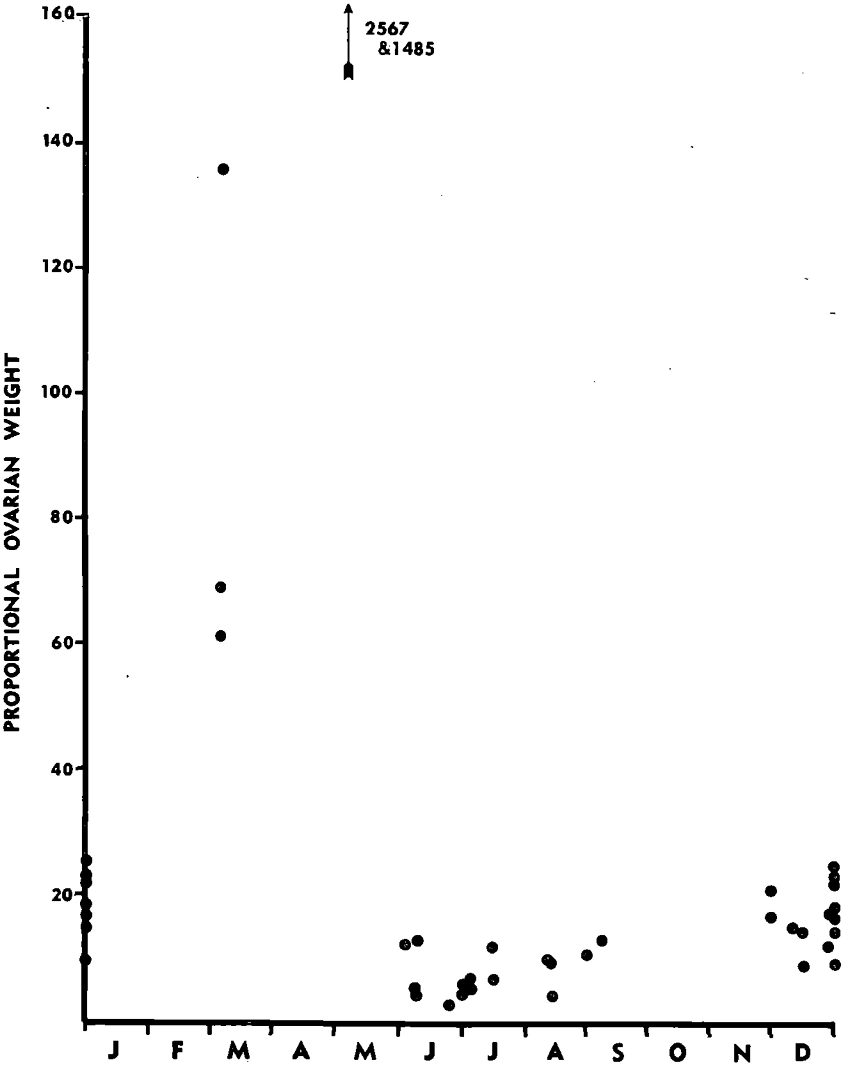

FIGURE 17.—Seasonal changes in proportional ovarian weight (grams x 10^{-4}/SVL in mm) in mature female *Cyclura carinata*. Each point represents one individual lizard.

unknown). Maturity in females at 185-200 mm SVL (200-300 gm) at an age of about six years (see GROWTH) is indicated. Nearly all females presumably oviposit their first clutch of eggs between age six and seven. Adult females averaged 225.4 mm SVL (190-292) and 475.6 gm (205-1135) body weight.

Courtship and Mating

From late March through April males became increasingly interested in females. During April males were frequently observed following females on the ground. At this time, the resident territory-holding male typically approached within 1 m of the female, but did not display or otherwise court the female. The approach usually caused the female to headbob (submissively; see SOCIAL ORGANIZATION), move a short distance away, stop, and again bob to the male. The male often reciprocated with a headbob, and again approached the female closely and the sequence was repeated (up to 12 times). The impression was that the male was attempting to insure his proximity to a female as the mating season approached. Perhaps this precourtship interest is necessary for the induction of receptivity as in

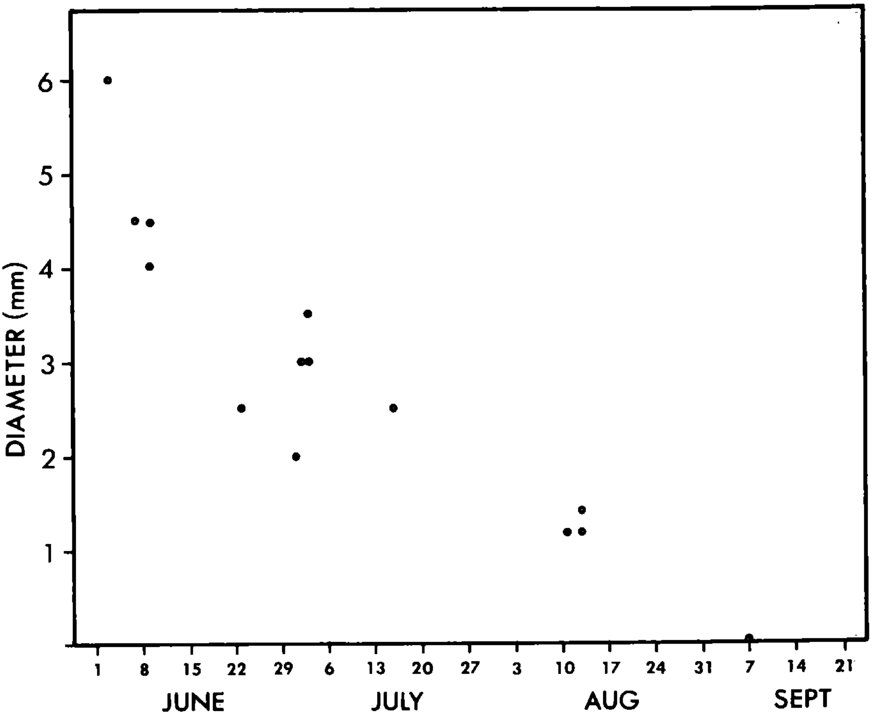

FIGURE 18.—Regression of ovarian corpora lutea in *Cyclura carinata* following oviposition. Maximum diameter is plotted.

Drosophila melanogaster (see Parker 1974:158) and *Anolis carolinensis* (Crews 1975b).

Resident males terminated their female-directed activity to displace neighboring males from their (the resident's) territory (hence away from the female) at this time of the year, just as they did during the remainder of the year. However, it was my subjective opinion that the males were more willing to defend at this time of the year than at any other. There was no question that the general level of activity was greatest at this time of the year (see ACTIVITY and MOVEMENTS). Following defense, the resident male returned to the female and resumed his interest in her.

In some cases, the male was so persistent in his attempts to closely approach the female, that she ultimately moved out of his territory and into that of a neighboring male. However, females sometimes also moved between males' territories without this pressure from the resident males. Perhaps female *Cyclura* were making active choices among courting partners at this time, as Trivers (1976) suggested for *Anolis garmani*.

The interest of males in females increased through April, presumably until the female tolerated the close approach of a male and active courtship could proceed. Unfortunately, neither active courtship nor copulation was observed in nature. However, they were frequently observed in captivity and the basic behavioral components are undoubtedly the same as those in non-captives.

Courtship was observed nearly 100 times (three times to completion) in the captive enclosure in Gainesville during nine days between 24 April and 9 May 1975 (Table 5). During this period, four mature females and at least two of four males were confined in a pen at any one time. The lizards were captured 5-9 April 1975 on the study islands.

TABLE 5.—AVERAGE NUMBER OF COURTSHIPS PER DAY ATTEMPTED BY EACH MALE WITH EACH FEMALE IN GAINESVILLE ENCLOSURE DURING NINE DAYS BETWEEN 24 APRIL AND 9 MAY 1975.

		MALES		
		#1	#3	#4
FEMALES[1]	SVL (mm)	349	286	219
#1	235	3.0	2.333	4.75
#2	235	1.67	1.222	0
#3	216	1.33	1.222	0.75
#4	185	—	1.000	0.75
Days male present		3	9	4

[1] All females were present everyday.

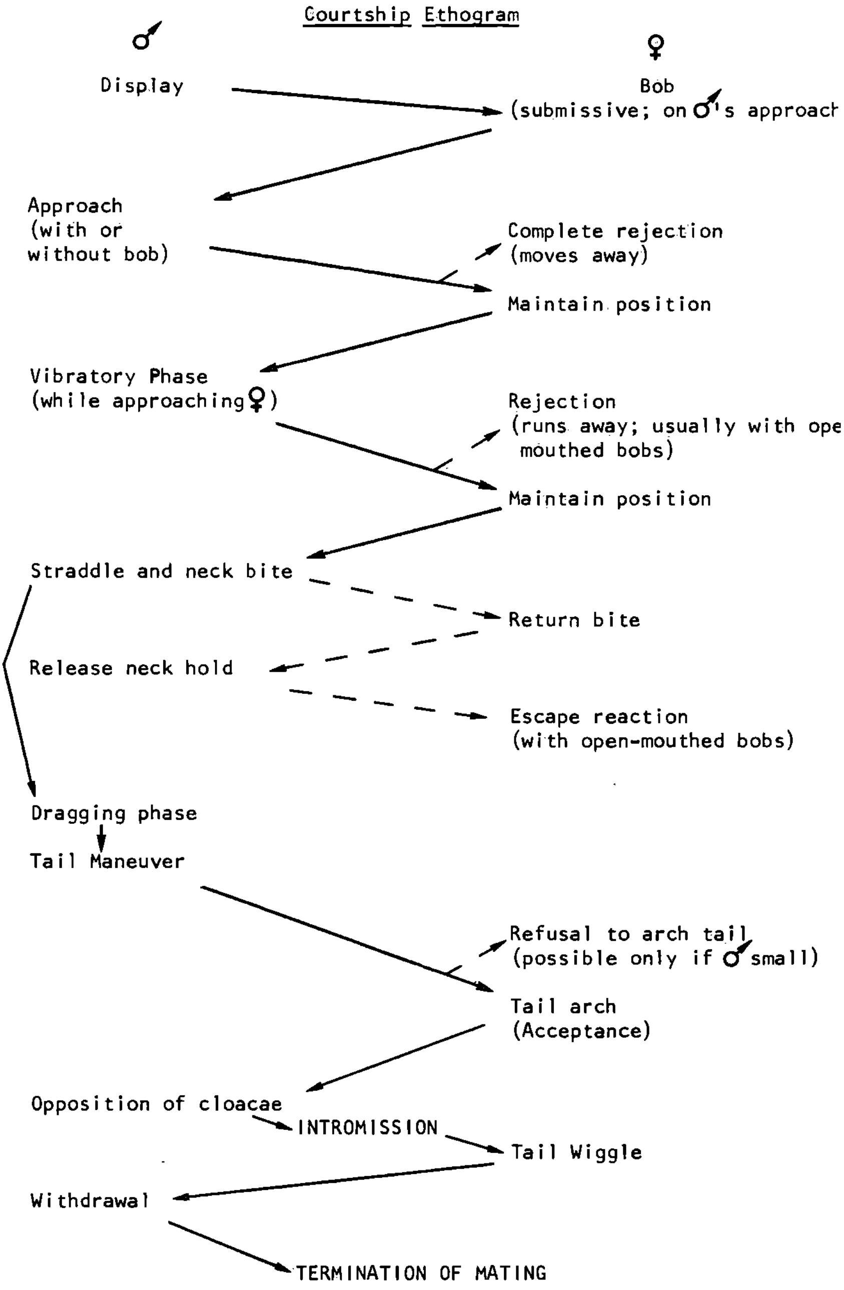

FIGURE 19.—Behavioral components of courtship in *Cyclura carinata.*

The females and smallest male (#4) were released into the captive enclosure on 17 April, while the other males were maintained separately in the laboratory. These males were introduced into the pen at various times between 24 April and 9 May to investigate dominance relationships (see SOCIAL ORGANIZATION).

Successful mating behavior can be divided into four basic stages: approaching, displaying, neck holding, and copulating. Figure 19 illustrates the male and female components of courtship behavior.

APPROACH.—In captivity the male and female did not always exchange headbobs prior to the male's approach to the female. In the field, the female always bobbed submissively at the appearance of the male; the male often did not reciprocate (see SOCIAL ORGANIZATION). The courting male typically approached the female laterally and from behind (their bodies aligned at approximately a 30 to 45° angle). The profile of the approaching male once within 0.5 m of the female was very low to the ground. The body was dorsoventrally flattened and the chin was kept less than 5 cm from the substrate. A few times the male turned his head to inspect the female's hip area, but usually approached until his head was lateral to her anterior trunk region. At this point the female often moved away, rejecting the male's advances. If she did not (or could not, as in some captive situations) the male began his courtship display and continued to approach the female.

DISPLAY OR VIBRATORY PHASE.—The courtship display of *Cyclura carinata* was stereotyped and very similar to that of most other iguanid and agamid lizards that have been studied (Carpenter 1967; Gonzales 1974). The male continued his approach toward the female while rapidly vibrating his head vertically. I have termed this behavior "vibratory" display due to the low amplitude of the headbobs. A typical display action pattern (DAP; see Carpenter and Grubitz 1961) of this head movement appears in Figure 20. Four videotaped displays, each including four oscillations of the head, averaged 0.36 seconds (0.32-0.40). Males sometimes performed displays with open mouths.

This vibratory courtship display is synonymous with the "jiggling" display described by Evans (1938) and Ruibal (1967), the "courtship nod" by Carpenter (1962b), and the "shudder sequence" by Ferguson (1970) for other lizards. In each case, the display consisted of a sequence of shallow, rapid headbobs. Male *Ctenosaura pectinata* (Evans 1951) and *Amblyrhynchus cristatus* (Carpenter 1966) also exhibit a similar courtship display. *Sauromalus obesus* (Berry 1974) is the only iguanine lizard studied to date that lacks this display.

Females rejected male courtship advances by a stereotyped rejection display or by simply running away. Either behavior was accompanied by vigorous headbobbing, typically with an open mouth. In the rejection display (Fig. 21), the female compressed her body laterally, postured high on all four legs with her back strongly arched and her tail on the ground, and headbobbed rapidly. In the field, as in many of the captive courtships, this display is probably sufficient to thwart the male's courting interests. However, captive males often continued the courtship sequence despite this display. If the female maintained her position during the male's vibratory display and approach, the male terminated the display, raised up and gripped the female's neck in his teeth.

Many iguanid lizard species have a similar rejection posture (Fitch 1956; Clarke 1963; Carpenter 1967). Noble and Bradley (1933) first described and illustrated this behavior but were unable to determine its significance. Within the subfamily Iguaninae, *Sauromalus obesus* (Berry 1974) also uses this rejection posture, while *Amblyrhynchus cristatus* apparently does not (Carpenter 1967); other members have not been sufficiently studied.

Only one homosexual courtship (with the smallest male) was observed and it was terminated by the courting male following his vibratory display.

Neck holding.—Following the vibratory phase of courtship, the male moved to straddle the female and secure a mouth grip on the dorsal region of the female's neck. The female could still terminate the

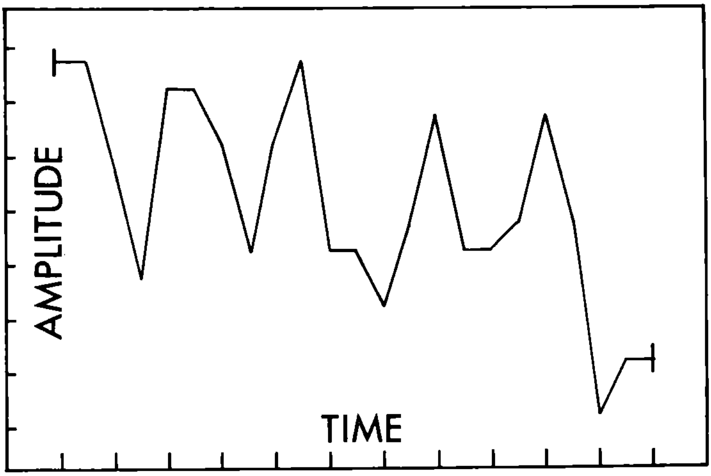

Figure 20.—Display action pattern of typical vibratory courtship display of a male *Cyclura carinata*. Time increments are 0.03 second. Amplitude is proportional to the distance from the lizard's eye to the substrate. Graph is accurate to 0.015 second.

courtship at this point by turning and biting at the male's head and/or struggling free. Females sometimes attempted to walk away, dragging the male for short distances.

Once the female's neck was securely held, the male attempted to maneuver his tail under that of the female to align their cloacae. The receptive female then arched her tail upward to facilitate the male's tail maneuvering. She could apparently still reject the male's advances, by refusing to arch her tail only if the courting male was smaller than herself; large males could force their tails under the female's tail even if she did not arch it. This was observed once in captivity during the forced copulation (rape) of one of the females (discussed later) by a large male. The refusal of a female to arch her tail to allow cloacal apposition was observed six times when a small male (219 mm SVL) had obtained a neck grip on a larger female. Once the cloacae were finally opposed, the neck grip was maintained until hemipenial withdrawal following copulation. The mating posture was exactly like that pictured for *Amblyrhynchus* by Schmidt (1935).

COPULATION.—Once the cloacae were opposed, intromission followed immediately and lasted from 40 to 76 seconds ($\overline{X} = 58.7$, $N = 3$). No thrusting by the male was observed. Wiggling of the distal portion of the female's tail immediately preceded withdrawal of the hemipenis. Uncoupling was rapid; the male released his neck grip and backed away from the female. His pelvis remained elevated from the ground until his hemipenis was fully retracted. Typically both lizards then moved very little and rested quietly. Their activity during the remainder of the day was generally depressed.

In all iguanine lizards, except *Iguana iguana*, for which data are available (Table 6), copulation (i.e. female receptivity) occurs approximately one month before oviposition. A distinct relationship with the female ovarian cycle is implied. It is suggested, but not known, that receptivity in *Cyclura carinata* immediately precedes ovulation as it

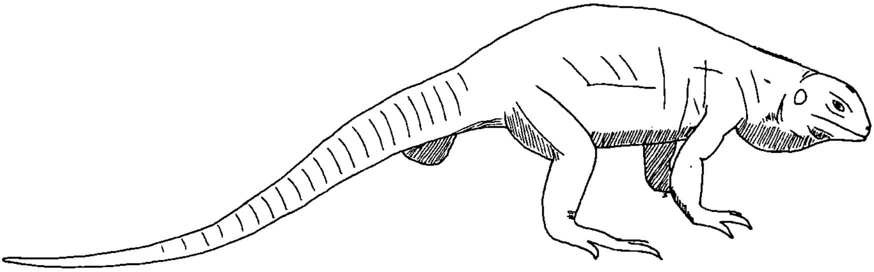

FIGURE 21.—Rejection posture of female *Cyclura carinata*.

Table 6.—Reproductive Data for the Lizard Subfamily Iguaninae.

SPECIES	LOCATION	MAXIMUM SIZE (mm SVL)	MAXIMUM WEIGHT (kg)	AVERAGE ADULT SIZE (mm SVL)	AVERAGE WEIGHT (kg)	AVERAGE CLUTCH SIZE	AVERAGE EGG SIZE (mm)	EGG WEIGHT (gm)
Amblyrhynchus cristatus	Galapagos	—	—	—	—	2	—	—
	Galapagos (Narborough)	—	3.118	—	—	2	—	80-120
	Galapagos (Hood)	♂=400	♂=2.948	♂=361	♂=2.01	2-3	—	—
	Galapagos (Narborough)	♂=430 ♀=350	♂=2.580 ♀=1.928	♂=341 ♀=290	♂=1.984 ♀=0.992	2.29 (2-3)	93 x 42	96.3 (79-121)
	Galapagos	—	—	♀=268	—	3n	86.0 x 42.5	82.0 (80.2-83.8)
	Galapagos	—	—	—	—	—	—	—
	Galapagos (Santa Cruz)	♂=510 ♀=350	—	—	—	—	—	—
Brachylophus fasciatus	Fiji Islands	160	—	—	—	3-4	40 x 30	—
	Fiji Islands	229	—	—	—	5 (n=3)	19 x 13	—
Conolophus pallidus	Galapagos (Barrington)	—	—	—	—	7,10	50-57 x 73-82	—
	Galapagos (Barrington)	—	—	—	—	7-10	64 x 35	—
	Galapagos	—	—	—	1.8-2.1	—	—	—
Conolophus subcristatus	Galapagos (South Plazas)	♂=420 ♀=380	♂=3.260 ♀=2.410	350	1.700*	—	—	—

TABLE 6.—EXTENDED.

INCUBATION TIME	HATCHLING SIZE (mm SVL)	HATCHLING WEIGHT (gm)	BREEDING SEASON	NESTING SEASON	HATCHING SEASON	SOURCE
—	—	—	—	—	—	Eibl-Eibesfeldt 1961
—	—	—	—	Feb. 3-4	—	Bartholomew 1966
—	—	—	Jan.-Mar.	early April	early July	Carpenter 1966
ca. 2 m	—	—	Dec.-Jan.	late Jan.-Feb.	April-May	Carpenter 1966
112-113 d (captive)	97.0	58.7	—	before Feb. 24	June (captive)	Shaw 1966
—	—	—	—	February	May	DeVries 1974
—	105-130	ca. 80-120	—	Feb.-early March	early May-early June	Bartholomew *et al.* 1976
17-23 w (captive)	65	—	—	—	—	Cogger 1974
—	—	—	Sept.-Mar. (captive)	Nov.-March (captive)	—	Cahill 1970; Bustard 1970a
—	—	—	—	Oct.-Nov.?	—	Van Denburgh & Slevin 1913
—	—	—	—	Dec.-Jan?	—	Slevin 1935
—	—	—	—	—	—	Wilhoft 1958
—	—	—	—	—	—	Carpenter 1969

TABLE 6.—CONTINUED.

Conolophus sp.	Galapagos	—	—	—	—	—	—	—
Ctenosaura acanthura	Veracruz, Mexico	—	—	—	—	17, 17, 28	30-35 x 15-20	—
Ctenosaura hemilopha	Sonora, Mexico	—	—	♀=179+	♀=0.215+	15n	25.5 x 12.8	4.67
Ctenosaura pectinata	Morelos, Mexico	♂=320 ♀=325	♂=1.000 ♀=0.950	—	—	49n	—	5.10*
	Morelos, Mexico	—	—	—	—	—	—	—
	Guerrero, Mexico	—	—	—	—	—	—	—
	Michoacan, Mexico	—	—	—	—	—	—	—
	Tamaulipas, Mexico	—	—	♀=191+	♀=0.315+	17n	28.0 x 18.0	4.41
Ctenosaura similis	Yucatan	—	—	—	—	—	—	—
	Yucatan, Nicaragua, Costa Rica	♀=335+	—	♀=306	—	—	—	—
	Chiapas, Mexico	—	—	—	—	20-30	—	—
	Belize	—	—	—	—	—	—	—
	Western Costa Rica	♂=440	—	♂=415 ♀=335	—	21-34	24-34 x 18-19	—
	Western Costa Rica	♀=350	—	♀=298	—	54.9 (34-87)	27.8 x 19.1	—
	Nicaragua, Costa Rica	♂=489 ♀=347	—	♂=345 ♀=276	♂=1.034 ♀=0.651	43.4	—	—

TABLE 6.—EXTENDED.

—	—	—	—	May-July	Oct.-Nov.	DeVries 1974
—	—	—	—	early May*	—	Smith & Burger 1950
—	—	—	—	early May	—	Iverson, unpubl. data
—	—	—	—	April 11	—	Evans 1951
—	—	—	—	—	July	Davis & Smith 1953
—	—	—	early spring	—	May-June	Davis & Dixon 1961
—	—	—	—	—	early July	Duellman 1961
—	—	—	—	—	—	Iverson, unpubl. data
—	—	—	—	—	June-July	Duellman 1965
—	54.0 (49-59)	—	—	—	early June	Fitch 1970
90 d	—	—	summer?	March-May	June-August	Alvarez del Toro 1972
—	53-61	—	February	—	June-July	Henderson 1973
≤90 d	57	—	—	Nov.?-Feb.	late April-June	Fitch 1973b
—	—	—	—	April	—	Hackforth-Jones (MS)
2.5 m	57	3+	—	late March-early April	June	Fitch & Henderson (MS)

TABLE 6.—CONTINUED.

Cyclura carinata	Caicos Islands, BWI	♂=360 ♀=292	♂=1.864 ♀=1.135	♂=276 ♀=225	♂=0.935 ♀=0.476	4.65 (2-9)	51.8 x 31.1	25.9 (19.0-29.9)
Cyclura collei	Jamaica	490+	—	—	—	—	—	—
	Jamaica	—	—	—	—	20n	—	—
Cyclura cornuta	Dominican Republic	—	—	—	—	17n	—	—
	Captive (?)	—	—	—	—	20n	85 x 38	—
	Hispaniola	—	—	—	—	11-23 N=3	68.6 x 45.9	77.7 (58.5-88.3)
	Mona Island	—	—	—	—	12n	78 x 47	—
	Mona Island	♂=545 ♀=510	♂=6.80 ♀=5.40	♂=517 ♀=475	♂=6.10 ♀=4.70	12 (6-19)	80.3 x 50.9	104.0 (82-159)
	Dominican Republic	—	—	—	—	13n	—	—
	Dominican Republic	♂=545 ♀=510	♂=6.24 ♀=4.76	♂=522 ♀=476	—	—	—	—
Cyclura cychlura	nr. Great Exuma, Exumas, Bahamas	—	—	290	—	7n	—	—
	Guana Cay, Exumas	—	—	—	—	3-4	—	—
	Guana Cay, Exumas	♂=355 ♀=320	♂=1.40 ♀=0.85	♂=303 ♀=283	♂=0.770 ♀=0.595	—	—	—

TABLE 6.—EXTENDED.

90 d	79.8 (76-83)	14.6 (12.5-15.0)	late April -early May	early June	early September	This study
—	—	—	—	—	—	Grant 1940a
—	—	—	—	April-May	—	Lewis 1944, 1946
9 w ?	—	—	—	—	—	Noble 1923
127 d	—	—	—	July 5	November 9	Haast 1969
106-129 d (captive)	101.3 (95-104)	54.1 (47.4-61.9)	—	July 31, Aug. 4, Aug. 11 (captive)	late Nov.-early Dec. (captive)	Shaw 1969
—	—	—	—	July*	—	Thomas *in* Carey 1975
82.6 d (78-89)	119 (105-127)	74.0 (60-92)	June	mid July-early Aug.	mid to late Oct.	Wiewandt, in prep.
—	—	—	—	—	—	Iverson, unpubl. data
—	—	—	—	—	—	Wiewandt and Gicca, unpubl. data
—	—	—	—	—	—	Carey 1975
—	—	—	—	early June	—	Coenen *in* Carey 1975
—	—	—	—	—	—	Windrow 1977

TABLE 6.—CONTINUED.

Cyclura nubila	Little Cayman	♀=420+	—	—	—	8-20	—	—
	Cuba	—	—	—	—	16n	76 x 44.5	—
	Cuba	—	—	—	—	17n	65.6 x 44.5	—
Cyclura pinguis	Anegada, British Virgin Islands	♂=550 ♀=500	♂=7.75 ♀=5.25	♂=534 ♀=468	♂=6.72 ♀=4.75	12-16	—	—
Cyclura ricordi	Dominican Republic	—	—	♀=340	—	4.67 (4-6) N=3	—	—
	Dominican Republic	460	3.18	354	1.74	—	—	—
Cyclura rileyi	San Salvador, Bahamas	—	—	—	—	5n	—	—
Dipsosaurus dorsalis	California	133	—	—	—	—	—	—
	California	—	—	—	—	5-6 N=2	28.0 x 16.8	—
	California, Arizona, & Nevada	—	—	—	—	3-8	—	—
	California	♂=145 ♀=142	—	♂=127 ♀=120	—	3-5	26.4 x 15.0	—
	Arizona	144	—	—	—	—	—	—
	Captive	—	—	♀=107.3	—	4.44 (4-5)	—	—

TABLE 6.—EXTENDED.

—	—	—	—	May - early June	—	Grant 1940b
93 d	—	—	March	June 23	Sept. 24	Street 1952
119-123 d	102.4 (95-110)	54.73 [48-59)	June (captive)	July 10 (captive)	Nov. 5-9 (captive)	Shaw 1954
—	100?	—	—	April-June?	Aug.-Sept.	Carey 1975
—	—	—	—	—	—	Carey 1975
—	—	—	—	—	—	Wiewandt and Gicca, unpubl. data
—	—	—	—	July	—	Stejneger 1903
—	—	—	August?	—	—	Smith 1946
—	—	—	—	Aug. 11 (captive)	—	Shaw 1952
—	—	—	April - early May	late June - early July?	August	Norris 1953
—	—	—	—	early June - mid August	—	Mayhew 1971
—	47-52	—	—	June?	August	Parker 1972
43.4 d (43-45)	47.4 (46-50)	4.62 (3.6-5.1)	—	—	—	Muth 1977

TABLE 6.—CONTINUED.

Enyaliosaurus clarki	Michoacan, Mexico	154	—	♂=147 ♀=135	—	—	—	—
	Michoacan, Mexico	♂=165+ ♀=150+	♂=0.200 ♀=0.150	♂=153 ♀=142	♂=0.131 ♀=0.108	7.5 (4-11) N=6	—	—
Iguana delicatissima	Leeward Islands	—	—	—	—	—	47.6 x 28.6	—
	Lesser Antilles	♂=345 ♀=346	—	—	—	22 (17-27)	ca. 35	—
Iguana iguana	Panama	—	—	—	—	32.25 (21-43) N=4	41.3 x 22.2	—
	British Guiana	—	—	—	—	4-7 N=2	—	—
	Panama	514	6.01	—	—	20-70	ca. 30	—
	Nicaragua	—	—	—	—	41n	—	—
	Eastern Costa Rica	—	—	♀=353	—	35.3 (29-40) N=7	38.0 x 26.2	—
	Columbia	—	—	—	1.20	41n	39 x 26	—
	Panama	—	—	—	—	33-45 N=2	—	—
	Captive	—	—	—	—	38n	—	—
	Chiapas, Mexico	—	—	—	—	25-60	—	—

TABLE 6.—EXTENDED.

—	ca. 46	—	—	April?	early to midJune	Duellman & Duellman 1959
—	—	—	—	—	—	Iverson, unpubl. data
—	—	—	—	—	—	Garman 1888
—	—	—	—	Aug.-Oct.?	Dec.-Feb.?	Lazell 1973
—	—	—	—	Feb.-March	—	Hallinan 1920
—	—	—	—	—	—	Beebe 1944
ca. 3 m	—	—	Oct.-Nov.	early Feb. March	June?	Swanson 1950
—	—	—	—	eggs found April 4	—	Carr 1953
ca. 3 m	—	—	—	March-early April	June 6	Hirth 1963
73 d @ 30°C	66	10.25	—	March 1 (captive)	May 18 (captive)	Licht & Moberly 1965
—	—	—	—	late Jan.-early Mar.	late April-early May	Rand 1968
65 d (captive)	254 (total length)	—	February (captive)	April 19 (captive)	July 3 (captive)	Van Aperen 1969
90 d	—	—	Oct.-Dec.	March-April	June-Aug.	Alvarez del Toro 1972

TABLE 6.—CONTINUED.

	Panama	—	—	—	—	—	—	—
	Colombia	♂=420	♂=3.20	♀=280	♀=1.10	14-70	—	13.0 (12.4-14.0)
	Panama	—	—	—	—	—	32-39 x 24-27	—
	Western Costa Rica	—	—	♂=530 ♀=390	—	—	—	—
	Nicaragua	♂=550 ♀=411	♂=2.60+ ♀=2.15	♂=361 ♀=327	♂=1.309 ♀=1.195	30.5 (11-54)	—	10.28
Sauromalus obesus	California	—	—	—	—	8-10	35.3 x 21.6	—
	California	210	—	—	—	6n	—	—
	Arizona	—	—	—	—	5n	38.25-40.0 x 21.6-24.75	—
	California	♂=197 ♀=185	♂=0.315 ♀=0.255	150-160	♀=0.05-0.25	7n	—	—
	California	♂=220 ♀=205	—	150-220	—	7.8 (6-13)	—	—
	California	♂=203 ♀=184+	—	170	♂=0.250 ♀=0.175	10n	—	—
	Arizona	♂=207 ♀=207	—	♂=176 ♀=189	—	6-10	28 x 14 (oviducal) 41 x 23 (in nests)	—

NOTE: Asterisks indicate values extrapolated or interpolated from cited source. All species probably lay at most a single clutch per year. Values in parentheses are ranges. Sample sizes for clutch size included where small, except where N = 1 (marked with n). Incubation times in days (d), weeks (w), or months (m).

TABLE 6.—EXTENDED.

ca. 3 m	—	—	—	February	late April-May	Rand 1972
—	68 (260 total)	—	Dec.	March	late May	Mueller 1972
100 d @ 28°C	—	—	—	late Feb.-early Mar.	mid-June (captive)	Ricklefs & Cullen 1973
—	60 (253 total)	—	—	Jan.-Feb.	mid-Dec.-early May	Fitch 1973
—	73-76?	—	—	Feb.-Mar.	April-June	Fitch & Henderson 1977b
—	—	—	—	late May	—	Shaw 1945, 1952
—	—	—	May-June	—	—	Smith 1946
—	60?	—	—	late June*	Sept.*	Gates 1957
—	68-70?	—	March 26-June 25?	June 22	—	Johnson 1965
168-171 d (captive)	46-60	—	Mar.-April	May-June	Sept.?	Berry 1974
—	—	—	—	—	—	Iverson, unpubl. data
85 d	64.6 (53.9-79.6)	—	May-June	—	August	Prieto and Sorenson 1977

does in *Anolis carolinensis* (Crews 1973a), and perhaps *Crotaphytus wislizeni* (Parker and Pianka 1976).

It is strongly suspected that female receptivity is terminated by copulation, as Crews (1973b) has shown to be the case in *Anolis carolinensis*. One captive female mated twice with the same male in three days, but she was an unwilling partner in the second mating. The male was able to "rape" the female due to his much larger size (286 mm SVL versus 235 mm) and the confinement of the enclosure. Since no female *Cyclura* was observed to accept a male more than once in captivity (mated females always rejected further courtship attempts), I suspect that females copulate only once, with only one male, during each breeding season.

Males, however, will copulate more than once during the breeding season, but apparently only once during any one day. On 24 April, male #3 had attempted to mate once (with another female) before he copulated successfully with female #1. He did not attempt courtship again that day. He courted unsuccessfully 3 times on the following day, and on the next day 11 times (with two females) before he forcibly mated #1 female. He did not try to court again that day, but did on several following days. On 9 May, #3 male copulated successfully with the first female (#3) he courted. She was very receptive and moved to him immediately after his morning emergence. He did not attempt courtship for the remainder of the day. It is suggested that males in the field are able to mate with more than one female if they are available.

In captivity, female #1 accepted male #3 on 24 April, and was raped (by the same male) on 26 April; female # 3 accepted male #3 on 9 May. The other two females were not observed to accept males, but both later nested. It is therefore presumed that they also mated. The earliest courtship attempt was observed on 24 April; none was attempted in two days of observation prior to that. Since the lizards involved were captured less than three weeks prior to that time, a two to three week mating season, centered about the first of May, is indicated.

POST-COPULATORY BEHAVIOR.—Captive males frequently dragged their cloacal regions on the substrate both prior to and following courtship behavior. Two captive males also exhibited a strange modification of normal defecatory behavior during the breeding season. The pelvic region was elevated above the ground in typical defecation posture; however, the abdominal contractions necessary to egest the fecal pellet resulted in eversion of the hemipenes. The organs remained everted until after the scat was deposited. As they were then withdrawn a small quantity of white viscous fluid (semen?) dripped from the region of each retracting hemipenis. I could not determine the significance of this behavior.

Probably the most significant post-copulatory behavior noted in the captive situation was when the male drove off males that courted the female with which he had copulated. This behavior was clearly observed after only one of the three captive matings. Following the other two copulations, other males did not attempt to court the mated female.

Two other males were present in the enclosure at 1237 hours on 26 April 1975 when male #3 copulated with female #1. Male #2 was old, senile, and subordinate to #3; he was never observed to court. Male #4 was young (first or second year post-maturity); he courted frequently (Table 5) but was never accepted by a female.

Approximately 8 min after #3's copulation, male #4 courted female #4 twice in less than 30 sec and was rejected each time following the vibratory display. Male #3, resting in the shade, showed no interest in this activity. However, at 1249 hr, #4 approached female #1 very rapidly and after an abbreviated vibratory display, jumped up and bit at her neck. Simultaneous with her attempts to reject him, #3 postured (see SOCIAL ORGANIZATION), charged from his resting place, and chased #4 away from "his" female. Following the short chase, #4 bobbed submissively, as #3 moved back to his resting place. Within 30 sec, #4 again moved to court #1 and again #3 postured, charged, and drove #4 from the vicinity of the female, and then moved into the shade to rest. This same sequence was repeated five times over the following 5 min; 20 to 60 sec separated each sequence. At that time (about 1256 hr), male #2 moved to the feeding station and this seemed to stifle #4's advances temporarily.

No interaction occurred until 1321 hr when #4 resumed his courting interest in #1, and #3 again chased him away from her. The sequence was repeated six more times, each separated by 60 to 150 sec, over the next 9 min. Male #4 dragged his cloaca on the substrate three times during the following 9 min and retreated to a burrow for the remainder of the day at 1341 hr. Number 3 male did not attempt to "guard" any female during any other day of observation. This protective behavior thus appears to be restricted to the day of copulation.

Assuming females are receptive for only a short time during the ovarian cycle, the practice of guarding a recently-copulated female by a male in the field would help guarantee that he, alone, contributed to that female's entire brood that year. Parker (1974) has discussed the significance of this behavior in his theoretical treatment of female-guarding as a male time-investment strategy.

The mating system of *Cyclura carinata* is apparently one of serial polygyny, with monogamy among some males (see Wilson 1975). There appears to be pair-formation during at least the breeding season.

Two females at the SW Blind lived within the home range of the same respective males for two years until all were killed by dogs and cats. Monogamy and/or polygyny seem to be the predominant systems among the iguanines. Although no breeding observations were made, pair bonding and monogamy have been suggested for *Cyclura pinguis* (Carey 1975). Johnson (1965) noted male-female pairing in *Sauromalus obesus*, but did not observe courtship. In a more complete behavioral study, Berry (1974) found a polygynous system with pair formation for the same species.

Male Mona Island *Cyclura cornuta* are generally polygynous but some are apparently promiscuous; females are monogamous, polyandrous, or promiscuous (Wiewandt 1977). Street (1952) implied that *Cyclura nubila* is promiscuous, but no supporting data were presented. His observations were based on tame, unrestrained lizards inhabiting a golf course in Cuba, but may not be representative of field populations. Alvarez del Toro's (1972) observations of *Iguana iguana* suggest a polygynous mating system for the species. However, Peracca (1891, cited in Noble and Bradley 1933) observed that captive male iguanas mated with more than one female, but did so more with one female than another. He also noted multiple insemination of females (up to 11 times). This suggests a polygamous if not totally promiscuous system, but it may have been an artifact of the captive situation. Mueller (1972) reported that the species is polygamous in Colombia. Further studies of courtship behavior as well as all aspects of social behavior are sorely needed for lizards of this subfamily if meaningful comparisons are to be made.

NESTING

Female *Cyclura carinata* oviposit their single annual clutch in early June. Two gravid Pine Cay females had fully shelled oviducal eggs on 3 and 9 June and four recently deposited nests were excavated on 5 June, 7 June, and 9 June (2) on Pine and Water cays. A female at the SW Blind site laid her eggs 6 June. A female captured 5 June on Water Cay nested in an observation pen four days later. Captive lizards tended to nest later than native lizards, perhaps due to subnatural thermal or photoperiod regimes. A Pine Cay female collected 4 April deposited her clutch on 12 June in Gainesville. A Water Cay female, captive for nearly one year, dropped her eggs on 25 July 1975 (David Auth, pers. comm.). Soil for burrowing was not available in the pen in 1975 and the eggs were deposited on the enclosure's substrate. The female had ceased feeding two weeks previous to oviposition and resumed immediately after laying.

Since copulation was not observed in the field, I have no way of knowing with certainty the relation of a female's nest site to the territory of the male with which she copulated. However, burrows, or branches thereof, offering optimum nesting conditions (see later) are limited in many areas due to substrate conditions and high lizard densities. Therefore, female nest site location is probably not closely determined by the location of the territory of the male with which she copulated, but rather by nest site availability. A clustered nest site distribution in areas with optimal nesting conditions would thus be expected, and was in fact observed at the SW Blind during the summer of 1974 (Fig. 22). The nest burrows were clumped in the strip of relatively deep friable soil lying midway between the rocky ledge adjacent to the lake and the rocky seashore. Availability of nest sites is probably an important factor limiting population size; the success of egg clutches laid in inferior nests is certainly reduced. The fact that several other iguanine lizard species migrate considerable distances to communal nesting areas (Rand 1968; Montgomery *et al.* 1973; Wiewandt 1977; Hackforth-Jones MS) suggests that suitable sites may be generally limiting to members of the subfamily.

Nesting activity is apparently confined to the morning. The previously mentioned SW Blind site female failed to emerge on 6 June at her usual time. Under continual observation, the female first emerged at 1045 hr EST. She climbed immediately into a small *Conocarpus* tree and began eating leaves.

In the afternoon she returned to the nest burrow to kick additional soil in to further close the nest chamber. The 5 June Water Cay captive female had finished nesting by 0900 hr EST 9 June, when she began to cover the nest. The female captured 4 April nested sometime during the early part of the day on 12 June.

Cyclura nubila on Little Caymen apparently oviposit late in the day; Lewis (*in* Grant 1940b) found nesting females between 1730 and 1800 hrs. *Cyclura cornuta* (Wiewandt 1977), *Iguana iguana* (Rand 1968; Alvarez del Toro 1972), and *Amblyrhynchus cristatus* (Carpenter 1966) will nest at any time during the day. *Sauromalus obesus* is known to nest at midday (Johnson 1965).

Nest burrows are not constructed specifically for that purpose by female *Cyclura carinata* as in *Cyclura nubila* (Street 1952; Shaw 1954), *Cyclura cychlura* (Carey 1975), *Sauromalus obesus* (Johnson 1965), *Iguana iguana* (Rand 1968; Hirth 1963a), *Amblyrhynchus cristatus* (Carpenter 1966), *Cyclura cornuta* (Noble 1923; Haast 1969; Wiewandt 1977), *Ctenosaura similis* (Hackforth-Jones MS), and apparently *Ctenosaura pectinata* (Evans 1951). *Cyclura cychlura* on Andros apparently utilizes termite mounds for nesting in the absence of soil for digging (Walter Auffenberg, pers. comm.). The terminal portion of a

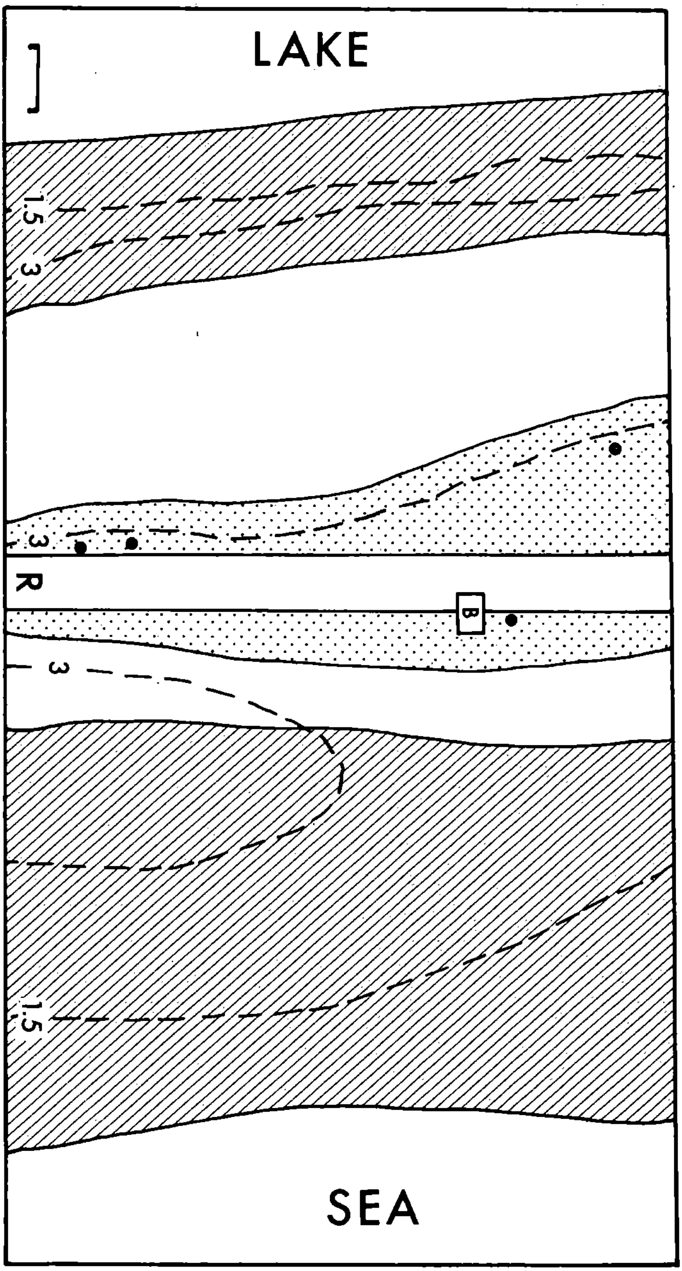

FIGURE 22.—Spatial relationship of known nest burrows to deep sandy soils (stippled) and rocky substrates (hatched) near SW Blind (B). Contour intervals (dashed lines) are in meters. Scale at left measures five meters. R indicates road.

retreat burrow is used for the nesting chamber in *C. carinata*. She may, however, dig a short branch off the main burrow for the nest chamber. Figure 23 illustrates a typical nest burrow found on Pine Cay on 9 June 1974. The general configuration of several nest burrows is diagrammed in Figure 14. As earlier described (see Burrows, under HABITAT), females tend to inhabit shallower burrows than males. This is certainly a function of the necessity for relatively shallow burrows by females for use as nest chambers; the roof of no nest chamber excavated was more than 25 cm below the ground surface.

Following the deposition of the egg complement at the end of the burrow (or a diverticulum of the same), the female kicks and pushes sand around the eggs and completely blocks the burrow just proximal to the eggs, forming a sealed air chamber above the eggs. A similar chamber is also present in the nests of *Amblyrhynchus cristatus* (Carpenter 1966) and *Ctenosaura similis* (Hackforth-Jones MS). This chamber apparently aids in the maintenance of high humidity and perhaps also functions to facilitate respiration of the eggs.

The female obtains the soil necessary for the nest plug from the area near the mouth of her burrow. The covering process was observed in part only once in nature. As the female walked through the burrow toward and out of its entrance, she pushed soil backward with her forefeet and alternately flung dirt backward with her hind feet. Once approximately a half meter outside the burrow she would turn and reenter the burrow and repeat the sequence. This process was repeated three times in the instance I observed.

The actual manipulation of the dirt at the nest plug was not observed. It is not known if female *Cyclura carinata* butt the soil with their heads while plugging the nest chamber to pack the earth as do *Amblyrhynchus* (Carpenter 1966), *Iguana* (Rand 1968), and *Cyclura cornuta stejnegeri* (Wiewandt 1977).

Female *C. carinata* demonstrated their digging instinct many times as nesting season approached during early June. Foraging females would frequently stop and scratch vigorously at the substrate in the same manner as that observed in the female covering her nest. This behavior was observed at no other time of the year.

One of the most interesting behaviors associated with nesting follows the completion of the nesting process itself. Although female *C. carinata* are not territorial during the remainder of the year they vigorously defend the area around their nest (and home) burrow.

A female *Cyclura carinata* at the SW Blind site defended her nest burrow against all conspecifics, female and male, at least until 2 July when daily observation was terminated. Perhaps my presence near her territory reinforced her defensive instinct and caused an atypical ex-

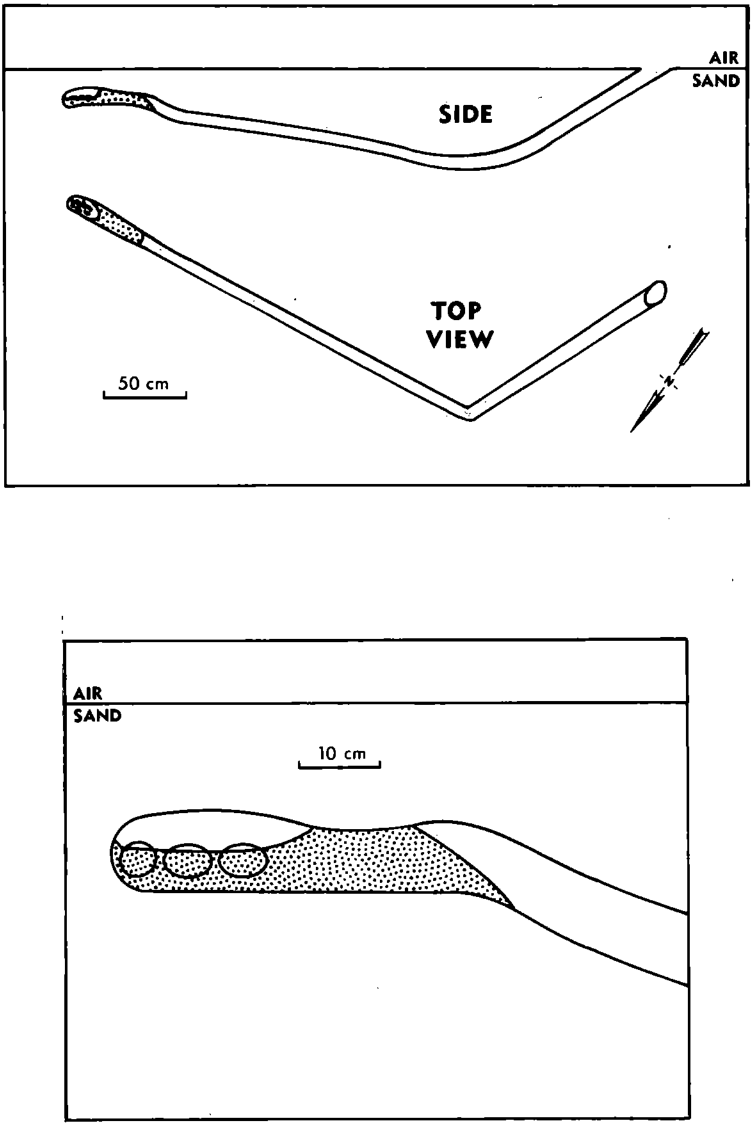

FIGURE 23.—Diagram of typical nest burrow of *Cyclura carinata* excavated June 9, 1974, on Pine Cay, Caicos Islands.

tension of this behavior. Two other undisturbed females near the SW Blind were last observed exhibiting this defensive behavior on 10 June and 12 June, respectively. It is not known when the behavior terminated as they were not seen again. A captive female in Gainesville exhibited this nest defense for three days following nesting when she was removed to another pen (David Auth, pers. comm.). Even though she was moved to a different enclosure she continued to exhibit occasional defensive behaviors for at least 35 days after the transfer.

Subsidence of nest defense behavior seems to be related to decreases in the number of intruding lizards (i.e. a lack of positive reinforcement). At the SW Blind site, as well as in captivity, the behavior seemed to remain as long as reinforcement from interaction was continual. The adaptive significance of such a behavioral mechanism seems apparent. It is clearly advantageous for a female lizard to expend energy guarding her nest site from other females seeking nest sites and from males which might inadvertently uncover the eggs during burrow cleaning activities. Once the nesting period is completed, however, and the resident male is aware of the female's burrow, this energy is better spent on other activities.

The defended area around a female's nest burrow was accurately mapped in two cases near the SW Blind. During June 1974 female #18 (222 mm SVL) maintained an activity range of only about 155.5 m^2, centered around a low perch overlooking her nest burrow (Fig. 24). I observed her defend the nest site eight times. Mean radius from the perch to the site where an intruder was defended was 3.79 ± 0.71 m (3.0 to 5.2). This radius defines a circular area of 45.1 m^2, only 29% of the female's activity range for the month.

During the same month, another female was observed to guard her nest eight times. Her defense was centered about a low brush pile directly above the entrance to her nest burrow. She defended against intruders which approached within an average of 4.60 ± 1.93 m (1.2 to 7.3). A circular area averaging 66.5 m^2 was thus defended. Her activity range for the month could not be accurately plotted.

Following nesting the female spends most of her time on a perch near her nest burrow vigilantly watching the area. Three females at the SW Blind site utilized piles of dead branches within 2 m of the entrance to their respective burrows for their elevated guard stations. For at least the next few days, these females could nearly always be seen occupying the same perch. A female which nested on 6 June spent 6 hr, 23 min (total active period = 9 hr) at her station on 10 June (with two defenses of her nest); 7 hr, 1 min on 12 June (with only one nest defense); 1 hr, 17 min on 16 June (a single defense); 43 min on 21 June (one defense); 1 hr, 29 min on 26 June (two defenses); and, 51 min on 2 July (one defense).

On the approach of a conspecific (male or female) the guarding female would make short lunging charges accompanied by vigorous open-mouthed bobbing and defensive posturing (see SOCIAL ORGANIZATION). Biting was never observed in these interactions and is apparently not part of the female's behavioral repertoire. Most intruding females and subadult males immediately ran when initially charged by the guarding female; however, males in whose territory the nest burrow occurred were more reluctant. In order to discourage the advance of a resident male, the female usually had to make several short charges, presenting her postured body laterally to the male between lunges, and bobbing vigorously with open mouth. The male always ultimately moved away, despite the small relative size of the female; a 222 SVL female (approximate weight, 400 gm) was repeatedly successful at driving off the 286 SVL resident male (weight, about 1 kg).

Nest defense was the rule for *Cyclura carinata* at the SW Blind, but it is not known if lizards at other locations on Pine Cay or on other

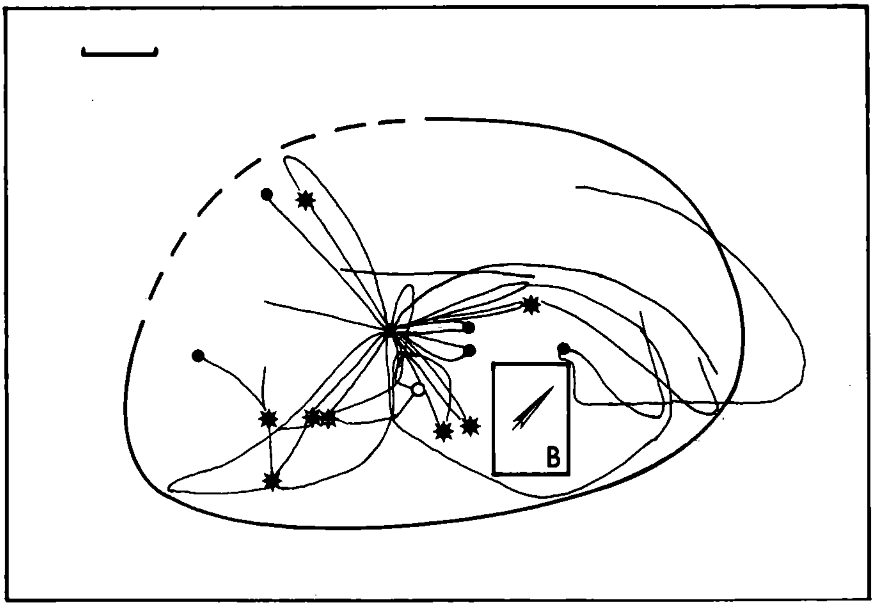

FIGURE 24.—Home range, movements and defense of a female *Cyclura carinata* during nesting season. Approximate home range is encircled; broken perimeter indicates questionable limits. Arrow in Blind (B) points due south. Bar scale represents two meters. Open circle marks nest burrow; solid dots indicate feeding sites. Stars designate sites of defensive encounters with intruders. Confluence of most movement lines marks the female's principal perch site when resting.

islands always exhibit the behavior. Eibl-Eibesfeldt (1966; see also Carpenter 1966) found that *Amblyrhynchus cristatus* on islands where potential nest sites were limited also defended their nests, while those on islands where nesting areas were plentiful did not. Lizard densities on Pine Cay were high and available burrows for nest sites were probably at a premium in many areas. This factor probably limited population growth to some extent in those areas.

Nest defense, either before or after oviposition, has also been reported for the iguanines *Cyclura cornuta* (Wiewandt 1977), *Cyclura cychlura* (Carey 1975), *Cyclura nubila* (Street 1952; Shaw 1954) and *Iguana iguana* (Rand 1968) in the field, and *Brachylophus fasciatus* (Cogger 1974), *C. cornuta* (Shaw 1969), and *C. nubila* (Shaw 1954) in captivity. In each of these, the aggression level apparently subsides within a few hours to a few days following oviposition.

The evolution of specialized nest guarding behaviors in at least the above species of the subfamily Iguaninae suggests that nest sites may commonly be limiting to all members of the group. Female iguanines undoubtedly actively seek optimum nest sites, i.e. areas with friable soil (Carpenter 1967), good insolation (Rand 1972), and/or decreased predator numbers (Rand and Robinson 1969; Sexton 1975).

Since these areas are often patchily distributed, communal nesting is common among iguanines: *Amblyrhynchus cristatus* (Carpenter 1966), *Cyclura cornuta* (Wiewandt 1977), and *Ctenosaura similis* (Hackforth-Jones MS). Sexton (1975) and Hackforth-Jones (MS) have discussed the advantages and disadvantages of communal versus dispersed nesting in *Iguana iguana*, and *Ctenosaura similis*, respectively; their comments pertain to other iguanines as well.

It should be clear that any behavior that decreases the energy spent in locating and constructing nest burrows should have a distinct selective advantage. A variety of strategies have apparently been employed by iguanines to reduce the cost of nesting. Female *Cyclura carinata* avoid excavating a complete nest burrow for each separate clutch by simply depositing the clutch in previously excavated retreat burrows (not necessarily one she has previously used as a retreat). A portion of the energy thus saved is then allocated to short-term nest defense which decreases the probability of interference with the nest by conspecifics.

Ctenosaura similis (Hackforth-Jones MS) nests communally; many females oviposit in the same connecting nest burrow system. Since many females contribute to constructing the nest burrow, average energetic cost of nest construction per individual is probably less than if separate burrows were constructed. Unfortunately, it is not known if ctenosaurs exhibit nest defense behavior within these burrow systems.

Iguana iguana (Rand 1968) nests communally; each female oviposits in a separate nest, which she may or may not have constructed. Since iguanas are physiologically incapable of completing the nesting process in a single bout, they must several times leave the partially constructed nest to rest. Since a rested female gains a considerable energetic advantage if she resumes digging in a burrow already partially completed, females compete for and dispute over these burrows. Disputes are generally settled via simple (not complex) displays rather than by actual fighting. Rand and Rand (1976) have argued stochastically that these competitive disputes are actually settled with a minimization of energetic cost to the individual. Their cost argument probably relates as well to the similar behavior of *Cyclura cornuta* (Wiewandt 1977) and *Amblyrhynchus cristatus* (Carpenter 1966).

EGGS, INCUBATION, AND HATCHING

No information is available in the literature concerning reproductive potential in *Cyclura carinata*. Only a single clutch of eggs is laid annually. Based on number of oviducal eggs and/or corpora lutea, clutch size in *C. carinata* averages 4.38 ± 1.95 (2-9; $N = 18$), and is positively correlated with SVL length (Fig. 25). An increase of one egg for about 16 mm SVL is indicated by the least square regression estimate (clutch size = 0.064 SVL - 10.018; $r = 0.741$, $p < 0.01$).

Estimation of clutch size by counting enlarged ovarian follicles from lizards collected during the spring tends to slightly overestimate the actual number of oviposited eggs ($\bar{X} = 4.80 \pm 0.98$; $N = 5$). Numerous excavated burrows contained hatched egg shells somewhere along their lengths, but their numbers were deemed unreliable as an estimate of clutch size and therefore were not included in any of the above calculations. The numbers of shells found in these cases were 1,1,3,5, and 7. It is doubtful that *Cyclura carinata* ever lays a single egg only and these shell records probably reflect my inability to find the entire clutch. The grand mean for clutch size from females with enlarged follicles, oviducal eggs, or corpora lutea; natural nestings observed; captive layings; and excavated nests is 4.65 ± 1.77 (2-9; $N = 26$).

Clutch information from two additional females was not included in the above calculations because of their captive maintenance, and the possible implications of their captive reproductive life. A 285 mm SVL, 770 gm lizard (the heaviest female encountered in the study) was captured 28 July 1974, by David Auth on Water Cay. Maintained in captivity on a generous diet, she laid seven eggs on the enclosure floor on 25 July 1975. She appeared very healthy until her sudden accidental death on 24 May 1976. Dissection revealed 11 yolked follicles of near-ovulatory size in the ovaries. A potential clutch size of 11 is indicated. Another Water Cay female, captured 16 February 1976, (292 mm SVL) laid 11 eggs in captivity 25 July 1976. Clutch sizes in these two females thus exceed by two the nearest record. This apparent jump in reproductive output could be related to the increase in quantity and quality of food resources available to them in captivity. The implications of these observations will be discussed later.

Twenty eggs (oviducal or freshly laid) averaged 51.8 mm (46.0-58) by 31.1 mm (28.5-33.5) and weighed an average of 25.9 (19.0-29.9) gm. Eggs are elongate ovals when laid; the elastic shell is thin and translucent and an embryonic disk 1.5 to 2.0 cm in diameter is faintly visible through the integument. The shell soon thickens, loses its translucent character, and becomes an immaculate white.

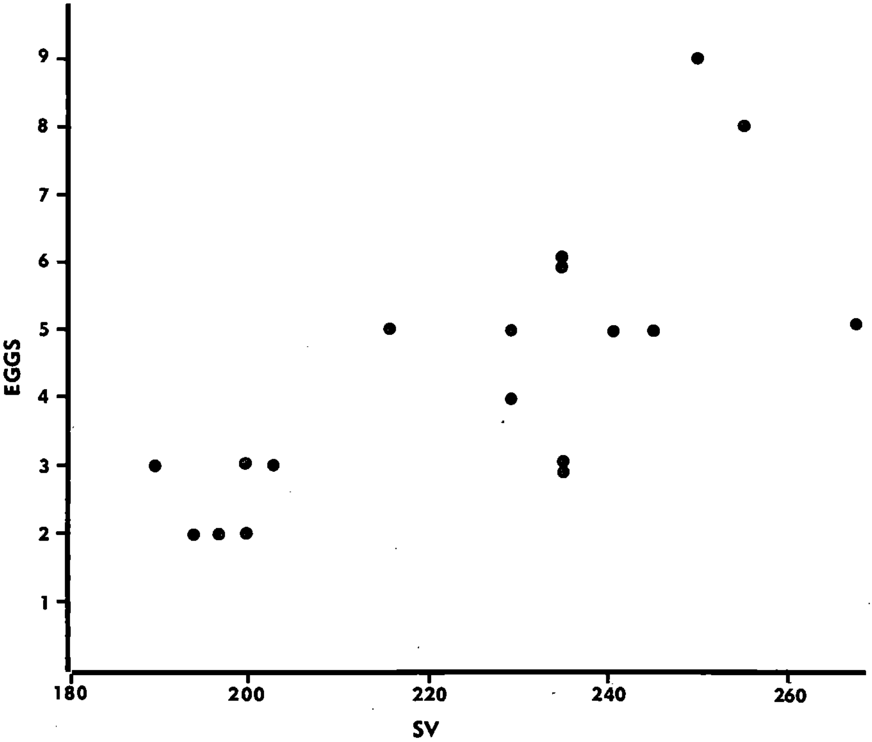

FIGURE 25.—Relationship of clutch size to snout-vent length (in mm) in *Cyclura carinata.* Number of eggs based on counts of oviducal eggs and/or corpora lutea only.

Two clutches of 6 eggs each were incubated to hatching in the manner of Zweifel (1961); only 3 of 6 hatched successfully in both cases. To minimize disturbance the widths of only 3 eggs were measured during incubation. Average width had increased to 38.3 mm at 18 days prehatching. This increase in diameter continued to a maximum at hatching; egg length increased very little during incubation. One egg, which increased exceptionally in size, weighed 46.0 grams just prior to hatching. Such an increase in egg size and weight is typical of iguanid lizard eggs (e.g. Crenshaw 1955).

One of the incubated clutches (Clutch A) was excavated from a nest burrow on Pine Cay 9 June (see Table 7) and was surely less than one week post-oviposition. Incubated at room temperature on Pine Cay until 20 July, the eggs were then transferred to a constant 28°C environment in the laboratory in Gainesville. Prior to 20 July, two eggs had developed fungus, collapsed, and were removed. The first had shriveled on 15 June (6 days after discovery) and contained an embryo of 34 mm total length. The second collapsed on 4 July (25 days post-location); the contained embryo measured 45 mm total length.

At 1800 hr, 2 September (85 days since discovery), hatching began. Two to four longitudinal slits were made in each egg shell by the lizard's egg tooth. Three young had completely emerged by noon on 4 September. On dissection the fourth egg was found to contain a fully developed, stillborn fetus which had apparently been unable to escape the egg. The first hatchling was completely out of his egg within 18 hours of slitting the egg; the second required 10 hours; the third, 19 hours.

The other incubated clutch (Clutch B) was laid in captivity on 12 June 1975, by a female captured 4 April 1975 on Pine Cay, and maintained in an outdoor observation enclosure in Gainesville. She was first copulated with on 26 April, and at least one more time on 27 April by a different male. Following deposition, the six eggs were removed immediately to an environmental chamber and incubated in sterile sand at 30°C. Three eggs spoiled during incubation and were discarded. During the afternoon of 22 September (101 days postoviposition), hatching began. By 1815 hr that evening, the heads of two hatchlings protruded from their respective eggs through a single longitudinal slit 16-19 mm long located dorsally on the eggs approximately 1/3 the distance from their ends (Fig. 26). Because of the continual disturbance while photographing the hatching process, the young required approximately 44 and 65 hours respectively to gain complete freedom from their eggs. The third egg had not been pipped by 0800 hr, 24 September, and was opened. The contained fetus was fully formed and alive, but had badly deformed hind limbs. In addition all three of the young had the distal portions of their tails twisted and shortened.

TABLE 7.—SELECTED REPRODUCTIVE DATA FROM FEMALE *Cyclura carinata*.

Location	Date Nesting	SVL (mm)	Pre-oviposition Weight (gm)	Clutch Weight (gm)	Post-oviposition Weight (gm)	Clutch Size	Mean Egg Size (mm)	Mean Egg Weight (gm)	RE	EPP x 10^2
Pine Cay	June 3 (O)	245	520	142	—	5	56.0 x 32.2 (54.5-58.0 x 31.0-33.5)	28.3 (27.2-29.9)	0.273	5.46
Water Cay	June 5 (N)	255	—	207.2*	645	8	—	—	0.243*	3.04
Pine Cay	June 7 (N)	200	—	51.8*	250	2	—	—	0.172*	8.60*
Pine Cay	June 9 (N)	200	—	77.7*	285	3	—	—	0.214*	7.13*
Pine Cay	June 9 (N)	—	—	155.4*	—	6	52.4 (51.5-54.0)	—	—	—
Pine Cay	June 9 (O)	235	510	126.2	380	6	49.1 x 29.5 (46.0-52.0 x 28.5-30.25)	21.0 (19.0-23.1)	0.247	4.12
Water Cay	June 9 (C; June 5)	250	815	250	568	9	49.5 x 31.5 (49-50 x 31-32)	27.8	0.307	3.41
Pine Cay	June 12 (C; April 4)	235	570	155.4*	—	6	51.0 x 32.2 (50.5-51.5 x 30.0-33.5)	—	0.273	4.55
Pine Cay	June 18, died with oviducal eggs (C; April 3)	235	560	77.7*	—	3	—	—	0.139*	4.63*
Pine Cay	Between June 13 - July 15 (C; April 5)	216	440	129.5*	—	5	—	—	0.294*	5.88*
Accumulated Averages		230	569.2	137.3 (excluding estimates = 172.7)	425.6	5.3	51.8 x 31.1	25.9	0.240 (excluding estimates = 0.275)	5.20 (excluding estimates = 4.33)

NOTE: (N) by date indicates date nest found; (O) indicates female with oviducal eggs; and (C) captive nesting (with date female collected). Observed range included in parentheses below means. Asterisks signify values estimated from overall average egg weight. Reproductive effort (RE) measures proportion of clutch weight in preoviposition weight of female. Expenditure per progeny (EPP) is the proportion of female weight made up by a single egg.

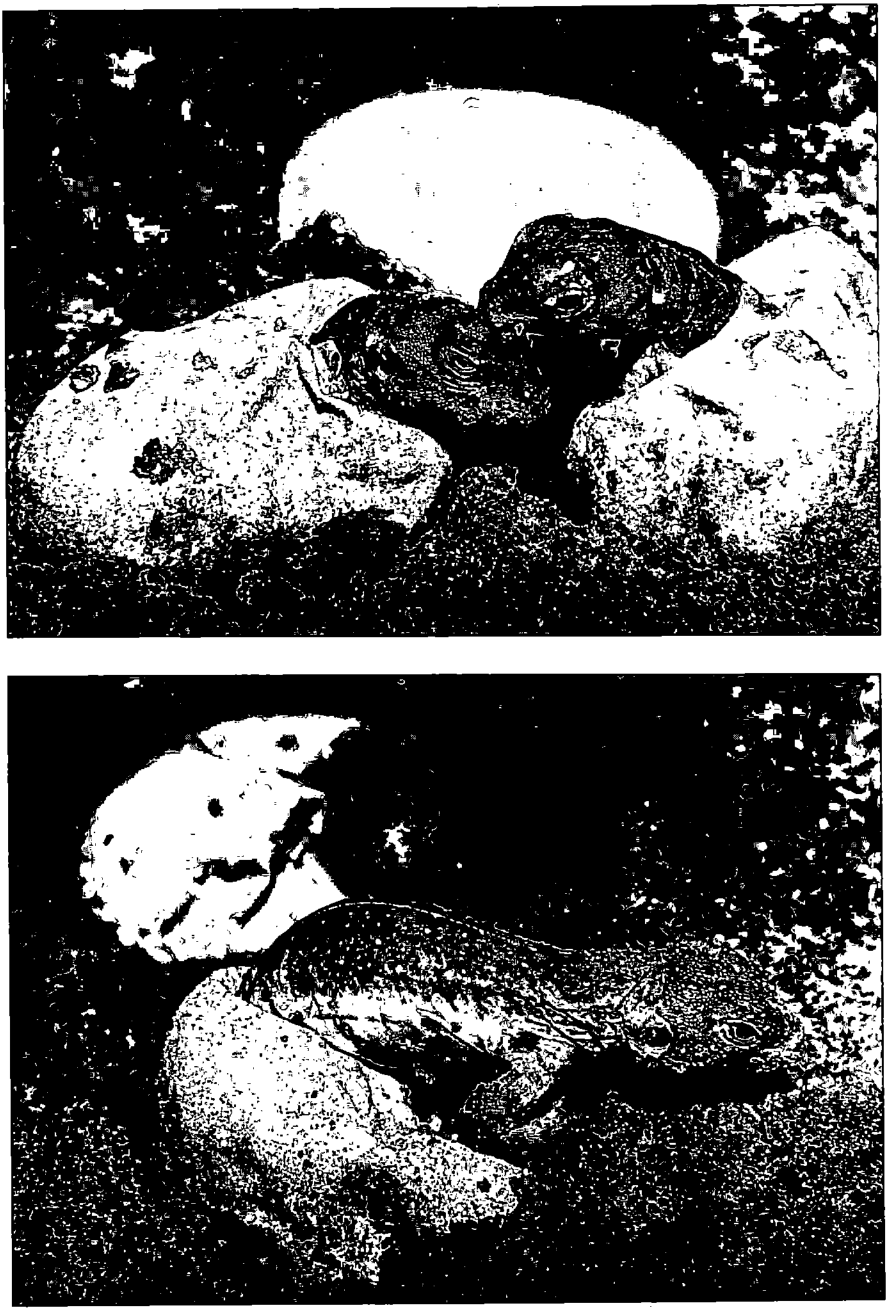

FIGURE 26.—Hatching in *Cyclura carinata*. See text for explanation. (A) 1815 hrs 22 September 1975; (B) 0815 hrs 23 September 1975.

Parker and Pianka (1976) found similar tail deformities among both captive hatchlings and wild *Crotaphytus wislizeni* in Utah. Bustard (1969) has suggested that such tail abnormalities may result from high temperature incubation of eggs. Field temperatures measured at depths representative of nest locations indicated a nearly constant 28-29°C through June and July. Incubation of the captive clutch at higher than natural temperatures (30°C) may have produced the observed deformities.

Incubation temperatures in natural nests have been recorded for several other iguanine lizard species. Bartholomew (1966) found temperatures in *Amblyrhynchus* varied between 28°C and 30°C. *Iguana iguana* nest temperatures in Panama (Rand 1972) were quite constant and ranged only between 31°C and 32°C; however, temperatures recorded in Costa Rica by Hirth (1963a, 1963b) and Mueller (1972) in Colombia at typical nest depths on nesting areas fluctuated from 27.8°C to 31.4°C, and 29.7°C to 30.3°C, respectively. Temperatures in nest burrows of *Ctenosaura similis* in Costa Rica ranged between 30.0°C and 31.5°C (Hackforth-Jones MS). Johnson (1965) found temperatures in a single nest of *Sauromalus obesus* varies from 32.2°C to 36.1°C. It is apparent that only minor temperature fluctuations characterize the nests of iguanine lizards.

No direct field data are available for the incubation period in *Cyclura carinata* but evidence indicates a term of about 90 days. A metal enclosure was placed around a recently laid nest burrow excavated on Water Cay on 5 June 1974. The nest had hatched and the young were above ground within the enclosure when checked on 30 August (86 days after discovery). Yolk remnants in their guts indicated they were very recently hatched. Hatchlings were seen emerging and dispersing from two previously unlocated nests at the SW Blind on Pine Cay on 1 September 1974.

Young of the year have been captured on Pine Cay on 31 August 1974 (2), 5 September 1974, 8 September 1974, and 18-20 September 1973 (10), and were very common during early and mid-September. The earliest collection date for a new hatchling was 10 August 1975, on Little Water Cay. On that date, 22 additional juveniles were captured and released, and all were at least one year old. An obviously recently hatched *C. carinata* with exposed umbilicus and remnants of yolk in its gut, was collected on Fort George Cay on 23 September 1973.

Since eggs are laid during the first two weeks of June and hatch during late August and early September, an incubation period of three months (approximately 90 days) is indicated. The captive hatching of Clutch A, estimated to be a week old when found, after 85 days, further supports this figure.

Hatchlings measured in early September ranged from 76 to 83 mm SVL ($\bar{X}$ = 79.80; N = 20) and 108 to 121 mm TL ($\bar{X}$ = 113.6; N = 17). Captive hatchlings were smaller than those naturally hatched; three from Clutch A averaged 74.1 mm SVL (73.0-76.2 mm) and two from Clutch B, 72.75 mm (72.0-73.5). Tail lengths from the Clutch A hatchlings ranged from 104.8 mm to 106.4 mm ($\bar{X}$ = 105.9).

Nine recently hatched lizards on Pine Cay weighed in early September averaged 14.62 gm (12.5-15.0). Three captive hatchlings averaged 15.69 gm (13.4-17.3) immediately after leaving their eggs. The higher weight is due to the bulk of the freshly absorbed yolk sac. The same three lizards weighed 10 days later averaged 14.34 gm (12.2-15.6).

Hatchling rock iguanas are basically identical to the adult female, except for the longer tail and the proportionately larger head (see GROWTH), the more brilliant laterally striped pattern and the presence of the egg tooth.

FERTILITY, PRENATAL AND NATAL MORTALITY

No oviducal eggs or freshly laid eggs (representing five clutches, totaling 32 eggs) examined lacked embryonic disk development. Although the sample size is quite small, a fertility rate close to 100 percent is indicated.

Estimates of natural prenatal mortality come from only four nest chambers excavated following the hatching period. Since spoiled eggs are easy to distinguish from the crisp parchment-like empty shells of successfully hatched eggs, mortality rates for these clutches during incubation were determined. Unsuccessful eggs and their respective total complement size included 3 of 3, 1 of 5, 1 of 8, and 0 of 7. Mortality rates therefore averaged 33.1 percent among these clutches (range 0 to 100%). However, this estimate is not weighted with respect to clutch size and tends to overestimate mortality. If we total the number of bad eggs and compare this to the total of all four complements, the mortality rate is 21.7 percent and may be a more reliable estimate despite the small sample size. Wiewandt (1977) found a 14 percent mortality rate in natural nests with single clutches for Mona Island *Cyclura cornuta*.

One of the most critical stages in the life history of *Cyclura carinata* occurs shortly after hatching, between the time the bulky yolk sac is drawn into the body cavity and the time the mid-ventral cleft through which the sac was drawn is securely closed. In that interval the lizard must necessarily rest since disturbances provoking movement by the hatchling, whether they be from siblings in nature or observers in the laboratory, will cause the closing umbilicus to rupture. The resulting hemorrhage and the subsequent inability of the lizard to successfully retract the yolk sac into his body cavity lead to the eventual death of the individual. Synchronization of hatching processes in a nest chamber providing little sensory input is therefore of utmost importance to successful hatching in *Cyclura carinata.*

Once the hatching process is complete, the lizards must still escape their incubation chamber. Their success at this time is reflected in the fact that of six nest burrows excavated after hatching, none contained a dead hatchling lizard. Freedom is gained via a narrow escape tunnel (or tunnels) dug by the hatchlings vertically from the nest chamber. The proximity of the nest chamber to the substrate surface simplifies the process (see Nesting). However, escape from the nest chambers constructed under flat limestone or compacted coral sand rocks is necessarily different. Only one such hatched nest was excavated. Considerable scratching at all walls of the chamber was evident and the excape tunnel had ultimately penetrated the nest plug and the lizards had apparently emerged through the main burrow. This alternative is always available should vertical escape be impossible.

The importance of sibling facilitation (as noted in sea turtles; Carr and Hirth 1961) in *Cyclura carinata* digging out of the nest is unknown, but it is logical to assume that the presence of more digging hands would increase the probability of a more rapid, successful emergence. Experimentation with monitored nests would be very interesting.

GENERAL SEASONAL REPRODUCTIVE PATTERN

The timing of the major events of the reproductive cycle of *Cyclura carinata* is illustrated in Figure 27. A general model relating environmental, physiological, and behavioral changes during the reproductive cycles of male and female *Cyclura carinata* is shown in Figure 28. Although partly hypothetical, this model describes well the

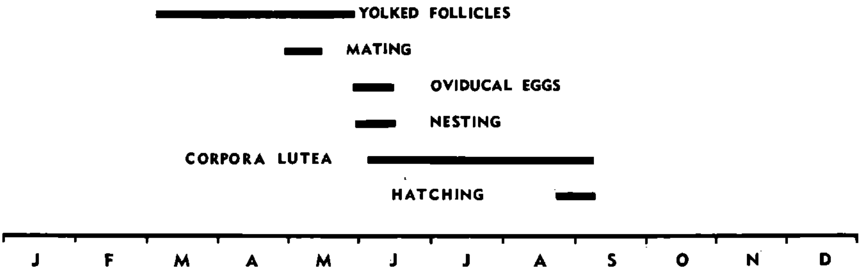

FIGURE 27.—Annual reproductive pattern of *Cyclura carinata.*

synchronization of biotic and abiotic events in the annual cycle of the rock iguana.

Three basic patterns in the timing of tropical iguanine reproductive cycles are evident. In the first, nesting coincides with the beginning of the rainy season, with hatching occurring well into that season. This is the pattern followed by *Cyclura cornuta* (Wiewandt 1977), *Cyclura cychlura* (Carey 1975), *C. pinguis* (Carey 1975), and *Cyclura carinata* (this study). For these species, the reproductive cycle appears to be seasonally timed to reduce the possibility of egg desiccation and to insure an abundant food supply, especially fruits, for hatchlings. The se-

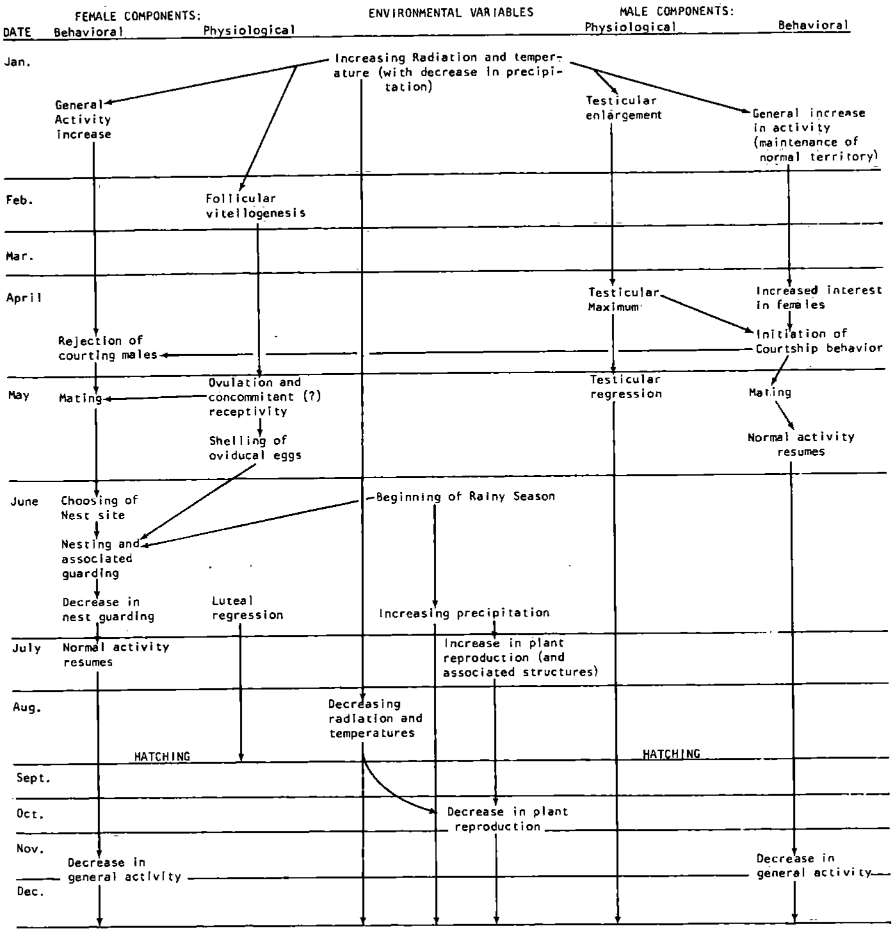

FIGURE 28.—A hypothetical model relating environmental, physiological, and behavioral changes to the reproductive cycles of male and female *Cyclura carinata*.

cond strategy involves nesting during the dry season, with hatching coincident with the beginning of the rainy season. *Iguana iguana* and *Ctenosaura similis* adhere to this schedule (Davis and Smith 1953; Hirth 1963a; Rand 1968; Alvarez del Toro 1972; Fitch 1973b). Both Rand (1972) and Fitch (1973b) agree that this cycle is dictated by the lack of optimal incubation temperatures during any other time of the year. In addition, the cycle is advantageous to hatchlings that are folivorous or insectivorous since these resources are available soon after the beginning of the rainy season.

In the last pattern, nesting occurs toward the end of the rainy season, and hatching early in the dry season. *Amblyrhynchus cristatus* is the only species known to conform to this schedule (Carpenter 1966). Unfortunately, since this species is a littoral feeder (mainly marine algae), and food resource productivity and availability have not been studied, the significance of the timing of its reproduction cycle is unknown.

There is some disagreement concerning the timing of the reproductive cycle in the genus *Conolophus;* nesting in November to January (the rainy season) is suggested by Van Denburgh and Slevin's (1913) and Slevin's (1935) data; however, DeVries (1974) reported nesting in May and June (during the dry season). This apparent paradox deserves further study.

REPRODUCTIVE EFFORT AND STRATEGY

Recent studies argue that the ratio of clutch weight to preoviposition body weight may not accurately reflect the proportion of energy allocated to reproduction, especially in lizards producing multiple seasonal clutches (Tinkle and Hadley 1973, 1975; Vitt 1974; Vitt and Ohmart 1975; Tinkle 1976). The clutch weight-body weight ratio (abbreviated RE, for reproductive effort) tends to underestimate a similarly derived ratio of actual calories (Tinkle and Hadley 1975; Vitt and Ohmart 1975). Unfortunately, the lizard literature contains considerably fewer of the latter estimates than the former. Nevertheless, the clutch-to-body-weight ratio is still of value in making general interspecific comparisons of reproductive effort.

A similar argument can be raised for estimates of expenditure per progeny (EPP) based on the proportion of preoviposition female weight in a single egg. However, for broad comparisons, this measure is probably adequate.

Selected reproductive data, including RE and EPP, for individual female *Cyclura carinata* appear in Table 7. RE in *Cyclura carinata* averaged slightly less than one-fourth and ranged from 0.139 to 0.307 for nine females. This value falls well within the range of similarly obtained values in the lizard literature as compiled by Pianka and Parker (1975: Range 0.05 to 0.30 $\bar{X} = 0.173$; N = 70+ species), Tinkle (1969: 0.10 to 0.40; N = 14) and myself (0.10 to 0.40; N = 27). However, the value obtained for *C. carinata* is greater than the average for those species. Unfortunately, speculation on specified reproductive strategies based on these data is complicated by the fact that the majority of the lizard species for which data on reproductive effort are available produce multiple clutches, while the values reflect only single clutches. Since all the iguanine lizards apparently oviposit only once per year, comparisons within the group should be more meaningful.

EPP values for *C. carinata* ranged from 3.04 to 7.13% and averaged 5.20%. This is a relatively high value among lizard species. Estimates of EPP for several species calculated from the literature averaged from about 2 to 7% (Telford 1969; Avery 1975a; Parker and Pianka 1975, 1976; Pianka and Parker 1975; Vinegar 1975; Vitt and Ohmart 1975). However, one value calculated from a single female *Tachydromus tachydromoides* (11.2%) exceeded this range (Telford 1969). This value is probably approaching the limit that is possible for lizards.

Among nine clutches, there is a significant negative correlation of EPP with female SVL length ($r = -0.92$, $p < 0.01$) and clutch size ($r = -0.85$, $p < 0.01$). Older females lay more eggs, but expend less energy per egg. As expected, RE is positively correlated with clutch size ($r = 0.74$, $0.05 > p > 0.01$. It is, however, not significantly correlated with female SVL ($r = 0.40$, $p > 0.05$). In comparison to other lizard species, *Cyclura carinata* demonstrates a high reproductive expenditure per clutch as well as per progeny; relatively few large eggs are produced annually.

The iguanine lizards have been poorly represented in previous analyses of reproductive strategies, due to a dearth in basic reproductive data for the included species. No species has been fully studied reproductively; basic reproductive parameters remain unmeasured (especially weights) even for otherwise well-studied iguanines like *Dipsosaurus* and *Sauromalus*. I have scoured the literature as well as the knowledge of my colleagues in an attempt to compile and analyze reproductive data for lizards of the subfamily Iguaninae. This information, supplemented by some of my own unpublished data, appears in Table 6.

This table illustrates the general deficiency of our knowledge of iguanine reproduction. Several comparisons can, however, still be drawn. *Cyclura carinata* lays the fewest eggs ($\bar{X} < 5$) of any studied iguanine except *Amblyrhynchus* (2-3) and perhaps *C. cychlura* (3-7). *Ctenosaura similis* can lay nearly 20 times as many eggs as *Cyclura carinata*. Only *Amblyrhynchus, Conolophus, Cyclura nubila,* and *C.*

cornuta are known to lay larger eggs than *Cyclura carinata*. However, the eggs of *Ctenosaura similis* are only half the length and one-fifth the weight of those of *C. carinata*. Each of these comparisons suggests considerable variation in reproductive expenditure among this otherwise homogeneous group of lizards. Within the subfamily reproductive strategies fall into two basic categories (after Iverson MS): the production of large clutches of relatively small eggs (as in *Iguana iguana* and *Ctenosaura similis*) and the deposition of small clutches of relatively large eggs (most of the remaining species, including *Cyclura carinata*). I am currently studying the selective advantages of these strategies to the species exhibiting each.

GROWTH

GENERAL PATTERN

Cyclura carinata ranges from about 80 mm SVL and 15 grams at hatching to over 290 mm SVL and 1100 grams in females and nearly 360 mm SVL and 1900 grams in males (Fig. 29). The relationship between the logarithm of snout-vent length and that of body weight is significantly linear:

$$\text{Log Wt} = 3.0336 \text{ Log SVL} - 4.496$$
$$(r = 0.987, \text{d.f } 176, P < 0.0001).$$

This equation is equivalent to $\text{Wt} = (3.202 \times 10^{-5})\ \text{SVL}^{3.0336}$, where Wt = weight in grams, and SVL = snout-vent length in mm. Curves for females (plus juveniles) and males (also with juveniles) are not significantly different from the overall curve.

An ontogenetic reduction in head size relative to body size occurs in *Cyclura carinata* from hatching to maturity in males and throughout life in females (Fig. 30). Older males, however, do exhibit a secondary increase in proportional head size. Hypertrophy of the head musculature contributes significantly to the visual image of a massive head in aging males. This cephalic enlargement in *Cyclura carinata* does not however reach the magnitude that it does in old male *Cyclura cornuta*, but as in that species (Wiewandt 1977), it may be important in social contexts, especially male-male interactions (see SOCIAL ORGANIZATION).

At hatching relative tail size is maximal, decreasing in length proportional to body length throughout life (Fig. 31). There is no sexual difference in relative tail length; however, the girth at the tail base is proportionately larger in males due to the presence of the hemipenes internally.

Variation in maximum size (and weight) between populations of *Cyclura* on the study islands is notable (Tables 8 and 9). Adult *Cyclura* *carinata* from Water and Little Water cays are larger (and more yellow; see Color under MORPHOLOGY) than those from Pine and Fort George cays. Since the islands are so similar phenetically, this divergence may be related to genetic differences in the colonizers of the two groups of islands.

The sexes of *Cyclura carinata* are strongly size dimorphic; female SVL and weight average 81.5 and 50.9% that of males, respectively

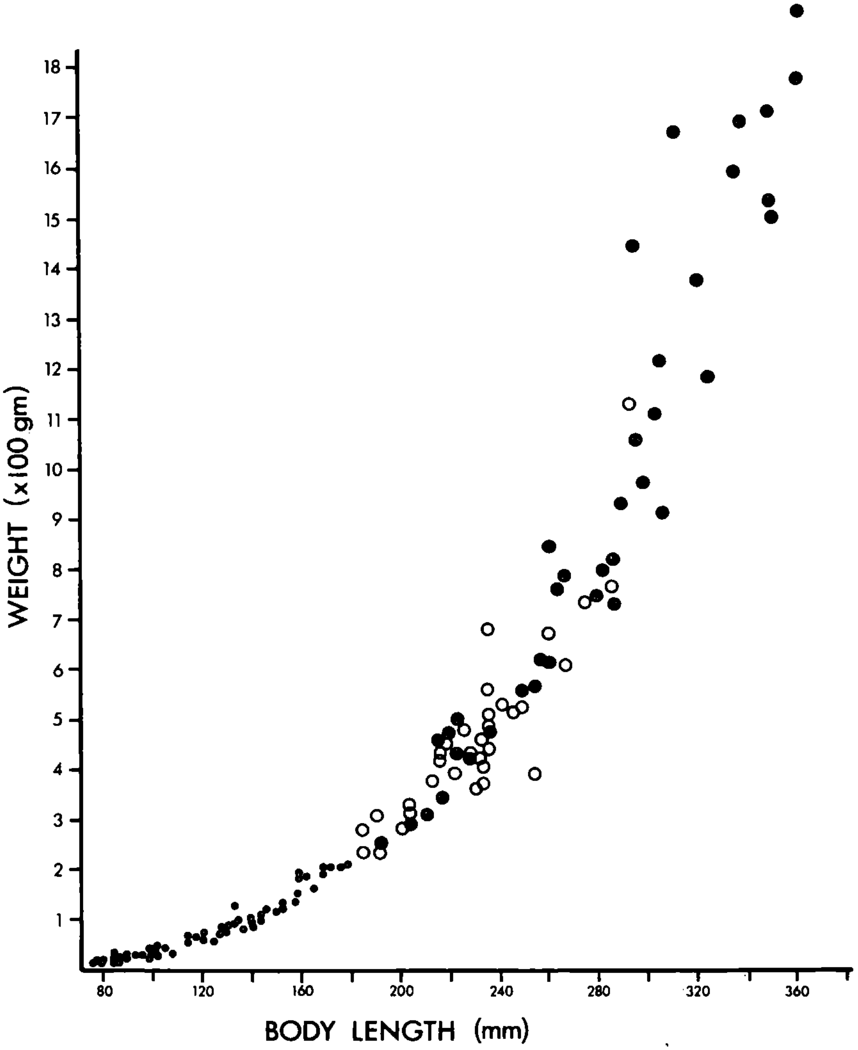

FIGURE 29.—Relationship of body length (SVL) to weight. Solid circles above 180 mm SVL indicate males; open circles, females. Each symbol represents at least one individual. Data from 181 lizards.

(Tables 8 and 9). *Amblyrhynchus, Ctenosaura similis*, and *Iguana iguana* all exhibit this great size dimorphism. Female *Amblyrhynchus* average 85.0% of male SVL and 50.0% of male body weight (Carpenter 1966); female *Ctenosaura similis* measure 80.0% and 55.6%, respectively (Fitch and Henderson 1977a); and *Iguana iguana* average 73.6% (Fitch 1973a) to 90.6% male SVL (Fitch and Henderson 1977b). Males are also larger than females in all the other iguanine species for which data are available (see Table 6); however the dimorphism is extremely reduced. Female *Cyclura cornuta, Cyclura pinguis, Conolophus subcristatus, Ctenosaura pectinata, Dipsosaurus dorsalis, Enyaliosaurus clarki*, and *Sauromalus obesus* all average only slightly smaller than males of the same species (references in Table 6).

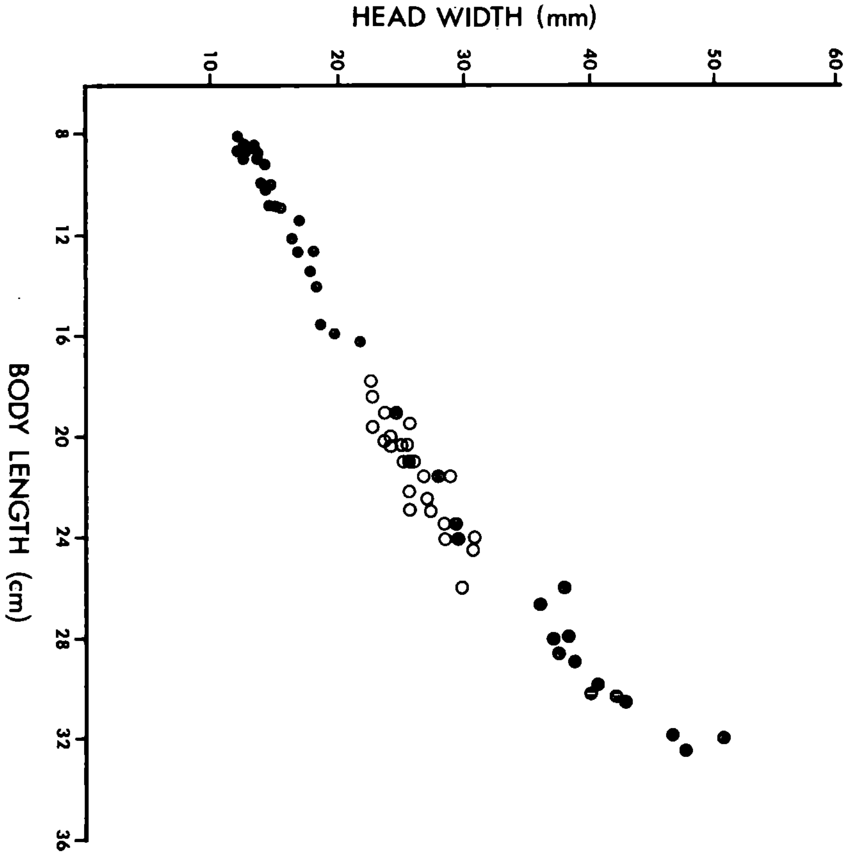

FIGURE 30.—Relationship of headwidth across tympanum to body length (measured snout to vent). Solid circles above 170 mm body length indicate males; open circles, females. Each symbol represents at least one individual. Data for 77 lizards.

The sexual size dimorphism observed for *C. carinata* may be the result of intense sexual selection as a consequence of its generally polygynous mating system and/or as a mechanism to reduce intraspecific competition for food (see later).

Comparisons of lizard size-frequency plots by month of capture suggest several discrete juvenile age classes. Although the use of these

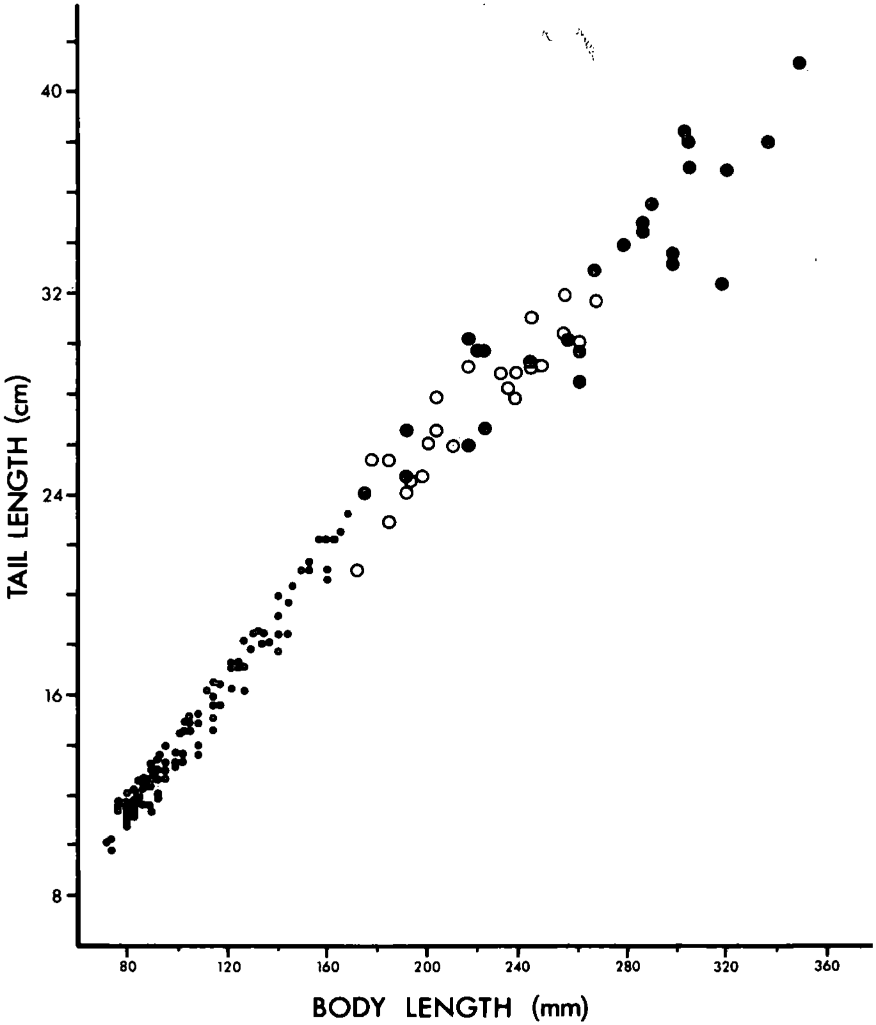

FIGURE 31.—Relationship of body length (measured snout to vent) to tail length. Solid circles above 170 mm body length indicate males; open circles, females. Each symbol represents at least one individual. Data from 179 full-tailed lizards.

TABLE 8.—COMPARISON OF SNOUT-VENT LENGTH IN *Cyclura carinata* ON FOUR OF THE STUDY ISLANDS.

	Fort George	Pine Cay	Water Cay	Little Water Cay	Total
♀	$\bar{X}=221.75 \pm 30.46$ 191 - 267 N=4	$\bar{X}=218.24 \pm 17.19$ 190 - 260 N=27	$\bar{X}=256.6 \pm 22.79$ 222 - 292 N=5	$\bar{X}=231.11 \pm 15.01$ 191 - 254 N=9	$\bar{X}=225.39 \pm 22.56$ 190 - 292 N=45
♂	$\bar{X}=237.17 \pm 28.64$ 203 - 286 N=6	$\bar{X}=270.12 \pm 32.29$ 216 - 318 N=17	$\bar{X}=314.69 \pm 44.84$ 191 - 360 N=13	$\bar{X}=261.64 \pm 43.61$ 191 - 318 N=11	$\bar{X}=276.26 \pm 46.37$ 191 - 360 N=47

NOTE: Data from lizards over 190 mm SVL only. Means ± one standard deviation appear with range and sample size.

TABLE 9.—COMPARISON OF BODY WEIGHT IN *Cyclura carinata* ON FOUR OF THE STUDY ISLANDS.

	Fort George	Pine Cay	Water Cay	Little Water Cay	Total
♀	$\bar{X}=366.25 \pm 160.68$ 205 - 610 N=4	$\bar{X}=433.46 \pm 97.63$ 250 - 570 N=13	$\bar{X}=749.83 \pm 187.80$ 535 - 1135 N=6	$\bar{X}=428.89 \pm 71.17$ 315 - 540 N=9	$\bar{X}=475.59 \pm 193.40$ 205 - 1135 N=32
♂	$\bar{X}=470.00 \pm 165.58$ 265 - 735 N=6	$\bar{X}=832.5 \pm 231.65$ 460 - 1110 N=8	$\bar{X}=1451.67 \pm 344.00$ 750 - 1864 N=12	$\bar{X}=646.3 \pm 319.84$ 256 - 1215 N=10	$\bar{X}=935.08 \pm 479.98$ 256 - 1864 N=36

NOTE: Data from lizards over 190 mm SVL only. Means ± one standard deviation appear with range and sample size.

size distributions to estimate growth rates can be misleading (Tinkle 1967b), when used in conjunction with mark and recapture data reliable growth information can be obtained. Actual growth data on *Cyclura carinata* are difficult to acquire even on islands uninhabited by man and his animals. Collection of such data on disturbed islands is nearly impossible. Slow adult growth and the difficulty in accurately measuring a struggling lizard with a total length of over half a meter and weighing over half a kilogram compound the difficulty in obtaining accurate natural growth information. On Pine Cay predation on juvenile lizards by feral mammals made abortion of a mark-release-recapture program there necessary early in this study; during four visits over one year 30 juveniles were marked and none recaptured. A similar recapture program initiated on uninhabited Little Water Cay (Fig. 5) proved satisfactory. A total of 103 lizards was marked on five visits (10 July and 4 December 1974, 10 August 1975, 5 May and 10 June 1976), and 19 were subsequently recaptured at least once.

Growth in juvenile *Cyclura carinata* based on actual recapture data as well as analysis of size-class information is plotted in Figure 32. Based on size at sexual maturity, males require 7 to 8 yr to reach maturity (about 220 mm SVL); females, 6 to 7 yr (185-200 mm SVL). Size-class data indicate an average hatching SVL of 80 mm (weight = 19.0 gm from regression equation); juveniles average 100 mm (37.4 gm) at 1 yr, 124 mm (71.8 gm) at 2 yr, 146 mm (117.8 gm) at 3 yr, 161 mm (158.5 gm) at 4 yr, 178 mm (214.9 gm) at 5 yr, and 195 mm (283.5 gm) at 6 yr. Only a slight decrease in growth rate (measured as change in SVL length) occurs from hatching to maturity. An average growth rate of approximately 19.2 mm SVL (range = 15-24) per year, or 1.6 mm per month, is indicated. Similar results are obtained from individual growth records of recaptured Little Water Cay lizards as well as of several captive Pine Cay juveniles (Fig. 33, Table 10). A single captive juvenile lizard maintained in captivity for 16 months increased in body length from 129 to 178 mm SVL, a growth rate of 5.5 mm/month. This atypically high value was not used in any of the calculations, since it presumably represents growth under optimum conditions. The slopes of each of the regression equations in Table 13 evidence the nearly constant juvenile growth rate.

Mean change in tail length per month for recaptured Little Water Cay lizards less than 180 mm SVL with complete tails was 2.365 ± 1.30 mm (N = 13). The data suggest relatively constant rates of tail growth in juvenile *Cyclura*.

Despite their tropical location, there is considerable seasonality in both temperature and moisture in the Caicos Islands. This is reflected in the phenology of the vegetation and ultimately in the growth and ac-

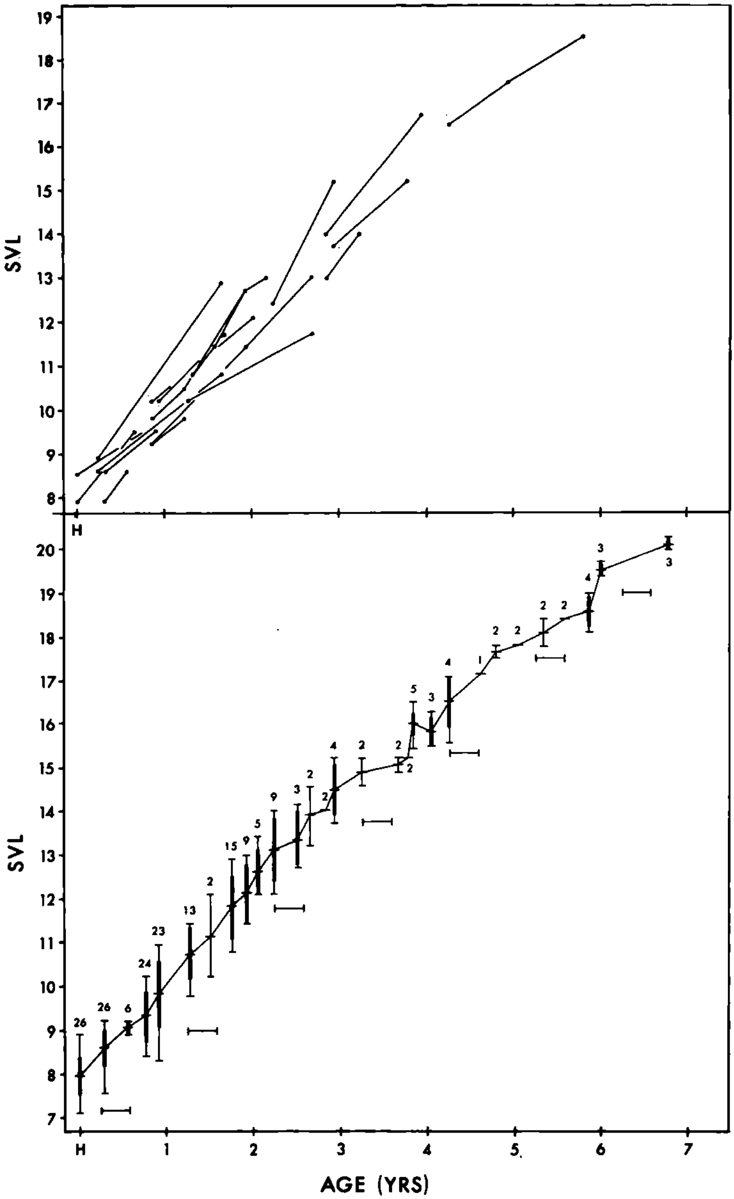

FIGURE 32.—Growth in juvenile *Cyclura carinata* based on actual recapture data (top) and size class distribution (bottom). Snout-vent lengths in centimeters. Means (horizontal lines connected by curve), range (vertical line), standard deviation (heavy solid vertical line) and sample size for each size range class sample are indicated. Horizontal bars below curve in lower graph mark annual period of slow growth (December to March). Total sample size = 206.

tivity of *Cyclura* in the islands. During the cold, dry season of late December through March, there is very little plant growth. Growth in juvenile lizards (and presumably adults) also slows considerably. This growth reduction in *Cyclura* is apparent in Figure 32 (bottom) if the slope of the curve during the harsh winter season (marked by horizontal bars below the growth curve) is compared to that for the remainder of the year. The slope of the curve (equivalent to growth rate) during the winter season ($\overline{X}$ = 0.992 mm/month; range 0.30-1.39) is significantly different ($p < 0.05$) from the slope for the remainder of the year ($\overline{X}$ = 1.855; range 1.15-2.30). This winter decrease in growth rate is related not only to a decrease in food quality and quantity (pers. observ.; Auffenberg MS) but also to a reduction in activity necessitated by the cooler temperatures (see ACTIVITY AND MOVEMENTS).

Mean body size (SVL) and weight for yearly intervals (see above) were utilized to construct a curve relating change in body weight to body size for juvenile *C. carinata*. Actual weight changes in recaptured lizards for the most part fit that curve very well (Fig. 34). Both sets of data indicate a nearly constant annual increase in body weight change

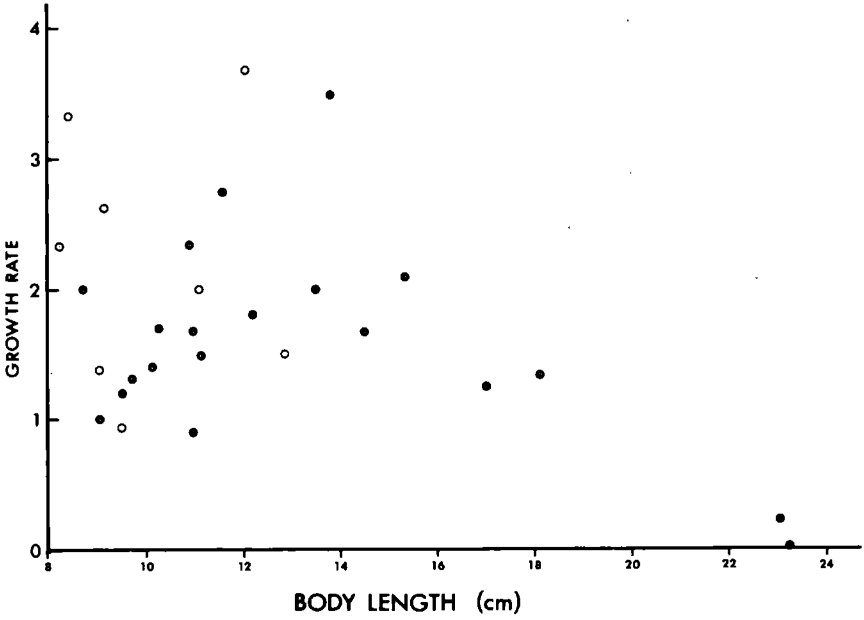

FIGURE 33.—Growth rate (mm SVL per month) of recaptured lizards on Little Water Cay (closed circles) and captive lizards from Pine Cay (open circles) plotted by the average of the body lengths at first capture and at recapture.

TABLE 10.—REGRESSIONS OF BODY SIZE ON GROWTH RATE FOR FOUR CATEGORIES OF DATA FROM FIGURE 33.

	$\bar{X}$ Growth rate (mm SVL/month)	Regression Equation ($\bar{X}$ = mm SVL; y = growth rate [mm SVL/month]; and r = correlation coefficient)	Critical value for r
Little Water Cay recapture data (lizards <200 mm SVL only)	1.74 ± 0.63 N=18	$y=0.0033X + 1.34$ $r=0.138$	0.468 (5%)
All Little Water Cay data	1.58 ± 0.77 N=20	$y=-0.0081X + 2.65$ $r=-0.439$	−0.444 (5%)
Little Water Cay and captive data (<200 mm SVL only)	1.85 ± 0.80 N=26	$y=-0.00083X + 1.98$ $r=-0.061$	−0.388 (5%)
All Little Water Cay and captive data	173 ± 0.90 N=28	$y=-0.0094X + 2.92$ $r=-0.718$	−0.496 (1%)

($\bar{X}$ = 10.03 gm/year) through at least the first 6 yr of life.

Very little information on growth rates of adult *Cyclura carinata* was obtained during the course of the study. Only one adult lizard of those few marked on Little Water Cay was recaptured. Although many lizards at the SW Blind site were remeasured, the value of the data is questionable due to the difficulty in accurately measuring the large lizards; negative growth rates (SVL change/month) were occasionally recorded. Nevertheless, an extremely slow adult growth rate is suggested. The mean change in SVL per month for males at the SW Blind was 0.18 mm (N = 12). However, all but three (4 recapture records) of these lizards were obviously old, territorial-holding males. I therefore believe that this extremely low estimate of mean growth rate reflects the very slow growth of older males. The mean growth rate (mm SVL/month) in the smaller males (250-270 mm SVL) is 0.659 (N = 4) and is probably a more accurate estimate of growth in adult male lizards.

A mean growth rate for females slightly more than half that of males (0.461 mm SVL/month; N = 4) is indicated by the SW Blind and Little Water Cay recapture data. This is as anticipated since the difference between SVL at maturity and maximum size in females is only half that for males.

In a further attempt to determine the rate of growth in adult iguanas, the relationships of body size to the mid-dorsal spines were investigated. As explained under MORPHOLOGY, once maturity is reached in males the spines on the neck begin elongation (Fig. 7).

Thereafter each time the skin is shed an annulus is formed around the base of the spine. The back spines begin a similar development (including rate) after the skin is twice cast (Fig. 35). Therefore, neck spines possess two more annuli than back spines. Tail spines also

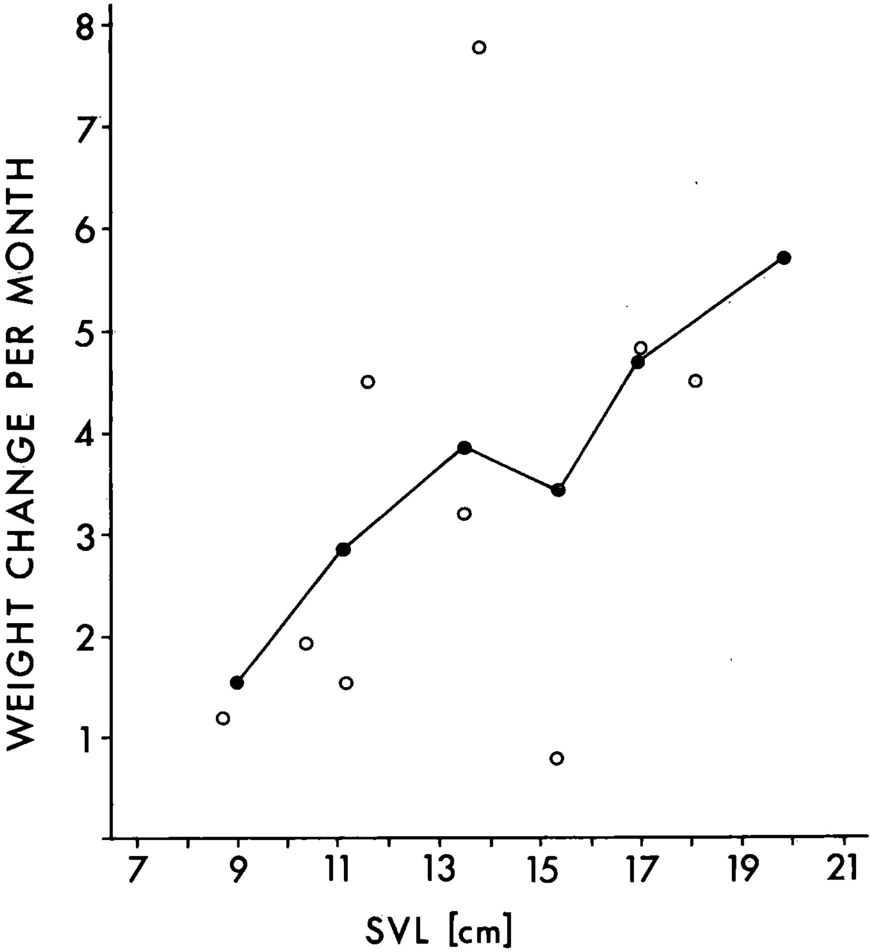

FIGURE 34.—Relationship of weight change (gm/month) to body size in juvenile *Cyclura carinata*. Hollow circles are actual weight change records from recaptured Little Water Cay lizards, plotted by the average of the original and the recapture snout-vent lengths. Solid circles represent calculated weight changes: mean snout-vent lengths for one year age intervals were used to calculate body weights with the regression equation: $Wt = (3.202 \times 10^{-5})SVL^{3.0336}$; consecutive yearly weight changes were divided by 12 to give monthly values. These are plotted by the average of the mean snout-vent lengths at the beginning and end of the sample year.

elongate in older males, but annuli are not formed. The dorsal spines of females develop little and generally do not bear annuli (Fig. 36). With age the dorsal spines are worn smooth and the number of annuli are uncountable. However, it is frequently possible to determine with some accuracy the number of annuli present. Unfortunately, the spine sheaths are not shed precisely at the time the adjacent skin is sloughed, and annuli counts therefore tend to be underestimated.

Since the spines indicate previous ecdyses, it should be possible to estimate age in male lizards by the number of annuli on their spines. But some knowledge of the time between molts is necessary. Accurate data on shedding frequency are difficult to obtain; Tinkle (1967b:43) has discussed the problems inherent in their estimation. From adult lizards painted both on Little Water Cay and at the SW Blind an annual slough is indicated. Furthermore, adult *Cyclura carinata* from Water Cay maintained in captivity by David Auth during the course of thermoregulatory studies shed their skin annually. Street (1952) also believed *Cyclura nubila* on Cuba shed only once a year (during the spring).

The onset of shedding in *Cyclura carinata* seems to be coincidental with the resumption of more rapid growth following the cold and dry winter. The skin is not sloughed rapidly; ecdysis may require several

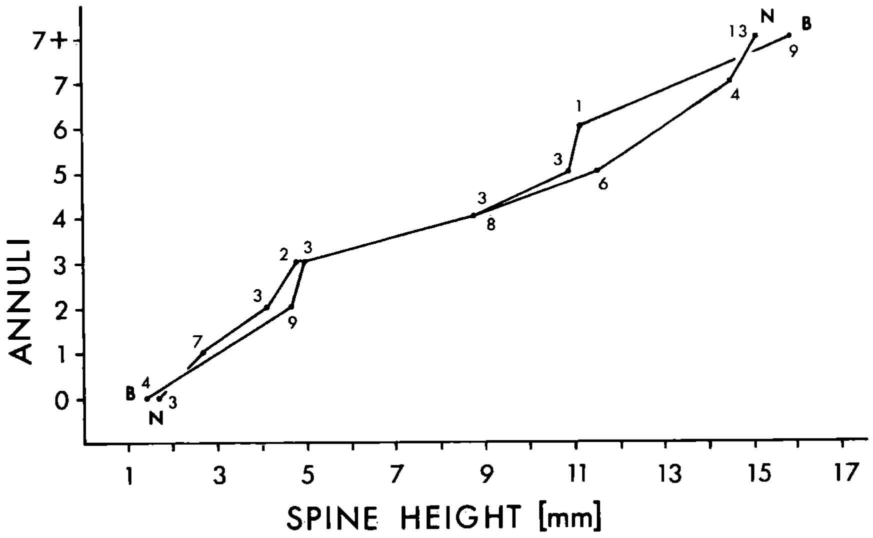

FIGURE 35.—Relationship of mean maximum dorsal back (B) and neck (N) spine heights to number of spine annuli in male *Cyclura carinata*. Numbers adjacent to curves are sample sizes.

months for completion. The skin of the head and upper trunk areas are shed first, followed by the lower trunk, then the limbs and ultimately the tail. In those instances where traces of paint were still visible during late summer or autumn on lizards marked the previous year, the paint remnants were always on the tail or distally on the limbs. Once initiated, juvenile shedding appeared more rapid than that of adults, as would be expected from the more rapid juvenile growth rate.

Because there is evidence that ecdysis is an annual phenomenon, the annuli on the dorsal spines are believed to represent yearly increments. Since annulus counts are therefore approximately equal to age post-maturity in male lizards, growth rate can be estimated by comparing these counts to lizard size. Figure 37 demonstrates the linear relationship between number of spine annuli and body length in *Cyclura carinata*. The least-squares regression equation for this data (y = 0.59x − 11.849) indicates an SVL change of approximately 1.7 cm with the addition of 1 annulus, i.e. 1 year. This is equivalent to a growth rate of 1.41 mm SVL per month, more than twice the 0.66 mm estimate for young adult males and only slightly less than the 1.85 mm estimate for juveniles based on actual recaptures. SVL lengths calculated from weights recorded from six captive adult male lizards by David Auth (pers. comm.) for periods totaling almost 60 months (Range 7.25 to 14) exhibited an average monthly change of 1.82 mm.

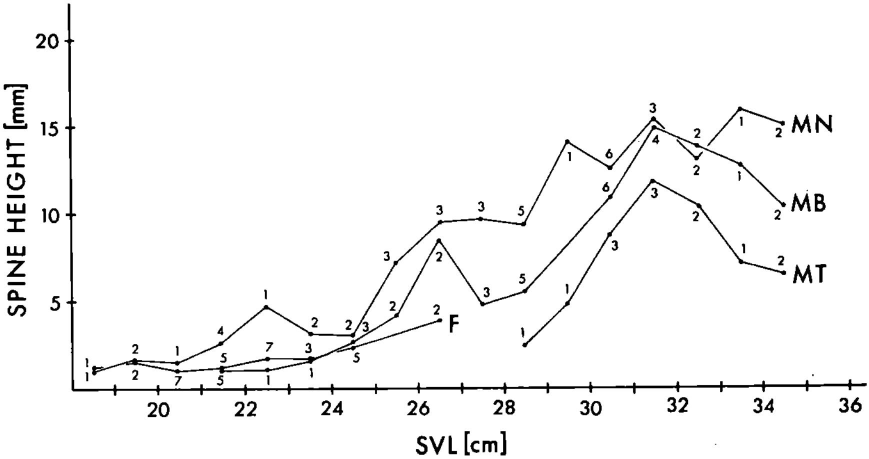

FIGURE 36.—Change in dorsal spine height with body size in *Cyclura carinata*. Means for maximum spine heights from neck (MN), back (MB), and tail spines (MT) of males and neck spines of females (F) are plotted by 1 cm body size classes. Numbers adjacent to curves are sample sizes.

This presumably overestimates actual growth rate, since captive animals receive more food of higher quality than do wild individuals. Therefore, the actual adult male growth rate is probably close to the 1.41 mm per month estimate from the annulus data.

Due to small sample sizes, it was impossible to relate social status to growth rate in wild populations. However, in captivity, subordinate male lizards (females do not exhibit dominance relationships in nature or captivity, except during nesting) often would not eat even when food was abundantly available. In addition, their activity was greatly reduced. Berry (1974) found that dominant male *Sauromalus* grew more rapidly than subordinates, and I suspect a similar relationship in wild male *Cyclura carinata*. Males unable to establish territories in primary habitat are forced to occupy inferior peripheral habitats, such as unstable sandy habitats. As an example, the distal two-thirds of the sand spit formed since 1967 at the northeast point of Little Water Cay is populated only by adult male lizards.

If the juvenile growth rate (through 6 yr) is 1.6 mm per month, as indicated by the Little Water Cay recapture data as well as age-size class analysis, and the adult male rate (after 6 yr) is 1.4 mm per month, the average adult male of 276 mm SVL (Table 8) is approximately 10 yr 10 mon of age.

Unfortunately growth rates of adult females are not so readily calculable. However, if a female lizard of mean adult female body size (225 mm SVL; Table 8) is the same age as a male of mean body size, an increment of monthly growth in adult females of 0.52 mm is indicated.

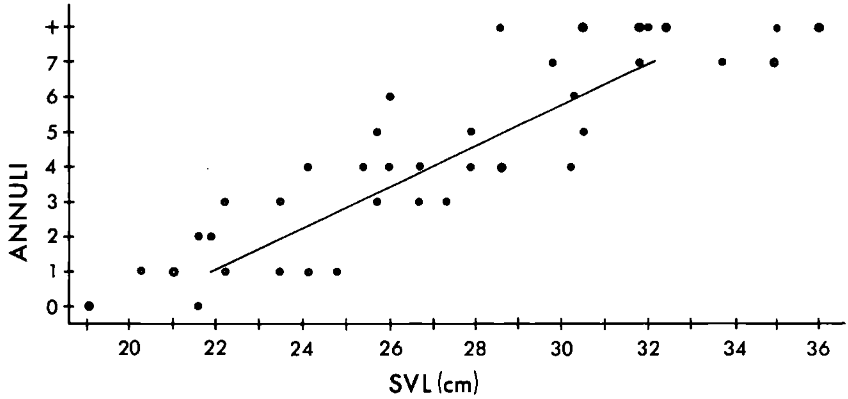

FIGURE 37.—Change in number of neck spine annuli with body size in male *Cyclura carinata*. Back spine annuli number is two less than neck spine count. Small dots indicate individual records; large dots, two or more. Least squares regression ($y = 0.59x - 11.849$; $N = 34$; $r = 0.8577$; $p = p < 0.01$) utilizing only that data for annuli numbering through seven is plotted.

It remains to be seen whether this assumption is a valid one. In any case, this estimate supports the rate determined from four recaptured adult females (0.36 mm/month).

SVL lengths calculated from weights recorded from four captive female lizards by David Auth (pers. comm.) for periods totaling more than 53 months (range, 7.25 to 26) indicated an average monthly increase of 1.11 mm. This value is over two times the estimated natural growth rates. One captive female gained 63 mm in SVL (and 562 gm body weight) in only 26 months (2.42 mm/mon). A similar-size female marked and recaptured on Little Water Cay gained only 3 mm over 24 of the same 26 months. This accelerated captive growth may indicate that natural food resources are limiting growth (see FOOD AND FEEDING).

From the SVL-body weight and the SVL-spine annuli regressions, calculated annual adult male weight changes constantly increase from about 14 gm/yr in newly maturing individuals to almost 24 gm/yr in older lizards ($\bar{X} = 18.9 \pm 3.1$, from ages 6 to 17 yr). Calculated yearly weight increases were 82 gm/yr during the sixth year and 252 gm/yr during the sixteenth year.

The slowing of the growth rate in adult females when compared to males is perhaps related to the high annual female reproductive expenditure; female *Cyclura carinata* deposit roughly 25% of their gravid body weight annually when nesting (see REPRODUCTION). Applying the SVL-body weight regression to the mean adult SVL for males (276.26 mm) and females (225.9 mm) calculates body weight at 815 gm and 440 gm, respectively. Age for males of this size was previously determined to be approximately 10 yr, 10 mon. Six-year-old subadult lizards average 195 mm SVL and 283.5 gm. Therefore, males increase their weight 531.5 gm in 4 yr, 10 mon. If we assume average-size adult females are also aged 10 yr. 10 mon, then they experience only a 156.5 gm increase in the same 4 yr 10 mon. (Even if this is not a strictly valid assumption, I believe its accuracy will not greatly affect the following discussion.) However, in that period of time, a female would have deposited five clutches of eggs. Since mean clutch size for females 195 to 225 mm SVL equals 3.42 and mean egg weight equals 25.9 gm, average clutch weight for those five clutches is approximately 88.6 gm. Add the weight of five average clutches (442.9 gm) to the 156.5 gm female increase during the 4 yr, 10 mon , and we observe that a potential weight increase of nearly 600 gm might be possible if reproductive output were rechanneled to growth (and maintenance costs were disregarded).

It is perhaps more than coincidental that this value is approximately equivalent to the male increase during the same five periods (531.5

gm). It is tempting to suggest that the observed sexual size dimorphism is explainable in terms of a simple shift of a portion of the potential energy available for growth to use in the reproductive output of females. Nevertheless, it would probably be better explained as a means of reducing intraspecific competition and/or as a correlate of the polygynous mating system.

Factors Affecting Growth

As shown above for juveniles, lizards grow little during the winter. This is probably due primarily to two factors. In response to the colder and drier conditions most plant species do not produce fruits or flowers. *Cyclura* must necessarily become more folivorous. Since digestion of fibrous leaves is presumably more difficult, as evidenced by the fact that leaves often pass through the entire gastrointestinal tract unaltered, and the caloric content of leaves is generally lower than that of fruits (Golley 1969; Auffenberg MS), the nutritive quality of the winter diet is much reduced. Secondly, lower winter environmental temperatures sometimes make it impossible for lizards to reach preferred temperatures for one to several days at a time. Feeding is therefore precluded, and digestive activity is presumably reduced (Harlow *et al.* 1976) as most activity certainly is. Thus, despite their tropical location, populations of *Cyclura carinata* are subjected to a distinct climatic seasonality which is reflected in a decrease in the physical and physiological availability of the food resources during the winter. Growth must necessarily slow during that period.

Longevity

If the previously estimated adult male growth rate (17 mm/yr) were maintained from age 6 yr (195 mm SVL) on, with no slowing in old age, it would require over 15 years to reach the approximate 350 mm maximum male SVL. Even if the mean juvenile growth rate was maintained throughout life, over 14 years would be required for a male to reach that 350 mm maximum SVL. These data suggest that large adult males commonly live 15 yr; many probably live 20 yr, with occasional individuals surviving 25 yr.

Regeneration

As in most other lizards (Fitch 1954:97; Tinkle 1967b:58), rate and extent of tail regeneration in *Cyclura carinata* is dependent on a variety of factors, including age and site of fracture. Figure 38 illustrates the relationships of tail break site in juveniles, females, and males on the total length of tails with regenerated portions. The data indicate that: (1) fully regenerated tails in juveniles are proportionately longer than those of adults, and (2) the longer the lost tail segment, the shorter the completely regenerated tail length will be.

Information on actual regeneration rates of broken tails is scanty and only data from juvenile lizards are available. Regeneration is very rapid in juveniles, exceeding 5 mm per month (maximum recorded 7.3). The fact that the majority of the broken-tailed adult lizards seen exhibited nearly maximal regeneration (note modal values in Fig. 38)

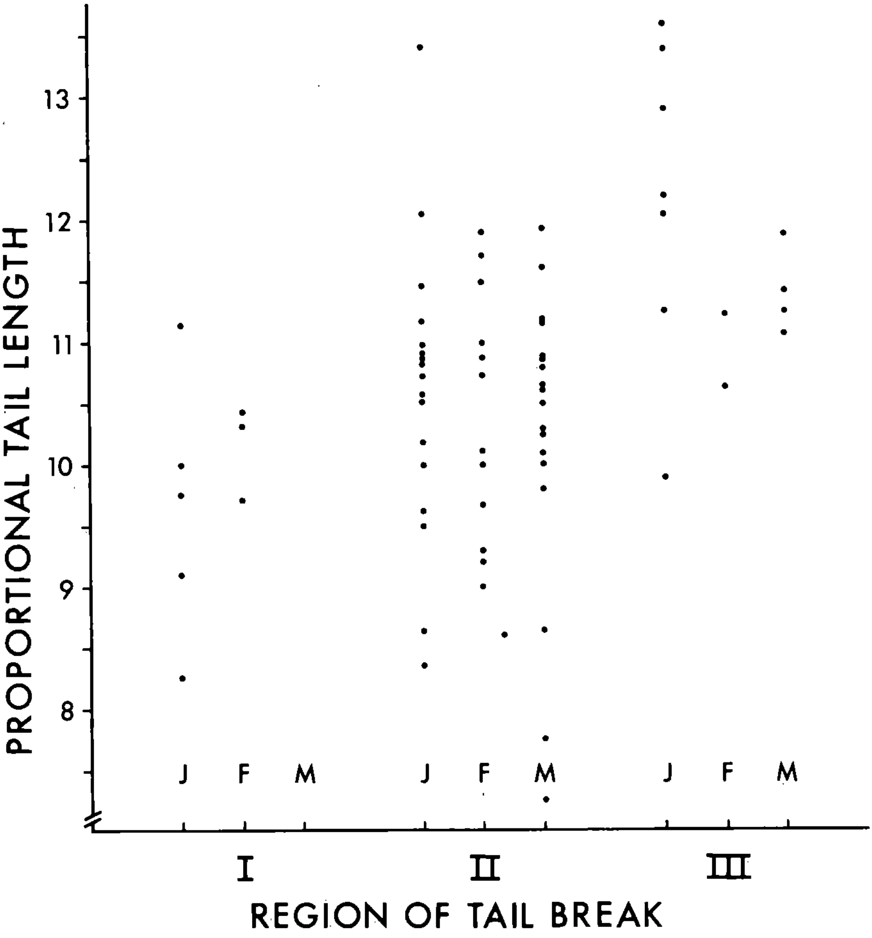

FIGURE 38.—Proportional tail length (TL x 10/SVL) in broken-tailed *Cyclura carinata* for juveniles (J), females (F), and males (M), based on region of break. Roman numerals refer to break position: I = proximal third (unregenerated portion of tail/SVL = 0 to 0.47), II = Middle third (0.47 to 0.93), and III = distal third (over 0.93). Data from tails with multiple breaks are not plotted. Unbroken tails have a mean proportional length of about 14.

suggests that regeneration rates in adults are also very rapid. The importance of the tail for balance when running, and as an escape mechanism from predators, as well as its use in social contexts (see SOCIAL ORGANIZATION) bespeaks the selective value of rapid tail regeneration.

Occasionally incompletely severed tails will begin regeneration, producing forked tails. In this study, three lizards were encountered with bifurcate tails; one additional iguana exhibited three tail forks.

COMPARISONS WITH OTHER IGUANINES

Cyclura carinata is a medium-sized iguanine lizard; the genera *Brachylophus* (one species), *Ctenosaura* (four species, except *C. similis*) *Enyaliosaurus* (four species), and *Sauromalus* (five species), and only one other species of *Cyclura* (*rileyi*) are smaller. *Cyclura carinata* exhibits greater sexual size dimorphism than any other iguanine (see above); adult females average only about 80% and 50% of adult male SVL and body weight, respectively. Male *Cyclura pinguis* are also larger than females (Carey 1975) but not to the extent found in *C. carinata*.

A juvenile growth rate of 1.6 mm SVL/mon (0.052 mm/day) in *Cyclura carinata* is among the slowest yet recorded among lizards (see review in Tinkle 1967b). This is undoubtedly an artifact of the much greater size of juvenile *Cyclura* compared to previously studied juvenile lizards. Comparisons of weight changes during juvenile growth are probably more meaningful to growth discussions involving lizard species of greatly varying sizes. Unfortunately, these data are not easily extracted from the literature. Nevertheless, the rates of body length change for juvenile *Cyclura carinata* compare favorably with those recorded for other juvenile iguanines (Table 11). Adult growth rates are similarly congruent (Table 12).

Very little information exists on age at maturity in iguanine lizards. Fitch (1970) theorized that three years is the minimum breeding age for *Ctenosaura similis* in Costa Rica. Mayhew (1971), Berry (1974), and Carey (1975) similarly postulated that *Dipsosaurus dorsalis, Sauromalus obesus*, and *Cyclura pinguis* require 5-6, 9, and 7-9 yr respectively. These data correspond well with my estimate of 6-7 yr for *Cyclura carinata* and Wiewandt's (1977) estimate of 6-7 yr for *C. cornuta.*

Longevity has been discussed previously for few iguanine species. Johnson (1965) and Berry (1974) postulated 25 and 20 years, respectively, as estimates of longevity for *Sauromalus obesus* in the Mojave Desert. Carey (1973) maintained two *Dipsosaurus dorsalis* (adults when obtained) in captivity for just over 14½ years; assuming at least

TABLE 11.—JUVENILE GROWTH RATES IN IGUANINE LIZARDS.

Species	Location	Growth rate (mm SVL/month)	Sample Size	Data Base	Reference
Ctenosaura similis	Western Costa Rica	9	2+	age class groupings	Fitch 1970
Ctenosaura similis	Belize	9.17	1	age class groupings	Henderson 1973
Ctenosaura similis	Western Costa Rica	9.86 (7.5 to 15.33)	8	field recaptures	Fitch 1973
Cyclura carinata	Caicos Islands British West Indies	1.6	206	age class groupings	Present study
		1.74	16	field recaptures	
		2.10	8	captive data	
Cyclura cornuta	Mona Island	4.4	8	captive	Wiewandt 1977
			6	noncaptive	
Cyclura pinguis	Anegada, British Virgin Islands	1.2 and 3.0	2	captives	Carey 1973, 1975
Dipsosaurus dorsalis	California	0.8 to 4.4*	23	captive	Mayhew 1971
		0.9 to 1.2*	?	field recaptures	
Dipsosaurus dorsalis	Arizona	2.7 (0.0 to 5.1)	22	field recaptures	Parker 1972
Iguana iguana	Belize	6.60	23	field recaptures	Henderson 1974
Sauromalus obesus	California	♂=3.8 (1.6 to 6.3)*	21	field recaptures	Berry 1974
		♀=1.8 (0.0 to 4.2)*	15	field recaptures	
Sauromalus obesus	California	2.5[1]	1	field recapture	Johnson 1965
Sauromalus obesus	California	3.5	1	captive	Mayhew 1963a

*Growth rates for growth season of six months only.

five years to reach adulthood (Mayhew 1971), at death the lizards were probably more than 20 years of age. Goin and Goin (1962) considered 15 yr to be the maximum age for *Conolophus subcristatus*, and Mueller (1968, 1972) believed that very few *Iguana iguana* lived more than 10 yr. Iguanine lizards of at least 13 species (including four species of *Cyclura*), each wild-caught as an adult, have been maintained in captivity from 4 to 17 yr (review in Bowler, 1977). Unfortunately Carey (1975) did not speculate on longevity for *Cyclura pinguis* in the British Virgin Islands. However, if longevity is computed by utilizing his values for size (400 mm) and age (7-9 yr) at sexual maturity, maximum size (about 540 mm),

Table 12.—Adult Growth Rates of Iguanine Lizards. Asterisk indicates Growth rates for Six Month Growth Season Only.

Species	Location	Growth rate (mm SVL/month)	Sample Size	Data Base	Reference
Sauromalus obesus	California	0-1.7	8	field recaptures	Johnson 1965
		1.6	1	captive	
		0.5-1.3	11	field recaptures	
Cyclura carinata	Caicos Islands British West Indies	0.18 (<270 mm SVL)	12	field recaptures	Present study
		0.66	4	field recaptures	
		1.41	34	spine annuli analysis	
		1.82	6	captives	
		0.36	4	field recaptures	
		1.11	4	captives	
Sauromalus obesus	California	(<170 mm SVL) 1.9 (0-4.3)*	14	field recaptures	Berry 1974
		(>170 mm SVL) 0.7 (0-2.3)*	31	field recaptures	
		(<170 mm SVL) 0.3 (0-0.5)*	6	field recaptures	
		(>170 mm SVL)- 0.04 (0-0.1)*	19	field recaptures	

and the average of his two captive subadult growth records (2.1 mm/month), a minimum longevity of nearly 14 yr is obtained. Following a similar procedure, *Cyclura carinata* must normally live from 15 to 20 yr.

FOOD AND FEEDING

DIET

GENERAL COMMENTS.—Food items eaten by *Cyclura carinata* are listed in Tables 13 and 14. A more comprehensive analysis of diet, based on stomach analysis, appears in Auffenberg (MS); therefore, only a few important points regarding diet are discussed here.

At least 95% of the diet (in volume or numbers of items) of lizards of all ages during all seasons is plant material (Auffenberg MS; this study). As expected, seasonal diet variation reflects food availability; fruits and flowers are necessarily infrequently represented (leaves frequently) in the winter diet. Ontogenetic diet changes are primarily related to the increasing size of the trophic apparatus with age; adults are more efficient leaf-croppers and can swallow much larger fruits than juveniles.

Strumpfia (bay cedar) is the single most important food item in the diet of *Cyclura carinata* during the first year of its life. *Erithalis* (Torch

TABLE 13.—PLANTS KNOWN TO BE EATEN BY *Cyclura carinata* on Pine Cay. Fecal Determinations by Gross Examination Only.

					Discovered		
Species	Leaves	Fruits	Flowers	Other	In GI tract	In feces	By observation
Acacia acuifera	++				X	X	
Ambrosia hispida	– –				X		
Amyris elemifera		– –			X		
Andropogon glomeratus		– –			X		X
Antirhea myrtifolia	– –	+			X	X	
Argythamnia sericea	– –						X
Bourreria ovata	– –				X		X
Bucida buceras	– –						X
Bumelia americana	– –						X
Byrsonima cuneata	– –	+			X	X	
Calyptranthes pallens		+			X	X	X
Casasia clusiaefolia		+	– –			X	X
Cassia lineata	– –				X	X	
Catesbaea foliosa	– –				X		
Chamaesyce buxifolia	– –		– –		X		
Chamaesyce vaginulata	– –		– –		X		
Chloris petraea	+	+			X	X	X
Coccoloba krugii		++			X	X	X
Coccoloba uvifera	– –	++			X	X	X
Conocarpus erectus	– –				X	X	X
Crossopetalum rhacoma	– –	+			X	X	X
Cuscuta americana	– –					X	
Cynanchum cf *eggersii*	– –				X		
Cyperus fuligineus	+	– –			X		X
Digitaria filiformis	+	+			X		X
Erithalis fruticosa	+	++	+	flower buds	X	X	X
Ernodia millspaughii	– –	+	++		X	X	X

Eugenia foetida	+	++			X	X	X
Evolvulus sp.	+				X		
Guaiacum sanctum	++				X		
Guapira obtusata	– –	+			X	X	
Guettarda krugii	– –				X		
Gundlachia corymbosa			– –		X		
Hippomane mancinella	– –	– –			X		
Hypelate trifoliata	– –				X		X
Jaquinia keyensis	– –	– –			X	X	X
Manilkara bahamensis	+	++		leaf buds	X	X	X
Maytenus buxifolia	+			shoots	X		X
Metopium toxiferum		– –			X		
Paspalum laxum	+	+			X	X	X
Phyllanthus epiphyllanthus	– –						X
Pithecellobium guadelupense	+			shoots	X		X
Plumeria obtusa				leaf buds and petioles			X
Psidium longipes	+	+			X	X	X
Rachiallis americana	+		+	stems	X		X
Reynosa septentrionalis	+	++			X	X	X
Rhizophora mangle	– –						X
Scaevola plumieri	– –	– –			X	X	X
Strumpfia maritima	– –	++	+		X	X	X
Tabebuia bahamensis			– –	flower buds	X		
Thrinax microcarpa		++			X	X	X
Thyralis sp.	– –				X		X
Tournefortia volubilis		+			X		X
Zizyphus taylori	++				X	X	X
2 mushroom species		(entire plant)			X		X
6 unidentified species	+	+	+		X	X	

NOTE: – – occasional
\+ common
++ abundant

TABLE 14.—ANIMALS KNOWN TO BE TAKEN BY *Cyclura carinata* ON PINE CAY.

	Discovered		
	In GI Tract	In Feces	By Observation
Mollusca			
unidentified slug	X		
Crustacea			
Decapoda			
Clibanarius (hermit crabs)	X	X	X
Cardisoma guanahumi (land crabs)	X	X	
Insecta			
Homoptera			
Ollanta caicosensis (Cicada) nymphs	X	X	
Ollanta caicosensis (Cicada) adults	X	X	
Lepidoptera			
Pseudosphinx tetrio larvae	X		
Hymenoptera			
unidentified honeybee	X		
Isoptera			
Nasutitermes costatus	X		
Coleoptera			
unidentified adult weevils	X		
unidentified beetles	X	X	
Diptera			
unidentified species	X	X	
Odonata			
unidentified wing fragments	X	X	
Arachnida			
Solpugidae		X	
Reptilia			
Cyclura carinata juveniles	X		X
Cyclura carinata skin	X	X	
Aves			
various species (as carrion)			X
unidentified feathers	X		X

wood) and *Ernodea* (guanaberry) are also very important. Of 6 neonates captured in September with food in their gastrointestinal tracts, 5 had eaten *Strumpfia* fruits, and two contained *Erithalis* and/or *Ernodea* in their digestive tracts. During December of their first year (approx. age, 3.5 mon), 7 of 12 juveniles had fed on *Strumpfia*, and 3 of 12 had eaten more than one of these three species. By March (age 6½ mon), each of 4 juveniles had eaten at least one of the three species; by June and July (age, 9-10 mon) this proportion was 2 of 6. This may reflect the occurrence of the three plant species in nearly all habitats, as well as the fact that fruit is produced throughout an extended reproductive season (Auffenberg MS; pers. observ.).

In additon to fruits of the above three species, adults are especially fond of fruits of *Antirhea, Casasia, Coccoloba, Eugenia, Manilkara, Psidium, Reynosa,* and *Thrinax*. Evidence of the fruits of at least one of these species was found in the gut of nearly every adult lizard dissected.

GEOPHAGY.—The guts of nearly all *Cyclura carinata* examined contained sand grains and/or other soil fragments. There is some controversy as to whether reptilian geophagy and/or lithophagy is intentional or accidental (see Kennedy and Brockman 1965; Sokol 1967; for literature review). Despite Sokol's (1971) observations (in captivity?) of apparently intentional geophagy in the iguanines *Iguana iguana* and *Ctenosaura pectinata*, I believe that *Cyclura carinata* does not purposely ingest particles of the substrate. I have never observed geophagy in this species either in captivity or in the field.

COPROPHAGY.—The intentional ingestion of feces, whether from their own or other species, has been documented for herbivorous tortoises (Auffenberg and Weaver 1969; Mares 1971) and has been reported in the herbivorous lizards *Amblyrhynchus cristatus* (Wilcox *et al.* 1973, bird feces), *Dipsosaurus dorsalis* (Norris 1953; Stebbins 1954; Minnich and Shoemaker 1970, mammal and reptile, including their own), *Iguana iguana* (Swanson 1950, believed by natives to eat human excrement), *Sauromalus obesus* (Nagy 1973, fecal origin unspecified; Sanburn 1972, *Neotoma lepida* droppings), and *Utomastix acanthinurus* (Dubuis *et al.* 1971, gazelle drippings). However, feces were not found in the upper gastrointestinal tracts of any *Cyclura carinata* dissected.

The importance of coprophagy to iguanines is unknown. Unfortunately Nagy (1973) did not speculate on the significance of the occurrence of feces in the stomachs of *Sauromalus*. Mares (1971) hypothesized that ingestion of the scats of herbivores by other herbivores might increase the latter's efficiency of assimilating the contained cellulose materials since they are already partially digested. Minnich and Shoemaker (1970) suggested that the ingestion of fecal materials may provide specific nutritional requirements (vitamins and proteins) otherwise lacking in a plant diet. Another possible benefit of coprophagy is that it provides a means of acquiring potentially symbiotic intestinal micro-organisms that might also increase assimilation efficiencies (see *Digestive Efficiency*, this section, and INTERSPECIFIC COACTIONS).

CANNIBALISM.—The inclusion of conspecifics in the diet of *Cyclura carinata* is of particular interest (Table 14): cannibalism is extremely rare among iguanid lizards, especially in non-captive situations (Burt 1928; Dodge 1938; Shaw 1950; Mayhew 1963c; C. Johnson 1965; Montanucci 1965, 1976; Groves 1971; Bowie 1973). No herbivorous lizard is known to exhibit cannibalism in nature; but Alvarez del Toro (1972) reported that *Ctenosaura similis* in captivity will eat "young iguanas" (species not given). However, a hatchling *C. carinata* was found in the stomach of a conspecific adult female (203 mm SVL) collected near the Ridge Area on Pine Cay on 2 January 1974.

In addition one natural observation of possible cannibilism was made. On 3 September 1974, while walking along a trail near the SW Blind, I flushed a hatchling *Cyclura* from a low perch near the trail's edge. He ran away from me into the bush, directly toward an adult male that he had apparently not seen. As the hatchling ran to within 1.5 m of the male, the adult charged and snatched the hatchling up in his mouth by its entire left foreleg. As the hatchling flailed in an attempt to escape, the male vigorously shook it. I stooped to get a better view, and frightened the adult, which ran off out of sight with the hatchling dangling in his mouth.

EPIDERMOPHAGY.—Shed skin is commonly found in the gastrointestinal tracts and/or feces of *Cyclura carinata*. Murphy (1969) observed *Cyclura cychlura* in captivity to pull shedding skin from other iguanines and feed on it, but in my study ingestion of skin was not observed in either wild or captive *C. carinata*. Of 54 adult iguanas dissected, 12 had skin fragments in their guts; 9 of those were females and 3 were young males (222-298 mm SVL). A shed male dorsal spine was found in the large intestine of another female. These observations suggest that females groom dead skin from males. Of all records of skin in guts or feces, 80 percent fell between 5 March and 13 August.

The adaptive significance of epidermophagy in reptiles is unknown; Bustard and Maderson (1965) reviewed the subject and speculated that, as in birds and mammals (Rawles 1960; Mercer 1961), the ingested skin represents an alternative source of Vitamin D.

CARRION FEEDING.—*Cyclura carinata* do not hesitate to feed on carrion when it is encountered. They are, in fact, attracted to carcasses by olfactory clues. I have observed iguanas locate and feed on the decaying soft part of hermit crabs. On several occasions birds shot for diet analysis and not immediately retrieved were found by foraging iguanas. In every case, the lizard immediately began feeding on the carcass. (See example under Social Feeding). Fish carrion was found in the stomach of one iguana. Several-day-old canned sardines were consumed as readily as fresh ones at the SW Blind.

Among iguanines, carrion feeding has been reported for *Iguana iguana* (Loftin and Tyson 1965) and *Dipsosaurus dorsalis* (Norris 1953). I suspect necrophagy is more common among iguanine lizards than the literature suggests.

COMPARISONS WITH OTHER IGUANINES.—An extensive literature, supplemented by dissections of previously unstudied forms, indicates that all 30± species of the subfamily Iguaninae are primarily herbivorous throughout their lives. Some iguanid and agamid species are believed to exhibit an ontogenetic change from carnivory to herbivory (Mertens 1960; Pope 1969; Fleet and Fitch 1974; Carey 1975; Fitch and Henderson 1977a; and review in Pough 1973), but this definitely is not the case in *Cyclura carinata*. Unfortunately, captive and anecdotal natural observations form the basis for suggesting this strategy for other iguanine species (*Iguana iguana, Amblyrhynchus cristatus*, and most species of *Cyclura*). Further study is necessary to determine whether the juveniles of other iguanines (or any other herbivorous lizards) ingest animal matter opportunistically or intentionally. Table 15 reviews the literature on diet in the genus *Cyclura*. Fruits of such widespread forms as *Coccoloba, Erithalis,* and *Opuntia* are probably eaten by iguanas wherever they co-occur. Auffenberg (MS) compares breadth of the food niche with respect to floral diversity within the genus *Cyclura*.

FEEDING BEHAVIOR

GENERAL COMMENTS.—*Cyclura carinata* will feed anywhere within its home range (see ACTIVITY AND MOVEMENTS), but males feed within their defended territories more often than outside them (see SOCIAL ORGANIZATION). Feeding activity is bimodal during the warmer months (because of high midday environmental temperatures) and unimodal during colder months. Lizards generally make one to several feeding forays away from their burrows each day. During the winter only one foray is usually possible. Weather permitting, iguanas will feed every day of the year (see ACTIVITY AND MOVEMENTS).

Hatchling lizards begin feeding soon after emergence from the nest. Of seven neonates collected on 18 September 1973, six contained food both in the stomach and intestines. Others collected 30 August 1974 (4), 31 August 1974 (2), and 5 and 8 September 1975 (1 each) either lacked food in the gut or produced no scats following capture. Of all the lizards examined, these were the only ones that lacked digesta in the gastrointestinal tract.

As in *Iguana* (Rand 1967b) and *Dipsosaurus* (Norris 1953), feeding may also be reduced in female *Cyclura carinata* carrying eggs. The entire gastrointestinal tract of a gravid female dissected 3 June con-

TABLE 15.—NATURAL FOODS RECORDED FOR LIZARDS OF THE GENUS *Cyclura*.

Species	Location	Diet[1]	Reference
C. collei	Jamaica	*Petiveria* sp. (leaves)	Hill *in* Gosse 1848
C. cornuta	Mona Island	*Tribulus cistoides*	Martin 1966
C. cornuta	Mona Island	74 species of vascular plants including fruits of 26 species; flowers eaten when available Sphingid moth larvae Scarab beetles	Wiewandt 1977
C. cornuta	Haiti	"fruits", crabs	Eyerdam 1954
C. cornuta	Dominican Republic	cactus fruits	Carey 1975
C. cychlura	Exumas, Bahamas	*Erithalis fruticosa* (flowers, buds, & leaves)	Wilcox *et al.* 1973
C. nubila	Little Cayman Island	*Ipomoae pes-caprae* (flowers and leaves) *Cordia caymanensis* *Ernodea littoralis*	Grant 1940b
C. nubila	Cayman Brac	plums, mangoes	Grant 1940b
C. nubila	Cayo de la Piedra, Cuba	*Opuntia* (all parts) crabs	Sutcliffe 1952
C. pinguis	Anegada B.V.I.	*Coccoloba* (leaves) *Opuntia* (fruit) "nutmegs"	Grant 1937
C. pinguis	Anegada	Cactus (all parts) *Coccoloba*	Underwood 1962
C. pinguis	Anegada	*Conocarpus erectus* (leaves) *Reynosa uncinata* *Erithalis fruticosa* *Coccoloba uvifera* (leaves) Unidentified grasses *Lantana reticulata* Insects (mainly Lepidopteran larvae) *Pisonia rotundata*	Carey 1975
C. ricordi	Dominican Republic	cactus fruits	Carey 1975

[1] Items in diet are listed in approximate decreasing order of useage. Plant parts (leaves, fruits, etc.) are included when possible.

tained only small bits of unidentifiable trash. However, the only other gravid female dissected (9 June) contained an almost normal load of digesta throughout its gut. Whether or not it is reduced, normal feeding is apparently resumed immediately after the eggs are laid. A female nesting alongside the SW Blind during the morning of 6 June 1974 climbed into the nearest *Conocarpus* and began eating leaves immediately after her first emergence, shortly following oviposition. It is not known how much nest covering was accomplished within the burrow before she emerged. She fed for approximately 18 min (until 1208 hr) and retired to the shade to rest for the next 4 hr and 12 min. She then resumed the nest-covering process (see REPRODUCTION) for an additional 22 min before again moving to an area of partial shade to rest for the remainder of the day.

Cyclura carinata is surprisingly macrosmatic. Observations indicate that lizards are able to accurately orient toward an odoriferous food source without visual cues as to its location. Lizards frequently moved directly to a can of sardines obscured from view by leaves from distances exceeding 20 m. A few iguanas moved to the bait from 50+ m. This ability allows the lizards to take advantage of rich, temporal food sources such as fruiting trees, even if they lie outside the normal home range of the lizard.

When foraging, *Cyclura carinata* apparently supplements narial reception of olfactory stimuli by frequently tonguing the substrate. Norris (1953) and Carey (1975) observed similar behavior in *Dipsosaurus dorsalis* and *Cyclura pinguis*, respectively. The relative importance of taste versus smell was not investigated.

Auditory stimuli can also be very important in initiating feeding responses in *Cyclura*, providing that the sounds simulate the fall of a fruit. Lizards were observed to abruptly run to the site of a freshly fallen fruit of the seven year apple (*Casasia clusiaefolia*) based only on an auditory cue. Since the fruits of this species are edible by iguanas only for a short period before and after being dropped, the ability to utilize such cues is important if the resource is to be used. Fruits, stones, a wad of paper—essentially any small object—can be used to invoke this response simply by throwing them in such a way that they fall through the canopy to the substrate within hearing range of the lizard. The immediate response is an investigative charge to the site of the sound's origin.

ARBOREAL FEEDING.—*Cyclura carinata* is an extremely capable arboreal feeder. Lizards were frequently observed cropping fruits or flowers as they walked across the tops of bushes or trees at heights up to 5 m. Their climbing dexterity and integrative learning is exemplified by several lizards observed to depart from trees simply by moving distally along a branch until the lizards' weight caused the branch to bend down to the ground. The lizard could then step or drop deftly to the ground, allowing the branch to swing upward to its normal position. If disturbed while above ground, however, they typically jump to the ground and flee. Lizards leaped, apparently unharmed, from heights of up to 5 m when I disturbed them. Seasonal and daily variation in arboreal activity (including feeding) is discussed under ACTIVITY AND MOVEMENTS.

It is my subjective opinion that arboreality in *Cyclura carinata* is inversely related to wind speed. Considerably fewer lizards were observed in trees during periods of high winds. Unfortunately, objective data were impossible to obtain due to the complicated relationship of arboreality to all aspects of the weather (not simply wind), time of day, and season of year. The decreased ability to hear lizards during such periods of increased background noise is in part responsible for these observations.

Jackson (1974) observed lizards of the genus *Sceloporus* using periods of high sensory complexity (such as wind gusts) to shift perch sites. This behavior was not evident in *Cyclura*. In fact, the noise created by strong gusts of wind often elicited a fright response (running away).

Among other iguanines, *Brachylophus fasciatus* (Cahill 1970; Cogger 1974) *Conolophus pallidus* (deVries 1974), *Ctenosaura pectinata* (Alvarez del Toro 1972), *Ctenosaura similis* (Tamsitt and Valdivieso 1963; Alvarez del Toro 1972), *Cyclura collei* (Gosse 1848; Lewis 1944), *Cyclura cornuta* (Thomas Wiewandt and Peter Meylan, pers. comm.), *Cyclura cychlura* (Wilcox *et al.* 1973), *Cyclura nubila* (Lewis 1944; Buide 1951; Cooper 1958), *Cyclura ricordi* (Diderot Gicca and Thomas Wiewandt, pers. comm.), *Cyclura rileyi* (Stejneger 1903; Paulson 1966), *Dipsosaurus dorsalis* (Cowles 1946), *Iguana iguana* (Rand and Humphrey 1968; Alvarez del Toro 1972; Henderson 1974), *Sauromalus hispidus* and *S. varius* (Norris and Dawson 1964), *S. obesus* (Shaw 1945; Johnson 1965; Berry 1974; Prieto and Sorenson 1975a) and even *Amblyrhynchus cristatus* (deVries 1974) are all known to climb into bushes, trees, and/or cactus thickets, presumably to feed. Iguanine lizards probably exhibit arboreality wherever the vegetation permits it.

HABITUAL USE OF FEEDING SITES.—Upon locating a particularly attractive food source, *Cyclura carinata* will frequent the site up to several times a day and for several days. This was particularly the case when trees began fruiting. Two iguanas (always a male and a female) often both habitually fed at such sites. The energetic benefit of not having to continually search for new food sources, perhaps even of lower quality, bespeaks the adaptive advantage of this behavior.

In several cases the attractiveness of an habitually used food source was not apparent to me. I often observed lizards at the SW Blind to climb completely through a tree to reach a particular branch on which to feed. The site would be utilized until no leaves (or fruit) remained. The entire tree would then be abandoned as a food source. What distinguished those particular portions of the tree remains a mystery. Perhaps the quality of the food source is not as important as the certainty on the part of the lizard that it is not a toxic one (see discussion of toxicity versus seed predators in Janzen 1971, and Freeland and Janzen 1974).

Iguanas often frequented a food source until branches or even whole bushes were completely defoliated; small trees and bushes were even killed as a result of this heavy foraging. Considerable information on food species was accumulated by investigating these sites.

Social Feeding.—The possibility that social interactions can influence feeding behavior in lizards has only recently come under scrutiny. Greenberg (1976) recognized three basic types of interactions related to feeding: (1) social facilitation, (2) food-stealing, and (3) social learning. Behavior classifiable under the first category was frequently observed in *Anolis* and *Leiocephalus* on Pine Cay, but not in *Cyclura*. However, the common occurrence of more than one iguana feeding simultaneously in the same tree suggests the possibility of facilitation in *Cyclura carinata*.

Food-stealing behavior was noted several times in the field, but in each case the circumstances were not entirely natural. This behavior could sometimes be induced by throwing a food item in the vicinity of more than one lizard. The following observation (abbreviated and paraphrased from my fieldnotes) best illustrates this behavior:

> The brief fluttering of a ground dove shot with an air pistol for diet analysis attracted the attention of two resident males at the SW Blind on 2 August 1975. The bird had not only fallen to a point nearly equidistant from each lizard, but almost exactly in the middle of the zone of overlap of their respective home ranges. As Male #2 looked on, Male #8 moved to the carcass immediately and dragged it 3 m in the direction of his territory (in the shade). He immediately began feeding on the bird, consuming several mouthfuls of feathers. He finally removed the bird's head and, as he was manipulating it for swallowing, the remainder of the bird's body was temporarily ignored. At this time Male #2 bolted from his position 5 m away (in the direction of its territory), grabbed the carcass in his mouth, and headed back toward his territory with #8 in hot

> pursuit. Apparently afraid #8 would overtake him due to his burden, #2 dropped the bird's body in a sunny area near where it had originally fluttered. Number 8 immediately stopped short of the carcass, and #2 moved only 2.5 m farther before turning to posture laterally. Number 8, seeing #2 terminate his retreat and posture, then retreated to a point 2.5 m from the carcass and also postured. After approximately 1 min, #8 abruptly ran at the bird in an attempt to grab it and flee. However, a lunge by #2 prompted #8 to again retreat without the bird. Immediately #2 charged for the bird, #8 lunged at him, and #2 again retreated without the prey. Both lizards then maintained their postured positions on either side of the carcass for nearly 90 sec, when #2, apparently disinterested, slowly moved off. Once #2 was out of sight, #8 resumed feeding on the carcass.

Although food-stealing was never observed under completely unaltered natural conditions in *Cyclura carinata*, the ease with which it was induced suggests it is a naturally occurring phenomenon.

Behavior suggesting social learning (or imitation) in *Cyclura carinata* was not observed. Early in the study it was hypothesized that hatchling iguanas might learn arboreal behavior from conspecifics; however, newly emergent hatchlings were observed to climb extensively in bushes and trees long before they actually began feeding. Social learning seems to be of little importance in at least this behavior. Its role in other behaviors, especially the establishment and maintenance of a defended area, deserves further study.

Food related social behavior in lizards is unfortunately much more frequently observed than recorded. It is hoped that Greenberg's (1976) paper will provide the impetus for documentation of social feeding and its evolutionary implications to natural lizard populations.

DEFECATION.—Defecation characteristically occurs during morning hours following emergence and basking. Most defecations occurring at other times of the day also occurred following a basking period (see ACTIVITY AND MOVEMENTS). Presumably the body temperatures near the maximum preferred temperature range facilitate elimination of wastes. Since defecation typically follows the morning basking period the distribution of scats is not random. Feces are more abundant in the area of a lizard's preferred basking sites.

Defecating posture is typical of iguanid lizards (Carpenter 1966; Greenberg 1973); the body is elevated above the substrate by hind limb extension and the proximal portion of the tail is arched sharply upward and the distal portion arched downward to the substrate. A single fecal pellet is typically egested, but sometimes two are eliminated. Whether these discrete pellets represent different feeding periods in unknown.

Fecal analysis has frequently been used to determine diet in mammals (e.g. Ward 1970; Free *et al.* 1970; and Steward and Stewart 1970) and birds (e.g. Forschgen 1962). Among reptiles, scat analysis has chiefly been used in food studies of herbivorous tortoises (see bibliography in Douglass 1975; Hansen *et al.* 1976), carnivorous snakes (Fitch 1960, 1963; Platt 1969; among others), and insectivorous lizards (Fitch 1954, 1956; Hall 1972; among others). Except for Hansen's (1974) analysis for *Sauromalus*, scats have not generally been utilized for food studies of herbivorous lizards (Carey 1975). This is certainly a result of the potential unreliability of fecal analysis due to a lack of representation of the softer food items in the diet. However, many of the above listed studies have shown scatological analysis to be nearly as reliable as stomach analysis, at least for tabulation of food species and information on frequency of occurrence. Despite the disadvantages of relying on fecal examination to represent an animal's actual diet, the advantage of not having to sacrifice study animals remains. This is not only very important when studying a natural population, but it becomes more important as populations continue to decline to sizes potentially critical for their survival. Other than direct feeding observations, scatological analysis is the only feasible approach to the diet of herbivores facing extinction. The feces of *Cyclura carinata* are typical of the scats reported for other lizards, except in their larger size. The compacted oblong fecal pellets may occasionally exceed 75 mm in length and 20 mm in diameter for large males. After deposition, the pellets dry out rapidly and, depending on the amount of rainfall, can resist decomposition for months. Thus, great stores of dietary information are available to the student without risk of damaging natural populations.

NASAL SECRETIONS.—*Cyclura carinata* frequently expel fluids from the nostrils in a sneezing manner similar to that described for *Amblyrhynchus cristatus* by Schmidt-Nielsen and Fange (1958), *Brachylophus fasciatus* by Cogger (1974), *Dipsosaurus dorsalis* by Norris and Dawson (1964), *Cyclura cychlura* by James B. Murphy (pers. comm.) and *Cyclura pinguis* by Carey (1975). Although no analysis of the expellent was made, it is presumably a secretion of the nasal salt gland functioning as an accessory kidney, mainly for potassium excretion as in several other iguanine lizards: *Ctenosaura pectinata, Dipsosaurus dorsalis, Iguana iguana, Sauromalus hispidus, S. obesus,* and *S. varius* (Schmidt-Nielsen and Fange 1958; Schmidt-Nielsen *et al.* 1963; Templeton 1964, 1967; Norris and Dawson 1964). High concentrations of salt ions (notably potassium) in the diet of these herbivorous lizards (including *Cyclura*) and the general unavailability of free water in their respective habitats make extrarenal salt secretion necessary for survival in physiologically xeric habitats. *Cyclura carinata* were never observed to drink fresh water (from lakes or rain pools) in nature, but they frequently did in the outdoor observation enclosure in Gainesville. No physiological explanation for this behavior is offered.

SEED PREDATOR OR DISPERSER?—The importance of *Cyclura carinata* as a seed predator and/or seed disperser is unknown. Aspects of this problem are under investigation by Walter Auffenberg. I have on numerous occasions failed to completely dry fecal samples before packaging them and have found, on laboratory examination several days later, that seeds had germinated. My subjective impression is that the seeds of *Coccoloba* were the most frequent germinators. Whether traversing an iguana's digestive tract increases or reduces seed viability in *Coccoloba* or in any other species awaits testing. Without study, it should never be flatly assumed that seeds from a particular species are so adapted to seed predation that their fitness is ultimately increased (Janzen 1976). The actual effects of seed eating by *Cyclura* on the survival rates of plant species cannot be known until increases or decreases in fitness for seeds passing through the vertebrate digestive tract are determined and then related to the advantages of dispersal. It must also be remembered that dispersal, even of eaten seeds with considerably reduced germination success, can still be advantageous to that species' survival (see Janzen 1971). Further discussion of herbivory as an adaptive strategy in *Cyclura* appears in Auffenberg (MS).

DIGESTIVE EFFICIENCY

Although this aspect of feeding was not investigated, certain observations relative to previous work are pertinent. Digestive efficiencies (relating ingested and egested caloric content) of carnivorous lizards are known to vary from about 70 to 90 percent (Table 16). Herbivorous lizards have as yet been poorly studied. Szarski (1962) suggested that perhaps only a small amount of the energy potentially available in the food is utilized by herbivorous lizards. Throckmorton (1973) has reported digestive efficiencies similar to those of carnivorous lizards from *Ctenosaura pectinata* fed sweet potato tubers. However, Minnich (1970), Nagy and Shoemaker (1975), and Harlow *et al.* (1976) found lower digestive efficiencies for *Dipsosaurus dorsalis* fed natural diets (mainly leaves), fed natural vegetation, and force-fed commercial rabbit food, respectively. Nagy and Shoemaker (1975) obtained similar results with *Sauromalus obesus* fed natural vegetation.

TABLE 16.—APPARENT DIGESTIBILITY COEFFICIENTS (ADC) OF LIZARDS, WHERE ADC = (CALORIES CONSUMED — CALORIES OF FECAL WASTE) x (100)/CALORIES CONSUMED.

Species	ADC (in %)	Food	Source
Anolis carolinensis	54.4 88.9 69.5	*Tenebrio* adults *Tenebrio* larvae crickets	Licht & Jones 1967
Dipsosaurus dorsalis	30-70*	natural diets	Minnich 1970 Porter *et al.* 1973
Sceloporus grasiosus and *S. occidentalis*	83	*Tenebrio* larvae	Mueller 1970
Ctenosaura pectinata	86.3 (77.8-94.0)	Sweet potato tubers (*Ipomoea*)	Throckmorton 1971, 1973
Lacerta vivipara	89 (84-91)	*Tenebrio* larvae	Avery 1971
Anolis carolinensis	69.9-72.2	*Tenebrio* larvae	Kitchell & Windell 1972
Crotaphytus wislizeni *Cnemidophorus tigris* *Uta stansburiana*	77.8-78 79.8 83.5-85.8	natural diets	Essghaier & Johnson 1975
Dipsosaurus dorsalis	57	natural vegetation (flowers)	Nagy and Shoemaker 1975
Sauromalus obesus	56	natural vegetation	Nagy and Shoemaker 1975
Sceloporus olivaceus	83.5	crickets	Dutton *et al.* 1975
Dipsosaurus dorsalis	54.3 @ 33°C 62.8 @ 37°C 69.5 @ 41°C	commercial rabbit food	Harlow *et al.* 1976

*Method of calculation of digestive efficiency was not indicated.

Cyclura carinata (for that matter, most herbivorous lizards) probably do not have such an easily digestible food source as sweet potato tubers readily available in nature. Like *Dipsosaurus*, many of these herbivores must rely for at least parts of the year on a diet of leaves that are fibrous and difficult to digest. Although Rand (1979) believes *Iguana iguana* is an efficient folivore, ingested leaves often pass through the entire gastrointestinal tract of *Cyclura carinata* intact. This is perhaps related to the more xerophytic nature of the vegetation in areas inhabited by *Cyclura*, as well as the more modified colon of *Iguana* (Iverson 1979). In any case, I support Szarski (1962) in my belief that digestive efficiencies in at least the herbivore *Cyclura carinata* (in natural populations) are probably lower than those of carnivorous lizards, and comparable to those found for *Dipsosaurus* and *Sauromalus*.

Another aspect of digestive efficiency which has received almost no attention is whether the massive "caecal" nematode faunas found in at least all iguanines contribute to the efficiency of cellulose digestion or have some other as yet unsuggested effects (favorable or deleterious). If nematode faunas are advantageous, the septa found in the colons of iguanines (Iverson 1979) would not only be adaptive in increasing relative absorptive surface area, but also in providing pockets in which those faunas can proliferate. Nematodes residing in these colic microhabitats are not as subject to egestion due to the peristaltic flow of digesta, as would be the case in the unpartitioned colon. Whether large nematode faunas evolved with, or in response to, colic modification in iguanine lizards remains unanswered. I believe that worm burdens in virtually all *Cyclura carinata* are too great for their effects to be detrimental and suspect a beneficial effect (see INTERSPECIFIC COACTIONS). The role of the intestinal microflora and fauna in lizard digestion is completely unknown. Microbial fermentation products may be as important to nutrition in herbivorous lizards as they are to nutrition in herbivorous birds and mammals (see review in McBee 1971).

FAT BODIES

Abdominal fat storage is typical not only of all temperate reptiles but also occurs in at least those tropical species inhabiting seasonally fluctuating environments. Some tropical forms from areas lacking seasonality (physical or biotic) do store fat in abdominal vesicles (Berry and Lim 1967; Smith 1968), while other species apparently do not (Church 1962). Many studies have been conducted on lipid deposition and utilization in reptiles, most of which have suggested that deposition is negatively correlated with gonadal activity (Dessauer and Fox 1959; Tinkle 1962; Hahn and Tinkle 1965; Smith 1968; Telford 1970; Aleksiuk and Stewart 1971; Minnich 1971; Goldberg 1972; Jameson 1974; among many others). However, a few studies have commented on the mobilization of lipids for maintenance metabolism, especially during hibernation (Dessauer 1955; Mueller 1969; Telford 1970). Stored lipids (particularly those in abdominal vesicles) are probably mobilized to some extent both for reproduction and maintenance (notably during hibernation), as in *Sceloporus graciosus* (Derickson 1974), *Cnemidophorus tigris* (Gaffney and Fitzpatrick 1973), and *Takydromus tachydromoides* (Telford 1969). This seems to be the case in *Cyclura carinata*, which does not hibernate, but nevertheless must considerably reduce its winter activity due to decreased temperatures (see ACTIVITY AND MOVEMENTS).

Abdominal fat body size shows a generally bimodal seasonal fluctuation in *C. carinata* (Table 17). Minimum levels are attained in

TABLE 17.—SEASONAL PROPORTIONATE FAT BODY WEIGHTS (.01 GM/MM SVL LENGTH) FOR *Cyclura carinata*.

	January 1	March 5	Apr. 30 - May 10	June 1-15	June 15 - July 15	Aug. 7 - Sept. 15	December 1 - 15
Mature Males							
Mean	7.08±3.56	24.1	29.6	4.90±1.56	6.73±7.53	15.98±2.74	22.53±15.71
Observed range	3.2 - 10.2			3.8 - 6.0	0.08 - 17.0	13.13 - 18.6	4.4 - 32.0
Sample size	N=3	N=1	N=1	N=2	N=5	N=3	N=3
Mature females							
	12.54±6.45	13.3	2.82	1.15±.92	4.28±5.22	9.85±1.40	14.65±11.67
	8.2 - 21.95		2.19 - 3.45	0.5 - 1.8	0.6 - 12.0	7.8 - 10.8	6.4 - 22.9
	N=4	N=1	N=2	N=2	N=4	N=4	N=2
Immature							
	8.06±4.15	11.78±1.67	1.65	1.79±1.18	2.15±2.19	4.23±4.49	7.78±9.26
	3.6 - 14.6	6.6 - 12.96	1.5 - 1.80	0.5 - 3.35	0.6 - 3.7	1.05 - 7.4	1.0 - 22.0
	N=5	N=3	N=2	N=4	N=2	N=2	N=6

January and June; maximum levels in March (or April?) and November (?) or December. Comparison of the fat body cycle with the reproductive cycle (Table 4, Figs. 16 and 17) reveals the expected negative correlation between fat body size and gonadal activity during spring and summer. Both sexes exhibit this relationship, although for obviously different reasons: females for egg production and males for increased activity associated with mating and territorial defense. Following the nesting season fat body reserves increase to maximum in late fall. Late December and January bring a decrease in fat body size, probably as a result of decreased activity related to environmental conditions. However, it may also be in part due to decreases in quantity and quality of available food resources. A second increase in lipid deposition in the fat bodies apparently occurs in February prior to reductions related to gonadal activity. This phenomenon of a second peak in fat storage has previously been reported among the reptiles only in the montane lizard, *Sceloporus graciosus* (Jameson 1974). It is certainly due to the existence of a period of activity (including feeding) early in the year at a time between the winter period of reduced activity and the spring period of vitellogenesis. Due to selection for early clutches, most lizards lack a spring activity period before vitellogensis, and their fat bodies therefore necessarily decrease from a prehibernation maximum continually and regularly through hibernation and vitellogenesis to a post-oviposition minimum. It should be pointed out that for *Cyclura carinata* maximum adaptive value does not lie in production of the earliest possible clutch following the winter season as in most temperate species; clutch deposition is cued by early summer rains that guarantee an energy-rich food supply for emerging hatchlings in September (see REPRODUCTION). More temperate species without a late winter period for the accumulation of extra energy must leave hibernation with vitellogenesis in full progress. thus precluding the possiblity of increasing lipid reserves prior to vitellogenesis.

Food As a Limiting Factor

The limiting effects of food supply on animal population numbers have received considerable discussion and experimentation (Lack 1954; Windberg and Keith 1976; and others). Several demographic features of *Cyclura carinata* populations suggest that food availability is one of the more important factors limiting population numbers and densities of this species.

Reproductive success has been shown to be related to food availability (usually as represented by rainfall) in several lizard species (Mayhew 1965, 1966a, 1966b; Zweifel and Lowe 1966; Hoddenbach and Turner 1968; Pianka 1970b; Vinegar 1975; and review in Mayhew

1968); populations of *Sauromalus obesus* are known not to reproduce at all during particularly harsh years (Nagy 1973). Increased reproductive rates with increased food supply in birds and other animals have also been discussed (Lack 1954). That the same relationship is true of *Cyclura carinata* is evidenced by the substantially higher fecundity of well-fed captive lizards (see REPRODUCTION). Fat reserves in these captives were also considerably greater and oscillated with much less amplitude than in field animals (see Fat Bodies, this chapter). The apparent failure of these lizards to fulfill these higher reproductive potentials in the field suggests that insufficient food resources (in quantity and/or quality) are imposing some restraint on fecundity.

Since body size in *Cyclura carinata* is directly correlated with fecundity, growth rate is ultimately related to reproductive success, and therefore, population levels. Any restriction of growth rate should reduce fecundity. Case (1976) showed that *Sauromalus obesus* in habitats with more diverse and abundant food resources grew faster than those in less productive environments. By artifically supplementing the diet of *Anolis* in the field, Licht (1974) has shown that natural growth rate and energy storage are probably limited by insufficient food. Andrews (1976) has even suggested that most island anoles are probably food limited. The same may be true of *Cyclura*, at least on the smaller islands inhabited, and certainly deserves further study. *Cyclura carinata* is unquestionably capable of much more rapid growth and energy storage in captivity (with unlimited food) than in the field (see GROWTH). This again suggests that food may limit population increase via its direct effects on growth.

Several herbivorous iguanine species show considerable sexual size dimorphism (see Table 7). Although this dimorphism may have evolved in response to strong sexual selection, I believe additional selective advantage to *Cyclura carinata* may lie in reducing intraspecific competition for limited food resources (see discussion by Wilson 1975:334).

Perhaps the strongest support for food limitation comes from the territorial behavior exhibited by adult males throughout the year. Dominant males probably defended territories to guarantee priority of access to (1) food and (2) females; access to both of these resources was restricted for subdominants. If access to food was not important, defense might be expected to coincide only with the breeding season. Since it was maintained year-round, and since most feeding occurred within this defended area, I believe that these areas were primarily feeding territories (see SOCIAL ORGANIZATION). Simon (1975) has demonstrated this to be the case in *Sceloporus jarrovi*, in which food abundance was inversely correlated with territory size. Unfortunately sample sizes made it impossible for me to make analogous comparisons in *Cyclura*; however, iguana density was found to vary directly with diversity and abundance of vegetation (i.e. potential food sources) in occupied habitats (see DENSITY AND DEMOGRAPHY). Furthermore, two areas on Pine Cay, where abundant unnatural supplemental food was available, supported local densities higher than any other place in the study islands. These were the island's refuse dump and a garden not far from the SW Blind (generally unsuccessful due to decimation by the abundant iguanas).

This evidence all suggests that food availability is extremely important in regulating population size and/or growth in *Cyclura carinata*. It is quite possible that food may be limiting to this species for only part of the year. Rand (1979) suggested the same possibility for *Iguana iguana* in highly seasonal habitats in the neotropics. For *Cyclura* during the winter, food resources are not only restricted to items more difficult to digest (see Digestive Efficiency) and of less quality energetically (Auffenberg, pers. comm.), but environmental temperatures may physiologically limit the effectiveness of the lizard's use of those resources which are available (see Harlow *et al.* 1976). Furthermore, even during optimal times of the year, i.e. when fruit may be temporarily super-abundant, lizards can eat and assimilate only so much. They may thus only be able to use but a small portion of the energy that is abundantly available at such times. The importance of these factors in predator-prey relations deserves further investigation under natural conditions.

HERBIVORY AS A FEEDING STRATEGY

Since Szarski's remarks on lizard herbivory in 1962, interest in and controversy concerning the evolution of this feeding strategy among lizards has escalated. Only a "dozen or so" lizard species were known to be herbivorous at that time (Ostrom 1963). Nearly 90 species are now known to feed at least occasionally on herbaceous material; about 60 of these (including all 30 members of the subfamily Iguaninae) are known to be primarily herbivorous.

A survey of the literature indicates that, among the extant lizards, at least 6.0% (19) of the species of the Agamidae, 7.9% (44) of the Iguanidae, 1.9% (4) of the Teiidae, 2.4% (4) of the Lacertidae, 1.6% (11) of the Scincidae, 33% (4) of the Xantusiidae, 6.4% (3) of the Cordylidae, and 0.3% (2) of the Gekkonidae are known to take plant matter.

Speculations on the adaptive relationships of an herbivorous feeding strategy in lizards have been numerous (Szarski 1962; Ostrom 1963; Sokol 1967; Pough 1973; Rand 1979). Unfortunately, an understanding of the mechanisms involved in the evolution of herbivory in lizards must necessarily await investigation of the many involved components. Among these are: (1) the relationships of the gastrointestinal flora and fauna to digestion; (2) digestive efficiencies for natural dietary materials and the energies available from those materials: (3) ability of lizards to detoxify secondary compounds; (4) relationships of ion and water balance to diet; (5) relationships of temperature (and hence metabolism) to the above; (6) the functional anatomy of the feeding apparatus (Throckmorton [1976] provides an excellent example); (7) actual predation pressures and intra- and interspecific competition; (8) ontogenetic and seasonal dietetic variation; (9) the effects of habitat productivity on 8; and (10) diet versus reproductive output.

Many of these components should not be difficult to pursue; hard data are badly needed. Auffenberg (MS) focuses attention on some of these previously neglected subjects for *Cyclura carinata*.

ACTIVITY AND MOVEMENT

LOCOMOTION

Although primarily terrestrial, *Cyclura carinata* are adept arboreal lizards. Climbing is commonly used to secure food (see discussion of Arboreality under FOOD AND FEEDING), as well as for thermoregulation (Auth, in preparation; pers. observ.). Lizards of all ages can climb. Hatchlings less than two weeks old were frequently observed climbing in *Erithalis* bushes to heights of 1.5 m. They had not yet begun feeding.

Natural aquatic activity in *Cyclura carinata* was never observed during this study. *Cyclura collei* (Hill, *in* Gosse 1848), *C. cornuta* (Noble 1923), *C. nubila* (Hardy 1956; Lando and Williams 1969) and *C. pinguis* (Carey 1975) are the only members of the genus known to enter freshwater, usually as a means of escape. However, Cuban fishermen claim that *C. nubila* swim between islands and the mainland of Cuba (Buide 1951). *Iguana iguana* (Swanson 1950, among others) is the only other iguanine lizard (exclusive of the marine iguana, *Amblyrhynchus cristatus*) which commonly uses water as an escape route. Alvarez del Toro (1972) has even observed *Iguana* at night "sleeping" under water.

Cyclura carinata could be made to enter the sea only if strongly pressed and then only if no other retreat was available. Once in the water, the body was typically inflated so that the lizard floated on the surface. If pursued further, it would attempt to "swim" away using serpentine body and tail undulations. The limbs were not used and trailed posteriorly along the body. This behavior rarely lasted more than three to five seconds. On several occasions, iguanas were carried into the water in order to observe aquatic behavior. The behavior was always that described above; as a result of body inflation, no lizard attempted to escape by submerging. When carried distances of 10–30 m out from shore and watched from below the water, *C. carinata* showed no inclination to return to land. They simply floated with the surf out to sea. The length of time these lizards can remain inflated and thus avoid drowning is unknown. This mechanism could potentially be important to dispersal, especially under hurricane conditions, and deserves further study.

RETREATS

Hollows in trees are known to be used as retreats by *Cyclura carinata* (present study, occasionally), *Cyclura collei* (Gosse 1848), and *Cyclura ricordi* (Gicca, pers. comm.); natural cavities (honeycomb limestone, rock crevices, crab burrows, etc.) are used by *C. carinata* (Cochran 1934; present study, occasionally), *C. cornuta* (Klingel 1929; Grant 1944; Wiewandt 1977), *C. cychlura* (Bailey 1925; Rabb and Hayden 1957; Carey 1975; Auffenberg, pers. comm.), *C. nubila* (Grant 1940b; Hardy 1956; Carey 1966), *C. pinguis* (Carey 1975); *C. ricordi* (Carey 1975), and *C. rileyi* (Cochran 1934; Carey 1975). Only *Cyclura carinata* (present study), *C. cornuta* (Noble 1923; Carey 1975), *C. nubila* (Hardy 1956, occasionally), *C. pinguis* (Carey 1972, 1975, occasionally); and *C. ricordi* (Noble 1923; Carey 1975) in this genus are known to completely excavate their own retreat burrows. Whether natural cavities or self-constructed burrows are used as retreats most likely depends on the physiography of the inhabited region; soils substantial enough for burrowing are often unavailable in some areas, and natural cavities often absent in others.

Cyclura carinata subadults and young adult males show little allegiance to a particular retreat. However, as adults, the older and, in the case of males, the more dominant they become, the greater retreat tenacity they exhibit.

HOME RANGE

Although the concept and measurement of an animal's home range has received extensive treatment and review, no method or model has received universal support or useage (for literature review, see Davis 1953; Kaufmann 1962; Jewell 1966; Southwood 1966; Jennrich and Turner 1969; Burge and Jorgensen 1973; Van Winkle 1975). Several studies have considered the subject of home range specifically in lizards (Stebbins 1944; Milstead 1961, 1970; Jorgensen and Tanner 1963; Tinkle 1967a; Tinkle and Woodward 1967; Tanner and Hopkin 1972). Most of the techniques for calculating home range size are based on isolated recapture or resite records. Only a few studies have utilized direct continuous observations in delineating home ranges. This is especially true among lizard species (Irwin 1965; Rand 1967b; Tinkle 1967b; Andrews 1971; Berry 1974; Mackay 1975). The advantages and disadvantages of this direct method are aptly discussed by Adams and Davis (1967) and Mackay (1975). My observations on home range in *Cyclura* are based either on direct observation or on maps of activity as recorded by tracks in the sand.

I define home range, or activity range, for *Cyclura carinata* as the area most frequented during a year's activity. This definition is fundamentally the same as Kaufmann's (1962) "core area." There is an area within which an iguana spends most of his time during a yearly cycle. The great majority of all activities are performed within this core area. However, lizards do make forays outside of this most-frequented area for food as well as other resources. Temporary high quality food resources (flowering of fruiting plants, for example) frequently lure them from their normal activity ranges. This made baiting successful in attracting lizards for marking and observation. Because of these extra-core area activities, lizards are familiar with the neighboring habitat and its occupants. The lizards' knowledge of locations other than their own burrows has previously been discussed (see HABITAT, Burrows). Since these burrows may occasionally offer the only route of escape available to a lizard, this information is important.

Home range size was determined from plots of observed movements during 34 days of observation at the SW Blind (on five trips) from June 1974 through August 1975. Area of the home range was calculated only for those lizards with the most complete movement records (Figs. 39 and 40). Home ranges for six dominant males (286-308 SVL) at the SW Blind averaged 0.159 ± 0.050 ha (0.103-0.248); five subdominant males (254-267 mm SVL) averaged 0.126 ± 0.041 ha (0.070-0.187); and four adult females (203-238 mm SVL), 0.098 ± 0.019 ha (0.078-0.118). Home range size among these lizards was significantly positively correlated with body size (Fig. 41). This was expected in light of similar interspecific correlations previously found for birds (Armstrong 1965; Schoener 1968), mammals (McNabb 1963), and terrestrial lizards (including *Sauromalus obesus*; Turner *et al.* 1969); however, the home range of *Cyclura carinata* was not even 1 percent of the area predicted by the body weight-home range correlation of Turner *et al.* (1969). Perhaps this correlation is only significant within specific trophic groups (i.e. frugivores, granivores, insectivores, etc.) for lizard species.

Auth (MS) calculated home ranges for four adult males (1.51 to 1.87 kg) in an area of Dense Scrub on Water Cay at between 0.233 and 0.379

ha. These home range sizes are larger than those at the SW Blind because the lizards are generally smaller and density is higher. and the habitat more productive at the latter site. Home range size for three additional adults living near the SW end of Pine Cay in a sparsely vegetated open scrub habitat was very accurately determined from plots of their movements as recorded by tracks in the sand. Calculated home ranges were 0.0943 ha (male, 260 mm SVL), 0.0895 ha (male, 257 mm SVL), and 0.0672 ha (female, 200 mm SVL). These values are low in comparison to those at the SW Blind. Higher values should be expected in this poorer habitat, since intuitively a greater area would be necessary to provide equivalent amounts of food energy. However, in this extremely open sandy habitat the food sources are distinctly clumped, and lizards usually excavate their burrows amid this vegeta-

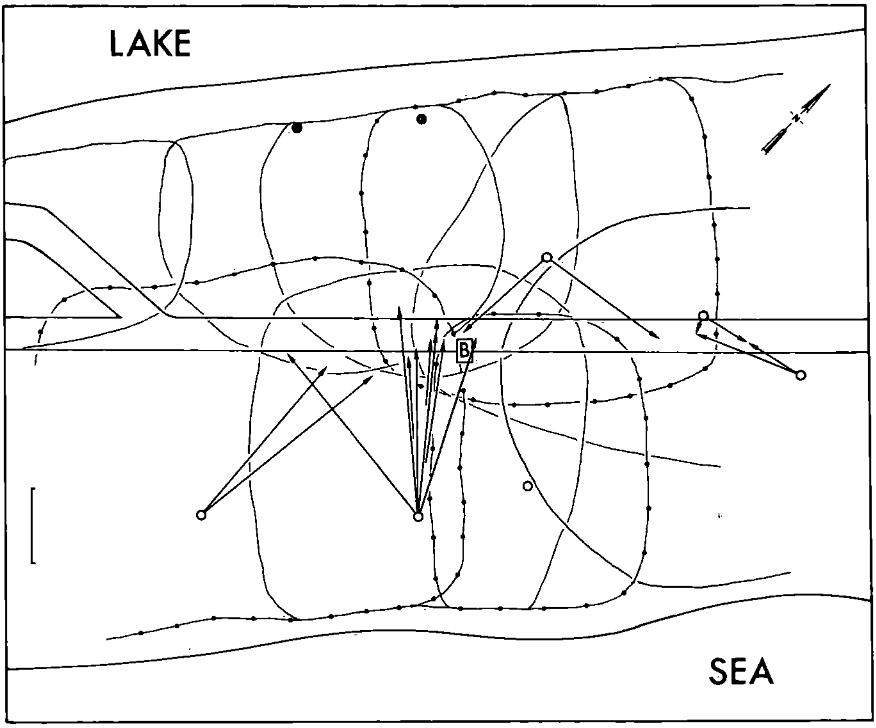

FIGURE 39.—Home ranges of dominant territorial males near SW Blind (B) from June, 1974, through August, 1975. Some home range perimeters are marked with dots for visual clarity. Open circles mark known retreat locations; solid circles are approximate locations of retreats in honeycomb of rocks along lake cliff. Arrows mark sites of active territorial defenses in respect to site of resident's retreat (source of arrow). Each arrow represents at least one defense. Scale at left measures ten meters.

tion. (Lizard densities are also lower.) Therefore, movement beyond the nearest patch of food is usually unnecessary.

Another estimate of adult home range size was obtained in June 1976, along a portion of a 950 m sand spit on Little Water Cay (Fig. 5). This peninsula has formed since 1967 by a redeposition of sand, as the northern point of the island is being eroded away. The vegetation is sparse and composed entirely of psammophilous, primary successors (*Uniola, Scaevola, Ernodea, Chamaesyce, Cenchrus,* etc.). Adult male lizards have colonized the spit as fast as it has formed. Lizard burrows are located along the main axis of the spit where altitude is greatest (but nowhere over 2 m above mean sea level). The mean distance between large active (presumably male) burrows was 43.83 ± 16.28 m (range 30.7–87.8; 16 measurements). However, the two longest interburrow distances (87.8 and 82.7 m) each are nearly twice the average remaining recorded distances. Perhaps the lack of an active burrow

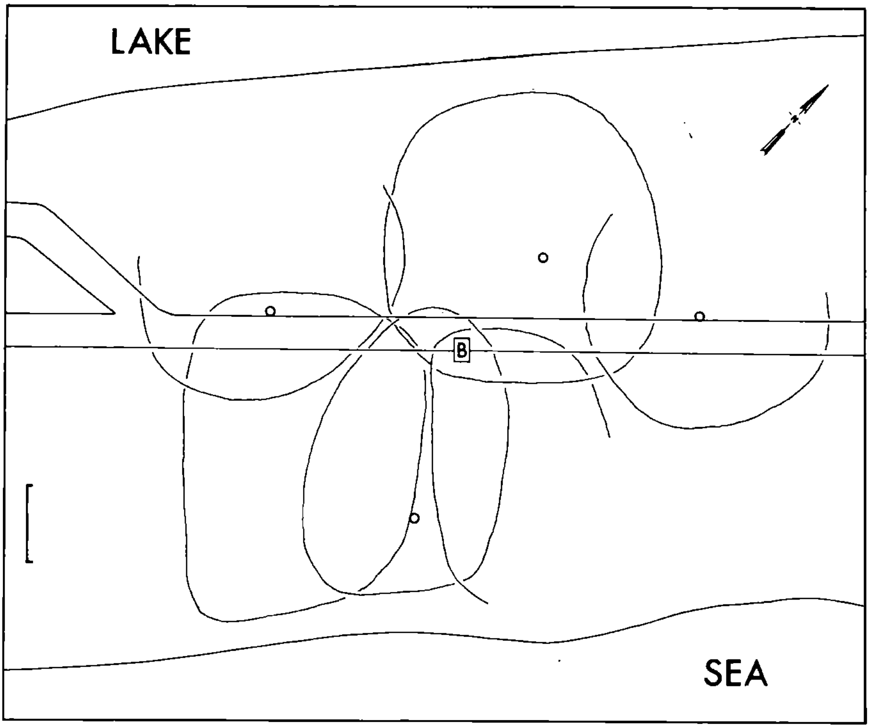

FIGURE 40.—Home ranges of adult females near SW Blind (B) from June, 1974, through August, 1975. Open circles mark burrows of females utilizing only a single retreat. Scale at left measures ten meters.

somewhere near the middle of these lengths indicates the death or emigration of a former occupant of the area, with subsequent destruction of his burrow. If these two measurements are omitted, the recalculated mean interburrow distance is 37.93 ± 4.73 m (range 30.7–48.3; N = 14 measurements). At the SW Blind the mean interburrow distance for males was 26.6 ± 6.9 m (13 measurements). If these same averages are considered approximately equal to the average diameter of male home range, areas of 1129.94 m^2 and 555.72 m^2 are indicated for the sand spit and SW Blind study areas, respectively. This method obviously underestimates male home range size, since it assumes no overlap of male ranges. However, it does suggest that

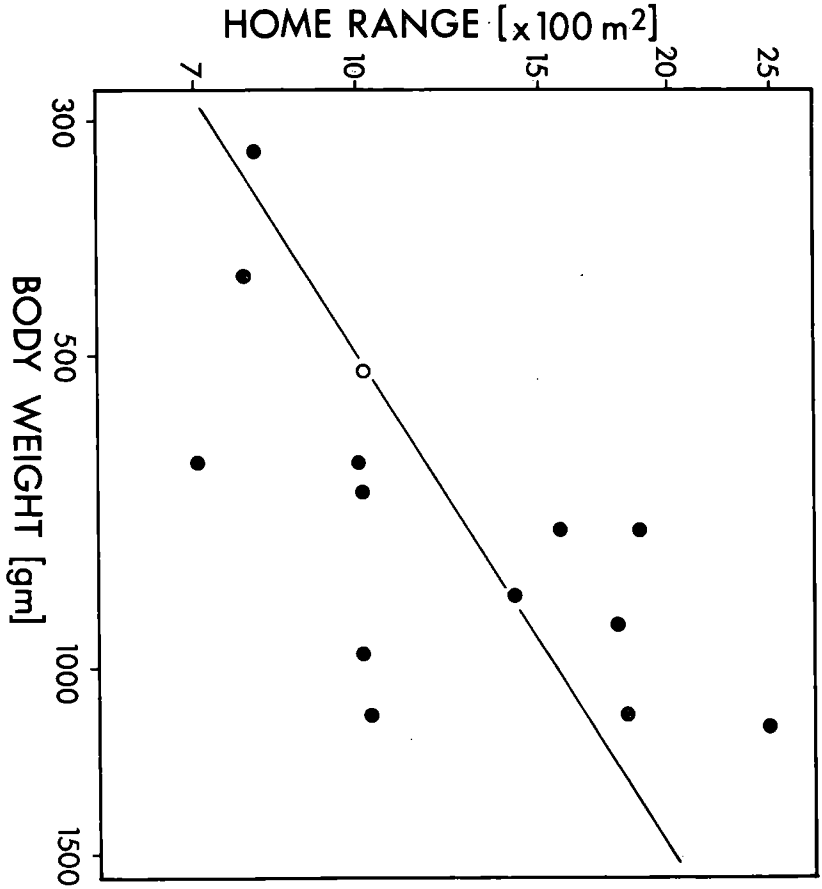

FIGURE 41.—Relationship of home range size to body size in adult *Cyclura carinata* at SW Blind (open circle denotes two individuals). The four lightest lizards are females; the rest are males. Least squares regression of log-log plot is significant ($p = 0.01$); Home range = $19.23\text{weight}^{0.635}$.

home range sizes on the spit are at least twice those at the SW Blind. This is certainly related to the lower lizard density on the sand spit due to its extremely low productivity and dispersed resources. Tinkle and Woodward (1967) found a similar inverse relationship between density and home range size in the lizard *Uta stansburiana.*

Movement and activity data for only a single juvenile lizard were complete enough to allow home range size determination (Fig. 42). Between hatching and seven months of age, this lizard maintained an activity range of 118.9 m^2. Although data from additional juveniles less than one year of age were fragmentary, they support this figure as representative of lizards of this age group. Home range data for subadult lizards greater than one year of age were very inconclusive. The lizards apparently show little philapatry. Juveniles frequently appeared near the SW Blind only to disappear after one to several days in the area. Although feral predators are at least in part responsible for this disappearance, I believe most of these juveniles were transients. The area covered during a year's activity probably greatly exceed that of most adults. This is possible since the social structure permitted complete freedom of juvenile movement (see SOCIAL ORGANIZATION).

Of the few species of iguanines for which data are available, only *Cyclura pinguis* is reported to utilize smaller adult ranges that *Cyclura carinata* (Table 18). However, home range size for *Cyclura pinguis* was determined from sightings during only a 5-week period (Carey 1975), and the values probably greatly underestimate areas inhabited during the entire year. Although *C. carinata* are slightly larger than *Sauromalus obesus*, the latter's home range is over ten times as large. Additional data both on activity range size and habitat productivity are sorely needed if meaningful comparisons among the iguanines are to be made.

Male home ranges overlapped broadly, as did those of females (Figs. 39 and 40). Although a female's home range was usually centered within a single dominant male's, they sometimes overlapped the ranges of more than one. Subdominant male home ranges overlapped those of dominant males, and tended to be centered in areas where the ranges of dominant males overlapped (i.e. away from the center of a dominant male's activity).

ACTIVITY CYCLE

SEASONAL PATTERNS.—Initiation and termination of daily activity in *Cyclura carinata*, as evidenced by times of burrow emergence and submergence, show considerable seasonal variation (Table 19). Average emergence times in early December, early April, and June-

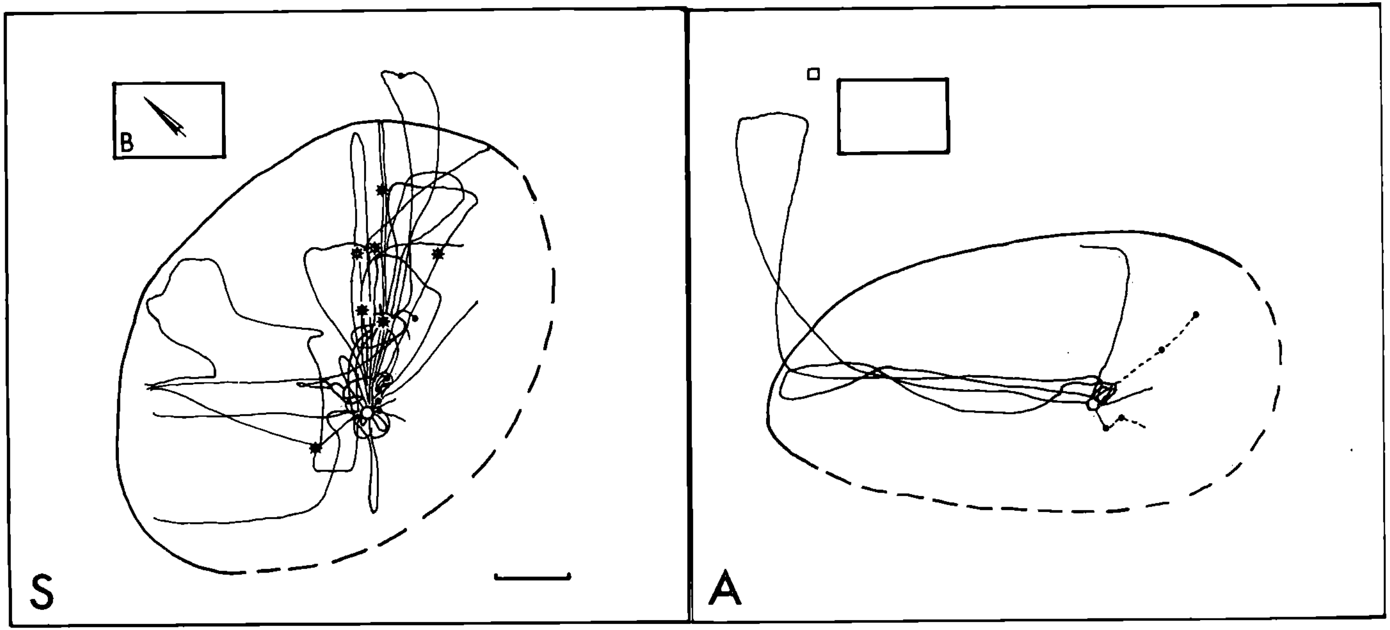

FIGURE 42.—Home range and movements of juvenile lizard in September, 1974 (S) at age 1 month (five days data) and in April, 1975 (A) at age 7 months (four days data). Approximate home range is encircled, broken perimeter indicates questionable limits. Scale (bar = two meters) and orientation (arrow points south) are the same in both diagrams. Open circle marks retreat; small solid dots and connected dashed lines indicate arboreal movement. Stars designate sites of defensive encounters with intruders. April foray outside home range is a result of bait (small box) near Blind (B).

TABLE 18.—HOME RANGES OF IGUANINE LIZARDS.

Species	Location	Juveniles	Adult	Authority
Ctenosaura pectinata	Morelos, Mexico	—	122.7*	Evans 1951
Ctenosaura similis	Belize	—	19.6*	Henderson 1973
Cyclura carinata	Caicos Islands Britist West Indies	1.19 (--; 1)	M(s) =12.6 (7.0-18.7; 5) M(D)=15.9 (10.3-24.8; 6) F = 9.8 (7.8-11.8; 4)	This study
Cyclura pinguis	Anegada British Virgin Islands	—	M = 5.5 (1.2-9.9; 5) F = 2.8 (1.6-4.1; 5)	Carey 1975
Dipsosaurus dorsalis	Arizona	6.2 (--; 25)*	—	Parker 1972
Dipsosaurus dorsalis	California	—	M =14.6 (2.0-43.7) F =15.6 (2.2-42.4)	Krekorian 1976
Iguana iguana	Belize	3.24 (0.4-12.1; 14)	—	Henderson 1974
Sauromalus obesus	California	—	M =57 (---; 8) F =17 (---; 5)	Johnson 1965
Sauromalus obesus	California	—	M =107 F = 67	Schallenberger 1970 (in Berry 1974)
Sauromalus obesus	California	—	M = 20 (---; 7) F = 17 (---; 4)	Nagy 1973
Sauromalus obesus	California	M=98 (85-150; 11) F=72 (61-110; 7)	M =190 (100-330; 22) F = 81 (40-160; 14)	Berry 1974

NOTE: Areas in ares (100 ares = one hectare). Ranges and sample sizes in parentheses. Asterisk indicates area of circle calculated from published recapture radii or longest movements (diameters). Data for dominant (D) and subdominant (s) male *Cyclura carinata* are presented separately.

TABLE 19.—SEASONAL DATA ON TIME (EST) OF INITIATION AND TERMINATION OF DAILY ACTIVITY IN *Cyclura carinata*.

	SPRING (March 5 - April 12)	SUMMER (June 4 - Aug. 5)	WINTER (Nov. 27 - Dec. 21)
MORNING			
Earliest records of activity	$\bar{X}$=0829.9±32.9 0725-0939 N=13	$\bar{X}$=0749.1±28.2 0710-0850 N=25	$\bar{X}$=0931.5±17.0 0910-0950 N=8
Emergence witnessed	$\bar{X}$=0911.1±61.3 0758-1052 N=11	$\bar{X}$=0753.0±43.9 0640-0920 N=28	$\bar{X}$=0937.6±38.1 0852-1100 N=10
Combined	$\bar{X}$=0848.8±51.0 0725-1052 N=24	$\bar{X}$=0751.2±37.0 0640-0920 N=53	$\bar{X}$=0934.8±29.9 0852-1100 N=18
AFTERNOON			
Latest records of activity	$\bar{X}$=1609.6±22.5 1530-1654 N=15	$\bar{X}$=1704.7±13.1 1645-1722 N=6	1536.5±20.5 1514-1600 N=4
Submergence witnessed	$\bar{X}$=1618.8±55.4 1527-1710 N=4	$\bar{X}$=1724.1±44.7 1600-1825 N=14	1505 — N=1
Combined	$\bar{X}$=1611.2±30.8 1527-1710 N=19	$\bar{X}$=1718.3±38.7 1600-1825 N=20	$\bar{X}$=1530.2±22.7 1505-1600 N=5

NOTE: Mean times are followed by one standard deviation in minutes, observed range, and sample size.

July were 0930, 0849, and 0751 hr, respectively. Corresponding submergence times were 1530, 1611, and 1718 hr. Lizards were never active before sunrise or after sunet. Time of extra-burrow activity averaged only 5 hr 55 min during the winter, 7 hr 22 min during the spring, and during summer 9 hr 27 min.

A bimodal diurnal activity cycle is exhibited by *Cyclura carinata* during the warmer parts of the year (Fig. 43); lizard activity is typically reduced during high midday temperatures. *Cyclura cychlura* (Wilcox *et al.* 1973) and *C. nubila* (Carey 1966) also demonstrate this bimodality during at least the warmer seasons of the year. During the winter *C. carinata* demonstrates a unimodal diel cycle; activity peaks during the warmest time of the day (Figs. 43 and 44).

General activity, i.e. lizard movement, is greatest during the warm, dry, spring months. A tally of the number of lizards entering or leaving my field of view at the SW Blind during different seasons of the year supports this (Fig. 43). During 11 spring days, an average of 30.4 arrivals and/or departures was logged per day. An average of 20.8 per day was recorded during the summer and only 13.75 during the winter. The spring activity peak is related to both courtship and optimal climate. I could detect no sexual differences in general activity levels.

Weather conditions have a profound effect on all phases of activity. Lizard emergence was only rarely precluded by cool, wet, and windy conditions (1 of 65 days) on summer days, but often so on winter days (4 of 19 days). Furthermore, on many winter days when emergence was observed, lizard activity was restricted to basking in the vicinity of the retreat; body temperatures high enough to permit other activities were apparently never reached. Cold weather effects a reduction in activity range size. An adult male at the SW Blind maintained a home range of 702 m^2 between June 1974 and August 1975, but occupied only about 40 percent (279 m^2) of that area in November 1974. Similar activity range reductions were typical of all lizards during the colder parts of the year.

Throughout most of the year an iguana is capable of traversing its entire home range within any single day. During the colder winter months (November-January) all phases of activity are reduced, and it

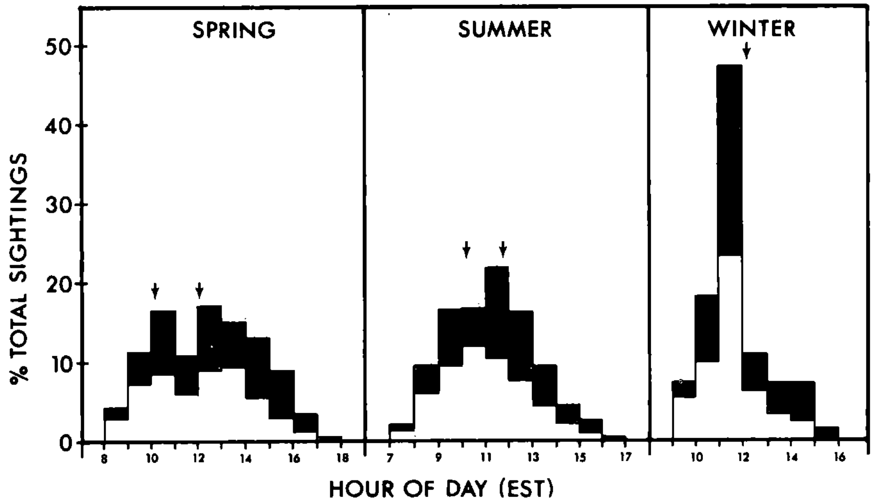

FIGURE 43.—Hourly activity in *Cyclura carinata* as represented by arrival and/or departure of lizards from the field of view at the SW Blind. Sample periods include 11 days between March 5 and April 12 (334 total arrival and departure sightings), 20 days between June 4 and September 6 (416 total sightings), and 8 days between November 27 and December 21 (110 sightings). Open bars indicate arrivals; closed bars, departures. Arrows indicate activity peaks from flush transect data. The absence of bimodality in the summer data is an artifact of lumping sightings by clock hour. Number of arrivals exceeds number of departures since lizards spooked by me or feral mammals were not tallied.

is unlikely that the entire home range will be visited in one day. Nevertheless, individual *Cyclura carinata* are active every day of the year, weather permitting. This is in contrast to *Sauromalus obesus* in California (Nagy 1973) and *Cyclura cornuta* on Mona Island (Wiewandt 1977), which may remain inactive for at least 2 or 3 days at a time, regardless of weather conditions.

DAILY ACTIVITY.—Diel activity patterns of *Cyclura carinata* reflect their heliothermic nature. The probability that a lizard will exhibit a particular behavior at a particular time during the day is directly related to the thermal regime. A detailed study of the thermoregulatory ecology of this species is in preparation by David Auth. My discussion of thermoregulatory behavior will therefore be limited.

Cyclura carinata are active and will feed on every day of the year that the weather permits. After morning burrow emergence, iguanas move immediately into the sun to bask. Morning basking usually lasts less that 45 min during the summer, but lizards were observed to bask for up to 5 hr (their entire time of emergent activity) on winter days. (Basking postures are discussed by Auth MS). Defecation most frequently occurs immediately following termination of morning basking (Fig. 44). Since the same basking site may be used for many days by the same lizard, large numbers of fecal pellets accumulate nearby, identifying the site.

Following basking (or defecation), lizards make forays through their home range to feed. Most of the remainder of the day is spent feeding, interacting with other lizards, and shuttling in the sun-shade

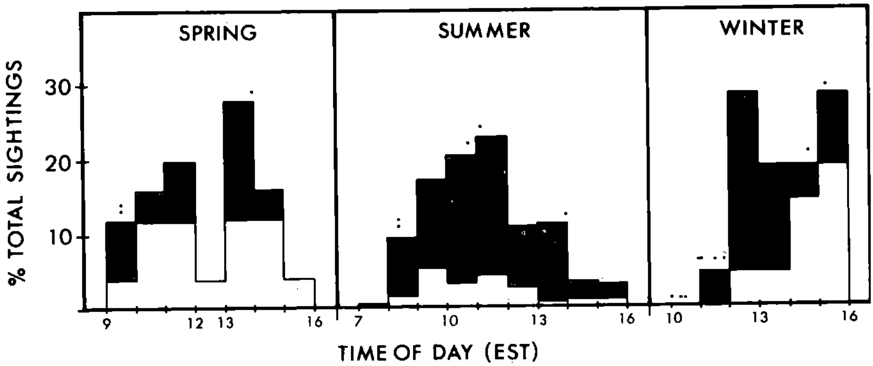

FIGURE 44.—Hourly feeding and/or arboreal activity in *Cyclura carinata* for Spring (March 5 - April 12; 25 total sightings), Summer (June 6 - September 6; 191 sightings), and Winter (November 27 - December 21; 21 sightings) seasons. Open bars indicate actual feeding observations; closed bars, arboreal sightings (not necessarily feeding). Black dots indicate times of observed defecations.

mosaic for thermoregulatory purposes. A similar daily routine is reported for *Cyclura cychlura* (Wilcox *et al.* 1973), *Cyclura nubila* (Grant 1940b; Carey 1966), and *Cyclura pinguis* (Carey 1975). As previously stated, there are usually two peaks in the iguana's diet activity cycle, with but a single peak during the winter. Midday temperatures during most of the year dictate a period of rest to prevent the lizard from overheating. This midday activity decline is illustrated in the decreasing number of lizards flushed on transects (Fig. 45) and moving into or out of my field of view from the SW Blind (Fig. 43), and the reduction in non-bait feeding (Fig. 44).

The winter feeding and/or arboreal activity record (Fig. 49) appears anomalously bimodal because of a morning burst in arboreal activity. The morning peak reflects the increased use of arboreal basking sites during the winter. The bushy vegetation of the low thick canopy reduced the flow of cooling air currents, and the green leaves absorb more warming radiation than the light coral sand substrates, providing a warmer microclimate in which to bask.

The midday resting location is usually not far from the retreat; morning and afternoon forays take the lizard to the periphery of his home range. During the winter there is usually no midday resting period, and lizards typically make only one foray a day.

Following the afternoon activity peak, as temperatures fall, lizards spend increasingly more time in the sun. Thigmotropic basking is often employed late in the afternoon in an attempt to maintain elevated body temperatures. When their body temperatures drop below the preferred range, the lizards enter their burrows.

Unlike *Cyclura nubila* (Grant 1940b) and *Sauromalus obesus* (Berry 1974), which avoid rain, *Cyclura carinata* (and *Cyclura pinguis*; Carey 1975) often endured temporary rain showers in prostrate postures. If the rain continued for more than 20 or 30 min and/or was especially intense or cold, the lizards would retreat to their burrows. As soon as the sun reappeared, the iguanas would re-emerge if the clearing preceded their normal submergence time. As that time approached, lizards were increasingly unwilling to re-emerge.

Re-emergence after disturbance by humans or feral mammals was similarly affected. Lizards usually left their burrows (if the threat was no longer present) within 45 min after retirement unless spooked shortly before normal submergence times.

ORIENTATION AND HOMING.—In order to test for homing ability, several lizards fitted with transmitters were displaced distances of 0.6 to 5.6 km and released into a burrow in the dune area of Pine Cay, 500 m NE of the Ridge Area. The lizards were subsequently relocated one to several times after intervals of approximately 1/2 to 5 diurnal periods. It was often possible to trace and map the lizard's travels by his tracks in the sand (Table 20). None of these animals homed successfully. Each of the first four took an immediate general southward heading toward their capture sites, suggesting homing capabilities, but this might simply reflect the avoidance of human activity (to the north and northeast) and the sea (northwest). To test this effect, lizards from Fort George Cay, north-northeast of the release site, were displaced. Their initial headings were homeward, toward the area of human activity. All lizards, during at least the first interval of freedom

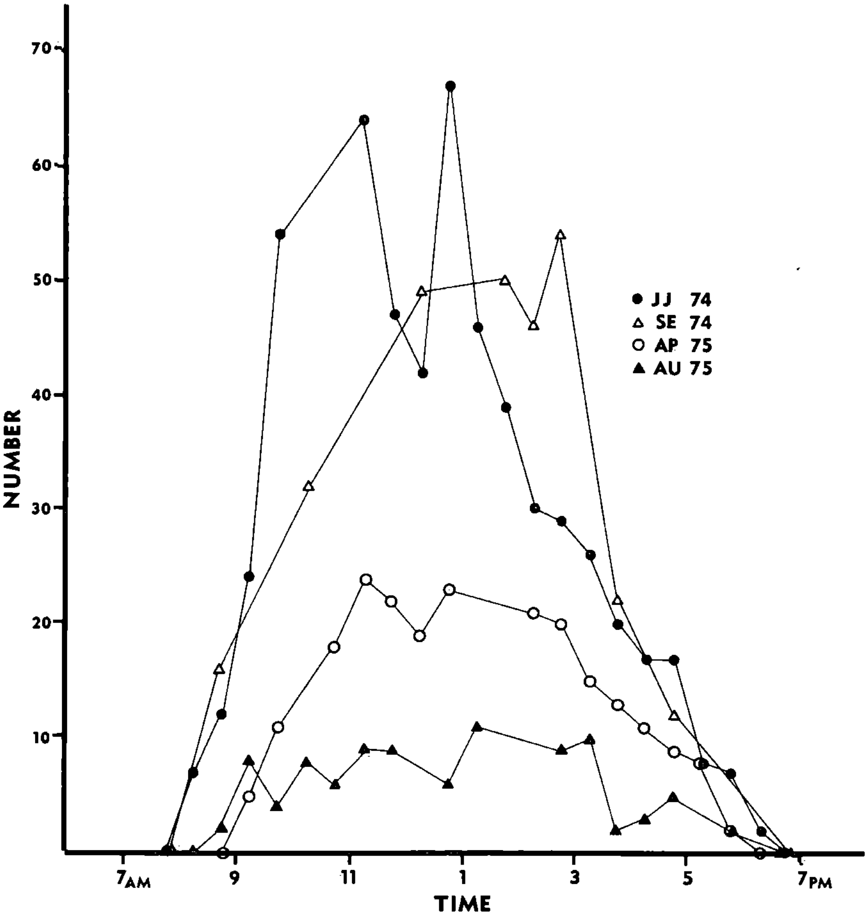

FIGURE 45.—Variation in total number of adult *Cyclura carinata* sighted during half-hour flush transects on four separate trips to Pine Cay; June-July, 1974; September, 1974; April, 1975; August, 1975. Times are EDT. See Figure 3 for transect location.

following displacement, moved in a direction within 43° of that to their original capture point (arithmetic mean = 20.5° ± 11.7, range 7-43; geometric mean = +0.5 ± 21.6°, range = 43° east to 14° west of home direction). In no case was it believed possible that displaced lizards had ever visited the area of their displacement. Therefore, despite the small sample size, directional homing abilities are strongly indicated.

However, the lizards did not maintain their initial directional movements. This might suggest a failure of their homing mechanism, but might also reflect their reactions to disturbances inherent to relocation. As these lizards often simply buried themselves in the leaf litter in the center of huge patches of *Coccoloba*, they were apparently well aware of my presence (and that of a beeping receiver) long before their precise location was determined.

Since females of at least *Cyclura cornuta* (Wiewandt 1977) and *Iguana iguana* (Montgomery *et al.* 1973), among the iguanines, migrate long distances year after year to the same nesting areas (and presumably return to their normal activity ranges), homing ability in *Cyclura carinata* might be expected. Further study is needed on the entire subject of homing in lizards (see review in Weintraub 1970).

With the present availability of biotelemetric equipment (including radioactive marking), structured experimentation using large sex and age samples displaced over a variety of distances could be very enlightening. Of particular importance is the relationship of the size of a lizard's normal activity range to his homing ability. Return success in *Sceloporus orcutti* decreased considerably for displacement distances not greatly exceeding the lizard's home range diameter (Weintraub 1970). *Dipsosaurus dorsalis* failed to home when displaced distances over five times the diameter of their normal activity range, but were fairly successful from distances three to four times that diameter (Krekorian 1977).

I observed *Cyclura carinata* make occasional forays beyond their normal activity range for distances up to twice its diameter in order to exploit a temporary food source. I believe that *Cyclura* could also home successfully after displacement up to three or four times the normal activity range diameter, but lizards in this study were displaced at least 20 times that diameter.

SOCIAL ORGANIZATION

DISPLAYS

Iguanid lizards are typically diurnal and communication is mainly via visual sensory modes. Tactile communication may be important in

TABLE 20.—MOVEMENTS OF DISPLACED LIZARDS BEARING TRANSMITTERS.

						Direction from release burrow (degrees E of N)		
Sex	SVL	Wt. (kg)	Island of Origin	Date	Length of Displacement	To Capture Point	To point of first relocation	Time from release to first relocation
F	229	0.495	Pine	Nov. 27, 1974	661.4m	236°	214°	17 hr
F	222	0.455	Pine	Nov. 27, 1974	604.6 m	223°	180°	17 hr
M	260	0.620	Little Water	Aug. 10, 1975	5.6 km	232°	239°	12 hr
M	349	1.720	Water	Aug. 7, 1975	2.5 km	229°	204°	3 days
M	286	0.735	Fort George	June 11, 1976	2.75 km	9°	21°	6 hr
M	248	0.555	Fort George	June 12, 1976	2.75 km	9°	25°	4½ hr

NOTE: All lizards were released within 8 hr of capture at the same site on Pine Cay. Times refer to daylight hours of freedom (this overestimates actual time of activity). Actual distance between locations of lizards (to nearest 10 m) determined by following the lizards' tracks in the sands.

some interactions, such as courtship, but in general, very little information is probably exchanged via the tactile, auditory, or chemical-olfactory sensory modes. All iguanid lizards apparently perform stereotyped displays, typically with head movements or "bobs" (Carpenter 1967; and others). These displays are believed to function primarily in intraspecific interactions, including aggression, assertion, and courtship. They exhibit both individual and geographic variation within lizard species (e.g. Ferguson 1971; Jenssen 1971; Crews 1975a) and are thought to serve in species recognition (Ferguson 1972) and, possibly, sexual and/or individual recognition (e.g. Berry 1974).

Displaying rock iguanas were videotaped in the field and laboratory. All head bob displays (except the male courtship display; see REPRODUCTION) contained the same basic units (Fig. 46). I follow Stamps and Barlow (1973) in calling these apparently species-constant headbobs the 'signature' displays or bobs. This term is preferred to the "assertion" display of Jenssen (1971) and others, since, in at least *Cyclura carinata*, it is rarely performed in an assertive context.

Unlike many anoline lizard species which exhibit complex display or headbob repertoires (Stamps and Barlow 1973; Jenssen 1975), that of *Cyclura carinata* was relatively simple, with complexity involving frequency of combination of only two signature units: a single, or a double vertical oscillation of the head. These units are illustrated in Figure 49 as they constitute a communication between two lizards.

Straight line distance to first relocation	Actual distance traveled to first relocation	Average speed (m/hr) to first relocation	Direction from release burrow to point of last relocation (°E of N)	Time from release to last relocation	Straight line distance	Actual distance	Average speed (m/hr) till last relocation
350.6 m	?	—	220°	5 days	187.2 m	?	—
341.0 m	?	—	180°	2 days	341.0 m	?	—
339 m	610 m	50.8	0°	3 days	99.9 m	1200 m	33.3
246.7 m	?	—	—	—	—	—	—
141.7 m	300 m	50	—	—	—	—	—
202.4 m	250 m	55.6	121°	1.5 days	50.6 m	450 m	25.0

Each of the two units was very stereotyped. The single bob unit ranged from 0.28 to 0.35 sec ($\overline{X}$ = 0.31). Male single bobs averaged slightly longer than females (0.33 versus 0.28), presumably because of the heavier heads of the larger males. Double bobs ranged from 0.37 to 0.50 sec ($\overline{X}$ = 0.44). The pauses between units of the same bobbing sequence ranged from 0.69 to 1.03 sec ($\overline{X}$ = 0.835).

Forty interactions, each involving only two lizards, were recorded in their entirety; the composition of a bobbing sequence differed between dominant males in their territories and other lizards. Dominant male sequences averaged 1.25 units (range 0 to 5; mode = 0; median = 1); other lizards averaged 5.48 units per sequence (range 1-13; mode = 3; median 5). Maximum length for a dominant male sequence was 5.5 sec (one single followed by four double units); maximum for other lizards was 12.3 sec (four single, eight double, and one single).

Dominant males in 17 of 40 interactions did not display to bobbing subdominant lizards. It they did display, the sequence consisted most frequently of one to four single units ($\overline{X}$ = 1.82; 11 of 40; Fig. 46, bottom), or one to three double units ($\overline{X}$ = 1.60; 5 of 40). In most of the remaining sequences one or two single units either preceded or followed one or two double units. In only one case did single unit(s) both precede and follow double units (two); the reverse was never true. The mean number of total single units in a sequence was 0.72; double units, 0.47.

Bobbing sequences of non-dominant lizards were much more variable. In most displays, (37 of 40) 0 to 5 single units preceded ($\overline{X}$ = 1.68) or followed ($\overline{X}$ = 0.84) (or both) 1 to 8 double units ($\overline{X}$ = 3.03). All but one sequence was composed of: (1) only single units (two cases of

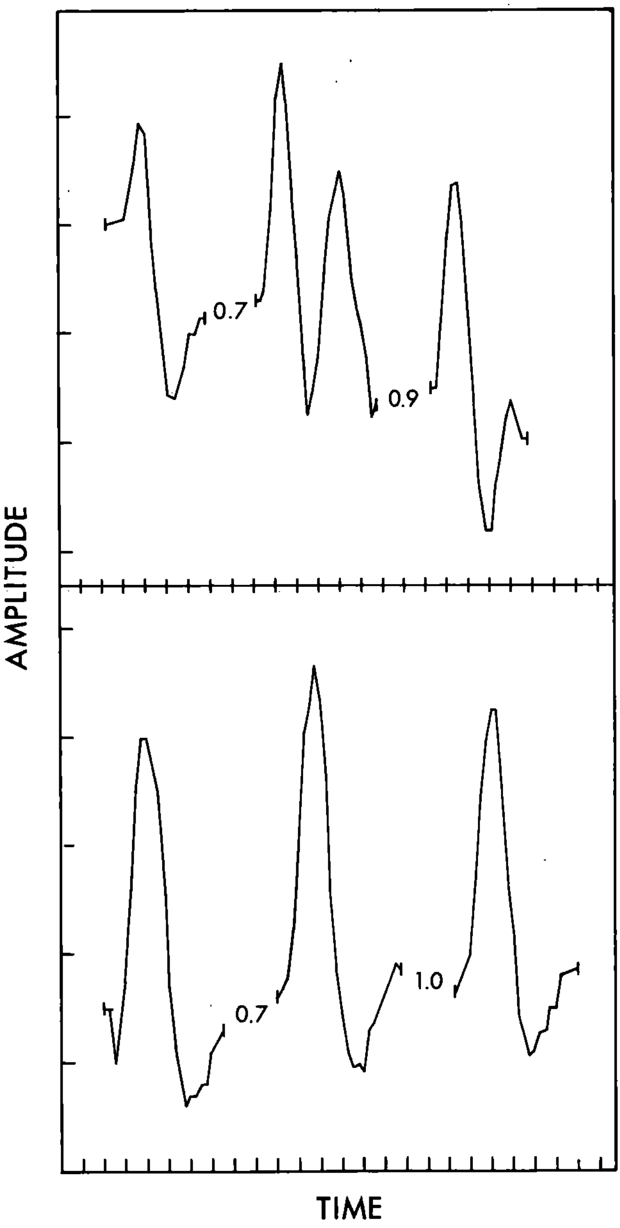

FIGURE 46.—Display action pattern graph (DAP) for *Cyclura carinata*. Top: headbobs of female displaying submissively to approaching male (single, double, and single unit bobs); bottom: headbobs of same male in response to female display (three single unit bobs). See discussion of units in text. Numbers are time between bobs in seconds. Time increments are 0.06 second. Amplitude is proportional to distance from lizard's eye to the substrate. Graph is accurate to 0.015 second.

40); (2) only double units (six cases); (3) single unit(s) preceding double unit(s) (12 cases); (4) single unit(s) following double unit(s) (seven cases); or (5) single unit(s) both preceding and following double unit(s) (11 cases; Fig. 49, top). The remaining sequence consisted of two single units, followed by two double units, then one single unit, one double unit and finally one single unit. No other sequences had double unit(s) both preceding and following single unit(s).

The sequence of units in a display was not constant for individuals; great variation, related to emotional state, existed. There was a tendency for more excited lizards to use longer bobbing sequences, but this relationship was impossible to quantify. The reaction of a male caged within the territory of male #8 at the SW Blind illustrated this trend. As #8 approached, the caged male bobbed a sequence including five single units followed by four double units. Male #8 postured threateningly but did not bob. The caged male responded with a four-single-six-double-unit sequence. Lacking a response from #8, the male made five single and three double unit bobs. Without responding further, #8 simply moved off.

Further display variation involved several modifiers including gular, nuchal, and roach extension; mouth opening; and other postural changes. These modifiers permitted the scaling of behavior in relation to aggression levels. *Cyclura carinata* did not perform pushups; bobs involved only the head and neck. Courtship and female rejection displays were discussed under REPRODUCTION; the other displays and their integration into behavioral patterns are discussed here. The frequency of use of each display type by each of several social categories appears in Table 21.

THREAT OR AGGRESSIVE DISPLAY.—In this primarily postural display the threatening male extended all four legs, raising and arching the body high above the ground; elevated the mid-dorsal roach, enhancing the prominence of the erect crests of neck and body

TABLE 21.—FREQUENCY OF DISPLAY TYPES RECORDED FOR SEVERAL CATEGORIES OF ADULT *Cyclura carinata* AT THE SW BLIND IN 1974 AND 1975.

	Dominant Males	Subdominant Males	Females (except nesting)	Total
Threat	73	8	0	81
Challenge	47	1	0	48
Submissive[a]	14	34	89	137
Total				266

[a] Excludes lizard that retreated without displaying

spines; bloated and laterally compressed the trunk region; and inflated the gular region (Fig. 47). The effect was an increase in the lizard's apparent size. These postural changes were most pronounced during the challenge display (see below). Headbobbing usually accompanied this posturing but was only rarely initiated by the resident or dominant male; the intruding lizard usually bobbed first. Females employed a similar display during mating (male rejection) and nesting season (nest defense), but modified it with intense open-mouthed headbobbing and, in nest defense, short side-stepping lunges in the direction of the intruder (see REPRODUCTION).

Challenge Display.—Performed by males only, this display was an intensification of the male threat display. The postures were the same but further modified by headbobs (only rarely), short side-stepping lunges (for maximum lateral presentation), and lashing of the tail on the ground from side to side.

Submissive or Appeasement Display.—Performed by both males and females, this display always included signature headbobs, which themselves served a submissive or appeasing function. Subordinate males modified the display by assuming a low profile with head and body on the ground. Sometimes the bobbing continued in the absence of response from a dominant. Large submissive males allowed their dorsal spines to lie to the side in an unerect position.

Exploratory Display.—Females and subdominant and young adult males often arched the distal two-thirds of their tails high in the air each time they stopped as they moved through the bush (Fig. 48). Dominant males arched their tails rarely and only when outside their territories. The tail was most often raised when the resident male was not in sight. I suspected this was a simple appeasement mechanism which prevented an attack on the explorer lizard by some undetected resident male before the explorer could display submissively by bobbing. As iguanas did not otherwise display in the absence of conspecifics as anoline and sceloporine lizards often do (pers. observ.), this explanation is feasible. I was unable to quantify this behavior in the field, and captive individuals never exhibited it.

The communicating function of these various displays in *Cyclura carinata* is clear in the following typical sequences. A dominant, territory-holding male, on detecting another lizard in its vicinity, did not display, but rather assumed a simple alert stance, with forelegs extended, head high, and pelvic and tail regions on the ground. If the intruder was a very young adult male or a female (i.e. relatively small and lacking dorsal spine development) the resident male's further response was determined by the behavior of the approaching lizard. On

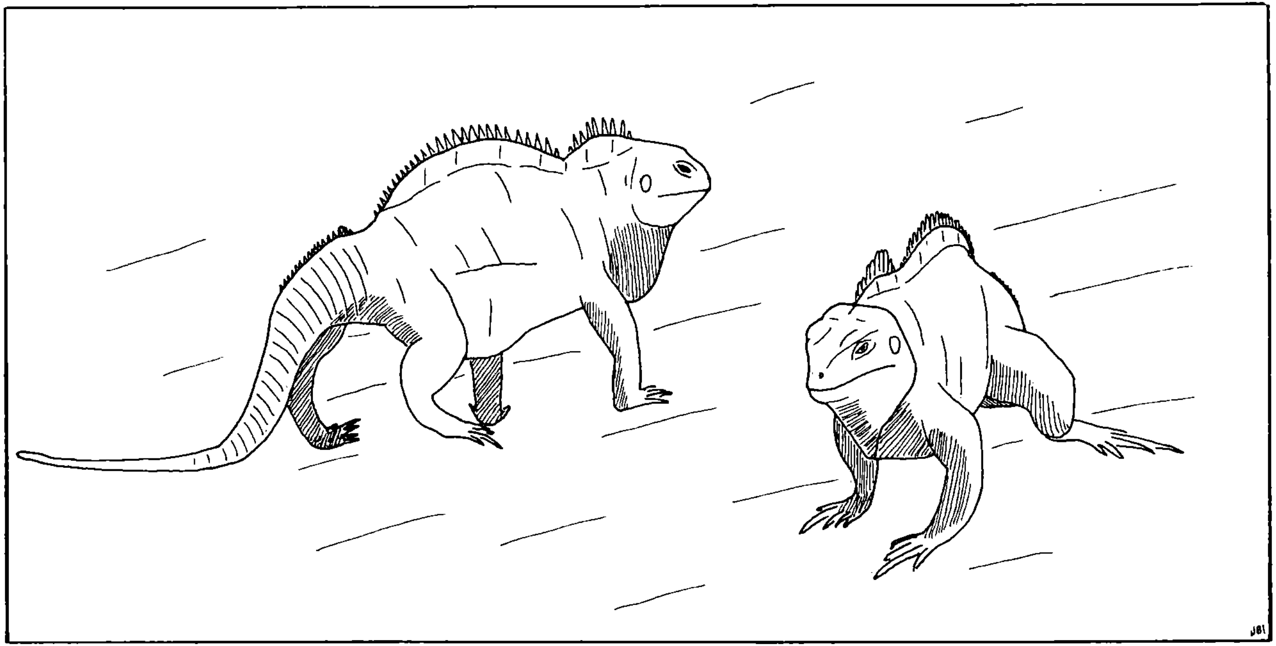

FIGURE 47.—Adult male *Cyclura carinata* in face-off position. Postures are typical of threat and challenge displays. Distance between lizards is reduced for illustration purposes. Drawn from kodachromes.

seeing the resident male, the intruder immediately displayed submissively. The resident male typically responded with a headbob display, and the two lizards exchanged up to five bobbing sequences, although the resident sometimes did not reciprocate with any bobbing. Perhaps he recognized the individual lizard; he certainly recognized it as no threat. This lack of response was typical in the case of juvenile intruders.

It was clear that dominant males: (1) bobbed much less frequently than females or subdominant males; and (2) initiated few bobbing exchanges. During 158 interactions, involving no more than two lizards, observed in their entirety at the SW Blind, dominant males performed only 18.4% of the bobs and initiated only 11.4% of the sequences; subdominant males performed 26.6% of the bobs and initiated 23.4% of the sequences. Females accounted for the remainder. Females and subordinate males also were most commonly the last to bob during these exchanges. Table 22 shows a similar relationship among captive lizards. This reduced display frequency by the most dominant individuals is contrary to the pattern found in most other iguanid species (e.g Carpenter 1962a). Since dominant male *Cyclura* are rarely challenged on their own territories, it is energetically advantageous for them to display only when necessary.

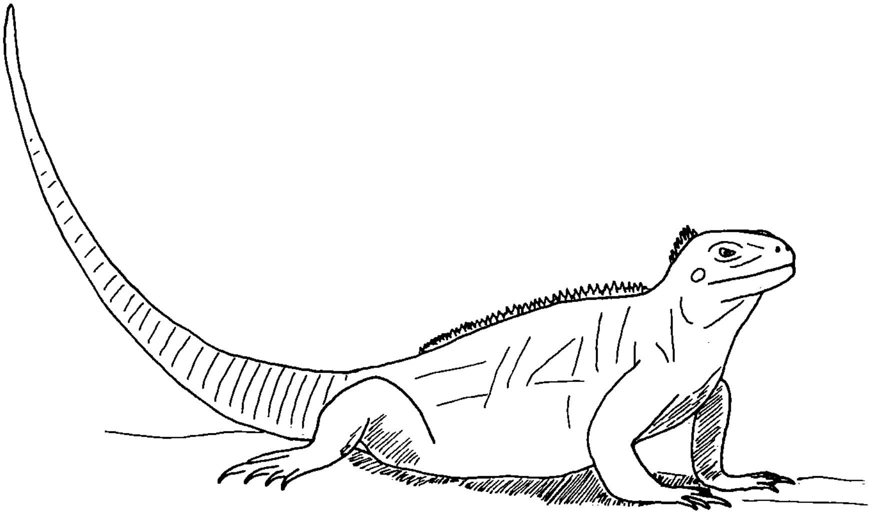

FIGURE 48.—Lizard posture during exploratory display. See text for explanation.

TABLE 22.—HEADBOB DISPLAYS INITIATED (LEFT OF SLASH) VERSUS THOSE ANSWERED (RIGHT) FOR VARIOUS CAPTIVE LIZARD PAIRS BETWEEN 23 APRIL AND 1 MAY 1975.

Initiator of Bobbing sequence		Intended Respondent			
Lizard #	SVL (mm)	1M	2M	3M	4M
1M	349	—	0	0	0
2M	324	1/1	—	0	0
3M	286	3/1	13/2	—	3/2
4M	219	61/13	4/0	39/20	—
FF	—	0	0	76/28	9/7

NOTE: Courtship bobs and sequences involving more than two lizards are not included. Male status in hierarchy is indicated by lizard number (1=most dominate). Note infrequenty of bob initiation and response by dominant males. M= male. FF= females.

If an intruding lizard was recognized as a male, the resident territorial male quickly shifted from his alert stance to a threat display. The components of the behavioral sequence that followed were very constant and determined by the actions of the intruder (Fig. 49). Since the sex of all but the youngest adult males is apparent (both to the observer and the iguanas) from the size of the dorsal neck and back spines (see GROWTH), spine development is probably the main criterion of sex recognition in the species. This is supported by the experiments performed at the SW Blind. Caged alien females or males without spine development placed in a male's territory never elicited a threat display; caged or tethered males with well-developed dorsal spines always did (one resident even attacked the cage). Females on which I mounted a crest of dorsal body spines (dissected from a preserved specimen) at first seemed to confuse resident males as they approached. The males sometimes approached rapidly in a very low-intensity threat display when they first saw the strange female, but terminated this approach quickly, apparently as they recognized the disguise. The smaller size, lack of neck spines, and submissive displaying of the modified female probably contributed to his recognition. I never saw a dominant male mistake the sex of a female and threat posture to her, or refrain from threat displaying to a male with observable dorsal spine development. Young adult males without spine development were treated as females.

Presentation of a threat display by a resident to an intruding male was usually sufficient to cause the intruding male to flee (with or without a submissive display), usually with the resident male chasing after him. The resident male never overtook the chased lizard, although in several cases he surely could have. If the encounter occurred just outside the intruder's territory, he retreated slowly, side-stepping as he went, in a low intensity threat posture. The resident did not chase the intruder in this case. If the intruder returned the threat display or simply ignored the male, the resident increased the intensity of his display and charged with side-stepping lunges (challenge display). In only six cases at the SW Blind did this challenge fail to induce the intruder to flee. The intruder that refused to run oriented his body perpendicular to the lunging resident and continued his threat display. The resident always stopped his charge short of this threaten-

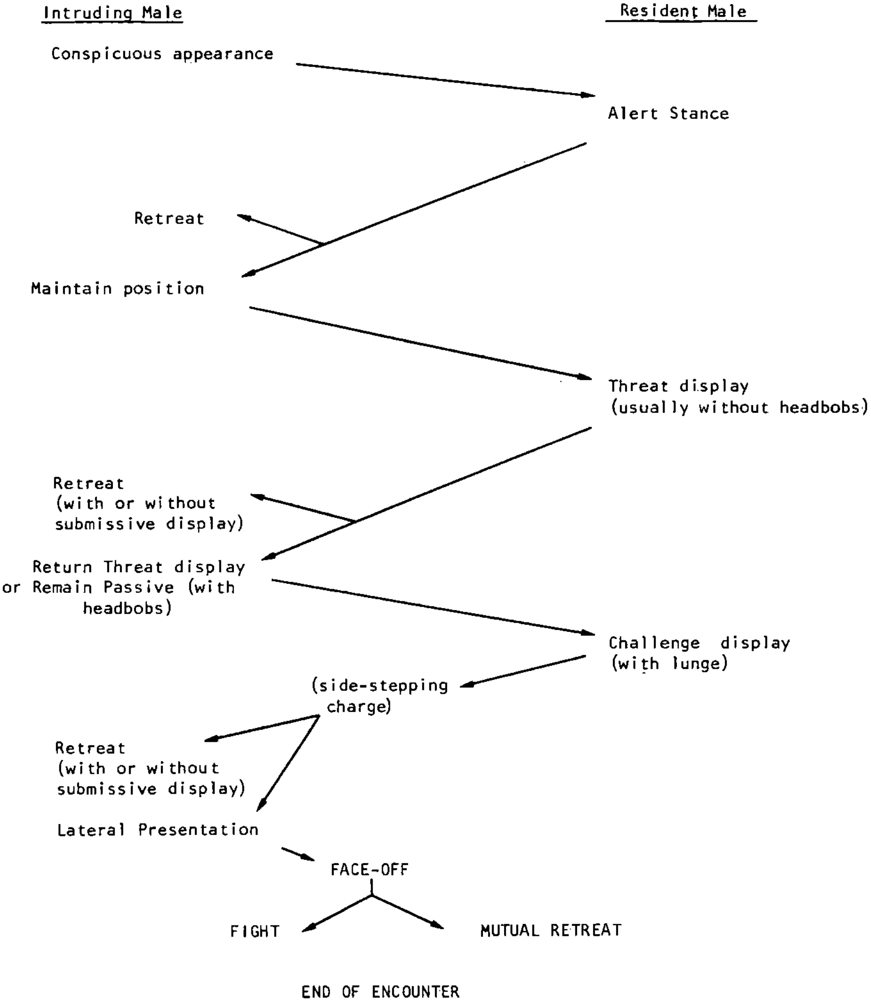

FIGURE 49.—Behavioral components of territorial defense in *Cyclura carinata*.

ing intruder and presented himself laterally in a "face-off" position (after Carpenter 1967; Fig. 47).

Fights followed four of the six face-offs observed in the field; both lizards withdrew following the other face-offs (2 July 1974 and 2 August 1975), side-stepping and threat posturing as they separated. In one of these instances, the lizards chased one another in circles from the face-off position before moving apart.

All four fights (16 July, 2 September, 29 November 1974 and 8 April 1975) were between the same two males (#33, and Y; both 285-290 mm SVL) and occurred between their respective burrows along the road northeast of the SW Blind (Fig. 39; intersection of arrows marks fights). Three of the four fights were observed in their entirety; one was video-taped as was part of another. Each fight was instigated when each male challenged the other, but neither withdrew. Lunging charges brought the lizards to face-off position. Bobbing was rare during face-offs or fights.

Fights began with the simultaneous open-mouthed charge of each lizard from the face-off position (about 0.6 m apart). Contact was either cheek to cheek (only one fight), as in the ritualized jaw-sparring of *Cyclura nubila* (photographed in Street 1952) and *C. cornuta* (Wiewandt 1977), or shoulder to shoulder (with adjacent forelegs interlocked) as in *Dipsosaurus dorsalis* (Norris 1953). Rostrum to rostrum contact, as in male *Amblyrhynchus* (Carpenter 1966; Eibl-Eibesfeldt 1955), was not observed. The lizards then attempted to push one another back. This was accompanied by tail thrashing, but the tail was not directed at the opponent as in *Dipsosaurus* (Carpenter 1961). Perhaps this tail movement increased momentum or traction, or was simply intended to intimidate the opponent. Although lizards had their mouths open during fights, I saw no biting. Scars and missing spines in the anterior trunk regions of several adult males suggest, however, that it does occur.

Pushing bouts (up to five) lasted from 4 to 10 sec before the combatants suddenly backed apart to a face-off position; 5 to 15 sec separated each pushing bout. The males missed each other's shoulders in the last three charges of one fight; they came to lie with their forelimbs on the posterior trunk and limbs of their opponents. This seemed to surprise them and they remained motionless for 2-3 sec before breaking to again face-off. The loser of the fight was that lizard that during a face-off began to back away (laterally) from his opponent (usually with his head inclined downward). Two of the fights were apparently draws as both lizards simultaneously withdrew, side-stepping and threat-posturing as they separated. Number 33 won the other two fights; after the first he remained stationary as Y left the area, but after the second he lunged several times at Y to prompt his retreat. From 30 to 70 sec elapsed between the beginning of the first pushing bout to the withdrawal of at least one of the combatants.

Fighting is obviously rare even in populations as dense as those at the SW Blind. The fact that all four fights I observed were between the same two males in the area between their burrows is probably related to the fact that the distance between their burrows was the least of any pair of dominant male burrows I located and was much less than the average radius of territorial defense by males at the SW Blind (see later). The area between them must have been in constant dispute.

The fights of the male iguanines *Cyclura carinata* (this study), *C. cornuta* (Wiewandt 1977), *C. nubila* (Street 1952), *Dipsosaurus dorsalis* (Norris 1953; Carpenter 1961), and *Amblyrhynchus cristatus* (Carpenter 1966) are highly stereotyped, whereas those of *Brachylophus fasciatus* (Cogger 1974), *Conolophus* (Carpenter 1969), *Ctenosaura similis* (Henderson 1973), and *Sauromalus obesus* (Berry 1974) are apparently not.

Displays in other species of *Cyclura* have been poorly studied. The display of *Cyclura rileyi* on San Salvador (smaller than *C. carinata*) includes both pushups and bobs (Gicca, pers. comm.); that of *C. cornuta* on Mona Island (larger than *Cyclura carinata*) consists only of slow rolling of the head (Wiewandt 1977). This information suggests a size-related display complexity within the genus. Purdue and Carpenter (1972) observed a similar correlation among 21 species of *Sceloporus*. Since it is more costly energetically for a large lizard than a small one to perform the same display, this decrease in display complexity in larger species is not unexpected. This energetic argument may explain the reluctance of large territorial male *Cyclura carinata* to bob. Whether or not other species of *Cyclura* or iguanines follow this trend must await further study; however, *Sauromalus, Enyaliosaurus,* and *Dipsosaurus* (Berry 1974; Carpenter 1961, 1977; and others) are smaller than *C. carinata* and employ pushups and headbobs, whereas *Iguana iguana* is larger and has a very simple bobbing pattern (Mueller 1972).

Male displays in *Cyclura carinata* are probably extremely important not only in attracting females (as suggested by Berry 1974 for *Sauromalus*), but in governing their reproductive physiology (as shown for *Anolis* by Stamps and Crews 1976; and others). These relationships within the Iguaninae deserve further attention since their longevity permits the formation of much more complicated male-female relationships than occurs in short-lived lizard species.

Displays were rarely used in interspecific interactions in the field, though iguanas sometimes bobbed at me when approached closely. Hunsaker and Burrage (1969) documented interspecific displaying among several species of iguanines, including *Cyclura nubila* and *C. cornuta*.

DOMINANCE RELATIONSHIPS

TERRITORIALITY AMONG MALES.—The concept of territoriality with respect to *Cyclura carinata* is precisely the same, whether defined functionally (an area where an individual or group has priority of access to the resources) or behaviorally (a defended area). The reader is referred to Kaufmann (1971) and Wilson (1975) for recent reviews and discussion of the concept.

Social structure in *Cyclura carinata* was controlled by dominant males, each with a large body size and a full or completely regenerated tail, a territory which he defended against other males, and a well-constructed burrow. Females defended their nest sites during the nesting season and exhibited no dominance relationships during the remainder of the year in the field or captivity. Dominance among young adult males (those subordinate to territorial males) was infrequently observed in the field, but commonly seen in captivity.

Territory sizes for dominant males at the SW Blind were calculated using, as the radius of a circle, the mean distance from the burrow to the site of defense (challenge display or chase) against a neighboring territory-holder. These defense radii ranged from 2.2 to 29.1 m (Table 23; Fig. 39). The mean radius for 21 defenses involving five males was 19.0 m, defining an average circular territory area of 1379 m^2. Home range data for three of those males were complete enough to indicate that about one half to all of the home range was defended. Incomplete data for other territorial males suggested this estimate was high.

Territorial males at the SW Blind did most of their feeding within their territories. The similarity between average defense and feeding radii values in Table 23 reflects the daily movements of dominant males at the perimeter of their territories (patrolling?). Territorial males have undeniable priority of access to food and any other resource found within their territories.

Except during the nesting season, *C. carinata*'s social system permitted freedom of movements for juveniles, adult females, and subadult males, while greatly restricting that of mature males. In order to avoid aggression, subdominant males shuttled between the territories of one or more dominants and apparently "free zones" between these territories. In many cases these subordinates had to occupy marginal or suboptimal areas, or colonize previously uninhabited

TABLE 23.—RELATIONSHIPS BETWEEN DEFENSE RADII, HOME RANGE SIZE, AND FEEDING RADII FOR THE DOMINANT MALES WITH THE MOST COMPLETE DATA AT THE SW BLIND.

Lizard	SVL (mm)	Defense Radius (m)	Calculated Defense Area (m²)	Observed Home Range (m²)	Estimated % of Home Range Defended	Feeding Radius (m)
8	305	24.48±1.99 (21.1-27.8) N=9	1883	1813	103.9	24.79±2.89 (19.9-27.2) N=4
2	286	16.13 (14.4-17.9) N=2	817	1773	46.1	14.06±3.86 (6.1-20.0) N=12
33	289	8.84±8.88 (2.2-23.8) N=5	246	—	—	22.71±10.56 (7.8-29.5) N=4
38	308	27.24 (25.4-29.1) N=2	2331	2484	93.8	—
Y	—	12.42±3.29 (7.8-14.8) N=3	485	—	—	—
Overall	297 (286-308) N=4	18.98±8.25 (2.2-29.1) N=21	1379.0±754.2[a] (485-2331) N=4	2023.3±326.1 N=3	81.3 68.2 N=3	17.68±7.19 (6.1-29.5) N=20

NOTE: Radii are measured from retreat burrow. Defended area is equivalent to the area of a circle with $\bar{X}$ defense radius. Only those defensive encounters between dominants seen in their entirety are included. Radius to a particular feeding site is used only once in calculations even if used by lizard more than once. Range in parentheses and sample size appear below mean ± one standard deviation.

[a] Excludes data from male #33.

areas. Thus the distal two-thirds of the recently deposited 950 m sandspit on Little Water Cay was inhabited only by males. Dominance among male rock iguanas was reinforced not by bob frequency, but by posturing, chasing, and, if necessary, fighting. The frequency of these aggressive acts among males at the SW Blind appears in Table 24. Threat displaying was the most frequent and least aggressive means by which dominant males intimidated intruders (54.5% of all encounters). When unsuccessful in driving off an intruder, the threat was followed by a challenge display and chase. A face-off or fight resulted in only 7.5 percent of the observed encounters.

Although four fights were observed, I found no evidence that any of the dominant territorial males at the SW Blind were ever completely displaced. The territories of males that disappeared during the course of the study (presumably dog- or cat-killed) were not immediately occupied by other big males. I believe that complete displacement of one male by another is rare in *Cyclura carinata*. Information on the rate of replacement of dominant residents in the field will require further study. Observations of one subdominant male at the SW Blind during each visit for two years provided some insight into the probable mechanism by which an adult male establishes dominance. The first lizard seen (December 1973) and marked (March 1974) at the SW Blind (#1) measured approximately 245 mm SVL and was at first mistaken by me as a female due to its undeveloped dorsal spines (see Fig. 36) and the lack of aggression toward it by dominant male residents. By March, and especially by June 1974 his sex became obvious both by the growth of his neck spines and by the increased male aggression toward him.

This lizard used retreats within the territory of dominant male #8 (305 mm SVL) during each of my visits to the islands from December 1973 through July 1974 but spent most of its active time in the area of

TABLE 24.—AGGRESSION AMONG MALE *Cyclura carinata* AT THE SW BLIND DURING 1974 AND 1975.

	Lizards Involved			
Encounter	Dominant to Dominant	Dominant to Subdominant	Subdominant to Subdominant	Total
Threat	41	32	5	78
Challenge (with chase)	27	24	1	52
Face-off	6	0	0	6
Fight	4	0	0	4
Total	78	56	6	140

home range overlap of the four nearest dominant males: #8; #6, 300 mm SVL; #2, 290 mm SVL; and #3, 305 mm SVL. This area was immediately to the west of the SW Blind (Fig. 39). Like most other subdominant males monitored, #1 used more than one retreat early in the study. In early June 1974, he maintained three retreats and often alternated between retreats from one night to the next. Each was only a small depression cleared beneath large flat rocks.

Aggression from dominants during June and July continued to restrict #1's activity to the area where their (the dominants') ranges overlapped and finally, between 20 July and 30 August 1974, he dug a burrow precisely in that area (due west of the blind at the road's edge). From that time until his disappearance between November 1975 and April 1976 (dogs dug his burrow up), he used only that retreat. During the same interval in which the burrow was dug, one of the nearby dominants disappeared (#6, to the west) and this allowed #1 additional freedom of movement in that direction. I believe that with further growth and experience #1 would likely have become a dominant.

Because these lizards are so long-lived, experience probably plays an important part in the establishment of dominance. The youngest territorial males at the SW Blind were estimated to be six to seven years post-maturity. Thus while the chances of a young male successfully displacing an older territorial male are small, his chances of outliving that male and inhabiting his area are good, especially if he avoids the aggression of the dominant. The transition of dominance in a particular area is clearly very slow, the abrupt displacement of one territorial male by another, rare. Maturing males, necessarily established in peripheral or socially "neutral" areas, apparently provide the major pool from which future dominant, territorial males will ascend.

THE EVOLUTION OF MALE TERRITORIALITY.—The cost of defending an area must necessarily be exceeded by the resources gained or that behavior would lose its selective advantage (Rand 1976b). The energetic cost of defense in *Cyclura carinata* has been minimized by a general reduction in displaying by the dominants and by settling disputes via simple displays rather than by fighting. Although the latter strategy is common among territorial lizards, the former has been reported for no other lizard species except *Varanus komodoensis* (Auffenberg, pers. comm.). Although access to other resources (e.g. basking sites) is also guaranteed, I believe that the primary advantages leading to the evolution of male territorial defense in this species have been in guaranteeing access to food, to females, and to permanent retreats (in probable order of decreasing importance).

Evidence presented under FOOD AND FEEDING suggests that food is probably the most limiting of these three and is the primary resource defended. I hypothesize that territorial defense evolved in *C. carinata* (or its ancestor) as an attempt to gain access to patchily distributed, limited food sources, such as the clumped thickets of *Scaevola, Coccoloba,* and *Strumpfia* found today in Open Scrub and Beach habitats on the study islands. A defending male would gain an immediate food and shelter advantage, and by permitting females to share the food source would also guarantee mating partners. The observed sexual dimorphism in this species would be expected as selection worked to reduce competition for food between males and their resident females (the evolution or retention of small female body size), and to increase the effectiveness of male-male defense (the evolution of large male body size and display modifiers, such as dorsal spines). Similarly female nest defense probably evolved in response to competition for limited nest sites (see REPRODUCTION).

JUVENILE AGGRESSION.—Hatchlings were aggressive as they emerged from nests. They were frequently seen chasing one another, as well as yearling *Cyclura* and adult *Leiocephalus*, during hatching season. Twenty such chases were observed during 24.5 hr of observation at the SW Blind between 1 and 6 September 1974. This agonistic behavior effectively dispersed the neonates from the nest site. It apparently subsided within a month following hatching, because it was not observed during November or December visits, and because up to four juveniles greater than three months of age could occasionally be found in the same retreat.

POPULATION EFFECTS OF SOCIAL SYSTEM.—Territoriality among male *Cyclura carinata* acts as an effective dispersal mechanism; nonterritorial males are always available for colonization of newly abandoned or otherwise available habitats. Aggression among neonates also functions in dispersal.

The social system in *Cyclura carinata* probably also functions to limit population size via its restrictions on access to food and nest sites. Male territoriality can limit male population size only by restricting the access of subordinates to food. Since it does not affect the number of nesting females, it cannot ultimately limit the population. However, the success of a female in locating and defending an optimal nest site is directly related to the success of her brood. This is probably the primary mechanism limiting population size in this species. Bustard (1970b) and Philobosian (1975) have also suggested that social behavior limits population size in several other species of lizards.

DOMINANCE HIERARCHIES.—Dominance hierarchies have been shown to develop under crowded laboratory conditions in many normally territorial lizards (review in Carpenter 1967). Among the iguanines, *Amblyrhynchus cristatus* (Pawley 1969), *Brachylophus fasciatus* (Cogger 1974), *Dipsosaurus dorsalis* (Carpenter 1961), and *Sauromalus obesus* (Carpenter 1967; Prieto 1971) have shown similar shifts in social structure in captivity. In a field population studied by Berry (1974), dominant tyrant male *Sauromalus obesus* were territorial, while subdominant males were organized in a predominately size-related dominance hierarchy. Evans (1951) and Schmidt (1935) observed hierarchies in field populations of usually territorial *Ctenosaura pectinata* and *Amblyrhynchus cristatus*, respectively, in areas with reduced space for basking and/or refuge. Brattstrom (1974) evoked this transition among male *Ctenosaura hemilopha* in an outdoor enclosure by combining numerous rock piles into one; each pile was originally defended by a single male. Although I found no evidence of dominance hierarchies in the field, adult male *Cyclura carinata* developed them in the laboratory.

Captive male hierarchies were linear; the dominant or tyrant male had unrestrained access to the entire enclosure, including the primary feeding and basking areas. He also had priority of access to females; only dominant males copulated with females in captivity (see REPRODUCTION). Dominant males rarely bobbed (Table 22); subordinates moved very little and were constantly displaying submissively. Because of their positions in the hierarchy, these subdominant males were often unable to bask or eat at will. In some cases they did not even leave their burrows for several days at a time. These lizards lost weight rapidly and would surely have died if I had not removed them from the socially stressful situation.

In order to observe behavior involved in dominance shifts, I repeatedly removed and reintroduced males to the enclosure. I also partitioned the pen, with high-ranking males on either side, and later removed it when the lizards were active. None of these manipulations induced challenge displays, chases, or fights; a few produced threat displays. Dominance shifts in captivity were immediate and lacked aggression. As soon as a new male emerged from the remotely operated release box, he immediately assumed his position in the predominately size-related linear hierarchy, despite having never previously seen the other lizards. The lack of aggression in the following specific example was characteristic of all introductions.

Male #3 (286 mm SVL) was introduced into the captive enclosure on 23 April 1974 and immediately established dominance over two smaller males. He had freedom of access to the primary feeding and basking stations and to the females for courting, and even chased smaller males away from females (see REPRODUCTION). At 1153 hr on 1 May, Male #1 (349 mm SVL) was introduced. During 3½ hr of observation during the 26 hr prior to releasing #1, #3 did not bob to other males. However, when #1 male carried only half of his body out of the release box, #3 immediately ran to the opposite end of the pen and bobbed submissively. Within the next hour he bobbed at least three more times to #1; #1 never responded. Number 3 remained at the far end of the pen in the shade for the remainder of the day, bobbing occasionally, while #1 moved freely between the main food source and the best patch of sunlight, without responding to #3. I know of no other lizard for which such a subtle unaggressive shift in dominance has been documented.

Since fights were so rarely observed in the field, I made many specific attempts to induce them in captivity, all without success. Despite continual manipulation (removal and reintroduction) of captive adult, similar-sized males in both David Auth's and my enclosures over 36 months, only one fight was induced in Auth's pen, entirely by chance. The following sequence of events leading to the fight in late August 1975 was provided by Auth:

Day 1: #10 male (about 1.45 kg), dominant in enclosure since September, 1973, was removed for laboratory experimentation. #7 male (same approximate weight) assumed dominance in pen.

Day 6: #7 male was removed for experimentation; #10 male was returned to pen and resumed dominance.

Day 8: #7 male was reintroduced into pen. As evidenced by scars on both lizards, #7 and #10 fought. #7 was thereafter dominant.

Very unusual physical, physiological, and psychological circumstances most obviously prevail for a male-male confrontation to result in actual combat.

A full or completely regenerated tail is extremely important to male social status. The rank of one male in the captive hierarchy decreased significantly when I accidentally broke his tail. He had been the dominant male, but following the break he greatly restricted his movements, appeared very nervous, and headbobbed more frequently. None of the dominant males at the SW Blind had tails freshly broken or incompletely regenerated.

MIRROR EXPERIMENTS.—Mirrors were used in an attempt to elicit aggressive behavior; however, no lizards responded to mirrors placed in their territories, either in the field or captivity. This was unexpected in light of the effectiveness with which mirrors evoke aggression in many other iguanids (Hunsaker 1962, among others), and since the introduction of an adult male *Cyclura* into a resident male's territory resulted in an immediate defensive reaction. *Cyclura carinata* may be able to detect the artificiality of the mirror and its images.

COMPARISONS WITH OTHER IGUANINES.—Some type of dominance relationships probably characterizes all natural populations of *Cyclura* (e.g. Hunsaker and Burrage 1969; Wiewandt 1977; Carey 1975), despite Carey's (1976) implication that neither territorial nor hierarchial behavior are important in *C. cychlura*, based on his 10-day visit to Guana Cay (Exuma Islands, Bahamas). I suspect that the Guana Cay population is only seasonally aggressive, perhaps in response to some seasonally limited resource such as mateable females or nesting sites. It may be too energetically costly for this species to defend territories or maintain hierarchies year-round. This might also be the reason that defense of territories by males is restricted to the breeding season in *Amblyrhynchus* and *Conolophus* (Wilson 1975; and others), some Mona Island *Cyclura cornuta* (Wiewandt 1977); *Cyclura nubila* (Street 1952); *Dipsosaurus dorsalis* (Norris 1953); and perhaps *Iguana iguana* (Alvarez del Toro 1972). Male *Cyclura carinata* (this study), some male *Cyclura cornuta* (Wiewandt 1977), and male *Sauromalus obesus* (Berry 1974), however, defend territories throughout their active seasons. In contrast, no female iguanines are known to exhibit territorial defense other than during the nesting season.

Our knowledge of the social organization of most iguanine species is very incomplete. Basic information on social behavior, complimented by quantitative analyses of the availability of potentially limiting resources, is necessary for our better understanding of the evolution of dominance relationships within this subfamily.

INTERSPECIFIC COACTIONS

NATURAL COHABITANTS

PREDATION.—The large size of adult *Cyclura* makes them almost invulnerable to predation by natural cohabitants; potential natural predators on adults are probably limited to birds. In addition to avian predators (and cannabalistic adults), juvenile iguanas may also fall prey to crabs, but no direct evidence of this was found. The Turks and Caicos Island boa, *Epicrates c. chrysogaster*, does not occur on Pine Cay, but probably feeds on *Cyclura* on islands where they are sympatric. No other reptiles reach a size large enough to take even the smallest iguana in these islands.

The Pearly-eyed thrasher (*Margarops furcatus*) was frequently seen successfully catching *Anolis* on Pine Cay and was once observed to capture and carry off an adult *Leiocephalus psammodrommus* in the same size range as one- to two-year-old *Cyclura carinata*. This bird probably does eat young iguanas. The remains of the diurnal lizard *Anolis* *scriptus* have been found in Barn Owl pellets (*Tyto albo*) from caves on Mayaguana Island, probably as a result of this lizard's habit of sleeping along exposed branches at night (Buden 1974). Since *Cyclura* are not exposed during the night, it is unlikely that they are included in the diet of the Barn Owl, or the Short-eared Owl (*Asio flammeus*), both of which have been recorded in the Turks and Caicos Islands (Buden, pers. comm.).

In the Galapagos Islands, the Lava Gull (*Creagrus furcatus*), the diurnal Short-eared Owl (*Asio galapagoensis*), the Galapagos Hawk (*Buteo galapagoensis*), and unidentified herons are all known to capture and feed on the marine iguana *Amblyrhynchus* and probably also on the two terrestrial species of *Conolophus* (Dowling 1964; Carpenter 1966). Ospreys (*Pandion halioetus*; Van Denburgh 1922 and Shaw 1945) and Sparrow Hawks (*Falco sparverius*; Prieto and Sorenson 1975b) prey on lizards of the iguanine genus *Sauromalus*. Both the Laughing and Herring gulls (*Larus atricilla* and *L. argentatus*) are known from the Turks and Caicos Islands and each is probably capable of subduing at least juvenile iguanas. Nine species of herons and egrets as well as the Frigate bird (*Fregata magnificens*) are also present and represent additional potential predators. Possible raptorial predators on *Cyclura* in the Turks and Caicos include the Osprey, Pigeon Hawk (*Falco columbarius*) and Sparrow Hawk. *Anolis scriptus* remains were found in the gut of a single Sparrow Hawk (Auffenberg, pers. comm.).

INTRODUCED COHABITANTS

The native flora and fauna of the Galapagos Islands are threatened with destruction by introduced goats, pigs, rats, dogs, cats, donkeys, and cattle (Dowling 1964). All of these are also feral in the Turks and Caicos, and each has had its destructive effects. In the Caicos Islands, feral goats, pigs, and cattle are generally uncommon. This is no doubt due to the premium placed on non-fish food sources by the local people; feral cattle are hunted on uninhabited East Caicos. The effects of these introductions on iguanas have therefore been minimal. Such has not been the case for *Cyclura cornuta stejnegeri* on Mona Island where nearly 100% of the lizards' nests in one area were destroyed by pigs in 1972, and the annual loss was about 25 percent (Wiewandt 1977).

Rats and mice are probably found on nearly every island in the Turks and Caicos. Rabb and Hayden recorded rats on uninhabited Fort George Cay in 1957. Previously destructively high rat densities on Pine Cay have recently decreased considerably due to the introduction and proliferation of feral cats. Although I was unable to detect any effects of these introduced rodents on Pine Cay lizard populations, Whitaker (1973) and Crook (1973) have documented decreased lizard densities (including *Sphenodon*) on islands off New Zealand inhabited by the introduced Polynesian rat (*Rattus exulans*). *Cyclura* is probably susceptible to predation by rats throughout its life.

As is the case for many of the world's wildlife species (Grant 1937; Hirth 1963b; Rand 1967a; Coman and Brunner 1972; Denny 1974; George 1974; Christian 1975; and review in McKnight 1964), dogs and cats represented the greatest threat to the lizard populations studied. The extirpation of the Pine Cay iguana population during the study period by feral cats and dogs is discussed in Iverson (1978).

Although not as efficient as cats and dogs, man represents the next most important predator. Natives capture lizards with snares or by excavating burrows to supplement their diets. This results only in the death of those lizards which are caught. Tourists and non-native residents use guns, usually pneumatic, to shoot iguanas. No better reason is offered than the novelty of providing the fare for an "iguana roast." Unfortunately, for every iguana that is shot and killed outright, many others are mortally wounded and destined to die in their retreats.

Some *Cyclura* populations have experienced predation by native fishermen for hundreds of years (Middleton and the Ambergris cays, for example) with no apparent threat of extirpation. However, iguanas have been extirpated or very nealy so on every island in the Turks and Caicos inhabited by feral cats or dogs. The effects of these unnatural predators cannot be underestimated.

DEFENSIVE BEHAVIOR.—When disturbed during early morning or late afternoon, or in sparsely vegetated areas, *Cyclura carinata* run directly to and into their burrows. During mid-day in thickly vegetated areas, however, the lizards simply run to a new location at some "safe" distance. Most of the attempts to chase adults into their burrows during mid-day at the SW Blind were unsuccessful. This behavior unfortunately contributes to the ease with which feral dogs and cats are able to capture the lizards.

Cyclura carinata exhibited considerable interisland differences in shyness. This phenomenon appeared to be related to past interference by man and domestic and feral mammals. Lizards on small islands rarely visited by humans were quite tame and would allow approach to within a meter or two. On those islands with heavy human traffic, the mere sight of a human often elicited an escape reaction in the lizards. The lizards on Pine Cay fell about midway between these two extremes.

Like *Sauromalus* (Van Denburgh 1922), *Cyclura* defend themselves by beating their adversaries with their tails. To prevent extraction from crevices and burrows, *Cyclura* inflate their bodies as do *Sauromalus obesus* and *Dipsosaurus dorsalis* (Van Denburgh 1922).

BROKEN TAIL FREQUENCY

Cyclura carinata commonly exhibited broken and regenerated tails; individuals with up to three tail forks have been captured. The incidence of broken and regenerated tails in lizards is often used as an indication of predation rates (Pianka 1967, 1970b; Tinkle and Ballinger 1972; Parker and Pianka 1973). As suggested by Parker and Pianka (1973), however, and substantiated by Vitt *et al.* (1974), social interactions, especially male territorial defense, are responsible for some broken tails.

Among the iguanids at least *Sceloporus magister* (Parker and Pianka 1973; Vitt and Ohmart 1974; Vitt *et al.* 1974), *Urosaurus graciosus* (Vitt and Ohmart 1974), *Urosaurus ornatus* (Vitt 1974), and some populations of *Sceloporus undulatus* (Tinkle and Ballinger 1972) exhibit increasing tail break frequencies with age, presumably due to greater exposure to predators and conspecific conflicts. Adult males of these species also had broken tails more often than females, probably because males are exposed more during territorial defense.

In *Cyclura carinata* there is a general tendency for increased frequency of tail breaks with age, but there appears to be a secondary decline in very large (presumably very old) lizards (Table 25; Fig. 50). This is perhaps because of the social ramifications of tail loss in this species. Experimental and natural observations indicate that social status declines in males experiencing tail loss; adult lizards with abbreviated tails were always subordinant to lizards of equal size (sometimes smaller) with intact tails under captive conditions (see SOCIAL ORGANIZATION). It would presumably be much easier for a challenging male to usurp the territory of a male who had just lost his tail. Considerable time and energy would then necessarily have to be expended by this lizard, first, to regenerate his tail, and second, to re-establish and maintain a territory. This does not even take into account the increased probability of conflict with other territorial males, the decreased certainty of food sources, and the concomitant increase in exposure to predators. Such a series of events must greatly reduce the likelihood of the lizard's survival to large adult size. An analogous decrease in social status, and therefore prospect for survival, would result from tail loss in females even though their territorial behavior is confined to the nesting season. With this information, it is not surprising that very large lizards tend to exhibit fewer broken tails than young adults.

The higher frequency of tail breaks among males of other lizard species is absent in *Cyclura carinata* (Table 25). No significant sexual differences in frequencies within size classes or island populations (or both) were found. Unlike males, which are territorial throughout the

Table 25.—Frequencies of Broken Regenerated Tails by Size Class, Sex, and Island for *Cyclura carinata*.

			SIZE CLASS															
			I		II		III		IV		V		VI		All size classes combined	
			75-124 mm SVL		125-164		F 165-189 M 165-199		F 190-214 M 200-249		F 215-239 M 250-299		F over 240 M over 300			
Island	Sex	Sample Size	Number broken	%	Number broken	%	Number broken	%	Number broken	%	Number broken	%	Number broken	%	Number broken	%
Pine Cay	F	N=56	2	10.0	1	33.3	0	—	5	41.67	8	57.1	1	25.0	17	30.4
	M	N=56	1	6.25	3	37.5	0	—	0	—	8	42.1	4	44.4	16	28.6
Little Water Cay	F	N=17	0	—	1	100.0	0	—	2	66.7	1	16.7	1	50.0	5	29.4
	M	N=16	0	—	0	—	0	—	4	80.0	2	50.0	2	50.0	7	43.8
Water Cay	F	N= 7	1	100.0	0	—	0	—	0	—	1	100.0	0	—	2	28.6
	M	N=10	0	—	0	—	0	—	0	—	2	50.0	1	20.0	3	30.0
All four study islands*	F	N=84	3	12.0	3	50.0	0	—	7	41.2	10	50.0	1	11.1	24	28.6
	M	N=86	1	5.56	3	33.3	0	—	4	36.4	14	48.3	6	35.2	28	32.6

Note: Percentages indicate proportion of particular size and sex sample with tail breaks. Only data for sexed lizards are included. Each juvenile size class (I, II, and III) represents a growth interval of approximately two years. Due to sexual dimorphism in size, adult size classes were defined to include females and males of approximately the same ages.

*Differences between totals shown for all four study islands and the three islands listed in this table represent data from Fort George Cay.

year, female *C. carinata* are territorial only during and following nesting. Females also have smaller activity ranges. However, both male and female strategies appear to be equally expensive with respect to tail breakage. The lack of territoriality in nesting females in lizard species for which tailbreak frequency has previously been studied perhaps accounts for the observed disparity in the proportions of males and females with broken tails in those species.

Interisland comparisons of tail break data indicate only slight differences. Even when all size classes were lumped together, approx-

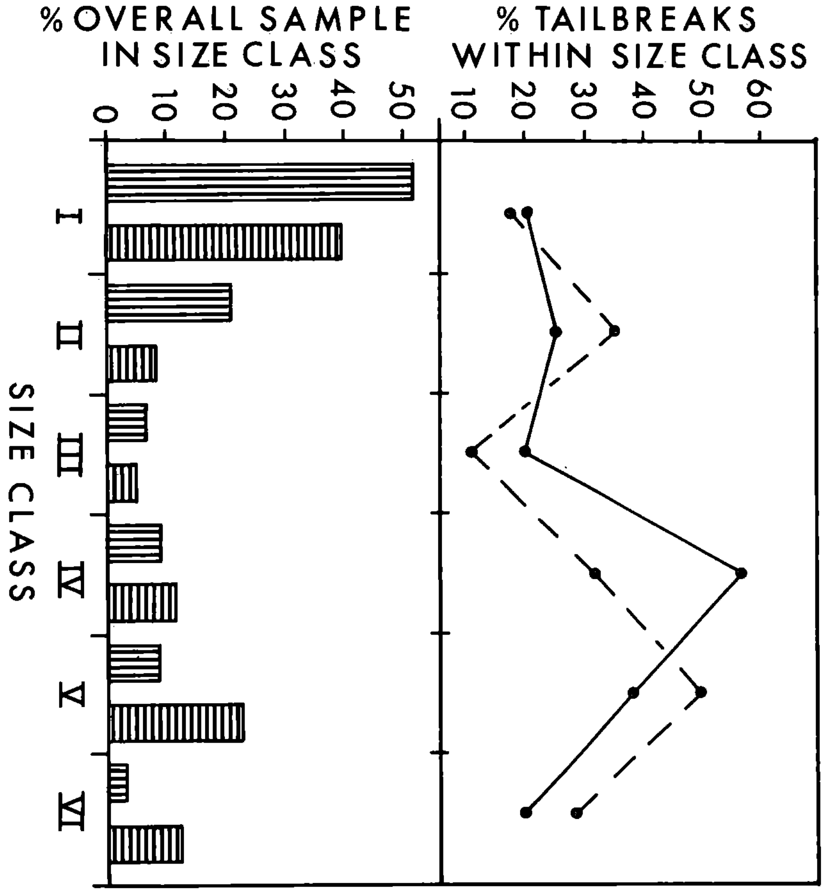

FIGURE 50.—Comparison by size class of tail break frequency in *Cyclura carinata* between islands inhabited by feral mammals versus those uninhabited. Limits of size classes are in Table 25. Vertically hatched bars and solid = Little Water and Fort George cays samples (N = 151 lizards); Horizontally hatched bars and dashed line = Pine and Water cays samples (N = 168). Sexes are lumped since they were not significantly different in any sample.

imately 30% of the captured lizards of each sex had broken tails, no matter on what island the collection was made. This might suggest similar rates of predation on all the islands, which is very definitely not the case. Little Water and Fort George cays are essentially free of introduced predators, while Pine and Water cays are overrun with them. The similar interisland tail break frequencies perhaps show the greater importance of causes other than predation in determining observed tail break frequencies.

EPIFAUNA

Ticks of the genus *Amblyomma* have been recorded as parasites of *Cyclura cornuta* (Robinson 1926; Carey 1975); *C. nubila* (Robinson 1926); *C. pinguis* (Kohls 1969); and *Cyclura cychlura* and *C. rileyi* (Carey 1975). *Amblyomma cruciferum* was found on *C. cornuta*, *A. albopictum* on *C. nubila* (Robinson 1926), and *A. antillorum* on *C. pinguis* (Kohls 1969); no specific identifications of the ticks occurring on the other lizard species are available. In the Caicos Islands, ticks were present on only a single specimen of *C. carinata* from Long Cay. The specimen bore approximately 15 ticks along the lateral regions of its abdomen and in its axillary and inguinal regions. No other ticks were found on over 250 additional lizards checked in the Caicos Islands. The low infestation rate, the proximity of Long Cay to the principal port of entry (by air or sea) to the Caicos Islands, and the frequency of human and pet visitation to the islands suggest the possibility that these ticks have been recently introduced in the Caicos.

ENDOFAUNA

Oxyuroid nematodes were found in the "caecae" of nearly all *Cyclura carinata* dissected. Infestation begins soon after hatching. Although neonates collected in September lacked intestinal worms, by late November and December nearly all lizards contained small caecal nematode faunas (less that 100 worms). The worm burden increases with age. From counts of nematodes in known homogeneous volumes of caecal digesta, estimates of total macroscopic worm burdens exceeded 15,000 in typical adults (300-320 mm SVL).

I isolated at least three different nematodes from the "caecae" of Pine Cay *Cyclura carinata*. Four species (*Cyrtosomum mega*, *Travassozolaimus travassori*, *Macracis microtyphlon*, and *Mamillomacracis cyclurae*) have been described from the intestinal tract of *Cyclura carinata*, but whether the described species correspond to the forms I noted was not determined (Table 26). Much confusion surrounds the taxonomy of the oxyuroid nematodes inhabiting the guts of iguanine lizards, especially within the genus *Cyclura* (Table 26). The systematics of these helminths and their implications to lizard zoogeography deserve attention.

The nearly 100 percent infection rate and the massive nematode infestions found in seemingly healthy *Cyclura carinata* suggest their relationships are not simply parasitic. Perhaps the role is mutualistic, with the nematodes functioning to increase the efficiency of the digestive process (by physical and/or chemical means) much as the microflora in the gut of an herbivorous mammal does (McBee 1971). No other helminths were found in *Cyclura carinata* during this study.

DENSITY AND DEMOGRAPHY

SEX RATIO

Males and females are almost equally represented in all age classes, but due to sexual size dimorphism the same is not true of adult size classes (Fig. 51). The observed sex ratio differs insignificantly from unity, with 51.5 percent of 167 sexed lizards being males.

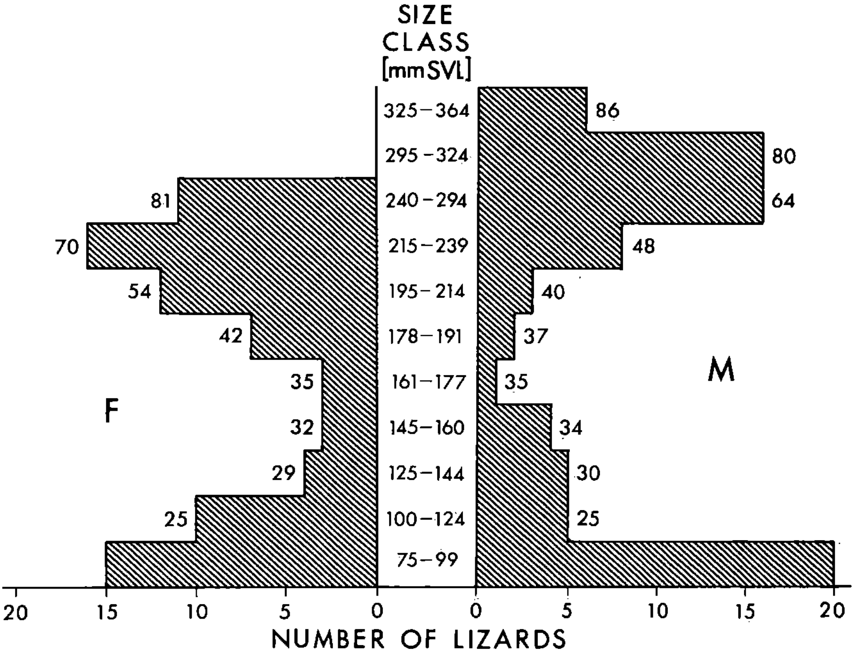

FIGURE 51.—Sex ratio of *Cyclura carinata* by size class. The five smallest size classes approximate yearly age classes. Cumulative totals for each sex are included. Lizards from all islands are combined.

TABLE 26.—NEMATODE PARASITES OF IGUANINE LIZARDS.

Parasite	Host	Source
Atractidae		
Atractis opeotura	*Cyclura nubila* *Cyclura cychlura* *Cyclura cornuta* *Iguana iguana* *Ctenosaura* sp.	Raillet and Henry (1912); Barus *et al.* (1969)
Atractis cruciata	*Cyclura cornuta*	Linstow (1902); Carey (1975)
Cyrtosomum longicaudatum	*Ctenosaura similis*	Brenes and Bravo Hollis (1960); Deloya (1971)
Cyrtosomum mega	*Cyclura carinata*	Bowie and Franz (1974)
Cyrtosomum scelopori	*Ctenosaura hemilopha* *Ctenosaura similis* *Ctenosaura acanthura* *Dipsosaurus dorsalis* *Enyaliosaurus quinquecarinatus* *Sauromalus obesus*	Bravo Hollis (1942); Gambino (1957, 1958); Gambino and Heyneman (1960); Yamaguti (1961)
Oxyuridae		
Aleauris iguanae	*Iguana iguana*	Thapar (1925); Yamaguti (1961)
Alaeuris yumanae	*Dipsosaurus dorsalis*	Edgerly (1952); Yamaguti (1961)
Macracis (=*Ozolaimus*) *ctenosauri*	*Ctenosaura acanthura*	Caballero (1938); Yamaguti (1961)
Macracis (=*Oxyuris*) *microtyphlon*	*Cyclura carinata* *Cyclura nubila*	Barus *et al.* (1969)
Macracis prolixa	"iguana" (Mexico)	Caballero (1943); Caballero and Zerecero (1943)
Ozolaimus monhystera	*Cyclura cornuta* *Cyclura nubila*	Linstow (1902); Perez Vigueres (1936); Barus *et al.* (1969)
Ozolaimus cirratus	*Iguana iguana*	Thapar (1926); Yamaguti (1961)
Ozolaimus magatyphlon	*Ctenosaura similis* *Iguana iguana*	Rudolphi (1819); Yamaguti (1961)
Mamillomacracis cyclurae	*Cyclura nubila* *Cyclura carinata*	Dosse (1939); Barus *et al.* (1969)
Paralaeuris cuckleri	*Cyclura cornuta*	Walton (1942)
Paralaeuris dorochila	*Conolophus subscristatus*	Cuckler (1938)
Pseudalaeuris caudata	*Iguana iguana*	Lent and Frietas (1948)
Pseudalaeuris conolophi	*Conolophus subcristatus*	Cuckler (1938); Walton (1942)
Pseudalaeuris galapogensis	*Conolophus subcristatus*	Cuckler (1938); Walton (1942)
Pseudalaeuris hirsuta	*Iguana iguana*	Walton (1942)
Pseudalaeuris longispicula	*Conolophus subcristatus*	Cuckler (1938); Walton (1942)
Pseudalaeuris vogelsangi	*Iguana iguana*	Lent and Frietas (1948)

TABLE 26, CONTINUED

Tachygonetria longiisthmus	*Iguana iguana*	Dosse (1939); Yamaguti (1961)
Travassozolaimus travassori	*Cyclura nubila* *Cyclura carinata*	Dosse (1939) Barus *et al.* (1969)
Filaroidea		
Oswaldofilaria brevicaudata	*Cyclura nubila* *Iguana iguana* *Ctenosaura* sp.	Frietas y Lent (1937); Rodhain and Vuylsteke (1937); Caballero (1939); Barus *et al.* (1969)

CHARACTERISTICS OF JUVENILE POPULATIONS

SURVIVORSHIP.—Too few juvenile lizards were recaptured to provide accurate estimates of mortality. Therefore, in an attempt to estimate juvenile survivorship, it was necessary to evaluate time-specific juvenile age class distributions (see Deevey 1947, or Giles 1971, for procedures). This assumes a stable age-class distribution, i.e. that age-specific immigration and emigration do not differ (Avery 1975b; among others). Since this species is predominately K-selected (Pianka 1970a), this assumption is probably justified. In all further discussion, it is assumed that mortality rate (proportion of a group which died during some interval) plus survivorship rate (proportion surviving through the same time interval) equals unity.

Age class distributions used to estimate juvenile survivorship in *Cyclura carinata* are in Table 27. Of the four samples presented, the most reliable is that from the Little Water Cay study area (other samples are biased due to small sample sizes and/or interference by man). The Little Water Cay data indicate the annual survivorship rates for the first six years of life as (in percent) 58, 53, 53, 67, 67, and 50, respectively. In general the rates calculated from the other samples support these estimates. Therefore, for simplicity in further discussions I have utilized the following survivorship schedule for juveniles, based mainly on the Little Water Cay results: 55% per year through the first three years of life and 67% per year for years 4 through 6. The age-class distributions observed in the other three samples (see Table 27) are insignificantly different from those expected by this schedule [X^2 for the September 1973 Pine Cay sample is 5.63 (df = 6; $X^2_{0.05}$ = 12.59); for the post-September 1973 captures from all islands except Little Water Cay it is 6.295 (df = 6; $X^2_{0.05}$ = 12.59); and for the dissected sample it is 1.209 (df = 4; $X^2_{0.05}$ = 9.49)].

The calculated juvenile survivorship schedule with its higher mortality in the smaller (and younger) size classes is a logical one. As juvenile iguanas grow, the number of potential natural predators is significantly reduced to a point where diurnal raptors (and large boid

TABLE 27.—JUVENILE AGE CLASS DISTRIBUTIONS FOR VARIOUS SAMPLES OF *Cyclura carinata*.

Age (yrs.)	LWC Study Area	Pine Cay captures Sept. 1973	Post-Sept. 1973 captures on all islands except Little Water Cay	Dissected lizards all islands (See Fig. 51)
< 1	55	14	12	35
< 2	32	6	5	15
< 3	17	5	2	9
< 4	9	0	0	7
< 5	6	0	0	4
< 6	4	2	2	—
< 7	2	1	1	—
Totals	125	28	22	70

NOTE: The first three samples are mutually exclusive; the fourth represents portions of each of the first three.

snakes on islands where they occur) are probably the only significant predators on adults. The schedule further estimates that only about 5 percent of the lizards hatched live to maturity (6 years).

Ctenosaura similis is the only other iguanine species for which population structure and survivorship have been investigated. Fitch (1973a) graphed the change in age structure throughout the year for *Ctenosaura* in Costa Rica. Based on extrapolation from his graph, an annual rate of survival between 25 and 30 percent is indicated for juvenile *Ctenosaura similis* (to age 2). The great pool of potential predators on the mainland undoubtedly accounts for this low survivorship.

DENSITY AND BIOMASS.—The simple Lincoln Index (Southwood 1966; Giles 1971) was employed to estimate juvenile (<195 mm SVL) population size from recapture data on Little Water Cay (Table 28). In all, 103 lizards, including adults, were marked; 15 were recaptured once, and 4 twice. Due to small sample sizes, population estimates based on the Jolly (1965) and Bailey (1951) triple catch methods proved unreliable and are not included in this analysis. The Lincoln Index was computed separately for each pair of consecutive mark-recapture periods. If a new hatchling cohort was added between censuses, however, captures of the neonates were not included in the calculations of original population size. Since juvenile survivorship has been calculated to be 0.55 per year for the first three years of life and 0.67 after age three, an estimate of yearly cohorts can be determined from the equation:

$$T = x + 0.55X + (0.55)^2X + (0.55)^3X + (0.55)^3(0.67)X + (0.55)^3(0.67)^2X + (0.55)^3(0.67)^3X$$

$$\text{or } T = 2.255X$$

TABLE 28.—POPULATION ESTIMATES OF JUVENILE (195 MM SVL) *Cyclura carinata* on Little Water Cay, Based on Mark-Recapture Data.

Original Census		Recensus					Original population estimate, excluding intercensus neonates (P)
Date	Number marked (a)	Date	Total number captured	Number intercensus neonates	Number captures less neonate cohort (n)	Number recaptures (r)	
July 10, 1974	15	Dec. 4, 1974	27	10	17	3	85.0
Dec. 4, 1974	27	Aug. 10, 1975	23	0	23	4	155.2
Aug. 10, 1975	23	June 10, 1976	50	25	25	5	115.0

NOTE: Estimates computed by Lincoln Index Method: P=an/r, where P=estimate, a=total number marked, n=total individuals in second sample, and r=recaptures.

where T = total population size, X = the youngest cohort, and the sum of the exponents in the coefficient of X = age (in years) of the cohort which it represents (Table 29).

It is also possible to apply the previously calculated survivorship schedule to population estimates for times of year other than at hatching in order to determine cohort and total population sizes immediately preceding and following hatching (Table 30). These calculations reveal that the Little Water Cay population typically consists of nearly 170 juveniles in September (post-hatching) and then decreases to just under 100 immediately prior to hatching a year later.

The mean of the extrapolated population estimates (including neonates) for hatching season (from Table 30) was used to estimate juvenile population structure on Little Water Cay study area immediately following hatching (Table 31), when maximum yearly densities obviously occur. Since the study area covers 1.848 ha, lizard density averages 90.3 juveniles/ha at this time. Immediately prior to the addition of the next hatchling cohort, the juvenile population size is estimated to be about 93 (Table 31; excluded neonate estimate) or 98 (Table 30; top). These estimates represent densities of 50.3 and 53.0 lizards/ha respectively. Although this is a considerable decline in lizard numbers (about 43%), biomass decreases relatively little (about 15%); biomass estimates for juvenile age classes during the hatching season are given in Table 31. Immediately following hatching, the Little Water Cay study area supports over 9.5 kg of juvenile lizards (5.15 kg/ha). This vegetatively simple, relatively unproductive Open Scrub habitat at the Little Water Cay study site therefore supports an extraordinary juvenile lizard biomass. This abundance is supported by observations made at the study site during each visit to the island; the lizards always seemed unbelievably abundant. Similar subjective

TABLE 29.—ESTIMATED JUVENILE COHORTS FOR THREE CENSUS DATES BASED ON 0.55 SURVIVORSHIP PER YEAR FOR AGE 0 TO THREE AND 0.67 FOR AGE THREE TO SIX, AND TOTAL POPULATION ESTIMATES FROM TABLE 27.

	Original census date		
Age (yrs.)	July, 1974	December, 1974	August, 1975
< 1	37.7	68.8	51.0
< 2	20.7	37.9	28.0
< 3	11.4	20.8	15.4
< 4	6.3	11.5	8.5
< 5	4.2	7.7	5.7
< 6	2.8	5.1	3.8
< 7	1.9	3.4	2.6
Total	85.0	155.2	115.0

TABLE 30.—POPULATION ESTIMATES FROM TABLE 29 EXTRAPOLATED TO HATCHING SEASON, BASED ON PREVIOUSLY CALCULATED SURVIVORSHIP SCHEDULE (0.55 PER YEAR TO AGE THREE; 0.67 YEAR THREE TO SIX).

	Original census date	Original population estimate	Hatching date extrapolated to	Months extrapolated	Extrapolated population estimate at hatching
Excluding neonates	July 1974	85.0	September 1974	+ 2	78.9
	December 1974	155.2	September 1975	+ 9	104.3
	August 1975	155.0	September 1975	+ 1	110.8
					$\bar{X}$=98.0+13.8
Including neonates	July 1974	85.0	September 1973	−10	134.0
	December 1974	115.2	September 1974	− 3	174.3
	August 1975	115.0	September 1974	−11	192.5
					$\bar{X}$=166.9±24.4

TABLE 31.—ESTIMATED POPULATION STRUCTURE AND BIOMASS OF JUVENILE *Cyclura carinata* Immediately Following Hatching at Little Water Cay Study Area (1.848 ha).

Age	Estimated Number (N)	% Total	$\bar{X}$ Cohort SVL	$\bar{X}$ Cohort Weight in grams (m)	Total Cohort Biomass in kg (N x M)	% Total Biomass
0	74.0	44.3	80	19.0	1.406	14.78
1	40.7	24.4	100	37.4	1.522	15.99
2	22.4	13.4	124	71.8	1.608	16.90
3	12.3	7.4	146	117.8	1.449	15.23
4	8.2	4.9	161	158.5	1.300	13.66
5	5.5	3.3	178	214.9	1.182	12.42
6	3.7	2.2	195	283.5	1.049	11.02
Totals	166.9	99.9	—	—	9.516	100.00

observations on Pine Cay at the beginning of the study, and on Fort George Cay several times during the study, indicate these densities to be typical for juveniles.

CHARACTERISTICS OF ADULT POPULATIONS

SURVIVORSHIP.—Long life and low adult mortality in *Cyclura carinata* made survivorship in adults difficult to determine. Due to the small number of adult recaptures, it was necessary to estimate survivorship from adult age class structure. Table 32 presents the observed population structure of a sample of randomly collected females early in the study. The data indicate the annual survivorship rate, if constant throughout adult life, is approximately 90%. The expected population structure, based on that schedule, also appears in Table 32, and is not significantly different from the observed structure (X^2 = 2.563, df = 6; p = 0.86). The expected adult female population structure with 95% constant annual survivorship is only slightly less significant (X^2 = 2.9995, df = 6; p = ≅ 0.81) than that with the 90% schedule. The assumption that adult mortality in females is constant is probably valid due to the relatively narrow adult size range. In addition this is the typical pattern recorded in most previous studies of lizard populations (Blair 1960; Turner *et al.* 1970; Fitch 1973a; among others), although others have documented changing survivorships from year to year (Turner *et al.* 1969; Turner *et al.* 1969, and Turner *et al.* 1970). A similar, though higher, rate of survival is indicated for males. Observed population structure of males (age-size classes based on average growth rate of field recaptures: 0.66 mm/mon), was significantly different from that expected with constant 90% annual survivorship (X^2 = 26.74, df = 6, p < 0.01). However, the structure ex-

TABLE 32.—POPULATION STRUCTURE OF RANDOMLY COLLECTED SAMPLE OF ADULT FEMALE *Cyclura carinata*.

Age (years)	Approximate SVL Range	Observed Number in Age Class	Expected, if mortality=10%
7-9	197-210	10	13.17
10-12	210-223	9	9.60
13-15	223-236	10	6.99
16-18	236-249	6	5.10
19-21	249-262	4	3.72
22-24	262-275	2	2.71
25 on	275+	1	0.73
Total		42	42.02

NOTE: Age-size classes based on mean adult growth rate of field recaptures (0.36 mm SVL/month). Expected population structure based on 90% annual survivorship is also indicated.

pected if survivorship were 95% annually is not significantly different from that observed ($X^2 = 8.4$, df = 6, $p \cong 0.21$). Survivorship is obviously extremely high in *Cyclura carinata* once maturity is reached. Subjective support for such a high rate of survival comes from my failure ever to find a dead adult or juvenile iguana on Little Water Cay, which to my knowledge, supports no feral mammals and has the highest lizard densities of any island I visited.

The highest adult annual survival rate previously suggested for lizards is approximately 80% for *Xantusia vigilis* in California (Zweifel and Lowe 1966) and *Lacerta vivipara* in England (Avery 1975b). Both are viviparous, relatively long-lived (11 to 12 yr), late-maturing (3 yr), seasonal breeders, with small brood sizes (1-2 and 7-8, respectively). The major difference between these two species lies in the ratio of adult to juvenile mortality. Annual juvenile mortality in *Xantusia* is similar to that of the adult, whereas in juvenile *Lacerta* it is over four times that of the adult. *Xantusia* therefore exhibits a Type I survivorship curve (Deevey 1947; Slobodkin 1962); *Lacerta*, a Type IV curve (Type III of Deevey 1947; Slobodkin 1962).

All other lizard population studies of which I am aware have shown adult annual survivorship to range between about 10 and 65% (*Uta stansburiana* in Texas, Tinkle and Ballinger 1972; and *Sceloporus poinsetti* in Texas, Ballinger 1973, respectively). Although adult survivorship in *Cyclura carinata* is higher that in any other previously studied lizard species, similar rates are likely to be found in other predominately K-selected (Pianka 1970a) species. I would speculate that at least the other undisturbed island-inhabiting iguanines probably also exhibit rates comparable to those in *C. carinata*. Unfortunately adult survivorship has been studied in no other iguanine species.

Because of the difficulty in both marking and observing a population large enough for adequate sample sizes at the SW Blind study site, as well as the interference from feral mammals, it was impossible to evaluate several factors that undoubedly relate significantly to survivorship. Among these are the effects of quality of the habitat, dominance-subdominance relationships among males, and female nest-guarding. Information on these and related factors in this or other island species could be important in understanding the evolution and adaptive significance of lizard social systems.

DENSITY.—Flush transect data were used to compute adult lizard densities by four methods. The first (Method A) was a modification of the Frye strip census method used by Overton (1953) for quail and utilizes the following formula:

$$\text{Density} = \frac{\text{Number}}{\text{Area}} = \frac{N}{2L(2d)} = \frac{N}{4Ld}$$

where N = total number of flushed lizards
L = length of the transect
d = average perpendicular distance from transect line to flushed lizard

This formula assumes equal probability of flushing a lizard anywhere in an area up to two times the average flush distance on either side of the transect line, and tends to underestimate actual lizard density. However, typical average distances were under 6 m, and one could be fairly certain that the majority of all lizards were flushed (and heard) up to twice that distance from the line of transect.

The second method (Method B) utilized only the number of lizards flushed within 10 m of the transect and assumed that all lizards within this boundary could be seen or heard. The density is expressed in the formula:

$$\text{Density} = \frac{\text{Number}}{\text{Area}} = \frac{N}{dL}$$

where N = number of lizards flushed within 10 m
L = length of transect
d = width of transect (in this case, 20 m)

A more direct census method, this formula assumes equal probability of flushing a lizard on the transect line as one 10 m from it. I believe this to be a valid assumption, and therefore accept the accuracy of the density estimate derived from this method. This is despite the argument of Eberhardt (1968) against restriction of the censused strip. A comparison of the results of this method with Method A supports the acceptability of this technique (Table 33).

Method C was a variation of the King strip census method as discussed by Hayne (1949) and expanded by Giles (1971). The following formula was used:

$$\text{Density} = \frac{1}{2L} \sum_{\text{obs}} \frac{1}{dj}$$

where L = transect length, and
dj = distance from transect route to jth animal

A density estimate derived from this formula is based on the generally logical idea that there is a decreasing probability of flushing an animal with increased distance from the transect route, and that the probability is inversely related to that distance (for further discussion and examples see Giles 1971). However, this argument is not strictly valid for *C. carinata*. There seemed to be a threshold distance inside of which nearly all lizards flushed. Only those lizards near (inside or outside)

TABLE 33.—CHANGE IN MAXIMUM CALCULATED DENSITY (NUMBER PER HECTARE) OF ADULT *Cyclura carinata* ALONG FLUSH TRANSECT ROUTE DURING THE COURSE OF FIELD WORK ON PINE CAY, CAICOS ISLANDS.

	Entire Transect				Sector F only			
Date	Method A	Method B	Method C	Method D	Method A	Method B	Method C	Method D
June-July 1974	12.109 N=67 (1130)	13.670 N=61 (1000 & 1130)	28.904 N=64 & 67 (1000 & 1130)	23.873 N=67 (1130)	24.650 N=17 (1200)	22.637 N=15 (1200)	58.093 N= 17 & 17 (1200)	41.987 N=17 (1200)
September 1974	9.795 N=54 (1330)	11.410 N=51 (1330)	22.122 N=50 & 54 (1230 & 1330)	19.657 N=54 (1330)	16.049 N=11 (1300)	19.623 N=13 (1230)	37.620 N=11,13 & 14 (1230, 1300, & 1330)	29.709 N=14 (1230)
April 1975	3.590 N=20 (1330)	3.983 N=18 (1130)	8.436 N=20, 22, 23, & 24 (1000, 1030, 1130 & 1330)	6.620 N=23 (1330)	12.378 N= 9 (1100)	13.584 N= 9 (1100)	27.801 N= 8 & 9 (0930 & 1100)	22.015 N= 9 (1100)
August 1975	2.293 N=11 (1200)	2.239 N=10 (1200)	8.930 N=10 & 11 (1200 & 1400)	4.130 N=11 (1200)	12.454 N= 7 (1200)	12.454 N= 7 (1200)	30.946 N= 7 & 7 (1200)	21.359 N= 7 (1200)
May 1976	0.036 N= 1 (1200)	0.219 N= 1 (1200)	0.072 N= 1 (1200)	— N= 1 (1200)	0 N= 0 —	0 N= 0 —	0 N= 0 —	0 N= 0 —

NOTE: See text for explanation of Methods. Values for Method C are averages of at least two estimates. Number of lizards flushed and time (EST) of transect yielding maximum density follow each estimate. See Figure 3 for transect locations.

this threshold limit seemed to obey a probabilistic model based on distance. Therefore, this method tended to slightly overestimate densities (Tables 33 and 34). The values do, however, provide an upper limit to the estimates.

The final method (Method D) was that of Gates *et al.* (1968) and utilized the formula:

$$\text{Density} = \frac{\text{Number}}{\text{Area}} = \frac{(n)(n-1)}{2L\Sigma d}$$

where n = number of flushed lizards
L = length of transect
d = perpendicular distance from transect line to flushed lizard

This method differs from Method C (basically the King method) only in its measure of 'average' flush distance (see equations). Which measure is the most reliable must await further testing (Gates *et al.* 1968).

Adult densities calculated by the above four methods for Pine Cay flush transect data during June and July 1974 are in Table 34.

Sector A of the transect route, because of its proximity to human activity, supported extremely low densities of lizards even at the beginning of the study. Therefore a reliable estimate of typical adult density should exclude that sector. The mean of all density estimates obtained for sectors B through F by all four methods was 26.88 (N = 20) per hectare. This was undoubtedly a fairly accurate estimate of the density of adult iguanas in the habitat adjacent to the transect route. The vegetative zone represented along most of the transect was Rocky Coppice and this habitat type supported the highest densities of iguanas on the study islands.

Based on the known adult inhabitants of the SW Blind area early in the study, a density of 31.1/ha was indicated. The vegetative type here is also Rocky Coppice. This value further substantiates the accuracy of those obtained from flush transect data.

If the mean distance between active male burrows is calculated and used as an estimate of spacing, another reliable density estimate is obtained. At the SW Blind, mean interburrow distance for males was 26.6 ± 6.9 m (N = 13 measurements) indicating an average male density of 17.99/ha. Since the sex ratio was 1:1, density of all adults should be 35.98. This value corresponds well with the density estimate for the area based on flush transects (Table 34, Sector F; $\overline{X}$ = 36.84). Similarly, mean interburrow distance for adult males on the Little Water Cay sand spit was 37.9 ± 4.7 m, giving a density of 8.85/ha. This is only 65.8% of the density of males expected along the flush transect route on Pine Cay (13.44). However, the dune habitat on this

TABLE 34.—DENSITIES (PER HA) OF ADULT *Cyclura carinata* ALONG FLUSH TRANSECT ROUTE IN PINE CAY, CAICOS ISLANDS, DURING JUNE-JULY 1974.

Sector	A	B	C	D	E	F	Total
Length	426.5 m	376.7 m	304.3 m	605.7 m	235.6 m	339.4 m	2288 m
Density (Method A)	1.130 N=1	12.056 N=8	13.832 N=10	19.267 N=28	18.557 N=8	24.650 N=17	12.109 N=67
Density (Method B)	1.206 N=1	10.882 N=8	15.177 N=9	23.691 N=28	19.580 N=9	22.637 N=15	13.670 N=61
Density (Method C)	2.260 N=1 & 1	26.960 N=8 & 8	29.082 N=10 & 10	45.019 N=28 & 29	40.620 N=8 & 9	58.093 N=17 & 17	28.904 N=64 & 67
Density (Method D)	2.025 N=2	21.021 N=8	24.889 N=10	37.160 N=28	32.491 N=8	41.987 N=17	23.873 N=67
Means	1.656	17.730	20.745	31.284	27.812	36.842	19.639

NOTE: See Figure 3 for location of transect sectors. The SW Blind is part of Sector F. Values for Method C are averages of two estimates. N = number of flushed lizards. Transects with the greatest number of lizards flushed were used for calculations.

spit was the most unstable, unproductive, and simplest of those inhabited by this species.

On Water Cay, in a Dense Scrub vegetational zone, David Auth (MS) calculated an adult density of 9.8/ha; mean male interburrow distances (33.1 ± 9.2 m) suggested a male density of 11.6/ha. These estimates are intermediate between those near the SW Blind and those on the Little Water Cay spit.

Iguana density on the study islands clearly was positively correlated with habitat productivity (i.e. food availability); highest densities occurred in the densely vegetated Rocky Coppice and lowest densities in sparsely vegetated beach areas. Intermediate habitats (e.g. Dense Scrub) had intermediate densities. Since this species was primarily food-limited (see FOOD AND FEEDING) this trend was expected. Lizard density was probably also related to burrow availability in some areas.

BIOMASS.—Since the sex ratio was unity and average adult female and male body weights on Pine Cay were 433.5 and 832.5 gm respectively, the density calculated from the flush transect data represents a biomass of approximately 17.01 kg/ha.

Iguanine lizards, especially those inhabiting islands, typically maintain population biomasses much higher than most lizard species (Table 35). This fact is undoubtedly related to their position in the food chain (primary consumers) as well as the structure of the food web itself (reduced predation on islands, for example). Unfortunately, more data on lizard species' biomass are needed before these relationships can be explored in detail.

Most of the previously studied populations of primarily carnivorous lizards maintain biomasses considerably less that 5 kg/ha (Fitch 1954, 1955, 1975; Harris 1964; Jenssen 1970; Tinkle 1972, 1973; Tanner and Hopkin 1972; Western 1974; Busack 1975; among others). However, *Anolis acutus* (St Croix, U.S. Virgin Islands) has been reported to reach densities of 2000-5600 individuals/ha, and a biomass of 13 to 23 kg/ha (Ruibal and Philobosian 1974); and *Hemidactylus garnoti* (Tinian, Mariana Islands) may reach densities exceeding 22,000/ha (Cagle 1946), over 67 kg/ha if average lizard weight is 3 gm.

Crook (1975) has reported densities of *Sphenodon punctatus* as high as 500 animals/ha or about 250 kg/ha. This is perhaps the greatest biomass known among all reptiles. However, Crook's estimate is based on only 30 individuals occupying an area of 625 m^2. It may represent an aggregation of burrow sites and therefore not accurately reflect the true density for the total area used by the lizards. Carpenter (1966) reported that the biomass of basking *Amblyrhynchus cristatus* may exceed 71,000 kg/ha (4.48 individuals/m^2). Since

TABLE 35.—ESTIMATED BIOMASS IN IGUANINE LIZARDS.

Species	Location	Density per hectare	Estimated Biomass (kg/ha)	Reference
Amblyrynchus cristatus (basking populations only)	Galapagos Islands	44,800	71,000[b]	Carpenter 1966
Cyclura carinata	Caicos Islands, British West Indies	Adults = 26.9 juveniles = 90.3	17.01 5.15 juvs.	Present study
Cyclura cychlura	Exuma Cays, Bahamas	Adults = 19.8	26.96	Carey 1976
Cyclura pinguis	Anegeda, British Virgin Islands	Adults = 2.03 juveniles = 25.00	11.63 21.07	Carey 1975
Dipsosaurus dorsalis	Arizona	juveniles = 10.0 neonates = 18.2	0.224[a] 0.069[a]	Parker 1972
Iguana iguana	Belize	juveniles = 25-41	ca. 2.500[b] to 4.100	Henderson 1974
	Colombia	80	?	Mueller 1972
Sauromalus obesus	California	Adults and immatures = 13.8	2.20[a]	Berry 1974
	California	7.1	1.111[a]	Johnson 1965

[a] Weights used in these calculations estimated from SVL-body weight regression for *Cyclura carinata*.

[b] Values in these calculations estimated from cited data.

this is an obvious aggregation, however, the estimate does not represent average habitat density.

There are few biomass data available for *Cyclura* species. Carey (1975) estimated 11.6 kg of adults and 21.1 kg of juveniles/ha for *C. pinguis*. An adult biomass of 27.0 kg is indicated from Carey's (1976) data on *Cyclura cychlura*. These values correspond well with the 17.0 and 5.15 kg/ha for adult and juvenile *Cyclura carinata*, respectively.

POPULATION SIZE.—It is possible to estimate Pine Cay's total adult *Cyclura* population since lizard density in each habitat type and the area of each habitat type on the island are both known. Densities early in the study in the Dense Scrub and Mesic Coppice habitat types were similar to that in the Rocky Coppice (26.9/ha); densities in areas of Open Scrub and Beach and Rocky Coasts were similar to those obtained from the Little Water Cay sand spit (7.7/ha); and almost no iguanas inhabited areas of Mixed Woodland. The area each habitat type occupies on Pine Cay appears in Table 3. From these data, a total adult population of nearly 5500 is indicated for Pine Cay (total area about 350 ha) in 1976. Since juveniles typically greatly outnumber adults, the total Pine Cay population certainly exceeded 15,000 individuals at the onset of this study.

LIFE TABLES

Based on the survivorship data previously calculated (prenatal mortality = 21.7%; juvenile mortality to age 3 = 45%; juvenile mortality age 3 to 6 = 33%; and adult mortality = 10%), a life table for *Cyclura carinata* was constructed (Table 36). Age-specific fecundity (Table 37) was determined from adult female growth rate and the body size-clutch size regression. Since the sex ratio is 1:1, one half of this age-specific fecundity represents potential female offspring (m_x) in Table 35. The life table data indicate a survivorship schedule fitting Slobodkin's (1962) Type IV curve (=Type III of Deevey 1947) with the incidence of mortality heaviest in the younger iguanas (Fig. 52).

Although the replacement rate value (0.721; Table 38) indicates a declining population, each of my mortality estimates is probably too high. The two estimates of which I am least confident are those of adult and prenatal mortality. A reduction in adult mortality of only 5% (10 to 5%) results in a much more stable age distribution (R_o = 1.155; Table 38). It was shown earlier that while both a 95% and 90% annual survivorship schedule produced age structures which were insignificantly different from the observed adult female population structure, the schedule assuming the 90% rate was less different.

The necessity for such high adult survival rates is apparent when it is realized that only about 4 of 100 offspring (five out of 100 hatch-

TABLE 36.—LIFE TABLE FOR *Cyclura carinata* ON THE STUDY ISLANDS.

X	l_x	d_x	q_x	m_x	l_xm_x	Xl_xm_x
oviposition	1.000	.217	.217	—	—	—
0	.783	.352	.450	—	—	—
1	.431	.194	.450	—	—	—
2	.237	.107	.450	—	—	—
3	.130	.043	.333	—	—	—
4	.087	.029	.333	—	—	—
5	.058	.019	.333	—	—	—
6	.039	.004	.100	1.23	.048	.288
7	.035	.003	.100	1.37	.048	.336
8	.032	.003	.100	1.51	.048	.384
9	.029	.003	.100	1.65	.048	.432
10	.026	.003	.100	1.78	.046	.460
11	.023	.002	.100	1.92	.044	.484
12	.021	.002	.100	2.06	.043	.516
13	.019	.002	.100	2.20	.042	.546
14	.017	.002	.100	2.34	.040	.560
15	.015	.001	.100	2.48	.037	.555
16	.014	.002	.100	2.61	.037	.592
17	.012	.001	.100	2.75	.033	.561
18	.011	.001	.100	2.89	.032	.576
19	.010	.001	.100	3.03	.030	.570
20	.009	.001	.100	3.17	.029	.580
21	.008	.001	.100	3.31	.026	.546
22	.007	.000	.100	3.44	.024	.528
23	.007	.001	.100	3.58	.025	.575
24	.006	.001	.100	3.72	.022	.528
25	.005	.001	.100	3.86	.019	.475

NOTE: X=age in years; l_x=proportion of original population surviving to age X; d_x=proportion of original population dying in age interval; $q_x=d_x/l_x$=proportional mortality of individuals during particular age interval; m_x=age specific fecundity; l_xm_x=contribution to replacement rate (ro) by animals of age X. l_x for age 0=1.000 due to prenatal mortality.

lings) survive to maturity (see Table 36). In order to replace herself successfuly, a newly matured female must produce about 50 eggs in her lifetime.

Reduction in prenatal mortality by one half increases the replacement rate to 0.826; if it is ignored completely, R_o = 0.919 (Table 38). Since the sample on which this mortality was estimated was small, egg mortality may well be overestimated.

Mean generation time ($\Sigma x\ l_xm_x/\Sigma l_xm_x$) for *Cyclura carinata*, calculated from the Life Table (Table 36), is 14.00 years, the longest for any lizard population yet studied.

LIFE HISTORY STRATEGY

The dichotomy of lizard life history strategies suggested by Tinkle *et al.* (1970) has been shown to represent correlates of the extremes of

TABLE 37.—SPECIFIC FECUNDITY OF FEMALE *Cyclura carinata* CALCULATED FROM CLUTCH SIZE-BODY SIZE REGRESSION.

SVL	Probable year class	$\overline{X}$ clutch size
195.0	6	2.46
199.3	7	2.74
203.6	8	3.02
208.0	9	3.30
212.3	10	3.56
216.6	11	3.84
220.9	12	4.12
225.2	13	4.40
229.6	14	4.68
233.9	15	4.96
238.2	16	5.22
242.5	17	5.50
246.8	18	5.78
251.2	19	6.06
255.5	20	6.34
259.8	21	6.62
264.1	22	6.88
268.4	23	7.16
272.8	24	7.44
277.1	25	7.72

NOTE: Age-class body sizes based on estimated female growth rate of 0.36 mm SVL per month.

the r-K selection continuum (Pianka 1970a). The dichotomy has and will necessarily continue to become less distinct as more lizard populations are studied (Tinkle and Ballinger 1972; Ballinger and Schrank 1972; Ballinger 1973; among others). Nevertheless, it remains a useful procedure to rank life history characteristics of a population along the selection continuum for comparison with other populations of the same or different species.

In its slower development, delayed maturity, production of a single annual brood many times, large body size, high intraspecific competition levels (evidenced by its sexual size dimorphism, for example), parental care (here nest defense), and longevity, *Cyclura carinata* is one

TABLE 38.—REPLACEMENT RATES IN *Cyclura carinata* WITH CHANGING COHORT MORTALITIES.

Prenatal Mortality	Juvenile mortality age 0 to 3 years	Juvenile mortality age 3 to 6 years	Annual Adult mortality	R_o
0.217	0.45	0.33	0.10	0.721
0.217	0.45	0.33	0.05	1.155
0.100	0.45	0.33	0.10	0.826
0.000	0.45	0.33	0.10	0.919

of the most K-selected species yet studied (Pianka 1970a). However, its survivorship schedule, with mortality greatest in juveniles, is more characteristic of an r-related strategy. This is undoubtedly related to size-dependent predation pressures and may bear on why *Cyclura carinata* does not produce fewer, larger young (see discussion of reproductive strategy under REPRODUCTION).

Most of the remaining undisturbed populations of other species of *Cyclura* are presumably also predominately K-selected, and I would expect their life-history tactics to be very similar to those of *Cyclura carinata*. It is important that demographic studies of these species, as well as all other iguanines, commence immediately if we are to learn more about these K-strategists; few undisturbed natural populations, at least of the island forms, remain. Of particular potential importance to understanding variation among K-related species is specific knowledge of the demography of the marine iguana (*Amblyrhynchus cristatus*) which, among other things, produces the fewest and largest eggs of all the iguanines (see REPRODUCTION).

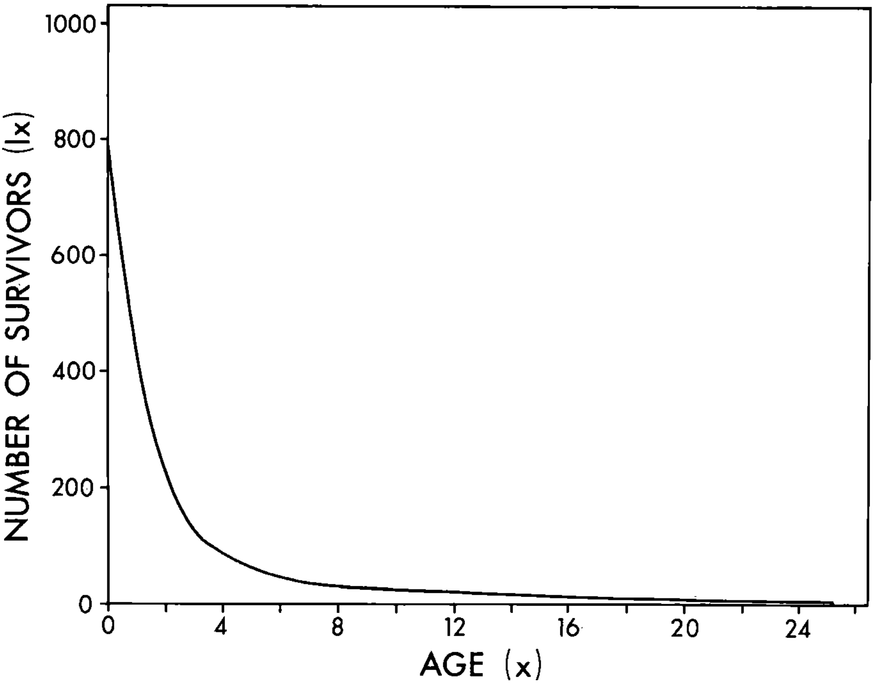

FIGURE 52.—Survivorship curve for 1000 zygotes of *Cyclura carinata*. Survivors (1x) at age 0 (in years) ≠ 1000 due to prenatal mortality.

LITERATURE CITED

Adams, L., and S. D. Davis. 1967. The internal anatomy of home range. J. Mammal. 48:529-536.

Aleksiuk, M., and K. W. Stewart. 1971. Seasonal changes in body composition of the garter snake (*Thamnophis sirtalis parietalis*) at northern latitudes. Ecology 52:485-490.

Alvarez del Toro, M. 1972. Los Reptiles de Chiapas. Inst. Zool. del Estado, Tuxtla Gutierrez, Chiapas, 178 p.

Andrews, R. M. 1971. Structural habitat and time budget of a tropical *Anolis* lizard. Ecology 52:262-270.

_________. 1976. Growth rate in island and mainland anoline lizards. Copeia 1976(3):477-482.

Arlton, A. V. 1936. An ecological study of the mole. J. Mammal. 17:349-371.

Armstrong, J. T. 1965. Breeding home range in the nighthawk and other birds: its evolutionary and ecological significance. Ecology 46:619-629.

Auffenberg, W., and W. G. Weaver, Jr. 1969. *Gopherus berlandieri* in southeastern Texas. Bull. Fla. State Mus., Biol. Sci. 13(3):141-203.

Avery, R. A. 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. J. Anim. Ecol. 40:351-365.

_________. 1975a. Clutch size and reproductive effort in the lizard *Lacerta vivipara* Jacquin. Oecologia (Berlin) 19:165-170.

_________. 1975b. Age-structure and longevity of common lizard (*Lacerta vivipara*) populations. J. Zool., London 176:555-558.

Avery, D. F., and W. W. Tanner. 1971. Evolution of the iguanine lizards (Sauria, Iguanidae) as determined by osteological and myological characters. Brigham Young Univ. Sci. Bull. 12:1-79.

Bailey, A. M. 1925. The iguanas of Bitter Guana Cay. Nat. Hist. 25:390-393.

Bailey, N. T. J. 1951. On estimating the size of mobile populations from recapture data. Biometrika 38:293-306.

Ballinger, R. E. 1973. Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). Ecology 54:269-283.

_________, and G. D. Schrank. 1972. Reproductive potential of female whiptail lizards, *Cnemidophorus gularis gularis*. Herpetologica 28:217-222.

Bartholomew, G. A. 1966. A field study of temperature relations in the Galapagos marine iguana. Copeia 1966(2):241-250.

_________, A. F. Bennett, and W. R. Dawson. 1976. Swimming, diving, and lactate production of the marine iguana, *Amblyrhynchus cristatus*. Copeia 1976(4):709-720.

Barus, V., A. C. Otero, and O. H. Garrido. 1969. Helmintofauna de *Cyclura macleayi* Gray (Sauria, Iguanidae) en Cuba. Torreia, Nueva Ser. 8:1-20.

Beard, J. S. 1949. The natural vegetation of the Windward and Leeward Is. Oxford Forestry Memoir 21:1-192.

Beebe, W. 1944. Field notes on the lizards of Kartabo, British Guinea, and Caripito, Venezuela. Part 2. Iguanidae. Zoologica 29:195-216.

Berry, K. H. 1974. The ecology and social behavior of the chuckwalla, *Sauromalus obesus obesus* Baird. Univ. of California Publ. Zool. 101:1-60.

Berry, P. Y., and G. S. Lim. 1967. The breeding pattern of the puff-faced water snake, *Homalopsis buccata* Boulenger. Copeia 1967(3):307-313.

Blair, W. F. 1960. The rusty lizard: A population study. Univ. Texas Press, Austin, 185 p.

Bond, J. 1961. Birds of the West Indies. Houghton Mifflin, Boston, 256 p.

Bowler, J. K. 1977. Longevity of reptiles and amphibians in North American collections. SSAR Misc. Publ., Herpet. Circular 6:1-32.

Bowie, A. 1973. Predation on lizards by *Sceloporus woodi.* J. Herpetol. 7:318.

_________, and R. Franz. 1974. *Cyrtosomum mega* sp. n. (*Nematoda: Oxyuroidea*) from the lizard, *Cyclura carinata.* J. Parasitol. 60:628-631.

Brattstrom, B. H. 1974. The evolution of reptilian social behavior. Amer. Zool. 14:35-39.

Bravo-Hollis, M. 1942. Acerca de un nematoda parasito de la iguana, *Ctenosaura acanthura* (Shaw). An. Inst. Biol. Mexico 13:533-537.

Brenes, R. R., and M. Bravo-Hollis. 1960. Helmintos de la Republica de Costa Rica. IX. Nematoda 3. Algunos nematodos de reptiles, con descripcion de dos nuevas especies: *Atractis caballeroi* n. sp. y *Cyrtosomum longicaudatum* n. sp. Edit. Politechnica Mexico Libro. Homenaje al Dr. E. Caballero y Caballero:451-464.

Buden, D. W. 1974. Prey remains of barn owls in the southern Bahama Islands. Wilson Bull. 86:336-343.

_________. 1975. A taxonomic and zoogeographic appraisal of the big-eared bat (*Macrotus waterhousii* Gray) in the West Indies. J. Mammal. 56:758-769.

Buide, M. S. 1951. Observations on habits of the Cuban iguana. Herpetologica 7:124.

Burge, J. R., and C. D. Jorgensen. 1973. Home range of small mammals: a reliable estimate. J. Mammal. 54:483-488.

Burt, C. E. 1928. Insect food of Kansas lizards with notes on feeding habits. J. Kansas Ent. Soc. 1:50-68.

Busack, S. D. 1975. Biomass estimates and thermal environment of a population of the fringe-toed lizard, *Acanthodactylus pardalis.* Brit. J. Herpetol. 5:457-459.

Bustard, H. R. 1969. Tail abnormalities in reptiles resulting from high temperature egg incubation. Brit. J. Herpetol. 4:121-123.

_________. 1970a. Turtles and an Iguana in Fiji. Oryx 10:317-322.

_________. 1970b. The role of behavior in the natural regulation of numbers in the gekkonid lizard *Gehyra variegata.* Ecology 51:724-728.

_________, and P. R. A. Maderson. 1965. The eating of shed epidermal material in Squamate reptiles. Herpetologica 21:306-308.

Caballero y C., E. 1938. Nematodes parasites des reptiles du Mexique. Ann Parasitol. 16:327-333.

_________. 1939. Nematodos de los reptiles de Mexico. II. An. Inst. Biol. Mexico 10:73-82.

_________. 1943. Nematodos de los reptiles de Mexico. VII. Acerca de la presencia de *Camallanus scabrae* MacCallum, 1918 en las tortugas de aguas dulce, del sureste de Mexico (English summary). An. Inst. Biol. Mexico 14:195-200.

_________, and M. C. Zerecero. 1943. Nematodos de los reptiles de Mexico. VIII. Descripcion de tres nuevas especies. An. Inst. Biol. Mexico 14:527-539.

Cagle, F. R. 1946. A lizard population on Tinian. Copeia 1946 (1):4-9.

Cahill, C. 1970. The banded iguana of Fiji. Fiji Mus. Educ. Ser. 2:1-14.

Carey, W. M. 1966. Observations on the ground iguana *Cyclura macleayi caymanensis* on Cayman Brac, British West Indies. Herpetologica 22:265-268.

_________. 1972. The herpetology of Anegada, British Virgin Islands. Carib. J. Sci. 12:79-89.

_________. 1973. Some notable longevity records for captive iguanas. Intl. Zoo Yearbook 13:154-156.

_________. 1975. The rock iguana, *Cyclura pinguis,* on Anegada, British Virgin Islands, with notes on *Cyclura ricordi* and *Cyclura cornuta* on Hispaniola. Bull. Florida St. Mus., Biol. Sci. 19(4):189-233.

_________. 1976. Iguanas of the Exumas. Wildlife 5:59-61.

Carpenter, C. C. 1961. Patterns of social behavior in the desert iguana, *Dipsosaurus dorsalis.* Copeia 1961(4):396-405.

_________. 1962a. Patterns of behavior in two Oklahoma lizards. Amer. Midl. Natur. 67:132-151.

_________. 1962b. A comparision of the patterns of display of *Urosaurus, Uta* and *Streptosaurus*. Herpetologica 18:145-152.

_________. 1966. The marine iguana of the Galapagos Islands, its behavior and ecology. Proc. California Acad. Sci. 34:329-376.

_________. 1967. Aggression and social structure in iguanid lizards. pp. 87-105 *In:* W. W. Milstead, ed. Lizard Ecology, a Symposium. Univ. Missouri Press, Columbia.

_________. 1969. Behavioral and ecological notes on the Galapagos land iguanas. Herpetologica 25:155-164.

_________. 1977. The display of *Enyaliosaurus clarki* (Iguanidae: Lacertilia). Copeia 1977(4):754-756.

_________, and G. Grubitz III. 1961. Time-motion study of a lizard. Ecology 42:199-200.

Carr, A. F. 1953. High jungles and low. Univ. Florida Press, Gainesville, 225 p.

_________, and H. Hirth. 1961. Social facilitation in Green Turtle siblings. Anim. Behavior 9:68-70.

Case, T. J. 1976. Body size differences between populations of the chuckwalla, *Sauromalus obesus*. Ecology 57:313-323.

Christian, D. P. 1975. Vulnerability of meadow voles, *Microtus pennsylvanicus*, to predation by domestic cats. Amer. Midl. Natur. 93:498-502.

Church, G. 1962. The reproductive cycles of the Javanese house gecko *Cosymbotus platyurus, Hemidactylus frenatus* and *Peropus mutilatus*. Copeia 1962(2):262-269.

Clarke, R. L. 1963. An ethological study of the iguanid lizard genera *Callisaurus, Cophosaurus* and *Holbrookia*. Emporia State Res. Stud. 13:1-66.

Cochran, D. M. 1931. New Bahaman reptiles. J. Washington Acad. Sci. 21:39-40.

_________. 1934. Herpetological collections from the West Indies made by Dr. Paul Bartsch under the Walter Rathbone Bacon scholarship, 1928-1930. Smithsonian Misc. Coll. 92:1-48.

Cogger, H. G. 1974. Voyage of the banded iguana. Australian Natur. Hist. 18:144-149.

Coman, B. J., and H. Brunner. 1972. Food habits of the feral house cat in Victoria. J. Wildl. Mgt. 36:848-853.

Cooper, J. E. 1958. Ecological notes on some Cuban lizards. Herpetologica 14:53-54.

Cope, E. D. 1896. On the hemipenes of the Sauria. Proc. Acad. Nat. Sci. Phila.:461-467.

Cowles, R. B. 1946. Notes on the arboreal feeding habits of the desert iguana. Copeia 1946(3):172-173.

_________, and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Natur. Hist. 83:261-296.

Crenshaw, J. W., Jr. 1955. The life history of the southern spiny lizard, *Sceloporus undulatus undulatus* Latreille. Amer. Midl. Natur. 54:257-298.

Crews, D. 1973a. Behavioral correlates to gonadal state in the lizard, *Anolis carolinensis*. Hormones and Behavior 4:307-313.

_________. 1973b. Coition-induced inhibition of sexual receptivity in female lizards (*Anolis carolinensis*). Physiol. Beh. 11:463-468.

_________. 1975a. Inter- and intraindividual variation in display patterns in the lizard, *Anolis carolinensis*. Herpetologica 31:37-47.

_________. 1975b. Effects of different components of male courtship behavior on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. Anim. Behav. 23:349-356.

Crook, I. G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the polynesian rat, *Rattus exulans* (Peale). Proc. New Zealand Ecol. Soc. 20:115-120.

________. 1975. The Tuatara. Biogeography and ecology in New Zealand Wildlife Publ. 167:331-352.

Cuckler, A. C. 1938. Nematode parasites of the Galapagos land iguana. Rep. Hancock Pacific Exped. (1932-1938) 2:137-165.

Cuellar, O. 1970. Egg transport in lizards. J. Morph. 130:129-136.

D'Arcy, W. G. 1975. Anegada Island: vegetation and flora. Atoll Res. Bull. 188:1-40.

Davis, D. E. 1953. Analysis of home range from recapture data. J. Mammal. 34:352-358.

Davis, W. G., and J. R. Dixon. 1961. Reptiles (exclusive of snakes) of the Chilpancingo region, Mexico. Proc. Biol. Soc. Washington 74:37-56.

________, and H. M. Smith. 1953. Lizards and turtles of the Mexican state of Morelos. Herpetologica 9:100-108.

Deevey, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.

Deloya, J. C. 1971. Redescripcion de *Cyrtosomum longicaudatum* Brenes y Bravo, 1960. An. Inst. Biol. Mexico, Ser. Zool. 42:29-34.

Denny, R. N. 1974. The impact of uncontrolled dogs on wildlife and livestock. Trans. 39th North Amer. Wildl. and Nat. Res. Conf.:257-291.

Derickson, W. K. 1974. Lipid deposition and utilization in the sagebrush lizard, *Sceloporus graciosus:* its significance for reproduction and maintenance. Comp. Biochem. Physiol. 49A:267-272.

Dessauer, H. C. 1955. Seasonal changes in the gross organ composition of the lizard *Anolis carolinensis.* J. Exp. Zool. 128:1-12.

________, and W. Fox. 1959. Changes in ovarian follicle composition with plasma levels of snakes during estrus. Amer. J. Physiol. 197:360-366.

DeVries, T. 1974. Opmerkingen over taxonomie en ecologie van de reptilien van de Galapagos-eilanden II. Landleguanen en Zeeleguanen. Lacerta 32:95-106.

Dodge, N. N. 1938. Amphibians and reptiles of Grand Canyon National Park. Grand Canyon Nat. Hist. Assoc., Nat. Hist. Bull. 9:1-55.

Dosse, G. 1939. Uber einige Nematoden aus *C. carinata* R. Harlan, 1824 (*Macracis monhystera* v. Linstow, 1902; *Travassozolaimus travassosi* Vigueras, 1938; *Mammillomacracis cyclurae* n. g., n. sp.). Zeitschrift fur Parasitenkunde 10:694-703.

Douglass, J. F. 1975. Bibliography of the North American land tortoises (genus *Gopherus*). Fish and Wildl. Serv. Spec. Sci. Rept. 190:1-60.

Dowling, H. G. 1964. Goats and hawks — a new theory of predation on the land iguana. Animal Kingdom 67:51-56.

Dubuis, A., L. Faurel, C. Grenot, and R. Vernet. 1971. Sur le regime alimentaire du lizard saharien *Uromastix acanthinurus.* C. R. Acad. Sci. Paris, Ser. D 273:500-503.

Duellman, W. E. 1961. The amphibians and reptiles of Michoacan, Mexico. Univ. Kansas, Publ. Mus. Nat. Hist. 15:1-148.

________. 1965. Amphibians and reptiles from the Yucatan peninsula, Mexico. Univ. Kansas, Publ. Mus. Nat. Hist. 15:577-614.

________, and A. S. Duellman. 1959. Notes on the variation, distribution, and ecology of the iguanid lizard *Enyaliosaurus clarki.* Occ. Pap. Mus. Zool. Univ. Michigan 598:1-10.

Dutton, R. H., L. C. Fitzpatrick, and J. L. Hughes. 1975. Energetics of the rusty lizard *Sceloporus olivaceus.* Ecology 56:1378-1387.

Eberhardt, L. 1968. A preliminary appraisal of line transects. J. Wildl. Mgmt. 32:82-88.

Edgerly, R. H. 1952. A new oxyurid nematode, *Alaeuris yumanae* n. sp. from the lizard *Dipsosaurus dorsalis.* Trans. Am. Micro. Soc. 71:341-343.

Eibl-Eibesfeldt, I. 1955. Der Kommentkampf der meerechse (*Amblyrhynchus cristatus* Bell) nebst einigen notizen zur biologie dieser art. Zeitschrift fur Tierpsychologie 12:49-62.

_________. 1961. Galapagos: The Noah's Ark of the Pacific. Doubleday, New York, 192 p.

_________. 1966. Das verteidigen der eiablageplatze bei der Hood-Meerechse (*Amblyrhynchus cristatus venustissimus*). Zeitschrift fur Tierpsychologie 23:127-213.

Essghaier, M. F. A., and D. R. Johnson. 1975. Aspects of the bioenergetics of Great Basin lizards. J. Herpetol. 9:191-195.

Evans, L. T. 1938. Courtship behavior and sexual selection of *Anolis.* J. Comp. Psychol. 26:475-496.

_________. 1951. Field study of the social behavior of the black lizard, *Ctenosaura pectinata.* Amer. Mus. Nov. 1493:1-26.

Eyerdam, W. J. 1954. With Dr. Eric Ekman in southern Haiti, in the summer of 1927. Field and Laboratory 22:85-105.

Ferguson, G. W. 1970. Mating behavior of the side-blotched lizards of the genus *Uta* (Sauria: Iguanidae). Anim. Behav. 18:65-72.

_________. 1971. Variation and evolution of the push-up displays of the side-blotched lizard genus *Uta* (Iguanidae). Syst. Zool. 20:79-101.

_________. 1972. Species discrimination by male side-blotched lizards *Uta stansburiana* in Colorado. Amer. Midl. Natur. 87:523-524.

_________. 1976. Color change and reproductive cycling in female collared lizards (*Crotaphytus collaris*). Copeia 1976(3):491-494.

Fitch, H. S. 1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus.* Univ. Kansas, Publ. Mus. Nat. Hist. 8:1-156.

_________. 1955. Habits and adaptations of the Great Plains skink *Eumeces obsoletus.* Ecol. Monogr. 25:59-83.

_________. 1956. An ecological study of the collared lizard (*Crotaphytus collaris*). Univ. Kansas, Publ. Mus. Nat. Hist. 8:213-274.

_________. 1960. Autecology of the copperhead. Univ. Kansas, Publ. Mus. Nat. Hist. 13:85-288.

_________. 1963. Natural history of the racer *Coluber constrictor.* Univ. Kansas, Publ. Mus. Nat. Hist. 15:351-468.

_________. 1970. Reproductive cycles in lizards and snakes. Univ. Kansas, Mus. Nat. Hist., Misc. Publ. 52:1-247.

_________. 1973a. Population structure and survivorship in some Costa Rican lizards. Occ. Papers Univ. Kansas Mus. Nat. Hist. 18:1-41.

_________. 1973b. A field study of Costa Rican lizards. Univ. Kansas Sci. Bull. 50:39-126.

_________. 1975. A demographic study of the ringneck snake (*Diadophis punctatus*) in Kansas. Univ. Kansas, Mus. Nat. Hist., Misc. Publ. 62:1-53.

_________, and R. W. Henderson. 1977a. Age and sex differences in the ctenosaur (*Ctenosaura similis*). Contrib. Biol. Geol. Milwaukee Public Mus. 11:1-11.

_________. 1977b. Age and sex differences, reproduction, and conservation of *Iguana iguana.* Contrib. Biol. Geol. Milwaukee Public Mus. 13:1-21.

Fleet, R. R., and H. S. Fitch. 1974. Food habits of *Basiliscus basciliscus* in Costa Rica. J. Herpetol. 8:260-262.

Free, J. D., R. M. Hansen, and P. L. Sims. 1970. Estimating the dry weights of foodplants in feces of herbivores. J. Range Mgmt. 23:300-302.

Freeland, G. L., and R. S. Dietz. 1971. Plate tectonic evolution of Caribbean-Gulf of Mexico Region. Nature 232:20-23.

Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. Amer. Natur. 108:269-289.

Freitas, J. F. Teixeira De, and H. Lent. 1937. Sobre *Oswaldofilaria brevicaudata* (Rodhain et Vuylsteke, 1937) n. comb. Mem. Inst. Oswaldo Cruz 32:439-442.

Gaffney, F. G., and L. C. Fitzpatrick. 1973. Energetics and lipid cycles in the lizard *Cnemidophorus tigris*. Copeia 1973(3):446-452.

Gambino, J. J. 1957 Relationships of North American Iguanidae as suggested by an analysis of their pinworm parasites, *Cyrtosomum* spp. Anat. Record 128:553-554.

_________. 1958. *Cyrtosomum readi* n. sp. and *Cyrtosomum heynemani* n. sp. (Oxyuroidea: Atractidae) two new pinworms of iguanids. J. Parasit. 44:439-445.

_________, and D. Heyneman. 1960. Specificity and speciation in the genus *Cyrtosomum* (Nematoda: Atractidae). Amer. Midl. Natur. 63:365-382.

Garman, S. 1888. On West Indian reptiles. Iguanidae. Bull. Essex Inst. 19:119-138.

Gates, G. O. 1957. Herpetofauna near Wickenburg, Arizona. Trans. Kansas Acad. Sci. 60:403-418.

Gates, C. E., W. H. Marshall, and D. P. Olson. 1968. Line transect method of estimating grouse population densities. Biometrics 24:135-145.

George, W. G. 1974. Domestic cats as predators and factors in winter shortages of raptor prey. Wilson Bull. 86:384-396.

Giles, R. H., Jr. (ed.). 1971. Wildlife management techniques. The Wildlife Society, Washington, D. C., 633 p.

Goin, C. J., and O. B. Goin. 1962. Introduction to herpetology. W. H. Freeman and Co., San Franscisco, 353 p.

Goldberg, S. R. 1972. Seasonal weight and cytological changes in the fat bodies and liver of the iquanid lizard *Sceloporus jarrovi* Cope. Copeia 1972(2):227-232.

Golley, F. B. 1969. Caloric value of wet tropical forest vegetation. Ecology 50:517-519.

Gonzales, R. B. 1974. Behavior notes on captive *Hydrosaurus pustulosus*. Silliman J. 21:129-138.

Gosse, P. H. 1848. On the habits of *Cyclura lophoma*, an Iguaniform lizard. Proc. Zool. Soc. London 16:99-104.

Grant, C. 1937. Herpetological notes with new species from the American and British Virgin Islands, 1936. J. Dept. Agric., Univ. Puerto Rico 21:503-522.

_________. 1940a. The herpetology of Jamaica. II. The reptiles. Bull. Inst. of Jamaica, Sci. Ser. 1:63-148.

_________. 1940b. The herpetology of the Cayman Islands. Bull. Inst. Jamaica, Sci. Ser. 2:1-65.

_________. 1944. *Cyclura stejnegeri* — a portrait. Herpetologica 2:139-140.

Greenberg, N. 1973. Behavior studies of the blue spiny lizard. Unpublished Ph.D. Dissertation. Rutgers Univ., Newark, N. J., 222 p.

_________. 1976. Observations of social feeding in lizards. Herpetologica 32:348-352.

Groves, J. D. 1971. Cannibalism in a captive *Sceloporus undulatus hyacinthinus*. J. Herpetol. 5:205.

Haast, W. E. 1969. Hatching rhinoceros iguanas (*Cyclura cornuta*) at the Miami serpentarium. Intl. Zoo Yearbook 9:49.

Hahn, W. E. 1964. Seasonal changes in testicular and epididymal histology and spermatogenic rate in the lizard *Uta stansburiana stejnegeri*. J. Morph. 115:447-460.

________, and D. W. Tinkle. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. J. Exp. Zool. 158:79-86.

Hall, R. J. 1972. Food habits of the Great Plains skink (*Eumeces obsoletus*). Amer. Midl. Natur. 87:258-263.

Hallinan, T. 1920. Notes on lizards of the Canal Zone, Isthmus of Panama. Copeia 83:45-49.

Hansen, R. M. 1974. Dietary of the Chuckwalla, *Sauromalus obesus*, determined by dung analysis. Herpetologica 30:120-123.

________, M. K. Johnson, and T. R. Van Devender. 1976. Foods of the desert tortoise, *Gopherus agassizii*, in Arizona and Utah. Herpetologica 32:247-251.

Hardy, J. D. 1956. Notes on the Cuban iguana. Herpetologica 12:323-324.

Harlan, R. 1825. Description of two species of Linnean *Lacerta*, not before described and construction of the new genus *Cyclura*. J. Acad. Nat. Sci., Phila. (1)4:242-251.

Harlow, H. J., S. S. Hillman, and M. Hoffman. 1976. The effect of temperature on digestive efficiency in the herbivorous lizard, *Dipsosaurus dorsalis*. J. Comp. Physiol. 1118:1-6.

Harris, V. A. 1964. The life of the rainbow lizard. Hutchinson Trop. Monogr., Hutchinson and Co., London, 174 p.

Hayne, D. W. 1949. An examination of the strip census method for estimating animal populations. J. Wildl. Mgmt. 13:145-157.

Henderson, R. W. 1973. Ethoecological observations of *Ctenosaura similis* (Sauria: Iguanidae) in British Honduras. J. Herpetol. 7:27-34.

________. 1974. Aspects of the ecology of the juvenile common iguana (*Iguana iguana*). Herpetologica 30:327-332.

Hirth, H. F. 1963a. Some aspects of the natural history of *Iguana iguana* on a tropical strand. Ecology 44:613-615.

________. 1963b. The ecology of two lizards on a tropical beach. Ecol. Monogr. 33:83-112.

Haddenbach, G. A., and F. B. Turner. 1968. Clutch size in *Uta stansburiana* in southern Nevada. Amer. Midl. Natur. 80:262-265.

Hotton, N. 1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. Amer. Midl. Natur. 53:88-114.

Hunsaker, D. 1962. Ethological isolating mechanisms in the *Sceloporus torquatus* group of lizards. Evolution 16:62-74.

________, and B. R. Burrage. 1969. The significance of interspecific social dominance in Iguanid lizards. Amer. Midl. Natur. 81:500-511.

Irwin, L. N. 1965. Diel activity and social interaction of the lizard *Uta stansburiana stejnegeri*. Copeia 1965(1):99-101.

Iverson, J. B. 1978. The impact of feral cats and dogs on populations of the West Indian rock iguana, *Cyclura carinata*. Biol. Cons. 14:63-73.

________. 1980. Colic modifications in Iguanine lizards. J. Morph.

Jackson, J. F. 1974. Utilization of periods of high sensory complexity for site change in two lizards. Copeia 1974(3):785-787.

Jameson, E. W. 1974. Fat and breeding cycles in a montane population of *Sceloporus graciosus*. J. Herpetol. 8:311-322.

Janzen, D. H. 1971. Seed predation by animals. Ann Rev. Ecol. Syst. 2:465-495.

________. 1976. Reduction of *Mucuna andreana* (Leguminosae) seedling fitness by artificial seed damage. Ecology 57:826-828.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. J. Theoret. Biol. 22:227-237.

Jenssen, T. A. 1970. The ethoecology of *Anolis nebulosus* (Sauria Iguanidae). J. Herpetol. 4:1-38.

_________. 1971. Display analysis of *Anolis nebulosus* (Sauria, Iguanidae). Copeia 1971(1):197-209.

_________. 1975. Display repertoire of a male *Phenacosaurus heterodermus* (Sauria: Iguanidae). Herpetologica 31:48-55.

Jewell, P. A. 1966. The concept of home range in mammals. Symp. Zool. Soc. Lond. 18:85-109.

Johnson, C. R. 1965. The diet of the Pacific fence lizard, *Sceloporus occidentalis occidentalis* (Baird and Girard) from northern California. Herpetologica 21:114-117.

Johnson, S. R. 1965. An ecological study of the chuckwalla, *Sauromalus obesus*, in the western Mojave Desert. Amer. Midl. Natur. 73:1-29.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration — stochastic model. Biometrika 52:225-247.

Jorgensen, C. D., and W. W. Tanner. 1963. The application of the density probability function to determine the home ranges of *Uta stansburiana* and *Cnemidophorus tigris tigris*. Herpetologica 19:105-115.

Kaufmann, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica* on Barro Colorado Island, Panama. Univ. Calif. Publ. Zool. 60:95-222.

_________. 1971. Is territoriality definable? pp. 36-40, *In:* A. H. Esser, ed., Behavior and Environment. Plenum Press, New York.

Kennedy, J. P., and H. L. Brockman. 1965. Stomach stone in the American alligator, *Alligator mississippiensis* Daudin. British J. Herpetol. 3:201-203.

Kitchell, J. F., and J. T. Windell. 1972. Energy budget for the lizard, *Anolis carolinensis*. Physiol. Zool. 45:178-188.

Klingel, G. C. 1929. Lizard hunting in the Black Republic. Nat. Hist. 29:450-464.

Kohls, G. M. 1969. A new species of *Amblyomma* from iguanas in the Caribbean (Acarina: Ixodidae). J. Med. Entomol. 6:439-442.

Korschgen, L. J. 1962. Food habits of greater prairie chickens in Missouri. Amer. Midl. Natur. 68:307-318.

Krekorian, C. O. 1976. Home range size and overlap and their relationship to food abundance in desert iguana, *Dipsosaurus dorsalis*. Herpetologica 32:405-412.

_________. 1977. Homing in the desert iguana, *Dipsosaurus dorsalis*. Herpetologica 33:123-127.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London, 343 p.

Lando, R. V., and E. E. Williams. 1969. Notes on the herpetology of the U. S. Naval Base at Guantanamo Bay, Cuba. Studies Fauna Curacao and other Caribbean Islands 31:159-201.

Lazell, J. O. 1973. The lizard genus *Iguana* in the Lesser Antilles. Bull. Mus. Comp. Zool. 145:1-28.

Lent, H., and J. F. Teixeira de Freitas. 1948. Una colecao de nematodeos, parasitos de vertebrados, do Museu de Historia Natural de Montevideo. Mem. Inst. Osev. Cr. 46:1-71.

Lewis, C. B. 1944. Notes on *Cyclura*. Herpetologica 2:92-98.

_________. 1946. Jamaican lizards. pp. 34-36, *In:* C. B. Lewis, ed., Glimpses of Jamican Natural History. Vol. II. Inst. of Jamaica.

Licht, P. 1974. Response of *Anolis* lizards to food supplementation in nature. Copeia 1974(1):215-221.

_________, and R. E. Jones. 1967. Effects of exogenous prolactin on reproduction and growth in adult males of the lizard *Anolis carolinensis*. Gen. Comp. Endocrinol. 8:228-244.

_________, and W. R. Moberly. 1965. Thermal requirements for embryonic development in the tropical lizard *Iguana iguana*. Copeia 1965(4):515-517.

Linstow, O. von. 1902. *Atractis cruciata* und *Oxyuris monhystera*, zwei Nematoden aus *Metopoceros cornutus*. Centralbl. Bakt. 1 Abt. Orig. 31:28-32.

Loftin, H., and E. L. Tyson. 1965. Iguanas as carrion eaters. Copeia 1965(4):515.

Lynn, W. G., M. C. O'Brien, and P. Herhenreader. 1966. Thyroid morphology in lizards of the families Iguanidae and Agamidae. Herpetologica 22:90-93.

MacKay, W. P. 1975. The home range of the banded rock lizard *Petrosaurus mearnsi* (Iguanidae). Southwestern Natur. 20:113-120.

Mares, M. A. 1971. Coprophagy in the Texas tortoise, *Gopherus berlandieri*. Texas J. Sci. 23:300-301.

Marshall, A. J., and R. Hook. 1960. The breeding biology of equatorial vetebrates: reproduction of the lizard *Agama agama* Boulenger at latitude 0°01'N. Proc. Zool. Soc. London 134:197-205.

Martin, F. W. 1966. Collecting the cacti of Mona Island. Cactus and Succulent J. 38:122-126.

_________. 1963b. Reproduction in the granite spiny lizard, *Sceloporus orcutti*. Copeia 1963(1):144-152.

_________. 1963c. Biology of the granite spiny lizard, *Sceloporus orcutti*. Amer. Midl. Natur. 69:310-327.

_________. 1965. Reproduction in the sand-dwelling lizard *Uma inornata*. Herpetologica 21:39-55.

_________. 1966a. Reproduction in the psammophilous lizard *Uma scoparia*. Copeia 1966(1):114-122.

_________. 1966b. Reproduction in the arenicolous lizard *Uma notata*. Ecology 47:9-18.

_________. 1968. VI. Biology of desert amphibians and reptiles. p. 195-356, *In:* G. W. Brown, ed. Desert Biology, Vol. 1. Academic Press, New York, 635 p.

_________. 1971. Reproduction in the desert lizard, *Dipsosaurus dorsalis*. Herpetologica 27:57-77.

McBee, R. H. 1971. Significance of intestinal microflora in herbivory. Ann. Rev. Ecol. and Syst. 2:165-176.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. Amer. Natur. 97:133-140.

McKnight, T. 1964. Feral livestock in Anglo-America. Univ. California Publ. Geog. 88:1-78.

Mercer, E. H. 1961. Keratin and Keratinisation. An essay in molecular biology. Pergamon Press, Oxford, N.Y., 316 p.

Mertens, R. 1960. The world of amphibians and reptiles. McGraw-Hill Book Company, New York, 207 p.

Milstead, W. W. 1961. Observations of the activities of small animals (Reptilia and Mammalia) on a quadrat in southwest Texas. Amer. Midl. Natur. 65:127-138.

_________. 1970. Late summer behavior of the lizards *Sceloporus merriami* and *Urosaurus ornatus* in the field. Herpetologica 26:343-354.

Minnich, J. E. 1970. Water and electrolyte balance of the desert iguana, *Dipsosaurus dorsalis*, in its natural habitat. Comp. Biochem. Physiol. 35:921-933.

_________. 1971. Seasonal variation in weight-length relationships and fat body size in the desert iguana, *Dipsosaurus dorsalis*. Copeia 1971(2):359-362.

_________, and V. H. Shoemaker. 1970. Diet, behavior and water turnover in the desert iguana, *Dipsosaurus dorsalis*. Amer. Midl. Natur. 84:496-509.

Montanucci, R. R. 1965. Observations on the San Joaquin leopard lizard, *Crotaphytus wislizeni silus* Stejneger. Herpetologica 21:270-283.

________. 1967. Further studies on leopard lizards, *Crotaphytus wislizenii.* Herpetologica 23:119-126.

________. 1968. Comparative dentition in four iguanid lizards. Herpetologica 24:305-315.

Montgomery, G. G., A. S. Rand, and M. E. Sunquist. 1973. Post-nesting movements of iguanas from a nesting aggregation. Copeia 1973(3):620-622.

Mueller, C. F. 1969. Temperature and energy characteristics of the sagebrush lizard (*Sceloporus graciosus*) in the Yellowstone National Park. Copeia 1969(1):153-160.

________. 1970. Energy utilization in the lizards *Sceloporus graciosus* and *S. occidentalis.* J. Herpetol. 4:131-134.

Mueller, H. 1968. Untersuchungen ueber Wachstum und Altersverteilung einer population der Gruenen Leguans *Iguana iguana iguana* L. (Reptilia: Iguanidae). Mittl. Inst. Colombo-Aleman Invest. Cient. 2:57-65.

________. 1972. Okologische und ethologische studien an *Iguana iguana* L. (Reptilia: Iguanidae) In Kolumbien. Zoologische Beitrage, Breslau. 18:109-313.

Murphy, J. B. 1969. Notes on iguanids and varanids in a mixed exhibit at Dallas Zoo. Intl. Zoo Yearbook 9:39-41.

Muth, A. 1977. Eggs and hatchlings of captive *Dipsosaurus dorsalis.* Copeia 1977(1):189-190.

Nagy, K. A. 1973. Behavior, diet and reproduction in a desert lizard, *Sauromalus obesus.* Copeia 1973(1):93-102.

________, and V. H. Shoemaker. 1975. Energy and nitrogen budgets of the free-living desert lizard, *Sauromalus obesus.* Physiol. Zool. 48:252-262.

Noble, G. K. 1923. Trailing the Rhinoceros iguana. Nat. Hist. 23:541-558.

________, and H. T. Bradley. 1933. The mating behavior of lizards; its bearing on the theory of sexual selection. Ann. New York Acad. Sci. 35:25-100.

________, and G. C. Klingel. 1932. The reptiles of Great Inagua Island, British West Indies. Amer. Mus. Nov. 549:1-25.

Norris, K. S. 1953. The ecology of the desert iguana *Dipsosaurus dorsalis.* Ecology 34:265-287.

________, and W. R. Dawson. 1964. Observations on the water economy and electrolyte excretion of chuckwallas (Lacertilia, *Sauromalus*). Copeia 1964(4):638-646.

Ostrom, J. H. 1963. Further comments on herbivorous lizards. Evolution 17:368-369.

Overton, W. S. 1953. Progress reports for investigations project, W-33-R, April 1 and July 1. Fla. Game and Freshwater Fish Comm., Tallahassee, 12 p.

Parker, G. A. 1974. Courtship persistence and female-guarding as male time investment strategies. Behavior 48:157-184.

Parker, W. S. 1972. Notes on *Dipsosaurus dorsalis* in Arizona. Herpetologica 28:226-229.

________, and E. R. Pianka. 1973. Notes on the ecology of the iguanid lizard, *Sceloporus magister.* Herpetologica 29:143-152.

________. 1975. Comparative ecology of populations of the lizard *Uta stansburiana.* Copeia 1975(4):615-632.

________. 1976. Ecological observations on the leopard lizard (*Crotaphytus wislizeni*) in different parts of its range. Herpetologica 32:95-114.

Paulson, D. R. 1966. New records of birds from the Bahama Islands. Not. Naturae 394:1-15.

Pawley, R. 1969. Further notes on a captive colony of marine iguanas *Amblyrhynchus cristatus* at Brookfield Zoo, Chicago. Intl. Zoo Yearbook 9:41-44.

Peracca, M. G. 1891. Osservazioni sulla riproduzione della *Iguana tuberculata*. Boll. Mus. Zool. Anat. Comp. Torino. 6:1-8.

Perez Vigueres, I. 1936. Sobre la validez de la especie *Atractis cruciata* Linstow 1902. Rev. Parasit. Clin. y Lab. Habana 1:188-190.

Philobosian, R. 1975. Territorial behavior and population regulation in the lizards, *Anolis acutus* and *A. cristatellus*. Copeia 1975(3):428-444.

Pianka, E. R. 1967. On lizard species diversity: North American flatland deserts. Ecology 48:333-351.

_________. 1970a. On r- and K- selection. Amer. Natur. 104:592-597.

_________. 1970b. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703-720.

_________, and W. S. Parker. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. Copeia 1975(1):141-162.

Platt, D. R. 1969. Natural history of the hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. Univ. Kansas, Publ. Mus. Nat. Hist. 18:253-420.

Pope, C. H. 1969. The Reptile World. A natural history of the snakes, lizards, turtles, and crocodilians. Knopf, New York, 324 p.

Porter, W. P., J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973. Behavioral implications of mechanistic ecology. Oecologia (Berlin) 13:1-54.

Pough, F. H. 1973. Lizard energetics and diet. Ecology 54:837-844.

Prieto, A. A. 1971. The ethology of the Arizona chuckwalla (*Sauromalus obesus tumidis*). Ph.D. Thesis, Univ. Missouri, Columbia, 176 p.

_________, and M. W. Sorenson. 1975a. Food preferences of the Arizona chuckwalla (*Sauromalus obesus tumidus*). Bull. New Jersey Acad. Sci. 20:8-11.

______________. 1975b. Predator-prey relationships of the Arizona chuckwalla (*Sauromalus obesus tumidus*). Bull. New Jersey Acad. Sci. 20:12-13.

______________. 1977. Reproduction in the Arizona chuckwalla, *Sauromalus obesus tumidus* (Shaw). Amer. Midl. Natur. 98:463-469.

Purdue, J. R., and C. C. Carpenter. 1972. A comparative study of the body movements of displaying males of the lizard genus *Sceloporus* (Iguanidae). Behavior 41:68-81.

Rabb, G. B., and E. B. Hayden, Jr. 1957. The Van Voast-American Museum of Natural History Bahama Islands expedition record of the expedition and general features of the islands. Amer. Mus. Nov. 1836:1-53.

Raillet, A., and A. Henry. 1912. Quelques nematodes parasites des reptiles. Bull. Soc. Path. Exot. 5:251-259.

Rand, A. S. 1967a. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc. U.S. Natl. Mus. 122:1-79.

_________. 1967b. The adaptive significance of territoriality in iguanid lizards. pp. 106-115, *In:* W. W. Milstead, ed., Lizard Ecology: A symposium. Univ. Missouri Press, Columbia.

_________. 1968. A nesting aggregation of iguanas. Copeia 1968(3):552-561.

_________. 1972. The temperatures of iguana nests and their relation to incubation optima and to nesting sites and season. Herpetologica 28:252-253.

_________. 1979. Reptilian arboreal folivores. *In* G. G. Montgomery, ed. The Ecology of arboreal folivores. Smithsonian Inst. Press, Washington, D.C.

_________, and S. S. Humphrey. 1968. Interspecific competition in the tropical rain forest: Ecological distribution among lizards at Belem, Para. Proc. U. S. Nat. Mus. 125:1-17.

Rand, W. M., and A. S. Rand. 1976. Agonistic behavior in nesting iguanas: a stochastic analysis of dispute settlement dominated by the minimization of energy cost. Z. Tierpsychol. 40:279-299.

_________, and M. H. Robinson. 1969. Predation on iguana nests. Herpetologica 25:172-174.

Rawles, M E. 1960. The Integumentary System. pp. 190-240, *In:* A. J. Marshall, ed. Biology and Comparative Physiology of Birds. Vol. 1. Academic Press, New York.

Ray, C. E. 1965. Variation in the number of marginal tooth positions in three species of iguanid lizards. Breviora 236:1-15.

Ricklefs, R. E., and J. Cullen. 1973. Embryonic growth of the green iguana *Iguana iguana.* Copeia 1973(2):296-305.

Robinson, L. E. 1926. The genus *Amblyomma. In:* G. H. F. Nuttal, C. Warburton, W. F. Cooper, and L. E. Robinson, eds. Ticks, a monograph of the Ixodidae. Cambridge Univ. Press, Pt. 4.

Rodhain, J., and C. Vuylsteke. 1937. Une filaire nouvelle d'*Iguana tuberculata (Breinlia brevocaudata* n. sp.). Ann. Par. 15:225-228.

Rudolphi, C. A. 1819. Entozoorum synopis cui accedunt mantissa duplex et indices locupletissimi. Berolini. 811 p.

Ruibal, R. 1967. Evolution and behavior in West Indian anoles. pp. 116-140. *In:* W. W. Milstead, ed. Lizard ecology: A symposium. Univ. Missouri Press, Columbia.

_________, and R. Philobosian. 1974. The population ecology of the lizard *Anolis acutus.* Ecology 55:525-537.

Sanburn, S. R. 1972. Food Habits of *Sauromalus obesus obesus* on the Nevada test site. J. Herpetol. 6:142-144.

Schmidt, K. P. 1935. Notes on the breeding behavior of lizards. Field Mus. Natur. Hist., Zool. Ser. 20:71-76.

Schmidt-Nielson, K., and R. Fange. 1958. Salt glands in marine reptiles. Nature, London 182:783-785.

_________, A. Borut, P. Lee, and E. Crawford, Jr. 1963. Nasal salt excretion and the possible function of the cloaca in water conservation. Science 142:1300-1301.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123-141.

Schwartz, A. 1968. The Geckos (*Sphaerodactylus*) of the southern Bahama Islands. Ann. Carnegie Mus. 39:227-271.

_________, and M. Carey. 1977. Systematics and evolution in the West Indian iguanid genus *Cyclura.* Stud. Fauna Curacao 173:16-97.

_________, and R. Thomas. 1975. A check-list of West Indian amphibians and reptiles. Carnegie Mus. Nat. Hist. Spec. Publ. 1:1-216.

Sexton, O. J. 1975. Black vultures feeding on iguana eggs in Panama. Amer. Midl. Natur. 93:463-468.

Shaw, C. E. 1945. The chuckwallas, genus *Sauromalus.* Trans. San Diego Soc. Nat. Hist. 10:269-306.

_________. 1950. Lizards in the diet of captive *Uma.* Herpetologica 6:36-37.

_________. 1952. Notes on the eggs and young of some United States and Mexican lizards, I. Herpetologica 8:71-79.

_________. 1954. Captive-bred Cuban iguanas *Cyclura macleayi macleayi.* Herpetologicia 10:73-78.

_________. 1966. The eggs and young of the marine iguana (*Amblyrhynchus cristatus*). Copeia 1966(3):585.

_________. 1969. Breeding the rhinocerous iguana *Cyclura cornuta cornuta* at San Diego Zoo. Intl. Zoo Yearbook 9:45-58.

Simon, C. A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi.* Ecology 56:993-998.

Slevin, J. R. 1935. An account of the reptiles inhabiting the Galapagos Islands. Bull. New York Zool. Soc. 38:2-24.

Slobodkin, L. B. 1962. Growth and regulation of animal populations. Holt, Rinehart & Winston, New York, 184 p.

Slobodkin, L. B. 1962. Growth and regulation of animal populations. Holt, Rinehart & Winston, New York, 184 p.

Smith, H. M. 1946. Handbook of lizards. Comstock Publishing Associates, Ithaca, N.Y., 557 p.

Smith, P. W., and W. L. Burger. 1950. Herpetological results of the University of Illinois Field Expedition, Spring 1949. III. Sauria. Trans. Kansas Acad. Sci. 53:165-175.

Smith, R. E. 1968. Experimental evidence for a gonodal-fat body relationship in two teiid lizards (*Ameiva festiva, Ameiva quadrilineata*). Biol. Bull. 134:325-331.

Sokol, O. M. 1967. Herbivory in lizards. Evolution 21:192-194.

________. 1971. Lithophagy and geophagy in reptiles. J. Herpetol. 5:69-71.

Southwood, T. R. E. 1966. Ecological methods. Chapman and Hall, London, 391 p.

Stamps, J. A., and G. W. Barlow. 1973. Variation and sterotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). Behavior 47:67-93.

________, and D. P. Crews. 1976. Seasonal changes in reproduction and social behavior in the lizard *Anolis aeneus*. Copeia 1976(3):467-476.

Stebbins, R. C. 1944. Field notes on a lizard, the mountain swift, with special reference to territorial behavior. Ecology 25:233-245.

________. 1954. Amphibians and reptiles of western North America. McGraw-Hill, New York, 536 p.

Steele, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York, 481 p.

Stejneger, L. 1903. A new species of large iguana from the Bahama Islands. Proc. Biol. Soc. Washington 16:129-132.

Stewart, D. R. M., and J. Stewart. 1970. Food preference data by fecal analysis for African plains ungulates. Zool. Afr. 5:115-129.

Street, G. B. 1952. Recent observations on the iguanas at Xanadu, Cuba. Privately Printed, 12 p.

Sutcliffe, R. 1952. Results of the Catherwood-Chaplin West Indies expedition. 1948. Part VI. Amphibia and reptilia. Not. Naturae 243:1-8.

Swanson, P. L. 1950. The iguana *Iguana iguana iguana* (L.). Herpetologica 6:187-193.

Szarski, H. 1962. Some remarks on herbivorous lizards. Evolution 16:529.

Tamsitt, J. R., and D. Valdivieso. 1963. The herpetofauna of the Caribbean Islands San Andres and Providencia. Rev. Biol. Trop. 11(2):131-139.

Tanner, W. W., and J. M. Hopkin. 1972. Ecology of *Sceloporus occidentalis longipes* Baird and *Uta stansburiana stansburiana* Baird and Girard on Rainier Mesa, Nevada test site, Nye County, Nevada. Brigham Young Univ. Sci. Bull., Biol. Ser. 15:1-39.

Telford, S. R. 1969. The ovarian cycle, reproductive potential, and structure in a population of the Japanese lacertid *Takydromus tachydromoides*. Copeia 1969(3):548-567.

________. 1970. Seasonal fluctuations in liver and fat body weights of the Japanese lacertid *Takydromus tachydromoides* Schlegel. Copeia 1970(4):681-688.

Templeton, J. R. 1964. Nasal salt excretion in terrestrial lizards. Comp. Biochem. Physiol. 11:223-229.

________. 1967. Nasal salt gland excretion and adjustment to sodium loading in the lizard, *Ctenosaura pectinata*. Copeia 1967(1):136-140.

Thaper, G. S. 1925. Studies on the oxyurid parasites of reptiles. J. Helm. 3:83-150.

________. 1926. *Ozolaimus* Dujardin, 1845 (= *Macracis* Gedoelst, 1916) a little known nematode from the caecum of *Iguana tuberculata*. J. Helm. 4:69-74.

Throckmorton, G. S. 1971. Digestive efficiency in the herbivorous lizard *Ctenosaura pectinata*. Herpet. Rev. 3:108.

________. 1973. Digestive efficiency in the herbivorous lizard *Ctenosaura pectinata*. Copeia 1973(3):431-435.

________. 1976. Oral food processing in two herbivorous lizards, *Iguana iguana* and *Uromastyx aegyptius*. J. Morph. 148:363-390.

Tinkle, D. W. 1962. Reproductive potential and cycles in female *Crotalus atrox* in northwest Texas. Copeia 1962(2):306-313.

________. 1967a. Home range, density, dynamics, and structure of a Texas population of the lizard *Uta stansburiana*. pp. 5-29. *In:* W. W. Milstead, ed. Lizard ecology: A symposium. Univ. Missouri Press, Columbia.

________. 1967b. The life and demography of the side-blotched lizard, *Uta stansburiana*. Misc. Publ. Mus. Zool., Univ. Michigan 132:1-182.

________. 1969. Concept of reproductive effort and its relation to the evolution of life histories of lizards. Amer. Natur. 103:501-516.

________. 1972. The dynamics of a Utah population of *Sceloporus undulatus*. Herpetologica 28:351-359.

________. 1973. A population analysis of the sagebrush lizard, *Sceloporus graciosus* in southern Utah. Copeia 1973(2):284-296.

________. 1976. Comparative data on the population ecology of the desert spiny lizard, *Sceloporus magister*. Herpetologica 32:1-6.

________, and R. E. Ballinger. 1972. *Sceloporus undulatus:* A study of the intraspecific comparative demography of a lizard. Ecology 53:570-584.

________, and N. F. Hadley. 1973. Reproductive effort and winter activity in the viviparous montane lizard *Sceloporus jarrovi*. Copeia 1973(2):272-277.

____________. 1975. Lizard reproductive effort: caloric estimates and comments on its evolution. Ecology 56:427-434.

________, H. M. Wilbur, and S. G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55-74.

________., and D. W. Woodward. 1967. Relative movements of lizards in natural populations as determined from recapture radii. Ecology 48:166-168.

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30:353-369.

Turner, F. B., G. A. Hoddenbach, P. A. Medica, and J. R. Lannom. 1970. The demography of the lizard, *Uta stansburiana* Baird and Girard, in southern Nevada. J. Anim. Ecol. 39:505-519.

Turner, F. B., R. I. Jennrich, and J. E. Weintraub. 1969. Home ranges and body size of lizards. Ecology 50:1076-1081.

Turner, F. B., J. R. Lannom, P. A. Medica, and G. A. Hoddenbach. 1969. Density and composition of fenced populations of leopard lizards (*Crotaphytus wislizenii*) in southern Nevada. Herpetologica 25:247-257.

Turner, F. B., P. A. Medica, J. R. Lannom, Jr., and G. A. Hoddenbach. 1969, Demographic analysis of fenced populations of whiptail lizard, *Cnemidophorus tigris*, in southern Nevada. Southwestern Natur. 14:189-202.

Van Aperen, W. 1969. Notes on the artificial hatching of iguana eggs, *Iguana iguana*, at Melbourne Zoo. Intl. Zoo Yearbook 9:44-45.

VanDenburgh, J. 1922. The reptiles of western North America. Vol. 1. Lizards. Occas. Pap. California Acad. Sci.:1-611.

________, and J. R. Slevin. 1913. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905-1906. IX. The Galapagoan lizards of the genus *Tropidurus;* with notes on the iguanas of the genera *Conolophus* and *Amblyrhynchus*. Proc. California Acad. Sci. 4(2):134-203.

Van Winkle, W. 1975. Comparison of several probabilistic home-range models. J. Wildl. Mgmt. 39:118-123.

Vinegar, M. B. 1975. Life history phenomena in two populations of the lizard *Sceloporus undulatus* in southwestern New Mexico. Amer. Midl. Natur. 93:388-402.

Vitt, L. J. 1974. Winter aggregations, size classes, and relative tail breaks in the tree lizard, *Urosaurus ornatus* (Sauria: Iguanidae). Herpetologica 30:182-183.

_________, J. D. Congdon, A. C. Hulse, and J. E. Platz. 1974. Territorial aggressive encounters and tail breaks in the lizard *Sceloporus magister*. Copeia 1974(4):990-993.

_________, and R. D. Ohmart. 1974. Reproduction and ecology of a Colorado River population of *Sceloporus magister* (Sauria: Iguanidae). Herpetologica 30:410-417.

_________. 1975. Ecology, reproduction, and reproductive effort of the iguanid lizard *Urosaurus graciosus* on the lower Colorado River. Herpetologica 31:56-65.

Walton, A. C. 1942. *Paralaeuris cuckleri* n. sp. (Nematoda) from the iguana (*Cyclura cornuta*). J. Parasit. 28:165-166.

Ward, A. L. 1970. Stomach content and fecal analysis: methods of forage identification. U.S. Dept. Agr. Misc. Publ. 1147:146-158.

Weintraub, J. D. 1970. Homing in the lizard *Sceloporus orcutti*. Anim. Behav. 18:132-137.

Western, D. 1974. The distribution, density and biomass density of lizards in a semi-arid environment of northern Kenya. E. Afr. Wildl. J. 12:49-62.

Whitaker, A. H. 1973. Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). Proc. New Zealand Ecol. Soc. 20:121-130.

Wiewandt, T. 1977. Ecology, behavior, and management of the Mona Island ground iguana, *Cyclura stejnegeri*. Ph.D. dissertation. Cornell Univ., Ithaca, N.Y., 338 p.

Wilcox, K., J. Y. Carter, and L. V. Wilcox, Jr. 1973. Range extension of *Cyclura figginsi* Barbour in the Bahamas. Carib. J. Sci. 13:211-213.

Wilhoft, D. C. 1958. Observations on preferred body temperature and feeding habits of some selected tropical iguanas. Herpetologica 14:161-164.

Wilson, E. O. 1975. Sociobiology, the new synthesis. Belknap Press, Cambridge, 697 p.

Windberg, L. A., and L. B. Keith. 1976. Snowshoe hare population response to artificial high densities. J. Mammal. 57:523-553.

Windrow, S. L. 1977. Winter Activity and behavior of the Exuman rock iguana, *Cyclura cychlura figginsi*. Master's Thesis. Rutgers University, New Brunswick, New Jersey, 52 p.

Yamaguti, S. 1961. Systema Helminthum. Volume III. The Nematodes of Vertebrates. Part II. Interscience Publishers, Inc., New York, 1261 p.

Young, F. N., and C. C. Goff. 1939. An annotated list of the arthropods found in the burrows of the Florida gopher tortoise, *Gopherus polyphemus* (Daudin). Fla. Entomol. 22:53-62.

Zweifel, R. G. 1961. Another method of incubating reptile eggs. Copeia 1961(1):112-113.

_________, and C. H. Lowe. 1966. The ecology of a population of *Xantusia vigilis*, the desert night lizard. Am. Mus. Nov. 2247:1-57.

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES SERIES, may be in any field of biology. Manuscripts dealing with natural history of systematic problems involving the southeastern United States or the New World tropics are solicited especially. Manuscripts should be of medium length—circa 35 to 200 pages (10,500-16,000 words). Examination for suitability is made by an Editorial Board. The BULLETIN is distributed worldwide through institutional subscriptions and exchanges. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this the author(s) receive(s) 50 copies free, and he may purchase additional separates at cost if ordered when page proof is returned. The author is also responsible for any charges incurred for alterations made by him on galley or page proofs. The Museum will send an invoice to the author for this amount upon completion of publication.

PREPARATION OF MANUSCRIPT

Contributors should consult recent numbers of the BULLETIN for preferred style and format. Highly recommended as a guide is the CBE Style Manual, 3rd Edition, 1972 (Washington, D.C., Amer. Inst. Biol. Sci.).

MSS must be submitted in duplicate (please no onionskin) and satisfy the following minimal requirements: They should be typewritten, double-spaced (*especially* tables, figure captions, and "Literature Cited"), on one side of numbered sheets of standard (8-1/2 x 11 in.) bond paper, with at least one-inch margins all around. Figure legends and tables should be typed on separate sheets. All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All illustrations should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lower case letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for illustrations is 8-5/8 x 14 in (twice typepage size); illustrations should not be less than typepage width (4-5/16 in.). Designate the top of each illustration and identify on the back with soft pencil by author's name, MS title, and figure number.

All manuscripts not submitted in BULLETIN format will be returned to the author for retyping.

Manuscripts and all editorial matters should be addressed to:

Managing Editor of the BULLETIN
Florida State Museum
Museum Road
University of Florida
Gainesville, FL 32611