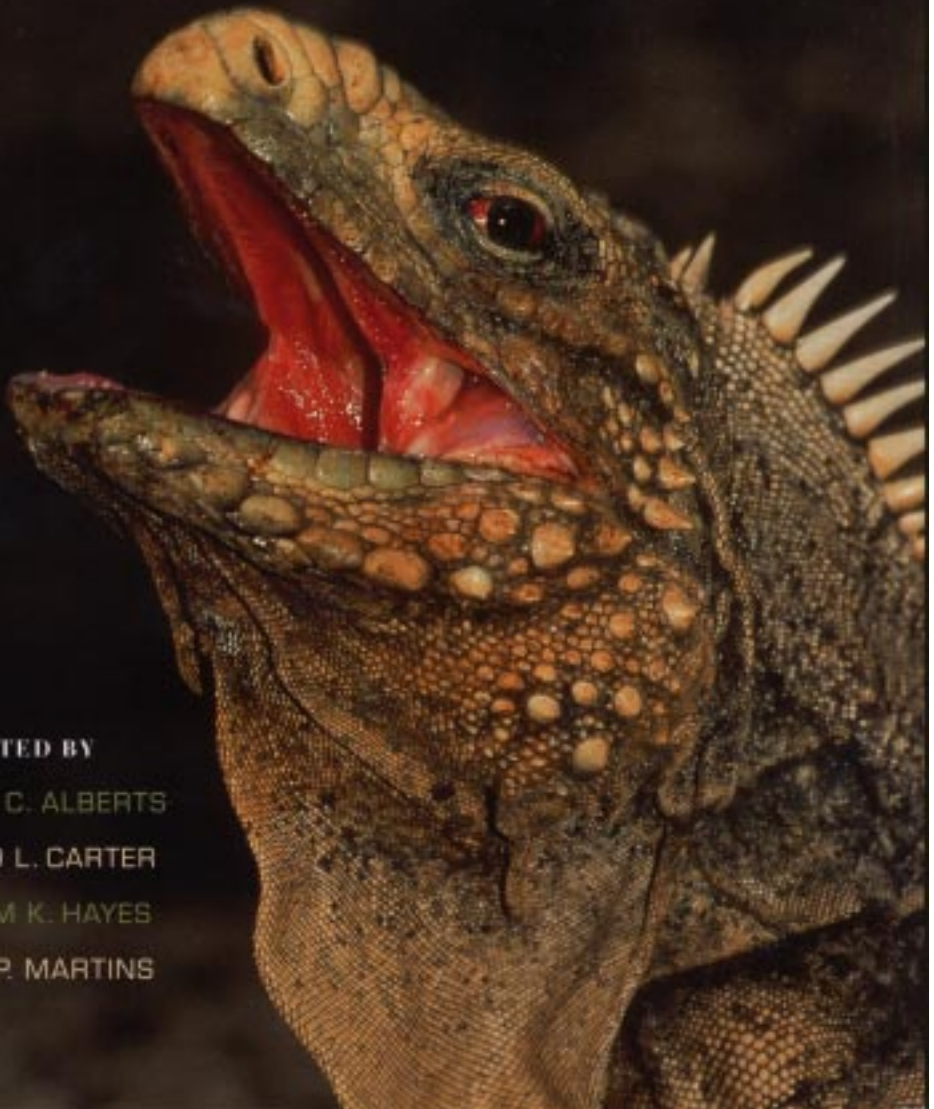# IGUANAS

BIOLOGY AND CONSERVATION

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17

Conservation of an Endangered Bahamian Rock Iguana, I

POPULATION ASSESSMENTS, HABITAT

RESTORATION, AND BEHAVIORAL ECOLOGY

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Samuel Cyril, Jr., and Benjamin Thornton

THE BAHAMIAN ENDEMIC *Cyclura rileyi* is one of the most threatened of the West Indian rock iguanas. Two of its three recognized subspecies, *C. r. cristata* and *C. r. rileyi,* are critically endangered, and the third, *C. r. nuchalis,* is endangered (Alberts, 2000). Although they formerly occupied large islands, today these lizards are confined to small, remote, uninhabited cays of three island groups in the Bahamas (the Exumas, San Salvador Island, and the Crooked and Acklins Islands; figure 17.1). The island groups, each harboring its own subspecies, are on separate banks and therefore were not connected during the most recent ice age when water levels were as much as 100 m lower than at present. The cays are currently separated from adjacent larger islands by shallow water and were probably formed within the past seven thousand years (when seas were more than 10 m lower than they are today; Kindler, 1995) from rising postglacial seas.

At present, *C. r. cristata* is restricted to a single cay (White = Sandy Cay, 14.9 ha) in the southern Exumas. This taxon almost certainly occupied adjacent islands (e.g., Leaf Cay, Hog Cay, possibly Little Exuma and Great Exuma) at one time, and has suffered substantial range contraction. *C. r. nuchalis* exists naturally on just two cays (North Cay, 51.7 ha; Fish Cay, 73.9 ha) in the Acklins Bight, the immense, shallow body of water between Crooked Island and Acklins Island. A third population, introduced to a small island (3.3 ha) within the Exumas Land and Sea Park, was established by five founders translocated from Fish Cay in the late 1970s by a private individual (S. Buckner, pers. comm.). This subspecies was found on nearby Long Cay (23 km^2) in the Acklins Bight in the early twentirth century (Schwartz and Carey, 1977; Schwartz and Henderson, 1991; Blair, 1992), and undoubtedly once occupied Crooked Island (238 km^2) and Acklins Island (311 km^2) as well. Thus, its current range represents a tiny fraction (0.2%) of its former range. The remaining populations of *C. r. rileyi* are presently confined to six tiny offshore cays and islets within the hypersaline lakes of San
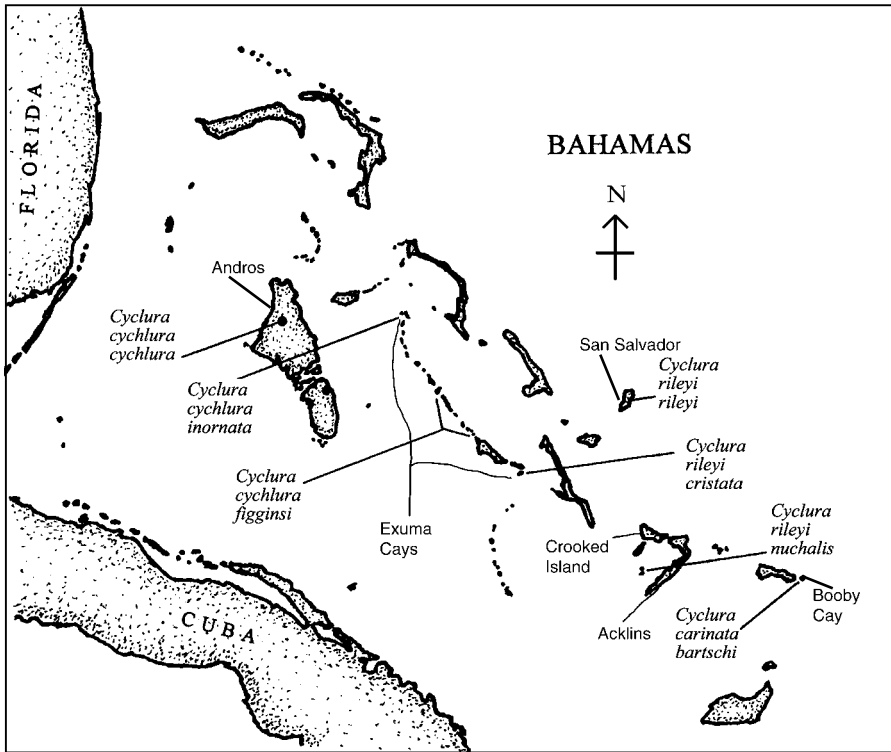
FIGURE 17.1. Distribution of *Cyclura* in the Bahamas, including the three subspecies of *Cyclura cychlura* (on Andros, northern Exumas, and southern Exumas) and the three subspecies of *C. rileyi* (on southern Exumas, San Salvador Island, and Acklins Bight). *C. carinata bartschi* exists only on Booby Cay off Mayaguana Island, Bahamas; the second subspecies of *C. carinata* occurs in the Turks and Caicos Islands to the east.

Salvador Island (31.5 ha total), although a few individuals are still encountered rarely on the main island (163 km²). Three additional populations have been extirpated in recent decades from Barn, High, and Gaulin Cays (30.3 ha total). Assuming the main island population is nonviable as a result of human habitation and environmental degradation, this taxon similarly occupies a mere fraction (0.2%) of its former range.

Although Amerindians apparently utilized iguanas for food and funerary offerings (e.g., Veloz Maggiolo, 1997; Winter et al., 1999) and possibly transported them between islands, their impact on iguanas is otherwise unknown. Most devastating was the large-scale destruction of habitat by European and American colonists, who cleared forests from entire islands to establish cultivation and introduced many non-native plants and animals. Today, in spite of protection

under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), hunting and smuggling for the pet trade continue (Alberts, 2000). However, the greatest threats appear to be related to invasive species that alter habitat and/or prey on iguanas.

In this chapter, we describe the findings of a long-term, ongoing research program on *C. rileyi*. At present, there are no legitimate collections of this iguana in captivity and all of our work has been in situ. We began our studies in 1993 with the short-term goals of identifying all remaining populations of *C. rileyi*, obtaining accurate population estimates, evaluating the general health of the iguanas and their habitats, and assessing the threats to each population. Our longer-term goals included more complete demographic analyses, measurement of morphological and genetic variation, mitigation of

TABLE 17.1
Summary of Annual Conservation Research Activities on the Three Subspecies of Cyclura rileyi

YEAR	TAXON	ACTIVITY
1993	*C. r. rileyi*	Capture/marking (May)
1994	*C. r. rileyi*	Capture/marking, population surveys (May, July)
1995	*C. r. rileyi*	Capture/marking, population surveys (March, June, November)
1996	*C. r. cristata*	Capture/marking (June)
	C. r. nuchalis	Capture/marking (May–June)
1997	*C. r. cristata*	Capture/marking, population surveys, behavioral ecology study (May–July)
	C. r. nuchalis	Capture/marking, population surveys (May)
1998	*C. r. cristata*	Rat eradication (April–May)
	C. r. nuchalis	Capture/marking, population surveys, behavioral ecology study (May)
	C. r. rileyi	Capture/marking, population surveys (June)
1999	*C. r. cristata*	Population survey (October)
	C. r. nuchalis	Capture/marking, population surveys, behavioral ecology study, post-hurricane assessment (May–July, October)
	C. r. rileyi	Capture/marking, population surveys, behavioral ecology study, rat eradication, post-hurricane assessment (June–July, October)
2000	*C. r. cristata*	Population survey (November)
	C. r. rileyi	Population surveys, rat eradication (May, June–July)
2001	*C. r. rileyi*	Population surveys, nest habitat restoration, behavioral ecology study (June–July, October)

Notes: Whereas the majority of expeditions were brief (one to two weeks) and sometimes several times per year, the behavioral ecology studies encompassed five ten-week field seasons.

threats to the habitats of several important cays, and detailed studies of behavioral ecology. A summary of our annual research activities is provided in table 17.1.

We begin by providing detailed assessments of all known *C. rileyi* populations, including demographic measures, habitat characteristics, and identified threats. Next, we describe and assess several projects undertaken to control non-native predators and restore damaged habitats. Subsequently, we provide highlights from our detailed studies of the behavioral ecology of several populations. In the following chapter (Carter and Hayes, this volume), we present analyses of morphological and genetic variation within and between the three taxa, and discuss conservation recommendations. Although some

of our findings appear in three student theses (Thornton, 2000; Cyril, 2001; Fry, 2001) and in an earlier paper (Hayes et al., 1995), most of our data remain to be published. Here, we summarize our major findings from years of field research and focus on how the findings benefit our understanding of iguanas in general and their conservation.

POPULATION ASSESSMENTS

We visited each of the known populations of *C. rileyi* to systematically survey population size, measure morphological features, and assess other demographic attributes (e.g., sex ratio, body-size distribution). We also informally surveyed the habitats of each cay and identified po-

tential threats to iguanas. The ownership and geophysical and ecological features of each cay are summarized in table 17.2. The demographic characteristics of and primary threats to each population are provided in tables 17.3 and 17.4. On the larger islands, there are additional problems related to human-commensal animals (pets and livestock) and substantial habitat alteration. Although the killing of iguanas for food persists in other regions of the Bahamas and Carribean (e.g., Alberts, 2000; Knapp, 2001b), we have found no evidence of current hunting of *C. rileyi*.

SAMPLING METHODS

DATA TREATMENT AND ANALYSES

Statistical tests were conducted using SPSS for Windows (release 8.0, 1997; SPSS Inc., Chicago, Illinois), with $\alpha = 0.05$. Both parametric and nonparametric tests were conducted, depending on the data properties. For some data, transformations (e.g., log or rank) were required prior to analyses. In some cases, we report parametric tests of data that failed to meet parametric assumptions, but when possible, we used nonparametric alternatives to confirm suitability of the parametric tests. For multivariate tests, effect size (proportion of variance explained by an independent variable) is indicated in some cases by η^2.

CAPTURE, MORPHOLOGICAL MEASURES, AND SEX DETERMINATION

Through 1999, we captured 484 iguanas (75 *C. r. cristata*, 198 *C. r. nuchalis,* and 211 *C. r. rileyi*) by noose (the majority) or by hand. Both methods proved effective and safe, with minimal injuries limited to occasional abrasions. Captured iguanas were immediately placed in cloth bags and taken to a shaded processing station. We weighed each iguana and obtained the following measurements (to the nearest mm) using a metric caliper or a folding metric ruler: snout-vent length (SVL), head length (posterior margin of tympanum to snout tip), and tail length (vent to tip). Iguanas were categorized into one of four size classes based on SVL: juveniles (<12 cm),

subadults (12–19.9 cm), adults (20–27.9 cm), and large adults (>28 cm). Most iguanas were probed for sex identification.

MARKING INDIVIDUALS

Prior to release at the site of capture, iguanas were marked semipermanently by affixing one to three colored glass beads on each side of the nuchal crest with an 80-lb nylon monofilament line melted into a ball at each end to retain the beads (Rodda et al., 1988; Hayes et al., 2000). When conducting home range and behavioral ecology studies, we additionally marked all individuals with a temporary alphanumeric code on each side of the dorsum, visible from a distance, using a nontoxic enamel paint that lasted several months or until ecdysis (Hayes et al., 2000). Our observations and those of others suggest that neither beads nor paint marks interfere with normal behavior or survival (but see Hayes et al., 2000; Murray and Fuller, 2000).

POPULATION SURVEYS

We estimated population sizes by three means, as summarized by Hayes and Carter (2000): (1) Lincoln-Petersen mark-resighting surveys on small cays (<12 ha) having sufficient marked iguanas; (2) classical transects (standard counts of all iguanas seen) that covered the entirety of small cays (<12 ha); and (3) distance transects (measurement of perpendicular distance between each iguana sighted and transect line) on large cays (≥12 ha), with adjustment for the proportion of habitat surveyed. Most surveys were conducted during the months of June or July. For several cays, we conducted repeated surveys and used multiple estimation methods to better understand the factors that influence our estimates. During surveys, we also recorded the approximate size class (juvenile, subadult, adult, large adult) of each iguana sighted. For classical transects and distance surveys, we adjusted our estimates based on detectability using the following general formula: N = iguanas seen/ detectability. We estimated detectability using two methods and are confident that it ranges between 0.33 and 0.5 under the usual conditions

TAXON	CAY (OWNER)	AREA (ha)	ELEVATION (m)	TYPICAL DOMINANT PLANTS[1]	BREEDING BIRD SPECIES[2]	OTHER REPTILE SPECIES	INVASIVE FAUNA
C. r. cristata	White (CL)	14.9	8	*Casuarina, Coccoloba, Coccothrinax, Strumpfia* (≥20)	Laughing gull, osprey, Antillean nighthawk, zenaida dove, white-crowned pigeon, gray kingbird, Bahama mockingbird, bananaquit (royal tern, gull-billed tern, Wilson's plover)	*Anolis sagrei, Sphaerodactylus* uncertain sp.	Raccoon,[3] rats,[3] house mice[4]
C. r. nuchalis	Fish (CL)	73.9	3	*Coccoloba, Coccothrinax, Strumpfia, Rhizophora* (>50)	Green heron, osprey, clapper rail, Antillean nighthawk, Bahama woodstar, gray kingbird, thick-billed vireo, Bahama mockingbird, blue-gray gnatcatcher, yellow warbler, bananaquit (yellow-crowned night-heron, Wilson's plover, zenaida dove, white-crowned pigeon, mourning dove, common ground-dove)	*Leiocephalus punctatus, Sphaerodactylus corticola*	House mice
	North (CL)	51.7	3	*Coccoloba, Coccothrinax, Strumpfia, Rhizophora* (>50)	Same as Fish Cay	*Leiocephalus punctatus, Sphaerodactylus corticola*	None known
	Transloc popn (NP)	3.3	7	*Coccothrinax, Conocarpus, Erithalis, Guapira, Jacquinia, Manilkara, Reynosia, Rhachicallis* (47)	Gray kingbird, thick-billed vireo, black-whiskered vireo, bananaquit (zenaida dove, white-crowned pigeon)	None known	Rats?
C. r. rileyi	Gaulin (CL)	1.6	3	*Coccoloba, Conocarpus, Sesuvium* (10)	Audubon's shearwater, roseate tern, bridled tern, sooty tern, brown noddy	None known	*Cactoblastis* moth

Island	(Area)	No.	Plants	Breeding birds	Reptiles	Introduced species
Goulding (P)	2.9	10	*Coccoloba, Conocarpus, Manilkara, Reynosia, Ximenia* (≥16)	Audubon's shearwater, bridled tern, yellow warbler (Bahama woodstar)	*Anolis distichus, Sphaero-dactylus corticola*	None known
Green (CL)	5.1	8	*Borrichia, Coccoloba, Conocarpus, Rhachicallis* (10)	Audubon's shearwater, tricolored heron, yellow-crowned night-heron, roseate tern, bridled tern, sooty tern, brown noddy, yellow warbler	*Anolis* uncertain sp., *Sphaero-dactylus corticola*	*Cactoblastis* moth
Guana (P)	1.6	9	Rich diversity (42)	(Green heron, white-crowned pigeon, Bahama woodstar, gray kingbird)	*Anolis distichus*	Rats
Low (P)	10.8	7	*Ambrosia, Coccoloba, Ipomoea, Sesuvium* (31)	Audubon's shearwater, Wilson's plover, bridled tern, yellow warbler (black-necked stilt, willet)	*Anolis* uncertain sp., *Leptotyphlops columbi, Sphaero-dactylus corticola*	Rats,[3] *Cactoblastis* moth
Manhead (P)	3.3	7	*Casasia, Coccoloba, Conocarpus, Sporobolus, Strumpfia* (15)	Audubon's shearwater, yellow-crowned night-heron, green heron, bridled tern, Antillean nighthawk, yellow warbler (sooty tern)	*Anolis sagrei, Sphaero-dactylus corticola*	*Cactoblastis* moth
Pigeon (CL)	7.8	1	*Rhizophora* (7)	Double-crested cormorant, tricolored heron, reddish egret, green heron, yellow-crowned night-heron, laughing gull, white-crowned pigeon, yellow warbler (little blue heron, Bahama mockingbird)	*Anolis distichus, Sphaero-dactylus corticola*	Rats

Sources: Auffenberg (1982b); Schwartz and Henderson (1991); Moyroud and Ehrig (1994, 1996); S. Buckner (pers. comm.); J. Iverson and S. Buckner (pers. comm.); W. Hayes (pers. obs.); this study.

Notes: CL = Crown lands; NP = national park; P = private lands. See Raffaele et al. (1998) for scientific names of birds.

[1] Numbers in parentheses are approximate numbers of total plant species.

[2] Unconfirmed breeder species are given in parentheses.

[3] Eradicated.

[4] Possibly eradicated.

TABLE 17.3

Population Data for All Known Populations of Cyclura rileyi cristata, C. r. nuchalis, and C. r. rileyi

| TAXON | CAY | CAPTURE DATA[2] | | | | | | POPULATION SURVEYS[3] | | | | |
		AREA (ha)[1]	N	MALES (%)	MEAN MASS (kg)	SVL RANGE (cm)	POPULATION SIZE (N)	JUVENILE (%)	SUB-ADULT (%)	ADULT (%)	DENSITY (N/ha)[4]	BIOMASS (kg/ha)[4]
C. r. cristata	White	14.9	61	95	0.403	10.2–28.0	136–204 (179)	17	17	66	9.1	3.7
C. r. nuchalis	Fish	73.9	49	51	0.459	9.0–31.4	9484–14226	10	15	74	128.3	58.9
	North	51.7	38	63	0.404	11.7–28.0	3036–4554	7	16	76	58.7	23.7
	Transloc popn	3.3	53	51	1.097	9.2–36.0	314–471 (299)	1	5	94	95.2	104.4
C. r. rileyi	Gaulin	1.6	3	66	0.650	22.8–25.8	Extirpated 1999	—	—	—	—	—
	Goulding	2.9	13	38	0.562	15.7–31.0	116–174 (130)	5	26	68	40.0	22.5
	Green	6.3	54	56	0.608	13.5–31.1	130–195 (257)	6	16	78	25.5	15.5
	Guana	1.6	5	40	0.665	12.1–35.2	30–45	20	27	53	18.8	12.5
	Low	10.8	13	77	1.481	26.3–39.5	42–63	0	0	100	3.9	5.8
	Manhead	3.3	19	47	0.268	16.0–27.0	38–57 (80)	14	43	43	11.5	3.1
	Pigeon	7.8	15	33	0.665	12.5–31.0	70–105 (62)	3	6	91	9.0	13.5

Notes: Excludes a very small population on the main island of San Salvador that could not be sampled. Sex ratio (% males) and body size measurements (mean mass and snout-vent length [SVL] range) are based on capture data during months of May and June only from 1994 to 1997. Population size and age structure are based on sighting data from population surveys from 1997 to 1998. Density and biomass are derived from population size, area (ha), and mean mass (kg).

[1] Based on weighing of paper cutouts from 1:10,000 scale maps published by the Bahamas Lands and Surveys Department.

[2] Sample size for captures (N) is for iguanas sexed by probing; N for body size was larger (by up to twofold on Goulding and Guana Cays).

[3] Population estimate based on number of iguanas seen multiplied by detectability of 0.33–0.50 (with Lincoln-Petersen mark-resighting estimate in parentheses); distance surveys were conducted for White, Fish, and North Cays (1997) and for all C. r. rileyi populations (1998); classical surveys were conducted for the translocated population (1997), the translocated population (1997), and three C. r. rileyi populations (1998); most recent Lincoln-Petersen mark-resighting estimates are shown in parentheses for White Cay (1997), the translocated population (1997), and three C. r. rileyi populations (1998).

[4] Density and biomass based on the assumption that 50% of iguanas were seen during survey (i.e., the lower estimate for population size).

TABLE 17.4

Identified Threats to Extant Populations of Cyclura rileyi cristata, C. r. nuchalis, *and* C. r. rileyi

TAXON	CAY	RATS, RACCOON	CACTOBLASTIS MOTHS	DISEASE	POPULATION FRAGMENTATION	HURRICANE DAMAGE	TOURIST VISITATION, SMUGGLING	RISING SEA LEVELS
C. r. cristata	White	(•)					•	
C. r. nuchalis	Fish							•
	North							•
	Transloc popn	•?						
C. r. rileyi	Gaulin		•		•	•		
	Goulding				•			
	Green		•		•	•	•	
	Guana	•	•	•	•			
	Low	(•)	•	•	•			
	Manhead		•		•			•
	Pigeon	•			•			•

Note: Parentheses indicate threats that may now be resolved.

TABLE 17.5
Proportion of Marked Iguanas Resighted during Lincoln-Petersen Surveys of Cyclura rileyi

PERCENTAGE	CAY	DATE	ELAPSED TIME
55	Pigeon	June 1998	31–39 months
52	Translocated population	May 1997	12 months
38	Manhead	August 1994	3–14 months
36	Goulding	June 1998	36–39 months
32	Green	August 1994	3–14 months
29	White	June 1997	5 days–12 months
22	Green	June 1998	31–60 months
13	Manhead	June 1998	31–60 months

Notes: The elapsed time between marking (initial to most recent) of iguanas and survey is indicated in the last column. Cays with duplicate surveys (Manhead, Green) had a lower resighting percentage after a greater period of elapsed time.

of our surveys. First, we learned from a number of Lincoln-Petersen surveys that we typically resight approximately one-third to one-half of the marked iguanas (table 17.5). However, the data indicate that the proportion resighted declines as the sampling interval increases (compare the repeated samples for Green Cay and Manhead Cay in table 17.5), presumably due to loss of beads (although we often detect a hole or scar in the nuchal crest in such animals) or to mortality. Unfortunately, we have limited knowledge about the rate of bead loss, but experience suggests that retention is better than 90% annually. We know that the plastic beads used in 1993 and 1994 lasted only a few years and suspect that loss of the more durable glass beads used thereafter is more rapid for larger individuals. Second, for two populations, we conducted repeated surveys of marked individuals at different times of the day. During fifteen surveys of *C. r. nuchalis* on North Cay in June 1998, the mean proportion of marked iguanas observed was 47% in the morning, 24% at mid-day, and 44% during the evening (Thornton, 2000). A two × three (sex × time of day) analysis of variance (ANOVA) showed that males were significantly more likely to be seen than females ($F_{1,24}$ =

5.87, $P = 0.023$) and detection varied with time of day ($F_{2,24} = 12.37$, $P < 0.001$), with fewest iguanas seen at mid-day. During thirty-seven surveys of *C. r. rileyi* on Green Cay in June and July 1999, the mean proportion of marked iguanas observed was 32% in the morning, 23% at mid-day, and 39% during the evening (Cyril, 2001). Similar analyses revealed that males and females were encountered equally often, but that detectability varied with time of day ($F_{2,74} = 14.83$, $P < 0.001$), with fewest iguanas seen at mid-day and most detected in the evening. In neither study was there an interaction between sex and time of day.

Because of inevitable variation in survey results, we have expressed our population estimates (table 17.3) as a range that is two to three times the number of iguanas seen during a survey (classical or distance transect). Lincoln-Petersen estimates generally fall within this range, except that loss of beads and mortality lead to overestimation, as is apparent for Green and Manhead Cays (table 17.3) because of the low resighting ratios during the 1998 surveys (table 17.5). Data obtained by Cyril (2001) from his repeated surveys on Green Cay provide coefficients of variation of 0.25 for the total num-

ber of iguanas sighted, 0.14 for Lincoln-Petersen (mark-resighting) estimates, and 0.86 for the numbers of juveniles sighted. These standardized measures of variance suggest that mark-resighting estimates are more reliable than counts and that juveniles are particularly challenging to survey with precision. We suspect that we underestimated juveniles in most surveys because of the difficulty detecting them, except on White Cay, where the leaf litter and minimal rock cover make audible detection quite easy.

CYCLURA RILEYI CRISTATA (WHITE CAY)

DEMOGRAPHIC ASSESSMENT

Of the three taxa, *C. r. cristata* is clearly the most threatened. In 1997, we discovered a crisis situation with our distance transects (conducted May 1997) and Lincoln-Petersen estimate (conducted June 1997), suggesting that two hundred or fewer iguanas remained (table 17.3). More alarming, approximately 95% of the noose and hand captures from 1996 to 1997 were of males. This male-biased ratio was not representative of other populations surveyed (table 17.3), and suggested that fewer than ten adult females remained. Our survey results may be biased by males being easier to see or capture than females on this particular cay, but given the extreme effort put into capture, we believe that a real imbalance between male and female numbers exists. In late June, five additional iguanas—four of which were female—were captured by glue traps placed in the entrance to freshly dug burrows subsequent to rain storms (the glue traps were carefully monitored to avoid subjecting captured lizards to excessive temperatures from direct sunlight). With these additional captures, our male representation based on capture data was 85.5% (Fry, 2001). The females captured were within a narrow size range (15.5–18.4 cm); all were considered subadults.

HABITAT AND THREAT ASSESSMENTS

Despite suffering a near-direct blow from Hurricane Lili in October 1996, the vegetation on White Cay appears to be diverse and healthy. At least twenty species of plants exist on the cay

(table 17.2; S. Buckner, pers. comm.). Vegetation density declines with elevation along a west-east gradient, along which the iguanas are evenly dispersed (Fry, 2001). Non-native Australian pine *(Casuarina)* flourishes along the south shore and on the offshore sand dunes. Although the iguanas appear unaffected by these trees at present, the trees must be removed eventually. The sand dunes are separated from the main island by tidal flats and are not utilized by iguanas. Several bird species potentially prey on the iguanas, including osprey *(Pandion haliaetus)* and laughing gulls *(Larus atricilla)* that nest on the cay (table 17.2), and merlin *(Falco columbarius)* and peregrine falcons *(F. perigrinus)* that frequently visit during winter and migration. However, non-native mammals clearly comprise the most immediate threat to this population. During our June 1996 visit, we found rats to be abundant, and John Iverson discovered tracks left by a raccoon *(Procyon lotor)*. When we returned in 1997, tracks of the single raccoon were seen daily about the island (the raccoon itself was never observed, despite extensive searching over a nine-week period). Iguana skin and claws were found in its feces. Fourteen adult iguana carcasses were located in 1997, some of which showed obvious gnaw marks. The number of iguanas was conspicuously fewer in 1997. Based on differences in capture rate between 1996 and 1997 and differences in resighting ratios of iguanas marked in each of the two years, we estimated annual mortality at 35–67% (Fry, 2001), indicating the loss of 96–363 iguanas in a single year! The raccoon, believed to be the primary culprit, was dispatched in July 1997. The rats were eradicated in May 1998. Mice (presumably *Mus musculus*) were also present and are assumed to be eradicated as well. Annual visits from 1998 to 2000 confirmed that the population decline ended abruptly after the raccoon was removed.

The population now suffers from a highly skewed sex ratio (few remaining females) and probable genetic bottlenecking, rendering it highly vulnerable to stochastic extinction processes. In addition, these iguanas have been

taken by smugglers for the pet trade: DNA evidence based on our samples led to the eventual sentencing of two individuals. Fortunately, the iguanas on White Cay are now exceptionally wary and exceedingly difficult to capture. Local residents are increasingly concerned about visitors to this island and are protective of its fauna. Moreover, the U.S. Drug Enforcement Agency routinely flies over this island to scrutinize suspicious activity.

CYCLURA RILEYI NUCHALIS (ACKLINS BIGHT)

DEMOGRAPHIC ASSESSMENT

Because this taxon occupies comparatively large islands, it is the least threatened of the three subspecies. The two populations in the Acklins Bight comprise approximately 12,500–18,800 individuals (table 17.3; the lower end of the range is probably closer to reality). Our estimates far exceeded the prior estimate of four hundred to six hundred total on the two islands (Blair, 1992); such discrepancies illustrate the need for rigorous population estimation. Our transects covered approximately 9.5% of Fish Cay and 14.3% of North Cay and were as representative as possible of the ecologically diverse habitats on these islands. The sex ratio is nearly 1:1, and each age category is adequately represented (table 17.3). Populations such as these give us a good understanding of what the demographic parameters should be for a healthy ecosystem. However, the density and biomass estimates are high compared with other populations of *Cyclura* (Iverson, 1979; table 17.3) and undoubtedly reflect the abundance and quality of food on these cays. The translocated population in the Exumas Land and Sea Park has now grown to three hundred or more iguanas, although juveniles and subadults appear to be poorly represented (table 17.3).

HABITAT AND THREAT ASSESSMENTS

The two natural populations in the Acklins Bight appear to be free of immediate threats. The habitats and vegetation on each cay are diverse and healthy, and their remoteness from human population centers leaves the iguana populations relatively undisturbed. A small population of Australian pine exists on Fish Cay, but none have been found on North Cay. Natural predation appears to be minimal. Laughing gulls and other seabirds regularly visit the cays, but none nest on them, although herons do (table 17.2). However, a resident population of osprey regularly preys on the adult iguanas. Kestrels *(Falco sparverius)* are frequently seen and may feed on juvenile iguanas, but we have not visited the cays during migration or winter to determine whether larger falcons regularly visit. Several shallow channels separate a few small islets on the north side of North Cay, and one iguana observed swimming across a channel was consumed by a barracuda *(Sphyraena barracuda)*. House mice *(Mus musculus)* are fairly common on Fish Cay, but appear to be absent from North Cay. Their impact on iguanas is likely negligible, but their presence suggests that rats could make it to the cays. Of more concern, these islands lack elevation relief (maximum of 3 m; table 17.2) and will be vulnerable in the long term to rising sea waters. Based on elevation contours of the most detailed maps available from the Bahamian government, we estimate substantial loss of habitat on both Fish (50%) and North Cay (40%) with an increase in sea level of 1 m, which is generally anticipated during the next one hundred years. This estimate, based solely on elevation relief, does not take erosion into account, which could further degrade the islands.

Although the introduced population in the Exumas occupies a much smaller island, the habitats there also appear to be diverse and healthy. Nevertheless, the scarcity of juveniles and subadults, and the discovery in 1997 of an iguana with a portion of rodent hide in its mouth, suggest that rats may be present. Unfortunately, rats are widespread among the Exuma Islands (Lee and Clark, 1995). In October 1999, we failed to live-trap any rats, but the full moon conditions were less than optimal for sampling. Fortunately, this cay is also remote and protected within the Exuma Land and Sea Park and is regularly patrolled by park wardens.

CYCLURA RILEYI RILEYI
(SAN SALVADOR ISLAND)

DEMOGRAPHIC ASSESSMENT

Our data indicate that this taxon is critically endangered, with an estimated 426–639 iguanas remaining (table 17.3; c.f. Blair, 1991). After conducting extensive searches throughout most of the inland cays within the hypersaline lakes and all eleven of San Salvador's offshore cays, we have verified that six viable populations remain (excluding Gaulin Cay, where they are thought to be recently extirpated, and the main island, where a few individuals persist). Two inland cays (Guana and Pigeon) and four offshore cays (Goulding, Green, Manhead, and Low) currently sustain iguana populations that vary in size from a few dozen to several hundred (table 17.3). Three additional cays supported iguanas in recent decades. Auffenberg (1982b) was told by local residents that iguanas were present on Barn Cay (14 ha, on Great Lake) in the early 1970s. Don Gerace (pers. comm.) reported that iguanas in the 1980s were still common on Gaulin Cay (offshore; up to eighteen seen at one time) and present on High Cay (13.4 ha, offshore). We have found up to three individuals on Gaulin (1994–95), but none since the habitat was severely damaged by Hurricane Floyd in September 1999. Although Sandra Buckner (pers. comm.) photographed tracks on High Cay in 1995, we have found no evidence of iguanas there, despite extensive searching. In addition to the six described populations, adult iguanas are occasionally reported (fewer than once per year) on the main island, usually at the Fortune Hill plantation ruins on the east side of the island, where extensive, but rat-infested, habitat remains. These iguanas are described as quite large in size. Iguanas are no longer seen on the southern end of the island. An adult iguana reported from the north end subsequent to Hurricane Floyd was undoubtedly washed ashore from Green or Gaulin Cay.

Some of the demographic parameters for this taxon offer additional reason for concern

(table 17.3). Sex ratios approach 1:1 on most of the cays, but Low Cay may be skewed toward males (77% of captures). The age structure appears healthy on all cays except Low and Pigeon, where rats are present and low recruitment of juveniles seems evident. On Low Cay, we seldom saw juveniles, subadults, or even small adults except in fall, when recent surveys have revealed an abundance of hatchlings. Iguanas on Low Cay attain the largest body size of any population (up to 39.5 cm SVL) and the population appears to be senescent (Hayes et al., 1995). The scarcity of juveniles on Pigeon Cay may result from recent wet years, which led to inundation of nests that are necessarily constructed close to emergent water. We estimate the maximum elevation of this cay to be less than 1 m, and eggs on other cays are typically deposited at depths greater than 0.2 m. The Guana Cay population suffered a severe die-off from an unknown cause (presumably a disease) in 1994 (Hayes et al., 1995; Hayes, 2000a), but appears to be recovering, as evidenced by the relatively high number of juveniles and subadults in the 1998 survey. Compared with our 1994 estimates of population size (Hayes et al., 1995), several populations appear to have experienced a decline (see table 17.3), including those on Green and Manhead Cays.

HABITAT AND THREAT ASSESSMENTS

The habitats occupied by these iguanas are remarkably varied (table 17.2), as are the threats to this subspecies (table 17.4). Owing to their small size, several of the cays support a low diversity of vegetation (table 17.2). Pigeon Cay in the interior lake is comprised almost exclusively of red mangrove *(Rhizophora mangle),* and scat examination shows heavy if not near-exclusive reliance on this plant by iguanas. Only six other plant species are present, and some of these are only on an isolated spit that has been separated from Pigeon Cay since 1995 by a shallow channel (about 10 m wide) that iguanas regularly traverse. Green Cay and Gaulin Cay support only ten species of plants. However, prickly pear cacti *(Opuntia stricta)* on these and other cays have

been greatly decimated by the larvae of an invasive moth species *(Cactoblastis cactorum)* introduced to the Caribbean region decades ago (Hayes et al., 1995). Monitoring of three 2-m² plots on Green Cay suggests that 75% or more of the cactus biomass has disappeared since 1994. Although we do not know how the cactus decline influences the iguana populations, we believe that substantial habitat on Gaulin and Low Cays in particular has been lost, thereby reducing carrying capacity and contributing to extirpation on Gaulin Cay. At present, these two cays have considerable barren habitat occupied by a residual forest of cacti, mostly less than 30 cm in height. Fortunately, no non-native plants have been detected on cays occupied by *C. r. rileyi*. When all eleven populations of *C. rileyi* were considered, we found a significant positive relationship between iguana density and number of plant species (r_s = 0.67, P = 0.025, n = 11). Diverse vegetation may be particularly important during winter, when cooler temperatures affect digestive efficiency and the more easily assimilated plant parts (fresh leaves, flowers, and fruits) decline in abundance (Iverson, 1979; Knapp, 2001a).

Black rats pose a suspected risk to several populations. Although rats have been seen on Guana and Pigeon Cays, their density is uncertain. However, rats were abundant on Low Cay prior to eradication in 2000, as determined from observational and trap data. The senescent iguana population on Low Cay and lack of juvenile recruitment suggest that the rats were detrimental to the iguanas. Auffenberg (1982b) reported that juveniles were commonly seen on Low Cay in 1980. The extirpation of iguanas on High Cay may have been a consequence of rat infestation (Auffenberg, 1982b), although rats presently seem scarce on High Cay, and in 2001 seabirds returned there to nest after an absence of some years (W. Hayes, unpubl. data). Although we have been unsuccessful in trapping rats on nearby Middle Cay, a formerly sizeable seabird colony has disappeared from there as well. Cree et al. (1995) report rat-associated lack of recruitment and island extirpations among

insular populations of tuatara *(Sphenodon punctatus)* in New Zealand. The tuatara is similar in size to *C. rileyi*.

Disease has been implicated as a problem for two populations. Auffenberg (1982b) noted a skin condition that afflicted a number of iguanas on Low Cay in 1980, which included skin sloughing, toe loss, and general disfigurement. However, when Auffenberg and his collaborators returned in 1982 to study the disease, it had resolved. The aforementioned die-off of adults on Guana Cay in 1994 (Hayes et al., 1995) was presumably caused by a disease, although it may have resulted from mosquito control efforts (Hayes, 2000a). The ticks that infest these iguanas have not been seen on any other cay examined and may have rendered the lizards more vulnerable to the agent(s) causing their death.

Several recent hurricanes have inflicted serious damage to iguana habitats. Hurricane Erin (August 1995) mangled several sections of mangrove on Pigeon Cay and rearranged the connection to a nearby sandspit. Hurricane Lili (October 1996) damaged stands of seagrape *(Coccoloba)* on Green Cay, which have since further deteriorated. Hurricane Floyd (September 1999), which struck with 155-mph winds, clearly caused the most damage, especially to Gaulin Cay and Green Cay and, to a lesser extent, Low Cay. On Gaulin Cay, we estimated 30–50% of the vegetation was destroyed, and no iguanas or their tail drags have been found there since the hurricane. Of more concern was the substantial damage to Green Cay, which supports the largest remaining population. Although a smaller percentage of vegetation was lost (roughly 5%), much of the free sand and soil used for nesting was swept away by a storm surge that washed over the cay. Fortunately, our surveys several weeks after the storm revealed that adult survivorship was excellent. However, the storm struck at the onset of the hatching season and apparently destroyed nearly all the 1999 cohort of hatchlings.

Although hatchlings were conspicuous on Manhead Cay (28.6% of twenty-eight iguanas seen) and Low Cay (45.8% of forty-eight iguanas)

in October 1999, they were virtually absent on Green Cay (1.4% of seventy-two iguanas), where they had always been well represented in the past. We observed a similar trend in November 2001, with hatchlings plentiful on Manhead Cay (29% of eighteen iguanas) and Low Cay (26% of fifty-three iguanas), but virtually absent on Green Cay (1% of ninety-six iguanas). We concluded that Hurricane Floyd inflicted substantial damage to the nesting habitat of Green Cay and that restoration of nesting habitat should be a high priority. The vulnerability of small lizards to Hurricane Floyd's storm surge was evident elsewhere in the Bahamas, where *Anolis* populations on low-relief cays (less than 3 m maximum elevation) suffered a high incidence of extirpation (Schoener et al., 2001).

Direct human impacts pose a serious threat to several *C. r. rileyi* populations. Manhead and Green Cays in particular are frequently visited because of their close proximity to guests of the Club Med Resort and students visiting the Gerace Research Center (formerly the Bahamian Field Station). Visitors during the nesting season (July–October) may trample nests, and we have found potentially dangerous food-related items (e.g., plastic wrap) left behind. Of greater concern, an unknown number of iguanas have been removed from Green Cay, including several individuals marked with color beads that turned up at the Club Med Resort and at a Nassau (New Providence Island) institution. In addition, iguanas were once confiscated from a European smuggler (D. Gerace, pers. comm.). Sadly, illicit smuggling for the pet trade will pose a perpetual risk for these populations, even though adults acquired from the wild fare poorly in captivity.

In the long term, perhaps the greatest threats to *C. r. rileyi* will be population fragmentation and lack of significant gene flow between cays.

INVASIVE SPECIES CONTROL AND HABITAT RESTORATION

As a result of our threats assessment, we have undertaken restoration efforts to remove invasive species and restore nesting habitat on several cays. Although more time is needed to assess our interventions, here we present our initial results.

INVASIVE SPECIES CONTROL

IMPACT OF RACCOON AND RATS ON IGUANA POPULATIONS

Clear evidence exists that larger predators, such as cats, dogs, mongooses, and hogs (e.g., Iverson, 1978; Henderson, 1992; Haneke, 1995; Tolson, 2000), as well as feral livestock (Mitchell, 1999), are devastating to insular iguana populations. Our studies on White Cay provide strong evidence for the raccoon's impact via predation on adults, but the evidence for harm caused by black rats remains less clear. In this section, we first discuss the impact of raccoon predation and then consider rats.

Although the raccoon's presence on White Cay was catastrophic for the iguanas, the extent to which it was responsible for the skewed sex ratio remains unclear. The raccoon was active only at night, when iguanas invariably became inactive. To assess how vulnerable the iguanas would be to a nocturnal predator, we conducted informal nighttime searches (about five hours total with two or three observers) on North Cay. Of twenty-three iguanas encountered, most were readily visible at the entrance to rock or sand burrows (57%). Others were on the branches of shrubs (9%), in the litter beneath shrubs (9%), or resting in the open on rock or soil (26%). Both males (48%) and females (30%) were readily discovered at night (22% were of undetermined sex). Using a custom-built burrowscope, we measured the dimensions of earthen and rocky retreat burrows on North Cay to determine how accessible they might be for a raccoon ($n = 10$ for each; Thornton, 2000). These burrows were distinct from and not used as nesting burrows. The dimensions (mean values) of earthen burrows (length = 55 cm, opening width = 26 cm, opening height = 9 cm) and rocky burrows (length = 66 cm, opening width = 17 cm, opening height = 6 cm) were statistically similar, but substantially shorter than burrows used by *C. carinata* (typically 3–4 m; Iverson, 1979). We imagine

that a raccoon would have little difficulty gaining access to iguanas within retreat burrows on North Cay. Thus, assuming comparable conditions on White Cay, we conclude that both males and females were highly vulnerable to the raccoon's nocturnal hunting activities. We further speculate that females were more vulnerable to the raccoon because of heightened visibility and exhaustion during the period of nest construction and egg laying. The nests were likely plundered as well, given that raccoons are notorious predators of reptile and bird nests (e.g., Hartman et al., 1997) and reportedly prey upon spiny-tailed iguana *(Ctenosaura similis)* nests on islands off Belize (Platt et al., 2000).

The evidence for a direct impact of black rats on iguanas is circumstantial at best. To our knowledge, no direct observation of predation in the wild has been reported. We chose to begin our behavioral ecology studies on White Cay, in part, to document rat predation (or its absence) upon iguana nests; however, the crisis situation we encountered in 1997 rendered it impossible for us to detect predation, as we could not find nests that summer! Nevertheless, rats are pernicious predators of other small vertebrates, and a considerable body of evidence points to their devastation of insular seabird and reptile populations (e.g., Case and Bolger, 1991; Cree et al., 1995).

We assessed the potential impact of rats on our study populations in two ways. First, excluding Gaulin Cay from consideration (now extirpated), we compared the mean density and biomass (± standard error [SE]) of iguanas on six cays believed to be rat-free (iguana density = 59.9 ± 18.1 per ha; iguana biomass = 38.0 ± 15.3 kg/ha) and four cays known to be rat-infested (iguana density = 10.2 ± 3.1 per ha; iguana biomass = 8.9 ± 2.4 kg/ha). Determination of rat absence was based on extensive trapping effort on all cays except North and Fish Cays, where we used minimal trapping but did not detect rats during lengthy periods of camping. Two-tailed Mann-Whitney U tests revealed that rat-free cays had significantly higher iguana density than did rat-infested cays ($U = 1.0$, $P =$

0.019), but iguana biomass was similar for the two groups ($U = 4.0$, $P = 0.114$). In a second study (Fry, 2001), ten rubber lizard models similar in size to hatchling iguanas (SVL 6–7 cm) were dispersed on White Cay (June, 1997) in open habitat ($n = 4$) and beneath vegetation ($n = 6$). Periodic monitoring during a two-week period revealed that 83% of the models beneath vegetation were attacked by rats, as evidenced by obvious incisor gnaw marks, and one model in the open habitat disappeared. Although the models did not represent the full stimuli of a live lizard, we conclude that rats are inclined to investigate and sample hatchling-sized objects encountered at night. At present, we do not know the sleeping habits of juvenile iguanas, but if they are accessible to rats and their arousal levels are elevated as in sleeping adults (which are slow to respond to tapping of our fingers), we suspect the juveniles are highly vulnerable to rats. Nocturnal attacks by rats on juvenile iguanas might also lead to tail loss. Although empirical data are lacking for iguanas, nests may also be vulnerable to rats.

RAT ERADICATION

In spring 1998, we assisted Fauna and Flora International (FFI) with the eradication of rats on White Cay. This was accomplished using the rodenticide brodifacoum, a second generation anticoagulant (Weatherblock XT® Rodenticide; donated by Zeneca Agrochemicals Products, United Kingdom) that was delivered in solid bait blocks over a 20-m grid system. To reduce the risk of incidental poisoning of iguanas and birds, we secured the bait blocks within rectangular plastic bait stations (about 25 cm × 7.5 cm × 7.5 cm). After four weeks of poisoning, the substantial reduction in bait take and lack of incisor marks on wooden sticks soaked in vegetable oil led the FFI team to conclude that the rats were eradicated (Day, 1999). During return visits in the fall of 1999 and 2000, our trapping efforts (twenty-seven trap nights) yielded no rats.

In the summer of 1999, Sam Cyril, then a graduate student, attempted to eradicate rats on Low Cay using the same delivery system.

TABLE 17.6
Numbers of *Cyclura rileyi cristata of Three Size Classes (and of Undetermined Size)*
Noted during Classical Strip Surveys on White Cay

DATE	JUVENILES	SUBADULTS	ADULTS	UNCERTAIN	TOTAL
May 1997	5	5	19	5	34
October 1999	10	5	17	4	36
November 2000	9	11	14	3	37

However, bait stations failed on this cay because of the dense population of hermit crabs that swarmed them and blocked access to the bait. Our rodent live-trap data show that hermit crabs are scarce on White Cay, but exceedingly abundant on San Salvador's cays (the crabs readily enter the traps). Cyril returned a year later with a modified bait delivery system, in which the same bait stations were elevated 15–20 cm above the ground on a single PVC stake. The design was successful at keeping hermit crabs out of the bait stations but still allowed access to the rats. The rodenticide initially was consumed quickly, but consumption had slowed noticeably by the end of the first week, when gnaw marks on bait, blue feces, and a dead rat were also observed. As noted on White Cay and elsewhere (M. Day, T. Bitzer, and K. Varnham, pers. comm.), direct evidence of rat poisoning is difficult to detect during eradication efforts, even under high levels of infestation. Trapping during the third week (thirty-seven trap nights) failed to record the presence of rats, and thus the eradication effort was deemed successful.

POPULATION RESPONSES TO PREDATOR REMOVAL
Following rat eradication, we returned to White Cay in the falls of 1999 and 2000 to conduct population surveys. The results of our surveys, summarized in table 17.6, were encouraging in that hatchlings and subadults were readily detected. Clearly, reproduction and recruitment were taking place, and the number of adults has stabilized since 1997. However, based on survivorship data for *C. carinata* in the Turks and Caicos Islands (Iverson, 1979), we can assume that up to 95% of the roughly several dozen hatchlings produced annually will die before attaining reproductive size. Of the few that survive, roughly half presumably will be female. Because of its small body size, reproduction in *C. r. cristata* may be limited to a clutch size of only two or three (see Behavioral Ecology, below). Will future recruitment of females (perhaps only one or two individuals per year) into the breeding population exceed the natural senescence and mortality of currently breeding females? We cannot answer this at present, but because this iguana is so small and its reproductive potential so limited, the risk of extinction will be high. However, as inferred from translocated populations (*C. r. nuchalis* in table 17.3; Iverson, 2001; Knapp, 2001a; Iverson et al., this volume), low density may promote more rapid growth, leading to larger adult size and greater fecundity. Higher survivorship of young might also occur in low-density conditions.

At present, we have little information to judge the benefit of rat eradication on Low Cay. We predicted that we would see greater survivorship of juveniles during the winter, as reflected by increased numbers during a spring 2001 survey. However, of twenty-seven iguanas detected, none were juveniles, although five (19%) were of undetermined size, representing iguanas that were heard but not seen clearly.

NESTING HABITAT RESTORATION
Near-direct hits by Hurricanes Lili (1996) and Floyd (1999) resulted in the destruction of soils,

vegetation, hatchlings, and juvenile iguanas. Most adults survived the destruction. Graduate student Eric Grove began Green Cay nest-restoration studies in April 2001. With his coordination and the aid of San Salvador Island Boy Scouts, we moved six hundred buckets of sand (approximately 5 m³) from the intertidal zone to nest sites eroded by hurricanes. Pure sand was not ideal, but importing soil from the main island, where fire ants and non-native plants abound, appeared risky, and we did not want to disturb remaining Green Cay soils. The sand was arranged similarly to nesting soils observed on other cays we have studied. However, the iguanas did not nest in the reconstructed habitat, although most other behaviors were exhibited there. One possible reason for lack of nesting use is that nest chambers on this cay are usually constructed directly beneath an overlying rock (E. Grove, unpubl. data), a situation we have not seen elsewhere. On Îlet Chancel in Martinique, Breuil (2000) artificially supplemented an existing *Iguana delicatissima* nest area with additional sand, and reported nesting use the same year with fewer eggs lost to nesting interference. We will continue to develop the restored areas on Green Cay by adding soil and rock features in proportions revealed by our recent substrate analysis of successful nest sites (E. Grove, unpubl. data).

BEHAVIORAL ECOLOGY

In this section, we summarize select data on foraging, predation, home range, retreat burrows, and reproduction. More detailed presentation of the methods and data can be found in three unpublished M.S. theses (Thornton, 2000; Cyril, 2001; Fry, 2001).

FORAGING AND DIET

Thus far, we have examined foraging in detail only on Green Cay, which supports the largest remaining population of *C. r. rileyi*. The dramatic loss of *Opuntia* on this cay and the low vegetation diversity (ten species) prompted us to undertake a quantitative assessment of diet and its potential impact on iguana body condition.

Diet was evaluated by examination of fecal deposits (collected July and October 1999 and May 2000) and by direct observation of foraging iguanas (Cyril, 2001). Seven plant species were found in the scats. Compared with their relative abundance (determined from 205 points at the intersections of 10 m² quadrants within a grid that covered approximately 80% of the cay), silver sea oxeye, *Borrichia arborescens* (flowers especially), and wild thyme, *Rhachicallis americana* (both flowers and leaves), were the most preferred items. *Opuntia stricta* (detected by spines and pads), although browsed less often, was also a preferred item despite its current scarcity. Plant content of the diet was similar during the three seasons. Nonplant food items taken by iguanas have included birds or their remains (five incidents on Green Cay, including a purple gallinule *[Porphyrula martinica]* and two unidentified songbirds that possibly died from other causes, and one bridled tern *[Sterna anaethetus]* chick that was likely predated), conspecific hatchlings (two observations on Green Cay in October 2001), the legs of a dead land crab (one observation on North Cay in May 1998), a grasshopper and a hermit crab (one of each present in scats on Low Cay in July 2000), unidentified insect material (22% of scats in October 1999, and 13% in May 2000, on Green Cay), sand particles, and soil fragments. We occasionally see iguanas lunge for grasshoppers, which are abundant on most of the cays occupied by *C. rileyi,* but their scarcity in the scats and apparent absence in the diet of *C. carinata* (Iverson, 1979; Auffenberg, 1982a) suggest they are seldom caught. More thorough studies of diet in other *Cyclura* (Wiewandt, 1977; Iverson, 1979; Auffenberg, 1982a) suggest that at least 95% of the diet of all age classes during all seasons consists of plant material.

To assess the possibility that the *Opuntia* cactus loss might affect body condition over time, we used an ANCOVA model to compare the relationship between log iguana mass (as the

dependent variable) and log SVL during 1993–95 (late May captures; $n = 51$) versus 1998–99 (mid-June captures; $n = 47$). During this time, we estimated a 75% (or greater) decline in the biomass of *Opuntia*. By pooling body condition data over several years, we hoped to dampen any differences that could result from annual variation in food conditions. The significant effect of time ($F_{1,95} = 12.46$, $P = 0.001$, $\eta^2 = 0.12$) suggested that iguanas prior to (or during) the cactus decline (1993–95) had comparatively more body mass than after the cactus decline (1998–99). As a control, we ran a similar ANCOVA for iguanas pooled from Goulding Cay and Pigeon Cay and found no difference ($P = 0.18$, $\eta^2 = 0.05$), although our sample size was smaller and number of intervening years lower ($n = 28$ for late May 1995; $n = 14$ for mid-June 1998). We recognize that factors other than or in addition to the *Opuntia* decline could contribute to the change in body condition. Nevertheless, our data suggest that iguanas are now in worse condition on Green Cay than they were in the mid-1990s, and this change is coincident not only with a reduction in *Opuntia* but also with a reduction in reproductive success. Because reproductive success is dependent to a large degree on food availability and quality (Iverson, 1979), we now suspect that the vegetation changes on Green Cay, in addition to lost nesting habitat from Hurricane Floyd, have contributed to reproductive failures in recent years.

A recent and remarkable observation was of an adult female that captured and ate its own hatchling in October 2001, on Green Cay. Although cannibalism appears to be rare in *Cyclura*, Auffenberg (1982a) reported one incident in his detailed study of the diet of *C. carinata* in the Turks and Caicos Islands, and Iverson (1979) witnessed a probably fatal attack on a hatchling by a male of the same species.

On North Cay, we witnessed aggregate feeding on two successive mornings at a small fruiting bush of undetermined species. Nine to twelve iguanas converged to feed between the hours of 0700 and 0830. One male defended the bush from other males, while allowing as many as five female iguanas to climb into the bush to feed. Several male iguanas were able to climb into the bush to feed when the defending male was driving off another intruding male. After two mornings of feeding, the bush was picked clean of its fruit and the iguanas did not aggregate there again. Auffenberg (1982a) reported aggregate feeding in *C. carinata* and concluded that conditions exist for social learning.

As is true for many taxa of iguanas (see Iverson, 1979, for review), *C. rileyi* on most cays routinely climbs into the vegetation to forage. Because at least one large rock iguana does not climb for food (*C. cornuta stejnegeri;* Wiewandt, 1977), Auffenberg (1982a) suggested that small body size may be advantageous for harvesting food above the ground on islands with low floral diversity. However, we have noted that the largest iguanas, especially those in the translocated population, climb trees to forage as readily as, and perhaps even more so than, the smaller iguanas.

NATURAL PREDATION

Although young iguanas clearly have more predators than do adults, the prevailing view is that natural predation can be virtually dismissed as an important factor shaping the natural history of *Cyclura*. Certainly, insular iguana populations exhibit life history traits that are presumably related to predation rates that differ from those of mainland populations (e.g., reductions in wariness, clutch size, growth rate, and tail loss rates; Iverson, 1979; Case, 1982; Wiewandt, 1982; Iverson and Mamula, 1989).

Osprey in the Acklins Bight (North and Fish Cays) regularly prey on adult iguanas (Hayes et al., unpubl. obs.). We have seen them feeding on a number of fresh adult carcasses and observed one take an adult iguana while on the wing. The significance of such predation remains unclear and likely has a trivial impact on these populations. However, if the osprey rely on iguanas to any extent on White Cay, this could pose a serious threat. Predation on nesting

Galápagos marine iguanas by the Galápagos hawk *(Buteo galapagoensis)* illustrates the susceptibility of female iguanas in particular to natural predators (Boersma, 1983). We have also noticed that iguanas tend to scan the sky, suggesting that they may have evolved strategies to avoid predation. Perhaps antipredator strategies of iguanas have shaped more of their natural history than has generally been recognized (see Rivas and Levin, this volume).

An unexpected observation was that of an adult iguana that was attacked and consumed by a large barracuda as she tried to swim across a mangrove channel to the small islets on the northern shore of North Cay. Although this particular event was precipitated by our attempt to capture the female, we tracked a radio-tagged iguana that traversed several mangrove channels on its own and iguanas are plentiful on these islets. Accordingly, marine predators, which abound in the shallow waters of the Acklins Bight, pose a credible risk to waterborne transport between cays and to movements by iguanas across narrow channels to and from the small islets on the northern shore of North Cay. As does *C. carinata* (Iverson, 1979), *C. rileyi* shows reluctance to enter water unless harassed, and then generally only as a last resort.

HOME RANGE AND HABITAT USE

Using radiotelemetry (White and North Cays) and direct observation (Green Cay), we quantified home-range sizes of male and female iguanas during the postmating and nesting seasons. Home-range size can be assessed by a variety of means (e.g., R. A. Powell, 2000), but recent developments indicate that the fixed kernel method (with least squares cross-validation for smoothing) is the best current estimator based on a preferred minimum of thirty resightings (e.g., Seaman et al., 1999). To compute kernel estimates, we used the Home Ranger software program (Hovey, 1998), which can be downloaded from the Internet. To compare our results more directly with prior studies, we also calculated minimum convex polygons (MCP) using the Calhome software program (Kie, 1994),

also available on the Internet. As a point of distinction, home-range values based on a small number of sightings are generally underestimated by MCPs and overestimated by kernel methods (Seaman and Powell, 1996).

Our largest and most informative data set was obtained for *C. r. rileyi* on Green Cay (Cyril, 2001), where we computed the home range size of fourteen males and twenty-four females (based on ten to twenty-six resightings for each individual) using four methods: maximum distance between any two points, 100% MCP, 95% MCP, and 95% fixed kernel. We found a high degree of correlation among all methods (all $r_s > 0.745$; $P < 0.001$). The mean 95% fixed kernel estimates for males and females, respectively, were 439 and 628 m². Mann-Whitney U tests revealed that all four measures of home range size were similar for males and females (all $P > 0.18$). The maximum distance traveled (373 m by a female) was more than one-half the length of the island. Some iguanas of both sexes were seen within a 100 m² area during the entire study (23 June to 22 July 1999).

Compared with *C. r. rileyi* on Green Cay, *C. r. nuchalis* on North Cay utilized larger home ranges (Thornton, 2000), where comparable fixed kernel estimates (based on twenty-three to thirty-seven fixes) were 2047 m² for gravid females ($n = 5$) and 397 m² for nongravid females ($n = 5$). Several gravid females and one nongravid female 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. *C. r. cristata* on White Cay also appeared to utilize larger home ranges, with adaptive kernel estimates (at the 85% level) of 2656 m² (five males and two females; the different estimator here was necessary because the number of resightings was small, ranging from four to eleven; Fry, 2001). Because of the recent population crash, the iguanas on White Cay were at much lower density than on Green Cay or North Cay. Mitchell (1999) reported that home range size of *C. pinguis* expanded one-hundredfold following a decline in density on Anegada, and a similar effect may have occurred on White Cay.

Our informal observations and those of others (e.g., Wiewandt, 1977; Iverson, 1979; Auffenberg, 1982b; Knapp, 2001a) clearly indicate that local iguana density varies with habitat quality. On Green Cay, we have observed a redistribution of iguanas corresponding to the decline in *Opuntia* cactus. Since 1994, it appears that more iguanas have moved from the formerly cactus-dense western end to the eastern end. Following the population crash on White Cay, we expected to see a similar redistribution, because we assumed that iguanas would seek to optimize resource utilization and males would seek out the handful of remaining females. The island has a distinct west-east gradient in terms of vegetation density. In 1997, the iguanas were evenly distributed across this gradient (Fry, 2001), and subsequent surveys in 1999 and 2000 indicate that the even distribution had persisted. The absence of redistribution or clustering suggests that the resources available to individuals at reduced iguana density are similar on this cay regardless of vegetation density, or that social pressures (e.g., territoriality) constrained movement patterns.

Iguanas often retreat to burrows that are formed by or excavated beneath rock or are excavated in loose soil (usually near vegetation and in soil with root penetration). The relative proportion of these burrows, although not quantified on any cay, varies considerably among the populations. For example, no earthen burrows are present on Green Cay, and few if any rock burrows are present on Pigeon Cay. On some cays, the number of iguanas present appears to far exceed the number of retreats available. In such circumstances, vegetation serves as an adequate retreat. Although the dimensions of rock and earthen burrows are similar, thermal differences may exist. To assess this possibility, we compared the temperature profiles of both burrow types ($n = 10$ for each) on North Cay by positioning temperature probes outside (10 cm above the entrance) and within (up to 110 cm from entrance or against the back wall) actively used burrows (Thornton, 2000). There was a significant three-way interaction between burrow

type (rock versus earthen), time of day (0800, 1200, 1600, 2000), and location (outside versus entrance; $F_{3,54} = 4.78$, $P = 0.005$), suggesting a complex relationship among the three variables. The earthen burrows were similar to the outside temperature at 0800 (mean of 28.4 and 28.8 °C, respectively), but warmed slowly and remained 2–3 °C cooler than the outside temperature at 1200 and 1600. The mean maximum temperature was reached at 1600 (31.0 °C). At 2000, the earthen burrows (30.8 °C) were several degrees warmer than the outside temperature (28.8 °C). Rocky burrows, in contrast, were coolest at 0800 (27.6 °C) but warmed up quickly and were similar to outside temperatures at 1200 and 1600 (32.6–34.1°C). At 2000, the rocky burrows (33.7 °C) were considerably warmer than both earthen burrows (30.8 °C) and outside temperatures (29.9 °C). These results suggest that earthen burrows are better suited for cooling during midday, whereas rocky burrows are better suited for rapid warming in the morning and heat retention at night.

Considering the importance of temperature to digestion rate, digestive efficiency, and growth in ectothermic herbivores (e.g., Harlow et al., 1976; Christian, 1986b), the presence of burrows in a territory may provide important thermoregulatory options. Growth rate of *C. nubila,* for example, is faster with increasing nighttime temperature (Christian, 1986b), and this species prefers to sleep in the warmest microhabitats available (Christian et al., 1986). Further study of the relationship between retreat burrow presence and territory quality seems warranted.

REPRODUCTION

Our studies of reproduction took place on North Cay in the Acklins Bight (*C. r. nuchalis;* 1998, 1999) and on Green Cay off San Salvador Island (*C. r. rileyi;* 1999, 2001). The research focused largely on the nesting season each year (late June and July). However, we conducted an ethological study from two observation towers during May and June 1998, on North Cay, and additional mating activities were observed opportunistically during population surveys and

capture studies in other years. Unfortunately, we found it difficult to observe copulations despite selecting a study area with high iguana density and low vegetation cover.

In contrast, nesting was much more conspicuous. On North Cay, we relied on radiotelemetry to track individual females. Despite the stress associated with capture, processing, and daily tracking, all telemetered females exceeding 300 g oviposited regardless of whether transmitters were installed (glued to the hip) fifteen to twenty-four days prior to oviposition ($n = 4$) or one to three days before oviposition ($n = 7$). On Green Cay, because of its small size, individually marked iguanas were more readily detected and radiotelemetry was not used. After females had laid their single clutch, easily recognized as having occurred by the obvious loss of body weight, we recaptured and weighed them. A number of nest burrows were very carefully dug open (usually via the excavation tunnel) to ascertain the structure of the burrows and determine the clutch size and weight and dimensions of the eggs. Digging was accomplished by hand in a manner so as not to damage the integrity of the egg chamber, which consisted of a small, hollow pocket in the sand where the eggs were deposited. Once the desired data were collected, the burrow was reconstructed to the best of our abilities. Unless indicated otherwise, most of the data were obtained during the 1998 season on North Cay (Thornton, 2000) and the 1999 season on Green Cay (Cyril, 2001).

PHENOLOGY OF REPRODUCTION

For *C. rileyi,* the mating season begins in May and continues into June. We have observed fifteen copulations by *C. r. nuchalis* from 21 May to 9 June and three copulations by *C. r. rileyi* from 26–30 May. Nest digging begins the last week of June for *C. r. nuchalis* on North Cay (1998 and 1999) and the first week of July for *C. r. rileyi* on Green Cay (1999 and 2001). Oviposition occurs several days after the onset of excavation and continues for at least two weeks. Hatching presumably commences eighty-five to ninety

days after egg laying (Iverson, 1979), from late September to mid-October.

As in *Iguana* (Rand and Greene, 1982), there is no general relationship between nesting date and latitude in *Cyclura*. Consideration of only those taxa that inhabit the Bahamas and the Turks and Caicos Islands seems bewildering. Moving from north to south, *C. cychlura inornata* in the northern Exumas begins nesting in mid-June (Iverson, 2001), *C. c. cychlura* on Andros nests as early as mid-May (Knapp, 2001b), *C. r. rileyi* on San Salvador starts in early July (Cyril, 2001), *C. r. nuchalis* in the Acklins Bight begins in late June, and *C. carinata* on Pine Cay in the Turks and Caicos Islands nests in early June (Iverson, 1979). Although annual variation may contribute to the variance, we are doubtful that a geographical pattern exists. Clearly, the seasonality of rainfall must exert an important role in the phenology of reproduction (e.g., Wiewandt, 1977; Iverson, 1979; Vogel, 1994), but its effect can be either beneficial or deleterious at several stages of reproduction. Moisture and temperature, for example, can affect not only nests during incubation (e.g., survival and incubation time of eggs, fitness of hatchlings; reviewed by Alberts et al., 1997), but also hatchlings following emergence (e.g., storm-associated mortality [this study; Breuil, 2000] and availability and quality of food). Excessive drought can be devastating at any time (Breuil, 2001). As pointed out by Rand and Greene (1982), because the timing of mating, nesting, incubation, and hatching have evolved together, the total response might represent an adaptive compromise. We suggest that future comparisons of nesting dates between translocated populations and their source cays would help us better understand the factors that govern the phenology of reproduction.

Curiously, the relationship between date of oviposition and female body size differed substantially between North Cay and Green Cay. On North Cay, the positive correlation ($r_s = 0.64$, $P = 0.024$, $n = 11$) indicated that larger females nested later, whereas the negative correlation on Green Cay ($r = -0.47$, $P = 0.028$, $n = 22$) revealed that larger females nested earlier. The pattern

of larger females ovipositing sooner was also reported for *C. nubila* (Alberts et al., 1997) and *C. cychlura inornata* (Iverson, 2001). There are a number of factors that could influence size-based differences in timing of reproduction (e.g., dominance relationships that affect time of mating, energetic or thermal influences on egg development rate, competition among females for suitable nest habitat, competition among young emerging at different times) that are deserving of future study.

In fall 2001 (2–10 October), we examined twelve nests from which hatchlings had recently emerged. Most nests were located by finding the small holes where the hatchlings had exited. We observed hatchlings emerge from two nests with known oviposition dates, giving us incubation times of ninety-one and ninety-two days.

SEXUAL MATURATION

Female *C. rileyi* attain sexual maturity at approximately 20 cm SVL and 300 g. On North Cay, the smallest measurements for a gravid female before oviposition were 19.5 cm and 260 g. Females on Green Cay possibly mature at a larger size (minimum measures were 21.5 cm and 340 g), perhaps because of the recent damage to vegetation or because they are somewhat larger (table 17.3) on this cay. In the absence of histological samples and sufficient mating data, we assume that males attain sexual maturity at a size similar to females or at a slightly larger size, as occurs in *C. carinata* (Iverson, 1979). Iverson (1979) estimated that female *C. carinata,* which mature at a size similar to *C. rileyi,* require six or seven years to attain reproductive size. This is probably a reasonable estimate for *C. rileyi*. However, Iverson (2001) recently concluded that *C. cychlura inornata,* which mature at a much larger size (closer to 29 cm SVL), require fourteen years to attain reproductive size. We suspect that female *C. rileyi* breed annually, but lack sufficient data to know this with certainty.

MATING SYSTEM AND TACTICS

Our observations on North Cay suggest that the mating system of *C. r. nuchalis* is polygynous,

and may even be polygamous. One male in our study area copulated with at least three females and another copulated with at least two. One female was seen to copulate with three different males, but we could not discern whether she actively solicited those copulations.

Because of competition among males for access to females, mate guarding (female defense) and forced copulation (particularly by smaller males) appear to be common strategies. The larger males are territorial and are more likely to guard their mates. We observed female defense by four males that repeatedly chased away rival males that approached a mated female in their territory. Both forced copulation and female defense appear to increase as the mating season progresses. Of the fourteen unsuccessful copulatory attempts observed between 21 May and 10 June, four of five that resulted from female escape efforts occurred prior to 27 May, and six of seven that resulted from interruption by a male conspecific occurred after 27 May (our notes do not clarify the cause of two other attempts). The difference in proportions approached significance (Fisher's exact test, two-tailed $P = 0.061$). One female was immediately subjected to forced copulation by two smaller males after we captured and temporarily removed (for processing) the large male that was aggressively defending her. This observation clearly illustrates the adaptive value of mate guarding by larger, territorial males. The tactic of forced copulation adopted by smaller iguanas is presumably a conditional mating strategy, based on phenotypic rather than environmental or genetic differences, and has been reported in *C. cornuta stejnegeri* (Wiewandt, 1977) and a number of other iguanas (e.g., *Amblyrhynchus:* Wikelski and Bäurle, 1996; *Conolophus:* Werner, 1982; *Iguana:* Dugan, 1982a; Rodda, 1992; *Sauromalus:* Berry, 1974).

The majority of copulations occurred in the morning ($n = 8$ between 0900 and 1200) and late afternoon ($n = 6$ between 1500 and 1800), with few during mid-day ($n = 2$ between 1200 and 1500). The duration of copulation was very brief in *C. r. nuchalis,* averaging 42.5 s (SE = 5.5) with a range of 20–90 s ($n = 13$). The duration of

copulation is probably longer in *C. r. rileyi;* although not timed precisely, two of the three observations lasted several minutes. Copulation time is relatively brief in some iguanas (e.g., *C. c. carinata:* 40–76 s, Iverson, 1979; *Conolophus:* 30–90 s, Werner, 1982) and considerably longer in others (e.g., *Amblyrhynchus:* 9 minutes, Wikelski and Bäurle, 1996; *Brachylophus:* 15–20 minutes, Gibbons and Watkins, 1982; *Iguana:* 7–9 minutes, Dugan, 1982a; Rodda, 1992). The relationships between duration of copulation, mating system, and alternative mating tactics deserve more consideration.

In addition to mate guarding, multiple mating of the same individual may represent another tactic to deal with sperm competition resulting from forced copulation. One male copulated with the same female twice, only two days apart. This particular female was mated at least four times by three different males over a five-day period. Although it appears to us that females are subject to intense harassment, we cannot rule out the possibility that females solicit multiple copulations. Multiple paternity is sought by females of other lizards because of the benefits of genetically diverse offspring (e.g., LeBas, 2001). Patterns of female receptivity, postcopulatory guarding by males, and number of males mated by females varies considerably among iguanas. At one extreme, female marine iguanas have a brief period of receptivity and are normally mated only once, postcopulatory guarding is absent, and hence multiple paternity is absent or rare (Wikelski and Bäurle, 1996). In contrast, many female green iguanas have an extended period of receptivity and may mate repeatedly with the same or different males, postcopulatory guarding is frequent, and hence multiple paternity seems likely (Dugan, 1982a; Rodda, 1992). Other iguanas, including *C. c. stejnegeri* (Wiewandt, 1977) and *Conolophus subcristatus* (Werner, 1982), appear to be more similar to *I. iguana*. Our observations and a report of multiple paternity in *C. collei* (Davis, 1996) suggest that sperm competition is an important determinant of mating tactics by both male and female *C. rileyi*. Genetic studies would be helpful in correlating the number, identity, and quality of males contributing to a clutch.

NESTING MOVEMENTS

None of the females on Green Cay made noteworthy movements prior to nesting, but a number of females on North Cay moved substantial distances prior to (or immediately after) nesting. In 1998, Thornton (2000) observed five of twelve gravid telemetered females make nesting movements of 145–1000 m. In 1999, we tracked four additional females that moved 500–1000 m away from the mating area to oviposit. One of the latter females crossed three shallow mangrove channels and stopped on one of the small sandy islets on the northern perimeter of North Cay, a journey of 700 m. Interestingly, the females clearly pass through an abundance of potential nest sites as they move to their final digging site. The advantages of these movements, perhaps related to outbreeding opportunities for their offspring, presumably outweigh the costs. Nesting movements of up to 15 km have been reported in other iguanas (e.g., *C. c. inornata:* Iverson, 2001; *C. c. stejnegeri:* Wiewandt, 1977, 1982; *Conolophus:* Werner, 1982; *Iguana:* Montgomery et al., 1973; Bock, 1989; Rand et al., 1989). In some species, nesting movements are essential to locate suitable nesting habitat, but in others, it remains puzzling as to why some females remain stationary and others pass up suitable habitat as they move a lengthy distance. Wiewandt (1982) suggested the involvement of an ontogenetic process, whereby neonates learn a hatching area through imprinting and/or females return yearly to a site where they previously nested.

NEST SITE CHARACTERISTICS

On North Cay, nests were widely distributed on the island, but excavation activities were more concentrated in some areas than in others. In 1999, we compared excavation activities in three different habitats: beachfront sandy habitat, interior sandy habitat, and interior rocky habitat. Within each habitat, we surveyed the number of excavations (including both nest burrows and abandoned burrowing efforts) in three 10 × 50 m

quadrants. The density of excavations differed significantly among the three habitats (median test $\chi^2_2 = 9.0$, $P = 0.011$), with the highest density of excavations along the beachfront sand (1822/ha), intermediate density in the interior sandy habitat (578/ha), and lowest density in the rocky interior habitat (244/ha). On Green Cay, nests were also widely distributed, but the habitat was much more rocky and nests were restricted to areas having loose sand and soil. However, some nests were constructed within rock crevices and would have been easily overlooked if not for the fresh earth present at the crevice entrance. The majority of nest burrows on Green Cay were dug beneath an overlying rock such that the rock itself formed the ceiling of the egg chamber (E. Grove, unpubl. data).

On both islands, females started multiple excavations prior to or during construction of the final nesting burrow. Exploratory and final nesting burrows could generally be distinguished because final nesting burrows were backfilled, whereas exploratory burrows were not (unless in close proximity to the nest burrow). Burrows were generally abandoned when females encountered rocks or dense root masses underground (c.f. Wiewandt, 1977; Christian, 1986a; Vogel, 1994). On Green Cay, Cyril (2001) found the entrance microhabitats of exploratory and final nesting burrows to be similar.

NEST CONSTRUCTION

Females typically dug their final nesting burrows in a single day and emerged having laid their eggs later in the day or the next morning, after spending the night in the burrow. When iguanas dug in sandy soil, the earth loosely filled the tunnel behind them such that they were entombed until they deposited their eggs and burrowed back out to the entrance. On North Cay, fourteen telemetered females emerged after oviposition approximately eight to thirty hours after entering the final nest burrow; of these, twelve (86%) appeared to spend the night in the burrow. To our knowledge, nests were always excavated and were never constructed in preexisting retreat burrows.

NEST BURROW CHARACTERISTICS

The final burrow in which eggs were laid varied substantially in shape, dimensions, and location of the egg chamber. Most burrow tunnels changed directions one or more times (92% of thirteen burrows on North Cay; 60% of five burrows on Green Cay) and in some (46% on North Cay), we detected multiple chambers. One burrow on North Cay had two clutches in separate chambers, and on Green Cay one chamber apparently contained two clutches. Some burrows contained old eggshell fragments (23% on North Cay; 60% on Green Cay). Total burrow length was longer on North Cay (69–235 cm, mean = 129 cm, $n = 13$) than on Green Cay (30–116 cm, mean = 53 cm, $n = 5$). Burrows on both cays were shorter in length than those dug by *C. carinata* on Pine Cay in the Turks and Caicos (Iverson, 1979) and *C. cychlura* in the northern Exumas (Iverson, 2001). Egg-chamber depth (from ground surface above to floor of chamber) was similar on North Cay (14–40 cm, mean = 22 cm, $n = 13$) and Green Cay (18–28 cm, mean = 22 cm, $n = 5$). Nest depth of *C. c. inornata* in the northern Exumas averaged deeper (27.5 cm; Iverson, 2001). On North Cay, burrow dimensions were associated with female size (burrow length: $r = 0.79$, $P = 0.060$; burrow depth: Spearman $r_s = 0.94$, $P = 0.005$).

On Green Cay, vegetation cover above the five nests (judged from a densiometer mirror placed on the ground above the nest chamber) ranged from 0 to 18%. Additional densiometer readings above estimated nest chamber placement (i.e., unexcavated nests; $n = 23$) averaged 19% and ranged from 0 to 82%. Iverson (2001) reported vegetation cover averaged 22% (range, 0–61%) for *C. c. inornata* in the northern Exumas. Vogel (1994) indicated that *C. collei* nests in soil devoid of vegetation. Variation in vegetation cover above nests could result from differences in substrate stability (sandy soils may need root tendrils for firmness), soil temperature gradients, or habitat availability. Iverson (2001) found that nest depth was inversely related to vegetation cover and suggested that females deposit eggs at depths of preferred temperatures (i.e., shadier sites require shallower nests).

Compared with other *Cyclura* species, the clutch size of *C. rileyi* is small because of the small size of adults in most populations. On North Cay in 1998, clutch size ranged from two to five with a mean of 3.1 ($n = 14$) and was positively correlated with female body size (SVL: $r_s = 0.66$, $P = 0.038$, $n = 10$; mass: $r_s = 0.77$, $P = 0.009$, $n = 10$). On Green Cay in 1999, clutch size ranged from three to six eggs ($n = 5$). A single clutch found on Low Cay contained ten eggs, reflecting the large size of animals in this population (most individuals >30 cm; table 17.3). Relative reproductive investment (change in body mass divided by mass before oviposition × 100) averaged 26.8% ($n = 11$) on North Cay and 21.7% ($n = 9$) on Green Cay and was associated with SVL (North Cay: $r_s = 0.66$, $P = 0.038$, $n = 10$; Green Cay: $r = 0.75$, $P = 0.02$, $n = 9$). These data suggest that iguanas on North Cay in 1998 invested more in reproduction than those on Green Cay in 1999.

Mean egg dimensions after oviposition were similar on North Cay (mass = 27.1 g, $n = 41$; length = 55.4 mm, $n = 43$; width = 30.2 mm, $n = 43$) and Green Cay (mass = 27.7 g; length = 53.4 mm; width = 29.5 mm; $n = 21$ for each mean). Three eggs found in a Green Cay nest at the time of emergence (October 2001) ranged from 42 to 47 g. Each of three recently hatched juveniles in a nearby nest had a mass of 21.5 g, with SVLs of 8.2–8.5 cm. Mean egg mass within individual clutches after oviposition was negatively correlated with clutch size (North Cay: $r_s = -0.70$, $P = 0.008$, $n = 13$; Green Cay: $r = -0.87$, $P = 0.05$, $n = 5$). Thus, larger females invested relatively more into reproduction by producing larger clutches with smaller eggs. In contrast, larger females produced both larger clutches and larger eggs in *C. cychlura* (Iverson, 2001) and in one study of *C. nubila* (Alberts, 1995). In another study of *C. nubila* (Alberts et al., 1997), egg mass was independent of female size, and larger females evidenced reproductive senescence with higher rates of infertility and greater mortality of initially viable eggs.

NEST DEFENSE

Female defense of nests is widespread among iguanas (reviewed by Wiewandt, 1982; see also Christian and Tracy, 1982; Werner, 1982; Christian, 1986a; Vogel, 1994; Iverson, 2001) and was exhibited by *C. rileyi* on both North Cay and Green Cay. It is thought to be a strategy that mitigates the loss of eggs resulting from the digging activities of females that prefer to enter a burrow that has already been excavated. On North Cay, at least five of fourteen females (36%) were observed to exhibit nest defense, even though nest defense was not carefully monitored on this cay. Curiously, all five females that made substantial nesting movements abandoned their nests and exhibited no defense. On Green Cay, at least eighteen of twenty-two females (82%) exhibited a degree of nest defense. Of these, thirteen (59%) remained near their nests and defended them for more than five days. The mean nest density of iguanas exhibiting more than five days' defense (3.6 nests within 10 m radius) was significantly greater than those exhibiting five or fewer days' defense (2.0 nests within 10 m radius; one-tailed *t*-test, $P = 0.03$). This latter observation is consistent with the proposed function of nest defense.

INCUBATION TEMPERATURES

On North Cay, we inserted a thermistor temperature probe into two nest chambers and measured temperatures over a forty-eight-hour period. Temperatures within the nests ranged from 25 to 33 °C. There was an inverse relationship between ambient air temperature and nest chamber temperature, with the eggs being warmer at night and cooler during the day. We suspect the inverse relationship between ambient temperature and nest temperature may result from the delay in transfer of heat between the air and the soil at the nest chamber depth. Although additional data are needed, these preliminary findings are similar to prior studies on incubation temperature (e.g., Christian and Lawrence, 1991) and give us meaningful information that may be of use in future captive breeding programs.

CONCLUSIONS

Our studies have provided a wealth of data on *C. rileyi* that are relevant to conservation programs. The population assessments indicate that two of the three recognized subspecies are critically endangered, with some populations becoming extirpated within recent decades and others continuing to dwindle. We have identified a number of threats to the remaining populations and have undertaken some efforts to ameliorate habitat degradation. Baseline data reported here are essential for continued monitoring.

Information regarding diet, predation, habitat use, and reproduction give us a more complete picture of the ecological requirements of the iguanas. As existing habitats change over time, or as new islands are sought for relocation programs, this information can help inform management decisions, such as the selection of appropriate islands for translocation. The social structure, mating system, and level of sperm competition can affect the genetic structure of a population, especially when only a subset of males is contributing to the gene pool. Removal of large males may be useful as a management tool for increasing the genetic diversity of a population (Alberts et al., 2002). The ability to predict clutch size and determine the timing of oviposition accurately and noninvasively is important not only to captive management programs, but also to field conservation efforts, in which estimates of population fecundity, collection of eggs for artificial incubation, or strict protection of nest sites at the time of laying are required (Alberts, 1995). For captive husbandry, knowledge of diet is essential, and consideration should be given to dominance relationships and the possible benefits of multiple insemination of females.

Finally, comparisons among populations can be useful to identify potential environmental problems that may need to be addressed. In our study, population differences in demography, body condition, and reproductive parameters appeared to be associated with environmental disturbances, such as catastrophic storms and non-native predators (e.g., rats, raccoons) and competitors (e.g., moths). However, many aspects of behavior and ecology are independent of phylogeny (e.g., Snell et al., 1984), and variation may often reflect local adaptation rather than problems in need of attention.