PROCEEDINGS

OF THE

TENTH SYMPOSIUM

ON THE

NATURAL HISTORY OF THE BAHAMAS

Edited by
Sandra D. Buckner
and
Thomas A. McGrath

Conference Organizer
Vincent J. Voegeli

Gerace Research Center, Ltd.
San Salvador, Bahamas
2005

Cover photograph – "Little Ricky" - juvenile dolphin, San Salvador, Bahamas (courtesy of Sandra Voegeli, 2003)

Printed in the Bahamas

ISBN 0-935909-76-1

BIOLOGY AND CONSERVATION OF *CYCLURA RILEYI*, AN ENDANGERED BAHAMIAN ROCK IGUANA

William K. Hayes and Ronald L. Carter
Department of Natural Sciences
Loma Linda University
Loma Linda, CA 92350 USA

ABSTRACT

Cyclura rileyi is one of the most threatened of iguanas, with two of its three recognized subspecies being critically endangered. Population and threat assessments suggest that all three taxa remain vulnerable to extinction. Threats identified include habitat degradation (from catastrophic storms and an introduced cactus-eating moth), feral mammals (particularly rats), disease, population fragmentation, ecotourism and smuggling, and habitat inundation by rising sea levels. Morphometric analyses reveal taxon, population, sex, age, and environment-related differences in body condition and injuries (toe loss and tail damage). Discriminant analyses of meristic data (head scales and femoral pores) confirm significant divergence among the three subspecies. Indirect evidence suggests a detrimental effect of rats on iguanas. Habitat restoration efforts (rat eradication and nest substrate replenishment) on several cays offer mixed results. Dietary diversity appears to be highly limited on some cays. Home range size seems similar for males and females but varies somewhat between populations. Females attain sexual maturity at approximately 20 cm SVL and 300 g. Mating takes place from late-May to mid-June. Both males and females seek multiple copulations, suggesting a polygamous mating system. Males often utilize forced copulation and mate-guarding. Egg-laying in relatively short nest burrows occurs mainly during July, with clutch size corresponding to female body size (both being relatively small in this species). Nest defense by females varies with nesting density. Hatching occurs from late-September to mid-October. Adults occasionally cannibalize young. Finally, we discuss management recommendations in urgent need of implementation.

INTRODUCTION

Among the eight species of West Indian rock iguanas, *Cyclura rileyi* is one of the most threatened, with two of its three recognized subspecies listed by IUCN (the World Conservation Union) as critically endangered (*C. r. cristata* and *C. r. rileyi*) and the other as endangered (*C. r. nuchalis*)(Alberts, 2000). Although they formerly occupied large islands, today these lizards are confined to small, remote, uninhabited cays of three island groups (Figure 1; Hayes et al., 2004). *Cyclura r. cristata* must have occupied other islands at one time, but is now restricted to a single cay in the southern Exumas, where fewer than 200 individuals persist. *Cyclura r. nuchalis* exists naturally on just two cays in the Acklins Bight of the Crooked/Acklins Island group. Although as many as 10,000 individuals may remain, their current habitat represents a tiny fraction (0.2%) of their former range. An introduced population of about 300 individuals thrives on an island within Exumas Cays Land and Sea Park. The remaining populations of *C. r. rileyi* are presently confined to four tiny offshore cays and two islets within the hypersaline lakes of San Salvador Island. Fewer than 600 individuals remain, and surveys suggest a continuing decline. Although a few individuals remain on the main island, this population appears to be non-viable. Thus, this taxon similarly occupies a mere fraction (0.2%) of its former range.

Shaped by tectonic forces and ice age-related sea level fluctuations, the Bahamian archipelago has undergone substantial change through time. For iguanas, no changes have been more significant than those caused by humans. Although Amerindians apparently utilized iguanas for food and funerary offerings (e.g., 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 CITES (Convention on the International Trade in Endangered Species) protection, hunting and smuggling of iguanas for the pet trade continue (Alberts, 2000). However, the greatest threats appear to be related to invasive species that alter the habitat and/or prey on iguanas. Ubiquitous human-commensal species (e.g., pigs, livestock, dogs, cats, mongooses, rats) have caused extirpation or near extinction of iguanas (and other vertebrates) throughout the West Indies (Alberts, 2000). In the Turks and Caicos Islands, Iverson (1978) documented one tragic example of the devastation caused by a handful of feral dogs and cats brought by hotel construction workers to Pine Cay. In less than five years, a population of more than 5,000 adult iguanas was nearly extirpated. Clearly, these iguanas are exceptionally vulnerable to anthropogenic influences.

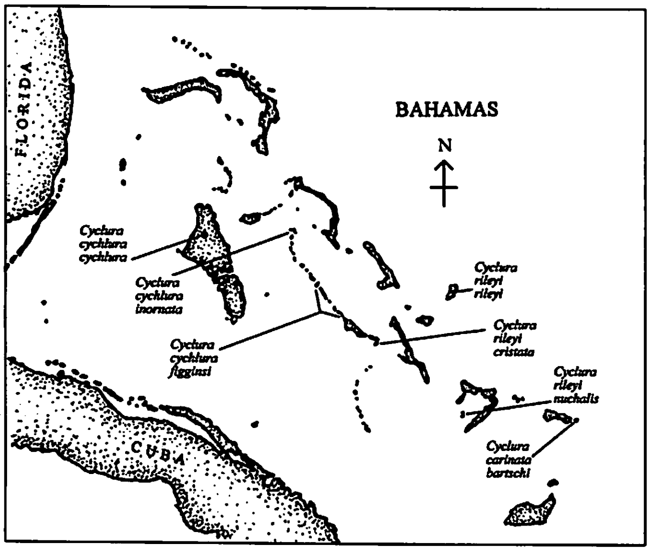

Figure 1. Distribution of Cyclura *in the Bahamas, including the three subspecies of* C. cychlura *(Andros, northern Exumas, southern Exumas) and the three subspecies of* C. rileyi *(southern Exumas, San Salvador Island, Acklins Bight).* Cyclura carinata bartschi *exists only on Booby Cay off of Mayaguana Island, Bahamas; a second subspecies of* C. carinata *occurs in the Turks and Caicos Islands to the south.*

In this article, we summarize the findings of a long-term, ongoing research program on *C. rileyi*. 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 threats to the habitats of several important cays, and detailed studies of behavioral ecology. More detailed analyses and discussion can be found in Hayes et al. (2004) and Carter and Hayes (2004).

METHODS

Population Assessments and Morphological Measurements

In our initial work, we visited each of the known populations of *C. rileyi* to survey population size, measure select morphological features, and assess other demographic attributes (e.g., sex ratio, body-size distribution). We also assessed the habitats of each cay and identified potential threats to the iguanas.

From 1993 to 1999, we captured 484 iguanas (75 *C. r. cristata*, 198 *C. r. nuchalis*, 211 *C. r. rileyi*) by noose (the majority) or by hand. 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 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.

Prior to release at the site of capture, iguanas were marked semi-permanently 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 (Hayes et al., 2000). When conducting home range and behavioral ecology studies, we additionally painted a temporary alphanumeric code on each side of the dorsum, visible from a distance, using a non-toxic enamel paint that lasted several months or until ecdysis (Hayes et al., 2000).

Population estimation was conducted by three means, as summarized by Hayes and Carter (2000) and Hayes et al. (2004): 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 or more), with adjustment for the proportion of habitat surveyed. Estimates based on classical transects and distance surveys were adjusted based on separate determinations of detectability (we usually saw one-third to one-half of the iguanas present during a given survey). During surveys, we also recorded the approximate size class (juvenile, subadult, adult, large adult) of each iguana sighted.

Invasive Species Control and Habitat Restoration

As a result of our population and threat assessments, 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 methods and initial results.

Potential impact and eradication of rats. To evaluate the potential impact of rats on iguanas, we compared the density and biomass of iguanas on six cays believed to be rat-free (Fish, Goulding, Green, Manhead, North, translocated population) and four cays known to be rat-infested (Guana, Low, Pigeon, White). Determination of rat absence was based on extensive trapping effort on all cays except North and Fish Cay, where we used minimal trapping but did not detect rats during lengthy periods of camping. To evaluate potential predation on juvenile iguanas, rubber lizard models similar in size to hatchling iguanas were placed beneath vegetation on White Cay. Rat attacks were evidenced by obvious incisor marks on the models.

In spring 1998, we assisted Flora and Fauna International with the eradication of rats on White Cay. This was accomplished using the rodenticide brodifacoum, a second generation anticoagulant (donated by Zeneca Agrochemicals) that was delivered in solid bait blocks over a 20 m grid system. Bait blocks were secured within rectangular plastic bait stations (ca. 25 x 7.5 x 7.5 cm) to reduce the risk of incidental poisoning of iguanas and birds. In the summer of 2000, Sam Cyril, then a graduate student, similarly eradicated the rats on Low Cay using bait stations elevated 15-20 cm above the ground on a single PVC stake. Following a failed eradication effort in 1999, we concluded that this design was necessary to keep hermit crabs out of the bait stations. Hermit crabs, which readily devour the bait, were far more abundant on San Salvador's offshore cays than on White Cay.

Nesting habitat restoration. Near-direct hits by Hurricanes Lili (1996) and Floyd (1999) resulted in the destruction of soils, vegetation, hatchlings, and juvenile iguanas on Green Cay. Most adults survived the destruction. In April 2001, with the aid of San Salvador Island Boy Scouts and coordination by graduate student Eric Grove, we moved 600 buckets of sand (approximately 5 m^3) from the intertidal zone to nest sites on Green Cay 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 similar to nesting soils observed on other cays we have studied. We returned during June and July to observe nesting behavior, and again in October to document hatchling emergence.

Behavioral Ecology

Diet and natural predation. Diet was evaluated by examination of fecal deposits (collected July and October 1999 and May 2000) and by direct observation of foraging iguanas, primarily on Green Cay. The dramatic loss of *Opuntia* on this cay and the low vegetation diversity (10 species) prompted us to undertake a quantitative assessment of diet and its potential impact on iguana body condition. Foraging bouts were opportunistically observed elsewhere as well. Several events of natural predation were also observed.

Home range size. Our graduate students estimated home range size of male and female iguanas on White Cay (1997), North Cay (1998), and Green Cay (1999). Radiotelemetry was used on White and North Cays, but Green Cay was small enough to rely solely on mark-resighting surveys. Further methodological details can be found in Thornton (2000), Cyril (2001), and Fry (2001).

Reproduction. We conducted ethological studies during the mating season (May and June) from observation towers on North Cay (1998) and on Green Cay (2002). Additional mating activities were observed opportunistically during population surveys and capture studies in other years. We studied female nesting during late June and July 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). Hatchling emergence was observed during October 2001 on Green Cay. Radiotelemetry was necessary to track gravid females on North Cay but was deemed unnecessary on Green Cay. A number of nest burrows were very carefully dug open (usually via the excavation tunnel) to ascertain the structure of the burrows and to determine the clutch size and weight and dimensions of the eggs. Digging was accomplished by hand and 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.

RESULTS AND DISCUSSION

Population Assessments

The demographic characteristics of each population and the non-native species that were detected are provided in Table 1. The primary threats identified include: (1) the presence of invasive (non-native) mammals (primarily black rats, *Rattus rattus*) and insects (*Cactoblastis cactorum* moths); (2) disease; (3) population fragmentation leading to small, isolated populations; (4) habitat damage from catastrophic storms; (5) vulnerability to ecotourism and smuggling; and (6) eventual inundation of habitat by rising sea levels. On the larger islands, there are additional problems related to human-commensal animals (pets and livestock) and substantial habitat alteration. Fortunately, we have found no evidence of humans currently hunting *C. rileyi*.

Cyclura r. cristata. Of the three taxa, this is clearly the most threatened. During our brief, June 1996 visit, we found rats to be abundant and John Iverson discovered tracks left by a raccoon (*Procyon lotor*). In 1997, we discovered a crisis situation with our distance transects (conducted May 1997) and Lincoln-Petersen estimate (conducted June 1997) suggesting that fewer than 200 iguanas remained (Table 1). More alarming, approximately 95% of the noose and hand captures from 1996-1997 were of males (additional females were caught by carefully-monitored glue traps set at burrow entrances; Fry, 2001). This male-biased ratio was not representative of other populations surveyed, and suggested that fewer than 10 adult females remained. The females captured were within a narrow size range (15.5-18.4 cm) and all were considered subadults. 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 between 1996 and 1997!

The raccoon, believed to be the primary culprit, was dispatched in July 1997. The rats were eradicated in May 1998. Visits from 1998-2000 confirmed that the population decline ended abruptly after the raccoon was dispatched.

Our most recent visit, in October 2002, suggested that population recovery is well underway. The numbers of juveniles (N = 28), subadults (N = 24), and adults (N = 24) detected in 2002 during our standardized survey were more than double those of November 2000 (N = 9, 11, and 14, respectively). Nevertheless, the population has been subject to recent demographic trauma (highly skewed sex ratio and few remaining females) and probable genetic bottlenecking, rendering it highly vulnerable to stochastic extinction processes.

Non-native *Casuarina* trees have begun to dominate the vegetation, and these attract numerous birds of prey (falcons) during winter and migration. Removal of the trees should be a high priority.

Cyclura r. nuchalis. Because this taxon occupies comparatively large islands, we found it to be the least threatened of the three subspecies. The two populations in the Acklins Bight comprise approximately 10,000-14,000 individuals (Table 1), but we suspect that actual population size is lower. The sex ratio is nearly 1:1 for both populations, and each age category is adequately represented. Populations such as these give us a good understanding of what the demographic parameters should be for a healthy ecosystem.

The relatively high density and biomass estimates compared to other populations of *Cyclura* (Table 1) undoubtedly reflect the abundance and quality of food on these cays. Juveniles and subadults appear to be poorly represented in the introduced Exumas Cays Land and Sea Park population, perhaps because of high population density or the suspected but not confirmed presence of rats. The two natural populations in the Acklins Bight appear to be free of immediate threats. However, these islands lack elevation relief (maximum of 3 m) 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 100 years. This estimate, based solely on elevation relief, does not take erosion into account, which could substantially degrade the islands further.

Cyclura r. rileyi. This taxon is critically endangered, with an estimated 426 to 639 iguanas remaining (Table 1). Only six viable populations occur. Two inland cays (Guana, Pigeon) and four offshore cays (Goulding, Green, Manhead, Low) currently sustain iguana populations that vary in size from a few dozen to several hundred (Table 1). Three additional cays supported iguanas in recent decades: Barn Cay (in Great Lake) in the early 1970's (Auffenberg, 1982b), High Cay in the 1980's (Don Gerace, pers. comm.; tracks were photographed in 1995 by Sandra Buckner, pers. comm.), and Gaulin Cay (the small population was extirpated by Hurricane Floyd in September 1999). Adult iguanas are occasionally reported (fewer than once per year) from the main island, usually at the Fortune Hill plantation ruins on the east side of the island where extensive, but rat-infested, habitat remains.

Some of the demographic parameters for *C. r. rileyi* offer additional reason for concern. 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 have resulted from a period of wet years that 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, 2000), but appears to be making a comeback, as evidenced by the relatively high number of juveniles and subadults in the 1998 survey. Compared to our 1994 estimates of population size (Hayes et al., 1995), several populations appear to have experienced a decline (see Table 1), including Green Cay and Manhead Cay.

Several populations of *C. r. rileyi* occupy cays with marginal food resources. 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 the 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 Hurricane Erin in August 1995 by a shallow channel (ca. 10 m width) that iguanas regularly traverse. Green Cay and Gaulin Cay support only ten species of plants. However, the 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 m^2 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 (height mostly < 30 cm) forest of cacti. When all 11 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, 2001).

Several recent hurricanes have inflicted serious damage to *C. r. rileyi* 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, and these stands have since deteriorated further. 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. (Vegetation critical for nesting seabirds was also destroyed on nearby White Cay, not to be confused with the White Cay that supports *C. r. cristata*.) No iguanas or their tail drags have been found on Gaulin since. Although a smaller percentage of vegetation was lost (roughly 5%) on Green Cay, 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 of the 1999 cohort of hatchlings. Reproductive failure observed again in 2000 bolstered our conclusion that the nesting substrate needed to be replenished. 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. 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. Sadly, illicit smuggling for the pet trade will pose a perpetual risk for these populations, despite the fact that 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.

Morphological Variation

Analyses of morphometric data, summarized more thoroughly by Carter and Hayes (2004), lead to a number of interesting conclusions.

Sexual dimorphism of body size and relative head size exists, with males being larger in both regards. Multivariate statistical models reveal that iguanas are heaviest in spring and leanest in fall, with males comparatively heavier in spring and females heavier in summer. Surprisingly, *C. r. nuchalis*, which thrives at high density on large islands with substantial food, exhibits a leaner body condition than the other taxa. Unpublished data obtained in October 2002 confirm that iguanas translocated to foliage-rich Club Med are substantially larger than those of their sparsely-vegetated source population on Green Cay.

Regarding injuries, *C. r. rileyi* suffers higher rates of toe loss than other subspecies, males (regardless of taxa) experience higher loss than females, and toe loss increases with age. Tail loss is similar among subspecies, sexes, and size classes, but populations coexisting with rats experience higher rates, again suggesting a possible detrimental effect.

Discriminant analyses of meristic data (head scales and femoral pores) suggest significant divergence among the three subspecies of *C. rileyi*, with reciprocal diagnosis of the three taxa at greater than 80% levels (Carter and Hayes, 2004). These levels exceed the preferred subspecies criterion of 75% diagnosability (Patten and Unitt, 2002).

Invasive Species Control and Habitat Restoration

Clear evidence exists that larger predators, such as cats, dogs, mongooses, and hogs (e.g., Iverson, 1978; Henderson, 1992, Haneke, 1995; Alberts, 2000), as well as feral livestock (Mitchell, 1999), are devastating to insular iguana populations. Our data from 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.

Potential impact and eradication of rats. Indirect evidence for the impact of rats was found by comparing the density and biomass (0 ± 1 S.E.) of iguanas on six cays believed to be rat-free (density = 59.9 ± 18.1 per ha; biomass = 38.0 ± 15.3 kg/ha) and four cays known to be rat-infested (density = 10.2 ± 3.1 per ha; biomass = 8.9 ± 2.4 kg/ha). Two-tailed Mann-Whitney U tests revealed that rat-free cays had significantly higher iguana density than rat-infested cays ($U = 1.0$, $P = 0.019$), but iguana biomass was similar for the two groups ($U = 4.0$, $P = 0.114$). On White Cay, Fry (2001) also found that rubber lizard models similar in size to hatchling iguanas were frequently bitten by rats after placement beneath vegetation, as evidenced by obvious incisor gnaw marks. 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 (see Hayes et al., 2004, for sleep habits of adults), 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. Although empirical data are lacking for iguanas, nests may also be vulnerable to rats. Raccoons are notorious predators of reptile and bird nests (e.g., Hartman et al., 1997) and prey upon spiny-tailed iguana (*Ctenosaura similis*) nests on islands off Belize (Platt et al., 2000).

As mentioned previously, the iguana population on White Cay has shown considerable rebound following raccoon (1997) and rat (1998) removal. However, because the raccoon was likely the greater threat, we can't fully assess the impact of rat removal. On Low Cay, we have seen very few juvenile iguanas during spring surveys each year from 2001-2003. Thus, the benefits of rat eradication remain unclear.

Nesting habitat restoration. Following nest habitat restoration on Green Cay in April 2001, the iguanas did not nest in the reconstructed habitat. One possible reason for lack of nesting use is that nest chambers on this cay are usually constructed directly beneath an overlying rock, a situation we have not seen elsewhere and did not recognize until after nest habitat reconstruction. In contrast to the reproductive failures in 1999 and 2000, there was a good hatch of iguanas on Green Cay in October 2001. Unfortunately, Hurricane Michelle washed away most of the restored sand in November 2001, thereby ending our experiment.

In contrast to our effort, Breuil (2000) artificially supplemented an existing *Iguana delica-*

tissima nest area with additional sand on Ilet Chancel in Martinique, and reported nesting use the same year with fewer eggs lost to nesting interference resulting from the high density of nesting females. Thus, the benefits of nest habitat restoration seem promising in spite of our results.

Behavioral Ecology

Diet. Seven plant species were found in the scats collected from Green Cay (Cyril, 2001). Compared to their relative abundance (determined from 205 points at the intersections of 10 m^2 quadrants within a grid that covered approximately 80% of the cay), *Borrichia arborescens* (flowers especially) and *Rhachicallis americana* (both flowers and leaves) were the most preferred items. *Opuntia stricta* (detected by spines and pads), though browsed less often, was also a preferred item despite its current scarcity. Plant content of the diet was similar during the three seasons. Iguanas also ingested the following animal items: birds (five incidents on Green Cay), 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), and unidentified insect material (22% of scats in October 1999 and 13% in May 2000 on Green Cay). More thorough studies of diet in other *Cyclura* (e.g., Iverson, 1979; Auffenberg, 1982a) suggest that at least 95% of the diet of all ages during all seasons consists of plant material.

To assess the possibility that the *Opuntia* cactus loss might affect body condition over time, we compared the relationship between log iguana mass (as the dependent variable) and log SVL during 1993-1995 (late May captures; N = 51) versus 1998-1999 (mid-June captures; N = 47) using an ANCOVA model. We found a significant effect of time (P = 0.001), suggesting that iguanas prior to (or during) the cactus decline (1993-1995) had comparatively more mass than after the cactus decline (1998-1999). As a control, we ran a similar ANCOVA for iguanas pooled from Goulding Cay and Pigeon Cay (N = 28 for late-May 1995; N = 14 for mid-June 1998) and found no difference (P = 0.18). Thus, iguanas appeared to be in better condition on Green Cay prior to the reduction in *Opuntia*, and this, in addition to lost nesting habitat from Hurricane Floyd, may have contributed to reproductive failures in recent years.

Natural predation. To our surprise, we learned that osprey in the Acklins Bight (North and Fish Cays) regularly prey upon adult iguanas. The significance of such predation remains unclear and likely has a trivial impact on these populations. Bryant Reynolds, then an undergraduate student, also observed 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, although iguanas may regularly enter water for relatively short excursions, marine predators pose a credible risk to water-born transport between cays and islands.

Home range size. On Green Cay during June and July, 1999, Cyril (2001) found that males (N = 14) and females (N = 24) occupied statistically similar home ranges (mean 95% fixed kernel estimates of 439 and 628 m^2, respectively, based on 10-26 resightings for each individual). The maximum distance traveled (373 m by a female) was more than half the length of the island. Some iguanas of both sexes were seen within a 100 m^2 area during the entire study (23 June to 22 July 1999).

On North Cay during June and July, 1998, Thornton (2000) observed larger home ranges, with comparable fixed kernel estimates (based on 23-37 fixes) averaging 2,047 m^2 for gravid females (N = 5) and 397 m^2 for non-gravid females (N = 5). Several gravid females and one non-gravid female undertook lengthy movements (up to 1 km), which were not possible on Green Cay where the length of the island is only 600 m.

On White Cay during May-July, 1997, Fry (2001) determined that iguanas may utilize even larger home ranges, with mean adaptive kernel estimates (at the 85% level) of 2,656 m^2 (N = 5 males and 2 females; the different estimator here was necessary because the number of resightings was small, ranging from 4-11). Because of the recent population crash, the iguanas on White Cay were in much lower density than on Green Cay or North Cay. Mitchell (1999) reported that home range size of *C. pinguis* expanded 100-fold following a decline in density on Anegada, and a similar effect may have been apparent on White Cay.

Reproduction. For *C. rileyi*, the mating season begins in May and continues into June. We observed 15 copulations by *C. r. nuchalis* on North Cay from 21 May to 9 June and 19 copulations by *C. r. rileyi* (with all but one observation from Green Cay) from 26 May to 16 June. Nest-digging begins the last week of June for *C. r. nuchalis* on North Cay (both 1998 and 1999) and the first week of July for *C. r. rileyi* on Green Cay (both 1999 and 2001). Oviposition occurs several days after the onset of excavation and continues for at least two weeks.

In Fall 2001 (October 2-10), we examined 12 nests from which hatchlings had recently emerged. Most nests were located by finding the small holes where the hatchlings had exited (Haneke, 1995). We observed hatchlings emerge from two nests with known oviposition dates, giving us incubation times of 91 and 92 days.

On both Green Cay and North Cay, females attain sexual maturity at approximately 20 cm SVL and 300 g (smallest gravid female before oviposition on Green Cay: 21.5 cm and 340 g; on North Cay: 19.5 cm and 260 g). We assume that males attain sexual maturity at a size similar to females or at a slightly larger size, as occurs in *C. c. carinata* (Iverson, 1979).

Our observations on both North Cay and Green Cay suggest that the mating system of *C. rileyi* is probably polygamous, with both males and females mating multiple partners. Repeat matings with the same partner are also observed frequently. Because of competition among males for access to females, mate-guarding (particularly by larger, territorial males) and forced copulation (particularly by smaller males) appear to be common strategies. Both forced copulation and female defense appear to increase as the mating season progresses. 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 a number of iguana taxa (Hayes et al., 2004). The duration of copulation is brief on North Cay, averaging 42.5 sec (SE = 5.5), with a range of 20-90 seconds (N = 13).

Nesting. 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 12 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. The females clearly passed through an abundance of potential nest sites as they moved to their final digging site. We assume that the advantages of these movements, perhaps related to outbreeding opportunities for their offspring, must outweigh the costs incurred. Nesting movements of up to 15 km have been reported in other iguanas (reviewed by Hayes et al., 2004), but such lengthy movements generally result from limited nesting habitat being distant from ideal foraging habitat.

The iguanas require loose substrate for nest-digging. On North Cay, nests were widely distributed on the island but excavation activities were more concentrated in beachfront sandy habitat than elsewhere (Thornton, 2000). On Green Cay, nests were also widely distributed, but the habitat was much rockier and nests were restricted to areas having loose sand and soil. However, some nests were constructed within rock crevices. Most nests were situated beneath an overlying rock such that the rock itself formed the ceiling of the egg chamber. On both cays, females often dug multiple burrows, abandoning those that encountered rocks or dense root masses underground.

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 13 burrows on North Cay; 60% of five burrows on

Green Cay) and in some (46% on North Cay) we detected multiple chambers. Total burrow length was longer on North Cay (69-235 cm, 0 = 129 cm, N = 13) than on Green Cay (30-116 cm, 0 = 53 cm, N =5). Egg-chamber depth (from ground surface above to floor of chamber) was similar on North Cay (14-40 cm, 0 = 22 cm, N = 13) and Green Cay (18-28 cm, 0 = 22 cm, N = 5). On Green Cay, vegetation cover above the five nests (judged from a densiometer mirror placed on the ground above the nest chamber) ranged from 0-18%. Additional densiometer readings above the estimated nest chamber placement (i.e. unexcavated nests, N = 23) averaged 19% and ranged from 0-82%.

Compared to 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 2-5 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 3-6 eggs (N = 5). A single clutch found on Low Cay contained 10 eggs, reflecting the large size of animals in this population, where most individuals exceed 30 cm snout-vent length.

Female defense of nests is widespread among iguanas and was exhibited by *C. rileyi* on both North Cay and Green Cay. Nest defense presumably mitigates the loss of eggs resulting from the digging activities of females that prefer to enter a burrow that has already been excavated. At least 36% of 14 females on North Cay exhibited nest defense, as did 82% of 22 females on Green Cay. Cyril (2001) determined that the mean nest density of iguanas on Green Cay exhibiting > 5 days defense (3.6 nests within 10 m radius) was significantly greater than those exhibiting $\leq$ 5 days defense (2.0 nests within 10 m radius; one-tailed t-test, P = 0.03).

CONSERVATION PRIORITIES

We have stated explicit conservation priorities elsewhere (Carter and Hayes, 2004), and will only summarize these here. In essence, we urge the implementation of conservation initiatives and new research foci that ideally will move *C. rileyi* from crisis management to full remediation and removal from the endangered species list. This task will require carefully prioritized planning, the cooperative efforts of many private and governmental entities, and must be data-driven. We suggest that a research-based approach to conservation is most beneficial in the long term and that *C. rileyi* can serve as a model species for developing conservation plans for other West Indian iguanas. Our priorities include the following recommendations.

<u>Clarification of systematic relationships</u>. We have argued, based on morphological data, that the three taxa represent, at a minimum, separate conservation management units (MU's) because of their genetic divergence and geographical isolation (Carter and Hayes, 2004). Whether they comprise evolutionarily significant units (ESU's) that represent full species remains to be clarified. Regardless of conservation designation or priority-setting criteria (such as maximizing preservation of genetic diversity; Malone et al., 2000), we must seek to conserve these lizards for their heuristic value and to protect the ecosystems that they depend on.

<u>Formal protection of existing populations</u>. We urge formal protection, preferably within a newly designated National Park, for the most threatened populations on White Cay (*C. r. cristata*) and San Salvador Island (*C. r. rileyi*). White Cay could be incorporated readily into an existing nearby park. A number of San Salvador's cays are Crown Land, which support not only endangered iguanas but also some of the largest and most species-rich seabird populations (Hayes, unpubl. data). Transfer of these cays to the National Park system would seem relatively straightforward.

<u>Continued research</u>. The basic biology of the organism—arguably the most important factor—is often the least appreciated and most neglected facet of recovery programs. Although our research has provided important and useful data on the biology of *C. rileyi*, we are far from fully understanding how iguanas interact with their en-

vironment. More research will be needed not only to benefit this species, but also to serve as a model for better understanding the conservation needs of other rock iguanas.

Invasive species control, habitat restoration, and monitoring. In spite of the lack of success for some of our efforts, invasive species remain a serious concern and habitats continue to deteriorate. Much more will need to be done.

Establishment of new populations. Reintroductions of iguanas in the form of relocation, repatriation, and translocation (RRT) programs represent a high priority of the West Indian iguana action plan proposed by the IUCN Iguana Specialist Group (Alberts, 2000). We recommend implementing such programs on behalf of all three taxa, but also urge that translocations be designed so as to experimentally evaluate several factors potentially important for success, including timing of translocation (e.g., before versus after the mating season) and under different conditions (into occupied and unoccupied habitats).

Establishment of captive headstarting programs. At present, headstarting programs have been established for a handful of West Indian iguanas (e.g., Alberts, 2000). For political and logistic reasons, no such program exists for any of the Bahamian species. Because of the success of headstarting programs with other iguanas, we strongly recommend that such programs be initiated specifically for *C. r. cristata* at a yet-to-be-determined facility and for *C. r. rileyi* at the Gerace Research Center on San Salvador Island. The latter institution is particularly well-suited for such a program. We anxiously await adequate funding to launch these programs.

Development and Implementation of Educational Programs. The success of our conservation programs will be measured ultimately by the degree to which the Bahamian people become invested in conservation activities, taking full ownership of the process of protecting and developing their national treasures. Clearly, local education will be essential to meet this goal.

ACKNOWLEDGMENTS

We are very much indebted to a host of individuals and institutions who have assisted or financially supported our work. Volunteers who assisted in the field, many at their own expense, included Mike Arct and Kathy Hayes, Pat Barry and Nico Barry-Yount, Sheila Brown, Sandra Buckner, Mike Cardwell, Linda Sturges Carney, Eric Chung, Jeff Francis and his family, Carl and Janet Fuhri, Danette Gallagher, Tim Haack, Jessica and Krista Hayes, Denise Heller, John and Sheila Iverson, Tom Lloyd, Charles Radcliffe, Scott and Ian Ray, Bryant Reynolds, Johnathan Rivera, and participants of the 1995 International Iguana Society Meeting. Graduate students Shawn Fry, Ben Thornton, Sam Cyril, Eric Grove, Roland Sosa, Neville Trimm, Naomi Balduff, and Jeremy Johnson rendered substantial help in the field. Local support, including boat transportation, was kindly provided or arranged by Kenneth Buchan, Don and Kathy Gerace, Dan Suchy, and Vince and Sandy Voegeli of the Gerace Research Center (San Salvador); Basil Minns, Raymond Sears, and Bailey Smith (Great Exuma); Cindy Bates, David and Nell Meadows, and Elwood Gibson (Crooked Island); and Sandra Buckner and Paul Harding (Nassau). Eric Carey and Maurice Isaacs, of the Bahamas Department of Agriculture, enthusiastically provided research permits and were always a delight to interact with. We thank especially Allison Alberts, Sandra Buckner, Don and Kathy Gerace, John Iverson, Charles Radcliffe, and Rich Reading for informative discussion, encouragement, and support. Funding was provided by out-of-pocket contributions, David Winters (donation of a boat motor), Southern Adventist University, Loma Linda University, the Denver Zoological Society, the Chicago Zoological Society, the Bahamas Department of Agriculture, and the Disney Foundation.

REFERENCES

Alberts, A. C., 2000, West Indian Iguanas: Status Survey and Conservation Action Plan: IUCN, Gland, UK.

Auffenberg, W., 1982a, Feeding strategy of the Caicos ground iguana, *Cyclura carinata*, *in* Burghardt, G. M. and Rand, A. S., eds., Iguanas of the World: Their Behavior, Ecology and Conservation: Noyes Publications, Park Ridge, New Jersey, p. 84-116.

Auffenberg, W., 1982b, Conservation of Bahamian rock iguanas (*Cyclura* sp.), Unpublished project report: U. S. Fish and Wildlife Service.

Breuil, M., 2000, Taxon reports: Lesser Antilles *Iguana delicatissima* and *Iguana iguana*: IUCN West Indian Iguana Specialist Group Newsletter, v. 3(2), p. 11-15.

Carter, R. L., and Hayes, W. K., 2004, Conservation of an endangered Bahamian rock iguana. II. Morphological variation and conservation priorities, *in* Alberts, A. C., Carter, R. L., Hayes, W. K., and Martins, E. P., eds., Biology and Conservation of Iguanas: University of California Press, Berkeley, in press.

Cyril, S., 2001, Behavioral ecology of the endangered San Salvador rock iguana (*Cyclura rileyi rileyi*) in the Bahamas. [M.S. thesis]: Loma Linda University, Loma Linda, CA.

Fry, S., 2001, Ecology of the endangered Sandy Cay rock iguana, *Cyclura rileyi cristata*, in the Bahamas, [M.S. thesis]: Loma Linda University, Loma Linda, CA.

Haneke, B., 1995, A study of Mona rock iguana (*Cyclura cornuta stejnegeri*) nesting sites on Mona Island, Puerto Rico: J. Internat. Iguana Soc., v. 4, p. 61-71.

Hartman, L., Gaston, A. J., and Eastman, D., 1997, Raccoon predation on ancient murrelets on East Limestone Island, British Columbia: J. Wildl. Mgmt., v. 61, p. 377-388.

Hayes, W. K., 2000, San Salvador iguana, *in* Alberts, A., ed., West Indian Iguanas: Status Survey and Conservation Action Plan: IUCN, Gland, UK., p. 56-58

Hayes, W. K., and Carter, R. L., 2000, Population monitoring. in Alberts, A., ed., West Indian Iguanas: Status Survey and Conservation Action Plan: IUCN, Gland, UK., p. 79-85.

Hayes, W. K., Carter, R. L., Cyril, S., and Thornton, B., 2004, Conservation of an endangered Bahamian rock iguana. I. Population assessments, habitat restoration, and behavioral ecology, *in* Alberts, A. C., Carter, R. L., Hayes, W. K., and Martins, E. P., eds., Biology and Conservation of Iguanas: University of California Press, Berkeley, in press.

Hayes, W. K., Carter, R. L., and Mitchell, N., 2000, Marking techniques, *in* Alberts, A., ed., West Indian Iguanas: Status Survey and Conservation Action Plan: IUCN, Gland, UK., p. 77-79.

Hayes, W. K., Hayes, D. M., Brouhard, D., Goodge, B., and Carter, R. L., 1995, Population status and conservation of the endangered San Salvador rock iguana, *Cyclura r. rileyi*: J. Intl. Iguana Soc., v. 4, p. 21-30.

Henderson, R. W., 1992, Consequences of predator introductions and habitat destruction on amphibians and reptiles in the post-Columbus West Indies, Carib. J. Sci., v. 28, p. 1-10.

Iverson, J. B., 1978, The impact of feral cats and dogs on a population of the West Indian rock iguana, *Cyclura carinata*: Biol. Conserv., v. 24, p. 63-73.

Iverson, J. B., 1979, Behavior and ecology of the rock iguana *Cyclura carinata*: Bull. Florida State Mus., v. 24, p. 175-358.

Knapp, C., 2001, Status of a translocated *Cyclura* iguana colony in the Bahamas: J. Herpetol., v. 35, p. 239-248.

Malone, C. L., Wheeler, T., Taylor, J. F., and Davis, S. K., 2000, Phylogeography of the Caribbean rock iguana (*Cyclura*): Implications for conservation and insights on the biogeographic history of the West Indies: Mol. Phyl. Evol., v. 17, p. 269-279.

Mitchell, N. C., 1999, Effect of introduced ungulates on density, dietary preference, home range, and physical condition of iguana (*Cyclura pinguis*) on Anegada: Herpetologica, v. 55, p. 7-17.

Patten, M. A., and P. Unitt., 2002., Diagnosability versus mean differences of sage sparrow subspecies: Auk, v. 119, p. 26-35.

Platt, S. G., Rainwater, T. R., Miller, B. W., and Miller, C. M., 2000, Notes on the mammals of Turneffe Atoll, Belize: Carib. J. Sci., v. 36, p. 166-168.

Schoener, T. W., Spiller, D. A., and Losos, J. B. 2001, Natural restoration of the species-area relation for a lizard after a hurricane: Science, v. 294, p. 1525-1528.

Thornton, B., 2000, Nesting ecology of the endangered Acklins Bight rock iguana, *Cyclura rileyi nuchalis*, in the Bahamas, [M.S. thesis]: Andrews University, Berrien Springs, MI.

Winter, J., Wing, E., and Newsome, L., 1999, *in* Winter, J. (Ed.), Proceedings of the 17th International Congress for Caribbean Archeology: Molloy College, Rockville Centre, New York, p. 197-210.

Table 1. Data for all populations of Cyclura rileyi cristata (Crc), C. r. nuchalis (Crn) *and* C. r. rileyi (Crr). *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 1994-1997. Population size is based on surveys taken during the period 1997-1998. Density and biomass are derived from population size (assuming 50% detectability, the lower end of ranges reported), area (ha) and mean mass (kg). A very small population on the main island of San Salvador could not be sampled. Data from Hayes et al. (2004).*

Taxon	Cay (location)	Area (ha)	Capture data				Population estimate	Density (N/ha)	Biomass (kg/ha)	Invasive fauna identified
			N	Males (%)	mass (kg)	SVL range (cm)				
Crc	White	14.9	61	0.95	0.403	10.2-28.0	136-204	9.1	3.7	Raccoon (erad), rats (erad), house mice (erad?)
Crn	Fish	73.9	49	0.51	0.459	9.0-31.4	9484-14226	128.3	58.9	House mice
	North	51.7	38	0.63	0.404	11.7-28.0	3036-4554	58.7	23.7	None known
	Transloc.	3.3	53	0.51	1.097	9.2-36.0	299	95.2	104.4	Rats?
Crr	Gaulin	1.6	3	0.66	0.650	22.8-25.8	extirpated 1999	–	–	*Cactoblastis* moth
	Goulding	2.9	13	0.38	0.562	15.7-31.0	116-174	40.0	22.5	None known
	Green	6.3	54	0.56	0.608	13.5-31.1	130-195	25.5	15.5	*Cactoblastis* moth
	Guana	1.6	5	0.40	0.665	12.1-35.2	30-45	18.8	12.5	Rats
	Low	10.8	13	0.77	1.481	26.3-39.5	42-63	3.9	5.8	Rats (erad), *Cactoblastis* moth
	Manhead	3.3	19	0.47	0.268	16.0-27.0	38-57	11.5	3.1	*Cactoblastis* moth
	Pigeon	7.8	15	0.33	0.665	12.5-31.0	70-105	9.0	13.5	Rats