

ECOLOGY AND CONSERVATION OF THE ANDROS IGUANA  
(*Cyclura cychlura cychlura*)

By

CHARLES R. KNAPP

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL  
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT  
OF THE REQUIREMENTS FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2005

Copyright 2005

by

Charles R. Knapp

This work is dedicated to my father and in loving memory of my mother.

## ACKNOWLEDGMENTS

Research on Andros would never have been possible without the contributions of many individuals, organizations, and philanthropic businesses. I wish to thank my committee (C. Kenneth Dodd, Jr.; Michael Moulton; Melvin Sunquist; Richard Franz; and Marianne Schmink) for their guidance and constructive comments. I also thank John Iverson, an ad hoc committee member, who provided valuable comments to the dissertation. The John G. Shedd Aquarium has been the largest benefactor of Andros Iguana research and their support is greatly appreciated. Financial assistance was made possible through the Shedd Aquarium and grants from the American Association of Zoos and Aquariums Conservation Endowment Fund, a Disney Research Fellowship, U.S. Fish and Wildlife Service International Conservation Fund, International Iguana Foundation, Chicago Zoological Society Board of Trade Endangered Species Fund, and the Chicago Herpetological Society. I thank the Bahamas Department of Agriculture for granting permission and research permits to conduct this study. Among many contributions, Mike and Petagay Hartman of Tiamo Resorts of South Andros have provided crucial logistical support and partial monetary prizes for the student contests. This research would never have succeeded without Tiamo Resorts and their staff.

I especially thank my field assistant, Audrey Owens, for her devotion to the project and making life in the bush bearable. Coleman Sheehy III stepped up and filled the role of field assistant in times of need. Maria Morera assisted greatly with designing the local interview questions and performing the ethnographic interviews. I also thank Heather

Tiszai and Joe Hoats for assisting in the field and providing logistical assistance on North Andros. John Bendon designed tee shirts, study area maps, and possessed passion for the project that rivaled my own. Sandra Buckner provided logistical and bureaucratic assistance throughout the entire study. I also thank the office staff in the Department of Wildlife Ecology and Conservation for all of their assistance throughout my graduate career. I thank the crew of the Shedd Aquarium's research vessel (Lou Roth, John Rothchild, and Charles Julian), who have been assisting beyond the call of duty for years. In addition, the volunteers participating in the John G. Shedd Aquarium research expeditions were responsible for discovering study sites and garnering large amounts of data in short time periods. Marinela Capanu provided statistical guidance and Kathleen Sullivan-Sealy, with the Coastal Ecology Project, provided satellite images. Rudi Scheffrahn identified the termites from South Andros Island. I also thank John Binns and Joel Friesch of the International Reptile Conservation Foundation for producing an invaluable conservation poster for the Andros iguana and tee shirts for the new Central Iguanas Football Club. This dissertation would never have been completed without the caffeinated mocha and work environment provided by Starbucks Coffee in downtown Gainesville.

I thank my family and friends for their steadfast support. Silvia Alvarez assisted with analyses and provided valuable comments on the dissertation. Most importantly, her love and encouragement in the difficult times kept me buoyant. Lastly, I thank my parents for giving me the tools to succeed and for their unconditional love and support.

## TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS .....	iv
LIST OF TABLES .....	ix
LIST OF FIGURES .....	x
ABSTRACT .....	xii
CHAPTER	
1 INTRODUCTION .....	1
2 HOME RANGE AND HABITAT ASSOCIATIONS OF A BAHAMIAN IGUANA: IMPLICATIONS FOR CONSERVATION .....	7
Introduction.....	7
Methods .....	8
Study Area and Habitat Delineations .....	8
Telemetry.....	10
Home Range Calculations .....	11
Habitat Association Analyses.....	12
Results.....	16
Home Range .....	16
Habitat Association .....	17
Discussion.....	18
Home Range .....	18
Habitat Association .....	20
3 OVIPOSITION OF THE ANDROS IGUANA ( <i>Cyclura cychlura cychlura</i> ) IN TERMITARIA .....	30
Introduction.....	30
Methods .....	32
Study Site.....	32
Field Data Collection.....	32
Statistical Analysis .....	35
Results.....	35
Pre-nesting Behavior .....	35

	Nesting Behavior .....	37
	Termitaria Excavation .....	38
	Oviposition and Back-Filling .....	39
	Defense .....	40
	Timing of Oviposition and Nest Location.....	41
	Termitarium and Internal Nest Characteristics.....	42
	Termitarium Fidelity .....	44
	Hatching Success.....	45
	Discussion.....	46
4	GEOGRAPHIC VARIATION IN NESTING BEHAVIOR AND REPRODUCTIVE BIOLOGY OF AN INSULAR IGUANA ( <i>Cyclura cychlura</i> ) ...	55
	Introduction.....	55
	Methods .....	58
	Study Species.....	58
	Study Sites.....	58
	Field Data Collection.....	59
	Statistical Analysis .....	60
	Results.....	61
	Variation in Reproductive Behavior.....	61
	Variation in Reproductive Traits .....	62
	Discussion.....	64
	Behavioral Variation .....	64
	Body-Size Variation.....	66
	Reproductive Life-History Variation .....	66
5	NEONATE SURVIVAL AND DISPERSAL OF AN INSULAR IGUANA: IMPLICATIONS FOR CONSERVATION .....	75
	Introduction.....	75
	Methods .....	76
	Results.....	80
	Discussion.....	82
6	POTENTIAL FOR IGUANA-BASED ECOTOURISM ON SOUTH ANDROS ISLAND, BAHAMAS.....	94
	Introduction.....	94
	Methods .....	99
	Tourist Surveys.....	99
	Local Interviews .....	99
	Results.....	101
	Tourist Profile and Attitudes .....	101
	Local Respondent Profile and Attitudes.....	102
	Discussion.....	104
	Tourism Potentials.....	104

Local Perception and Attitude .....	106
Conclusions .....	109
7 CONSERVATION RECOMMENDATIONS FOR THE ANDROS IGUANA.....	115
LIST OF REFERENCES.....	123
BIOGRAPHICAL SKETCH .....	140

## LIST OF TABLES

<u>Table</u>	<u>page</u>
2-1 Morphometrics, number of relocations, cumulative home ranges, and 50% and 95% Kernel home range Cole indices for the Andros iguana.....	23
2-2 Seasonal home range and overlap comparisons for male and female Andros iguanas. ....	24
2-3 Ranking matrix including t-statistics and (P-values) for pairwise comparisons of Andros iguana habitat. Final habitat row ranks included. ....	25
2-4 Plants eaten by <i>Cyclura cychlura cychlura</i> on Andros Island, Bahamas.....	26
2-4 Continued.....	27
3-1 Termite mound parameter means with standard deviations for mounds used and unused for nesting by the Andros iguana.....	51
3-2 Yearly ambient and iguana nest temperatures (°C) recorded from 6 June to 10 August on Andros Island. ....	52
3-3 Causes of individual egg mortality in nests by year for Andros iguanas. ....	52
4-1 Mean female reproductive and hatchling parameters for <i>C. cychlura cychlura</i> and <i>C. cychlura inornata</i> . ....	70
6-1 Demographic profiles and primary motivation for visitors to Andros Island. ....	111
6-2 Source of iguana awareness and willingness to pay for guided tours and national park entrance fees for visitors to Andros Island. ....	112

## LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1 Andros Island with highlighted study areas .....	28
2-2 Breeding and non-breeding seasonal minimum convex polygon home ranges for iguanas inhabiting Sandy Cay, Andros Island. ....	29
3-1 Daily temperatures from within two 2003 exemplar Andros iguana nests .....	53
3-2 Dorsal and lateral schematic views of representative termitaria used as oviposition sites by female Andros iguanas.....	54
4-1 Map of the Bahamas depicting the Great Bahama bank .....	71
4-2 Correlations of log scale clutch parameters with log snout-vent length.....	72
4-3 Correlations of log scale egg parameters and relative egg mass with log snout-vent length.....	73
4-4 Correlations of (A) log scale hatchling snout-vent length and (B) log hatchling body mass with log egg mass.....	74
5-1 Kaplan-Meier survival curves with 95% confidence intervals for Andros iguana hatchlings using combined 2003 and 2004 data. ....	89
5-2 Weekly fates of Andros iguana hatchlings with number of hatchlings confirmed killed per week by snakes species.....	90
5-3 Distance away from corresponding nests and fate of Andros iguana hatchlings surviving a minimum of 14 days. ....	91
5-4 Individual dispersal distances away from nests for Andros iguana hatchlings surviving a minimum of 14 days. ....	92
5-5 Histogram depicting habitat use for hatchling iguanas surviving a minimum of four days.....	93
6-1 Map of Andros Island, Bahamas depicting the three terrestrial protected areas of the Central Andros National Parks. ....	113

6-2 Age demography for the local respondents from Andros Island, Bahamas with relative attitudes towards exclusionary protected areas.....	114
7-1 Grayscale version of conservation poster for the Andros iguana that incorporates student murals in the lower left corner. ....	121
7-1 Soccer team tee shirts. ....	122

Abstract of Dissertation Presented to the Graduate School  
of the University of Florida in Partial Fulfillment of the  
Requirements for the Degree of Doctor of Philosophy

ECOLOGY AND CONSERVATION OF THE ANDROS IGUANA  
(*Cyclura cyclura cyclura*)

By

Charles R. Knapp

December 2005

Chair: C. Kenneth Dodd, Jr.

Major Department: Wildlife Ecology and Conservation

The Bahamian iguana (*Cyclura cyclura cyclura*) is a large, endangered lizard threatened by habitat loss, illegal hunting, and predation by feral animals. In order to formulate a science-based management and conservation strategy, I investigated iguana home range size, habitat use, reproductive ecology, and hatchling dispersal and survival on South Andros Island. I further investigated local resident and visitor perceptions of the iguanas and to potential national parks on the island. Home ranges were the largest reported to date for free-ranging *Cyclura* iguanas (30.58 ha for males, 5.63 ha for females). Telemetry results revealed that open pine was the only habitat type where iguanas occurred more than expected by chance. However, iguanas were found significantly closer to open pine and shrubland than to closed pine.

Andros iguanas were found to use termitaria as oviposition sites, a unique behavioral pattern among iguanid lizards. Andros iguanas selected nests nonrandomly with respect to termitarium height and surrounding soil depth; these variables had a

significant effect on the probability of a mound being used by an iguana. Oviposition in termitaria has important implications for iguana demographics and spacing, and must be considered in conservation planning. The probability of hatchling survival to 55 days post release was 0.15 or 0.25, depending on the model used. Mortality was greatest during the first two weeks post-hatching and resulted primarily from snake predation, a heretofore unrecognized selective factor. Hatchlings moved a median distance of 510 m from their nests (range 156–1090 m). Most hatchlings (> 53%) confirmed alive at the end of the study were relocated in mangroves; such areas may provide important, but previously undocumented, developmental habitats. Tourists were willing (89%) or somewhat willing (11%) to pay entrance fees into national parks; of these, 57% were willing to pay for guided iguana tours. Local residents were either supportive or cautious about establishing national parks, especially if the use of natural resources was excluded. Based on biological and human-dimension results from this study, management recommendations for long-term iguana conservation were formulated.

## CHAPTER 1 INTRODUCTION

West Indian iguanas of the genus *Cyclura* are a group of large, herbivorous lizards that inhabit islands throughout the Greater Antilles and the Bahamas. *Cyclura* iguanas are among the most endangered lizards in the world, with some taxa verging on extinction. Under the International Union for the Conservation of Nature (IUCN) criteria, all but four taxa are listed as either critical or endangered (Alberts, 2000). Threats include competition with and predation by feral animals, smuggling for the wildlife trade, subsistence hunting, and stochastic processes influenced by isolation, restricted ranges, and small population sizes. Of the West Indian iguanas categorized as endangered, the majority inhabit the Bahamas.

The Bahamian Andros iguana (*Cyclura cyclura cyclura*) is the largest native terrestrial vertebrate, and the only iguana (of 3 species, 7 subspecies) in the Bahamas, that is not confined presently to small cays. It is among the least-studied of the Bahamian species of iguanas and virtually no life history data are available. In addition, scientists have no indication of how many iguanas inhabit Andros, and arbitrarily estimated between 2500 and 5000 individuals for the IUCN West Indian Iguana Action Plan (Buckner and Blair 2000). Before 1999, the only information scientists could garner was that the Andros iguana faced particularly severe anthropogenic threats relative to other iguanas in the archipelago. These included habitat loss, illegal hunting, predation by feral animals (e.g., cats, dogs, and hogs), and impact from historic, large-scale, logging practices for Caribbean Pine (*Pinus caribaea* var. *bahamensis*), which destroyed large

tracts of iguana habitat in the 1960s and 70s. Recent accounts from the island presented grim scenarios featuring iguanas either already in cooking pots or in cages (J. Barichivich, S. Buckner, pers. communication). Some individuals were even discovered in a hunting camp with their arms and legs tied behind their backs and their mouths sewn shut (L. Roth, pers. communication).

Little regard has been given to the Andros Iguana by international conservation organizations, mainly because reliable life-history and population-trend data were lacking and no scientist was doing the necessary research. Walter Auffenberg initiated preliminary field expeditions in the early 1970s, but the surveys were short-lived and generated only cursory observations (see his field notes deposited in the Florida Museum of Natural History). The lack of field data on the life history of the Andros iguana is easily understandable. Andros is the fifth largest island (~ 165 km long by 65 km wide) in the West Indies; travel is expensive, and logistics are extremely difficult even to the accessible areas of the remote island. Andros actually is a composite of three main inhabited islands (North Andros, Mangrove Cay, and South Andros) and dozens of associated uninhabited cays separated by saline tidal channels termed bights. Except for North Andros, no roads extend beyond the eastern edge of the island making the remote interior accessible only by shallow-draft boats.

The Bahamas Department of Agriculture and Bahamas National Trust are responsible for protecting terrestrial biodiversity and maintaining the national park system, respectively. Both organizations are greatly interested in establishing protected areas on Andros Island, in part, to protect the iguana. Both organizations requested

assistance to study the iguana, identify areas of extraordinary biological richness, and incorporate local views into protected area boundary demarcation.

The goal of this project was to develop a multidisciplinary program for protecting the endangered Andros Island iguana using both ecological and human dimension-based methods. To accomplish this goal, research was conducted to evaluate present distribution patterns throughout the island and to collect data on the ecology, viability, and threats to isolated populations. Data from the ecological studies will ideally be incorporated into a science-based management program to help protect not only the iguana and its habitat, but also other species inhabiting the island. Local residents and tourists were interviewed to help gauge receptiveness towards establishing national parks to protect the iguana and generate revenue through responsible ecotourism. Although some iguana surveys were conducted on North Andros, the primary ecological investigations were conducted in the South Andros region because the area is characterized by large and small isolated cays accessible only by boat. These isolated cays are free from large feral mammals and not visited as frequently by humans as areas farther north (pers. observation). Therefore, studies were conducted in a relatively unaffected region of the island and prior to severe perturbations.

Adequate habitat is a primary requirement for survival of wildlife populations (Morrison et al., 1992), and the relationships between habitat and a species must be determined to develop management strategies, especially the demarcation of protected areas. Chapter 2 provides a detailed habitat association description of iguanas within their home ranges and in relation to the entire study area. These spacial data will be

incorporated into a science-based management strategy for the Andros iguana and may be applied to congeners throughout the West Indies.

The study of nest-site selection and nesting behavior is important when establishing conservation and management programs for endangered taxa that have obligatory, habitat-specific nesting requirements (Garcia et al., 2003; Troeng and Rankin, 2005). For example, iguanas of the genus *Cyclura* are characterized by a uniform nesting strategy of depositing eggs in subterranean chambers. However, the Andros iguana is the only iguanine that deviates from the standard nesting behavior through its use of termitaria as incubation chambers. A critical aspect of iguana conservation relies on knowledge of available nesting areas, the migration patterns to nest sites, and the behavioral mechanisms influencing nest-site selection. Chapter 3 examines the distribution and density patterns of termitaria to identify their effects on the nesting distribution of iguanas. Environmental variables influencing nest-site selection also are reported, along with movement patterns pre- and post-oviposition. Additionally, I describe this unique nesting behavior in detail because the nesting strategy for the Andros iguana is novel for any iguana.

Comparisons among geographically separated populations of wide-ranging species may be particularly useful in elucidating proximate and ultimate causes in the variation of behavioral and reproductive life history traits. Discerning mechanisms influencing variation in life-history traits, including behavior (Carroll and Corneli, 1999), are important to understand the ecology, adaptive responses, and factors limiting the distribution of species. The objective of Chapter 4 is to describe geographic variation in reproductive life histories and nesting behavior for two subspecies of the Bahamian

iguana (*C. c. cyclura* and *C. c. inornata*) inhabiting two distinct island systems varying in area, topography, and rainfall.

Distances traveled and the concomitant survival of juvenile animals during natal dispersal are factors that must be considered fully to understand the distribution, population dynamics, and implications of management practices on organisms (Johnson and Gaines, 1990; Ruckelshaus et al., 1997; Macdonald and Johnson, 2001; Berry et al., 2005). To date, the survival and dispersal behavior of free-ranging iguana hatchlings immediately post emergence is one of the least-studied aspects of their biology (but see Greene et al., 1978; Christian and Tracy, 1981; Drummond and Burghardt, 1982). This knowledge gap in hatchling survival is a crucial component that affects population dynamics and a variety of conservation efforts. Chapter 6 describes early survival patterns of Andros iguana hatchlings and quantifies dispersal distances away from corresponding nest sites. Results from this chapter may be applied to local management strategies and also to other endangered insular iguana species inhabiting large islands throughout the Caribbean and Pacific.

The success of most endangered species programs depends significantly on consideration of various human attitudes and values rather than just assessing biological elements. Wildlife ecologists/managers often ignore or view these social variables as marginally important when attempting to protect and recover species threatened with extinction (Clark, 1992). The major causes for this neglect include the biological and technical bias of most wildlife professionals, the difficulty of understanding and interpreting human behavior, and the political risks associated when attempting to manage socioeconomic and cultural factors (Kellert, 1994). Therefore, Chapter 6

addresses local perceptions of the Andros iguana, historic and contemporary hunting practices, and potential support for protected areas. The assessment of local responses toward protected areas, including knowledge, perceptions, attitudes, and expectations are viewed widely as a crucial step in achieving the goals of national parks. The chapter also addresses the possibility of establishing protected areas and promoting ecotourism using the Andros iguana as a flagship species. The willingness of tourists to pay for guide services and entrance fees into hypothetical national parks also was evaluated with the assumption that revenue generated from park fees could ultimately be directed back to conservation initiatives and park management.

Finally, recommendations are made in Chapter 7 that will ideally influence and guide management decisions designed to protect the Andros iguana. Examples of outreach programs, implemented while conducting this study, also are provided with suggestions for future programs.

CHAPTER 2  
HOME RANGE AND HABITAT ASSOCIATIONS OF A BAHAMIAN IGUANA:  
IMPLICATIONS FOR CONSERVATION

**Introduction**

West Indian rock iguanas of the genus *Cyclura* are among the most endangered lizards in the world, with some taxa verging on extinction (Alberts, 2000). The Bahamian Andros iguana (*Cyclura cyclura cyclura*) is the largest native terrestrial vertebrate, and the only iguana in the Bahamas that is presently not confined to small cays (Alberts, 2000). The lizards face unique anthropocentric pressures relative to other islands in the archipelago such as habitat loss, illegal hunting, and impacts from historic large-scale logging practices for Caribbean pine (*Pinus caribaea* var. *bahamensis*), which destroyed large tracts of iguana habitat in the 1960s and 70s for saw lumber and pulpwood (Little et al., 1976; Knapp et al., 1999). These deleterious effects have been compounded further by predation by feral animals (e.g., cats, dogs, and hogs). Consequently, the Andros iguana is listed as Endangered according to International Union for the Conservation of Nature (IUCN) Red List criteria (Knapp and Buckner, 2004) and also placed under Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES).

The Bahamas National Trust (BNT), the non-government organization mandated with managing national parks in the country, established protected areas on North Andros in 2002. Because no detailed ecological studies have been conducted on the endemic iguana, little input concerning habitat requirements was incorporated into delineating

protected area boundaries. Adequate habitat is a primary requirement for survival of wildlife populations (Morrison et al., 1992) and the relationships between habitat and a species must be determined to develop management strategies.

Currently, the BNT is pursuing the creation of protected areas in the South Andros area. The area is characterized by a closely linked mosaic of habitat types (Nickrent et al., 1988) thus facilitating habitat association studies across hierarchical selection levels (Johnson, 1980). Johnson's (1980) 2nd Order resource selection evaluates the selection of a home range within a study area or geographical range, whereas 3rd Order resource selection evaluates the importance of habitat components within the home range of an animal. Additionally, correlating temporal movement patterns with habitat use can provide detailed insights into a potential fluctuating continuum of behavior and improve understanding of the behavioral mechanisms motivating animals to use particular resources (Marzluff et al., 2001).

My objectives were to provide a detailed habitat association description across Johnson's (1980) 2nd and 3rd selection orders for iguanas inhabiting the South Andros area. I also present exploratory, temporally-referenced, spatial, organization data of iguanas studied in two distinct and biologically informative seasons. These space-use data will then be applied in a science-based management strategy for the Andros iguana and may be applied to congeners in the West Indies.

## **Methods**

### **Study Area and Habitat Delineations**

Andros is the largest island in the Bahamian archipelago (~ 165 km long by 65 km wide) encompassing an area of 5,959 km<sup>2</sup>, and supporting a human population between 7,000 and 8,000, concentrated along the eastern coast. This subtropical island is actually

a composite of three main islands (North Andros, Mangrove Cay, and South Andros), along with dozens of associated cays, separated by saline tidal channels termed bights. The substrate consists of oolitic and bioclastic limestone, subject to severe solution weathering (Sealey, 1994). Much of the low-relief island (~ 90% < 6 m above mean sea level) is punctuated with small cavities and large blue holes (vertical shafts with rounded surface features created by dissolution; Boardman and Carney, 2000).

Although ten plant communities have been recognized on Andros (Nickrent et al., 1988), this study was conducted in areas containing the four most prominent habitat types. Additionally, the extreme low-density population constrained me to use areas where enough iguanas could be captured and followed to facilitate analyses. Iguanas were radio-tracked in two locations from the South Andros area, Sandy and Mangrove Cays. Sandy Cay (310 ha; 24°05' 24"N; 77°41'44"W) is located in the South Bight of Andros, whereas the second study site is a tri-lobed peninsula (175 ha; 24°09'03"N; 77°43'30"W) extending from the south/southeast side of Mangrove Cay (Figure 2-1). Both areas are dominated by four main habitat types as defined by Sullivan-Sealey et al. (2002): pine woodland with open broadleaf understory (open pine; OP), pine woodland with closed broadleaf understory (closed pine; CP), dry evergreen shrubland (SH), and mangrove (MAN).

Predominant plants of open pine woodlands (< 60% canopy cover) include *Bumelia salicifolia*, *Cassytha filiformis*, *Erithalis fruticosa*, *Exostema caribaeum*, *Metopium toxiferum*, *Pinus caribaea* var. *bahamensis*, *Pithecellobium keyense*, *Savia bahamensis*, and *Thrinax morrisii*. Closed pine woodlands (> 60% canopy cover) are dominated by *Acacia choriophylla*, *Bourreria ovata*, *Bursera simaruba*, *Coccoloba diversifolia*,

*Eugenia confusa*, *Metopium toxiferum*, *Pinus caribaea* var. *bahamensis*, and *Randia aculeata*. Shrubland communities are represented primarily by *Bucida spinosa*, *Byrsonima lucida*, *Coccothrinax argentata*, *Erithalis fruticosa*, *Jacquinia keyensis*, *Manilkara bahamensis*, *Reynosa septentrionalis*, *Rhachicallis americana*, and *Strumfia maritima*. Mangrove community plants are generally short (< 1.5 m) and include *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, and *Rhizophora mangle*. Various karst limestone areas where mangroves occur remain above mean high tide levels, although their roots anchor in submerged solution holes. Throughout our study, thermal data loggers hung 1.5 m above the ground in indirect sun recorded a mean daily temperature of 29.5 °C (range 26.0–31.2°C).

### **Telemetry**

Adult iguanas were captured using fish-landing nets in May 2003 and a series of morphological measurements were recorded, including snout-vent length (SVL), tail length (TL), and body mass (BM) to the nearest 5 g. Sex was determined by cloacal probing for hemipenes. For visual identification at a distance, iguanas were marked by painting numbers on each lateral side of the body using white correction fluid and by affixing two colored 4 mm glass beads on each side of the nuchal crest using nylon coated stainless steel leader wire (Rodda et al., 1988). Eighteen iguanas (10 males, 8 females) were fitted with 14 g radio transmitters (Model F2050, Advanced Telemetry Systems, Isanti, MN, USA) using a modified suture technique to the posterior dorsal crest as described in Goodman (2005). While this sample size may be considered low for habitat use analysis, this is the longest telemetry investigation of *Cyclura* iguanas in natural habitats. Difficulties arise from the remoteness and severity of terrain, and subsequent difficulty in securing radio transmitters to lizards over multiple months.

I tracked the radio-tagged animals between 4 May and 10 October 2003. The study was divided into a breeding season (4 May to 3 July) and non-breeding season (1 August to 10 October) based on observed courtship and oviposition dates from the previous three years. Iguanas were tracked using a hand-held 3-element Yagi directional antenna and a Wildlife Materials, Inc. (Carbondale, IL, USA) TRX-48S receiver. The animals were located visually using telemetry during the day (0900 to 1830 h) at a mean interval of 2.8 days (range 1 to 7). I considered iguana positions to be independent since we recorded occasional movements greater than the diameter of the average home range in a 24-hour period (White and Garrott, 1990). After locating an iguana, I recorded the location using a WAAS-enabled Garmin® e-trex Legend GPS receiver with an accuracy of  $\pm 5$  m. In conjunction with location, I also recorded time, activity, and habitat association. Each animal was tracked for an average ( $\pm$  standard deviation) of  $48.9 \pm 13.2$  days in the breeding season and  $59.2 \pm 12.6$  days in the non-breeding season. Tracking ended when transmitters detached or were removed by my team at the end of the study.

### **Home Range Calculations**

I estimated cumulative and seasonal 100% minimum convex polygon (MCP; Jennrich and Turner 1969), and fixed kernel (Kernel; Worton, 1995) core 50% and 95% utilization distributions using the universal transverse-mercator coordinates from each animal relocation. Only animals with  $\geq 11$  relocations per season were used in the analysis. I made home range estimates using the Arcview GIS 3.2a and Spatial Analyst programs, and the Animal Movement Analysis Extension (Hooge et al., 1999). Default least-squares cross validation was used as the smoothing parameter for individual Kernel home ranges. MCPs were calculated to facilitate comparisons with past conspecific studies (Knapp, 2000) and future investigations (Perry and Garland, 2002), and to

delineate home range boundaries for generating random points for the habitat association investigation. I calculated the degree of home range overlap between lizards, and the seasonal stability of individual core 50% and 95% Kernel home ranges using the XTools extension (version 9/15/03) in Arcview. Seasonal stability was determined by calculating a Cole index for each animal:  $C\% = 100 \cdot 2AB/(A + B)$ , where A and B are the areas of consecutive home ranges and AB is the area in common to both periods (Cole, 1949). The value ranges between zero (no coincidence) and 100% (total coincidence).

For non-normal data, I applied the Box-Cox procedure to yield the optimal transformations to normality (all square root transformations in this study; Sokal and Rohlf, 1995). Percentage data were arcsine-square root transformed. The MCP, 50% and 95% Kernel home range variables were analyzed using two-way ANOVA with repeated measures to test the main and interaction effects of sex and season. Percentage of 95% Kernel home range overlap was analyzed for males only using one-way ANOVA with repeated measures. Cole indices were analyzed using one-way ANOVA. Simple effects were tested in the presence of significant interactions. I used Pearson product-moment correlations to test relationships between lizard morphometrics and cumulative home range sizes.

### **Habitat Association Analyses**

Understanding habitat selection is fundamentally important to elucidate the natural history of animals (Manly et al., 1993). Because of this importance, many techniques using nonparametric, multivariate, multiresponse permutation procedures, log log-linear modeling, logistic regression, and Euclidean distance methods have been devised and tested (see Alldredge and Ratti, 1986; 1992; McClean et al., 1998; Conner et al., 2002; Bingham and Brennan, 2004). In the last decade, compositional analysis (Aebischer et

al., 1993) has become one of the most popular habitat analysis procedures (Conner et al., 2002) because it (1) uses radio-marked animals as the sampling unit, (2) uses log-ratio transformations for habitat use and availability compositions to negate the potential problems on non-independence of proportional data, (3) permits hypothesis testing among meaningful groups (e.g., sexes or age classes), and (4) works at multiple scales.

Recently, compositional analysis has been criticized because of the need to arbitrarily modify the data by entering a value (usually 0.01 or 0.001) when no observations for some animals are recorded in available habitat types (Bingham and Brennan, 2004). This arbitrary procedure is required so that the log-ratio representing use of a habitat category can be calculated. Bingham and Brennan (2004) discovered inflated Type I error rates when arbitrary substitutions were made for 0% use of available habitat values. Consequently, the authors do not recommend using compositional analysis if some animals are not detected in available habitat, and also call into question the results of studies using an arbitrary substitution rate for non-used habitat values.

Conversely, the Euclidean distance approach (Conner and Plowman, 2001) of analyzing habitat use is virtually identical to compositional analysis regarding the multivariate nature of the analysis, but is not hampered by the unit-sum constraint of proportional data analysis (see Conner and Plowman, 2001; Conner et al., 2002 for additional benefits). The method involves simulating points randomly to estimate expected distances to selected habitat types. If habitat use occurs at random, the distances between observed animal locations and each habitat type should equal the distances between random points and the same habitat types. Additionally, the ratio of used distances to random distances for each habitat type should equal 1.0. If habitat use is

nonrandom, the ratios can be used to determine which habitats are used disproportionately. If the observed/random ratio is low ( $< 1.0$ ), the animal is associated with the habitat more than expected. If the same ratio is high ( $> 1.0$ ), the animal is associated with the habitat less than expected.

I used the Euclidean distance method after calculating home ranges for each iguana to detect annual nonrandom habitat use. Landstat 7 digitized images of both study areas were imported into Arcview GIS and polygons were constructed around each previously described habitat type. I then layered the MCP home ranges and radio telemetry relocations of each iguana over the habitat base map. To determine if iguanas selected for habitat types within their MCP home ranges (3rd order selection) I generated 500 locations randomly within the MCP boundary of each iguana ( $i$ ) using the Arcview animal movement extension (Hooge et al., 1999). For each lizard, I then computed the distance from each random point to the nearest representative of each habitat type. I calculated the average distance from random points to each habitat type to create a vector of mean distances ( $\mathbf{r}_i$ ) for each animal. This vector represents the vector of expected distances for the  $i$ th iguana. I performed the same procedure using observed animal locations to generate ( $\mathbf{u}_i$ ) for each iguana. This vector represents the average distance from every relocation for the  $i$ th iguana to each habitat type. I created a vector of ratios ( $\mathbf{d}_i$ ) for each iguana by dividing each element of  $\mathbf{u}_i$  by the corresponding element in  $\mathbf{r}_i$ . The expected value of each element in the  $\mathbf{d}_i$  is 1.0 under the null hypothesis of no selection.

I pooled  $\mathbf{d}_i$  data across both study areas because paired  $t$  tests failed to detect significant distance ratio differences to habitat types for our 3rd order (OP,  $P = 0.474$ ;

CP,  $P = 0.183$ ; SH,  $P = 0.422$ ; MAN,  $P = 0.158$ ) or 2nd order selection investigation (OP,  $P = 0.784$ ; CP,  $P = 0.717$ ; SH,  $P = 0.797$ ; MAN,  $P = 0.119$ ; M. Conner, pers.

communication). The mean of the  $\mathbf{di}$  was calculated as  $\mathbf{\rho}$  and multivariate analysis of variance (MANOVA) was used to determine if  $\mathbf{\rho}$  differed from a vector of 1's. A significant Wilks' lambda test statistic indicated nonrandom resource selection (Conner and Plowman, 2001). To determine which habitat types were used disproportionately, I tested each element within  $\mathbf{\rho}$  to determine if it differed from 1 using a paired t-test. If a statistically significant element in  $\mathbf{\rho}$  was  $< 1$ , or  $> 1$ , then the corresponding habitat was preferred or avoided, respectively. To test whether a particular habitat was selected significantly more than other habitats, I used pair-wise t-tests to compare relative habitat selection. These pair-wise tests provided a habitat-ranking matrix similar to the compositional analysis approach of Aebischer et al. (1993).

To determine if iguanas selected home range placement based on habitat types throughout the entire study area (2nd order selection), I performed the same analysis using the same random distance points within each MCP and compared them to distances calculated from 1000 randomly generated points throughout the study area. My study area for this habitat association investigation was delineated using the composite home range of all lizards. Since my sample size was reduced in the non-breeding season because of transmitter loss, I did not perform a Euclidean Distance analysis to detect seasonal trends but instead made exploratory inferences by examining seasonal home range orientation. All statistical tests in this study were analyzed using SAS (vers. 8, SAS Institute, Inc., Cary, NC, 1999). All means are presented with  $\pm$  standard deviation (S.D.) unless otherwise noted.

## Results

### Home Range

Transmitter loss reduced my sample size to 15 (8 males, 7 females) and ten (7 males, 3 females) iguanas during the breeding and non-breeding seasons, respectively. The MCP cumulative home-range estimator was correlated with both core ( $r = 0.766$ ,  $P = 0.001$ ) and 95% Kernel ( $r = 0.890$ ,  $P < 0.001$ ) estimates (Table 2-1). Males had larger cumulative home ranges than females, but neither male nor female morphometrics (SVL and BM) were correlated with MCP, 50 and 95% Kernel home-range estimators, or the Cole index of interseasonal stability (all  $> 0.05$ ).

My seasonal home range analysis (Table 2-2) revealed that MCP home range size differed only by sex ( $F_{1,13} = 15.98$ ,  $P = 0.001$ ) but not by season ( $F_{1,8} = 0.73$ ,  $P = 0.419$ ). No interaction between sex and season was detected ( $F_{1,8} = 1.37$ ,  $P = 0.275$ ). Core area (50%) Kernel home range estimates were similar in that they differed only by sex ( $F_{1,13} = 12.70$ ,  $P = 0.003$ ) but not by season ( $F_{1,8} = 0.12$ ,  $P = 0.742$ ), nor was an interaction between sex and season detected ( $F_{1,8} = 3.73$ ,  $P = 0.089$ ). The 95% Kernel estimates were significant for sex ( $F_{1,13} = 14.10$ ,  $P = 0.002$ ) but not for season ( $F_{1,8} = 0.00$ ,  $P = 0.989$ ). However, a significant interaction between sex and season was detected ( $F_{1,8} = 12.97$ ,  $P = 0.007$ ). Tests of the simple effects revealed that the 95% Kernel home ranges were larger for males in the breeding season than in the non-breeding season ( $t = 3.23$ ,  $P = 0.012$ ), whereas female home ranges appeared to increase in the non-breeding season, though not significantly ( $t = -2.16$ ,  $P = 0.062$ ).

The degree of home range overlap for males in this study is defined as the percentage of an individual's home range that is shared with lizards of the same sex (Knapp, 2000). Female home range overlap includes males since no telemetered females

had overlapping home ranges with other females. The degree of male home range overlap did not appear to differ significantly between seasons ( $F_{1,6} = 1.90$ ,  $P = 0.216$ ), yet an increased sample may suggest otherwise since home range overlap in the non-breeding season decreased between 2 and 49% (mean  $32.5 \pm 17.3\%$ ) for six of seven males. One enigmatic male increased his non-breeding home range and almost overlapped another lizard's home range entirely. Analyzing the data without this male revealed a significant decrease in male home range overlap during the non-breeding season ( $F_{1,5} = 40.41$ ,  $P = 0.001$ ).

The interseasonal stability (Cole index) percentages of core 50% and 95% Kernel home ranges suggest that iguanas expand or use different areas between seasons (Table 3-1). Stability of core (50% Kernel) home range areas for males averaged  $17.7 \pm 23.5\%$  (range 0.0–55.9%) and  $22.3 \pm 7.6\%$  (range 17.9–31.0%) for females. Male stability of 95% Kernel home ranges averaged  $45.9 \pm 20.4\%$  (range 10.6–70.5%) while females averaged  $31.9 \pm 12.4\%$  (range 21.5–45.7%). Neither 95% Kernel ( $F_{1,8} = 0.98$ ,  $P = 0.351$ ) nor core area ( $F_{1,8} = 0.66$ ,  $P = 0.439$ ) home range stability differed by sex.

### **Habitat Association**

The 3rd order selection analysis using Euclidean Distance indicated that habitat selection occurred within individual home ranges ( $F_{4,11} = 4.12$ ,  $P = 0.028$ ). Examining distances to habitat types indicated that iguanas were found closer to pine woodland with open broadleaf understory more ( $\rho_{\text{open pine}} = 0.798 \pm 0.07$  (mean  $\pm$  standard error),  $t = -2.76$ ,  $P = 0.015$ ) than expected. The data also suggest that iguanas avoided areas of pine woodland with closed broadleaf understory ( $\rho_{\text{closed pine}} = 1.312 \pm 0.15$ ,  $t = 2.14$ ,  $P = 0.05$ ). There were no significant differences in regard to observed and random distances to

shrubland ( $\rho_{\text{shrubland}} = 0.942 \pm 0.07$ ,  $t = -0.82$ ,  $P = 0.425$ ) or mangrove ( $\rho_{\text{mangrove}} = 1.156 \pm 0.16$ ,  $t = 0.99$ ,  $P = 0.337$ ).

A ranking of habitats based on the elemental values in  $\rho$  indicated that open pine areas were used more proportionately followed by shrubland, mangrove, and closed pine habitats. Pair-wise comparisons of distance ratios associated with habitat types indicated that iguanas were found significantly closer to open pine ( $P = 0.002$ ) and shrubland ( $P = 0.049$ ) than to closed pine. Proportional habitat use did not differ among other pair-wise comparisons (Table 2-3). Although iguanas appeared to be selecting habitat within respective home ranges, I found no evidence that iguanas were selecting where they established home ranges throughout the study sites (2nd order selection;  $F_{4,11} = 1.95$ ,  $P = 0.171$ ).

## Discussion

### Home Range

This study represents the longest telemetry investigation on a natural *Cyclura* population in the West Indies. Prior to this study, the largest *Cyclura* home range recorded from a natural population was for *C. pinguis* on Anegada Island, British Virgin Islands ( $\bar{\rho}$  mean = 8.2 ha, max. = 18.5; Mitchell, 1999). The relatively few studies that have attempted to estimate *Cyclura* home ranges were hampered with transmitter attachment failures and thus occurred only over limited time periods ranging from days to approximately four weeks (Wiewandt, 1977; Iverson, 1979; Goodyear and Lazell, 1994; Mitchell, 1999; Hayes et al., 2004). Accurate estimates should improve in the future as attachment technologies are refined and tested.

Home range estimates for the Andros iguana are considerably larger than previously published for natural populations of West Indian iguanas. An inadequate

number of relocation sightings via telemetry are most likely responsible for the low estimates on some islands (see Carey, 1975; Wiewandt, 1977; Goodyear and Lazell, 1994; Mitchell, 1999), or for other estimates this phenomenon is likely an artifact of island size and population density (see Knapp, 2000; Hayes et al., 2004). West Indian iguanas inhabit islands ranging from < 1 ha cays in the Bahamian Archipelago to the > 110,000 km<sup>2</sup> landmass of Cuba. On smaller islands iguana movements are constrained consequentially by island size and population density.

Andros Island contains one of the largest tracts of wilderness in the Caribbean region, thus allowing iguanas to regulate their spatial orientation via territorial behavior (Knapp, 2000). As expected for a territorial and polygynous lizard (Perry and Garland, 2002), males roamed over significantly larger core and 95% Kernel home range areas. Although home range size may be driven by multiple variables (Stamps and Buechner, 1985; Schoener, 1987), the data suggest that males expanded their home ranges during the breeding season, presumably in search of females (Carpenter, 1987; Baird et al., 2001; Figure 2-2). Although not significant statistically, larger home range areas resulted in increased overlap. The data suggest a masked trend because 95% Kernel home range overlap in the breeding season increased for six of seven males and was seasonally significant when an enigmatic male (MSC1) inhabiting a low-quality vegetated area was removed from the analysis. Contrary to breeding season estimates, no iguanas overlapped their core area home ranges in the non-breeding season (Table 2-2). The increase in home ranges and subsequent overlap also increased observed male intrasexual aggressive encounters in the breeding (n = 6) versus the non-breeding season (n = 2).

In contrast to male iguanas, nesting females in this study contracted their home ranges during the breeding season, which I attribute to nest site defense. Female Andros iguanas are the only iguanas documented to oviposit in active termite mounds (Chapter 3). Suitable nesting mounds are sparsely distributed and may be a limiting factor regulating population size. Consequently, females defended mounds vigorously from intrasexual conspecifics for up to 10 weeks. During the first two-weeks of nest defense, females rarely strayed more than 10 meters from defended mounds.

The low interseasonal stability (Cole index) percentages of male core ( $17.7 \pm 23.5\%$ ) and 95% Kernel ( $45.9 \pm 20.4\%$ ) home ranges are a result of interseasonal shifts in home range use. Four of seven males shifted entirely their core area of movement between seasons (Table 2-1). Three of these four males represented peripheral individuals inhabiting marginal mangrove habitats during the non-breeding season (Figure 2-2). I conclude that males seeking to mate expanded and shifted their activity ranges to include, or be closer to, open pine and adjacent scrub habitats. These habitats contained the majority (82%) of limited and suitable nesting sites for females (Chapter 4).

Although low core ( $22.3 \pm 7.6\%$ ) and 95% Kernel ( $31.9 \pm 12.4\%$ ) home range stability percentages were recorded for females, they exhibited a higher degree of philopatry than males. All breeding season core areas were incorporated into the non-breeding season ranges of nesting females but were eclipsed by a larger, expanded core area of use. However, data concerning home range philopatry are unavailable for non-nesting females.

### **Habitat Association**

Within iguana home ranges (3rd order selection), open pine was the only habitat type where iguanas occurred more than expected by chance. However, the pair-wise

comparisons of habitat types reveal that iguanas were found significantly closer to open pine and shrubland than to closed pine (Table 2-3). This result suggests that there is heterogeneity in habitat quality but that certain (e.g., submissive males) iguanas may rely on marginal habitats to survive. Bahamian open pine and shrubland habitats contain a productive array of terrestrial plant species compared to mangroves (Correll and Correll, 1982). Mangrove leaves also are typically regarded as a poor food source for herbivores (Skov and Hartnoll, 2002), thus perhaps driving expanded foraging bouts.

In closed pine habitats, foliage, fruits, and flowers of understory plants are higher (~ 2 m) from the ground and less productive than open pine habitats (Correll and Correll, 1982; pers. observation). Closed pine understory plants have relatively thin trunks, which cannot support the body mass of a climbing iguana. Thus iguanas are forced to feed on fruits and flowers that do not become lost in thin crevices or holes after falling to the ground. Finally, iguanas are ectothermic animals that require solar radiation to facilitate metabolic processes (Pough et al., 2001). Iguanas use thermoregulatory behavioral mechanisms that rely on optimal basking platforms adjacent to retreats (Alberts, 2000). The dense closed pine understory restricts light reaching the ground whereas sunlight is unlimited in the other described habitats.

I failed to uncover 2nd order selection of cumulative home range placement throughout our study areas. I attribute this result to herbivory, retreat requirements, and territorial behavior with subsequent spatial orientation. Andros iguanas consume a minimum of 44 plant species including mangrove representatives (Table 2-4). The capacity to consume plants from less productive areas facilitates the ability to use all representative habitat types. Suitable retreat sites are a requirement for all member of the

genus (Alberts, 2000) and are not limited on Andros because of the plethora of holes and splintered crevices created by dissolution of the limestone substratum. Thus regardless of habitat type, iguanas are never far from a suitable retreat site.

Although small sample sizes precluded my ability to analyze seasonal habitat choice, no habitat types were excluded from seasonal core areas. Females used core areas that included one or all of the following types- open pine, closed pine, and shrubland. Male core areas included at least one of all four-habitat types. Two males (MSC1 and MSC3) shifted entirely their core area, which included open pine and shrubland in the breeding season to predominantly mangrove in the non-breeding season. Consequently, those animals exhibited the two largest non-breeding season home ranges. Mangrove habitat is presumably less productive than the other three types and the lizards inhabiting these areas may be compensating for the lack of habitat quality with larger home range areas necessary to provide equivalent amounts of food energy (Iverson, 1979; Schoener, 1987).

Table 2-1. Morphometrics, number of relocations (n), cumulative home ranges, and 50% and 95% Kernel home range Cole indices for the Andros iguana.

Iguana	SVL (cm)	BM (kg)	n	MCP (ha)	50% Kernel (ha)	95% Kernel (ha)	50 Kernel Cole index (%)	95 Kernel Cole index (%)
MSC1	44.6	4.1	52	24.15	6.44	30.58	0.0	45.3
MSC2	42.5	2.8	58	11.76	2.47	13.43	28.2	53.6
MSC3	44.5	4.1	36	7.62	3.71	12.56	0.0	70.5
MSC4	46.2	3.9	55	5.35	0.68	5.00	55.9	65.3
MSC5	46.4	4.5	46	9.62	0.56	5.00	40.0	31.9
MMC1	49.4	4.8	52	18.02	1.35	8.58	0.1	43.9
MMC2	53.2	6.8	35	6.23	1.51	6.54	0.0	10.6
MMC3	55.0	7.3	11	5.94	2.36	7.12	—	—
<b>mean</b>	<b>47.7</b>	<b>4.8</b>	<b>43.1</b>	<b>11.08</b>	<b>2.38</b>	<b>11.53</b>	<b>17.7</b>	<b>45.9</b>
S.D.	4.43	1.52	15.5	6.72	1.94	8.22	23.5	20.4
FSC1	39.6	2.8	43	2.23	0.10	1.64	—	—
FSC2	36.1	1.8	57	0.74	0.03	0.42	17.9	28.6
FSC3	41.6	3.3	20	2.78	0.95	4.57	31.0	21.5
FSC4	38.5	1.1	15	1.14	0.34	1.63	—	—
FMC1	38.7	2.9	51	9.56	0.45	5.63	—	—
FMC2	41.6	3.2	22	0.81	0.17	1.40	17.9	45.7
FMC3	43.0	3.3	20	0.04	0.01	0.07	—	—
<b>mean</b>	<b>39.4</b>	<b>2.6</b>	<b>32.6</b>	<b>2.47</b>	<b>0.29</b>	<b>2.19</b>	<b>22.3</b>	<b>31.9</b>
S.D.	2.09	0.85	17.2	3.26	0.33	2.10	7.6	12.4

MSC and FSC = male and female Sandy Cay, respectively. MMC and FMC = male and female Mangrove Cay, respectively.

Table 2-2. Seasonal home range and overlap comparisons for male and female Andros iguanas.

Iguana	No. relocations	MCP (ha)	50% Kernel (ha)	95% Kernel (ha)	50 Kernel overlap (%)	95 Kernel overlap (%)
<u>Breeding season</u>						
Male (n = 8)						
<b>mean</b>	<b>16.9</b>	<b>6.87</b>	<b>1.70</b>	<b>11.26</b>	<b>2.7</b>	<b>45.5</b>
S.D.	3.7	1.98	0.74	5.18	4.6	23.8
range	(11–20)	(6.1–10.11)	(0.64–2.70)	(4.39–19.17)	(0.0–9.8)	(2.0–71.8)
Female (n = 7)						
<b>mean</b>	<b>19.3</b>	<b>1.94</b>	<b>0.31</b>	<b>1.72</b>	<b>2.4</b>	<b>58.5</b>
S.D.	2.2	2.67	0.35	1.76	4.5	36.2
range	(15–20)	(0.4–7.65)	(0.01–0.95)	(0.1–4.6)	(0.0–11.2)	(0.0–100.0)
<u>Non-breeding season</u>						
Male (n = 7)						
<b>mean</b>	<b>30.7</b>	<b>5.89</b>	<b>1.43</b>	<b>8.38</b>	<b>0.0</b>	<b>24.3</b>
S.D.	7.7	3.15	1.08	6.46	0.0	34.5
range	(16–38)	(2.24–10.93)	(0.19–2.96)	(2.30–21.36)	0.0	(3.9–99.9)
Female (n = 3)						
<b>mean</b>	<b>31.0</b>	<b>2.18</b>	<b>0.53</b>	<b>3.51</b>	<b>2.97</b>	<b>37.3</b>
S.D.	7.2	1.81	0.35	2.81	5.1	41.5
range	(23–37)	(0.64–4.16)	(0.13–0.77)	(0.91–6.49)	(0.0–8.9)	(12.1–85.2)

Table 2-3. Ranking matrix including t-statistics and (P-values) for pairwise comparisons of *Andros iguana* habitat. Final habitat row ranks included.

	Open pine	Closed pine	Shrubland	Mangrove	Final Rank
Open pine	—	-3.73 (0.002)	-1.33 (0.204)	-1.79 (0.096)	1
Closed pine	3.73 (0.002)	—	2.15 (0.049)	0.61 (0.553)	4
Shrubland	1.33 (0.204)	-2.15 (0.049)	—	-1.52 (0.151)	2
Mangrove	1.79 (0.096)	0.61 (0.553)	1.52 (0.151)	—	3

Table 2-4. Plants eaten by *Cyclura cyclura cyclura* on Andros Island, Bahamas.

Family name	Scientific name	Leaves	Flowers	Fruits
Aizoaceae	<i>Sesuvium portulacastrum</i>	●		
Anacardiaceae	<i>Metopium toxiferum</i>	●		●
Annonaceae	<i>Annona glabra</i>			●
Apocynaceae	<i>Angadenia sagraei</i>	●		
Apocynaceae	<i>Echites umbellata</i>		●	
Asteraceae	<i>Gundlachia corymbosa</i>	●		
Avicenniaceae	<i>Avicennia germinans</i>	●		
Bignoniaceae	<i>Tabebuia bahamensis</i>		●	
Burseraceae	<i>Bursera simaruba</i>	●		
Chrysobalanaceae	<i>Chrysobalanus icaco</i>			●
Combretaceae	<i>Conocarpus erectus</i>	●		●
Euphorbiaceae	<i>Euphorbia blodgettii</i>	●		
Euphorbiaceae	<i>Croton linearis</i>			●
Euphorbiaceae	<i>Dalechampia scandens</i>	●		
Euphorbiaceae	<i>Savia bahamensis</i>	●		●
Gramineae	—	●	●	
Lauraceae	<i>Cassytha filiformis</i>			●
Leguminosae	<i>Acacia choriophylla</i>	●		
Leguminosae	<i>Leucaena leucocephala</i>	●		
Malpighiaceae	<i>Byrsonima lucida</i>	●		●
Meliaceae	<i>Swietenia mahagoni</i>			●
Myrtaceae	<i>Myrcianthes fragrans</i>	●		
Myrtaceae	<i>Psidium longipes</i>			●
Nyctaginaceae	<i>Guapira discolor</i>		●	
Orchidaceae	<i>Cattleyopsis lindenii</i>			●
Palmae	<i>Thrinax morrisii</i>	●		●
Passifloraceae	<i>Passiflora bahamensis</i>			●
Polygonaceae	<i>Coccoloba diversifolia</i>			●
Rhamnaceae	<i>Auerodendron northropianum</i>	●		
Rhamnaceae	<i>Reynosia septentrionalis</i>	●		●
Rhizophoraceae	<i>Rhizophora mangle</i>	●		●
Rubiaceae	<i>Antirhea myrtifolia</i>			●
Rubiaceae	<i>Randia aculeata</i>	●		

Table 2-4. Continued.

Family name	Scientific name	Leaves	Flowers	Fruits
Rubiaceae	<i>Chiococca parvifolia</i>	●		●
Rubiaceae	<i>Erithalis fruticosa</i>	●		●
Rubiaceae	<i>Exostema caribacum</i>	●		●
Rubiaceae	<i>Psychotria ligustrifolia</i>	●		●
Rubiaceae	<i>Rhachicallis americana</i>	●		●
Rubiaceae	<i>Strumpfia maritima</i>	●		●
Sapotaceae	<i>Bumelia salicifolia</i>			●
Sapotaceae	<i>Manilkara bahamensis</i>			●
Sapotaceae	<i>Manilkara zapota</i>			●
Smilacaceae	<i>Smilax auriculata</i>	●		
Theophrastaceae	<i>Jacquinia keyensis</i>	●		

Family and scientific names *sensu* Correll and Correll (1982).

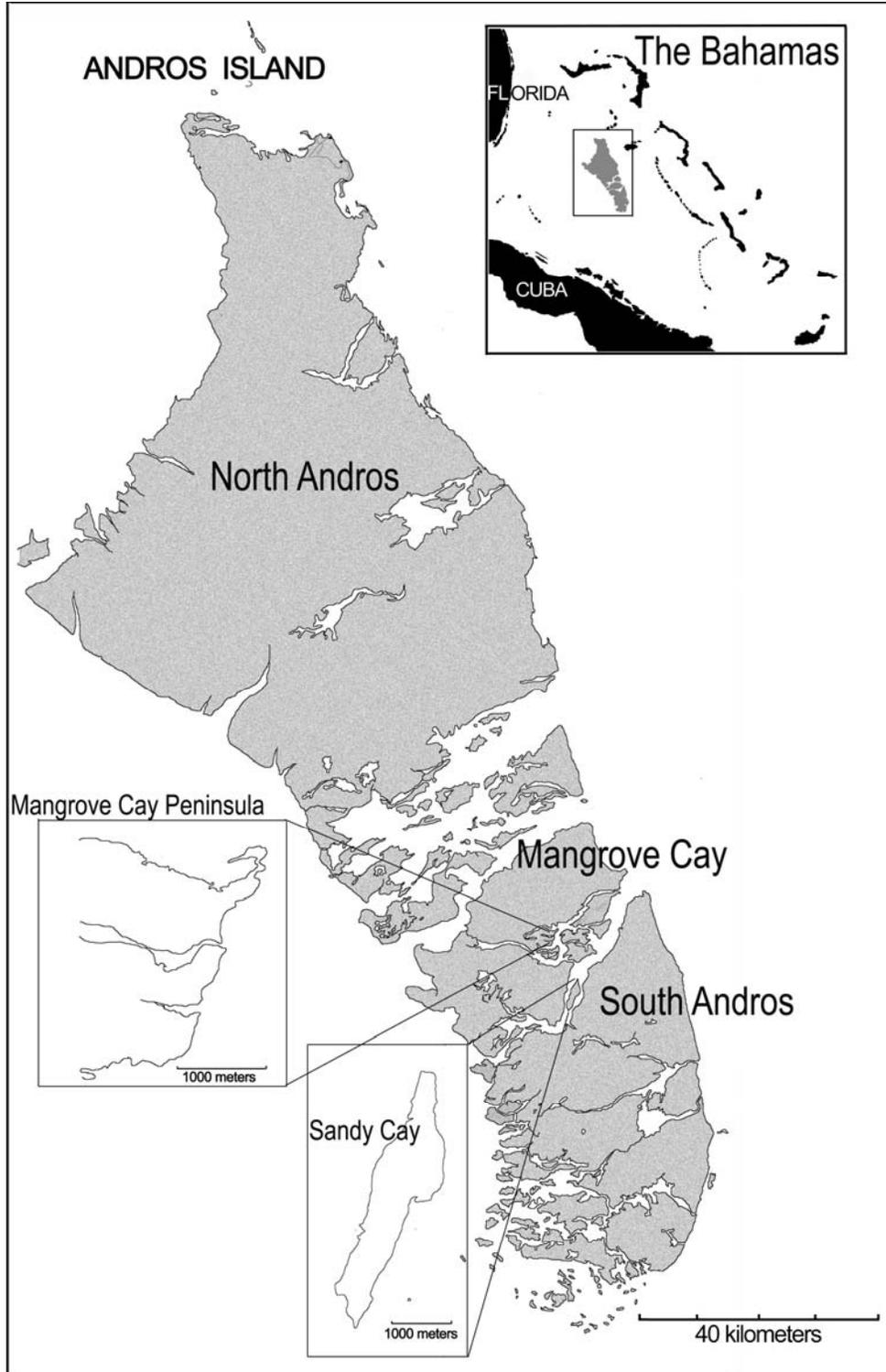


Figure 2-1. Andros Island with highlighted study areas that include Sandy Cay (310 ha) in the South Bight of Andros, and the tri-lobed peninsula (175 ha) extending from the south/southeast side of Mangrove Cay.



Figure 2-2. Breeding (A) and non-breeding (B) seasonal minimum convex polygon home ranges for male and female iguanas inhabiting Sandy Cay, Andros Island. Females FSC3 and FSC4 are excluded because non-breeding season data are absent. The depicted area is the composite of all home ranges used in the habitat selection analysis. Dark gray areas represent closed pine, shaded gray represent open pine, white areas indicate shrubland, and stippled areas represent mangrove.

CHAPTER 3  
OVIPOSITION OF THE ANDROS IGUANA (*Cyclura cyclura cyclura*)  
IN TERMITARIA

**Introduction**

The ecology of reproduction is a critical aspect of an organism's life history strategy and has received substantial scientific interest. Reproductive ecology studies in reptiles have focused primarily on reproductive investment (e.g., Andrews and Rand, 1974; Vitt and Congdon, 1978; Seigel and Fitch, 1984), reproductive costs (e.g., Madsen and Shine, 2000; Olsson et al., 2000; Olsson et al., 2001; Shine, 2003a, 2003b), physiological trade-offs between offspring size and number (e.g., Elgar and Heaphy, 1989; Sinervo, 1994), and functional and phylogenetic constraints on offspring size (e.g., Vitt and Congdon, 1978; Shine 1992). Nest-site selection and the behavioral mechanisms behind selection, however, has received considerably less attention, possibly because of the difficulty in observing nesting behavior in the wild (but see Burger, 1993; Madsen and Shine, 1999; Harlow and Taylor, 2000; Randriamahazo and Mori, 2001). Nest-site selection and associated behavioral studies are important because they have demonstrated that female choice can influence phenotype (e.g., Bull et al., 1988, Roosenburg, 1996; Reinhold, 1998; Deeming, 2004) and survival probability of offspring (e.g., Burger, 1993). Studies also have quantified the cost of reproduction associated with migration or exposure to predation risk during nesting forays (e.g., Parker and Brown, 1972; Madsen, 1987; Gibbs and Steen, 2005).

The study of nest-site selection and nesting behavior is also important when establishing conservation and management programs for endangered taxa that have obligate habitat-specific nesting requirements (e.g., Garcia et al., 2003; Troëng and Rankin, 2005). For example, iguanas of the genus *Cyclura* are characterized by relatively uniform nesting strategies on the islands they inhabit. These strategies include migration from normal activity centers to limited areas suitable for oviposition, construction of nesting burrows, and nest site defense (Wiewandt, 1982; Iverson et al., 2004a). The two most endangered species of *Cyclura* (*Cyclura collei* and *Cyclura lewisi*) nested historically along coastal areas of Jamaica and Grand Cayman (Lewis, 1944), respectively, but are now restricted to the island interior. The only two contemporary nesting sites known for *C. collei* were discovered in 1990 and consist of areas of only 12 m<sup>2</sup> and 60 m<sup>2</sup> (Vogel, 1994). No natural nesting areas on Grand Cayman are currently known (F. Burton, pers. communication). Consequently, a critical aspect of conservation for *Cyclura* iguanas relies on knowledge of available nesting areas, the migration patterns to nest sites, and the behavioral mechanisms influencing nest site selection.

The Bahamian Andros iguana (*Cyclura cychlura cychlura*) is the only iguanine that deviates from the standard nesting behavior model for the genus by its use of termitaria as incubation chambers. Only anecdotal accounts exist concerning this behavior (Wiewandt, 1982; Auffenburg, unpublished field notes), and nothing is known about the number of suitable oviposition sites, and the habitat and physical characteristics that influence the selection of nest sites in this species. Data on these and other aspects of the reproductive ecology of females are necessary for making informed decisions regarding its management and conservation. In this study, I examined the distribution and

density patterns of termitaria to identify their effects on the nesting distribution of iguanas. I also documented environmental variables for termitaria to elucidate factors influencing nest site selection. Pre- and post-oviposition movement patterns were also studied. Finally, because the nesting tactic for the Andros iguana is novel for any iguanid, I describe this unique nesting behavior in detail.

## **Methods**

### **Study Site**

Fieldwork was conducted in a southerly cross-island swath of area between Mangrove Cay (24°10'15"N) and Sandy Cay (24°05' 18"N). The majority of work was concentrated in three study locations- Sandy Cay, Linder Cay, and Mangrove Cay. Sandy Cay (310 ha; 24°05' 24"N, 77°41'44"W) is located in the South Bight of Andros and Linder Cay (1300 ha; 24°10'14"N, 77°41'40"W) is located in Lisbon Creek, South Andros area. Three main habitat types, including pine woodland, evergreen shrubland, and mangrove, characterize both areas. The third primary study site is a tri-lobed peninsula (175 ha; 24°09'03"N; 77°43'30"W) extending from the south/southeast side of Mangrove Cay. In addition to the three aforementioned plant communities, this location contains broadleaf forest and marsh habitats. Knapp and Owens (2004) provided descriptions of plant communities from each site.

### **Field Data Collection**

Preliminary field investigations began in May 2001, and April/May 2002. Based on observed courtship and oviposition dates from those two years, field work was concentrated in May/June and August/September 2003–04. Prior to the 2004 field season, termitaria used by nesting females were located primarily by searching all habitat types. Locating a termite mound was difficult initially, but once discovered, those currently in

use as iguana nests were conspicuous and easy to identify by the presence of old eggshells and/or a buttress of pine needles, leaf litter, and soil accumulation on one side of the mound. Females were usually in the area and when approached, aggressively held their ground instead of fleeing. Termitaria used by nesting females in 2003 and 2004 were also discovered while radio tracking females in conjunction with a concurrent habitat preference and home range study (see Chapter 2 for methods).

In 2004 (and to some extent in preceding years) I was able to monitor nest sites from previous years every 1 to 3 days to observe nesting behavior, verify oviposition dates, and document nest site fidelity. Based on the lack of defending females, and the characteristic substrate disturbance associated with nesting, I am confident that nesting did not occur before the May investigations. I am also confident that no nesting occurred after departing the island in 2003 (3 July), but I know of one nesting event after the 2004 departure date (13 June).

After discovering an iguana nest, attendant female iguanas were captured using fish-landing nets and a series of morphological measurements were recorded, including snout-vent length (SVL to the nearest mm), tail length (TL to the nearest mm), and body mass (BM in grams). Although female body mass was recorded primarily post oviposition ( $n = 27$ ), some females ( $n = 11$ ) were weighed from 2 to 7 days prior to nesting. Therefore, gravid body mass (GBM) for females recorded after egg deposition was estimated as post oviposition BM + associated clutch mass and was used in statistical analyses to facilitate comparisons with other studies (e.g., Iverson et al., 2004a). Implantable passive integrated transponder tags were injected beneath the epidermis on the right dorsolateral side directly anterior to the pelvis. For visual identification at a

distance, iguanas were marked by painting numbers on each lateral side of the body using white correction fluid and by affixing two colored 4 mm glass beads on each side of the nuchal crest using nylon coated stainless steel leader wire (Rodda et al., 1988).

I excavated nests and removed the eggs to record clutch size and condition, egg mass (to the nearest g), and egg length and width (to the nearest mm). With eggs removed and covered to prevent desiccation, I mapped the internal three-dimensional structure of the mound. When available, an Optic StowAway® temperature logger was reburied with the eggs inside the mound to record hourly incubation temperatures. Another temperature logger was deployed directly above the mound to record corresponding ambient air temperatures.

In 2003, I documented physical nest and surrounding vegetation parameters for each termite mound used as a nest as well as for mounds unused by nesting females. I recorded mound height (to the nearest cm) and circumference (to the nearest cm at the widest position). Skirt depth was recorded as the mean organic soil depth in front of the tunnel entrance at the base of the mound and at 15 cm away (to the nearest 0.5 cm). For unused mounds, I recorded skirt depth using the area with maximum deposition. A spherical densiometer was placed directly on top of mounds and four readings (at each cardinal direction) were taken to estimate percent canopy cover. Distance to the closest area with < 50% canopy cover was measured (to the nearest 0.5 m). The three nearest plant species also were recorded.

I returned to nests approximately 75 days post-oviposition to re-excavate and retrieve eggs or hatchlings. In some nests, all hatchlings were liberated completely from eggs and in the nest chamber. In others, a portion of the clutch had hatched and was free

in the nest, while the remaining eggs were still incubating. Eggs from partially hatched and un-pipped clutches were placed in plastic containers containing surrounding soil and carton from the mound, and incubated until hatching (1 to 7 days). Time to emergence from eggs after pipping (mean =  $1.9 \pm 0.7$  days, range 0 to 4, n = 68) and closure of the umbilical opening following emergence (mean =  $3.9 \pm 0.9$  days, range 3 to 6, n = 70) were used to estimate incubation times for nests found with hatchlings. When excavated, if the neonates had already hatched and emerged from the nest, eggshells and failed eggs were counted to determine hatching success.

### **Statistical Analysis**

I used logistic regression to model probability of termite mound usage by nesting female iguanas based on the five recorded parameters of mound height, circumference, soil skirt depth, canopy cover, and distance to nearest 50% canopy cover. I used stepwise selection with backward elimination to choose the best set of predictors. The dependent variable, mound usage, was a binomial response in all models. The final model was selected using likelihood ratio tests. Analyses of variance (ANOVA) and student t-tests were used to test for temperature differences among years and locations, and hatchling success among years. Least-squares linear regression was used to test for correlations between body size and date of oviposition and termite mound characteristics. Means are presented with  $\pm$  one standard deviation. Statistical tests were performed using SAS (vers. 8, SAS Institute, Inc., Cary, NC, 1999).

## **Results**

### **Pre-nesting Behavior**

Courtship occurred from the first week of April until the first week of May with one copulation event observed on 24 April 2005 (P. Hartman, pers. communication).

During this period, males were captured with high incidences of fresh lacerations seemingly due to male-male combat. Furthermore, in a South Andros study area, characterized subjectively by extremely low iguana densities ( $< 0.2$  iguanas/ha), male mate-guarding was observed by myself and colleagues in April 2002–2005 (P. Hartman, per. communication). One male was recorded following the same female continuously (as confirmed via radio telemetry) and sharing a nocturnal retreat. Although the nocturnal retreats changed between years, the guarding behavior of the same male to the same female remained consistent. Any approach by a rival male would cause the guarding attendant male to charge the intruder and give chase for long-distances (recorded up to 150 m). Mate-guarding was observed occasionally at other study sites suggesting facultative guarding behavior influenced potentially by iguana densities.

Females roamed large areas prior to oviposition, presumably in search of nest sites. Using radio telemetry, females in 2004 were recorded traveling up to 916 m in one day and roaming a mean area of  $12.48 \pm 4.69$  ha (95% Kernel estimator, range 6.7–19.8 ha,  $n = 4$ ) three-weeks prior to oviposition. These extensive movement patterns eclipsed those reported in the 2003 non-breeding season (95% Kernel estimator:  $3.51 \pm 2.81$  ha, range 0.91–6.49 ha,  $n = 3$ ; see Chapter 2). Within-year comparisons of 2003 females also demonstrate that movements two-weeks prior to oviposition (95% Kernel estimator:  $5.16 \pm 9.56$  ha, range 0.06–22.16 ha,  $n = 5$ ) were significantly greater than two-week post-oviposition movements ( $0.06 \pm 0.06$  ha, range 0.01–0.14 ha). Female iguanas were encountered making rapid movements crossing all four habitat types (closed pine, open pine, dry evergreen shrubland, mangrove; habitat parameters defined in Chapter 2) while apparently searching for suitable oviposition sites. In the month of May, females also

were noted swimming water channels and crossing mangrove areas prior to oviposition, presumably in search of suitable nest sites.

### **Nesting Behavior**

Although iguanines are fairly uniform in their nesting strategies (Wiewandt, 1982), the Andros iguana deviates from the standard model because of its use of termitaria as incubation chambers. Females predominantly use active *Nasutitermes rippertii* (Termitidae: Isoptera) termite mounds. However, two of 45 iguana nests recorded in this study (plus one old nest) were discovered in coarse sand consisting primarily of gastropod (*Batillaria* sp.) shell fragments. The sand nests were all located < 1 m above msl and under *Rhizophora mangle*, *Strumpfia maritima* bushes, or unidentified beach grass. Only nest-covering and defense were observed in these instances with identical behavior as described by Iverson et al. (2004a) for *C. c. inornata*, and I suspect that the entire sand-nesting episode mimics the behavior of that subspecies. One nest did not have a well-defined tunnel due to the non-compactable sand. The nest was primarily a chamber (28 cm wide x 8 cm high) with the eggs located 15 cm below the surface to the top of the chamber. The second nest consisted of a 52 cm long tunnel angling 90° at 15 cm and terminating in a chamber (9 cm wide x 10 cm high) 20 cm below the surface to top of the chamber.

For oviposition in termitaria, a general nesting pattern was documented based on a composite of observations from multiple females. I divided the nesting event into three phases: 1) excavating; 2) oviposition and back-filling; and 3) defense. I did not time individual phases specifically for fear of disturbing females engaged in nesting.

### **Termitaria Excavation**

The excavation technique of the Andros iguana differs from most documented varanid digging behavior (Auffenberg, 1994; Ehmann et al., 1991; King and Green, 1993 but see Cowles, 1930), which includes excavating an entrance tunnel from the upper lateral, or curved surface of the termite mound. Female Andros iguanas initiate digging at ground level but the tunnel can veer up or laterally depending on rock or wood obstructions within the mound. Females often performed test digs on several mounds, or on the mound eventually used for oviposition. A maximum of three exploratory holes were documented on a single mound, although the same tunnel entrances were used in 93% (13 of 14) of mounds that were used in consecutive years (regardless if by a different female). These repeated uses of the same tunnel entrances suggest that annual excavation may ease digging efforts in subsequent years.

Three to seven days prior to final excavation, females remained within 20 m of chosen termitaria. Once initiated, intermittent digging could last five days. Females scraped termitaria with their front claws and performed frequent tongue flicks on the mound and substrate. Loose carton (i.e., a construction material created by termites from partly chewed or digested woody tissue, salivary secretions, and feces) and soil was kicked out of the tunnel with backward thrusts of the female's arms, and then legs, once at the entrance opening. Excavating females were sometimes injured during the process and discovered with open puncture wounds on their backs, shoulders, or dewlaps caused by sticks embedded in the mound. Carton and substrate material from termitaria were displaced in an apron around the tunnel entrance and frequently contained empty egg shells from previous years. During excavation (and back-filling), curlytail lizards (*Leiocephalus carinatus*) and brown anoles (*Anolis sagrei*) often gravitated to termitaria

and consumed defending termite soldiers from mound surfaces or from the backs of iguanas.

Usually, tunnels were only of sufficient diameter to allow females access into the mound without the ability to turn around. However, in three instances I documented females excavating a chamber large enough to enter and disappear completely. At times, iguanas remained overnight, and also excavated from within the mound. The within-mound excavations were sometimes extreme and iguanas were observed breaking through lateral or upper surfaces. One of these females oviposited five-days later in coarse sand 400 m away from the damaged mound. Forceful digging may be responsible for the destruction of termite colonies by removal of the queen because 13% (6 of 45) of termitaria documented as used in 2002 and 2003 were without termites in 2004. Additionally, two inactive termite mounds were found with eggshells in the crumbling carton.

### **Oviposition and Back-Filling**

I was unable to observe an oviposition event from the onset and therefore unable to report precise timing. However, oviposition and egg placement in termitaria appears unique compared with other reptiles. Instead of depositing eggs directly into termitaria (King and Green, 1993), female iguanas oviposited at the tunnel entrance and subsequently pushed eggs into the central mound chamber. Pushing was performed using alternating rapid thrusts of the forelimbs and prodding with the snout. Loose soil and carton were pushed along with the eggs into a central chamber within the mound leaving a pocket of air above the eggs. While eggs were pushed into the mound, females intermittently packed the tunnel by bracing with their hind legs and thrusting their head and snout into the plug, at times causing the snout to bleed. When the eggs were no

longer visible from the outside, females turned from the mound and scratched substrate toward the entrance using alternating movements of the forearms followed by reciprocal movements of the back legs. Back-fill material consisted of carton from termitaria, associated soil, pine needles, twigs, leaf litter, palm fronds, and limestone fragments (ranging up to 14 cm in diameter) from the surrounding area. Scratching and kicking of the surrounding substrate was alternated with packing the tunnel. Females often patrolled the perimeter of the mound and plugged any holes if present. Back-filling would continue (for up to five hours) until there was a large buttress of aforementioned material piled against the side of the mound. The affected termite colonies usually encapsulated the chamber and repaired the tunnel after one-week. In large clutches  $> 9$  eggs, peripheral eggs are sometimes encased and incorporated into the existing structure. Depending on placement within the mound, entire clutches  $< 9$  eggs are sometimes encased. In some instances, the tunnel opening was not repaired by the colony but remained occluded with the nest back-fill.

Since eggs are vulnerable to desiccation and predators while exposed outside the mound, I suspect that back-filling of the tunnel is completed the same day eggs are oviposited, as observed similarly for the varanid *Varanus gouldii rosenbergi* (King and Green, 1979). Back-filling was always observed in the morning (as early as 0930 h EST) or early afternoon, suggesting that oviposition occurs in the morning.

### **Defense**

Females are aggressive and protective of their mounds pre- and post-oviposition. On numerous occasions, females charged and chased approaching females for long distances if the latter ventured within 10 m of their termite mound. In cases where females were of equal size, I observed head-bobs and open-mouthed face-offs with lateral

head pushing similar as reported elsewhere (Wiewandt, 1977; Iverson, 1979). In these cases, the resident iguana drove the intruder from the mound. However, on two occasions prior to oviposition, but after initiating digging and defense, iguanas were driven from their mounds by larger females. Another iguana, defending a nest that had been destroyed by crabs, was driven off by a same-sized individual, which eventually nested in the mound.

Although the usual female defense behavior toward human observers consisted of approach and head-bobbing, the behavior ranged from passive observation under the protection of vegetation to head-bobbing, hissing, charging, and biting of boots. Females normally remained in the area of the nest for six weeks (max. = 12.5) following oviposition and often would stay perched on top, or within three meters of the nest mound. Iguanas with nests were observed on top of termitaria during thunderstorms. At night attendant females would retreat to adjacent limestone crevices or under vegetation. Near the time of hatchling emergence, 23% (9 of 40) of nesting females were still in the immediate area of their nest and approached the termitarium while I investigated the mound. In these cases, aggression was normally subdued, although some females still actively charged, perched atop the mound, and performed head-bob displays. One female is suspected to have removed nesting back-fill from the entrance of her nest burrow at the time of hatchling emergence (see discussion).

### **Timing of Oviposition and Nest Location**

Nesting females averaged  $38.7 \pm 4.2$  cm SVL (range 31.0 to 47.7 cm,  $n = 32$ ) and  $3006 \pm 1185$  g GBM (range 1279 to 6657,  $n = 31$ ). Iguanas initiated nest excavation and deposited eggs in early May. The first nests discovered in 2001, 2002, 2003, and 2004 were on 12, 8, 10, and 8 May, respectively. In all cases, iguanas most likely oviposited

one or two days prior to discovery. The earliest nest discovered in 2003 and 2004 were from the same female. I was able to remain on the island throughout the nesting season in 2003 and recorded nesting events from 10 May to 13 June (mean = 30 May, median = 3 June,  $n = 9$ ). Other nests were found serendipitously after 13 June 2003 but an exact oviposition date could not be verified. I was able to monitor nests for oviposition more accurately in 2004 but only remained on the island until 12 June. I recorded 2004 nesting events from 8 May to 12 June (mean = 29 May, median = 31 May,  $n = 21$ ) but I am aware one mound that was used for nesting after I left the island. Date of oviposition was not related to SVL in 2003 ( $r = -0.08$ ,  $P = 0.84$ ,  $n = 9$ ) or 2004 ( $r = -0.37$ ,  $P = 0.27$ ,  $n = 11$ ).

Nests were located primarily in open pine habitats (46%) followed by dry evergreen shrubland (36%) and closed pine (18%; habitat parameters defined in Chapter 3). Twenty-two plant species were recorded < 1 m from termitaria with the most frequent species being *Metopium toxiferum*, *Thrinax morrisii*, and *Savia bahamensis* (20, 13, and 12% of termitaria, respectively). The association of termitaria and vegetation was responsible for extremely high percentages of canopy cover over nests (mean =  $72 \pm 20\%$ , range = 28 to 96%,  $n = 30$ ).

### **Termitarium and Internal Nest Characteristics**

The logistic regression results for indicate that there was a significant relationship between termite mound usage and recorded parameters (Table 3-1). Based on likelihood tests, only the parameters of height, circumference, and soil skirt depth were used in the final odds ratio model. Height and skirt depth had a significant effect on the probability of a mound being used by an iguana (Table 3-1). With the other factors fixed, a one-centimeter increase in mound height decreased the estimated probability of mound usage

by 0.855 (95% Wald Confidence Limits = 0.747, 0.979) while a one-centimeter increase in soil depth increased the estimated probability of mound usage by 2.38 (95% Wald Confidence Limits = 1.061, 5.355).

Thermal loggers within and above nests from 6 June to 10 August recorded uniform temperatures between years (Table 4-2). Mean daily ambient temperatures above termitaria were not significantly different between 2003 and 2004 ( $t = 0.06$ ,  $P = 0.96$ ). Likewise, mean daily nest temperatures were not significantly different among years 2002–2004 ( $F_{2,13} = 0.03$ ,  $P = 0.97$ ). Combined mean daily temperatures were significantly greater in nests than ambient temperatures (unequal variance  $t = 60.13$ ,  $P < 0.0001$ ). Nest temperatures also experienced less fluctuation than ambient temperatures (Figure 3-1) both within and among years combined (Levene homogeneity-of-variance test,  $F > 5150.2$ ,  $P < 0.0001$ ). Combined nest temperatures were not correlated with percent cover ( $r = -0.32$ ,  $P = 0.40$ ,  $n = 16$ ) or mound circumference ( $r = 0.11$ ,  $P = 0.77$ ,  $n = 16$ ). Mean incubation temperature for the one recorded sand nest was  $30.8 \pm 1.5$  °C.

Termitaria used as incubation chambers ranged from 23.0 to 71.0 cm in height ( $n = 25$ ) and 55.0 to 214.0 cm in circumference ( $n = 25$ ; Table 3-1). Excavated tunnel entrances in termitaria averaged  $8.3 \pm 1.6$  cm in height (6 to 11 cm,  $n = 19$ ) and  $14.9 \pm 2.9$  cm in width (12 to 23 cm,  $n = 19$ ). Body size was not correlated with entrance height (for SVL,  $r = -0.12$ ,  $P = 0.63$ ; for BM,  $r = 0.25$ ,  $P = 0.31$ ) or width (for SVL,  $r = -0.23$ ,  $P = 0.35$ ; for BM,  $r = -0.34$ ,  $P = 0.16$ ). There was also no correlation between body size and termite mound circumference (for SVL,  $r = -0.13$ ,  $P = 0.50$ ,  $n = 30$ ; for BM,  $r = -0.13$ ,  $P = 0.51$ ,  $n = 30$ ). Tunnel structure was highly variable and depended on the internal characteristics of the mound (Fig. 3-2). In some cases, limestone slabs, tree

trunks, or branches obstructed tunnels forcing females to excavate a diverse array of tunnel trajectories ranging from multiple lateral bends to upward pathways. Regardless of the tunnel shape, the eggs were pushed into a wider chamber (usually the hollowed natural chamber of the mound). There was always an initial air pocket over the eggs but some eggs eventually became encased by the working termite colony depending on the clutch location within the chamber. Egg incubation length in 2004 averaged  $76.3 \pm 3.5$  days (range 72 to 82 days,  $n = 12$ ). Incubation lengths for the two nests recorded reliably in 2003 were both 72 days.

### **Termitarium Fidelity**

Eighty percent (12 of 15) of termitaria that were used for nesting from 2001 to 2003, and still supported active termite colonies, also were used in 2004. Repeat mound use may have been higher, however, because one of the previously-used termitaria was damaged in 2004 by an overly aggressive excavating female. Another mound was the smallest recorded in the study and was used by the smallest nesting female in 2003. Fifty percent (6 of 12) of consecutive-year nests in termitaria were used by the same female. The other mounds were used by different females in each year. Three nesting females from 2003 that nested in 2004 used different sites (up to 300 m away from previous sites), because the mounds were inactive, defended by a larger female, or damaged while excavating.

At least for some locations, population growth rate in Andros iguanas may be limited by availability of nest sites. In 2004, there were 10 active termitaria (0.147 per ha) within my concentrated study area (68 ha) on north Sandy Cay, of which nine were used by nesting iguanas (90%). One mound was used twice after the defending female was forced from her mound (although the eggs were destroyed earlier by crabs). Three of the

six total active mounds (50%) observed on Sandy Cay in 2003 were used by the same females in 2004. Other nesting options do not exist in the area, which is characterized by an extreme lack of soil or sand. Therefore, females either migrate to other areas, or alternate nesting years as documented in *C. c. inornata* (Iverson et al., 2004a) and this study. For example, two adult females (SVL 38.5 and 41.6 cm) from Sandy Cay telemetered in 2003 did not nest prior or by 3 July when I left the island.

The other two concentrated study areas on Linder and Mangrove (65 ha) Cays had concentrations of termitaria per hectare of 0.875 and 0.292 per ha, respectively. Five of seven (71.4%) termitaria documented from the Linder Cay site (8 ha) were used by nesting females in 2003 and 2004. Two of the termitaria were used by the same respective females in 2003 and 2004. At the Mangrove Cay site (65 ha), three of 19 (15.8%) mounds documented in 2004 were used. Some of these termitaria were associated with depths of surrounding soil suitable for nesting, suggesting that iguana densities are either lower than at the other study locations or that females are using the limited shallow sand areas adjacent to the water edge. However, only two active sand nests have been found with three years of search effort on Mangrove Cay.

### **Hatching Success**

I documented hatching in 2003 from 3 August to 2 September and from 4 to 30 August in 2004. Mean hatching success for clutches was 100% (n = 2), 75.2% (n = 15), and 69.9% (n = 17) in 2002, 2003, and 2004, respectively, and did not differ significantly among years ( $F_{2,31} = 0.59$ ,  $P = 0.56$ ). Hatching success > 75% for all years combined was independent of habitat type ( $\chi^2 = 1.29$ ,  $P = 0.52$ ). Hatchling success for the two 2004 nests deposited in sand was 100 and 69%. Clutch mortality in 2003 and 2004 ranged from 0 to 100%. Egg mortality occurred because eggs were flaccid and died immediately after

oviposition, desiccated during development, ruptured by the nesting female, attacked by fungus, flooded (one mound nest located adjacent to a tidally-flooded mangrove), depredated by crabs (*Cardisoma guanhumi*), or removed from their nests (presumably by crabs; Table 3-3).

### **Discussion**

Andros iguanas selected nest sites nonrandomly with respect to termitarium height and soil skirt depth. Termitaria used as iguana nest sites were not as tall as those not used (Table 3-1), however, this may be an artifact of use rather than a selection choice by iguanas. A typical defense position for females is resting on top of termitaria. The annual movement of iguanas on and off termitaria continually for up to 12 weeks post-oviposition may reduce the height because of scratching involved when climbing up the side and while on top of the mound. Although not significant in the final logistic regression model, the circumference of used termitaria also is less relative to the unused mounds (Table 3.1), which may reflect the same artifact of iguana movement patterns.

Andros iguanas selected termitaria that were associated with more surrounding soil relative to the unused mounds (Table 3-1). Soil is required to back-fill the nest tunnel and construct the buttress of material over the entrance. The overall lack of soil associated with Andros Island is evident; the mean soil depth surrounding termitaria used as oviposition sites, which are areas with the most soil accumulation, was < 6 cm to the limestone substratum. The selection process for suitable termitaria is likely an instinctive trait that also is plastic because of the inconsistent availability of termitaria. As demonstrated in this study, at least three females were forced to relocate from nests used in the previous year. Most secondary nests were less than 400 m from the previously-used termitarium and one of the nests was excavated in sand.

How *Varanus* hatchlings emerge through the gallery walls of termitaria has been mostly conjecture. Cowles (1930) speculated that leakage of amniotic fluids soften the termite galleries and allow hatchlings to escape via a “chimney” excavated up to the top of the mound. It also has been reported that certain female *Varanus* lizards return to their termitarium nest during the period of hatchling emergence presumably to assist in liberating the young from the mound (Cogger, 1967; Ehmann et al., 1991). During an unrelated hatchling telemetry study, I documented conspicuous squeaking noises from hatchling iguanas from two clutches in 2003 and two in 2004. I returned the next day after placing and reburying the hatchlings from one of the 2004 clutches into their corresponding termitaria and discovered the adult female (confirmed with identification beads) adjacent to the mound. The female did not flee upon my approach and telemetry confirmed that the hatchlings were still in the mound. I examined the tunnel entrance and it appeared as if the buttress of soil and limestone fragments were moved away from the outside to such an extent that it implied a larger animal was responsible. All the hatchlings eventually left the mound from the tunnel opening. Although I cannot confirm that the female liberated the hatchlings, this behavior should be furthered studied.

The propensity for using termitaria for oviposition sites appears to be well established for lizards in the genus *Varanus* (e.g., Cowles, 1928; Ehmann et al, 1991; King and Green, 1993; Auffenburg, 1994) but also occurs in other reptilian (see reviews in Riley et al., 1985) and avian taxa (e.g., Weaver, 1982; Reed and Tidemann, 1994). A purported benefit of using termitaria for brood incubation is protection from predators (Riley et al., 1985). In this study, crab predation appeared to impact clutch survivorship more than most factors, especially if missing eggs are pooled in the crab predation

category (Table 3-3). I have observed crabs returning to a nest on consecutive nights and removing one or two eggs at a time until the clutch was depleted. Although not quantified, Andros is well known for its abundance of crabs (*C. guanhumi* and *Gecarcinus lateralis*) that are observed frequently in the crepuscular hours or in the shade of closed pine forests during the day. Unfortunately, sample sizes were too small to compare crab predation rates between clutches deposited within termitaria and in the few areas of sand.

Termites are well known for their ability to regulate the environmental conditions of their nests (Korb and Linsenmair, 2000) and studies pertaining to termitaria use by reptiles have focused primarily on the thermal and humidity advantages associated with selecting those sites for oviposition. The Andros iguana uses only active termite mounds and apparently gains similar temperature and humidity benefits for the eggs as described in other studies (see Riley et al., 1985). A thermal data logger placed within a 2003 inactive termite mound demonstrates the ability for the colony to regulate nest temperatures. The mean temperature for the inactive mound was only  $29.1 \pm 1.4$  °C compared to  $32.6 \pm 1.2$  °C for combined 2003 active termitaria nests (Table 3-2). The elevated temperatures of termite nests, rather than variation in temperature, may have a larger influence on nest site selection because the variation in temperature of the 2003 inactive (and unused) mound (S.D. = 1.4 °C) was actually less than that of the 2004 sand nest ( $30.8 \pm 1.5$  °C).

The benefits to reptilian eggs deposited within the regulated environmental conditions of termitaria appear to be universal and well-studied relative to the proximate or ultimate factors influencing the use of termitaria. This is especially intriguing in taxa

where the behavior is facultative or specific to one population. West Indian iguanas inhabit areas of karst limestone with limited areas of sand/soil accumulation. Nest-site selection is therefore constrained by the physical structure of the associated habitat, which has shaped fairly uniform nesting tactics for *Cyclura* iguanas. The Andros iguana deviates from the usual *Cyclura* nesting strategy of depositing eggs in subterranean chambers excavated in sand or organic soil (references in Alberts, 2000) by selecting predominantly termitaria over sand/organic soil areas (41 of 43 documented nests). Conspecifics inhabiting the small cays (< 88 ha) of the Exuma Islands (*C. c. figginsi* and *C. c. inornata*) deposit eggs only in sand areas despite termitaria being present on the islands (Iverson et al., 2004a; pers. observation).

I suspect that rainfall and topography differences between Andros and the Exuma Islands are responsible for the difference in nesting tactics between the populations. Andros is the largest island in the Bahamian archipelago and receives considerably more rainfall than the Exumas, partly because of convective precipitation associated with large islands. Andros also offers little vertical relief and the karst limestone provides few areas for soil accumulation (predominant elevation above msl at study sites = 1.5 m). The island receives between 1100 and 1300 mm of precipitation annually (Shaklee, 1996) and has a distinct wet season from May to October when heavy rainfall often results in a raised water table that continually breaches the limestone surface throughout the rainy season (pers. observation). In contrast, the Exuma Islands share the same wet season, but receive less than 600 mm of rainfall annually. Additionally, the only standing water on most cays comes from rain that is collected temporarily in small rocky depressions after rain events (Iverson et al., 2004a; pers. observation). There are also many more areas of

oolitic and bioclastic sand deposits above msl that are suitable for nest burrow construction (pers. observation). Ovipositing in termitaria on Andros may be advantageous because mounds are elevated above flood level and remain dry (except for one documented case) throughout the rainy season. Consequently, even small curlytail lizards (*Leiocephalus coryi*) on Andros have been documented exploiting termite mounds for oviposition (Owens and Knapp, 2004).

Geographic variation in *C. cyclura* nesting behavior most likely reflects the effects of local climatic history or topography on reproductive attributes such as nest success. The loss of traditional nesting areas due to eustatic sea level change during the Pleistocene may have forced female iguana on Andros to oviposit in the only available location that remained dry and warm. Whether the behavior is now genetically entrenched or a plastic response to the environment will require future experimentation (see Chapter 4). Nonetheless, the requirement for dry, well-drained oviposition sites and the use of termitaria by the Andros iguana, when available, most likely reflects a history of selection favoring individuals nesting in mounds that remain dry and provide relatively high and constant internal temperatures for egg incubation.

Table 3-1. Termite mound parameter means with standard deviations for mounds used and unused for nesting by the *Andros iguana*.

Parameter	Used (n = 21)	Unused (n = 22)	Wald's $\chi^2$	P
Circumference (cm)	148.9 ± 32.9	161.7 ± 29.6	2.66	0.10
Height (cm)	40.3 ± 8.6	62.1 ± 17.7	5.16	0.02
Soil depth (cm)	5.6 ± 1.9	2.6 ± 1.2	4.42	0.04
Distance to 50% canopy cover (m)	2.1 ± 2.5	1.6 ± 1.8	—	—
Percent canopy cover	71.3 ± 22.2	71.6 ± 20.2	—	—

Logistic regression final-model results of the relationship between termite mound use and mound parameters are presented with P values.

Table 3-2. Yearly ambient and iguana nest temperatures (°C) recorded from 6 June to 10 August on Andros Island.

Temperature (°C)	2002 (n = 2)	2003 (n = 6)	2004 (n = 8)	All years (n = 16)
Ambient	—	29.0 ± 3.7 (21.5–46.9)	29.4 ± 5.7 (17.3–46.4)	29.2 ± 4.8 (17.3–46.9)
Nest	32.4 ± 1.8 (27.5–37.4)	32.6 ± 1.2 (27.9–36.6)	32.4 ± 1.9 (26.2–40.7)	32.6 ± 1.5 (26.2–40.7)

Means are followed by standard deviations with hourly ranges in parentheses. All nest temperatures were taken within termitaria. Mean temperature for the one 2004 nest in sand was 30.8 ± 1.5 °C. Mean temperature for a 2003 inactive mound was 29.1 ± 1.4 °C.

Table 3-3. Causes of individual egg mortality in nests by year for Andros iguanas.

Cause	2003	2004
Eggs missing	14 (40.0)	8 (15.4)
Crab predation	6 (17.1)	18 (34.6)
Desiccated	2 (5.7)	8 (15.4)
Fungus	7 (20.0)	0 (0.0)
Flooded	0 (0.0)	8 (15.4)
Flaccid	2 (5.7)	8 (15.4)
Ruptured by female	4 (11.4)	2 (3.8)

Total eggs in 2003 and 2004 were 144 and 165, respectively. Number lost by each cause is followed by the percent of total eggs lost to that cause.

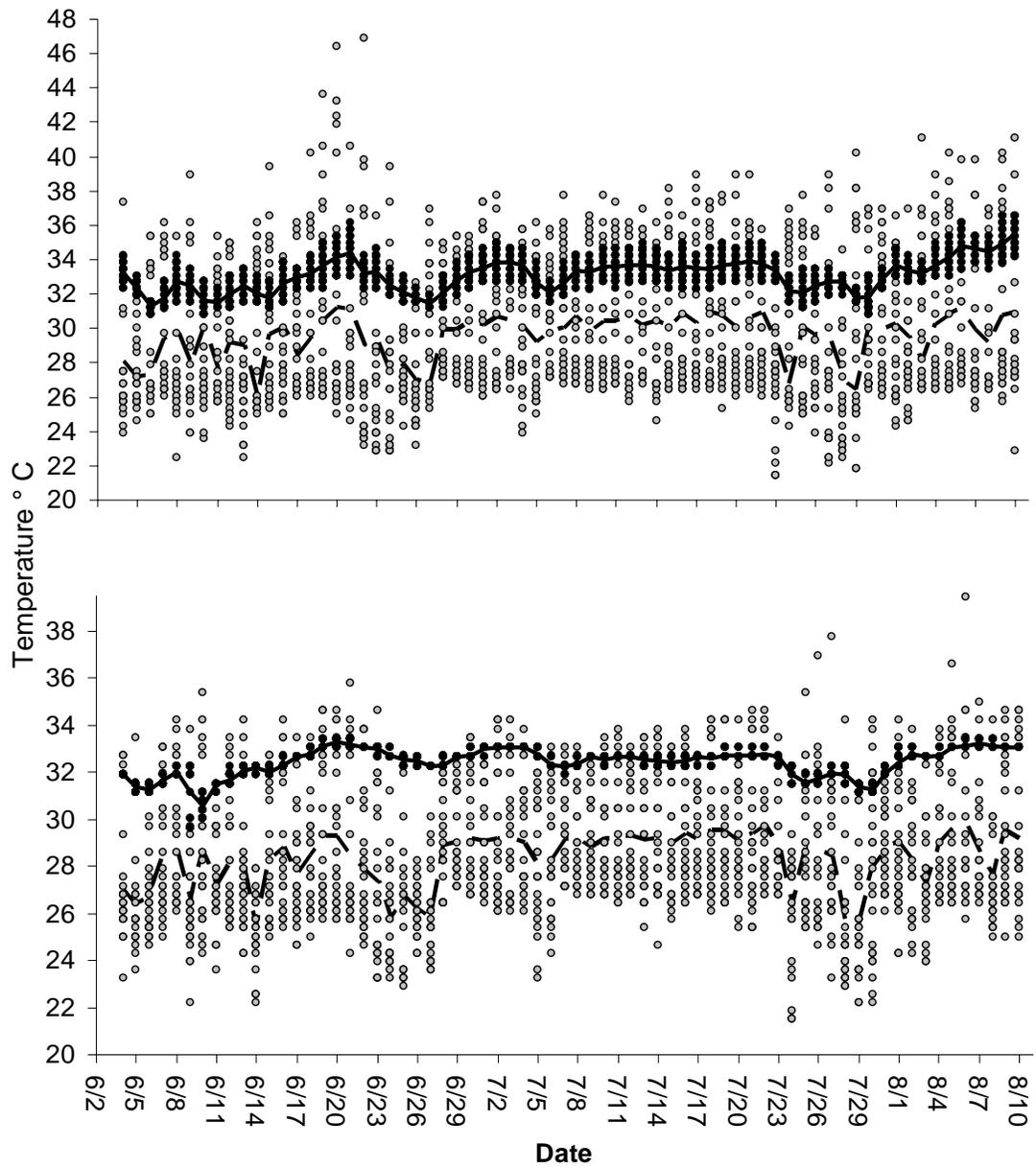


Figure 3-1. Daily temperatures from within two 2003 exemplar *Andros iguana* nests oviposited in termitaria along with their corresponding ambient temperatures. Solid and broken lines represent mean nest and ambient temperatures, respectively. Solid and shaded circles represent hourly recordings in and above nests, respectively.

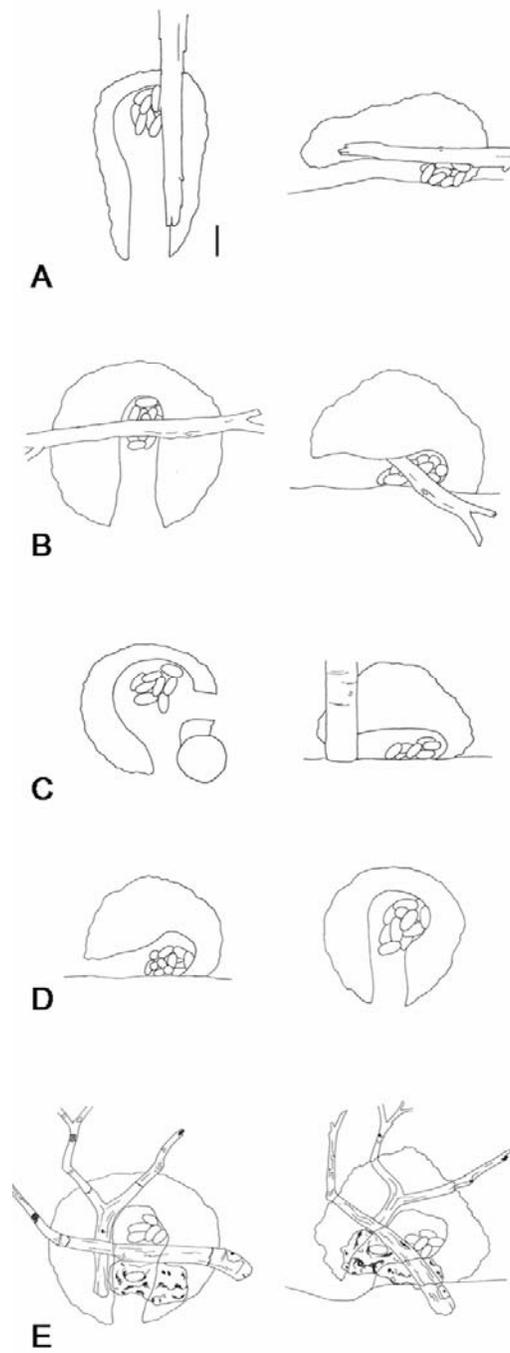


Figure 3-2. Dorsal and lateral schematic views of representative termitaria used as oviposition sites by female *Andros iguanas* in 2004. Bar adjacent to mound A represents 12 cm.

CHAPTER 4  
GEOGRAPHIC VARIATION IN NESTING BEHAVIOR AND REPRODUCTIVE  
BIOLOGY OF AN INSULAR IGUANA (*Cyclura cychlura*)

**Introduction**

Variation in life history traits is common in geographically separated populations of wide-ranging species (Roff, 1992; Stearns, 1992). This variation is either the result of plastic responses of a genotype to environmental conditions (i.e., phenotypic plasticity), local adaptations of genotypes to specific environmental situations, or both (Berven and Gill, 1983; Via and Lande, 1985; Stearns, 1989; Conover and Schultz, 1995). Geographic variation in phenotypes can be due to differences in availability and quality of resources or to differences in biotic interactions among disparate habitats, because no single phenotype will likely confer high fitness in all environmental situations (Via et al., 1995). The mechanistic associations between specific environments and expressed phenotypes are complex and the resulting interpretations controversial (Via et al., 1995). Despite these obstacles, the ability to discern the mechanisms influencing variation in life history traits, including behavior (sensu Carroll and Corneli, 1999), is important to understand the ecology, adaptive responses, and factors limiting the distribution of species.

Comparisons among geographically separated populations of wide-ranging species are particularly useful in elucidating variation in behavioral and reproductive life history traits resulting from proximate (e.g., climatic conditions, food supply) and ultimate (genetic) causes. Investigations that focus on intraspecific geographical differences may present the greatest opportunity for elucidating the causes of life history

evolution (Arnold, 1992). Although interspecific dissimilarities in life histories are usually more pronounced than intraspecific variation, species-level differences are often confounded by phylogeny (Miles and Dunham, 1992). Thus, life history traits of closely-related species may be correlated as a result of inheritance from a common ancestor rather than as a result of contemporary selective environments. Intraspecific investigations of geographic variation in life histories also are advantageous because evolution can be studied on a microevolutionary scale and offer the most elementary data (Arnold, 1992).

The strongest evidence for adaptive variation in life histories to local environments is found in systems that experience low levels of gene flow (Downes and Adams, 2001). Investigations of life history variation of terrestrial vertebrates on islands (e.g., the West Indies) are particularly valuable because the high levels of island endemism suggest sporadic overwater dispersal or vicariance due to rising sea levels, low levels of gene flow, followed by divergence in allopatry (Hedges, 1996; Pregill and Crother, 1999; Glor et al., 2005; but see Calsbeek and Smith, 2003). Indeed, comparative studies on islands can be unique in providing insights into the evolution of life history variation among populations of a species currently inhabiting regions of differing physiography or biotic complexity (e.g., Snell et al., 1988; Stone et al., 1994).

Reptiles in general, and squamates in particular, have been useful models in investigating and interpreting reproductive life history variation across geographic gradients (e.g., Ballinger, 1977; Drummond and Burghardt, 1983; Fitch, 1985; Gregory and Larsen, 1993; Stone et al., 1994; Martins et al., 1998; Seigel and Ford, 2001; Bissell and Martins, 2004). However, among the lizards, investigations of reproductive

parameters have concentrated primarily on small (mean adult snout-vent length (SVL) < 60 mm; e.g., Tinkle and Ballinger, 1972; Dunham, 1982; Gillis and Ballinger, 1992; Downes and Adams, 2001; Niewiarowski et al., 2004) to moderate-sized species (mean adult SVL < 190 mm; e.g., Vitt and Colli, 1994). The body size of a species has considerable life history implications, and comparative analyses have revealed robust associations between body size and life history traits such as age to maturity, fecundity, and the degree of sexual size dimorphism (Shine, 1994; Shine and Seigel, 1996; Shine et al., 1998; Du et al., 2005). Investigating geographic variation in reproductive life history traits among larger lizards with broad adult size variation may reveal differences too subtle to discern in smaller species.

The objective of this study was to investigate geographic variation in reproductive life histories and nesting behavior of a large-bodied (♀ max. SVL- 47.7 cm; ♀ max. body mass- 6657 g) Bahamian iguana (*Cyclura cyclura*) inhabiting two distinct island systems varying in area, topography, and rainfall. Investigations conducted on islands of the Bahamas Archipelago can facilitate the isolation of selective influences on life history traits, which likely evolved during the Pleistocene (approximately 8,000–10,000 years before present) as eustatic sea level change isolated terrestrial populations on islands of dissimilar physiography (Sealey, 1994; Malone et al., 2003; Figure 4-1). The isolated populations most likely occupy the same physiographic areas where differentiation in life histories occurred initially, which provides the opportunity to correctly identify causative selective agents. Reproductive biology and nesting ecology studies of *C. c. cyclura* were conducted on Andros Island (ca. 6,000 km<sup>2</sup>) and the results were compared with *C. c.*

*inornata* inhabiting two cays (each < 4 ha) in the northern Exuma Island chain (ca. 140 km distant).

## **Methods**

### **Study Species**

The Bahamian iguana (*C. cyclura*) is distributed currently in a series of isolated populations throughout islands of different sizes occurring on the submerged Great Bahama bank. Of the approximately 365 cays in the Exuma Island chain, only 12 are inhabited by *C. cyclura*, traditionally separated into two subspecies (*C. c. inornata* and *C. c. figginsi*; but see Malone et al., 2003 for a molecular phylogeographic analysis). Andros Island is inhabited only by *C. c. cyclura*. The Andros and Exuma iguana subspecies are protected by Bahamian law, formally listed as Endangered under 2004 IUCN Red List criteria and listed under Appendix I of the Convention on International Trade of Wild Fauna and Flora (CITES). The primary threats to their existence are poaching or smuggling for the pet trade, the potential effects of supplemental feeding by tourists, introduction of mammalian predators, and vulnerability to stochastic perturbations (Iverson et al., 2004a; Chapter 1).

### **Study Sites**

Andros fieldwork was conducted in conjunction with, and in the same area, as the nesting ecology study described in Chapter 3. The northern Exuma Island sites of Leaf (24°44'55"N; 76°50'11"W) and U Cays (24°44'33"N; 76°50'24"W) are significantly smaller islands (ca. 4 and 3 ha, respectively) and constitute the most northerly natural occurrence for the genus. Similar to Andros, Leaf and U Cays are composed of oolitic and bioclastic limestone, are subject to severe solution weathering, and contain large areas of sand deposits above mean sea level (msl; Sealey, 1994; Iverson et al., 2004a).

However, unlike Andros with plant diversity of more than 800 species (Eshbaugh and Wilson, 1990), vegetation on the Exuma study islands consists of approximately 51 species of evergreen shrubland plant species on Leaf Cay and only 13 species on U Cay (Iverson et al., 2004b). Iverson et al. (2004a; 2004b) provided complete descriptions of the vegetation on Leaf and U Cays. Although both islands share the same rainy season (May to October), precipitation on Andros ranges between 1100 and 1300 mm annually (Shaklee, 1996) whereas the islands of the Exumas are too small to attract moisture or create convection cells so they are drier than larger islands in the same latitude. Rainfall in the Exumas is low, averaging less than 600 mm annually.

### **Field Data Collection**

Fieldwork in the Exuma Islands was conducted by John Iverson's (Earlham College) research team in May/July and October 2001-02 (see methods in Iverson et al., 2004a). I initiated preliminary reproductive ecology investigations on Andros in May 2001 and April/May 2002, with concentrated study efforts, based on observed courtship and oviposition dates from the previous two years, in May/June and August/September 2003-04. After discovering an iguana nest, attendant female iguanas on Andros were captured using fish-landing nets and a series of morphological measurements were recorded, including snout-vent length (SVL to the nearest mm) and body mass (BM in grams). I excavated nests and removed eggs to record clutch size, egg mass (to the nearest g), and egg length and width (to the nearest mm). Eggs were excluded from the morphometric analyses if not measured within 48 hours of oviposition. I returned to nests approximately 75 days post-oviposition to re-excavate and retrieve eggs or hatchlings. Eggs from partially hatched and un-pipped clutches were placed in plastic containers containing surrounding soil and termitaria carton (i.e., a construction material created by

termites from partly chewed or digested woody tissue, salivary secretions, and feces) from the associated nest, and incubated until hatched (1 to 7 days). The resulting hatchlings were measured as described above for adult females.

Adult female body mass was recorded prior to oviposition in the Exuma populations. Although some adult female iguanas were weighed prior to oviposition ( $n = 11$ ) in the Andros population, most were recorded post oviposition ( $n = 27$ ). Gravid body mass (GBM) for spent females was calculated as post oviposition BM + associated clutch mass. There was no significant difference between true gravid BM ( $n = 11$ ) and calculated GBM ( $n = 27$ ; Mann-Whitney U:  $Z = -0.756$ ,  $P = 0.45$ ) in the Andros iguana sample. There also was no SVL difference in Andros iguanas measured pre- and post-oviposition (Mann-Whitney U:  $Z = -1.545$ ,  $P = 0.12$ ). Measures of reproductive output included relative clutch size (RCS; ratio of clutch size to BM x 100), relative egg mass (REM; ratio of mean egg mass in the clutch to BM x 100), and relative clutch mass (RCM; ratio of total clutch mass to BM x 100).

### **Statistical Analysis**

There was no significant interannual difference in SVL for nesting females in the Andros (Mann-Whitney U:  $Z = -0.760$ ,  $P = 0.45$ ) or Exumas (Mann-Whitney U:  $Z = -1.410$ ,  $P = 0.16$ ) female samples, so the data were pooled among years for each island group. I excluded the second-year of data for consecutively nesting females in both island samples to avoid potential non-independent sampling. Simple linear regression was used to examine the relationships between female SVL and recorded reproductive parameters. In circumstances where SVL was correlated with reproductive parameters in both the Andros and Exuma populations, analyses of covariance (ANCOVA) were used to test for island effects on reproductive parameters, with SVL as the covariate. In analyses where

the slopes were not significantly different ( $P > 0.05$ ), interaction terms were deleted and the analyses recalculated to investigate possible differences in intercepts (Sokal and Rohlf, 1995). Partial correlation analyses were used to remove the effect of female body size to test the effect of clutch size on egg size, clutch mass, and hatchling size. Prior to regression and ANCOVA analyses, morphological and egg data were log transformed to meet the assumptions of normality and homogeneity of variance (King, 2000). I report regression results using log transformed measures for clutch parameters.

## Results

### Variation in Reproductive Behavior

Iguanas of the genus *Cyclura* are iteroparous, depositing one clutch of eggs per year (Alberts, 2000; but see Burton, 2004). For *C. cyclura*, the timing of reproductive events and the mode of oviposition differed conspicuously between the Andros and Exuma populations. Female iguanas on Andros consistently initiated oviposition six weeks earlier (earliest dates 8 to 12 May) than females from the Exumas (earliest dates 17 to 20 June; Chapter 3; Iverson et al, 2004a). Oviposition dates between Leaf and U Cays in the Exumas also differed by seven days with iguanas depositing eggs on U Cay first (Iverson et al., 2004a).

The Andros iguana deviated from the usual *Cyclura* nesting strategy of depositing eggs in subterranean chambers excavated in sand or organic soil (references in Alberts, 2000). Although facultative, the nesting behavior of the Andros iguana is unique among all iguanines because of its use of termitaria as oviposition sites (see Chapter 3), whereas females from the Exumas construct nest chambers in sand typical of other *Cyclura* (Iverson et al., 2004a). After oviposition, females from both populations vigorously defended their nests. Iguanas from Andros normally defended nest sites for six weeks,

while females from the Exumas normally defended for at least four weeks. The study in the Exumas did not last the entire summer so prolonged and extensive nest site defense was not able to be observed. The reproductive behavior of the Andros and Exuma iguana populations is described in detail in Chapter 3 and Iverson et al. (2004a), respectively.

### **Variation in Reproductive Traits**

Nesting female iguanas on Andros were significantly larger (SVL) than those from the Exumas (Mann-Whitney U:  $Z = -6.301$ ,  $P < 0.001$ ). Minimum recorded size to maturity also was greater for the Andros than the Exuma populations (Table 4-1). However, female iguanas on Andros reached sexual maturity at a younger age (approximately 8 years) than those in the Exumas (approximately 12 years; Iverson et al., 2004a).

In both the Andros and Exumas populations, maternal body size was correlated significantly with the reproductive parameters of clutch size (figure 4-2A), clutch mass (Figure 4-2B), egg width (Figure 4-3A), and REM (Figure 4-3D). For both populations, the slopes of the regressions were not significantly different for clutch size ( $F_{1,88} = 0.476$ ,  $P = 0.49$ ), clutch mass ( $F_{1,84} = 0.024$ ,  $P = 0.88$ ), and egg width ( $F_{1,83} = 0.279$ ,  $P = 0.60$ ). However, the slope for REM was significantly steeper for the Exuma population ( $F_{1,78} = 16.164$ ,  $P < 0.001$ ). Correlations varied among other reproductive parameters with respect to egg size and individual populations. Egg mass was significantly positively correlated with maternal body size in the Andros ( $P = 0.005$ ) but not the Exuma population ( $P = 0.22$ ; Iverson et al., 2004a; Figure 4-3B). Conversely, egg length was negatively correlated in the Exuma ( $P < 0.001$ ; Iverson et al., 2004a), but not the Andros population ( $P = 0.27$ ; Figure 4-3C).

In general, female iguanas from Andros deposited larger and heavier clutches with larger eggs, but hatchlings of equal size, than female iguanas from the Exumas (Table 4-1). Adjusting for maternal body size where data permitted, female iguanas from Andros deposited significantly more eggs per clutch (ANCOVA:  $F_{1,89} = 13.53$ ,  $P < 0.001$ ), heavier total clutches (ANCOVA:  $F_{1,85} = 23.99$ ,  $P < 0.001$ ), and wider eggs (ANCOVA:  $F_{1,84} = 29.86$ ,  $P < 0.001$ ) than conspecifics from the Exumas.

Using partial correlations to correct for maternal SVL, clutch size was not correlated significantly with mean egg mass in either the Andros ( $r = -0.25$ ,  $P = 0.21$ ) or Exuma populations ( $r = -0.09$ ,  $P = 0.49$ ). However, clutch size was correlated significantly with clutch mass in both the Andros and Exuma populations ( $r = 0.84$ ,  $P < 0.001$  and  $r = 0.91$ ,  $P < 0.001$ , respectively) suggesting that an increase in clutch mass relates primarily to an increase in clutch size but not mean egg mass. These data are supported further by the lack of significant correlations between RCM and maternal SVL in either the Andros or Exuma populations ( $r = 0.07$ ,  $P = 0.75$  and  $r = 0.15$ ,  $P = 0.30$ , respectively), indicating that females with large clutches in both populations tend to produce relatively small eggs, such that RCM remains constant with maternal body length.

The population of origin contributed very little to variation in offspring characteristics. Mean hatchling SVL was not correlated significantly with mean egg mass in either the Andros ( $r = 0.296$ ,  $P = 0.31$ ) or the Exuma populations ( $r = 0.102$ ,  $P = 0.81$ ; Figure 4-4A). Hatchling SVL per clutch also did not differ significantly between the Andros ( $n = 14$ ) and Exuma ( $n = 8$ ) populations (Mann-Whitney U:  $Z = -0.681$ ,  $P = 0.68$ ). Mean hatchling BM was correlated significantly with mean egg mass in both the

Andros ( $r = 0.635$ ,  $P = 0.02$ ) and the Exuma populations ( $r = 0.836$ ,  $P = 0.01$ ; Figure 4-4B). After adjusting for egg mass, mean BM of hatchlings also did not differ among populations (ANCOVA:  $F_{1,19} = 0.002$ ,  $P = 0.51$ ).

## Discussion

### Behavioral Variation

Behavioral traits are often more complex than many physiological and life-history components of fitness (e.g., Price and Schluter, 1991), because they are often more plastic and yet can evolve rapidly (Martins et al., 1998). This flexibility of behavior is of great importance in evolution because it may increase the variety of habitats to which a species has access, ultimately enhancing a population's potential for evolutionary change (West-Eberhard, 1989; Carroll and Corneli, 1999). Geographic variation in the nesting behavior of *C. cythlura* most likely reflects the effects of local climatic history and island topography on reproductive attributes such as nest success.

Andros is the largest island in the Bahamian archipelago and receives considerably more rainfall than the Exumas, partly because of convective precipitation associated with large islands. Andros also offers little vertical relief (90% < 6 m above msl) and the karst limestone provides few areas for soil accumulation. The island has a distinct wet season from May to October when heavy rainfall often results in a raised water table that continually inundates the limestone surface (pers. observation). In contrast, the Exuma Islands share the same wet season, but the islands are too small to create convection cells and thus receive half the amount of rainfall as Andros (E. Carey, unpublished data). Additionally, the only standing water on the cays is what is collected temporarily in small rocky depressions after rain events (Iverson et al., 2004a; pers. observation). There are also relatively more areas of oolitic and bioclastic sand deposits above msl that are

suitable for nest burrow construction (pers. observation). Ovipositing in termitaria on Andros (in areas devoid of sand deposits) is advantageous because mounds are elevated above flood level and remain dry throughout the rainy season. This adaptive flexibility of nesting behavior for the Andros iguana has facilitated their occupation of areas that would be unsuitable for typical iguanine nesting behavior.

Additional investigations are needed to isolate mechanisms behind the behavioral variation in nest site choice between the Andros and Exuma iguana populations. However, it appears that the behavioral disparities between the two iguana populations reflect the effects of island topography and local climatic history on reproductive attributes such as nest success. The requirement for dry, well-drained and warm oviposition sites, and the use of termitaria by the Andros iguana when available, most likely reflects selection favoring individuals that nest in mounds that provide relatively high and constant internal temperatures for egg incubation.

The discrepancy in nesting dates between the Andros and Exuma populations is difficult to explain. The timing of reproductive activity is highly variable in tropical reptiles, both within a given geographical area, as well as between distant sites, suggesting that multiple factors may influence reproductive timing (Censky, 1995). There is no general relationship between nesting date and latitude in the three *Cyclura* species inhabiting the Bahamas (Hayes et al., 2004). However, the degree of rainfall differences between the Andros and Exuma *C. cychlura* populations must influence the phenology of reproduction (e.g., Wiewandt, 1977; Iverson, 1979; Vogel, 1994). Because the timing of mating, nesting, incubation, and hatching have evolved together, the total response

probably represents an adaptive compromise within each respective population (Rand and Greene, 1982).

### **Body-Size Variation**

Evidence from other studies (e.g., Knapp, 2001; Iverson et al, 2004a) supports the hypothesis that the disparity in body size between the Andros and Exuma iguana populations is most likely because of proximate environmental effects and that the two populations have not diverged in their capacity for individual growth. Increased opportunity for foraging on Andros (mediated by lower iguana densities, increased rainfall, and greater plant species diversity) should result in more energy that can be allocated to both growth and reproduction. Thus iguanas inhabiting Andros Island may be expected to exhibit higher rates of growth, larger body size, and relatively younger age to maturity than iguanas in the Exumas.

The differences in minimum size to maturity between the Andros (31.0 cm SVL) and Exuma (26.5 cm SVL) populations could be the result of faster growth and/or may reflect disparities in nest site availability and subsequent nest site defense pressures. Densities of termitaria suitable for oviposition are extremely low relative to sand nesting areas in the Exumas. Larger minimum nesting female body sizes for the Andros population is likely an artifact of intrasexual competition for the extremely limited nest sites, and selection pressure toward larger females and advantages gained defending nests (Isaac, 2005). The limited nest sites may also explain the increased recorded duration of nest site defense for the Andros iguana versus the Exuma populations.

### **Reproductive Life-History Variation**

Simple, collective explanations of intraspecific patterns of geographic variation in life histories are difficult, especially considering the multiple trade-offs that result from

interactions of individuals with their environment (Sears, 2005) and the difficulty in interpreting results because of uncontrollable variables (Ford and Seigel, 1994).

However, there is widespread agreement that the degree of phenotypic variation across environments can differ among characters such as clutch and offspring size (Ford and Seigel, 1994; Seigel and Ford, 2001), and may be either adaptive or non-adaptive (Via et al., 1995). While clutch size, clutch mass, and egg width (to a lesser extent) increased with maternal body size in both the Andros and Exuma populations, egg mass and egg length displayed different relationships between the two populations.

Egg mass was correlated with maternal body size in the Andros but not the Exuma populations. The possibility exists that larger females inhabiting an island with greater plant species diversity are of higher quality (relatively greater total lipid reserves) than smaller females, which could translate into higher relative total reproductive allocation (i.e., egg mass; Vitt and Colli, 1994; Thompson and Speake, 2004). Conversely, there was an inverse relationship between egg length and maternal body mass in the Exumas but not on Andros. Smaller females in the Exuma population produced longer and narrower eggs than larger females in the same population, presumably an adaptation to produce the largest egg possible given the constraints of the pelvic opening (Iverson et al., 2004a). The pelvic opening has been demonstrated to constrain egg size in other lizards (Michaud and Echternacht, 1995) but is presumably not a constraint in the larger iguanas from the Andros population. Thus, egg length remains constant as egg width increases.

Interestingly, despite the differences in egg dimensions between the two populations, hatchling body masses and lengths were canalized, supporting the

hypothesis that smaller females in the Exumas are depositing longer eggs to compensate for smaller cloacal openings. The data also suggest that hatchling size may be under genetic control while other reproductive parameters such as clutch size and clutch mass are influenced more by proximate causes.

Unambiguous tests of life-history variation arising from resource availability are difficult without field manipulations (Olsson and Shine, 1997) or unless resource abundance is measured simultaneously with demographic life-history studies (Dunham, 1982). However, as demonstrated in other studies of *Cyclura*, resource limitation on small islands such as the Exumas impinges initially on adult body size in these lizards in response to reduced resource availability and/or reduced resource processability (see Iverson, 1982; Knapp, 2001; Iverson et al., 2004a). Low-density populations of *Cyclura* inhabiting areas of greater resource diversity (i.e., larger islands) are free from the constraint of limited resources and are generally larger (Iverson et al., 2004a). Consequently, the larger maternal body size in these lizards in response to proximate causes translates to larger RCM, clutch sizes, and clutch masses because of greater resource allocation available for reproduction.

In general, RCM is constant across sizes, ages, and geographic ranges of lizard species (Vitt and Congdon, 1978; Vitt and Price, 1982; Dunham, 1982; Dunham et al., 1988). Intraspecific variation of RCM (i.e., seasonal or geographic), as demonstrated in this study, usually reflects phenotypic plasticity in response to varying resources (Swingland, 1977, Vitt and Colli, 1994). Additionally, clutch size was correlated significantly with clutch mass but not with mean egg mass in either the Andros or Exuma populations, suggesting that an increase in clutch mass relates primarily to an increase in

clutch size and not mean egg mass. These data suggest that clutch size and clutch mass are more plastic than egg and hatchling size, which may have a much greater genetic basis and are the products of much more intense selection for optimal offspring size. Plasticity of reproductive investment stemming from the effects of food resources can be considered a physiological constraint and thus uninteresting from an adaptive point of view (Gotthard and Nylin, 1995; Via et al., 1995). However, plasticity in allocation to number and/or size of offspring could be adaptive in the sense that it may lead to increased fitness under varying environments.

Data from this study support the hypothesis that proximate environmental factors play an important role in determining geographic variation associated with not only reproduction biology (e.g., Ballinger, 1983; Berven, 1988), but also reproductive behavior. Additional investigations need to be conducted to isolate mechanisms behind the canalization of offspring size and the behavioral variation in nesting strategies between the Andros and Exuma iguana populations. Since reciprocal transplant or common garden experiments (reviewed in Conover and Schultz, 1995; Gotthard and Nylin, 1995) on large bodied and endangered taxa are improbable, the conservation strategy of translocation (Knapp and Hudson, 2004) may provide the opportunity to explore further the effects of proximate and ultimate causes on life history variation in insular lizard populations.

Table 4-1. Mean female reproductive and hatchling parameters for *C. cychlura cychlura* and *C. cychlura inornata*.

Parameter	<i>C. cychlura cychlura</i>	<i>C. cychlura inornata</i>
SVL (cm)	38.7 ± 4.2 (32) [31.0–47.7]	31.5 ± 3.0 (70) [26.5–38.9]
BM (g)	3006 ± 1185 (31) [1279–6657]	1283 ± 413 (57) [749–2370]
Clutch size	9.8 ± 3.3 (34) [4–19]	4.5 ± 1.7 (73) [1–10]
Egg length (mm)	70.7 ± 3.6 (34) [60.4–80.9]	67.5 ± 4.6 (63) [57.5–80.0]
Egg width (mm)	40.3 ± 2.8 (34) [33.8–47.3]	34.8 ± 1.8 (63) [30.2–40.6]
Egg mass (g)	59.8 ± 4.9 (34) [50.5–71.0]	49.1 ± 3.9 (63) [37.2–57.3]
Clutch mass (g)	618.9 ± 230.0 (34) [229–1220]	223 ± 85 (73) [56–426]
RCS	0.33 ± 0.08 (31) [0.16–0.57]	0.35 ± 0.07 (53) [0.12–0.52]
REM	2.3 ± 0.8 (31) [1.0–4.4]	4.1 ± 1.2 (51) [1.7–6.7]
RCM	20.3 ± 4.1 (31) [12.2–31.1]	16.9 ± 3.4 (53) [6.7–22.1]
Hatchling SVL (cm)	9.6 ± 0.42 (37) [8.1–10.6]	9.5 ± 0.24 (12) [9.1–9.9]
Hatchling BM (g)	42.4 ± 4.9 (37) [31.0–55.0]	35.4 ± 3.3 (12) [30.8–42.9]

Sample sizes are in parenthesis after mean ± SD with range below in brackets. Sample sizes of clutches are provided for hatchling parameters. RCS = clutch size/body mass x 100; REM = mean egg mass/body mass x 100; RCM = clutch mass/body mass x 100.

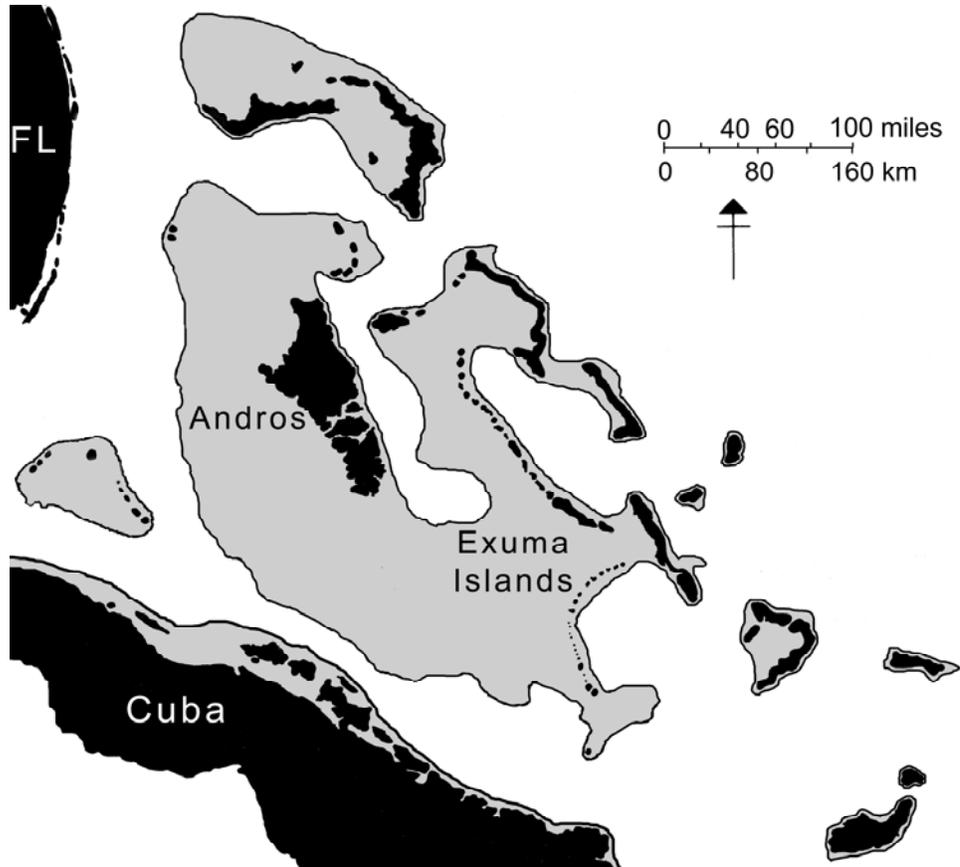


Figure 4-1. Map of the Bahamas depicting the Great Bahama bank (grey scale), which was last exposed during the Last Glacial Maximum (approximately 8,000–10,000 years before present). The positions of Andros Island and the Exuma Island chain are identified on the bank.

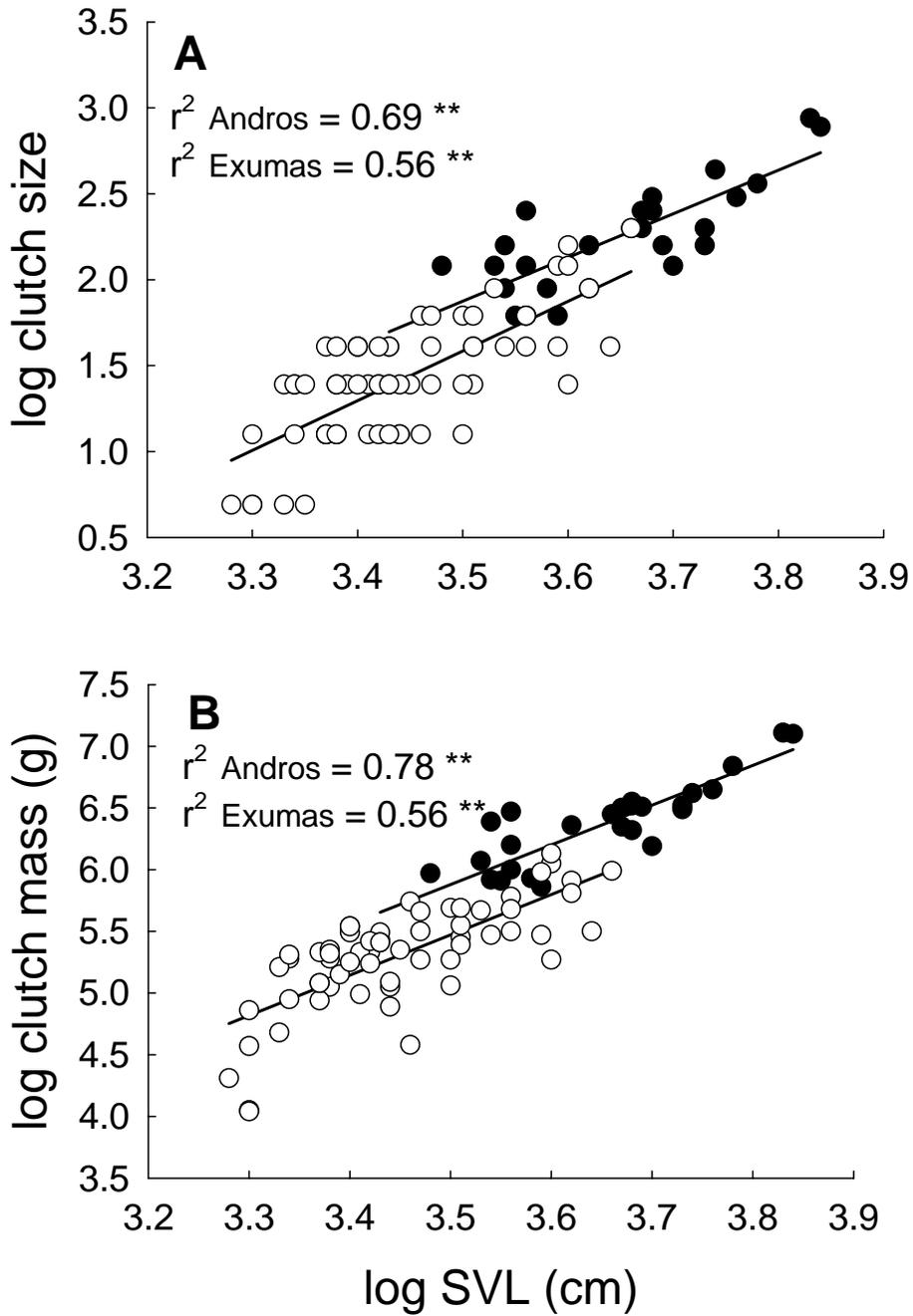


Figure 4-2. Correlations of log scale clutch parameters with log snout-vent length (SVL). Dark and open circles represent the Andros and Exuma Iguana populations, respectively. Double asterisk denote statistical significance at  $P < 0.001$ .

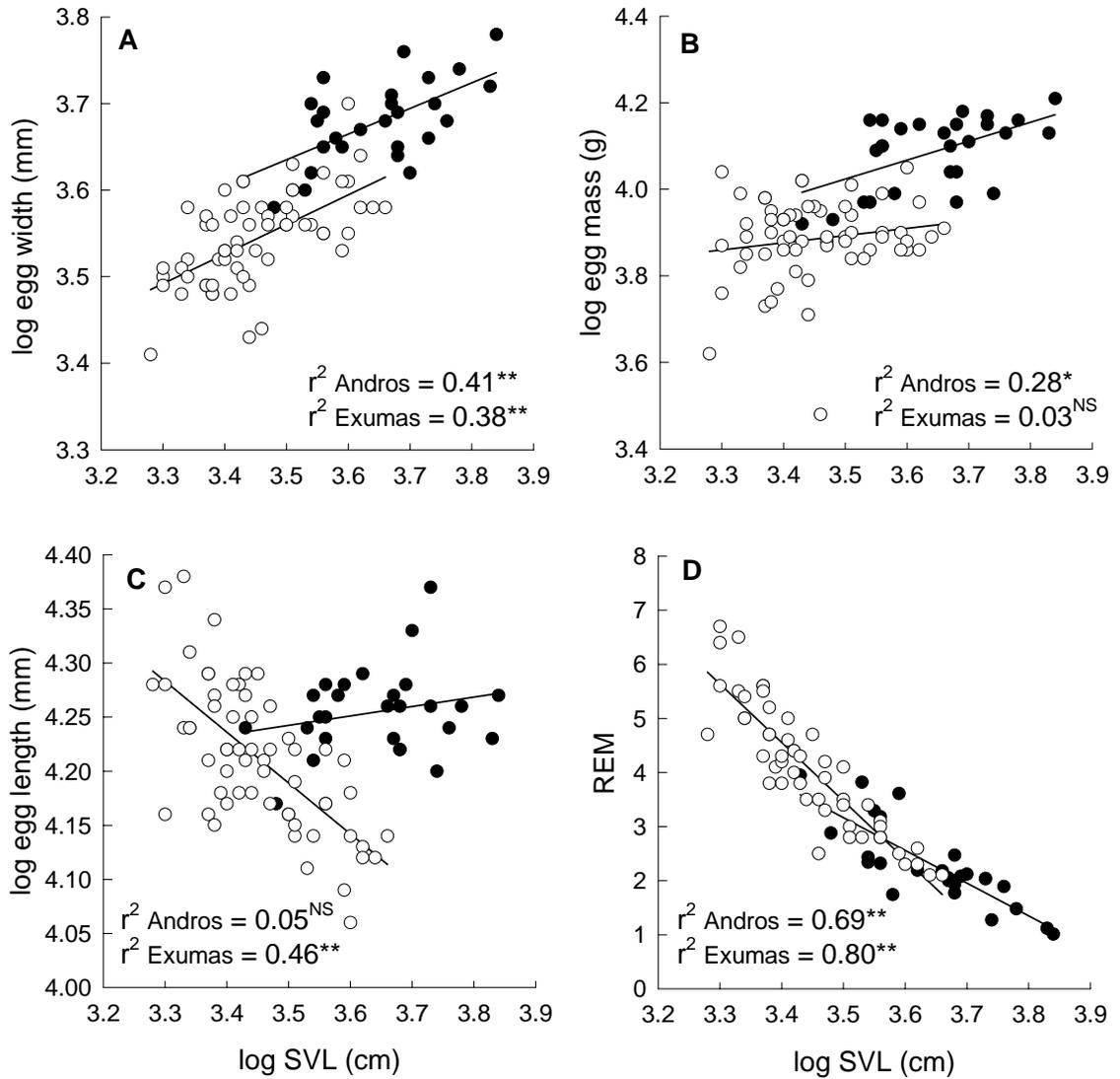


Figure 4-3. Correlations of log scale egg parameters and relative egg mass (REM) with log snout-vent length (SVL). Dark and open circles represent the Andros and Exuma Iguana populations, respectively. Single and double asterisk denote statistical significance at  $P < 0.01$  and  $< 0.001$ , respectively.

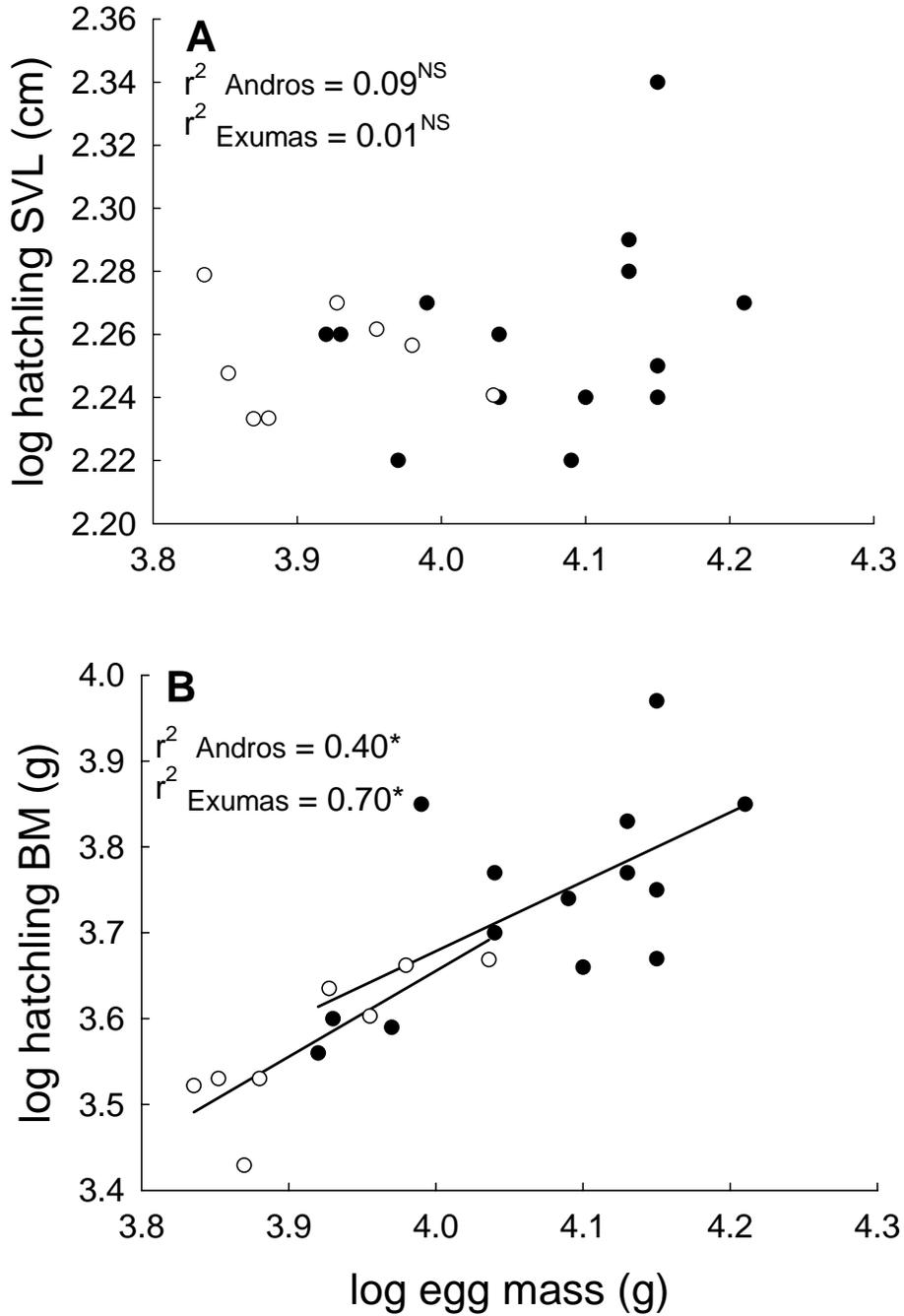


Figure 4-4. Correlations of (A) log scale hatchling snout-vent length (SVL) and (B) log hatchling body mass (BM) with log egg mass. Dark and open circles represent the Andros and Exuma Iguana populations, respectively. Single asterisk denotes statistical significance at  $P < 0.05$

CHAPTER 5  
NEONATE SURVIVAL AND DISPERSAL OF AN INSULAR IGUANA:  
IMPLICATIONS FOR CONSERVATION

**Introduction**

Distances traveled and the survival of juvenile animals during natal dispersal are factors that must be considered by population ecologists and conservation managers wanting to understand the distribution, population dynamics, implications of management, and abundance of organisms (Johnson and Gaines, 1990; Ruckelshaus et al., 1997; Macdonald and Johnson, 2001; Berry et al., 2005). Understanding these attributes requires knowledge of how survival rates vary in relation to factors such as sex, age, season, and habitat occupied during dispersal.

Although there have been numerous investigations pertaining to natal dispersal in amphibians (e.g., Lowe, 2003; Vasconcelos and Calhoun, 2004), tortoises (e.g., Bjurlin and Bissonette, 2004), birds (e.g., Webb et al., 2004; Brøseth et al., 2005; Withey and Marzluff, 2005), and mammals (e.g., Haughland and Larsen, 2004; Martin and Heske, 2005), the survival and natal dispersal behavior of free-ranging lizard hatchlings immediately post emergence remains the least studied aspects of their biology (but see Greene et al., 1978; Christian and Tracy, 1981; Drummond and Burghardt, 1982). The lack of data on juvenile dispersal distances and habitat-specific survivorship of endangered lizards while dispersing needs to be addressed in order to construct accurate demographic models and make informed management decisions.

Iguanas in the genus *Cyclura* compose a group of lizards (nine species) endemic to the Bahamas and Caribbean that are recognized as among the most endangered lizards in the world (Alberts, 2000). Juvenile survivorship estimates for any *Cyclura* species are only now available from a long-term study of the Allen Cays iguana (*Cyclura cychlura inornata*) though the data are restricted to post six-month old juveniles (Iverson, unpublished data). Additionally, Iverson's long-term study (Iverson et al., 2004a; 2004b) is being conducted on small islands ( $\leq 4$  ha) thus presumably restricting juvenile dispersal opportunities. The islands also lack non-avian predators and may therefore not represent a realistic model for other iguana species inhabiting large islands with complex predator assemblages.

The primary objectives of this study were to describe the early survivorship of Andros iguana hatchlings (*C. c. cychlura*) and to quantify dispersal distances away from nest sites. Other objectives included examining survival rates in relation to hatchling body size and to qualitatively examine the influences of habitat on survival. Results from this study will then be applied to science-based management programs (e.g., establishing protected areas) for the Andros iguana. Additionally, results from this study are more applicable to other insular iguana species inhabiting large islands because Andros is the fifth largest island in the West Indies ( $\sim 6,000$  km<sup>2</sup>) and thus dispersal is less restricted by island size and predator interactions are assumed to be more complex because of the presence of non-avian predators.

## Methods

Iguanas were radio-tracked at three locations from the South Andros area- Sandy Cay, Linder Cay, and Mangrove Cay. Sandy Cay (310 ha; 24°05' 24"N, 77°41'44"W) is

located in the South Bight of Andros. Linder Cay (1300 ha; 24°10'14"N, 77°41'40"W) is located in Lisbon Creek, South Andros. The third study site is a tri-lobed peninsula (175 ha; 24°09'03"N; 77°43'30"W) extending from the south/southeast side of Mangrove Cay. Each site is characterized by three main habitat types: pine woodland, dry evergreen shrubland, and mangrove (see Chapter 2 for a detailed description of the study sites and associated vegetation).

Forty-one hatchlings in 2003 and 36 hatchlings in 2004 were collected for radio tracking directly before emerging from nests or from incubated eggs (see Chapter 3). The snout-vent length (SVL to the nearest mm), tail length (TL to the nearest mm), and body mass (BM in grams) were recorded prior to release. Hatchlings ranged from 31 to 57 g in BM (mean =  $44 \pm 5.56$  g), 84 to 106 mm in SVL (mean =  $97 \pm 0.41$  mm), and 122 to 171 mm in TL (mean =  $153 \pm 0.97$  mm). To radio track lizards, I secured BD-2 and PD-2 model transmitters (Holohil Systems Ltd., Ontario, Canada) to the inguinal region of hatchlings as described by Knapp and Owens (2005). Transmitters represented  $6.0 \pm 0.7\%$  of hatchling body mass.

An assumption common to any method involving marked animals is that capturing the animal or having it carry a radio tag does not influence its future movements or survival (Pollock et al., 1989; White and Garrott, 1990). Although not quantified, the transmitter attachment appeared to have no significant effect on iguana hatchling behavior or movement (see Knapp and Owens, 2005). Hatchlings were released from 12 August to 8 September 2003 and from 7 to 27 August 2004 after they had emerged from eggs and their umbilical openings had healed (mean =  $3.9 \pm 0.9$  days). I was able to use a release-relocation method that enabled me to record the exact initial

position of dispersal. Andros iguanas are the only iguana to deposit their eggs within termitaria (see Chapter 3). For 2003 releases, hatchlings were positioned directly on the dorsal surface of their corresponding nest termitaria. A conditioning period (Pollock et al., 1989) of one day was incorporated into the 2003 data set to minimize the potential of short-term negative survival biases of tagging and releasing directly on the nest. Therefore, only 2003 hatchlings surviving a minimum of 24 hours post release were included in the analyses. In 2004, the conditioning period consisted of reburying hatchlings in their nests and allowing them to emerge on their own (up to 24 hours post release). The majority of termitaria where iguanas were released occurred in pine woodland (71%,  $n = 12$ ), followed by evergreen shrubland (29%,  $n = 5$ ).

I tracked iguanas using a hand-held 3-element Yagi directional antenna and a Wildlife Materials, Inc. (Carbondale, IL, USA) TRX-48S receiver. Iguanas were located with telemetry during the day and early evening (0830 to 1900 hrs) at a mean interval of  $1.3 \pm 0.5$  days (range 1 to 3). Days tracked for each animal ranged up to 55 days in 2003 and 34 days in 2004. After locating an iguana, I recorded time, activity, habitat association, and location using a WAAS-enabled Garmin® e-trex Legend GPS receiver with an accuracy of  $\pm 5$  m. Hatchling locations were confirmed by visual observation to ensure that I was recording actual hatchling movement patterns and not predators with ingested transmitters (see Knapp and Owens, 2004). Additionally, I verified that transmitters were not causing visible stress (e.g., abrasions in the inguinal region) to the lizards.

Survival estimates were calculated using the standard Kaplan-Meier procedure (Kaplan and Meier, 1958) even though staggered entry designs are common for survival

analysis because of the ability to add new animals after initiation of the study (Pollock et al., 1989). An assumption of the staggered entry design is that newly-tagged animals have the same survival function as previously-tagged animals. In my case, survival estimates would be negatively biased using staggered entry because survival of hatchlings immediately following release was lower than that of longer-lived hatchlings. Additionally, this study is unique relative to other telemetry studies because of a natural time origin consisting of the systematic release of hatchlings at their nests after emergence from the egg (Collett, 2003).

Known fates of hatchlings were documented typically either as direct evidence of snake predation or captured alive at the end of the study. In 2003 and 2004, the fates of nine and seven lizards, respectively, were unknown and considered censored. Unknown fates were the result of signal loss or the inability to confirm death because of stationary transmitter signals emitting from underneath the fragmented limestone surface. Bounds of the Kaplan-Meier survival curves were thus generated to allow interpretation of extreme rates (Pollock et al., 1989). A pessimistic bound was obtained by assuming that every censored observation was a death, and an optimistic bound by assuming that every censored observation was not a death and that the hatchling survived to the end of the study. The log rank test was used to compare survival distribution functions between years. Percentage of relocations in each of the three habitat types were graphed to make qualitative comparisons of potential influences of habitat on survival. Only hatchlings surviving  $\geq$  four days were used to construct the habitat graph because the median distance from nests at day four was 94 m. All three habitats in the study area were within

94 m of every nest where hatchlings were released, thus hatchlings had the potential to disperse into all areas under study.

I calculated four movement indices using ArcView GIS 3.2a software (Environmental Systems Research Institute, Redlands, CA, USA). Dispersal distance was calculated as the straight-line distance from the nest to the last recorded location of a living hatchling. Total distance moved was calculated by summing the linear distances between fixed locations. Mean daily movement rates were calculated by dividing the total distance moved by the number of days individual hatchlings were tracked. I categorized hatchlings as “dispersers” using the site fidelity test with the Animal Movement Analysis Extension (Hooge et al., 1999) in ArcView. The test compared actual movement paths with 100 simulated random walks using corresponding nests as the start point. The test used a Monte Carlo simulation and parameters from the original data to determine if the observed movement patterns displayed a more constrained or dispersed pattern ( $P < 0.05$ ) than should occur randomly. Linear regression was used to compare hatchling morphometrics (i.e., SVL, BM) with maximum linear dispersal distance from the nest. All hatchlings used in dispersal analyses were at least 14 days old. All analyses were performed using JMP IN 4.0 (SAS Institute Inc., Cary, NC, USA). Means are presented with  $\pm$  one standard deviation.

## Results

The probability of survival using both the pessimistic and optimistic categorizing themes did not differ by year (pessimistic: log rank test  $\chi^2 = 3.34$ ,  $P = 0.07$ ; optimistic: log rank test  $\chi^2 = 0.09$ ,  $P = 0.77$ ); thus, the data were combined to increase sample size. Probability of survival to 55 days post release using the pessimistic categorizing theme

was 0.15 (95% C.I. = 0.09–0.26), and 0.25 (95% C.I. = 0.16–0.40) using the optimistic categorizing theme. The highest rates of hatchling death were during the first two weeks post release at nests (Figure 5-1). All confirmed sources of mortality were from two native snakes, the colubrid, *Alsophis vudii*, and the boid, *Epicrates striatus*. Two confirmed deaths with ambiguous causes were thought to be the result of an avian predator based on the location and state of the carcasses.

Hatchling deaths confirmed as a result of snake predation were not independent by species ( $\chi^2 = 8.81$ ,  $P = 0.003$ ). Predation by *A. vudii* accounted for 73.2% ( $n = 30$ ), whereas *E. striatus* accounted for 26.8% ( $n = 11$ ) of hatchlings killed during the study. The last recorded predation event by *A. vudii* occurred 27 days after release from the nest, whereas hatchling predation by *E. striatus* ceased 13 days after release (Figure 5-2). The mean total lengths of captured *A. vudii* and *E. striatus* preying on hatchlings were  $89.1 \pm 10$  cm (range 69–104 cm,  $n = 14$ ) and  $108.4 \pm 17.9$  cm (range 82–130 cm,  $n = 8$ ), respectively.

Hatchlings that survived at least 14 days ( $n = 18$ ) moved a median distance of 510 m from their nests (mean =  $550 \pm 277$  m, range 156–1090 m; Figure 5-3). The median daily movement rate and total distance moved was 15 m (mean =  $35 \pm 60$  m, range 0–390 m) and 716 m (mean =  $805 \pm 478$  m, range 210–1987 m), respectively. There were no annual differences in SVL ( $t = 1.262$ ,  $P = 0.23$ ), BM ( $t = -0.426$ ,  $P = 0.68$ ) or in maximum distance moved from nest ( $t = 1.117$ ,  $P = 0.28$ ), so data were combined for regression analyses. Neither SVL ( $r = 0.029$ ,  $P = 0.91$ ) or BM ( $r = -0.089$ ,  $P = 0.73$ ) were correlated with maximum dispersal distance from nests.

Although movements were analyzed only for hatchlings surviving a minimum of 14 days, extensive dispersal was recorded for individuals preyed on before 14 days and thus was excluded from the analysis. The most extensive confirmed movement of the study was recorded from a 2004 individual, censored because of signal loss at four days. After entering the water on the third day after its release, the hatchling moved 1723 m in one day, and 2300 m from its nest. It was discovered resting on a red mangrove root but the signal was lost the following day. Single day over-water movements ranging from 5 to 1723 m were recorded from seven hatchlings, of which three were recorded alive for more than 14 days.

Of hatchlings that survived a minimum of 14 days, 89% (n = 16) were classified as dispersers based on their non random (all  $P < 0.05$ ) over-dispersed movements away from nests. The remaining two hatchlings displayed random movement patterns ( $P > 0.05$ ). One hatchling that moved randomly was eaten by an *Alsophis*. The remaining randomly-moving hatchling traveled 410 m away from the nest within 10 days and then remained relatively inactive (maximum distance 693 m from nest) until it was recaptured 45 days later to remove the transmitter. Given the length of monitoring this individual, it may be that hatchlings make extensive movements away from nesting sites before settling in an area (Figure 5-4). This individual was relocated last in a tidal mangrove, as were eight other hatchlings surviving until the end of the study. Most hatchlings (8 of 10) confirmed alive at the end of the study were relocated  $> 53\%$  in mangrove systems (Figure 5-5).

### **Discussion**

The lack of quantitative assessments of natal dispersal and survival of organisms directly from nests or birthing areas is most likely because of the difficulty in accurately monitoring small animals over large areas and failing to detect long-distance movements

away from study areas (Koenig et al., 1996). Non-experimental lizard-dispersal studies predominantly use mark-recapture techniques (Doughty and Sinervo, 1994; Massot et al., 2003), whereas estimates of first year survival rates of iguanas have only been calculated using age class structure (Iverson, 1979; Abts, 1987), recapture percentage (Harris, 1982; Krekorian, 1984; Iverson, unpublished data), or Jolly-Seber (Laurie and Brown, 1990) methods. This is the first study using the advantages of radio telemetry to determine dispersal distances and the fate of hatchling iguanas. Evidence from other organisms suggests that predation is one of the major causes of mortality for dispersing individuals (Weisser, 2001). This study demonstrates specifically that snake predation, in areas free from feral mammalian predators, is the most significant cause of mortality in hatchling iguanas dispersing away from nest sites on Andros Island.

High snake-related mortality is responsible for the lower than expected survival rates for dispersing hatchlings on Andros. The pessimistic and optimistic survival estimates of 0.15 and 0.25 are the lowest reported for an insular iguana species. Hatchling survival rates reported for insular iguana species range from 46.9 (Galapagos Islands; Laurie and Brown, 1990) to 95.3% (Exuma Islands, Bahamas; Iverson, unpublished data). However, both studies used recapture methods and Iverson's study was conducted on small, snake-free islands and only with hatchlings at least 6 months of age. The limitations of recapture studies have been discussed previously (Koenig et al., 1996), and I stress that more survival studies of dispersing hatchlings from nest sites are needed to provide survival estimates for insular iguanas. The extreme high rate of survival for Iverson's population (95.3%) may be because high mortality was missed during the first six months, or because of the lack of snake predators on his small study islands.

Conversely, the low survival rates of hatchlings on Andros could be an artifact of unmeasured negative influences caused by transmitters that reduced the ability to escape predation attempts.

Tracking periods and survival rates were not sufficient to describe overall dispersal using philopatry or emigration models. Despite the low number of surviving hatchlings, some aspects of their dispersal were recognized. As reported in other studies of iguanid hatchlings (Doughty and Sinervo, 1994), hatchling body size of Andros iguanas was not related to dispersal distance. Most hatchlings displayed rapid, nearly linear, movements away from nests for a minimum of 14 to 21 days (Figure 5-4), during which predation rates were highest (Figure 5-2). Most hatchlings (53%) surviving a minimum of four days were not reluctant to move and disperse through at least two of three area habitats (Figure 5-5). The two hatchlings surviving the longest in this study (47 and 55 days) appeared to reach an asymptotic distance from their corresponding nest sites after 28 to 33 days. Both hatchlings were last relocated and spent the majority of their time in tidal mangrove systems. Six other surviving hatchlings were relocated > 53% in mangroves. Further studies are needed to quantitatively describe hatchling behavior mechanisms and predator densities in all habitat types in order to infer causation for the purported benefits of remaining in mangrove systems on Andros Island. Although snakes were never observed in mangroves (Knapp and Owens, 2004), I hypothesize that these habitats may act as refugia for dispersing hatchlings.

Mathematical models predict that high predation rates and risk of population extinction generally increase dispersal rates (Johnson and Gaines, 1990; Weisser, 2001). Although predation rates were highest during initial movements away from nests, the

active dispersal of iguana hatchlings rapidly increased their presence from concentrated emergence points to widespread areas. The initial and rapid movements away from nests could reduce relative predation by dispersing neonates from a zone where predators learn to exploit them. There are numerous examples of avian and snake predators exploiting newly emerging, or recently emerged, iguana hatchlings from mainland and island locales (e.g., Christian and Tracy, 1981; Drummond and Burghardt, 1982; Werner, 1983; Rivas et al., 1998; Henderson and Powell, 2004). Although multiple, often synergistic, causes likely influence dispersal (Ronce et al., 2001), predation pressure in the vicinity of nest sites appears substantial enough to be an important selective force favoring vigorous and immediate dispersal in iguanas (Drummond and Burghardt, 1982).

Although avian and squamate predation appears to be a significant threat to mainland iguanine hatchlings (Drummond and Burghardt, 1982; Van Devender, 1982; Rivas et al., 1998), snakes appear to be a major and potentially underestimated predator of insular iguanas. The colubrid snake *A. anomalus* has been observed preying on hatchling iguanas (*C. cornuta*) as they emerge from beach nests (Henderson and Powell, 2004). On Grand Cayman Island, *A. cantherigerus caymanus* was seen attempting to capture a hatchling iguana (*C. lewisi*) minutes after release from an enclosure (Goodman and Burton, 2005). In this study, *Alsophis* were documented converging on nests minutes after iguana emergence and preying on hatchlings (pers. observation). Werner (1983) observed up to 85 snakes migrating “long distances” to attack emerging Galapagos marine iguanas (*Amblyrhynchus cristatus*). However, the low detectability of snakes at other Galapagos study sites led her to believe that snakes were not a significant predator of hatchling Galapagos land iguanas (*Conolophus pallidus*).

This study demonstrated that underestimating potential impacts of snake predation on insular iguana hatchlings is ill-advised. Snakes are uncommonly observed on Andros because of the fragmented limestone topography of the island. Despite low detection, snakes were the primary predator of iguana hatchlings. Since relative snake predation of iguana hatchlings in this study appeared to taper after three weeks and with distance from nest, future investigations are needed to determine the underlying physiological mechanisms responsible for the ability of snakes to detect and trail newly emerged hatchlings.

This study also provides baseline data to investigate the role of dispersal and predation on conservation management for iguanas on Andros Island and throughout islands of the Caribbean and Pacific. Particular to Andros, studies (Chapter 2) have demonstrated the importance of protecting pine woodland habitats for adult iguanas, while results from this study suggest protecting mangroves because they serve as relatively safe dispersal conduits for hatchling iguanas. Additional studies are needed to investigate potential ontogenetic habitat selection and attempt to isolate selective factors behind individual dispersal behavior.

This study was conducted in an area free from non-native mammalian predators and large-scale anthropogenic disturbances. Under these natural conditions on Andros, the low hatchling survivorship is most likely compensated by a long life span, low adult mortality, and the persistence of extensive and unchanging habitat (Iverson, 2004a). Much of Andros, however, is affected directly by anthropogenic impacts (Chapter 2) and feral mammalian predators, which are common throughout much of the island and have been demonstrated to effectively reduce iguana densities or extirpate populations on other

islands (e.g., Wiewandt, 1977; Iverson, 1978). The low survival rates of hatchlings when interacting only with native predators may have a multiplicative effect when non-native mammalian predators are established in the environment. Studies should be conducted in areas close to human settlements to determine the impact of non-native mammals on the predators of hatchlings, and also on area hatchlings. Survival data can and will be used in future population viability analyses to increase prediction accuracy stemming from potential management decisions.

Iguanas inhabiting island systems are endangered typically because of habitat loss and increased predation pressure from introduced non-native mammals (Alberts, 2000). Dispersal distances from nest sites and habitat preferences while dispersing are important considerations when attempting to establish protected areas on islands becoming increasingly fragmented because of habitat destruction or degradation. Conservation programs for *Cyclura* iguanas increasingly involve translocating lizards to augment declining populations or establish new ones (Knapp and Hudson, 2004). The dispersal distances in this study (maximum = 2300 m in four days) should serve as a guide when attempting to establish protected areas because hatchlings may not stay in predetermined areas but disperse to unsuitable habitats.

The impacts of non-native mammalian predators are well documented (Iverson, 1978), but we are unaware of predation impacts stemming from native fauna. These native impacts may play a role in shaping translocation programs, which rely typically on islands free only of non-native mammalian predators (Knapp and Hudson, 2004). For a small, slowly reproducing population recently adjusting to a translocation, any reduction in recruitment could hinder the success of the program. Therefore, both non-native and

native predators should be evaluated prior to translocation or relocation programs for endangered insular iguana species.

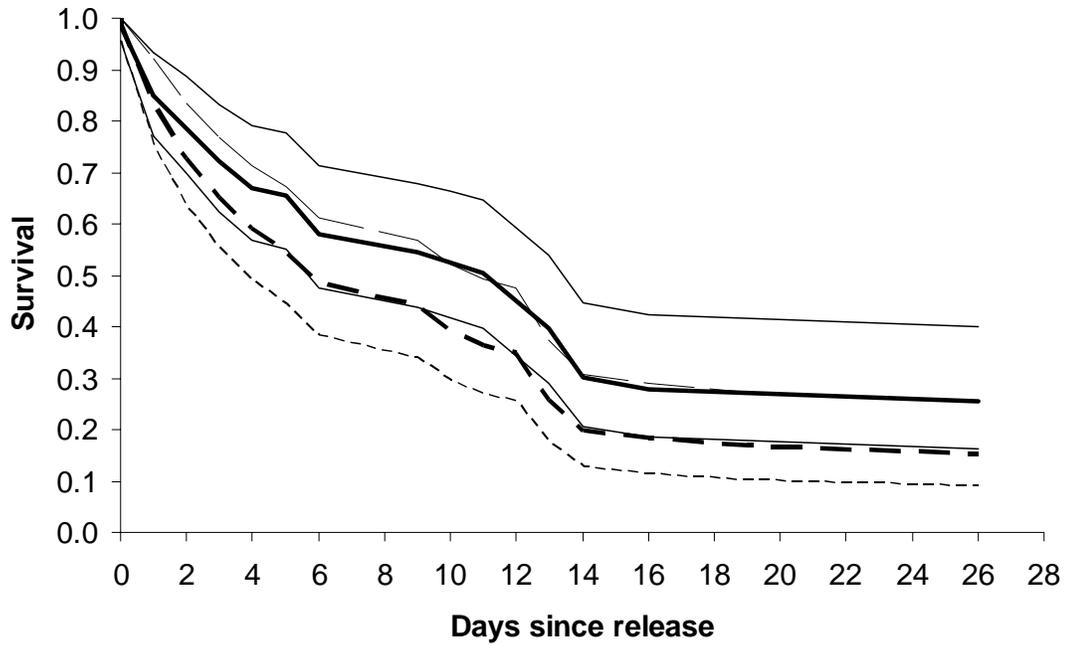


Figure 5-1. Kaplan-Meier survival curves with 95% confidence intervals for Andros iguana hatchlings using combined 2003 and 2004 data. Hatched lines represent the pessimistic estimate (with 95% C.I.) where all censored hatchlings were assumed dead. Solid lines represent the optimistic estimate (with 95% C.I.) where every censored observation was assumed not a death and that the hatchlings survived to the end of the study.

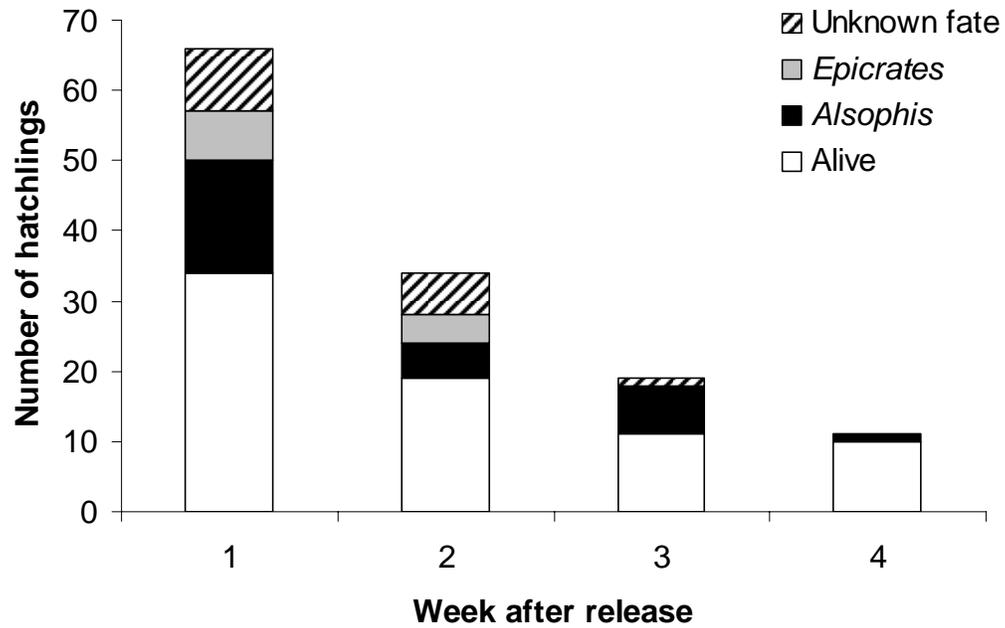


Figure 5-2. Weekly fates of Andros iguana hatchlings with number of hatchlings confirmed killed per week by snakes species.

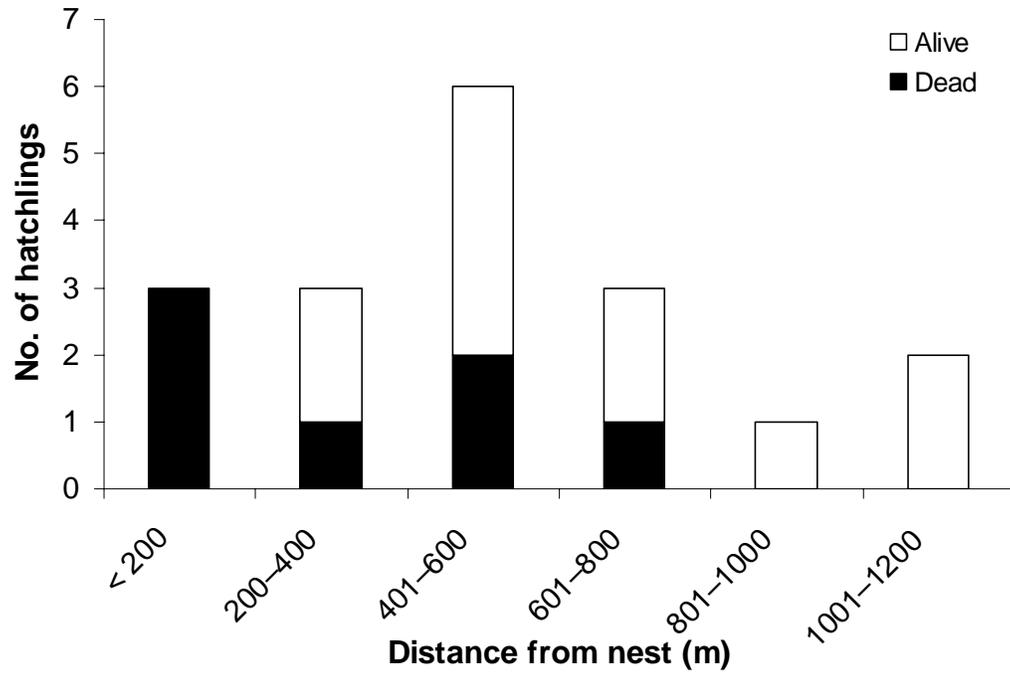


Figure 5-3. Distance away from corresponding nests and fate of Andros iguana hatchlings surviving a minimum of 14 days (n = 18).

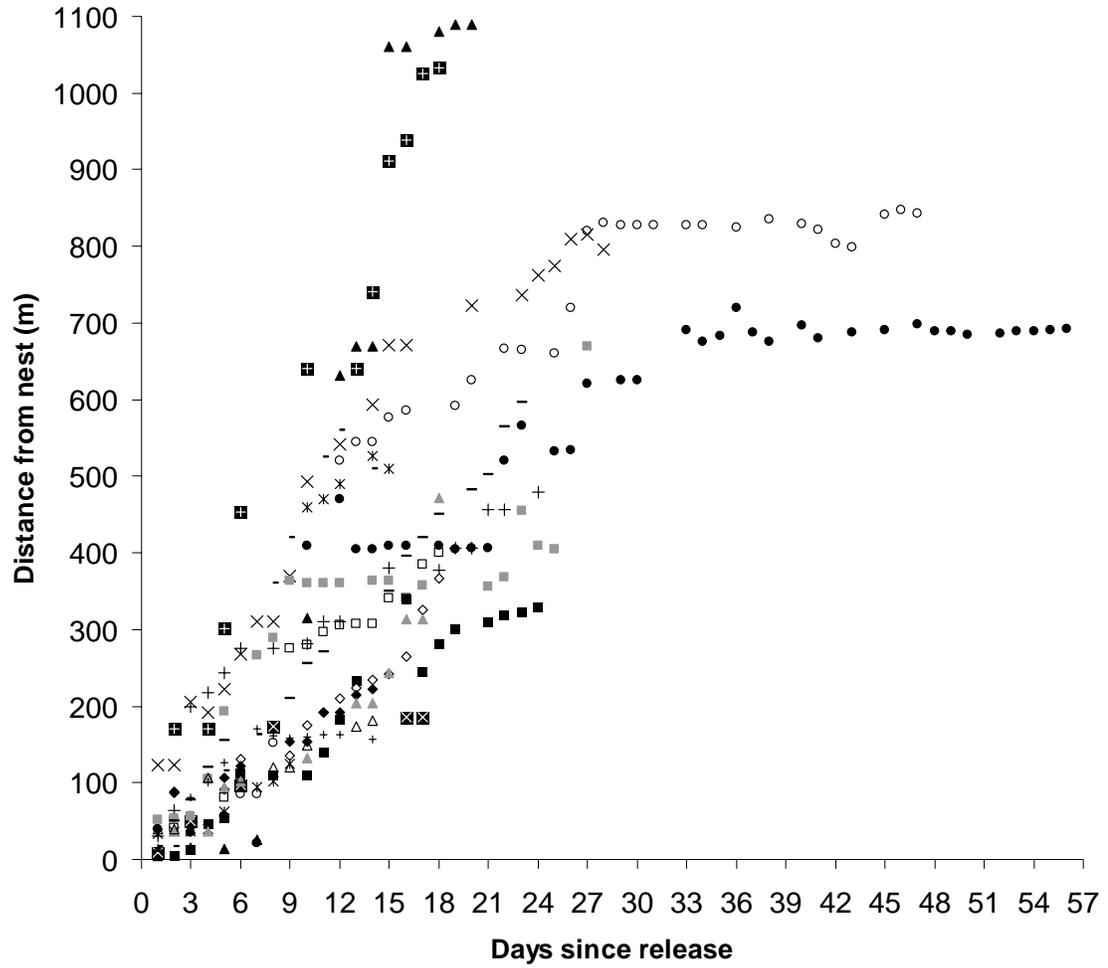


Figure 5-4. Individual dispersal distances away from nests for Andros iguana hatchlings surviving a minimum of 14 days. Symbols series represent individual iguanas.

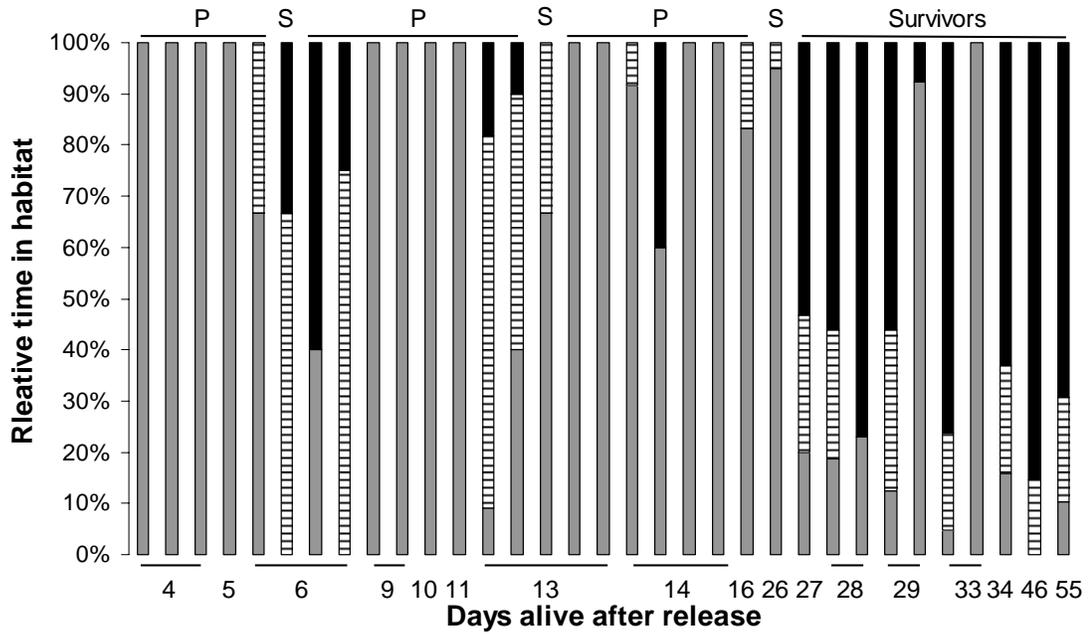


Figure 5-5. Histogram depicting habitat use for hatchling iguanas surviving a minimum of four days (see methods). The lower horizontal axis represents days alive since release and are grouped when applicable using lines. The upper horizontal axis represents location of death or depicts survivors. Pine woodland = "P" and evergreen shrubland = "S." Grey bars depict pine woodlands, hatched bars evergreen shrubland, and black bars depict mangroves.

CHAPTER 6  
POTENTIAL FOR IGUANA-BASED ECOTOURISM ON SOUTH ANDROS  
ISLAND, BAHAMAS

**Introduction**

In tropical island systems such as the Caribbean, tourism is primarily a coastal industry focusing on cruise ship and resort clientele (Lowe and Sullivan-Sealy, 2003). However, although not traditionally considered a destination for ecotourists, the Caribbean is currently encountering a surge of travelers interested in natural areas and wildlife (Knapp, 2004). Studies have demonstrated that revenues earned through ecotourism, if managed properly, have potential to augment local economies, positively influence local attitudes, and fund conservation initiatives (Honey, 1999; Archabald and Naughton-Treves, 2001; Walpole and Goodwin, 2001; Walpole et al., 2001).

One major component attracting ecotourists is a flagship species (Krüger, 2005) and if such species are absent, the market for ecotourism can be severely limited (Munn, 1992). Large charismatic bird and mammal species typically are associated with flagship species, and thus with sustainable ecotourism initiatives (Krüger, 2005). However, not all biodiversity-rich areas retain traditional charismatic megafauna. For example, the Caribbean Islands (including the Bahamas) are a biological hotspot because of the large number of endemic species occurring in rapidly disappearing habitats (Hedges and Woods, 1993; Myers et al., 2000). The area lacks traditional megafauna and instead supports the smallest species of frog, lizard, and bird (Estrada and Hedges, 1996; Hedges and Thomas, 2001). The Caribbean Islands also have dozens of highly threatened species,

including two species of solenodon (giant shrews), four species of nesting sea turtles, the Cuban crocodile, and the most endangered group of iguanas in the world (genus *Cyclura*; Alberts, 2000).

As the largest native terrestrial vertebrate on the islands, the long-lived Caribbean iguanas qualify as a potential flagship species (Caro and O'Doherty, 1999). The Caribbean iguanas of the genus *Cyclura* include many of the largest, most impressive lizards in the Western Hemisphere. The lizards inhabit tropical dry forest and beach scrub habitats on the Greater Antillean Islands, Puerto Rico Bank, Grand Cayman, Bahama Islands, and Turks and Caicos Islands. Under International Union for Conservation of Nature and Natural Resources (IUCN) criteria, all but four taxa are listed as either critically endangered or endangered (Alberts, 2000). Threats include competition with and predation by feral animals, smuggling for the wildlife trade, subsistence hunting, and stochastic processes influenced by isolation, restricted ranges, and small population sizes. With one exception (Hispaniola), each island supports only one species of iguana. Of the nine species in the genus *Cyclura*, three inhabit the Bahamas.

The Andros iguana (*C. cyclura cyclura*) is the only iguana in the Bahamas that is not confined to small cays but faces unique pressures relative to the remaining archipelago. Predation by feral animals (e.g. cats, dogs, and hogs), habitat loss, and illegal hunting severely threaten this species. Subsistence hunting of the iguana dates back to the Lucayan Indians and the first European settlers (Campbell, 1978). Although formally protected by the Bahamian government in 1968, illegal hunting still persists though at unquantified levels. Consequently, the Andros iguana is listed as Endangered

according to IUCN Red List criteria (Knapp and Buckner, 2004) and also placed under Appendix I of CITES.

This study addresses the possibility of establishing protected areas and promoting ecotourism using the Andros iguana as a flagship species. Since realistic potentials of certain flagship species must be assessed (Krüger, 2005), this initial pilot study was carried out using questionnaires distributed to Andros visitors to assess tourist perceptions of the native iguana and iguana-related activities including guided tours. The willingness for tourists to pay for guide services and entrance fees into hypothetical national parks also were evaluated with the assumption that revenue generated from park fees could ultimately be directed back to conservation initiatives and park management. Additionally, using in-depth interviews, I assessed local perceptions of the Andros iguana, historic and contemporary hunting practices, and potential support for protected areas. The assessment of local responses toward protected areas, including knowledge, perceptions, attitudes, and expectations is viewed widely as a crucial step in achieving the goals of national parks (Fletcher, 1990; Sah and Heinen, 2001; Jim and Xu, 2002; Weladji et al., 2003). Historic and contemporary hunting pressures have never been quantified on Andros and their effects on ecotourism and the ultimate survival of the Andros iguana remain equivocal. Results from this study could provide insight to the governments of other Caribbean Islands interested in using iguanas as flagship species for ecotourism and as surrogates for habitat conservation.

The Bahamas currently leads the Caribbean region in both number of tourists and tourism revenues. In 2000, the Bahamas received 4,056,582 tourists, and tourist expenditures accounted for a total of US\$ 1.8 billion (Lowe and Sullivan-Sealy, 2003).

The Bahamas has great potential to promote two tourism markets because of the fragmented, insular geography of the country (Lowe and Sullivan-Sealy, 2003). The two markets include 1) the mass tourism sector for resort and cruise ship clientele centered in Nassau and Freeport and, 2) the ecotourism market concentrated in the Out Islands (islands other than New Providence and Grand Bahama). Visitation to the Out Islands comprises approximately 16% of all Bahamian tourism (Lowe and Sullivan-Sealy, 2003) but is projected to increase as more development projects gain momentum on islands away from New Providence and Grand Bahama.

In 2002, the size of the national park system of the Bahamas was doubled with the addition of 10 new protected areas. These new areas, incorporating both marine and terrestrial habitats, increased the total national system to more than 283,280 ha and the total number of sites to twenty-five. All national parks in the Bahamas come under the jurisdiction of the Bahamas National Trust (BNT). The BNT was mandated by an act of Parliament in 1959 with the responsibilities and legal authority to manage the national parks of the country. The BNT is the only non-governmental organization in the world to have the ultimate responsibility for a country's entire national park system. Although the expansion of protected areas is admirable in principle, most areas are not staffed with educators or wardens and remain "parks on paper." Because of the island geography of the country, it is expensive and nearly impossible currently for the Bahamas to staff and monitor all national parks.

Andros is the largest island in the Bahamian archipelago (~ 165 km long by 65 km wide) encompassing an area of 5,959 km<sup>2</sup>, supporting a human population between 7,000 and 8,000 concentrated in 22 settlements along the eastern coast and one on the

northwest coast. This subtropical island is actually a composite of three main inhabited islands (North Andros, Mangrove Cay, and South Andros), along with dozens of associated cays, separated by saline tidal channels termed bights. From east to west, a coastal ridge (to 30 m elevation) gives way to a flat and pine-forested interior. Approximately halfway across the island, forest grades into extensive mangroves as the water table reaches the surface, and then is reduced to extensive mud flats.

Andros contributes significantly to the collective natural resource wealth of the Bahamas. The third longest barrier reef in the world trails down its eastern margin and the island contains the highest known density of blue holes in the world. The extensive mangrove, and shallow water flats system are responsible for the island being known as the “bonefishing capital” of the world. The island also contains the largest reservoir of freshwater in the archipelago.

With the doubling of the park system, the Central Andros National Parks (total area 115,770 ha) were established, which protect inland forest, coral reef, and wetland nursery areas on North Andros Island (Figure 6-1). Unfortunately, these protected areas are not ideal for iguana conservation because they are located on North Andros Island, which is severely degraded habitat for iguanas because of feral animals, loss of habitat, logging roads that allow access to the island interior, and illegal hunting pressure. The South Andros area is relatively pristine in comparison and the BNT is presently considering additional protected areas in the region. Therefore, this study is expected to influence management decisions concerning future protected areas.

## **Methods**

### **Tourist Surveys**

The survey methods were developed as part of a pilot project to outline basic information that can be used to develop management strategies for the current and future national parks on Andros. A formal questionnaire was designed that targeted Andros tourists. The questionnaire emphasized the Andros iguana; however, attitudes towards wildlife in general and national parks also were addressed. The questionnaire consisted of 18 questions that were intended to document tourist characteristics such as 1) general profile, 2) motivations for visit, 3) knowledge of the Andros iguana, and 4) willingness to pay fees for both guided excursions to observe wildlife, and entrance fees into national parks. The questions developed were primarily closed-ended with a maximum of six response options. The questionnaire was designed to require only a few minutes to complete and general comments were welcomed.

Seven resorts and hotels, both locally and foreign owned, were approached to participate in the survey. Ultimately, four resorts/hotels and one private guest house located on Mangrove Cay and South Andros distributed the questionnaire to their guests between December 2003 and May 2005. Questionnaires were distributed one per family at time of guest check-in to minimize influences from external sources during their stay on the island.

### **Local Interviews**

Opportunistic interviews were used to gauge respondent's attitudes towards national parks and also to quantify current and historic iguana hunting pressures. Respondents were limited to one per household and no more than four people were interviewed per settlement. Thirty-one interviews of male (74%, n = 23) and female

(24%, n = 8) respondents, varying in length from 10 to 55 minutes, were conducted in October 2002 and May 2004. The majority of interviews (65%, n = 20) were conducted in nine settlements on South Andros followed by three settlements on Mangrove Cay (26%, n = 8) and two settlements on North Andros (9%, n = 3). All respondents were initially informed that their responses would be confidential. Respondents were interviewed in an in-depth, semi-structured and open-ended approach to garner important qualitative information and to increase comfort levels. This format also allowed respondents to answer some target questions without prompting and reduced the duration of “formal” question inquiry.

After a series of demographic questions (age, sex, profession, family composition, perception of wealth), respondents were asked about their contact with iguanas. A series of dichotomous (yes/no) questions were asked regarding respondent’s historic and contemporary use of iguanas. Two categories of questions were asked: 1) questions regarding historic use of iguanas including whether respondents hunted, ate, sold, or bought iguanas, and 2) questions pertaining to current uses of iguanas including whether respondents currently hunt, eat, sell, or buy iguanas. The dichotomous questions were followed by one open-ended question to gauge attitudes toward protected areas. Protected areas were explained as areas set aside to protect wildlife (e.g., fish, crab, iguanas, white-crown pigeons) and excluded all hunting or fishing in order to provide for future generations and to attract tourists. Based on respondent’s open-ended response, answers were categorized as positive, cautious, negative, or did not know. Pre-testing was conducted on a small subset of residents on South Andros prior to the study to ensure that all questions were clear, and a final version was prepared for sampling. Some interviews

were recorded on tape (with consent) and later transcribed, or reconstructed from notes taken during interviews.

Data were analyzed in SPSS 11.0 by cross tabulation and when requirements were met, chi-square tests were applied to combinations of independent (i.e., gender) and dependent variables. Dependent variables were the answers to multiple choice questions. Answers to other open questions were used for qualitative interpretation. Insights from dozens of additional informal conversations from other local representatives between 2001 and 2004 pertaining strictly to hunting iguana also were used for qualitative interpretation.

## **Results**

### **Tourist Profile and Attitudes**

Survey results indicate that 90% of the study population came from the United States followed by the Bahamas (7%) and the United Kingdom (3%). Among respondents, 57% were males and 43% females, traveling mostly as couples (37%) or in groups of two or more friends (25%). During the survey, Andros Island tended to receive middle age to older clientele with tourists ranging primarily from 50–59 (28%), 40–49 (24%), and 30–39 yrs (20%). Reported annual household income was generally greater than US\$ 90,000 (34%) or between US\$ 30,000 and US\$ 60,000 (28%). Most respondents had previously visited the Bahamas (50%) two to four times but the majority (53%) was making a first visit to Andros Island. Primary motivations for visiting Andros were significantly different for males and females ( $\chi^2 = 31.92$ ,  $df = 3$ ,  $P < 0.0005$ ). The deviation from independence was influenced primarily by more males (50%,  $n = 29$ ) than females (2%,  $n = 1$ ) listing “fishing” as their primary reason for visiting the island followed by more females (28%,  $n = 12$ ) than males (5%,  $n = 3$ ) listing “other water

activities.” However, combined gender responses indicate that the primary motivation for visiting the island was to “relax” (36%) followed by “fishing” (30%; Table 6-1).

Only 34% of respondents reported awareness that an endemic iguana inhabited Andros Island. This awareness appeared to stem from a variety of sources (Table 7-2). No trends were uncovered for differences in iguana awareness between gender ( $\chi^2 = 0.395$ ,  $df = 1$ ,  $P = 0.53$ ) or primary motivation for visit ( $\chi^2 = 1.488$ ,  $df = 3$ ,  $P = 0.69$ ). The majority of tourists were interested (74%) or somewhat interested (21%) in observing iguanas on the island. Of tourists that were interested, 57% ( $n = 43$ ) were willing, and 28% ( $n = 21$ ) were somewhat willing to pay for a guided tour to observe iguanas and other wildlife. Of tourists that were willing to pay for a guided wildlife tour, 52% ( $n = 23$ ) were willing to pay from US\$ 20–39, 32% ( $n = 14$ ) were willing to pay from US\$ 40–59, 9% ( $n = 4$ ) were willing to pay less than US\$ 20, and 7% ( $n = 3$ ) were willing to pay from US\$ 60–79. All respondents were willing (89%) or somewhat willing (11%) to pay an entrance fee into a national park if the money benefited wildlife. The majority of respondents were willing to pay from US\$ 10–14 (52%,  $n = 52$ ), and US\$ 5–9 (27%,  $n = 27$ ; Table 6-2).

### **Local Respondent Profile and Attitudes**

Ages of local respondents ranged from 24 to 93 yrs with the majority ranging from 40–49 yrs (32%,  $n = 10$ ) followed by 80–89 yrs (16%,  $n = 5$ ) and 30–39 yrs (13%,  $n = 4$ ; Figure 6-2). Most people interviewed were fisherman (29%,  $n = 9$ ), worked in the hotel industry (16%,  $n = 5$ ), or owned their own small businesses (16%,  $n = 5$ ). The majority of respondents (74%,  $n = 23$ ) considered themselves “comfortable” in terms of wealth followed by poor (23%,  $n = 7$ ) and rich (3%,  $n = 1$ ).

According to the surveys, hunting does not appear to be a female-related activity as no women reported hunting iguanas currently or in the past. However, among males 17% (n = 4) admitted to hunt iguanas currently, while 38% (n = 8) reported hunting iguanas in the past. Of men that reported to still hunt, 75% (n = 3) were fishermen and the other listed “mechanic” as his profession. Fifty-percent of the men reported to hunt currently were from the ages of 40–50 yrs, while the two others were from 30–39 and 60–69 yrs.

No women reported to eat iguanas currently but six men (21%) aged 30 and over admitted they still eat iguanas (including the four men hunting currently). Eating iguana was more common in the past, with 63% (n = 5) of women and 57% (n = 13) of men aged 20 years and over, spanning all reported professions, stating that they have eaten iguana. One mechanic reported to sell iguanas currently, although one fisherman admitted to having sold iguanas in the past. Currently, two men aged between 60 and 79 years reported buying iguanas currently. Four men and one woman aged 40 and over reported buying iguanas for consumption in the past. Virtually all respondents were aware that hunting occurred in the past, and 55% (n = 17) were aware that hunting still occurs on the island.

The majority of local respondents (45%, n = 14) expressed cautious attitudes concerning national parks followed closely by positive (42%, n = 13), and distantly by negative attitudes (7%, n = 2). Women (50%, n = 4) had relatively positive attitudes toward national parks compared to men (39%, n = 9). Men (52%, n = 12) were relatively more cautious about the formation of national parks than females (25%, n = 2). Younger

respondents from 20–29 and 30–39 years appeared relatively more positive about the benefits of national parks (67 and 75%, respectively) than older respondents (Figure 6-2).

## **Discussion**

### **Tourism Potentials**

Visitors to Andros are interested in a variety of outdoor activities, including fishing, relaxing, and water sports instead of mass market tourism such as casinos, resorts, or shopping opportunities associated with Nassau and Freeport. This trend toward interest in the outdoors also is evident in the Exuma Island chain of the Bahamas where visitors are interested primarily in “natural beauty” (Lowe and Sullivan-Sealy, 2003). Tourists interested in the environment, outdoor activities, and ecotourism are generally well educated and enjoy a high income (Wearing and Neil, 1999), which results in a greater willingness to spend money in destination countries (Boo, 1991; Wight, 1996). This type of tourist also possesses an environmental ethic and willingness not to degrade the natural resources responsible for their interest in visiting an area (Wearing and Neil, 1999). Data from this study suggest that visitors to Andros Island possess high household incomes and are generally interested in paying for guided wildlife tours to see iguanas and other natural features. However, currently there are limited opportunities for visitors to participate in tours operated by local entrepreneurs.

Promoting non-traditional flagship species such as reptiles tends to be more difficult than for their high-profile mammalian counterparts (but see Tisdell and Wilson, 2002; Walpole and Leader-Williams, 2002 for exceptions with nesting sea turtles and the Komodo dragon, respectively). However, because iguanas are large, photogenic, and charismatic, they have the potential to serve as flagship species for ecotourism endeavors and surrogates for promoting conservation of the tropical dry forest and beach scrub

ecosystems they inhabit. A small ecotourism market exists currently in the form of annual “citizen scientist” research expeditions dedicated to study Bahamian iguanas. Participants of these research expeditions pay (~ US\$ 2,000) to participate in long-term iguana research projects on Andros and several islands in the Exuma Island chain (Knapp, 2004). Additionally, tour companies based in Nassau and Great Exuma offer one-day excursions to islands in the northern and central Exuma chain to view iguanas (Iverson et al, 2004a; pers. observation). While promoting conservation is not the focal point of the one-day iguana viewing excursions, the willingness of tourists (e.g., as many as 500 per week) to pay (~ US\$ 100) to observe iguanas underscores the potential for a sustainable ecotourism market if company actions are modified to promote conservation and sustainable activities.

The majority of Andros tourists were interested (74%) or somewhat interested (21%) in observing iguanas on the island. Most tourists interested were willing or somewhat willing to pay from US\$ 20–39 for a guided tour to observe iguanas and other wildlife. Andros contains one of the largest tracts of wilderness in the Caribbean and current surveys demonstrate that it harbors a vast amount of biological diversity (Currie et al., 2005) and potential for wildlife conservation facilitated through ecotourism. An ecotourism market using the iguana as a focal species, yet involving also the abundant avian fauna, near shore coral reefs, and terrestrial blue hole systems has great potential to lure visitors to the island throughout the year. Successful flagships are those that can be readily seen (Krüger, 2005) and the Andros iguana in particular employees a unique nesting behavior of depositing eggs in termitaria and then guarding the mound for up to six weeks (Chapter 3). This behavior is consistent, predictable,

unique, and provides visitors with exceptional photographic and personal encounters with the lizards. However, other insular markets (i.e. Galapagos Islands) have exposed the negative impacts of ecotourism such as animal behavior modification and habitat degradation (Kenchington, 1989). Therefore, any potential impacts on wildlife and habitats have to be evaluated and monitored for ecotourism programs to be sustainable (e.g., Romero and Wikelski, 2002; Müllner et al., 2004).

Tourists to Andros are overwhelmingly in favor of paying entrance fees into national parks if the money goes towards conserving wildlife and natural areas. All respondents in this study were willing (89%) or somewhat willing (11%) to pay an entrance fee into a national park if the money benefited wildlife. The majority of respondents was willing to pay from US\$ 10–14 and US\$ 5–9 for entrance fees. Revenue generated via entrance fees could be circulated back into park facilities, education programs, staff, and equipment. For example, in the Exuma Cays Land and Sea Park located in the Central Bahamas, all revenues earned currently from mooring fees (equated to an entrance fee) for yachtsmen and gift shop sales are circulated back into the operating budget and fund the entire operating costs of the Park (at limited staff and operations; T. Barbernitz, pers. communication). Statistics provided by the Bahamas Ministry of Tourism ([tourismbahamas.org](http://tourismbahamas.org)) indicate that 10,690 tourists visited Andros Island in 2004. Conservatively, if only 75% of Andros visitors paid entrance fees of US\$ 10, a total of US\$ 80,170 would be generated and could be circulated back into operational costs.

### **Local Perception and Attitude**

A reoccurring theme during the interview process with local residents was that the practice of hunting iguana was not as common as in the past and that it was becoming

slowly obsolete. It appeared that hunting iguana was tied to farming, fishing, and crabbing while men camped away from settlements or were in their farm plots deep inland. Yet Andros is no longer tied as closely to the land because food is imported primarily from Nassau. Respondents overwhelmingly stated “you have to go out back into the bush to find iguana.” Earlier generations lived closer to the land in the 1920s–50s, which is most likely why older respondents had more knowledge of hunting iguana and accounts of how the lizards were captured and prepared for meals. Iguanas were reported to be captured typically using dogs or by smoking the lizards out of their limestone retreats or subterranean holes. Iguanas were, and currently are, kept alive until eaten by sewing their mouths shut and tying their limbs behind their backs (S. Buckner, pers. communication).

Perceived hunting declines should be viewed with caution. In 1973 Walter Auffenburg (field notes deposited in Florida Museum of Natural History) reported that hunting iguana was becoming less common on Andros. Despite more than 30 years since these observations, 17% of men interviewed in this study hunt iguana. In addition, recent anecdotal accounts (with personal documented evidence) of locals collecting up to 41 iguanas on two forays into the island interior emphasize the importance of continued monitoring. Although iguanas are taken most often opportunistically by people associated with the island interior (e.g., fishermen, crabbers), a 13 year old boy recently bragged to my field assistant about hunting iguanas with dogs. I also was informed from five independent sources that iguanas, depending on the size, are sold for US\$ 50 and that the meat could be purchased in local restaurants under the pseudonym “hush hush.”

The success of management strategies depends on whether various stakeholders are positively or negatively affected by conservation (see Walpole and Goodwin, 2001). Thus, the attitudes and perceptions of the stakeholders towards a conservation area and the policies being implemented are an important element for sustainable conservation (Weladji et al., 2003). The local respondents in this study were mostly optimistic or cautious about national parks, with the knowledge that they were areas set aside for wildlife protection and excluded hunting or fishing. Most of the older respondents observed a decline in marine resources over the years and were remarkably astute about the benefits of exclusion zones. Cautious attitudes were linked primarily to the marine resources followed by the ability to collect the semi-terrestrial land crab (*Cardisoma guanhumi*), which is a substantial socio-cultural event on the island. Many respondents resonated that “the people of Andros fish for a living—you can’t take that away from them—they need it.” Other respondents believed in excluding commercial fishing but allowing sustenance fishing for families. A fear of exclusionary take zones was that the zones would exclude most people, but that others with special connections would still be able to hunt/fish and take the “lion’s share.” These attitudes suggest that people perceive potential parks as beneficial if they do not limit their activities. These results corroborate surveys around parks in Ecuador and Africa, where people agreed on the necessity to protect forest for future generations, but showed negative attitudes towards the daily manifestations and consequences of conservation (Fiallo and Jacobson, 1996; Ite, 1996, Bauer, 2003).

Imposing regulations that restrict legitimate resource-usage rights, while giving little in return to local inhabitants, can generate hostility from local stakeholders (Alberts,

1996; Jim and Xu, 2002). In 1986, after 27 years as a National Park, the Exuma Cays Land and Sea Park in the Bahamas was designated a “no take” zone both in the sea and on the islands. The benefits of the change in policy were not communicated adequately to local inhabitants and heavy poaching ensued followed by strict enforcement. The lack of communication and local input perpetrated violent threats against the park warden and necessitated intervention by the Bahamian Defense Force. Local Andros responses underscore the importance of good communication between park, project, and local communities with regard to the rights and responsibilities in natural resource management. The local respondents on Andros expressed the desire to be involved with protected area planning and enforcement. Efforts should be made to include local stakeholder opinions in designating protected areas and regulations. Minimally, outreach programs should be installed to not only convey the benefits of protected areas, but also promote and help market sustained ecotourism endeavors.

### **Conclusions**

This study served as an effective tool for gathering initial information to assist with developing tourism management strategies designed to facilitate wildlife and habitat conservation. However, the tourism market is dynamic and information on the current visitor structure is reliable for only a specific period of time (Lowe and Sullivan-Sealy, 2003). A procedure for monitoring visitors should be developed to update tourism information. The local government on North Andros is diligent in distributing post-stay questionnaires at airports. These questionnaires should be expanded to Mangrove Cay and South Andros, and include information concerning ecotourism interest. Additionally, potential impacts to wildlife and habitat must be evaluated to ensure a long-term sustainable program.

With notable exceptions, I conclude cautiously that contemporary hunting on Andros is an opportunistic event and occurs at lower levels than in the past; however, additional interviews are needed to further support this conclusion. Known hunting camps in the island interior should be monitored for illegal poaching and known perpetrators persuaded to stop the activity. Illegal hunting of an endangered animal that experiences additional external perturbations, slow growth, and extended age to maturity is detrimental to the survival of the species.

Although this study did not reveal many negative attitudes towards future protected areas, it was undertaken before area demarcation. Patterns of attitude, both of tourism and conservation, may change as the realities of protected areas materialize. It is therefore important that longitudinal monitoring of attitudes towards protected areas and ecotourism, as well as the effectiveness of protected areas be implemented throughout the entire process.

Provided that opportunistic poaching pressure is curtailed and the other threats perturbing iguana populations are mitigated, Andros Island has the potential to highlight a large charismatic reptile as a flagship species to support an ecotourism market that ideally facilitates conservation. The Andros iguana relies on diverse habitats for survival (Chapter 2) and the responsible promotion of the iguana as an ecotourism flagship will benefit island-wide biodiversity. More detailed studies, taking into account other relationships between people, parks, and wildlife might provide greater insights into the mechanisms that shape visitor and local attitudes towards conservation in the Bahamas and the greater Caribbean region.

Table 6-1. Demographic profiles and primary motivation for visitors (n = 101) to Andros Island.

Characteristics	n	Sample %
<b>Age</b>		
Under 20	4	4.0
20–29	13	12.9
30–39	20	19.8
40–49	24	23.8
50–59	28	27.7
Over 60	12	11.9
<b>Party Size</b>		
Couple	37	36.6
Family	16	15.8
Friends of 2 or more	25	24.8
Individual	12	11.9
Tour group	11	10.9
<b>Household income (US\$)</b>		
< 30K	5	5.0
30–60K	28	27.7
60–90K	18	17.8
> 90K	34	37.7
No response	16	15.8
<b>Number of Visits to the Bahamas/Andros</b>		
First	26/53	25.7/52.5
2–4	50/34	49.5/33.7
5–7	9/6	8.9/5.9
8–10	1/1	0.9/1.0
> 10	4/4	4.0/4.0
N/A	7/–	6.9/–
No response	4/3	4.0/3.0
<b>Primary motivation for visiting</b>		
Fish	30	29.7
Other water activities	15	14.9
Relax	36	35.6
Other	20	19.8

Table 6-2. Source of iguana awareness and willingness to pay for guided tours and national park entrance fees for visitors (n = 101) to Andros Island.

Special issue	n	Sample %
Source of Iguana Awareness		
Friend	6	22.2
Guide book	1	3.7
Magazine	3	11.1
Travel agent/tour operator	3	11.1
World wide web	5	18.5
Other	9	33.3
Interest in observing iguanas		
No	5	5.0
Somewhat	21	20.8
Yes	75	74.3
Willingness to pay for guided tours		
No	25	24.8
Somewhat	31	30.7
Yes	44	43.6
No response	1	1.0
Amount willing to pay for guided tour (US\$)		
< 20	9	11.4
20–39	46	58.2
40–59	18	22.8
60–79	4	5.1
No response	2	2.5
Amount willing to pay for NP entrance fee (US\$)		
< 5	7	6.9
5–9	27	26.7
10–14	52	51.5
15–19	2	2.0
> 20	9	9.0
No response	4	4.0

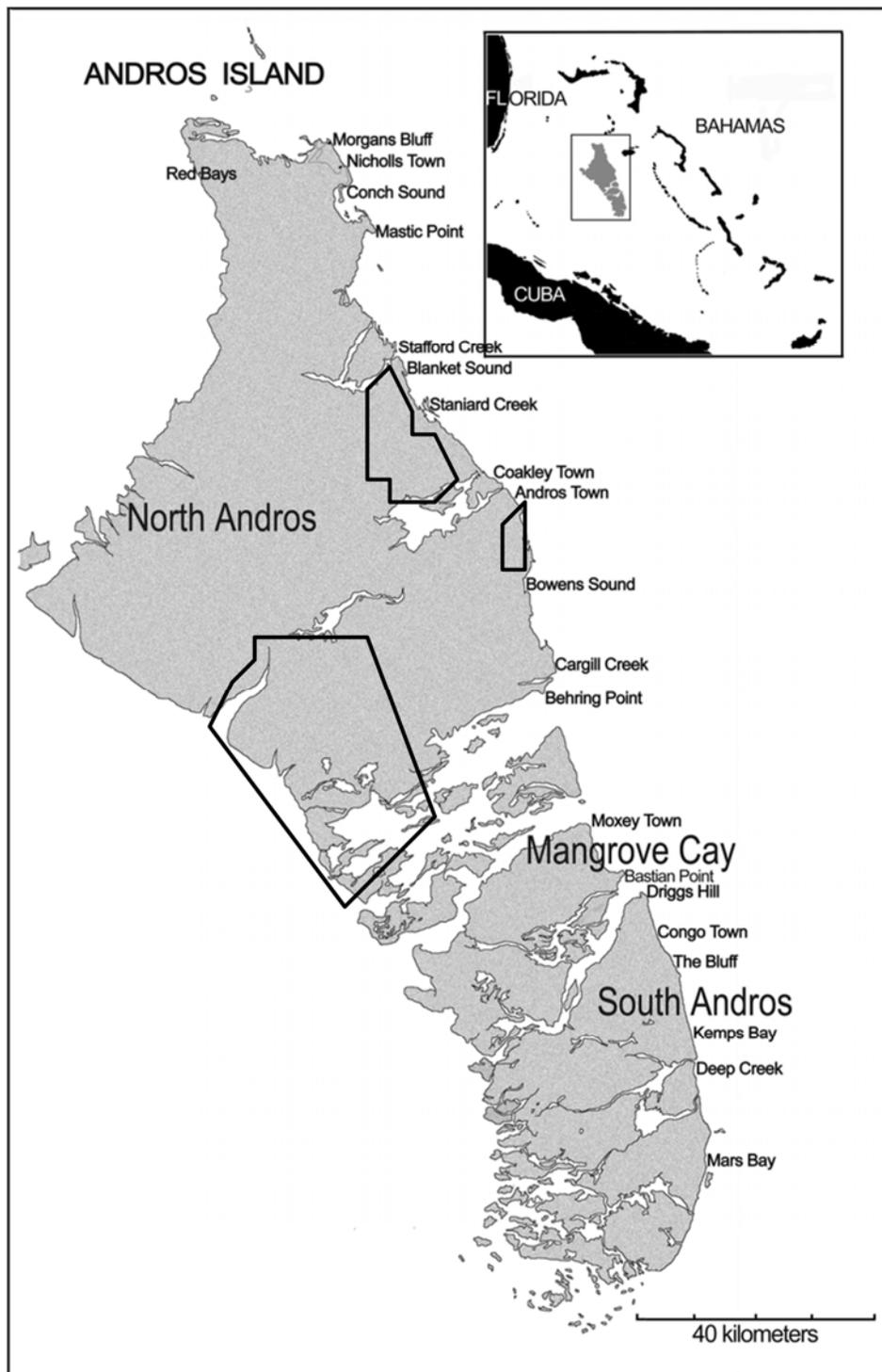


Figure 6-1. Map of Andros Island, Bahamas depicting the three terrestrial protected areas of the Central Andros National Parks. Not shown are the two offshore protected marine areas.

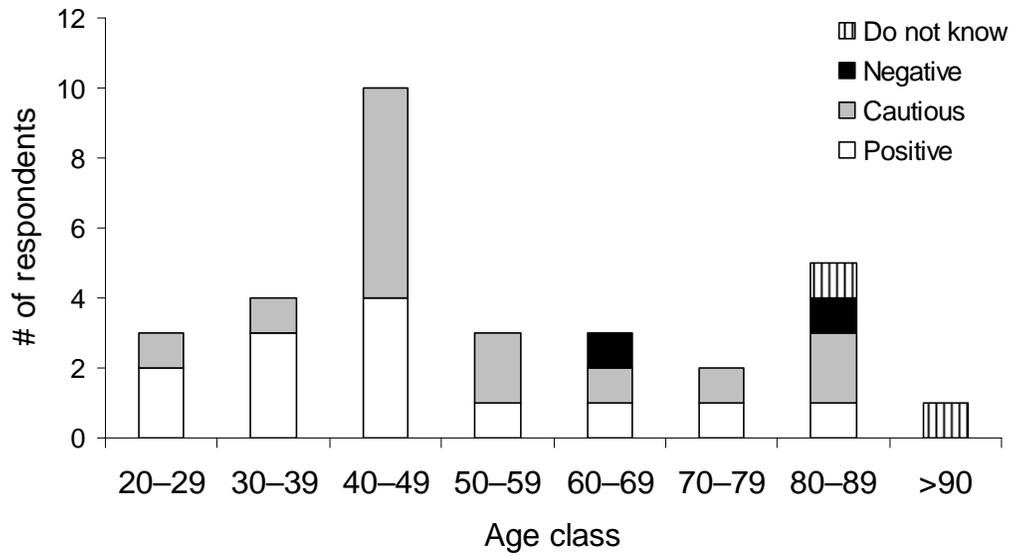


Figure 6-2. Age demography for the local respondents from Andros Island, Bahamas with relative attitudes towards exclusionary protected areas.

## CHAPTER 7 CONSERVATION RECOMMENDATIONS FOR THE ANDROS IGUANA

The purpose of this study was to conduct basic life history studies to acquire data germane in assisting conservation management decisions for the Andros iguana (*Cyclura cyclura cyclura*). The study focused specifically on habitat requirements of adult iguanas, reproductive ecology, and survival probabilities and dispersal of hatchlings. Attempts also were made to investigate the potential for human involvement in the active conservation of the iguana. Below are conservation recommendations specifically for the Andros iguana but also knowledge gaps that require attention in the future. The benefits of data garnered through this study for other iguana species inhabiting insular systems throughout the Caribbean and Pacific are also outlined.

Results from this study demonstrate that the Andros iguana selects pine woodland with open broadleaf understory. This habitat should be a conservation priority when developing protected areas on the island. However, open pine woodlands also are extremely important for resource land managers who view the areas as premium sites for pine extraction. North Andros contained one of the largest virgin stands of open pine habitat in the Caribbean region. In the 20<sup>th</sup> century, this area was impacted continually by human activity including sisal production, large scale, government-subsidized land clearing for agriculture, and logging (Eshbaugh and Wilson, 1996). Crisscrossed logging tracts over secondary and tertiary pine forests can still be seen from the air over North Andros (pers. observation). Large-scale clearing operations not only destroyed iguana habitat but also opened up the impenetrable island interior to people. Access to the

interior is possible via thousands of kilometers of historic hard-packed primary and secondary logging roads. Local residents use the old roads when hunting feral pigs but also shoot iguanas when seen. Iguana survival on north Andros is hampered further by predation from feral cats, dogs, and pigs. Consequently, iguana densities on North Andros are extremely low causing even experienced illegal subsistence hunters to travel south in search of iguanas (Knapp et al., 1999; W. Colebrooke, pers. comm.).

The southern and southwestern portion (south of Mangrove Cay) of Andros is relatively pristine in comparison to North Andros (Eshbaugh and Wilson, 1996). Although feral cats have been observed in the interior of Mangrove Cay up to 20 km from the nearest settlement, feral pigs have yet to reach this area because of the North Bight water separation. Additionally, commercial logging practices were not initiated in the area because much of the pineland is on hummocks of high ground surrounded by lower elevated mangrove and marsh. These isolated “pine islands” support the largest pines remaining in the Bahamas (Campbell, 1978) and are areas of high conservation priority for iguanas.

Open pinelands are important for iguanas but I found that iguanas use all represented habitat types. Other *Cyclura* species have been reported inhabiting mangrove systems on San Salvador, Bahamas (S. Buckner, pers. comm.) and Cuba (J. Thorbjarnarson, pers. comm.) but my 3rd order selection results suggest that mangroves may be marginal habitat on Andros and used year-round by submissive or senescent males. These areas may be extremely important for the ontogenetic cycling structure of male iguanas and should be protected. In addition, we have observed large male and female iguanas inhabiting isolated “pine islands” without noted termite nest mounds. I

also have encountered adult iguanas 800 m into emergent limestone mangrove areas. I strongly suspect that these mangrove systems are dispersal corridors that allow access to isolated habitats. As previously noted, females actively seek out suitable termite mounds and have been noted swimming water channels and crossing mangrove areas speculatively in search of mounds for oviposition. In addition, preliminary data suggest that mangroves may be important habitat for the survival of newly hatched iguanas (Chapter5).

Further, the home range data may be applied to population survey techniques. Iguana orientation across the landscape is characterized by temporal and spatial heterogeneity, which ultimately affects detectability. Sampling designs should benefit from this a priori knowledge of iguana movement patterns and be structured accordingly (Williams et al., 2002).

The predominant use of termitaria by female iguanas for oviposition sites should be addressed in conservation management planning. Although it appears that in at least some subpopulations the behavior is facultative, it is unknown how the island-wide population would adapt to wide-spread environmental change such as the loss of termitaria. Furthermore, there are no ancillary nesting options for many subpopulations because of a complete lack of soil, which is characteristic of Andros Island. Therefore, the monitoring and protecting of termitaria, through local education, should be incorporated into management initiatives. Knowledge of nest-site characteristics preferred by females and the associated habitats where termitaria are found also will assist managers in designing areas of formal protection such as national parks.

Andros Island harbors a vast amount of terrestrial biological diversity in general, and the south Andros area in particular holds great potential for iguana conservation. The isolated small and large cays of the south/southwestern area lack feral animals and are far from human settlements. Protecting iguana habitat preserves large-scale ecosystems since iguanas are found in, and rely on multiple habitat types comprised of economically important species (i.e., land crabs, *Cardisoma guanhumi* and *Gecarcinus lateralis*), Bahamian-endemic plants (e.g., *Cephalocereus bahamensis*, *Crossopetalum coriaceum*, *Eupatorium bahamense*, *Heliotropum eggersii*, *Neobraccia bahamensis*, *Vanilla correllii*, and *Vernonia arbuscula*; Correll and Correll, 1982; E. Freid, pers. communication) and reptiles (i.e., *Alsophis vudii*, *Anolis smaragdinus*, and *Tropidophis canus*; Schwartz and Henderson, 1991), and migratory bird species (e.g., *Dendroica coronata*, *Dumetella carolinensis*, *Icteria virens*, *Limnothlypis swainsonii*, and *Passerina ciris*; Wunderle and Waide, 1993).

If people value surrounding natural areas and wildlife, they are more prone to protect those areas and wildlife. Establishing businesses that profit from responsibly showcasing the natural environment of Andros potentially can generate vested interest in environmental protection. Data from this study suggest that visitors to Andros Island are generally interested in paying for guided wildlife tours to see iguanas and other natural features. However, currently there are limited opportunities for visitors to participate in tours operated by local entrepreneurs. Efforts should be made to increase the opportunity local businesses on Andros that cater to eco-oriented visitors. Currently, there is a business on South Andros that specializes in inland blue hole tours focusing on geology and medicinal plants in the area. Similar enterprises should be expanded to North Andros

Island, which receives more visitors than South Andros. Terrestrial activities have not been promoted as rigorously on Andros as water-related activities. Organized terrestrial-related excursions would diversify business opportunities for the local population and activities for visitors.

Additionally, the Bahamas National Trust should initiate an entrance fee program for current and future parks on Andros geared toward foreign visitors. Tourists to Andros are overwhelmingly in favor of paying entrance fees into national parks if the money goes towards conserving wildlife and natural areas. Currently, the parks on Andros are merely “parks on paper” but revenue generated via entrance fees could be circulated back into park facilities, education programs, staff, and equipment.

Although the term “umbrella species” and its effectiveness towards ecosystem protection is debated (Simberloff, 1998), others have argued that a species-driven approach to conservation draws attention to only a small part of the biodiversity crisis and that a more comprehensive approach is needed (Meffe and Carroll, 1997). Only multiple species-specific studies, comprehensive ecosystem function investigations, and law enforcement will ensure that we have adequate knowledge and determination to protect entire ecosystems (Simberloff, 1998). However, protecting the mosaic of iguana-required habitat in the south Andros area is the best alternative until adequate investigations are conducted.

Lastly, the local Andros community must take stewardship and assume the role of actively protecting their iguanas. Only in this manner will the long-term survival of this impressive lizard be realized. To reach this goal, education programs should be initiated on the island that advocate protecting the Andros iguana and other wildlife. I attempted to

facilitate the process by giving presentations in schools using a live iguana to capture and retain the attention of students. Dozens of students eventually participated in a contest to create murals for a conservation poster that was distributed throughout the island (Figure 7-1). I also have encouraged students to participate in iguana field research and have had up to three student assistants at a time in the field with me (Knapp, 2005). I have worked with a local teacher on North Andros to organize a soccer program at the Central Andros Middle School. The new team is named the “iguanas” and we obtained funding through the Shedd Aquarium in Chicago to provide equipment costs and team tee shirts promoting a conservation message (Figure 7-2). I am proud of the individuals on Andros that have taken a proactive role in promoting the conservation of the wildlife of Andros Island. It will, however, require sustained efforts from local communities to insure the long-term protection of iguanas and natural areas on the island. My hope is that the Andros iguana and associated programs act as a catalyst for further local involvement.

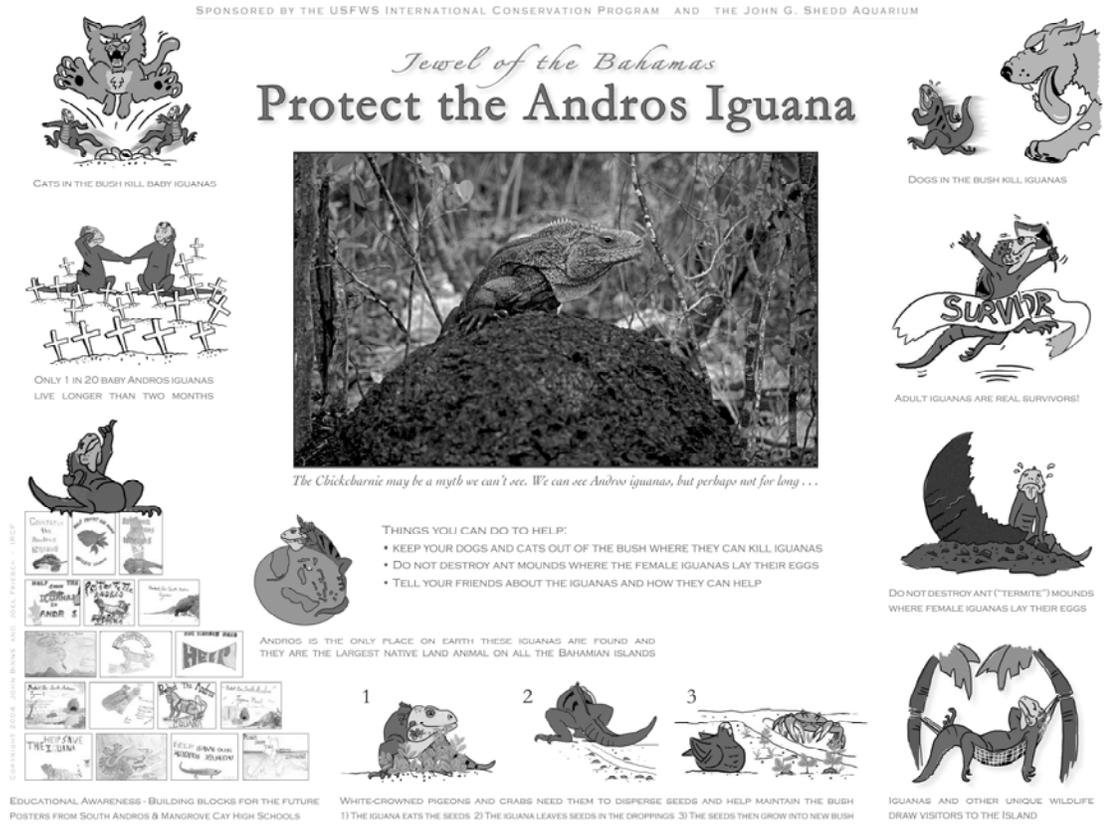


Figure 7-1. Grayscale version of conservation poster for the Andros iguana that incorporates student murals in the lower left corner.



Figure 7-1. Soccer team tee shirts to be distributed to student players on North Andros.

## LIST OF REFERENCES

- Abts, M. L. 1987. Environment and variation in life history traits of the chuckwalla, *Sauromalus obesus*. *Ecological Monographs* 57:215-232.
- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Alberts, A. C., (ed.). 2000. West Indian Iguanas: status survey and conservation action plan. IUCN-the World Conservation Union, Gland, Switzerland.
- Allredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 50:157-165.
- Allredge, J. R., and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 56:1-9.
- Alpert, P. 1996. Integrated conservation development projects: examples from Africa. *Bioscience* 46:845-855.
- Andrews, R., and A. S. Rand. 1974. Reproductive effort in anoline lizards. *Ecology* 55:1317-1327.
- Archabald, K., and L. Naughton-Treves. 2001. Tourism revenue-sharing around national parks in western Uganda: early efforts to identify and reward local communities. *Environmental Conservation* 28:135-149.
- Arnold, S. J. 1992. Behavioral variation in natural populations. VI. Prey responses by two species of garter snakes in three regions of sympatry. *Animal Behavior* 44:705-719.
- Auffenberg, W. 1994. *The Bengal Monitor*. University of Florida Press, Gainesville, Fla., USA.
- Baird, T. A., Sloan, C. L., Timanus, D.K., 2001. Intra- and inter-seasonal variation in the socio-spatial behavior of adult male collard lizards. *Crotaphytus collaris* (Reptilia, Crotaphytidae). *Ethology* 107, 15-32.
- Ballinger, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 58:628-635.

- Ballinger, R. E. 1983. On the nature of life history variation in lizards. Pages 241-260. In Huey, R. B., E. R. Pianka, and T. W. Schoener (eds.), *Lizard ecology: studies on a model organism*. Harvard University Press, Cambridge, Mass., USA.
- Bauer, H. 2003. Local perceptions of Waza National Park, northern Cameroon. *Environmental Conservation* 30:175-181.
- Bernardo, J. 1996. Maternal effects in animal ecology. *American Zoologist* 36:83-105.
- Berry, O., M. D. Tocher, D. M. Gleeson, and S. D. Sarre. 2005. Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. *Conservation Biology* 19:855-864.
- Berven, K. A. 1988. Factors affecting variation in reproductive traits within a population of wood frogs (*Rana sylvatica*). *Copeia* 1988:606-615.
- Berven, K. A., and D. E. Gill. 1983. Interpreting geographic variation in life-history traits. *American Zoologist* 23:85-97.
- Bingham, R. L., and L. A. Brennan. 2004. Comparison of Type I error rates for statistical analyses of resource selection. *Journal of Wildlife Management* 68:206-212.
- Bissell, A. N., and E. P. Martins. 2004. Behavior and ecology of rock iguanas, II: population differences. Pages 109-118. In Alberts, A. C., R. L. Carter, W. K. Hayes, and E. P. Martins (eds.), *Iguanas: biology and conservation*, University of California Press, Berkeley, Calif., USA.
- Bjurlin, C. D., and J. A. Bissonette. 2004. Survival during early life stages of the desert tortoise (*Gopherus agassizii*) in south-central Mojave Desert. *Journal of Herpetology* 38:527-535.
- Boardman, M. R., and C. K. Carney. 2000. Joulter Cays and North Andros Island, Bahamas. Bahamian Field Station, Ltd., San Salvador, Bahamas.
- Boo, E. 1991. Planning for ecotourism. *Parks* 2:4-8.
- Brattstrom, B. H. 1974. The evolution of reptilian social behavior. *American Zoologist* 14:35-49.
- Brøseth, H., J. Tufto, H. C. Pedersen, H. Steen, and L. Kastdalen. 2005. Dispersal patterns in a harvested willow ptarmigan population. *Journal of Applied Ecology* 42:453-459.
- Buckner, S., and D. Blair. 2000. Species account: *Cyclura cychlura cychlura*. Pages 31-32. In Alberts, A. (ed.), *West Indian Iguanas: status survey and conservation action plan*. IUCN-the World Conservation Union, Gland, Switzerland.

- Bull, J. J., W. H. N. Gutzke, and M. G. Bulmer. 1988. Nest choice in a captive lizard with temperature-dependent sex determination. *Journal of Evolutionary Biology* 2:177-184.
- Burger, J. 1993. Colony and nest site selection in lava lizards *Tropidurus* spp. In the Galapagos islands. *Copeia* 1993:748-753.
- Burton, F. J. 2004. *Cyclura lewisi* (Grand Cayman blue rock iguana) Reproduction. *Herpetological Review* 35:388-389.
- Calsbeek, R., and T. B. Smith. 2003. Ocean currents mediate evolution in island lizards. *Nature* 426:552-555.
- Campbell, D. G. 1978. *The ephemeral islands: A natural history of the Bahamas*. MacMillan Education, Ltd. London, UK.
- Carey, M. W. 1975. The rock iguana, *Cyclura pinguis*, on Anegada, British Virgin Islands, with notes on *Cyclura ricordi* and *Cyclura cornuta* on Hispaniola. *Bulletin of the Florida State Museum, Biological Sciences* 19:189-233.
- Caro, T., and G. O'Doherty. 1999. On the use of surrogate species in conservation. *Conservation Biology* 13:805-814.
- Carpenter, F. L. 1987. The study of territoriality: Complexities and future directions. *American Zoologist* 27:401-409.
- Carroll, S. P., and P. Showers Corneli. 1999. The evolution of behavioral norms of reaction as a problem in ecological genetics: theory, methods, and data. Pages 52-68. In Foster, S. A., and J. A. Endler (eds.), *Geographic variation in behavior: perspectives on evolutionary mechanisms*. Oxford University Press, Oxford, UK.
- Censky, E. J. 1995. Reproduction in two Lesser Antillean populations of *Ameiva plei* (Teiidae). *Journal of Herpetology* 29:553-560.
- Christian, K. A., and C. R. Tracy. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia* 49:218-223.
- Clark, T. W. 1992. Practicing natural resource management with a policy orientation. *Environmental Management* 16:423-433.
- Cogger, H. G. 1967. *Australian reptiles in colour*. Sydney, Australia.
- Cole, L. C. 1949. The measurements of interspecific association. *Ecology* 30:411-424.
- Collett, D. 2003. *Modelling survival data in medical research*. Chapman and Hall/CRC, Boca Raton, Fla., USA.

- Conner, L. M., and B. W. Plowman. 2001. Using Euclidean distances to assess nonrandom habitat use. Pages 275-290. In Millsbaugh, J. J., and J. M. Marzluff (eds.), Radio tracking and animal populations. Academic Press, San Diego, Calif., USA.
- Conner, L. M., M. D. Smith, and L. W. Burger. 2002. A comparison of distance-based analyses of habitat use. *Ecology* 84:526-531.
- Conover, D. O., and E. T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology and Evolution* 10:248-252.
- Correll, D. S., and H. B. Correll. 1982. Flora of the Bahama Archipelago. J. Cramer, Vaduz, Liechtenstein.
- Cowles, R. B. 1928. The life history of *Varanus niloticus*. *Science* 67:317-318.
- Cowles, R. B. 1930. The life history of *Varanus niloticus* (Linnaeus) as observed in natal South Africa. *Journal of Entomology and Zoology* 22:1-31.
- Currie, D., J. M. Wunderle, Jr., D. N. Ewert, M. R. Anderson, A. Davis, and J. Turner. 2005. Habitat distribution of birds wintering in central Andros, the Bahamas: implications for management. *Caribbean Journal of Science* 41:75-87.
- Deeming, D. C. (ed.). 2004. Reptilian incubation: environment, evolution and behaviour. Nottingham University Press, Nottingham, UK.
- Doughty, P., and B. Sinervo. 1994. The effects of habitat, time of hatching, and body size on the dispersal of hatchling *Uta stansburiana*. *Journal of Herpetology* 28:485-490.
- Downes, S. J., and M. Adams. 2001. Geographic variation in antislake tactics: the evolution of scent-mediated behavior in a lizard. *Evolution* 55:605-615.
- Drummond, H., and G. M. Burghardt. 1982. Orientation in dispersing hatchling green iguanas, *Iguana iguana*. Pages 271-291. In Burghardt, G. M., and A. S. Rand (eds.), Iguanas of the world: their behavior, ecology, and conservation. Noyes Publications, Park Ridge, N.J., USA.
- Drummond, H., and G. M. Burghardt. 1983. Geographic variation in the foraging behavior of the garter snake, *Thamnophis elegans*. *Behavioral Ecology and Sociobiology* 12:43-48.
- Du, W., J. Xiang, Y. Zhang, X. Xu, and R. Shine. 2005. Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (*Takydromus septentrionalis*, Lacertidae). *Biological Journal of the Linnean Society* 85:443-453.

- Dunham, A. E. 1982. Demographic and life-history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life-history phenomena in lizards. *Herpetologica* 38:208-221.
- Dunham, A. E., Miles, D. B., and D. N. Reznick. 1988. Life history patterns in squamate reptiles. Pages 441-522. In C. Gans and R. B. Huey (eds.), *Biology of the Reptilia*. Vol. 16. Ecology B. Defense and life history. Alan R. Liss, Inc., New York, N.Y., USA.
- Ehmann, H., Swan, G., Swan, G., and B. Smith. 1991. Nesting, egg incubation and hatching by the heath monitor *Varanus rosenbergi* in a termite mound. *Herpetofauna* 21:17-24.
- Elgar, M. A., and L. J. Heaphy. 1989. Covariation between clutch size, egg weight and egg shape: comparative evidence for chelonians, *Journal of Zoology* 219:137-152.
- Eshbaugh, W. H., and T. K. Wilson. 1990 The tropical tree flora of Andros Island, Bahamas: observations and notes. Pages 17-23. In Smith, R. R. (ed.), *Proceedings of the Third Symposium on the Botany of the Bahamas*. Bahamian Field Station, Ltd., San Salvador, Bahamas.
- Eshbaugh, W. H., and T. K. Wilson. 1996. On the need to conserve Bahamian floral biodiversity. Pages 77-82. In Elliott, N. B., D. C. Edwards, and P. J. Godfrey (eds.), *Proceedings of the sixth symposium on the natural history of the Bahamas*. Bahamian Field Station, Ltd. San Salvador, Bahamas.
- Estrada, A. R., and S. B. Hedges. 1996. At the lower size limit in tetrapods: a new diminutive frog from Cuba (Leptodactylidae: *Eleutherodactylus*). *Copeia* 1996:852-859.
- Ferguson, G., and S. F. Fox. 1984. Annual variation of survival advantage of large side-blotched lizards, *Uta stansburiana*: its causes and significance. *Evolution* 38:342-349.
- Fiallo, E. A., and S. K. Jacobson. 1995. Local communities and protected areas: attitudes of rural residents towards conservation and Machililla National Park, Ecuador. *Environmental Conservation* 22:241-249.
- Fitch, H. S. 1985. Variation in clutch and litter size in New World reptiles. University of Kansas Museum of Natural History Miscellaneous Publications 76:1-76.
- Fletcher, S. A. 1990. Parks, protected areas and local populations: new international issues and imperatives. *Landscape and Urban Planning* 19:241-249.

- Ford, N. B., and R. A. Siegel. 1994. Phenotypic plasticity: implications for captive-breeding and conservation programs. Pages 175-182. In Murphy, J. B., K. Adler, and J. T. Collins (eds.), *Captive management and conservation of amphibians and reptiles*. Society for the Study of Amphibians and Reptiles, Ithaca, N.Y., USA. *Contributions to Herpetology*, Volume 11.
- Garcia, A., G. Ceballos, and R. Adaya. 2003. Intensive beach management as an improved sea turtle conservation strategy in Mexico. *Biological Conservation* 111:253-261.
- Gibbs, J. P., and D. A. Steen. 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. *Conservation Biology* 19:552-556.
- Gillis, R., and R. E. Ballinger. 1992. Reproductive ecology of red-chinned lizards (*Sceloporus undulatus erythrocheilus*) in Southcentral Colorado: comparisons with other populations of a wide-ranging species. *Oecologia* 89:236-243.
- Glor, R. E., J. B. Losos, and A. Larson. 2005. Out of Cuba: overwater dispersal and speciation among lizards in the *Anolis carolinensis* subgroup. *Molecular Ecology* 14:2419-2432.
- Goodman, R. M. 2005. Attachment of radio transmitters in a rock iguana, *Cyclura nubila lewisi*. *Herpetological Review* 36:150-152.
- Goodman, R. M., and F. J. Burton. 2005. *Cyclura lewisi* (Grand Cayman blue iguana) Hatchlings. *Herpetological Review* 36:176.
- Goodyear, N. C., and J. Lazell. 1994. Status of a relocated population of endangered *Iguana pinguis* on Guana Island, British Virgin Islands. *Restoration Ecology* 2:43-50.
- Gotthard, K., and S. Nylin. 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* 74:3-17.
- Greene, H. W., G. M. Burghardt, B. A. Dugan, and A. S. Rand. 1978. Predation and the defensive behavior of green iguanas (Reptilia, Lacertilia, Iguanidae). *Journal of Herpetology* 12:169-176.
- Gregory, P. T., and K. W. Larsen. 1993. Geographic variation in reproductive characteristics among Canadian populations of the common garter snake (*Thamnophis sirtalis*). *Copeia* 1993:946-958.
- Harlow, P. S., and J. E. Taylor. 2000. Reproductive ecology of the jacky dragon (*Amphibolurus muricatus*): an agamid lizard with temperature-dependent sex determination. *Austral Ecology* 25:640-652.

- Harris, D. M. 1982. The phenology, growth, and survival of the green iguana, *Iguana iguana*, in northern Columbia. Pages 150-161. In Burghardt, G. M., and A. S. Rand (eds.), *Iguanas of the world: their behavior, ecology, and conservation*. Noyes Publications, Park Ridge, N.J., USA.
- Haughland, D. L., and K. W. Larsen. 2004. Ecology of North American red squirrels across contrasting habitats: relating natal dispersal to habitat. *Journal of Mammalogy* 85:225-236.
- Hayes, W. K., R. L. Carter, S. Cyril, Jr., and B. Thorton. 2004. Conservation of an endangered Bahamian rock iguana, I: Population assessments, habitat restoration, and behavioral ecology. Pages 232-257. In Alberts, A. C., R. L. Carter, W. K. Hayes, and E. P. Martins (eds.), *Iguanas: biology and conservation*, University of California Press, Berkeley, Calif., USA.
- Hedges, S. B. 1996. The origin of West Indian amphibians and reptiles. Pages 95-128. In Powell, R., and R. W. Henderson, (eds.), *Contributions to West Indian Herpetology: a tribute to Albert Schwartz*, Society for the study of amphibians and reptiles, Ithaca, NY, USA. *Contributions to Herpetology*, volume 12.
- Hedges, S. B., and C. A. Woods. 1993. Caribbean hotspot. *Nature* 364:375.
- Hedges, S. B., and R. Thomas. 2001. At the lower size limit in amniote vertebrates: a new diminutive lizard from the West Indies. *Caribbean journal of Science* 37:168-173.
- Henderson, R. W., and R. Powell. 2004. Thomas Barbour and the Utowana voyages (1929-1934) in the West Indies. *Bonner Zoologische Beiträge* 52:305-309.
- Henderson, R. W., and R. A. Sajdak. 1996. Diets of West Indian racers (Colubridae: *Alsophis*): composition and biogeographic implications. Pages 327-338. In Powell R., and R.W. Henderson (eds.), *Contributions to West Indian herpetology: a tribute to Albert Schwartz*. Society for the Study of Amphibians and Reptiles, *Contributions to Herpetology*, volume 12, Ithaca, N.Y., USA.
- Honey, M. 1999. *Ecotourism and Sustainable Development: Who Owns Paradise?* Island Press, Washington, D.C., USA.
- Hooge, P. N., B. Eichenlaub, and E. Solomon. 1999. *The animal movement program*. USGS, Alaska Biological Science Center, Anchorage, Alaska, USA.
- Hudson, R. D., and A. C. Alberts. 2004. The role of zoos in the conservation of West Indian iguanas. Pages 274-289. In Alberts, A. C., R. L. Carter, W. K. Hayes, and E. P. Martins (eds.), *Iguanas: biology and conservation*, University of California Press, Berkeley, Calif., USA.
- Isaac, J. L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review* 35:101-115.

- Ite, U. E. 1996. Community perceptions of the Cross River National Park, Nigeria. *Environmental Conservation* 23:351-357.
- Iverson, J. B. 1978. The impact of feral cats and dogs on populations of the West Indian rock iguana, *Cyclura carinata*. *Biological Conservation* 14:63-73.
- Iverson, J. B. 1979. Behavior and ecology of the rock iguana, *Cyclura carinata*. *Bulletin of the Florida State Museum, Biological Sciences* 24:175-358.
- Iverson, J. B. 1982. Adaptations to herbivory in iguanine lizards. Pages 60-76. In G. M. Burghardt and A. S. Rand (eds.), *Iguanas of the world: their behavior, ecology, and conservation*. Noyes Publications, Park Ridge, N.J., USA.
- Iverson, J. B., K. N. Hines, and J. M. Valiulis. 2004a. The nesting ecology of the Allen Cays rock iguana, *Cyclura cyclura inornata* in the Bahamas. *Herpetological Monographs* 18:1-36.
- Iverson, J. B., G. R. Smith, and L. Pieper. 2004b. Factors affecting long-term growth of the Allen Cays rock iguana in the Bahamas. Pages 176-192. In Alberts, A. C., R. L. Carter, W. K. Hayes, and E. P. Martins (eds.), *Iguanas: biology and conservation*. University of California Press, Berkeley, California, Calif., USA.
- Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology*. 22:227-237.
- Jim, C. Y., and S. S. W. Xu. 2002. Stifled stakeholders and subdued participation: interpreting local responses toward Shimentai Nature Reserve in South China. *Environmental Management* 30: 327-342.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* 21:449-480.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457-481.
- Kellert, S. R. 1994. A sociological perspective: valuational, socioeconomic, and organizational factors. Pages 371-389. In Clark, T. W., R. P. Reading, and A. L. Clarke (eds.), *Endangered species recovery: finding the lessons, improving the process*. Island Press, Washington, D. C., USA.
- Kenchington, R. A. 1989. Tourism in the Galapagos Islands: the dilemma of conservation. *Environmental Conservation* 16:227-236.

- King, D., and B. Green. 1979. Notes on diet and reproduction of the sand goanna, *Varanus gouldii rosenbergi*. *Copeia* 1979:64-70.
- King, D., and B. Green. 1993. Goanna: The biology of varanid lizards. New South Wales University Press, Kensington, Australia.
- King, R. B. 2000. Analyzing the relationship between clutch size and female body size in reptiles. *Journal of Herpetology* 34:148-150.
- Knapp, C. R. 2000. Home range and intraspecific interactions of a translocated iguana population (*Cyclura cyclura inornata* Barbour and Noble). *Caribbean Journal of Science* 36:250-257.
- Knapp, C. R. 2001. Status of a translocated *Cyclura* iguana colony in the Bahamas. *Journal of Herpetology* 35:239-248.
- Knapp, C. R. 2004. Ecotourism and its potential impacts on iguana conservation in the Caribbean. Pages 290-301. In Alberts, A. C., R. L. Carter, W. K. Hayes, and E. P. Martins (eds.), *Iguanas: biology and conservation*, University of California Press, Berkeley, Calif., USA.
- Knapp, C. R. 2005. Working to save the Andros iguana. *Iguana* 12:8-13.
- Knapp, C. R., and S. D. Buckner. 2004. *Cyclura cyclura* ssp. *cyclura*. In 2004 IUCN Red List of Threatened Species. [www.redlist.org](http://www.redlist.org).
- Knapp, C., S. Buckner, A. Feldman, and L. Roth. 1999. Status update and empirical field observations of the Andros rock iguana, *Cyclura cyclura cyclura*. *Bahamas Journal of Science* 7:2-5.
- Knapp C. R., and R. D. Hudson. 2004. Translocation strategies as a conservation tool for West Indian iguanas: Evaluations and recommendations. Pages 199-209. In A. C. Alberts, R. L. Carter, W. K. Hayes, and E. P. Martins (eds.), *Iguanas: biology and conservation*, University of California Press, Berkeley, Calif., USA.
- Knapp, C. R., and A. K. Owens. 2004. Diurnal refugia and novel ecological attributes of the Bahamian Boa, *Epicrates striatus fowleri* (Boidae). *Caribbean Journal of Science* 40:265-270.
- Knapp, C. R., and A. K. Owens. 2005. An effective new radio transmitter attachment technique for lizards. *Herpetological Review* 36:264-266.
- Koenig, W. D., D. van Vuren, and P. N. Hodge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* 21:449-480.

- Korb, J., and K. E. Linsenmair. 2000. Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? *Insectes Sociaux* 47:357-363.
- Krekorian, C. O. 1984. Life history of the desert iguana, *Dipsosaurus dorsalis*. *Herpetologica* 40:415-424.
- Krüger, O. 2005. The role of ecotourism in conservation: panacea or Pandora's box? *Biodiversity and Conservation* 14:579-600.
- Laurie, W. A., and D. Brown. 1990. Population biology of marine iguanas (*Amblyrhynchus cristatus*). II. Changes in annual survival rates and the effects of size, sex, age and fecundity in a population crash. *Journal of Animal Ecology* 59:529-544.
- Lewis, C. B. 1944. Notes on *Cyclura*. *Herpetologica* 2:93-98.
- Little, B. G., D. K. Buckley, A. Jefferiss, J. Stark, and R. N. Young. 1976. Land resources of the Commonwealth of the Bahamas. Volume 4a Andros Island. Land Resources Division, Tolworth Tower, Surrey, UK.
- Lowe, A. M., and K. Sullivan-Sealy. 2003. Establishing sustainable tourism in the Exuma Cays, Bahamas. *Bahamas Journal of Science* 11:17-24.
- Lowe, W. H. 2003. Linking dispersal to local population dynamics: A case study using a headwater salamander system. *Ecology* 84:2145-2154.
- Macdonald, D. W., and D. D. P. Johnson. 2001. Dispersal in theory and practice: consequences for conservation biology. Pages 358-372. In Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols (eds.), *Dispersal*, Oxford University Press, Inc., New York, N.Y., USA.
- Madsen, T. 1987. Cost of reproduction and female life-history tactics in a population of grass snakes, *Natrix natrix*, in southern Sweden. *Oikos* 49:129-132.
- Madsen, T., and R. Shine. 1999. Life history consequences of nest-site variation in tropical pythons (*Liasis fuscus*). *Ecology* 80:989-997.
- Madsen, T., and R. Shine. 2000. Energy versus risk: costs of reproduction in free-ranging pythons in tropical Australia. *Austral Ecology* 25:670-675.
- Malone, C. L., C. R. Knapp, J. F. Taylor, and S. K. Davis. 2003. Genetic consequences of Pleistocene fragmentation: isolation, drift, and loss of diversity in rock iguanas (*Cyclura*). *Conservation Genetics* 4:1-15.
- Manly, B. F. J., L. L. McDonanld, and D. L. Thomas. 1993. Resource selection by animals. Chapman and Hall, London, UK.

- Martin, J. M., and E. J. Heske. 2005. Juvenile dispersal of Franklin's ground squirrel (*Spermophilus franklinii*) from a prairie "island." *American Midland Naturalist* 153:444-449.
- Martins, E. P., A. N. Bissell, and K. K. Morgan. 1998. Population differences in a lizard communicative display: evidence for rapid change in structure and function. *Animal Behaviour* 56:1113-1119.
- Marzluff, J. M., S. T. Knick, and J. J. Millspaugh. 2001. High-tech behavioral ecology: Modeling the distribution of animal activities to better understand wildlife space use and resource selection. Pages 309-326. In Millspaugh, J. J., and J. M. Marzluff (eds.), *Radio tracking and animal populations*. Academic Press, San Diego, Calif., USA.
- Massot, M., R. B. Huey, J. Tsuji, F. H. van Berkum. 2003. Genetic, prenatal, and postnatal correlates of dispersal in hatchling fence lizards (*Sceloporus occidentalis*). *Behavioral Ecology* 14:650-655.
- McClellan, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management* 62:793-801.
- Meffe, G. K., and C. R. Carroll. 1997. *Principles of conservation biology*. Sinauer Associates, Inc., Sunderland, Mass., USA.
- Michaud, E. J., and A. C. Echternacht. 1995. Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. *Journal of Herpetology* 29:86-97.
- Miles, D. B., and A. E. Dunham. 1992. Comparative analyses of phylogenetic effects in the life history patterns of iguanid lizards. *American Naturalist* 139:848-869.
- Mitchell, N. C. 1999. Effect of introduced ungulates on density, dietary preferences, home range, and physical condition of the iguana (*Cyclura pinguis*) on Anegada. *Herpetologica* 55:7-17.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. *Wildlife-habitat Relationships: concepts and applications*. University of Wisconsin Press, Madison, Wis., USA.
- Müllner, A., K. E. Linsenmair, and M. Wikelski. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biological Conservation* 118:549-558.
- Munn, C. A. 1992. Macaw biology and ecotourism, or when a bird in the bush is worth two in the hand. Pages 47-72. In Beissinger, S. R., and N. F. R. Snyder (eds.), *New World parrots in crisis: solutions from conservation biology*. Smithsonian Institution Press, Washington, D. C., USA.

- Myers, N. R., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Nickrent, D. L., W. H. Eshbaugh, and T. K. Wilson. 1988. The vascular flora of Andros Island, Bahamas. Kendall/Hunt, Dubuque, Iowa, USA.
- Niewiarowski, P. H., M. J. Angilletta, and A. D. Leache. 2004. Phylogenetic comparative analysis of life-history variation among populations of the lizard *Sceloporus undulatus*: an example and prognosis. *Evolution* 58:619-633.
- Olsson, M., and R. Shine. 1997. The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). *American Naturalist* 149:179-188.
- Olsson, M., R. Shine, and E. Bak-Olsson. 2000. Locomotor impairment of gravid lizards: is the burden physical or physiological? *Journal of Evolutionary Biology* 13:263-268.
- Olsson, M., R. Shine, and E. Wapstra. 2001. Costs of reproduction in a lizard species: a comparison of observational and experimental data. *Oikos* 93:121-125.
- Owens, A. K., and C. R. Knapp. 2004. *Leiocephalus carinatus coryi* Nest location. *Herpetological Review* 35:392-393.
- Parker, W. S., and W. S. Brown. 1972. Telemetric study of movements and oviposition of two female *Matsicophis t. teaniatus*. *Copeia* 1972:892-895.
- Perry, G., and T. Garland, Jr. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. *Ecology* 83:1870-1885.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7-15.
- Pough, F. H., R. M. Andrews, L. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 2001. *Herpetology*, 2<sup>nd</sup> edition. Prentice Hall. Upper Saddle River, N.J., USA.
- Price, T., and D. Schluter. 1991. On the low heritability of life-history traits. *Evolution* 45:853-861.
- Pregill, C. K., and B. I. Crother. 1999. Ecological and historical biogeography. Pages 335-356. In Crother, B. I. (ed.), *Caribbean amphibians and reptiles*. Academic Press, New York, N.Y., USA.
- Rand, A. S., and H. W. Greene. 1982. Latitude and climate in the phenology of reproduction in the green iguana (*Iguana iguana*). Pages 142-149. In Burghardt G. M. and A. S. Rand (eds.), *Iguanas of the world: their behavior, ecology, and conservation*. Noyes Publications, Park Ridge, N.J., USA.

- Randriamahazo, H. J. A. R., and A. Mori. 2001. Egg-laying activities and reproductive traits in females of *Oplurus cuvieri cuvieri*. *Journal of Herpetology* 35:209-217.
- Reed, M. A., and S. C. Tidemann. 1994. Nesting sites of the hooded parrot *Psephotus dissimilis* in the Northern Territory. *Emu* 94:225-229.
- Reinhold, K. 1998. Nest-site philopatry and selection for environmental sex determination. *Evolutionary Ecology* 12:245-250.
- Riley, J., A. F. Stimson, and J. M. Winch. 1985. A review of Squamata ovipositing in ant and termite nests. *Herpetological Review* 16:38-43.
- Rivas, J. A., C. R. Molina, and T. M. Avila. 1998. *Iguana iguana* (Green Iguana) Juvenile predation. *Herpetological Review* 29:238-239.
- Rodda, G. H., G. M. Bock, G. M. Burghardt, and A. S. Rand. 1988. Techniques for identifying individual lizards at a distance reveal influences of handling. *Copeia* 1988:905-913.
- Roff, D. A. 1992. *The evolution of life histories*. Chapman and Hall, New York, N.Y., USA.
- Romero, L. M., and M. Wikelski. 2002. Exposure to tourism reduces stress-induced corticosterone levels in Galápagos marine iguanas. *Biological Conservation* 108:371-374.
- Ronce, O., I. Olivieri, J. Clobert, and E. Danchin. 2001. Perspectives on the study of dispersal evolution. Pages 341-357. In Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols (eds.), *Dispersal*, Oxford University Press, Inc., New York, N.Y., USA.
- Roosenburg, W. H. 1996. Maternal condition and nest site choice: an alternative for the maintenance of environmental sex determination? *American Zoologist* 36:157-168.
- Ruckelshaus, M., C. Hartway, and P. Kareiva. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* 11:1298-1306.
- Sah, J. P., and J. T. Heinen. 2001. Wetland resource use and conservation attitudes among indigenous and migrant peoples in Ghodaghodi Lake area, Nepal. *Environmental Conservation* 28:345-356.
- Schoener, T. W. 1987. Time budgets and territory size: some simultaneous optimization models for energy maximizers. *American Zoologist* 27:259-291.
- Schwartz, A., and R. W. Henderson. 1991. *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history*. University of Florida Press, Gainesville, Fla., USA.

- Sealey, N. E. 1994. Bahamian landscapes: an introduction to the geography of the Bahamas. Media Publishing, Nassau, Bahamas.
- Sears, M. W. 2005. Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity. *Oecologia* 143:25-36.
- Seigel, R. A., and H. S. Fitch. 1984. Ecological patterns of relative clutch mass in snakes. *Oecologia* 61:293-301.
- Seigel, R. A., and H. S. Fitch. 1985. Annual variation in reproduction in snakes in a fluctuating environment. *Journal of Animal Ecology* 54:497-505.
- Seigel, R. A., and N. B. Ford. 2001. Phenotypic plasticity in reproductive traits: geographical variation in plasticity in a viviparous snake. *Functional Ecology* 15:36-42.
- Shaklee, R. V. 1996. Weather and climate: San Salvador Island, Bahamas. The Bahamian Field Station Limited. San Salvador, Bahamas.
- Shine, R. 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? *Evolution* 46:828-833.
- Shine, R. 1994. Allometric patterns in the ecology of Australian snakes. *Copeia* 1994:851-867.
- Shine, R. 2003a. Effects of pregnancy on locomotor performance: an experimental study on lizards. *Oecologia* 136:450-456.
- Shine, R. 2003b. Locomotor speeds of gravid lizards: placing 'costs of reproduction' within an ecological context. *Functional Ecology* 17:526-533.
- Shine, R. P. S. Harlow, J. S. Keogh, and Boeadi. 1998. The allometry of life-history traits: insights from a study of giant snakes (*Python reticulatus*). *Journal of Zoology* 244:405-414.
- Shine, R., and R. A. Seigel. 1996. A neglected life-history trait: clutch-size variance in snakes. *Journal of Zoology* 239:209-223.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? *Biological Conservation* 83:247-257.
- Sinervo, B. 1994. Experimental tests of reproductive allocation paradigms. Pages 73-90. In Vitt, L. J. and E. R. Pianka (eds.), *Lizard ecology: historical and experimental perspectives*. Princeton University Press, Princeton, N.J., USA.
- Sinervo, B., P. Doughty, R. B. Huey, and K. Zamudio. 1992. Allometric engineering: a causal analysis of natural selection on offspring size. *Science* 258:1927-1930.

- Skov, M. W., and R. G. Hartnoll. 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? *Oecologia* 131:1-7.
- Snell, H. L., R. D. Jennings, R. D., H. M. Snell, and S. Harcourt. 1988. Intrapopulation variation in predator-avoidance performance of Galápagos lava lizards: the interaction of sexual and natural selection. *Evolutionary Ecology* 2:353-369.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*, 3<sup>rd</sup> edition. W. H. Freeman, New York, N.Y., USA.
- Stamps, J. A., and M. Buechner. 1985. The territorial defense hypothesis and the ecology of insular vertebrates. *The Quarterly Review of Biology* 60:155-181.
- Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. *BioScience* 39:436-445.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University of Press, Oxford, UK.
- Stone, P. A., H. L. Snell, and H. M. Snell. 1994. Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. *Conservation Biology* 8: 569-573.
- Sullivan-Sealey, K., B. Brunnick, S. Harzen, C. Luton, V. Nero, and L. Flowers. 2002. *An ecoregional plan for the Bahamian Archipelago*. Taras Oceanographic Foundation, Jupiter, Fla., USA.
- Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4:16.
- Swingland, I. R. 1977. Reproductive effort and life history strategy of the Aldabran giant tortoise. *Nature* 269:402-404.
- Thompson, M. B., and B. K. Speake. 2004. Egg morphology and composition. Pages 45-74. In Deeming, D. C. (ed.), *Reptilian incubation: environment, evolution and behaviour*. Nottingham University Press, Nottingham, UK.
- Tinkle, D. W., and R. E. Ballinger. 1972. *Sceloporus undulates*: A study of the intraspecific comparative demography of a lizard. *Ecology* 53:570-584.
- Tisdell, C., and C. Wilson. 2002. Ecotourism for the survival of sea turtles and other wildlife. *Biodiversity and Conservation* 11:1521-1538.
- Troëng S., and E. Rankin. 2005. Long-term conservation efforts contribute to positive green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica. *Biological Conservation* 121:111-116.

- Van Devender, R. W. 1982. Growth and ecology of spiny-tailed and green iguanas in Costa Rica, with comments on the evolution of herbivory and large body size. Pages 162-183. In Burghardt, G. M. and A. S. Rand (eds.), *Iguanas of the world: their behavior, ecology, and conservation*. Noyes Publications, Park Ridge, N.J., USA.
- Vasconcelos, D., and A. J. K. Calhoun. 2004. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. *Journal of Herpetology* 38:551-561.
- Via, S., R. Gomulkiewicz, G. De Jong, S. M. Scheiner, C. D. Schlichting, and P. H. Van Tienderen. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology and Evolution* 10: 212-217.
- Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505-522.
- Vitt, L. J., and G. R. Colli. 1994. Geographical ecology of a Neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* 72:1986-2008.
- Vitt, L. J., and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *American Naturalist* 112:595-608.
- Vitt, L. J., and H. J. Price. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38:237-255.
- Vogel, P. 1994. Evidence of reproduction in a remnant population of the endangered Jamaican iguana, *Cyclura collei* (Lacertilia, Iguanidae). *Caribbean Journal of Science* 30:234-241.
- Walpole, M. J., and H. J. Goodwin. 2001. Local attitudes towards conservation and tourism around Komodo National Park, Indonesia. *Environmental Conservation* 28:160-166.
- Walpole, M. J., H. J. Goodwin, and K. G. R. Ward. 2001. Pricing policy for tourism in protected areas: lessons from Komodo National Park, Indonesia. *Conservation Biology* 15:218-227.
- Walpole, M. J., and N. Leader-Williams. 2002. Tourism and flagship species in conservation. *Biodiversity and Conservation* 11:543-547.
- Wearing, S., and J. Neil. 1999. *Ecotourism: impacts, potentials and possibilities*. Butterworth Heinemann, Oxford, UK.
- Weaver, C. M. 1982. Breeding habitats and status of the golden-shouldered parrot *Psephotus chrysopterygius*, in Queensland. *Emu* 82:2-6.

- Webb, W. C., W. I. Boarman, and J. T. Rotenberry. 2004. Common raven juvenile survival in a human-augmented landscape. *The Condor* 106:517-528.
- Weisser, W. W. 2001. The effects of predation on dispersal. Pages 180-188. In Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols (eds.), *Dispersal*, Oxford University Press, Inc., New York, N.Y., USA.
- Weladji, R. B., S. R. Moe, and P. Vedeld. 2003. Stakeholders attitudes towards wildlife policy and the Bénoué Wildlife Conservation Area, North Cameroon. *Environmental Conservation* 30:334-343.
- Werner, D. I. 1983. Reproduction in the iguana *Conolophus subcristatus* on Fernandina Island, Galapagos: clutch size and migration costs. *American Naturalist* 121:757-775.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* 20:249-278.
- White, G. C., and R. A. Garrott. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego, Calif., USA.
- Wiewandt, T. A. 1977. Ecology, behavior, and management of the Mona Island ground iguana, *Cyclura stejnegeri*. Ph.D. dissertation. Cornell University. Ithaca, N.Y., USA.
- Wiewandt, T.A. 1982. Evolution of nesting patterns in Iguanine lizards. Pages 119-141. In Burghardt G. M. and A. S. Rand (eds.), *Iguanas of the world: their behavior, ecology, and conservation*. Noyes Publications, Park Ridge, N.J., USA.
- Wight, P. 1996. North American ecotourists: market profile and trip characteristics. *Journal of Travel Research* 34:2-10.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations: modeling, estimation, and decision making*. Academic Press, London, UK.
- Withey, J. C., and J. M. Marzluff. 2005. Dispersal by juvenile American crows (*Corvus brachyrhynchos*) influences population dynamics across a gradient of urbanization. *The Auk* 122:205-221.
- Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794-800.
- Wunderle, J. M., and R. B. Waide. 1993. Distribution of overwintering neartic migrants in the Bahamas and Greater Antilles. *Condor* 95:904-933.

## BIOGRAPHICAL SKETCH

Charles Knapp was born in Winfield, Illinois, on November 11, 1969. He attended Southern Illinois University and earned a Bachelor of Science degree in Zoology. He began his professional career as an aquarist/diver at the John G. Shedd Aquarium in Chicago, Illinois. He became fascinated with West Indian iguanas while working with the animals under his care at the aquarium. He left Shedd in 1997 to enter graduate school at the University of Florida. The Shedd Aquarium retained Charles as a part time employee in the Conservation Department where he is in charge of annual “citizen scientist” research excursions to the Bahamas and also the aquarium’s in-situ iguana research program.

In 1999, Charles earned his Masters of Science degree in Wildlife Ecology and Conservation at the University of Florida. His work focused on a population biology study of a translocated iguana colony in the Bahamas. He continued his work in the Bahamas for his doctorate and hopes to remain active in Bahamian conservation issues for many more years. Charles is a founding member of the International Union for the Conservation of Nature (IUCN) Iguana Specialist Group and was the co-organizer of the group’s 2005 meeting on South Andros Island. The meeting incorporated results from his doctorate research to guide conservation action to help protect the Andros iguana. Charles will be accepting a post doctorate position at the San Diego Zoo in the department of Conservation Research of Endangered Species. His work will focus on hatchling dispersal and survival of the critically endangered Grand Cayman iguana.