LOMA LINDA UNIVERSITY
Graduate School

Behavioral Ecology of the Endangered San Salvador Rock Iguana (*Cyclura rileyi rileyi*) in the Bahamas

by

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A Thesis submitted in partial satisfaction of
the requirements for the degree of
Master of Science in Biology

June 2001

Each person whose signature appears below certifies that this thesis in his opinion is adequate, in scope and quality, as a thesis for the degree Master of Science.

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ACKNOWLEDGMENTS

I am very grateful for all the many individuals who assisted me in many ways for the success of this project. My mother, Lucienne Cyril, was there pushing for me to do my best and to keep focused. The presence of my son, Lucas Amano-Cyril, encouraged me to push forward.

While in the field collecting data, a long time friend, Eric Chung, helped me immensely in setting up and planning my research. Eric’s input, hard work, and support proved to be crucial in helping me to collect the data needed for my research. Denise Heller and Johnathan Rivera dedicated a portion of their time to helping me collect data, which would have proved difficult without their help. My colleague, Roland Sosa, pushed me and encouraged me to succeed. Dr. William Hayes challenged my thoughts, views, and ideas into constructing the best experience I’ve ever had. I am very grateful for the countless hours that he took to help me prepare and review my manuscript. Dr. Ronald Carter and Dr. Cowles were appreciated members of my committee, who were always there when I needed advice and guidance. Financial support was provided by the Denver Zoological Foundation and by the Loma Linda University Department of Natural Sciences. The Bahamian Field Station provided logistical and hospitality support. Eric Carey of the Bahamas Ministry of Agriculture encouraged the undertaking of this study and arranged the necessary permits for fieldwork.

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ABSTRACT OF THE THESIS

Behavior Ecology of the Endangered San Salvador Rock Iguana (*Cyclura rileyi rileyi*) in the Bahamas

by

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Loma Linda University, June, 2001
Dr. William K. Hayes, Chairman

In this thesis I present the results of a study on the reproductive ecology, activity levels, population estimates, home range size and diet of the endangered San Salvador rock iguana (*Cyclura r. rileyi*). This lizard is one of three subspecies of *C. rileyi* that are endemic to the Bahamas. With fewer than 600 individuals remaining in 7 populations on small, remote islands, this iguana is one of the rarest lizards in the world. During the summer of 1999, I studied the population on Green Cay, a 5.1 ha island that supports the largest remaining population (roughly 200 animals). Nesting took place during the month of July, with larger females ovipositing earlier in the month than smaller females. Minimum reproductive size was approximately 22 cm snout-vent length (SVL) and 340 g. Many females dug exploratory burrows in microhabitats similar to nesting burrows. The nesting burrows were located in loose sand, though some were found in rock crevices. Three of five excavated nest burrows contained old eggshell fragments from previous years. Clutch size ranged from 3-6 eggs. Relative parental investment was positively correlated with SVL. Egg dimensions were negatively associated with clutch size. Females that defended their nests for more than five days (n=13 were found in areas of higher nest density than those defending their nests fewer than 5 days (n = 8). Male and female iguanas exhibited similar levels of activity. However, iguanas were more active during morning and evening hours than at mid-day. Population estimates based on mark-resighting ratios (Lincoln-Petersen estimates) were more precise than those based on numbers of iguanas observed during daily surveys. Detectability rate during the surveys averaged 33%. Estimates of home range size were similar for males and females, as evaluated by fixed kernel methods and minimum convex polygons. Vegetation on Green Cay was comprised of only ten species, of which seven were utilized by iguanas. *Borrichia arborescens*, *Rhachicallis americana,* and *Conocarpus erectus* were the most frequent food items in the diet. Compared to its relative abundance, *Opuntia stricta* was also browsed heavily.

INTRODUCTION

The Caribbean rock iguana, genus *Cyclura*, is represented today by eight species. These iguanas are the largest native herbivores on the islands where they exist (Barbour & Nobel, 1916; Iverson, 1979; Phillips, 1994). Although their range was formerly greater than it is today (Auffenberg, 1976; Blair, 1991; Schwartz & Carey, 1977), these members form a small group that are restricted to islands of the Bahamas, Greater Antilles, and the Virgin Islands. Several species have already become extinct (Wiewandt, 1982), and those that still exist are designated as endangered and are protected by CITES (Convention on the International Trade of Endangered Species).

In the mid-1700's, *Cyclura* thrived in vast numbers in the West Indies (Barbour & Nobel, 1916). In 1743, a report of the Natural History of the Carolina's and Bahamas stated that, "Iguanas were abundant upon many islands throughout the Bahamas, so common in fact that schooners were cargoed with them and were carried to the Carolinas for food" (Barbour & Nobel, 1916). In the early 1900's a group of scientists from the Museum of Comparative Zoology sought to study and collect specimens of *Cyclura*. Upon arrival to the West Indies they found that populations on many islands that once supported iguanas were extirpated (Barbour & Nobel, 1916). The remaining populations appeared to be thriving. The hunting of iguanas for food by the Arawak and Lucayan Indians was thought to be a major reason for the extinction of various species of *Cyclura* (Barbour & Nobel, 1916). They are also vulnerable to habitat destruction as well as predation by introduced predators (cats, dogs, rats, mongooses; Alberts, 2000; Iverson, 1978; Townson, 1980) and competition by feral livestock (e.g., goats, cattle, sheep; Alberts, 2000; Carey, 1975; Mitchell, 2000).

Cyclura rileyi, An Endangered Bahamian Endemic

Regarded as the smallest of all rock iguanas, *C. rileyi* is amongst the most threatened of the remaining species. There are three recognized subspecies that occur on three major island groups in the Bahamas (see Figure 1). At one time presumably hundreds of thousands or millions of iguanas thrived on the larger islands (Hayes et al., 1995), but today the remaining populations are largely confined to tiny, remote islets uninhabited by humans. Hayes and Carter (unpublished data) recently obtained population estimates for all remaining populations of these *C. rileyi* (Table 1).

Cyclura r. rileyi is confined to seven small offshore/inshore cays of San Salvador (Figure 2), with 500-600 iguanas remaining (Gicca, 1980; Hayes et. al., 1995). Populations on these cays vary in size, with the largest estimated at 200 iguanas (Green Cay) and the smallest estimated at 10 iguanas (Gaulin Cay), though this latter population may have recently become extirpated (Hayes et. al. 1995; Hayes & Carter, unpublished data). These populations are currently threatened by vegetation damage caused by an introduced moth (*Cactoblastis cactorum*), recent catastrophic storms, and feral rats that have been implicated in the extirpation of one population and senescence of another population (Hayes et al., 1995).

Cyclura r. cristata, the most threatened subspecies, is confined to the tiny island of Sandy Cay in the southern Exumas where fewer than 200 individuals and possibly less than 10 females remain (Fry, 2001; Hayes, 1998, 2000b). The major cause for its decline was predation by a single raccoon and feral rats. Since eradication of the raccoon (July, 1997; Fry, 2001) and feral rats (May, 1998; Day, 1998), recovery of this population appears to be in progress but will be slow due to the small body size and, consequently (Thornton, 2000), limited reproductive potential of this species.

Cyclura r. nuchalis is a resident of Fish and North Cay in the Acklins Bight (Hayes and Montanucci, 2000). This is the most abundant and least threatened of the three subspecies, with at least 10,000 individuals remaining and no recognized threats to its survival (Hayes & Carter, unpublished data). An introduced population of *C. r. nuchalis,* started by five iguanas in the 1970's on an unnamed cay in the northern Exumas, now has an estimated population of 300 iguanas (Hayes & Carter, unpublished data).

Given the highly threatened status of these taxa, natural history studies are urgently needed to better understand the factors that contribute to population health or decline. The fact that most remaining populations exist on very small islands makes them more vulnerable to stochastic processes such as disease and inbreeding depression. Recent declines in some populations appear to be the result of human-related pressures, which are compounded by small population size (Fry, 2001; Hayes, 1998; Hayes et al., 1995). We know relatively little, for example, about the reproductive, spatial and dietary requirements of the species. Such basic information is needed to develop sound management guidelines that may include, for example, translocation to new islands and captive propagation to serve as a safeguard against extinction.

Reproductive Ecology

Rock iguanas reproduce once a year, laying a single clutch of eggs. Breeding starts in spring, when mature males are brightly colored and females are inconspicuous (Auffenberg, 1976; Iverson, 1979; Wiewandt, 1982). Since mating is believed to occur around the same period each year, it is thought that photoperiods accompanied by seasonal changes initiate the mating season (Blair, 1991, 1994). In *C. rileyi*, mating usually occurs from mid-May through mid-June (Hayes et al., 1995, unpublished data; Thornton, 2000), when females appear to travel into male territories to seek copulation. Males frequently engage in territorial behavior that includes head bobs, face-to-face agonistic displays, and chasing. Copulated females appear to remain in close proximity to the male, who defends her from other males (Cyril, unpublished data; Thornton, 2000). The female may be mated repeatedly by the territorial male and may also be raped by other males (Cyril, unpublished data; Thornton, 2000).

Females nest approximately forty days after copulation (Iverson, 1979), usually between late-June and late-July in the Bahamas (Thornton, 2000). Females at this time seek areas suitable for nesting, which may take them well outside their usual home range (Christian, 1986; Haneke, 1995; Iverson, 1979; Thornton, 2000; Wiewandt, 1982). Pre-nesting movements have been recorded in some iguana species to extend beyond several kilometers, although not all species of iguanas make such lengthy pre-nesting movements (Christian & Tracy, 1982; Iverson, 1979;

Montgomery et al., 1973; Thornton, 2000; Werner, 1983; Wiewandt, 1982). Female *C. r. nuchalis* often dig several exploratory burrows in sand before choosing one to oviposit in (Thornton, 2000). In some instances where sand is not available for nest burrows, iguanas have been reported to nest in hollow logs, humus, rock crevices, and even termite mounds (Auffenberg, 1976; Iverson, 1979). Once the appropriate nest site is found, females dig burrows that range from 0.4 m to 1.5 m in length in *C. r. nuchalis* (Thornton, 2000; see also Blair, 1991; Iverson, 1979). Nest chambers are large enough for females to turn around in and deposit their eggs. Clutch size is strongly correlated with snout-vent-length (SVL) (Alberts, 1995; Blair, 1991; Iverson, 1979; Thornton, 2000). Once oviposition has occurred, the female fills the nest chamber as she moves out of the burrow. Females are known to exhibit nest-guarding behavior for up to a month (Iverson, 1979; Wiewandt, 1982) to protect nests from other females seeking nest-sites and from predators.

The incubation of eggs occurs over the next 80-90 days in *Cyclura* (Iverson, 1979), with egg chamber temperatures ranging from 25-33°C (Christian, 1991b; Thornton, 2000). Within the first week after hatching, the neonates excavate through the ceiling to emerge from the burrow (Iverson, 1979; Wiewandt, 1982). The weeks that follow hatching will be a crucial time for survival, when mortality rates are higher than at any other life stage (Iverson, 1978).

Movements and Spatial Relationships

Rock iguanas are generally regarded as territorial organisms. Their home ranges vary in size, presumably depending on sex, body size, season, population density and reproductive status (Carey, 1975; Fry, 2001; Iverson, 1979; Mitchell, 1999; Thornton, 2000). However, the factors that influence territoriality, home range size and nesting movements have not been studied adequately in any rock iguana species. These same factors may also influence iguana social structure in ways that are poorly understood.

Vegetation and Diet

Rock iguanas are mainly herbivorous, eating leaves, flowers, and fruits of many different plants (Auffenberg, 1982; Mitchell, 1999; Iverson, 1979; Wiewandt, 1982). Some plant species toxic or unpalatable to mammals are readily consumed by iguanas (Auffenberg, 1982). These lizards also eat some insects and carrion, but this occurs mainly during the juvenile stage of life. The vegetation found on many Caribbean islands is diverse, with several distinct communities (Smith, 1992). Consequently, the diet of these iguanas is typically diverse (Auffenberg, 1982), which is also true of other iguana species (Van Devender, 1982; von Lichtenbelt, 1993; Rand, 1989). However, vegetation density is often very limited on small Bahamian cays and may constrain maximum body size of iguanas (Hayes, 2000a).

Conservation Concerns and Objectives of Study

The iguanas on Green Cay comprise the largest remaining population of *C. r. rileyi*, but ongoing surveys suggest the population is declining (Hayes et al., 1995, unpublished data). Recent vegetation damage due to an introduced moth (Hayes et al., 1995, unpublished data) and severe storms (Hurricane Lily, 1997, and Hurricane Floyd, 1999) has altered the landscape of this tiny island. Suitable nesting substrate (loose sand and soil) appears to be scarce on this cay and may impose a limit on the carrying capacity of this cay. Only ten species of plants occur on this island (Moyroud & Ehrig, 1994), which represents a constrained diet compared to other iguana populations (Auffenberg, 1982). One important food source, the prickly-pear cactus (*Opuntia stricta*), has undergone a substantial decline in biomass on this cay (between 75 and 90%) due to the larvae of an introduced moth, *C. cactorum* (Hayes et al., 1995, unpublished data). The iguanas are also vulnerable to disturbance from increasing levels of ecotourism on Green Cay, and several smuggling efforts have been documented in the past decade.

With these concerns in mind, the purpose of this study was to learn more about the basic behavioral ecology of the San Salvador rock iguana, *C. r. rileyi*, on Green Cay. An improved understanding of three aspects in particular were deemed important for developing a conservation plan for this population and for the taxon. These included study of the reproductive ecology, home range size, and foraging ecology.

MATERIAL AND METHODS

Study Site Description

Green Cay, a small islet of 5.1 ha with a maximum elevation of 6.5 m above sea level, is located off the northern shore of San Salvador, Bahamas. Green Cay arises from the sea floor as an ancient highly eroded eolain (wind blown) sand dune that was formerly heavily vegetated. Large trunks and root masses are well-preserved in the lithified limestone. Today, the island is comprised of jagged limestone rock with approximately one-half of the surface covered by vegetation. Loose soil is scarce and limited. Temperatures on the main island average 31 C during summer and 17 C during the coolest month, December (Smith, 1992). Annual precipitation varies considerably, generally ranging from 100-180 cm, with a definite rain (hurricane) season from August to November and a lesser rain season in May and June (Smith, 1992).

The plant fauna on this cay is limited to 10 species (Table 2). Vegetation is sparsely distributed over rocky areas on the island (Figure 3). The dominant vegetation consists of two large areas of Silver Buttonwood (*Conocarpus erectus* var. *sericeus*). Small numbers of Bridled Terns (*Sterna anaethetus*) nest in the sparsely vegetated areas, and in some years large numbers of Sooty Terns (*S. fuscata*), Brown Noddies (*Anous stolidus*), and Roseate Terns (*S. dougallii*) will nest on the easternmost portion of the island. Tricolored Herons (*Egretta tricolor*) and a few Yellow-crowned Night Herons (*Nyctanassa violacea*) nest in the eastern-most Silver Buttonwood forest. Small numbers of Audubon's Shearwater (*Puffinus lherminieri*) nest beneath rocks throughout the island. Two additional reptiles, an anole (*Anolis distictus*) and a gecko (*Sphaerodactlylus corti*), are also present in small numbers.

This study was conducted between 17 June and 21 July 1999. During this span, temperature (using an electronic minimum and maximum thermometer placed in the shade of Buttonwood trees) and rainfall readings (from a rain gauge) were obtained on 19 occasions (Figure 4). Temperatures did not vary much during the study period, with a mean high (and range) of 34 C (28 – 37 C), and a mean low of 24 C (21-26 C). Rain was recorded on 19 of the 35 days on the cay, with a mean daily rainfall for the study period of 0.64 cm/day (0.1-6.4 cm).

Grid System and Vegetation Surveys

For the purpose of this study I constructed a 10 m grid system, which covered approximately 80% of the cay. Each of the 205 points was marked by flagging tape. The grid did not cover points east of the easternmost Silver Buttonwood forest because a large tern colony was in residence during the time of my study. Much of the southern portion of the eastern Silver Buttonwood forest was also omitted because of an active heron rookery. The rocky perimeter of the island was excluded from the grid system. At each point of the grid I took microhabitat measurements (plant species or rock) to map areas of vegetation and rock. When vegetation was present, I recorded not only the species but also the tallest height (cm) of that species within one meter of the point. Relative abundance of each plant species was determined from the point counts (excluding rock points). The approximate volume (m^3) of each species was calculated as total number of points (each representing 100 m^2) multiplied by the mean vegetation height (m). Because of incomplete vegetation sampling due to nesting birds, the relative abundance and volumes of Buttonwood, Sea Ox-eye Daisy (*Borrichia arborescens*), and Seaside Purslane (*Sesuvium portulacastrum*) were underestimated.

Capture, Processing, and Marking of Iguanas

Most of the iguanas were captured and processed during the first week of the study, but I continued to capture and process iguanas during the entire period. Most iguana captures were accomplished by hand using food as bait, whereas the rest were captured by monofilament noose attached to the ends of 2.5 m poles. Both methods appeared to be effective and safe for capturing iguanas with minimal injuries (abrasions). Each iguana was weighed in a cloth bag with a Pesola spring scale (100 g or 1000 g, depending on iguana size) and the following measurements obtained using a metric caliper or a folding metric ruler: snout-vent length (SVL), head length (from posterior margin of eye to snout tip), tail length (from vent to tip), left foreleg and left hindleg lengths (from midline of venter to base of thumb), and head width (between lateral margins of supraocular scales). Iguanas were categorized into one of four size classes based on SVL: juveniles (< 12 cm), subadults (12-19.9 cm), small adults (20-27.9 cm), and large adults (>

28 cm). The lengths of the longest nuchal spine and longest dorsal spine were also recorded with a set of calipers. The number of femoral pores on the right and left legs was counted. Many of these measurements were taken for comparisons with other taxa and thus are not reported in this thesis. Damage to the toes and any regeneration of the tail was recorded. A 1 ml sample of blood was drawn from the caudal vein for future genetic work.

Iguanas were marked semi-permanently by affixing colored glass beads to the nuchal crest with an 80 lb nylon monofilament line that was melted into a ball at each end to retain the beads (Hayes & Carter, 2000). Iguanas were also marked temporarily with an alphanumeric code on each side of the dorsum using a non-toxic enamel paint that lasted several months or until ecdysis (Hayes & Carter, 2000). This was done to aid us in identifying and recording the iguana's activities from a distance.

Reproductive Ecology

When nesting started, as indicated by digging activities of females, I recorded a number of variables for each female and each nesting burrow. All retreat burrows on Green Cay were beneath rock. No retreat burrows were apparent in the limited sandy habitat and no digging activities were observed prior to commencement of nesting. Thus, any freshly exposed earth was considered to be a nest excavation.

Many females dug multiple burrows, but I was able to distinguish between exploratory and nesting burrows. Nesting burrows were backfilled by females after oviposition had occurred, whereas exploratory burrows were abandoned and left uncovered. For each excavation I observed, I recorded the location, time, date, and iguana identity if a marked individual was in close proximity. I also recorded several microhabitat features. These included percent vegetation cover and the presence of rock and each plant species within 0.3 m of the burrow entrance. Vegetation cover was determined using a densiometer mirror. The densiometer was held on the ground and viewed from several angles overhead to count all 1 cm squares in which overhead vegetation was present. Percent cover was calculated as the number of squares out of the total possible (22 squares) that showed vegetation. To approximate the location of the egg chamber, the densiometer was positioned 0.3 m from the burrow entrance in the direction the female dug. However, the densiometer was positioned directly above the chamber for five nests that were excavated (see comments below). For all nesting burrows, I counted the number of all other burrows (both nesting and exploratory) within a 10 m radius. This number was updated regularly as more burrows were discovered over time.

For females observed in the act of digging, I studied them closely for signs that oviposition had occurred, such as backfilling the entrance of a burrow, an apparent loss of body mass (that often was not obvious), and signs of nest guarding. Some females appeared to immediately abandon their burrows, and thus I was unable to identify the individual who had dug the burrow. After I was confident that a female had oviposited, she was then captured so that I could record the loss in body mass. Relative parental investment of females that oviposited was calculated as change in body mass divided by original body mass multiplied by 100.

I carefully excavated five of the burrows, working inward from the entrance in a manner so as not to damage structural integrity of the egg chamber. I knew the identity of only two of these females. I measured the approximate contour and length of the burrow as well as the depth of the egg chamber (to the floor) from the ground surface above. Individual eggs were carefully retrieved and their dimensions measured with calipers. Eggs were also placed in a small plastic bag to determine their mass using a 100 g Pesola scale. Eggs were returned to the chamber in the same orientation they were found in. The burrows were then carefully backfilled so as to leave the chamber intact.

Nest guarding behavior was exhibited by many of the females. This was apparent from the agonistic responses toward approaching iguanas of either sex or by their approach toward me. For each female, I assigned a relative score of nest defense. A score of zero was assigned to females that appeared to abandon their burrows immediately, a score of one was applied to females that exhibited nest guarding for 1-5 days, and a score of two was given to females that defended their nests for >5 days.

Activity Surveys, Population Estimates and Home Range Estimates

Activity surveys of the entire study (grid) area were conducted regularly by a single investigator during the period 23 June to 22 July. Surveys were done during the morning (0800-1030), mid-day (1300-1430), and evening (1700-1930) hours, and required 30-75 minutes to complete. I subdivided the grid areas of the cay into three general regions (western, central and eastern) for daily randomizing the sequence of areas surveyed. Usually two but up to three surveys were conducted per day. Surveys were typically separated by 6 hr or more but always a minimum of 3 hr to maintain independence between successive surveys. During each survey, all iguanas seen were identified as marked or unmarked with their position recorded in the study grid area. The size class of each iguana was also recorded.

To evaluate how activity levels varied with gender and time of day, the proportion of marked iguanas resighted during each survey was compared using a 2 X 3 (sex X time of day) ANOVA treating each factor as a between-subjects variable. Proportions were arcsine transformed prior to analysis. The numbers of marked iguanas of each sex on the island were adjusted each day that new iguanas were captured and marked. Correlation analyses were employed to learn whether the proportion of iguanas active changed during the course of the study.

For each survey, population estimates were also derived based on the Lincoln Peterson equation: $N_{total} = (N_{seen} / N_{resighted}) \times N_{marked}$ (Hayes et al., 1995; Hayes and Carter, 2000). In this equation, N_{seen} was the number of iguanas seen during a given survey (excluding juveniles, none of which were marked, and poorly seen iguanas), $N_{resighted}$ was the number of marked iguanas seen, and N_{marked} was the number of iguanas marked on the cay at the time of the survey. The inclusion of subadults in N_{seen} inflated the estimates because only one subadult iguana was marked during the course of the study. However, the population estimates were underestimates for the cay as a whole because they were restricted to the grid area only and did not include juveniles. A one-way ANOVA was used to compare population estimates for the three times of day, and correlation analyses were used to learn whether estimates varied during the course of the study.

For all iguanas with a minimum of 10 sightings (males: 0 = 19, range = 10-26; females: 0 = 19, range = 10-24), home ranges were quantified using three methods. First, I determined the maximum distance between any two points. Second, I used the CalHome software program (Kie, 1994) to estimate home range based on minimum convex polygons (MCP) at the 100% and 95% levels. Third, I used the Home Ranger v. 1.5 software program (Hovey, 1998) to determine fixed kernel estimates using least squares cross-validation (LSCV) for smoothing and the data standardization option. To comply with constraints on LSCV for kernel methods, locality data for points with multiple sightings were randomly varied by up to 1 m. Autocorrelation measures were obtained from Home Ranger. The fixed kernel approach is preferred to other estimators of home range size (Seaman et al., 1999), but the minimum sample size for reliability should be close to 30 sightings (Seaman and Powell, 1996). The MCP method, though less reliable, is widely used even for small sample sizes and is reported because it can be compared more readily to other studies. With a small number of sightings, MCP's generally underestimate home range size whereas kernel methods usually overestimate home range size (Seaman and Powell, 1996). Home range size for male and female iguanas was compared by Mann-Whitney U tests. Spearman correlation analyses were used to compare similarity of the four estimates obtained by the three methods and to compare the influence of number of sightings on home range size. Because my study was confined to a limited period of time during the pre-nesting and nesting seasons, these home range values reflect seasonal rather than annual use of habitat.

Vegetation and Diet

Diet was evaluated by examination of fecal deposits and by direct observation of foraging iguanas. Fecal samples were randomly collected from the study area by myself in July 1999, and by W. K. Hayes in October 1999 and May 2000. Fecal samples in close proximity (within 0.5 m) were assumed to be from the same individual and were pooled. Fecal examination was initially done at the study site where comparisons could be made to live plant material. Some material was preserved and examined under microscope at the Bahamian Field Station. Content of each feces was examined qualitatively, noting the absence or presence of the plant species and their parts (leaves, fruits, and flowers). Presence of invertebrates and inorganic material was also noted. During the duration of the study period, I recorded the time of day and food items consumed by iguanas.

Statistical Analyses

All statistical analyses were conducted using Windows SPSS version 8.0 software. The alpha level was set to 0.05 for all tests.

RESULTS

Capture Data

Between 16 June and 21 July, a total of 65 iguanas were captured of which 27 (41.5%) were recaptured from studies made in previous years. The numbers of marked iguanas of each sex and size class are provided in Table 3. Nearly all captures (98.5%) during my study period were of adults (> 20 cm) because I focused the study on adult iguanas. Juveniles were present but not readily observed, and when seen they were skittish and difficult to capture.

Several size relationships were examined for adult male and female iguanas above 20 cm SVL. The data represents all captures from 1993 to 1999 during the months of May, June and July. Three separate analyses of covariance (ANCOVA's) were used to compare the relative body mass, relative head length, and relative tail length of adult males and females. In these linear equations, mass, head length, and tail length were separately treated as the dependent variable with sex as an independent variable and SVL as a covariate. In each ANCOVA, the dependent measure (body mass, head length and tail length) was significantly associated with SVL (all P's < 0.0001; Figure 5). There was no difference in the relationship between mass and SVL for males and females, although the standardized coefficient (beta) approached significance (Beta = -0.118, P = 0.066). The relationships between head length and SVL and between tail length and SVL were similar for both sexes (P's > 0.11; Figure 5). In all measures (mass, SVL, head length, tail length), males attained a larger body size than females (Mann-Whitney U tests: all P's < 0.008). Adult females averaged 74.6% of adult male body mass (means of 524 g and 702 g, respectively) and 89.5% of adult male SVL (means of 23.8 cm and 26.6 cm, respectively).

Reproductive Ecology

Nesting Activity

Signs of nesting activity were first noticed on 29 June, as evidenced by signs of exploratory digging. The first completed nests were found on 3 July. Nesting activity progressively increased and then leveled off as the season continued (see Figure 6). Nests were located throughout the cay (Figure 7), but were confined to areas having loose sand and soil, which sometimes were within rock crevices and would have been easily overlooked as potential nest sites if not for the fresh earth present at the crevice entrance. Of the 90 burrows found on Green Cay, 41 (45.6%) were identified as nesting burrows. Oviposition date was negatively correlated with SVL (r = -0.47, P = 0.028, n = 22; Figure 8). Thus, larger females oviposited earlier than smaller females. Nesting density averaged 2.9 nests (range = 1-8, n = 41) within a 10 m radius (314 m^2) of individual nests. There was no correlation between burrow density and female SVL (r = 0.35, P = 0.15, n =19).

Burrow characteristics

The microhabitat features of exploratory and nesting burrows are compared in Table 4 and in Figure 9. In Figure 9, numbers indicate the representation of each microhabitat relative to other microhabitats for nesting and exploratory burrows. Superficially, the microhabitats appeared to be similar for both types of burrows. Figure 10 shows the variation in burrow morphology of five excavated nests. Two burrows followed a straight path, while the other three burrows varied in the number of turns dug by females. Of the five nests excavated, three (60%) contained old eggshell fragments from previous years. Total burrow length ranged from 30-116 cm with a mean of 53 cm (Table 5). Egg chamber depth ranged from 18 - 28 cm with a mean of 21.6 cm. Vegetation cover of these five nests varied from 0-18%. Vegetation cover above all nest burrows averaged 19% (S.E. = 5%; range = 0-82%) and was independent of oviposition date (r = -0.21, P = 0.33, n = 23), female SVL (r = -0.38, P = 0.20, n = 13) and nesting density (r = -0.23, P = 0.29, n = 23).

Clutch size relationships.

Clutch size ranged from 3-6 eggs (n = 5 clutches). Because three clutches were produced by females of unknown size, I could not evaluate the relationship between body size and clutch size. During a visit to Low Cay, San Salvador Island, on 11 July, I excavated a single nest containing 10 eggs. Iguanas on this cay are substantially larger than on Green Cay with most individuals exceeding 30 cm SVL (Hayes et al., 1995; Hayes & Carter, unpublished data). Relative parental investment, determined by weighing females before and after oviposition, averaged 21.7% (S.E. = 2%, range = 14-31%) and was positively associated with SVL (r = 0.748, P = 0.02, n = 9; see Figure 11).

Egg size relationships

Mean (± SE) egg mass was 27.7 ± 0.77 g (n = 21), mean egg length was 53.4 ± 0.67 mm (n = 21), and mean egg width was 29.5 ± 0.32 mm (n = 21). Egg length was weakly correlated with egg width (r = 0.43, p = 0.05), egg mass was positively correlated with egg length (r = 0.687, $p < 0.001$) and width (r = 0.565, p = 0.008), and average egg mass was negatively correlated with clutch size (r = -0.870, p = 0.5). Thus, larger clutches were comprised of smaller eggs.

Nest defense

I was able to assign nest defense scores to 21 female iguanas. Of these, four exhibited no defense, four defended their nests fewer than 5 days, and 13 defended their nests more than five days. To analyze these with sufficient sample sizes, I re-categorized females as being “low” defense (<5 days; n = 8) and “high” defense (>5 days; n = 13). Several variables were examined by t-tests for their influence on nest defense behavior. I hypothesized that high defense females would have larger SVL, nest earlier in the season, and be in areas of higher nest density than low defense females; hence, these were all one-tailed tests. I also used a two-tailed test to compare vegetation cover for low versus high-defense females. Results of the comparisons are shown in Table 6. The only hypothesis supported by the data was that high defense females were found in areas of higher nest density (P = 0.03). This conclusion, however, should be regarded as tentative because with four tests, the experimentwise alpha level could arguably be reduced by reducing the alpha level of individual tests to 0.0125 using the Bonferroni adjustment (i.e., 0.05 / 4 tests; Lentner & Bishop, 1986).

Activity Surveys, Population Estimation and Home Range Estimates

Activity surveys and population estimation

During the activity surveys, there were a total of 1,795 iguana sightings (of all size classes), of which 854 (47.6%) were of marked iguanas. Table 7 lists the descriptive statistics for these sightings. During the study there was no apparent decline in the proportion of marked iguanas resighted, which suggests that our repeated sampling did not influence surveying results. The mean proportion of marked iguanas resighted was 32 ± 1.8% (range = 19-48%; n = 16) in the morning, 23 ± 2.9% (17-30%; n = 5) during midday surveys, and 39 ± 1.7% (25-48%; n = 16) during the evening hours (Table 8; Figure 12). A 2X3 (sex X time of day) ANOVA, treating both variables as between subject factors, was used to compare the effects of time of day and sex. The results suggest that activity levels were similar for males and females and there was not a significant interaction between sex and time of day. However there was a significant difference in the time of day that surveys were conducted ($F_{2,74}$= 14.83, $p < 0.001$, Figure 12), with fewest iguanas active at mid-day and the most iguanas active during the evening. Post hoc (Scheffe) contrasts indicated that each time of day was significantly different from the other times.

Correlation analyses revealed changes in the proportion of iguanas seen during the course of the study. For morning surveys (n = 16), the proportion of marked males resighted did not vary over time, but the proportion of marked females (r = 0.65, P = 0.007) resighted increased during successive surveys. Consequently, for morning surveys the proportion of all marked iguanas resighted increased over time (r = 0.65, P = 0.007), as did the total number of iguanas encountered (r = 0.53, P = 0.03). For afternoon surveys (n = 16), the proportion of marked males resighted and the total number of all iguanas sighted remained consistent over time, but the proportion of marked females (r = 0.70, P = 0.003) and therefore the proportion of all marked iguanas (r = 0.57, P = 0.02) resighted similarly increased during successive surveys. Thus, whereas males appeared to maintain consistent levels of activity during the course of the study, females either became more active as the nesting season progressed or they were more likely to be detected by the observer. The number of midday surveys (n = 5) was deemed too few for correlation analyses.

The results of Lincoln-Petersen population estimates are summarized in Table 9. Population estimates within the grid area ranged from 107-184 iguanas, with a mean (± S.E.) of 133 (± 3) iguanas for all surveys combined (n = 37). Assuming that 133 iguanas was the actual population size, detectability of iguanas (number of iguanas seen per survey / 133) averaged 0.33 (± 0.01), with a range of 0.15-0.46. Detectability did not change over time (r = 0.15, P = 0.374). The maximum estimation error for an individual survey was 19.5% (26 iguanas) below the estimate of 133 iguanas and 38.3% (51 iguanas) above this estimate. The number of marked iguanas varied from 63 with the first survey to 77 for the last survey. Thus, with an estimated 133 iguanas present, 47.4% were marked at the time of the first survey and 57.9% were marked by completion of the study. A one-way ANOVA revealed that population estimates were consistent regardless of the time of day that surveys were conducted ($F_{2,34} = 0.12$, P = 0.88; Table 9). However, because marked females were more likely to be seen later in the season, this might be expected to influence Lincoln-Petersen estimates. For morning surveys (n = 16), correlation analyses indicated that population estimates were consistent during successive surveys (r = -0.33, P = 0.21). In contrast, for afternoon surveys (n = 16), there was a significant decline in estimates of population size during the course of the study (r = -0.58, P = 0.019). When surveys were pooled for all times of the day, the population estimates were consistent (marginally) over the duration of the study (r = -0.32, P = 0.055).

To compare variation between iguana counts (total iguanas observed) and Lincoln-Petersen estimates, the coefficient of variation (CV = standard deviation / mean) was computed for each measure (n = 37 surveys total). With a mean of 44.3 iguanas sighted per survey, the CV for iguana counts was 0.253. With a mean Lincoln-Petersen estimate of 133 iguanas, the CV was 0.137.

Juvenile iguanas were not so readily detected during surveys, in part because of the focus on locating adults. The number of juveniles seen varied from zero (23.7% of surveys) to five (2.6% of surveys), with a mean of 1.6 (± 0.2) per survey and a CV of 0.855.

Home range estimates

Four measures of home ranges of male (n = 14) and female (n = 24) iguanas were evaluated by three methods: maximum distance between any two points, minimum convex polygon (100% and 95%) and fixed kernel estimation (95%). The results of these comparisons are shown in Table 10 for all iguanas with 10+ sightings. Smoothing (LSCV) values ranged from –3.61 to –0.04, with a mean of –0.34 (± 0.11). Autocorrelation values for t^2/r^2 ranged from 0.38-2.64 (only one animal was < 1.12) with a mean of 1.77 (± 0.08); values substantially less than 2.0 are indicative of time dependence between successive relocations (Swihart & Slade, 1985). Swihart and Slade autocorrelation values ranged from –0.62-2.61 (four animals exceeded 1.0), with a mean of 0.49 (+ 0.10); independent data should be near zero whereas autocorrelated data can be as high as 4 (Hovey, 1998). Mann-Whitney U tests indicated that all four measures of home range size were similar for males and females (Table 10; all P's > 0.18). Spearman correlation analyses for all iguanas (n = 38) showed that all four measures of home range were highly correlated (all rhos > 0.745, all P's < 0.001). Spearman correlations also revealed that home range estimates were negatively associated with the number of observations of an individual (all rho's < -0.37; all P's < 0.045). Thus, animals sighted most often were those having smaller home ranges. At the 95% level, MCP estimates were higher than fixed kernel estimates for male iguanas but smaller for females. Iguanas with large home ranges moved along the long axis of the island, with maximum distances traveled (up to 373 m) exceeding more than half the island length. In contrast, some iguanas of both sexes were seen within a 100 m^2 area during the entire study.

Vegetation

The vegetation of Green Cay is comprised of 10 species, located in patches throughout the cay. The spatial and quantitative relationships of the plant species and rocky/soil substrates within the grid system are provided in Figure 3 and Table 11. Although not apparent from the figure, many plants showed overlap, particularly *B. arborescens*, *R. americana*, *S. portulacastrum* and *S. patens*. Although not detected in the point surveys, a small area of *Hymenocallis* sp. was present in the SW area, as reflected on the map. *Opuntia stricta* was also present but was not encountered at any points of the survey. This cactus has declined dramatically since 1994 (Hayes et al. 1995) but small plants are distributed throughout much of the western and central areas of *B. aborescens* and along the periphery of *C. uvifera* clumps. Vegetation covered approximately 58% of the study area and rock occupied the remainder (42%). The most abundant plant species in the study area were *C. erectus* var. *sericeus* (40% of area), *R. americana* (16%), and *B. arborescens* (14%). Volumetrically, *C. erectus* var. *sericeus* was the dominant plant species, even though it was underestimated by exclusion of some habitat from the grid area. Iguanas were fairly evenly distributed across the cay although they avoided the rocky periphery of the island. Somewhat fewer iguanas were seen in the middle of the dense *C. erectus* var. *sericeus* on the eastern part of the island.

Diet

Food items consumed by *C. r. rileyi* during three times of the year are provided in Table 12. Of the 10 plant species present on Green Cay, seven were found in the scats of iguanas. Relative abundance of each plant species was determined from the vegetation survey (Table 12), using number of points occupied by each species divided by total points comprised of vegetation. Compared to their relative abundance, *B. arborescens* (flowers especially), *O. stricta* and *Rhachicallis americana* (both flowers and leaves) were heavily browsed by iguanas. The diet appeared to be similar during the three times of the year that scats were sampled. I occasionally observed adult iguanas attempt to catch grasshoppers. Insect remains were evident in some scats (22% in October 1999 and 13% in May 2000). Inorganic material such as sand particles and/or soil fragments was also found some scats.

DISCUSSION

Capture Data

The sexes of *C. r. rileyi* are size dimorphic. Adult males are significantly larger than adult females in all aspects of size measurements (mass, SVL, head length, tail length). This should be expected because the growth rates for males are generally greater than for females (Carey, 1975; Christian, 1986; Iverson, 1979, 1989). Other iguanas, including *C. carinata*, also exhibit sexual dimorphism in size (Iverson, 1979). Several studies have shown that female rock iguanas average between 80-90% of male SVL and between 50-55% of male body weight (Iverson, 1979). Female *C. r. rileyi* fell within this average for SVL (89.5%) but had a higher average for body mass (74.6%), perhaps because of their gravid state. This size dimorphism is different from most other reptile species for which females are usually larger then males (Fitch, 1981; Shine, 1978; Berry and Shine, 1980). Sexual dimorphism resulting in larger male iguanas may be the result of greater reproductive success of larger males due to local mate competition (Dugan, 1982; Trivers, 1976).

Reproductive Ecology

Nesting Activity

The nesting season for *C. r. rileyi* appeared to begin in late June but completed nests were not seen until July 3rd. Nesting continued throughout the study period and likely continued for another week or two after my departure. The onset of the nesting season was found to be later than in *C. r. nuchalis* which began nesting in late June in 1998 (Thornton 2000) and the same year of my study (Hayes and Carter, unpublished data). Since there is limited space where *C. r. rileyi* can nest, we noticed some diversity in habitat selection for nesting sites. The sites chosen ranged from sandy areas to rock crevices, usually with sparse or no vegetation cover. In several cases it appeared to me that nests were built beneath rock slabs that were entered through a small crevice. Perhaps because ideal nesting habitat can be limited, iguanas may utilize a diversity of microhabitats for nesting. Thornton (2000) showed that *C. r. nuchalis* preferred to nest in the loose sand of beachfront dunes, but nests of other *Cyclura* species have been found in hollow logs and termite mounds (Auffenberg, 1976; Iverson, 1979). Burger and Gochfeld, (1991) found that *Ctenosaura similis* use earth banks, logs and rock crevices as nest burrows.

My data showed that larger females oviposit earlier then smaller females. This was in contrast to the findings by Thornton (2000) with *C. r. nuchalis*, where larger females nested later than smaller females. Alberts (1995) found that larger *Cyclura nubila* oviposited earlier then smaller females. The extent to which nest sites are limiting may influence the timing of egg-laying, since females that oviposit earlier should have the first opportunity of preferred nest sites. However, females nesting early face the risk of having their eggs disturbed or destroyed by the digging efforts of subsequent nesters, which may explain why many post-oviposition females remain in close vicinity to their nests to defend them (as discussed below). Because of nest defense, the larger females that nested earlier might have been expected to nest in areas with fewer nearby females, but no such relationship between female SVL and relative nest density was found.

Burrow Characteristics

The burrows that I excavated showed some variation in morphology. The average burrow length was shorter for *C. r. rileyi* on Green Cay (53 cm; range = 30-116 cm) than those of *C. r. nuchalis* on North Cay (129 cm; range = 69-235 cm; Thornton, 2000). This could be for several reasons, one being that the soil on Green Cay appears to be much more limited in distribution and depth. However, the average chamber depth for burrows on Green Cay (22 cm; range = 18.0-28.0 cm) was similar to those of *C. r. nuchalis* on North Cay (22 cm; range = 14-40 cm). Nest chamber depth is likely more critical to incubation success than is burrow length.

The burrow dimensions of iguanas vary considerably within and among species. Of the five burrows I excavated, two followed a straight path while the other three had one or more turns. In green iguanas (*I. iguana*), Bock and Rand (1989) found some burrows very short, barely the length of the nesting female, whereas others were relatively sophisticated with a network of side chambers. Similar variation has been reported in other studies of *Cyclura* (Iverson, 1979;

Thornton, 2000). While digging burrows, females frequently run into obstacles (rocks, packed sand), which can result in the abandonment of burrows or a change in digging direction (Iverson, 1979; Thornton, 2000). This was observed on Green Cay when females were searching for nesting sites. I found that many of the exploratory burrows were apparently abandoned because of obstacles encountered while digging, but others were found abandoned for no apparent reason.

Several studies have shown that during the nesting season females seek out old burrows from the previous nesting season (Christian et al., 1986; Thornton, 2000). Previously used burrows undoubtedly have looser soil and would be easier to excavate. However, because of the limited amount of nesting sites, iguanas may randomly encounter (without intent) previously used burrows and egg chambers. Iguanas often begin multiple excavations before choosing one to nest in (Thornton, 2000; Vogel, 1994, 2000). This behavior may represent an effort to locate relatively loose soil. Alternatively, it may represent an effort to dissuade other females from nesting too close. While excavating nesting burrows I encountered old eggshell fragments that were found either in the path of the burrow or in the egg chamber. These shell fragments were from a previous year's clutch, but not necessarily from the same female. A longer term study would be necessary to confirm whether individual females use the same burrows year after year.

Construction of the burrow can be done in a little as one day. Once it is completed, the iguana stays in the burrow overnight and emerges the following day, refilling the burrow tunnel as it emerges (Blair, 1991b; Thornton, 2000). The exact time of egg-laying (e.g., evening, night or morning) could not be determined in this study. Most nesting burrows I found were already completed, with the exception of one iguana that was found in a burrow tunnel on its way out while I was attempting to excavate the burrow. Since iguanas infill the burrows after ovipositing it would seem difficult for the hatchlings to emerge from the burrow. Blair (1991b) found that hatchlings may require as much as two weeks to dig out after hatching. Some have argued whether the hatchlings emerge vertically through the chamber roof or out the burrow tunnel (Iverson 1979). My findings, and those of Thornton (2000) for *C. r. nuchalis*, were not consistent with a vertical escape because all nesting chambers, including those with old egg shells, had an intact roof of hard impacted sand.

Clutch Size Relationships

Clutch sizes for *C. r. rileyi* on Green Cay ranged from 3-6 eggs. This clutch size is amongst the smallest of all species of *Cyclura*. *Cyclura r. nuchalis* on North Cay had a slightly smaller clutch size, which ranged from 2-5 eggs (Thornton, 2000). Larger species of rock iguanas, such as *C. collei*, *C. cornuta* and *C. nubila*, can produce clutches of 20 or more eggs (Alberts, 1995; Christian, 1991; Vogel, 1994, 2000; Wiewandt, 1982). Clutch size in all lizards is clearly associated with SVL (e.g., Iverson, 1979; Alberts, 1995). Nevertheless, clutch size relative to body size is small for *Cyclura* compared to other iguanid genera (e.g., *Ctenosaura*, *Iguana*, *Sauromalus*), but exceeds that of the marine iguana *Amblyrhynchus* (Wiewandt, 1982). As suggested by Wiewandt (1982), insular populations of iguanas produce smaller clutches than those living in mainland habitats, and this is likely the result of differences in predation and survivorship.

An improved understanding of clutch size can benefit management of endangered iguana populations. For example, because *C. r. rileyi* on Low Cay are considerably larger than those on Green Cay (as well as those on other cays; Hayes et al., 1995, unpublished data) and produce larger clutch sizes (10 in one burrow that I found), iguanas on Low Cay should be deemed a high priority for conservation. Their high reproductive potential would be beneficial for captive headstarting and repatriation efforts should any such programs be undertaken in the future. Further, the small body size of *C. r. cristata*, for which as few as 10 females may exist (Fry, 2001), suggests that population recovery will be especially slow due to their limited reproductive potential. Thus, captive headstarting and translocation programs should be implemented to hasten recovery of this taxon.

Relative parental investment (change in body mass/ original body mass) is a good indication of the proportion of energy used for reproduction (e.g., Iverson, 1979). The mean value for *C. r. rileyi* (0.22; n =9) was somewhat less that that found in *C. r. nuchalis* (0.27; Thornton,

2000) and *C. c. carinata* (0.24; Iverson, 1979). However, relative parental investment was correlated with female SVL (see also Thornton, 2000; Wiewandt, 1977) and thus comparisons among different species are confounded by differences in body size. Relative parental investment in lizards ranges from 0.05-0.40 (Pianka & Parker, 1975; Tinkle, 1969; Iverson, 1979). However, in contrast to iguanas, which produce only one clutch per year, many lizards produce multiple clutches in a year.

The minimum reproductive size for *C. r. rileyi* was 22 cm and 340 g. Female *C. r. nuchalis* on North Cay appeared capable of breeding at a smaller size (19.5 cm, 260 g; Thornton, 2000), as did *C. carinata* (18.5-20 cm) studied by Iverson (1979). Larger iguanas generally mature at larger body sizes. *Cyclura pinguis* has a minimum reproductive size of 35-40 cm SVL (Carey, 1975) and *I. iguana* matures at 25-27 cm SVL (Dugan, 1980).

Egg Size Relationships

Egg measurements (mass, length, and width) showed high levels of covariance, as expected (c.f., Thornton, 2000). However, the mean mass of individual eggs decreased with increasing clutch size (or increasing SVL), a pattern similar to that found in *C. r. nuchalis* by Thornton (2000) but opposite of that reported for *C. nubila* (Alberts, 1995; Christian, 1991) and *I. Iguana* (Fitch and Henderson, 1977). Thus, in both studies of *C. rileyi* (this and Thornton, 2000), larger females increased their reproductive effort by producing larger clutches with smaller egg size. The demographic consequences of this pattern are unclear but warrant closer scrutiny in the future.

Nest Defense

Female nest defense subsequent to oviposition has been widely reported among iguanas (reviewed by Wiewandt, 1982). Among rock iguanas, nest defense has been reported for *Cyclura carinata* (Iverson, 1979), *C. collei* (Vogel, 1994, 2000), *C. cornuta stejnegeri* (Wiewandt, 1977), *C. cyclura* (Carey, 1975), and *C. rileyi nuchalis* (Thornton, 2000). Nest defense has been viewed largely as a strategy to protect the nest from damage inflicted by other nesting iguanas (Wiewandt, 1982). Wiewandt (1982) reported that roughly 10-15% of the egg-filled nests of *C. cornuta stejnegeri* are dug into by intruding gravid females.

The extent of engagement in nest defense may vary considerably within a single taxon. For example, female marine iguanas *(A. cristata)* on Hood Island exhibit nest defense (Eibl-Eibesfeldt, 1966), whereas those studied on Fernandina do not (Eible-Eibesfeldt, 1966; Carpenter, 1966). Within a single population, some individuals of *C. r. nuchalis* exhibit aggressive nest defense whereas others abandon their nest immediately (Thornton, 2000). Individual variation was also apparent in *C. r. rileyi* on Green Cay, where the duration of nest defense was highly variable. The reasons for variation in the duration of nest defense remain unclear. Although my sample size was limited, I was able to evaluate several factors that might influence the duration of nest defense, including female body size, nesting date, vegetation cover above the nest, and relative density of nest burrows. Of these, only the relative density of nest burrows differed significantly between females exhibiting brief (<5 days) versus lengthy (> 5 days) nest defense (Table 6). Females that exhibited lengthy nest defense had a greater number of other nest burrows in close proximity. Although other variables may be important for influencing nest defense, the most important one appears to be the relative density of nearby females, whose digging efforts and apparent preference for loose substrate pose a tangible risk to a completed nest. However, I suspect that other variables have an influence as well. For example, since larger females invest more into reproduction than smaller females and nest earlier in the season, they should be more willing to invest additional time and energy guarding their nests. Further study is necessary to confirm these relationships.

Activity Surveys, Population Estimation and Home Range Size

Activity Surveys and Population Estimation

The daily activities of iguanas are organized on a circadian rhythm that may vary seasonally. During hot weather, for example, many iguanas restrict their activities to the mornings and evenings, but during cooler weather they may remain active throughout the day (e.g., Iverson, 1979; Wiewandt, 1977; see also Burger and Gochfeld, 1991; Burghardt and Rand, 1985; Dugan, 1980). Behavioral differences may also exist between the sexes. Because many population estimates are based on the detection of active iguanas (e.g., classical transects, distance transects, and mark-resighting methods; Hayes & Carter, 2000), it is important to understand the factors that influence detectability.

In this study, I compared the activity levels (detectability) of male and female iguanas at different times of the day during the pre-nesting and nesting seasons. My results, based on the proportion of marked iguanas resighted during repeated surveys, indicated that male and female iguanas exhibited similar levels of activity during morning, mid-day and evening. However, there was a significant difference between the different times of days, with iguanas more active in the morning (0800 – 1030) and evening hours (1700 – 1930), but less active during the mid-day hours (1300 – 1430). The proportion of marked iguanas sighted during the surveys averaged 32% during morning surveys, 23% during mid-day surveys, and 39% during evening surveys, with a pooled mean of 33.7% for all surveys (Table 8).

The Lincoln-Petersen estimates suggested that 133 iguanas were present within the study area. With an average of 44.3 iguanas sighted per survey, a mean of 33.3% of the iguanas present were sighted on each survey. Thus, the mean proportion of marked iguanas resighted (33.7%) and the mean proportion of total iguanas sighted (33.3%) were remarkably equivalent. These findings are important because they are similar to the mark-resighting data from other *C. rileyi* populations (Fry, 2001; Hayes et al., 1995, unpublished data; Thornton, 2000), which suggest that during standard surveys we see approximately one-third to one-half of the iguanas (adults and subadults) present. Thus, when using classical and distance surveys, population estimates for *C. rileyi* can be adjusted based on a detectability rate of 0.33 to 0.5 (i.e. the number of iguanas detected during a survey can be multiplied two-fold or three-fold to derive a better estimate of actual population size; Hayes & Carter, 2000). Since iguanas are generally less active during mid-day, population estimates based on mid-day surveys should be adjusted with a higher multiplication factor, counter-balanced by surveys taken at other times of day, or avoided altogether.

My data indicate that the detectability of males remained consistent throughout the study period. However, female detectability increased over the duration of the study period. This may have been an artifact of observer familiarity with the specific location of marked females late in the season, but was more likely the result of the increased activities--and therefore visibility--of females during nest construction, nest defense and resumption of foraging during later stages of the study period. Thus, detectability of iguanas can vary to some extent during different stages of the reproductive cycle, and this needs to be taken into account when estimating population size (Hayes & Carter, 2000).

I found no evidence that the handling and marking of iguanas affected their subsequent detectability. There are two ways in which detectability might have changed: the marked iguanas could have avoided me (i.e., under-represented in surveys), or they could have become more conspicuous to me (i.e., over-represented in surveys). Neither consequence was apparent to me. The proportion of sightings represented by marked iguanas when all surveys were pooled (47.6% of 1795 sightings, including juveniles and subadults; Table 7) was reasonably close to the proportion of iguanas in the study area that were marked (47.4% at the start of the surveys to 57.9% by completion of the study, based on the Lincoln-Petersen estimate of 133 total iguanas). Moreover, the detection rate for marked iguanas (33.7%) was equivalent to that of all iguanas in the population (33.3%).

The two major approaches for estimating iguana populations are transect surveys (using classical or distance methods applied to animal counts) and mark-recapture methods (Hayes & Carter, 2000). The coefficients of variation from my repeated surveys suggest that Lincoln-Petersen estimates (CV = 0.137) are more precise than survey estimates based on numbers of iguanas sighted (CV = 0.253). However, there are many considerations when selecting a method for surveying iguanas, including available time, manpower and funding. Mark-recapture methods, though more precise, are more time-consuming, labor-intensive and costly. The appropriate choice of method should depend on the level of precision required for the estimate and, insofar as can be estimated, the level of accuracy required. Unfortunately, I do not know the true population size of iguanas on Green Cay, in part because iguanas could move in and out of the defined study area. Thus, I was unable to compare the accuracy of the two methods.

Unfortunately, on many cays juvenile iguanas seem particularly difficult to find, and as a result are likely under-represented in our population surveys (Hayes et al., 1995; Iverson, 1979; Thornton, 2000). The CV for counts of juveniles (0.855) was much higher than that of the entire population (0.253), which illustrates the difficulty in surveying this size class. Compared to previous years (Hayes & Carter, unpublished data), numbers of juvenile iguanas seemed low, but small differences in direct counts may not be suitable for year-to-year comparisons. Clearly, more work needs to be focused on this age class.

Because additional iguanas were present in areas excluded from my study (the eastern portions of Green Cay), my estimate of 133 iguanas in the study area was an underestimate for the entire cay. The actual population size on Green Cay is probably closer to 200 (Hayes & Carter, unpublished data). Visits at other times of the year to the dense stand of *C. erectus* on the eastern part of the island (where the heron rookery was) indicate that iguana numbers are comparatively low in this area, with most iguanas found on the periphery of these stands (Hayes & Carter, unpublished data). The highest density of iguanas occurs in areas with more diverse plant species, particularly on the southwestern third of the cay. However, several dozen iguanas are typically present in the *Borrichia* and *Sesuvium* dominated habitat on the northeastern end of the island, where seabirds were nesting during the period of my study (Hayes & Carter, unpublished data). Whether any iguanas were present there during my study remains uncertain, as I chose not to disturb the nesting birds.

Home Range Analysis

Estimates of home range size on Green Cay were similar for males and females. Mean home range size (at the 95% level) for all iguanas was 647 m^2 using MCP and 557 m^2 using the fixed kernel method. *Cyclura r. nuchalis* on North Cay utilized larger home ranges (Thornton, 2000), where comparable fixed kernel estimates were 2,047 m^2 for gravid females (n = 5) and 397 m^2 for non-gravid females (n = 5). One reason for this difference was that several gravid and one non-gravid females on North Cay undertook lengthy movements (up to 1 km), which were not possible on Green Cay where the length of the island is only 600 m. Although females on Green Cay exhibited higher levels of variation in home range size than males (Table 10), there were no obvious migrations by females to find suitable nesting sites. *Cyclura r. cristata* on Sandy Cay also appeared to utilize larger home ranges (Fry, 2001), where adaptive kernel estimates (at the 85% level) were 2,656 m^2 (n = 7). Because of recent heavy predation by a raccoon, the iguanas on Sandy Cay were in much lower density than on Green Cay. Mitchell (1999) reported that home range size of *C. pinguis* expanded substantially (100-fold) following a decline in density on Anegada, and a similar effect may have been apparent on Sandy Cay. Presumably, home range size can be affected by factors other than population density, including food availability, shelter, energy expenditure, age, social status and season.

In my study, minimum convex polygons and fixed kernel estimates were similar. The fixed kernel approach is preferred to other estimators of home range size, including MCP's (Seaman et al., 1999), but both are recognized as being sample size dependent. With a small number of sightings, MCP's generally underestimate home range size whereas kernel methods usually overestimate home range size (Seaman and Powell, 1996). Simulation studies suggest that the minimum sample size for fixed kernel estimates should be close to 30 sightings (Seaman and Powell, 1996), and therefore my estimates (mean = 19 sightings) may have been biased as larger than actual size. Autocorrelation can also influence home range estimates, and some iguanas clearly showed dependence between successive locations. However, some degree of autocorrelation reflects biological reality, as temporal independence can seldom be achieved in studies of home range size (De-Solla et al., 1999; Powell, 2000). Although I was unable to evaluate spatial independence, the apparent territoriality of many adult iguanas suggests that individuals can substantially influence the use of space by other iguanas. Statistical methods are now available to evaluate spatial independence (Powell, 2000), and these should be considered in future studies of iguana home range size.

Vegetation and Diet

From fecal analyses and direct observation, the iguanas were found to browse on at least seven of the 10 species of plants on Green Cay (Table 12). The most common food items in the iguana's diet were the flowers and leaves of *B. arborescens* and *R. americana*. These plants were widely distributed on Green Cay, and occupied 17% and 20% of the vegetation surface area, respectively. Though *C. erectus* was much more abundant (50% of the vegetation surface area) than *Borrichia* and *Rhachicallis,* the leaves and fruit of this plant were consumed less. Although this could mean that *Borrichia* and *Rhachicallis* were preferred in the diet, *C. erectus* was more restricted in its distribution and therefore dietary preference cannot be assumed. Indeed, the home range of some iguanas did not encompass any *C. erectus* plants. The two individual seven-year apples (*Casasia clusiifolia*) on the cay were also unavailable to many of the iguanas. Thus, unless occasional forays that escaped my detection were made, many individuals were unable to consume the full range of plants available on Green Cay.

Compared to other populations of *Cyclura* (e.g., Auffenberg, 1982; Iverson, 1979), these iguanas have a highly restricted diet. The same is true for *C. r. rileyi* on Pigeon Cay in the hypersaline lake on the main island of San Salvador, where only five species of plants are known (S. Buckner, personal communication). In a detailed study of the feeding habits of *C. carinata*, Auffenberg (1982) indicated that a greater proportion of plant species are consumed when fewer species are present. Thus, the iguanas on Green Cay may consume plants that otherwise would not be selected if more species were available. Curiously, *Borrichia* was a major staple in the diet of iguanas on Green Cay, yet it was not among the 58 species of plants utilized by *C. carinata* at Auffenberg's study site despite its presence.

Coccoloba uvifera, *C. clusiifolia*, *C. erectus*, and *O. stricta* are the only plant species on Green Cay that produce fruit. Of these, only the berries of *C. erectus* were identified in fecal samples, which was probably because the fruits had not set on the other species. Iguanas in other populations are known to feed on these fruits (e.g., Auffenberg, 1982; Iverson, 1979; Mitchell, 1999; Thornton, 2000). Although parts of prickly-pear cacti (*O. stricta*) are still consumed, this plant was formerly more abundant and assumed to be a major part of the iguana's diet (based on seeds found in iguana feces; Moyroud and Ehrig, 1994; Hayes et al., 1995). Since 1994, there has been an estimated 70-80% decline in the biomass of this plant on Green Cay (Hayes, unpublished data) as the result of infestation by the introduced moth, *C. cactorum* (Hayes et al., 1995). The extent to which the loss of this food source has affected the iguanas remains unclear. I suspect that the carrying capacity of Green Cay and other cays (including Low Cay, where a large area of very small *Opuntia* persists in an area seldom utilized by iguanas; Cyril, personal observations) has been reduced because of the cactus decline.

Some invertebrate fragments were found in the fecal contents (Table 12), but their representation in the data was small. However, throughout the duration of the study, iguanas were seen making attempts to capture insects. During a subsequent rat eradication effort on Low Cay (June 2001), I found parts of a grasshopper in one scat and parts of a hermit crab in another. Auffenberg (1982) reported that animal prey represent a very small portion of the diet (4.4%). Since the dietary selection on Green Cay is limited, iguanas may be more inclined to supplement their diet with insects than on other cays, but my data are insufficient to support this view. Inorganic material such as sand and soil fragments was observed in a few fecal samples. The ingestion of this material was likely incidental, as concluded by Iverson (1979) who also found instances of soil in the feces of *C. carinata*.

With the recent passage of several severe hurricanes (Lily in 1996, Floyd in 1999), the landscape of Green Cay appears to be undergoing change (Hayes & Carter, unpublished data). The impact of Hurricane Floyd in particular was traumatic, with much of the iguana's nesting substrate (soil and sand) being swept away with the storm surge. Some of the vegetation was damaged as well. Hopefully, my data can serve as a baseline for evaluating future changes in the habitat and iguana population on Green Cay.

Table 1. Population (N) estimates and density (N/ha) for all known populations of *Cyclura rileyi*, based on data collected 1995-1997.

Taxon	Cay	Area (ha)	N	Density (N/ha)
C. r. cristata	Sandy	14.9	136	9
C. r. nuchalis	Fish	73.9	9484	129
	North	51.7	3036	59
	Unnamed	3.3	299	91
C. r. rileyi	Gaulin	1.6	10	6
	Goulding	2.9	174	60
	Green	5.1	195	38
	Guana	1.6	45	28
	Low	10.8	63	6
	Manhead	3.3	57	17
	Pigeon	7.8	105	14

Table 2. Species list for plants of Green Cay, San Salvador, Bahamas. *Source:* Ehrig & Moyroud, 1994.

Plant Species	Common Name
Borrichia arborescens	Sea Ox-eye Daisy Bay Marigold
Casasia clusiifolia	Seven-year Apple
Coccoloba uvifera	Seagrape
Conocarpus erectus var. *sericeus*	Silver Buttonwood
Hymenocallis sp.	Spider Lily
Opuntia stricta var. *dillenii*	Common Prickly-pear
Rhachicallis americana	Hog-bush, Sandfly Bush
Sesuvium portulacastrum	Seaside Purslane
Spartina patens	Saltmeadow Cordgrass
Sporobolus viginicus	Seashore Dropseed
Total known species	10

Table 3. Number of marked iguanas on Green Cay based on size class and sex.

Sex	Juveniles (< 12cm)	Sub-adults (12-19.9cm)	Small adults (20-27.9cm)	Large adults (> 28cm)	Totals
Males	0	1	17	7	25
Females	0	0	39	1	40
Total	0	1	56	8	65

Table 4. Microhabitats associated with nesting (N=41) and exploratory (N=49) burrows. Numbers represent the proportion of burrows having the vegetation or rock within 0.3 m of the burrow entrance.

Micro-habitat	Nesting (%)	Exploratory (%)
Borrichia arborescens	16.7	14.8
Conocarpus erectus var. *sericeus*	5.6	9.3
Opuntia srticta var. *dillenii*	0	1.9
Rhachicallis americana	36.1	26
Sesuvium portulacastrum	25.0	9.3
Spartina patens	5.6	1.9
Sporobolus virginicus	11.1	14.8
Rock	47.2	35.2
Rock-crevice	8.3	11.1

Table 5. Characteristics of excavated nests (n=5), including data on females, percent vegetation cover, depth of chamber (to floor), and egg dimensions.

					Egg		
Date	Nest	Vegetation Cover (%)	Length (cm)	Chamber Depth (cm)	Mass (g)	Length (mm)	Width (mm)
07/09/99	3	0	40	28.0	26.0	49.9	27.9
Female: F-45 24.9 cm (SVL) 450 g					26.0	50.3	29.6
					26.0	51.2	28.0
					22.5	51.8	28.8
					22.5	47.7	27.0
07/16/99	15	0	30	18.0	34.0	59.1	31.7
Female: unknown					34.0	52.1	29.5
					32.0	56.7	31.9
07/14/99	60	18.1	69	20.0	32.0	57.2	31.3
Female: unknown					30.0	56.1	27.3
					32.0	54.6	31.3
07/14/99	61	9.1	116	18.0	26.0	50.5	29.8
Female: F-50 25.1 cm (SVL) 440 g					30.0	57.1	29.5
					24.0	50.5	30.4
					28.0	55.1	31.0
					28.0	53.4	30.6
					24.0	51.8	30.0
07/15/99	84	0	55	24.0	26.0	51.7	28.7
Female: unknown					25.0	56.2	27.2
					27.0	51.8	29.0
					27.0	55.9	29.0
					0.0	0.0	0.0

Table 6. Comparisons of variables (mean ± S.E.) associated with females exhibiting low (< 5 days) versus high (> 5 days) of nest defense. Nesting date corresponds to the calendar date of July 1999.

Variable	N	Low Defense (<5 days)	High Defense (>5 days)	P
SVL (cm)	7,13	23.7 ± 0.3	24.7 ± 0.6	0.11[a]
Nesting Date	8,13	13.5 ± 1.4	11.4 ± 1.0	0.11[a]
Vegetation Cover (%)	3,8	7.6 ± 7.6	25 ± 1.0	0.34[b]
Nest Density (N/314m^2)	6,12	2.0 ± 0.4	3.6 ± 0.5	0.03[a]

[a] One-tailed t-test

[b] Two-tailed t-test

Table 7. Breakdown by sex, time of day, and presence or absence of marks for 1,795 iguana sightings pooled across 37 surveys on Green Cay.

Category		N	%
Sex			
(marked iguanas)	Male	326	38.2
	Female	528	61.8
Time of Day			
(marked iguanas)	AM	350	41.0
	Noon	79	9.3
	PM	425	49.7
Marked vs. unmarked	Marked	854	47.6
(all iguanas)	Unmarked	941	52.4

Table 8. Proportion of marked iguanas resighted during activity surveys undertaken between 18 June and 21 July 1999.

Time of Day		Percent Males			Percent Females			Total		
	N	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Morning	16	32.4	1.72	22-50	30.7	2.68	11-47	31.6	1.85	19-48
Midday	5	21.3	5.17	6-38	24.1	2.95	16-34	23.1	2.90	17-30
Evening	16	41.0	1.89	28-53	37.3	2.32	21-49	39.2	1.73	25-48

Table 9. Lincoln-Peterson population estimates based on surveys conducted during morning (0800-1030), midday (1300-1400), and evening (1700-1930).

Lincoln-Peterson Estimates			
	N	Mean ± SE	Range
Morning	16	134± 4	113-170
Midday	5	129 ± 15	107-184
Evening	16	133 ± 4	112-164
Total	37	133 ± 3	107-184

Table 10. Home range estimates (m^2) for adult male, female and all iguanas based on three methods: Maximum Distance (m) between any two points, Minimum Convex Polygon (Calhome software, at 100% and 95% levels) and Fixed Kernel (Home Ranger software, at 95% level). Individual iguanas were sighted on 10 or more occasions (males: 0 = 19, range = 10-26; females: 0 = 19, range = 10-24).

<u>Method</u>	Sex	N	Mean	SE	Minimum	Maximum
Maximum Distance	Male	14	38	8	9	123
	Female	24	58	18	5	373
	Total	38	51	12	5	373
MCP (100%)	Male	14	402	100	58	1076
	Female	24	852	408	9	8690
	Total	38	686	261	9	8690
MCP (95%)	Male	14	384	104	45	1076
	Female	24	800	405	9	8690
	Total	38	647	259	9	8690
Fixed Kernel (95%)	Male	14	439	139	14	1853
	Female	23	628	217	2	4139
	Total	37	557	144	2	4139

Table 11. Point counts (N = 205) of vegetation and rock cover for 10 m grid system on Green Cay.

		Height (cm)			Percent of Points [a]	Percent of Vegetation [b]	Volume [c] (m^3)
Plant	N	Mean	SE	Range			
Borrichia arborescens	28	52	3	20 – 76	14	17	1456
Casasia clusiifolia	1	102	0	102	< 1	< 1	102
Coccoloba uvifera	9	128	45	61 – 262	4	6	1152
Conocarpus erectus var. *sericeus*	81	164	11	23 – 320	40	50	13284
Hymenocallis sp.	0	0	0	0	0	< 1	>0
Opuntia stricta var. *dillenii*	0	0	0	0	0	< 1	>0
Rhachicallis americana	33	46	5	3 – 119	16	20	1518
Sesuvium portulacastrum	7	11	3	3 – 26	3	4	77
Spartina patens	1	15	0	15	< 1	< 1	15
Sporobolus virginicus	3	25	1	23 – 28	1	2	75
Rock/Soil	87				42		

[a] Percent of points = number of points / 205 total points x 100.

[b] Percent of vegetation = number of points / 118 point occupied by vegetation x 100

[c] Approximate volume (m^3) = number of points (each represents 100 m^2) x mean vegetation height (m).

Table 12. Food items eaten (proportion of samples in descending order of preference) by iguanas on Green Cay, as determined from fecal samples and direct observation. Relative abundance of plant species is the percent of vegetation cover in Table 11.

		Proportion of samples (%)					
Plant Species	Parts of Plants	July[a]	October[b]	May[c]	Directly observed	Preference Rank	Relative abundance
Borrichia arborescens	Flowers Leaves	62 0	78 11	63 17	+	1	17
Rhachicallis americana	Flowers Leaves	31 62	67 56	50 46	+	2	20
Conocarpus erectus var. *sericeus*	Leaves Fruit	15 8	0 0	25 0	+	3	50
Coccoloba uvifera	Fruits Leaves	0 15	0 0	0 17	-	4	6
Opuntia stricta var. *dillenii*	Pads/spine	31	22	0	-	4	< 1
Invertebrates	Skeletons	0	22	13	+	6	
Sesuvium portulacastrum	Leaves	0	11	0	+	7	4
Inorganic material	Sand, rocks, etc.	0	22	0	+		

[a.] N=13 samples of 1-3 pellets; samples taken between June 25-July 15, represented from 10 grids in SW half; assumed to be from different animals.

[b.] N=9 samples of 1-2 pellets; samples taken in mid-October, randomly collected throughout the cay; assumed to be from different animals.

[c.] N=24 samples of 1-2 pellets; samples taken in May 2000, randomly collected throughout the cay, assumed to be from different animals.

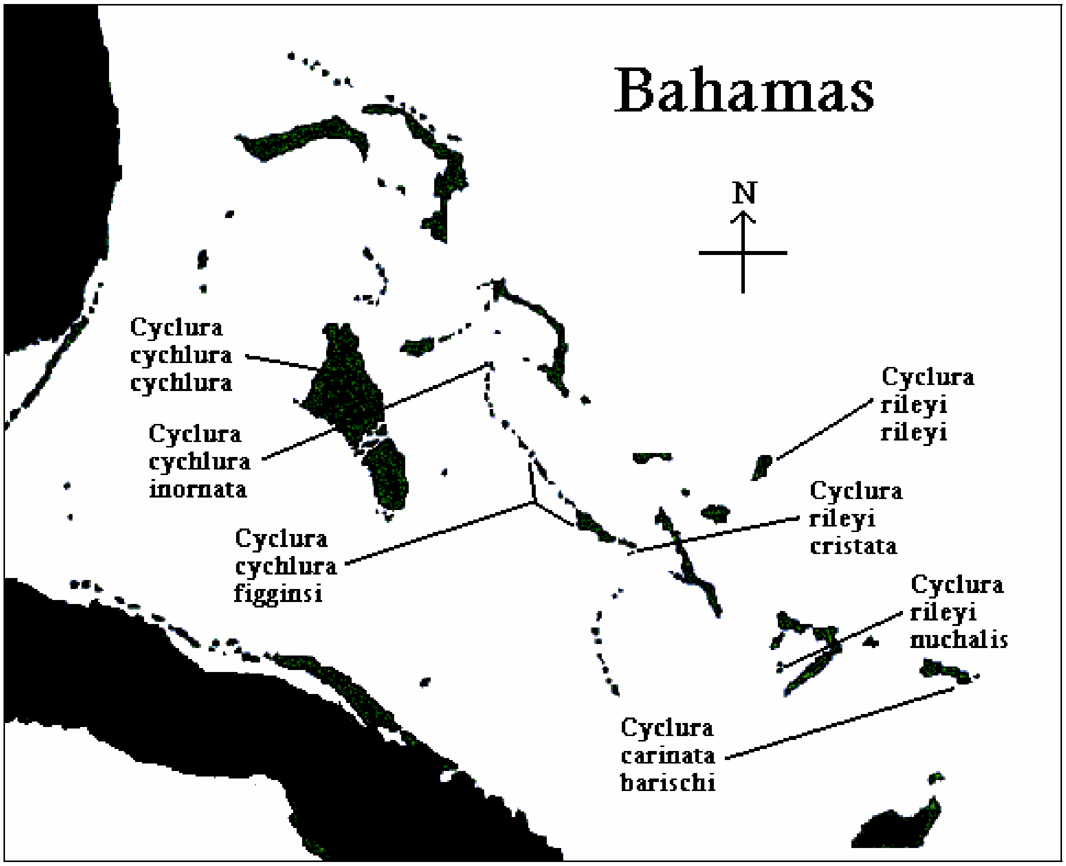


Figure 1. Distribution of *Cyclura* throughout the Bahamas.

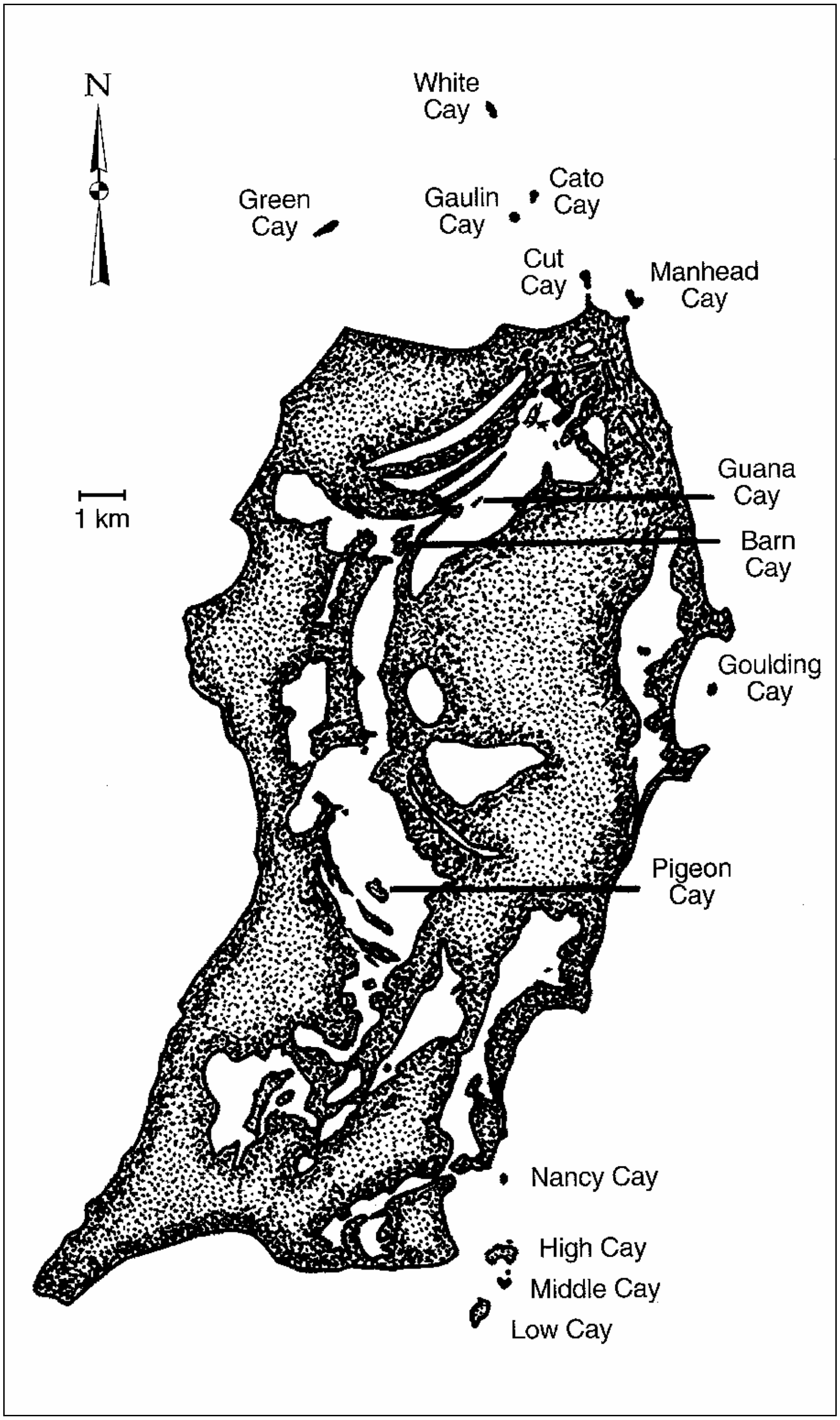


Figure 2. San Salvador Island, Bahamas.

Figure 3. Microhabitat map of Green Cay showing areas of rock (white) and dominant vegetation.

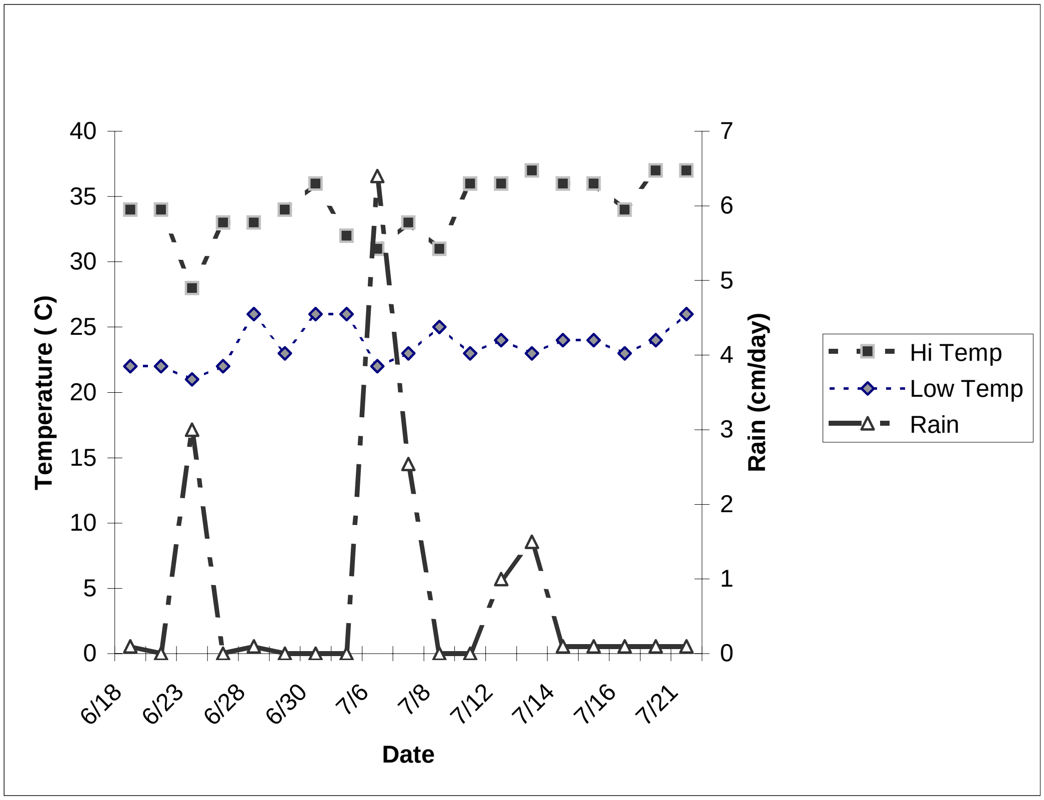


Figure 4. Daily temperature and rainfall measurements during June and July, 1999 on Green Cay.

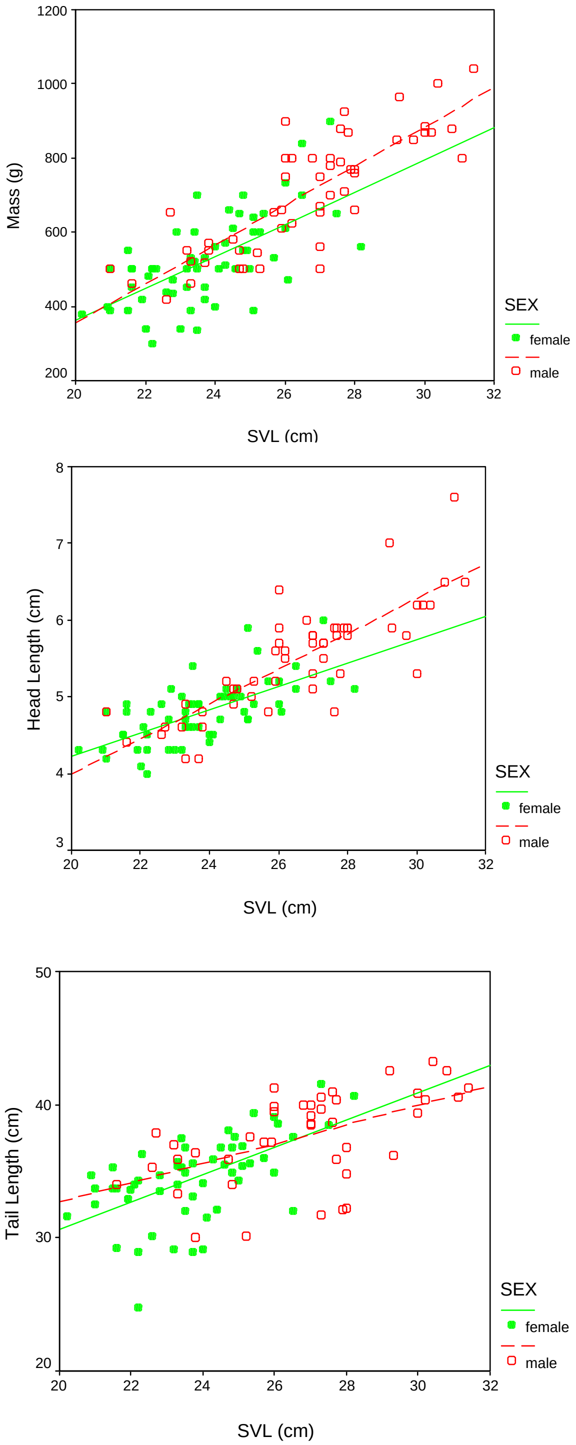


Figure 5. Body size relationships of adult (>20 cm SVL) male (open circles, dashed lines) and female (closed circles, solid lines) iguanas on Green Cay.

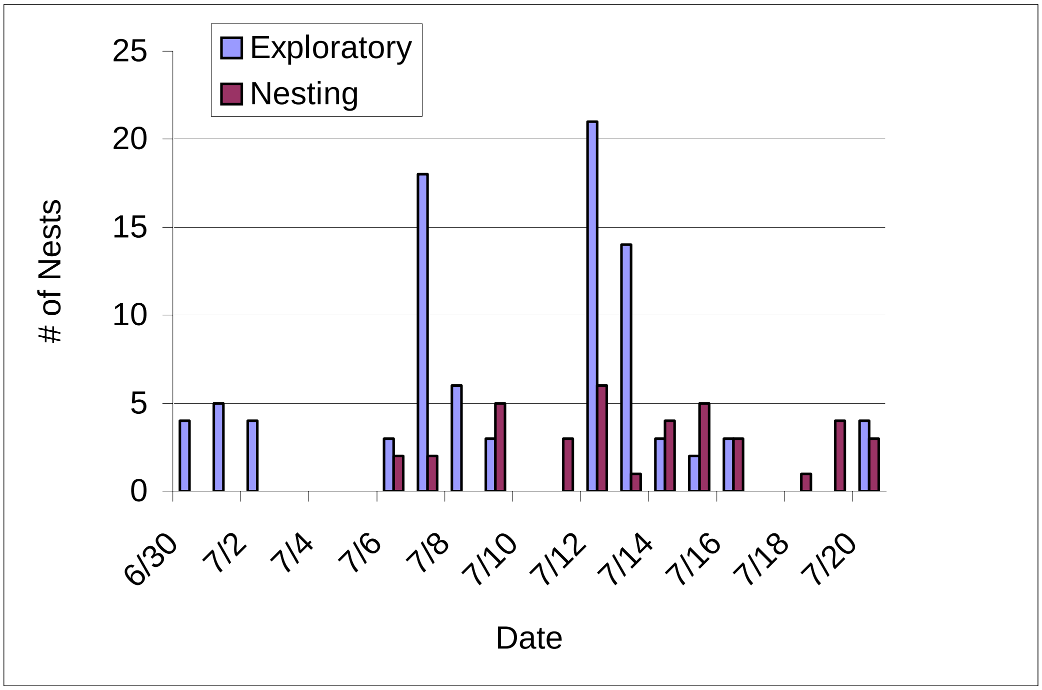


Figure 6. Number of nesting (n=41) and exploratory (n=49) burrows found on Green Cay per day throughout the study period. Missing bars represent absence from the study site.

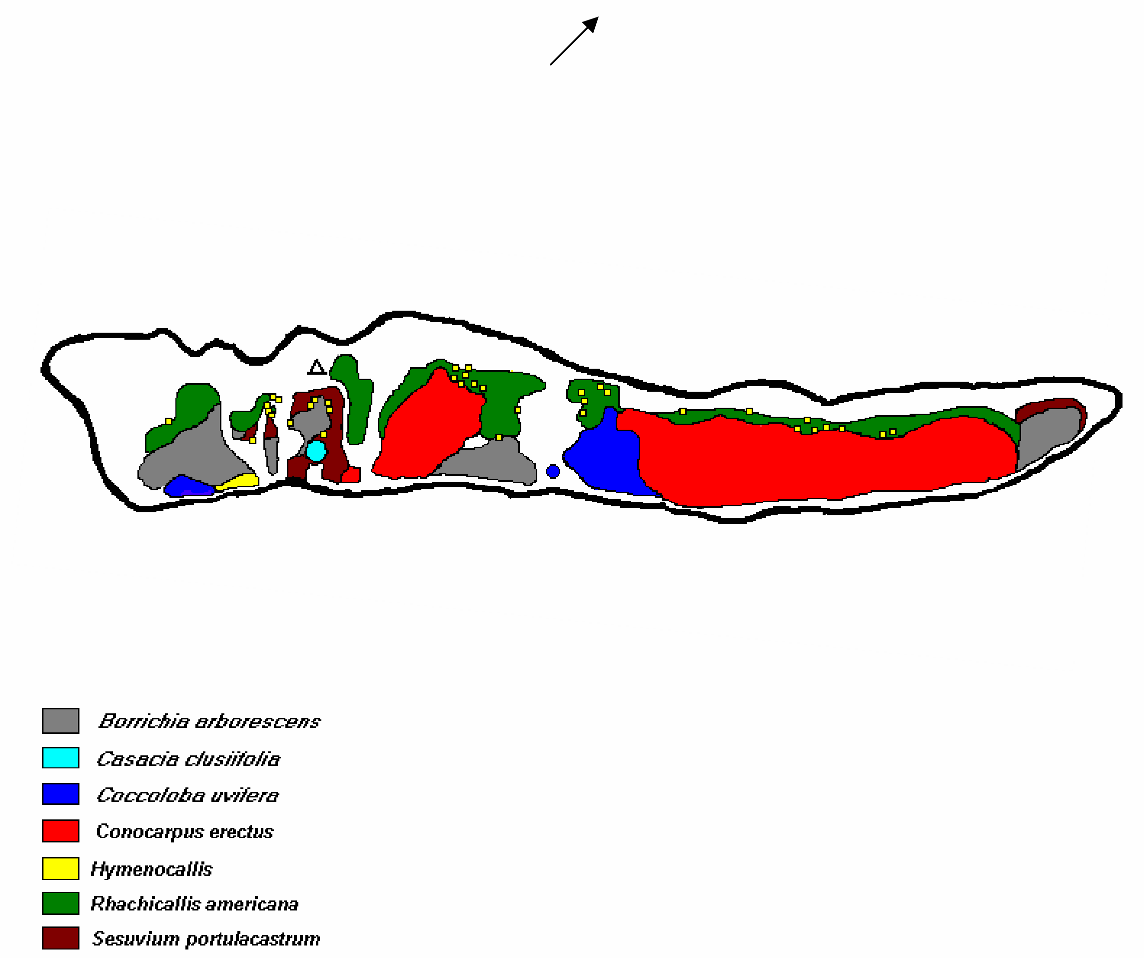


Figure 7. Distribution of nest sites (n=41) on Green Cay.

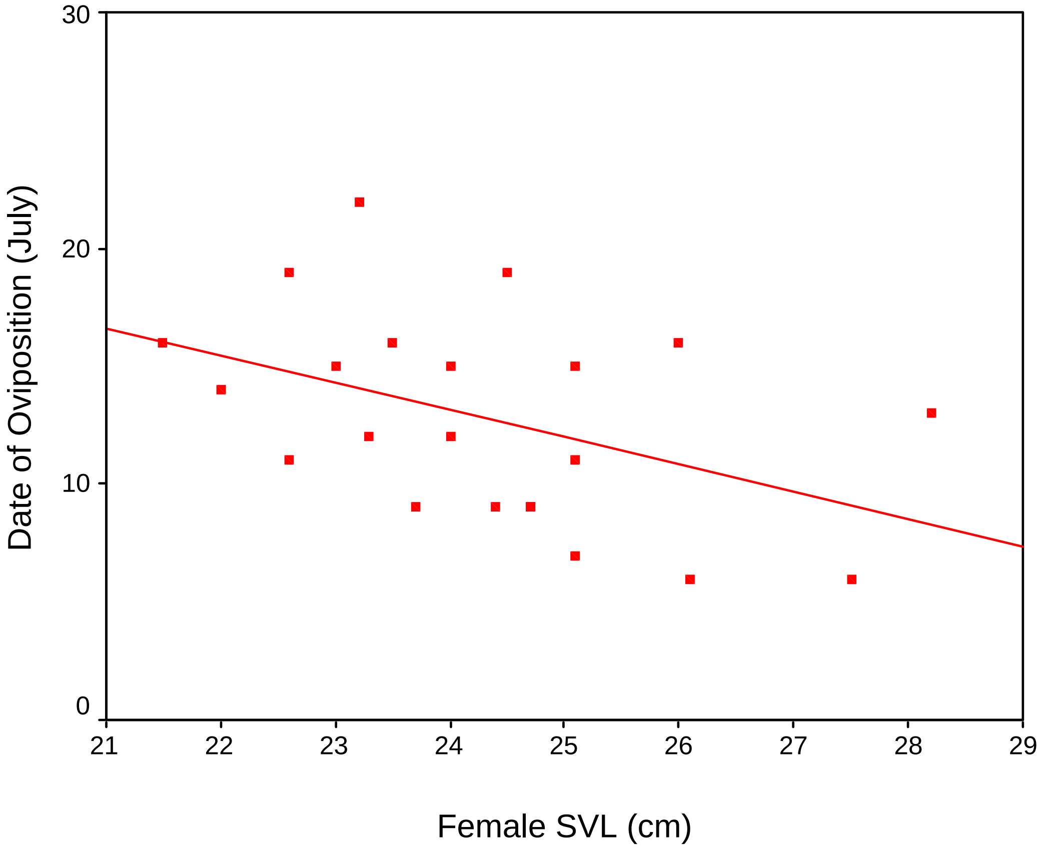
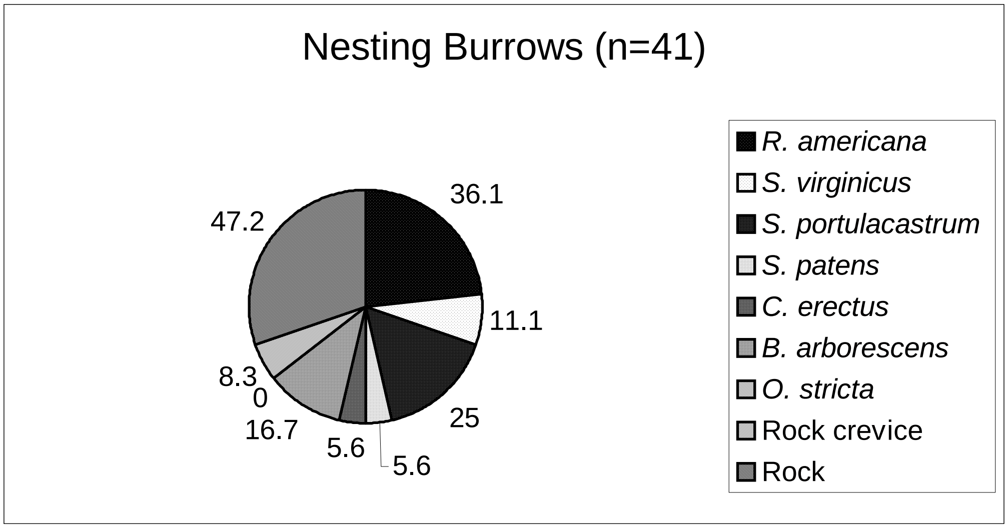


Figure 8. Relationship between female size and date of oviposition (r = -0.47, P = 0.028, n = 22).



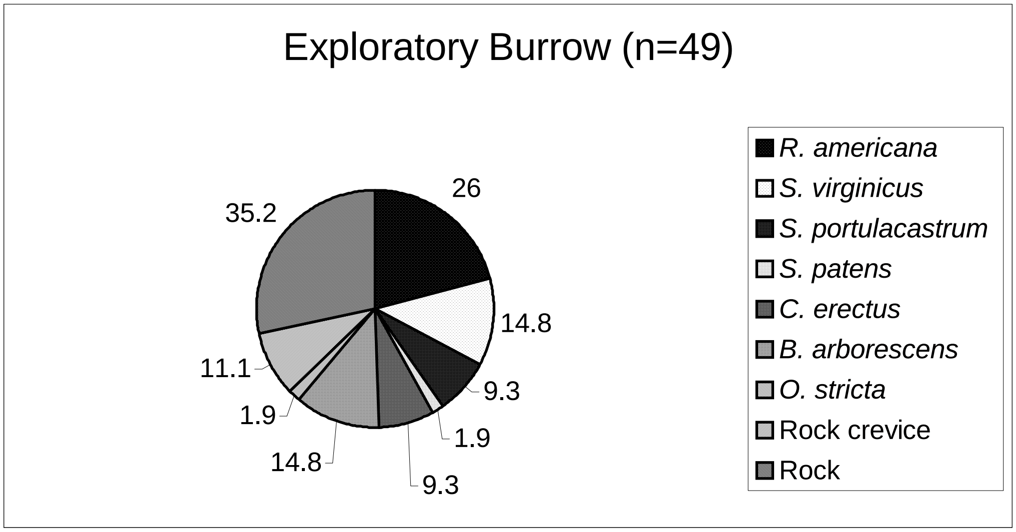


Figure 9. The relative representation of microhabitat features (within 0.3 m of entrance) for nesting and exploratory burrows (see also Table 4).

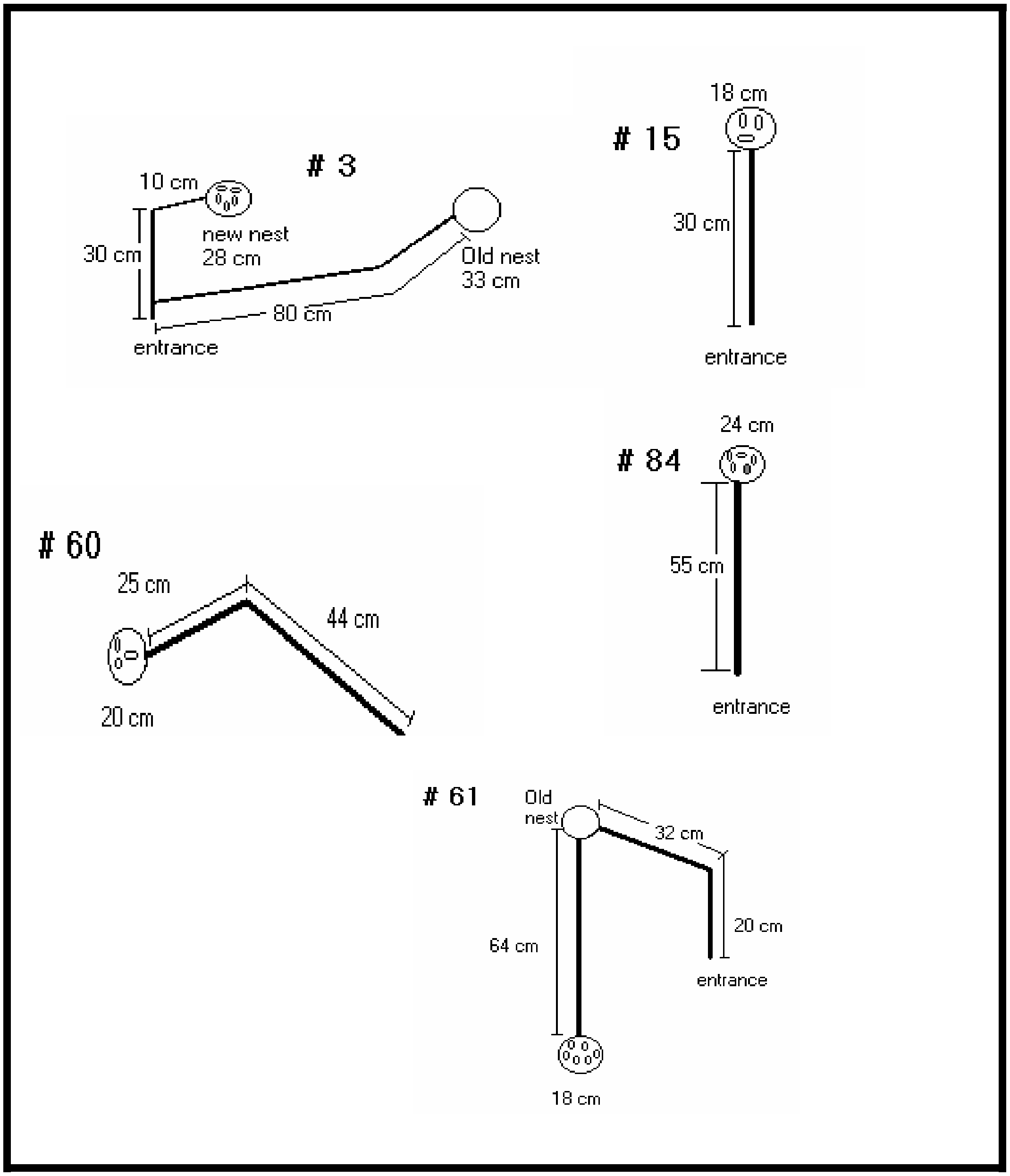


Figure 10. Morphology of five nesting burrows excavated during this study, including length of nest chamber from ground above to floor of chamber. Old nests were evident from eggshell remnants.

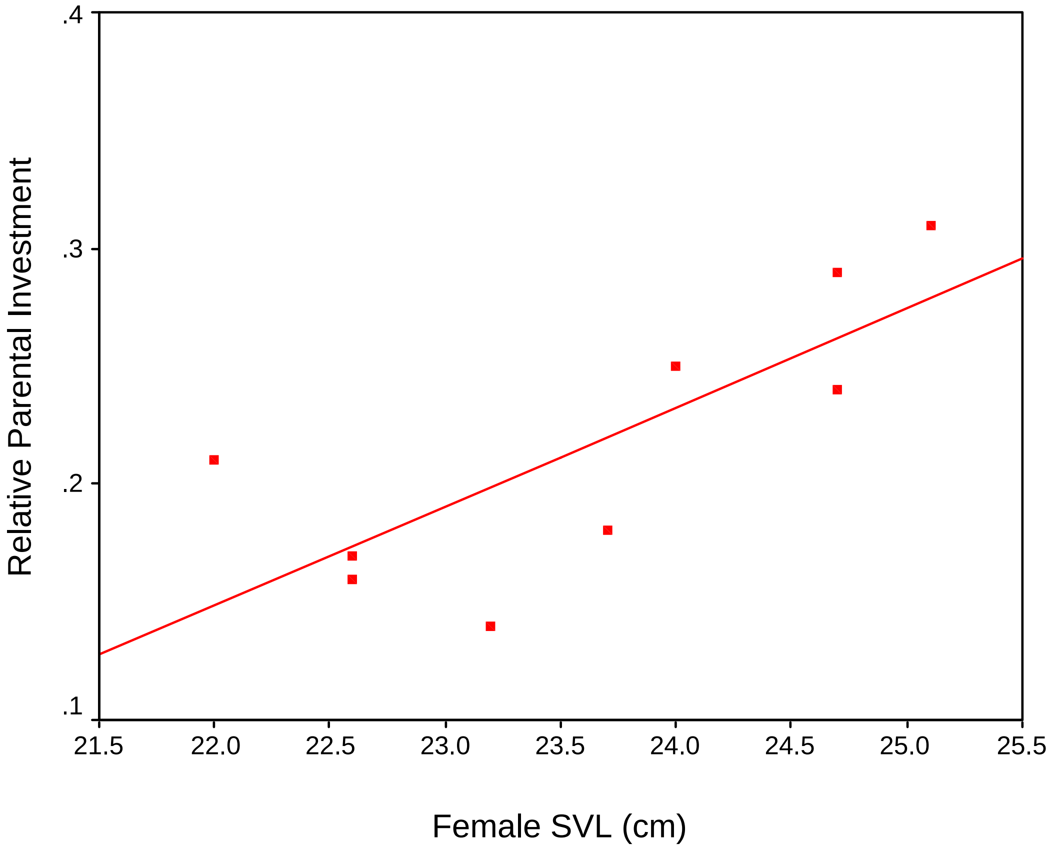


Figure 11. Relationship between female size relative parental investment (r = 0.748, P = 0.02, n = 9).

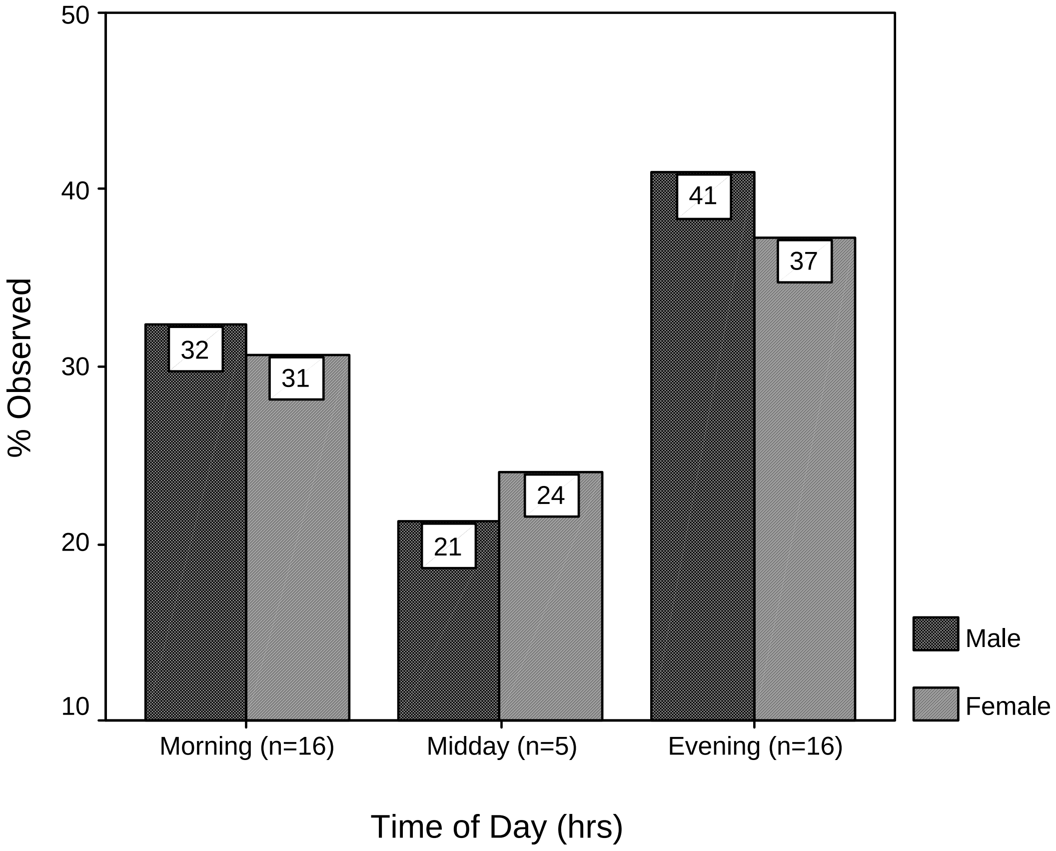


Figure 12. Activity levels of iguanas (percent of marked iguanas seen) observed during morning (0800- 1030), midday (1300- 1430), and evening (1700- 1930) surveys.

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