To the Graduate Council:

I am submitting herewith a thesis written by Rachel M. Goodman entitled, "Spatial Ecology and Habitat Use of the Endangered Iguana, *Cyclura lewisi*, in an Unnatural Setting." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

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SPATIAL ECOLOGY AND HABITAT USE OF THE ENDANGERED IGUANA, *CYCLURA LEWISI*, IN AN UNNATURAL SETTING

A Thesis
Presented for the
Master of Science Degree
The University of Tennessee, Knoxville

Rachel M. Goodman
May 2004

This work is dedicated to Slugger, who sleeps underneath an office building, survived being running over by a car, learned to discriminate between agoutis and dogs, and thrived on supplemental food without becoming mean. These characters are what *Cyclura lewisi* needs in order to survive in the coming age.

ABSTRACT

The Grand Cayman blue iguana, *Cyclura lewisi*, is critically endangered with an estimated 7-25 individuals remaining in the wild. This taxon is in need of intensive management, but little has been published on any aspect of its biology, and the remaining wild population is too small to be the basis of a research program. In order to aid in the conservation of this and other iguanid species, I investigated the spatial ecology and habitat use of a population of captive-bred, released *C. lewisi* in a botanic park on Grand Cayman. Movements and locations of these iguanas were verified through routine monitoring, radio tracking, and focal animal observation in the mating and post-mating seasons of 2001 and 2002.

Male iguanas had larger home ranges and moved greater distances than did females during the breeding season. Although home range size varied by two orders of magnitude among individuals, larger maximum home range size estimates were found in this population than have been previously reported for any species of *Cyclura*. Radio tracking revealed that several iguanas, especially males during the breeding season, used areas outside of the park where they are vulnerable to increased predation, death by vehicle, and hunting or collection by humans.

The reintroduced iguanas in this study preferred modified habitat to unmodified habitat throughout the year, both within the landscape and within their home ranges. Potential threats in modified and human-occupied habitats that were identified in this study included uncontrolled supplemental feeding, predation by nonnative predators,

and vehicular collision. Iguanas frequently used artificial retreats and nests, and commonly occupied retreats in modified areas. The use of modified habitats and artificial retreats by reintroduced *C. lewisi* is encouraging, because this species may depend on disturbed landscapes and supplemental resources for future survival.

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Bridget Donaldson collected data on iguana movements during the summer of 2001 and introduced me to using Arcview® GIS. Katie Benbow helped monitor

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CHAPTER I:

INTRODUCTION

Human modification and fragmentation of landscapes is a substantial and growing threat to ecosystems, with an estimated one-third to one-half of the Earth's terrestrial surface already transformed by humans (Vitousek et al. 1997). Because natural habitats are increasingly limited, many species must survive in modified and human-dominated habitats in order to escape extinction in the wild (Rosenzweig 2003). Scientists are, therefore, expanding their research and conservation efforts beyond pristine habitats into disturbed areas which, if properly managed, may aid in preserving biodiversity (Marzluff and Ewing 2001, Pickett et al. 2001, Melles et al. 2003, Rosenzweig 2003, Zerbe et al. 2003). Species differ in sensitivity to fragmentation and disturbance of habitats, in which some species are expected to persist and even thrive while other species are expected to face great difficulty and even extinction. Among reptiles, iguanas of the genus *Cyclura* (Sauria: Iguanidae: Iguaninae) are especially vulnerable. These endangered lizards inhabit islands in the West Indies which are subject to habitat modification and other human influences. In order for these iguanas to persist, research and conservation measures must be undertaken to improve the coexistence of iguanas and humans. This is especially true for the Grand Cayman blue iguana, *Cyclura lewisi*, one of the most highly endangered reptilian species.

ECOLOGY AND STATUS OF ROCK IGUANAS, *CYCLURA*

The rock iguanas of the genus *Cyclura* are a unique group of lizards on which intense conservation efforts and studies on life history, mating systems, diet, and evolutionary relationships have recently focused. Rock iguanas are found on islands throughout the West Indies (Schwartz and Henderson 1991). They differ from most other members of the family Iguanidae in containing entirely oviparous, primarily herbivorous, large lizards with an unusual life history (Burghardt and Rand 1982). Most species are larger members of the Iguaninae, ranging from 77-150 cm in total length, up to 57 cm snout-vent length (SVL), and 1.7–10.0 kg in mature adults (Alberts 2000).

Rock iguanas can be long-lived, with individuals of some species estimated to survive in excess of 40 years (Carey 1975, Wiewandt 1977). Social systems are variable among species, some of which are territorial and others non-territorial (Carey 1975, Wiewandt 1977, Iverson 1979, Knapp 2000, Alberts et al. 2002). All species are oviparous and deposit their eggs in burrows dug into the ground, which females may actively defend for days or weeks (Wiewandt 1982).

Rock iguanas are primarily herbivorous, although known to opportunistically prey on slow-moving insect larvae and scavenge carrion (Carey 1975, Wiewandt 1977, Iverson 1979, Auffenberg 1982, Alberts 2000, Gerber et al. 2002). They feed on a large variety of plant species representing several families (range of 25-100 species for those that have been studied), and the diversity of diet varies by species and by island (Carey

1975, Iverson 1979, Auffenberg 1982, Rodríguez Schettino 1999, Alberts 2000). Because of their diverse diet of plant material and the viability of some seeds after consumption, rock iguanas may serve as important seed dispersers (Iverson 1985, Hartley et al. 2000, Benitez-Malvido et al. 2003, Oleson and Valido 2003). Furthermore, on most islands where they occur, rock iguanas are the largest native land vertebrates. In healthy populations, population density can reach over 60 iguanas per hectare and biomass may reach nearly 40 kg per hectare (Table 1; see Appendices for all tables and figures). Therefore, rock iguanas of the West Indies must be considered an important component of healthy West Indian ecosystems.

In many populations that have been studied and surveyed, population densities of rock iguanas are well below the potential carrying capacity and much lower than historical accounts and observations (Table 1). In many places, cycluran species have experienced local extirpations during the previous century (Iverson 1978, Alberts 2000). Currently, all nine species of *Cyclura* are considered threatened or endangered according to the IUCN and are protected under CITES Appendix I and various forms of local protection (Alberts 2000). The main historic threats to rock iguanas include habitat loss and degradation; predation by introduced cats, dogs, mongoose and rats; competition with introduced goats, sheep and cattle; hunting and collection by humans; and vehicular collisions (Wiewandt 1977; Iverson 1978, 1979; Henderson 1992; Knapp et al. 1999; Mitchell 1999; Alberts 2000). Most of these continue to threaten rock iguanas, although hunting of iguanas is now less prevalent. The outlook has improved

recently with the formation of groups like the IUCN/SSC Iguana Specialist Group and the International Iguana Society in the last two decades, and the increased involvement of the academic community and several local government and non-government organizations. Although much work must be done to ensure the recovery and survival of this taxa, the support base for this work is growing.

From a conservation perspective, rock iguanas are important not only because of their ecosystem function, but also because of their potential function as flagship species. They are often the largest terrestrial vertebrates on islands where they live. Furthermore, they readily survive in captivity and alternatively retain their natural behaviors entertaining with behavioral displays, or become tame and habituated to humans allowing up-close encounters or even petting in controlled circumstances (pers. obs., Burton pers. comm.). Such iguanas can be used to draw public attention to their own plight for survival and extend that public interest to other local environmental issues.

THE GRAND CAYMAN BLUE IGUANA, *CYCLURA LEWISI*

The Grand Cayman blue iguana**,** *Cyclura lewisi,* is a large rock iguana (over 50 cm SVL and up to 9 kg; Schwartz and Henderson 1991, Burton pers. comm.) that is endemic to Grand Cayman, where it was once widely distributed (Morgan 1994). Adults are dark blue to sky blue in color, particularly when warm or during the breeding season. Previous observations (mostly unpublished) of captive and captive-bred,

reintroduced *C. lewisi* have yielded some information on its diet and reproductive cycle. Fossil remains and historical sightings suggest that the original distribution of the iguana included dry habitats throughout the island (Burton in Alberts 2000, Morgan 1994). However, little is known of the general ecology or behavior of this iguana, especially in a natural setting, because it is so rare. *Cyclura lew*isi was considered to be nearly extinct even when first described in 1940 (Grant 1940). The island-wide population was estimated to be 100-175 individuals in 1992 (Alberts 2000), but a census in 2002 estimated that only 7-25 wild iguanas remain on Grand Cayman. The species is currently considered critically endangered by the IUCN and endangered by the U.S. Fish and Wildlife Service, and it is protected by CITES Appendix I and the Cayman Islands Animals Law, section 68 (Morgan 1994, Alberts 2000). The presumed threats to *C. lewisi* are a subset of those which threaten *Cyclura* elsewhere, specifically habitat loss and degradation, predation by introduced mammals, and hunting and persecution by humans.

Because of the low estimate of the wild population size and threat of impending extinction, a captive breeding program was initiated for *C. lewisi* in 1990 by the National Trust for the Cayman Islands. The first releases of trial iguanas into the Queen Elizabeth II Botanic Park occurred in 1996, and 55 iguanas had been released between then and the completion of this study. Between 15 and 20 of these iguanas were sighted (after the initial release period) during any one season of the current study (for population density estimate, see Chapter II). Those iguanas which were not seen after

release may be either deceased or inhabiting surrounding areas, though instances of the latter have not been reported.

Iguanas that were included in this study were two to seven years old, and their ages, release dates, sexes, and body sizes are listed in Table 2. Because of releases of new iguanas in the spring of 2001 and 2002 and their emigration from the study site over time, the population size and age structure varied throughout this study. However, estimates of home range size and analysis of habitat use were restricted to iguanas that were 3-7 years of age, since they were sexually mature and had potentially settled into the park since their release at least one year prior. This criterion also helped ensure that study subjects remained in the park and therefore could be studied during both field seasons in 2002.

RATIONALE FOR STUDY

Because *Cyclura lewisi* had been reduced to few and small surviving subpopulations at the time of its original description and this trend continued to the present, little is known of the ecology, behavior, and general biology of this iguana, except for information gathered by the captive breeding program and inference from knowledge of related species. The remaining wild population of *C. lewisi* is too small and fragmentary to be the basis of research program. Furthermore, many of these remaining "wild" iguanas are found in disturbed habitats and so are likely to differ in their habits from truly wild iguanas in an intact ecosystem. Therefore, the reintroduced

population of iguanas in the Queen Elizabeth II Botanic Park provides an important opportunity to gather basic information on this species that is necessary for its future management. The amount of space used by iguanas needs to be known in order to plan protected areas which are suitable to maintain reintroduced populations elsewhere on the island. Also, knowledge of iguanas' habitat preferences will be useful in deciding which parcels of land will be appropriate for reintroducing iguanas.

This study was undertaken to examine the spatial ecology and habitat use of a reintroduced population of C. *lewisi* in order to assist in conservation efforts. The human modified and occupied setting of the botanic park and the captive-bred origin of the iguanas represent conditions that are currently faced by many populations of *Cyclura* throughout the West Indies. These rock iguanas increasingly depend on active management, including captive-breeding, head-starting, and reintroduction programs. Therefore, information gathered in this study should prove useful to the conservation of this group. For *C. lewisi* in particular, captive-bred, reintroduced populations of the next few decades are the only hope for the survival of this species, and so this study will certainly aid in its conservation.

STUDY SITE

This study was conducted during May - November of 2001 and 2002 at the Queen Elizabeth II Botanic Park in the east interior of Grand Cayman (Figure 1). The park is located at 19°19'N, 81°10'W, approximately 2 m above sea level. The park

includes 24.3 ha of relatively unmodified and heavily modified land, and is surrounded by additional tracts of mostly unmodified land that were included in the study site (55.2 ha; Figure 2). Beyond the study site, mostly unmodified habitats border, including a buttonwood swamp to the east and south. However, human residences and roads, where dogs and cats are found roaming, border to the west and northwest less than 0.5 km from the edge of the study site. While unmodified habitats border the park to the north, a large paved road with 40-60 mph traffic is found 0.5 km to the north and northwest of the study site.

Although not quantified, during this study I observed tens (rather than hundreds) of daily visitors in the park, except during school group visits and infrequent special events, when numbers of visitors were greater. Approximately 10-20 staff members where on site during regular work hours, 07:00-17:00 every day. Staff and iguanas overlapped largely in their hours and locations of activity, and were highly habituated to each other.

Grand Cayman has a warmer wet season in May-November and a cooler dry season in December-April (Burton 1994). This study took place during the wet season, when monthly temperatures average 25.8 °C minimum and 33.7 °C maximum (Burton 1994). The eastern portion of the island, where the study site was located, receives mean annual rainfall of 1107 mm, with the heaviest rainfall typically occurring in October (Burton 1994).

Heavily modified habitat makes up approximately 13% of the study site (defined as all area used by iguanas in this study; see Chapter III), and a larger portion of the botanic park proper. Modified habitat in the study site includes roads, trails, parking lots, ornamental gardens, manicured lawns, and buildings and facilities for staff and visitors. Additionally, I designated within modified habitat the ecotone subhabitat, which contains natural habitats, but wherein vegetation has been thinned to enhance viewing by visitors.

Unmodified types of habitat within the study site include buttonwood (*Conocarpus erectus*) dominated, seasonally flooded swamp; logwood (*Haematoxylum campechianum*) dominated, seasonally flooded swamp; dry semi-deciduous forest on rock and soil substrates; and xerophytic shrubland. Additional details on the habitats found in the park and the surrounding land are found in Chapter III. The habitats are illustrated in Figures 3-10.

The botanic park proper claims to contain about 40% of Grand Cayman's 678 species of indigenous and endemic plants, both in the natural tracts of habitat that remain and in special displays. In addition, the park contains hundreds of species of exotic plants, planted in displays and growing as weeds in the modified areas of the park.

Dogs and cats have been introduced to Grand Cayman, and they are abundant. These animals are actively excluded from the park by management, but the property is not fenced, and dogs, cats and their feces were infrequently sighted during the study.

Two other introduced mammals, agoutis (*Dasyprocta punctata*) and rats (*Rattus* sp.) reside in the park, although iguana program management began serious efforts to suppress the latter toward the end of this study. At least three native species of snakes (*Alsophis cantherigus caymanus*, *Tropidophis c. caymanensis*, *Tretanorhinus variabilis lewisi*), one species of turtle (suspected introduced: *Trachemys decussata angusta*), five species of lizards (native: *Anolis conspersus*, *Sphaerodactylus argivus lewisi*, *Aristelliger p. praesignis*; introduced: *Anolis s. sagrei;* native but presumed introduced to the park: *Leiocephalus carinatus varius*), two species of frogs (introduced: *Osteopilus septentrionalis*; native: *Eleutherodactylus p. planirostris*), many resident and migratory avian species (including the endemic Grand Cayman Amazon parrot, *Amazona leucocephala caymanensis*) and unknown species of bats have been sighted in the park (Goodman, Burton, and Echternacht, pers. obs.).

CHAPTER II:

SPATIAL ECOLOGY OF THE ENDANGERED IGUANA, *CYCLURA LEWISI*, IN A DISTURBED SETTING ON GRAND CAYMAN

This chapter is a modified version of a paper submitted for publication. The use of "we" refers to myself and two co-authors, Arthur C. Echternacht and Frederic J. Burton. My contributions to this chapter include 1) the selection of this topic and development of the project, 2) the majority of the field work including all radio tracking, 3) the data analysis, and 4) the writing of the manuscript.

INTRODUCTION

Human modification of landscapes is a substantial and growing threat to ecosystems, with an estimated one-third to one-half of the Earth's terrestrial surface already transformed by humans (Vitousek et al. 1997). Habitat destruction and fragmentation result in small, disturbed populations which are subject to numerous genetic, demographic, and stochastic threats (Franklin 1980, Primack 2002). Accordingly, conservation biologists are often faced with the task of studying, monitoring, and managing compromised populations.

Such disturbed populations are increasingly characteristic of species in the genus *Cyclura* (Iguanidae), which contains some of the most endangered lizards in the world (Alberts 2000). These large, herbivorous iguanas are widely distributed in the West

Indies where they are threatened by habitat loss and degradation (Alberts 2000), competition with and predation by introduced species (Iverson 1978, Mitchell 1999), and hunting and collection by humans (Carey 1966, Knapp et al. 1999, Alberts 2000).

The Grand Cayman blue iguana, *Cyclura lewisi*, is critically endangered and is thought to have numbered in the low hundreds of individuals since the taxon was first described (Grant 1940). These long-lived, sexually dimorphic, and primarily herbivorous lizards are endemic to the island (Schwartz and Henderson 1991). A census conducted in 2002 estimated that 7-25 individuals remained in the wild, either as isolated individuals or in very small groups (Burton 2002). Their current distribution is highly fragmented and reveals little about the original distribution or ecology of *C. lewisi*. Management of these iguanas requires information on their basic ecology, but little has been published, and the opportunity to study natural populations in the wild no longer exists. Therefore, we studied the spatial ecology of a captive-bred, reintroduced population in a disturbed but protected setting on Grand Cayman, the Queen Elizabeth II Botanic Park.

The spatial distribution of iguanids may be influenced by many biotic and abiotic factors, including age, sex, climate, breeding season, and density of food resources and potential mates (Dugan 1982, M'Closkey et al. 1987, Perry and Garland 2002). Temporal shifts in food resources may also influence the spatial ecology of widely foraging, herbivorous iguanas in the subfamily Iguaninae (Krekorian 1976, Wiewandt 1977). Thus we expected that *C. lewisi* would have more temporally

variable home ranges than have been reported for insectivorous lizards. Accordingly, sampling in this and other iguana species may need to be more intensive and cover a whole season or year for accurate representation of space use (Rose 1982).

We investigated two components of the spatial ecology of *C. lewisi*, home range sizes and movement rates, by monitoring and radio tracking iguanas during the summer and fall of 2001 and 2002. We compared space use and movements of adult males and females. Polygyny is common in the genus *Cyclura,* and males typically travel to, court, and defend several females during the mating season (Carey 1975, Iverson 1979, Dugan and Wiewandt 1982). Therefore, we predicted that male *C. lewisi* would have larger home ranges and movement rates than females in the mating season.

METHODOLOGY

Study site and study population

The Queen Elizabeth II Botanic Park is located in the east interior of the island of Grand Cayman (19°19'N, 81°10'W) at ca. 2 m above sea level (Figure 1). The park includes 24.3 ha, approximately 16 ha of which is preserved in a relatively undisturbed state. Our study site encompasses approximately 55.2 ha, which includes the park and the mostly undisturbed surrounding land that was used by iguanas initially found in the park (Figure 2). Habitats designated as modified include ornamental gardens, manicured lawns, buildings and other structures for visitors and staff, and roads and trails. Habitats designated as unmodified include xeric forest and shrubland habitats, as

well as seasonally flooded wetlands dominated by logwood (*Haematoxylum campechianum*) and buttonwood (*Conocarpus erectus*). Further descriptions of all habitats are found in Chapter III.

Iguana capture and attachment of transmitters

Iguanas were located during 2001 and 2002 by walking a circular transect of the park several times per day, and during related research conducted throughout the entire study area. Only iguanas that used the park regularly or occupied the park's perimeter were included in this study. Iguanas were captured by hand or using a landing net or Havahart® single door trap. All iguanas were tagged with unique combinations of colored beads as described by Rodda et al. (1988), weighed to the nearest 0.1 kg, measured for snout-vent length (SVL) and total length (TL), and probed to determine sex.

Radio transmitters (Holohil Systems, Ltd. model AI-2) were attached to large males (36-49 cm SVL, 80-118 cm TL, 2.2-5.1 kg) by suturing them below the posterior dorsal crest, along with an aluminum backing plate and neoprene pads for protection. More details on this method of radio transmitter attachment can be found in Goodman (submitted). A similar method of attaching radio transmitters has been used with salmon (Erkinaro et al. 1999), and suturing radio transmitters to snakes has been reported (Ciofi and Chelazzi 1991).

Transmitters were attached to females and small males (27-38 cm SVL, 69-93

cm TL, 0.9-2.7 kg) by encasing the transmitters in plastic and gluing the transmitter package to the posterior dorsum with cyanoacrylate gel. Sutures were not used on these smaller iguanas because their less developed dorsal crests would be vulnerable to tearing if the transmitters became caught on rocks or vegetation. The total mass of the transmitter packages before application averaged 40 g, which was less than 5 % of the body mass of all iguanas and acceptable within common standards (Macdonald and Amlaner 1980). Details on the reliability of the two methods of transmitter attachment and their effects on iguanas can be found in Goodman (submitted).

Population monitoring and tracking

All iguanas in the population (n = 23 over all seasons) were monitored walking a transect made of park trails and roads from May - July (summer) and August - November (fall) of 2001 and 2002. Transects were walked 2-8 times daily outside of radio tracking periods, with sampling spread over the iguanas' active hours, 07:00-19:30. Additionally, incidental sightings of iguanas were collected throughout the study site, including the undisturbed area immediately outside of the park, while conducting focal animal observations and habitat surveys for related research (see Chapter III). Locations of iguanas were recorded using GPS coordinates and when possible, bearings to local landmarks.

All iguanas that had been released at least one year prior were tracked using radiotelemetry (Wildlife Materials, Inc. TRX-1000S tracking receiver and collapsible,

hand-held yagi antenna) in two periods in the summer and the fall of 2002. Iguanas in this class were sexually mature and potentially more settled in their surroundings than iguanas that had been recently released. Males (n = 5) were tracked from May 28 - June 13 and from Oct 5 - 20, 2002. Females (n = 6) were tracked from July 19 - Aug 2 and from Oct 23 - Nov 5, 2002. Females could not be radio tracked during the mating season because of a limitation in number of radio transmitters. They were therefore radio tracked in the summer after all had nested. Males were tracked during the end of the mating season; the last mating was observed on June 23, although courtship and mating peaked in May.

Radiotelemetry was only conducted on days with mostly clear weather (no precipitation and less than 75% cloud cover estimated visually; 57 of 62 days during tracking periods). All iguanas were radio-located 4-8 times daily, with hours of tracking standardized to ensure an even distribution over the iguanas' active hours. These multiple locations within days were collected in order to more accurately calculate movement rates. Frequent, successive sampling of animal locations has been shown to be necessary for adequate approximations of true movement rates (Reynolds and Laundre 1990). Positive autocorrelation between successive locations has been suggested to bias home range (Swihart and Slade 1985); however, studies comparing sampling methods have indicated this bias is negligible when sample sizes are large, as in our study (Andersen and Rongstad 1989, Reynolds and Laundre 1990).

Iguanas were not tracked more than 20 m into dense vegetation to avoid

disturbance. To estimate iguana locations when visual verification was not possible, 2-4 bearings were taken from known locations in the park with a ten-minute maximum period between the first and last bearing. The majority of bearings (95.3 %, n = 1237) were taken from locations with GPS coordinates obtained multiple times and verified with aerial photography of the study site provided by the Cayman Islands Government's Land Information System (image date 1999). Triangulation of iguana locations was performed with TELEM88 (Coleman and Jones 1988) for only those locations with one set of bearings forming an angle of 30-165 degrees. Error of triangulation was estimated by tracking and estimating 36 dummy locations (unknown to the tracker) with the same methods as those used for tracking and triangulating real iguana locations. The 95% confidence intervals for triangulation error were 23-39 m and 20-34 m for two and three vectors, respectively.

Home range and movement rate analyses

In this study, home range refers to the area used by an individual during foraging, mating, and other regular activities over the course of a year (Burt 1943). The term "usage area" is analogous to home range, but applies to the area used by an individual over a shorter period of time, herein a tracking period (Powell 2000). All home ranges, usage areas, and movements were estimated using the Animal Movement extension (Hooge and Eichenlaub 1997) in Arcview® GIS version 3.2. Home range sizes of all iguanas were estimated using sightings and radiotelemetry data in the

summer and fall of 2001 and 2002 and for both seasons combined in each year. Additionally, movement rates and usage areas were estimated for each tracking period in 2002 to provide a more detailed and less biased estimate of space use and movement of settled adult iguanas (3-7 yrs age) in the population. Minimum convex polygons (MCP) were created using all locations (100% MCP), and also after omitting 5% of outlying locations (95% MCP) using the harmonic mean method (Dixon and Chapman 1980). To estimate usage areas, fixed kernel utilization distributions were created from radiotelemetry data (Worton 1989) using smoothing parameters of Silverman (1986), in addition to 100% and 95% MCP's. By convention, the area within 95% kernel contours was considered the usage area, and the area within 50% contours was considered the core area for each tracking period (Powell 2000).

To compare the efficiency of monitoring iguanas through transect walks only, versus transect walks plus radio tracking, home range estimates produced with and without radiotelemetry data were compared for iguanas radio tracked in 2002. Additionally, home range size estimates were compared between 2001, during which no iguanas were radio tracked, and 2002, during which adult iguanas were intensively radio tracked. To examine the relationship between sex and home range size, we compared estimated home range, usage area, and core area sizes between sexes in each season and year.

The average distance between consecutive locations was calculated by measuring and averaging distances between all locations within each day over a

tracking period. Overall movement was the sum of all distances traveled, including those between days, in a tracking period. We compared these rates of movement between sexes in each tracking period.

To determine whether sexes differed in their fidelity to home ranges, we compared shifts in usage area centers between the two tracking periods. We calculated distances between centers of usage areas using 100% MCP's and kernel contours for radio tracked iguanas. Harmonic mean centers of activity, which have been indicated as more biologically meaningful compared to other methods (Lair 1987), were calculated for MCP's in Animal Movement. Additionally, centers of kernel areas were estimated by visually determining the central point within 5% kernel contours. This novel method of estimating activity center is justified, because the average maximum length of 5% contours for all iguanas in both seasons was 8.8 m, and two estimates of centers on different days averaged less than 1 m apart.

We tested for relationships among variables with nonparametric tests because data did not conform to normality assumptions required for parametric statistics. Mann-Whitney U tests were performed for unpaired data, and Sign tests or Wilcoxon sign rank tests were performed for paired data in SAS version 8.2 (2002) with a designated alpha of 0.05.

RESULTS

Home ranges and usage areas

In 2001, when adult iguanas were not radio tracked, home range estimates varied in size from 270-113,510 m^2 (average = 20,110 m^2, SD = 36,460 m^2; see Tables 3, 4 for home range estimates of all iguanas in 2001 and 2002). In 2002, when a portion of the population was radio tracked, home range estimates varied from 150-376,010 m^2 (average = 47,920 m^2, SD = 94,130 m^2; see Table 3). When examining home ranges constructed with and without radiotelemetry data for iguanas in 2002, radio telemetry data significantly increased home range size estimates (average difference = 56,242 m^2; Sign test, M = 6, n = 13 , p = 0.0005). Larger maximum estimates of home ranges were evident in 2002, with the inclusion of radiotelemetry, as compared to 2001 (Table 3; Figures 11, 12). However, when comparing average home ranges in 2001 to those that included radiotracking in 2002, there were no significant differences between estimates (Sign test, M = 2.5, n = 9, p = 0.1797).

Different methods of observing iguanas also produced different results with respect to location of home ranges. In 2001, MCP's of all iguanas were mostly contained within the park (Figure 11). However, in 2002, MCP's constructed from data including radiotelemetry revealed that several iguanas used area outside the boundaries of the park (Figure 12). In some cases kernel usage areas constructed from radiotelemetry data also identified some area used by iguanas outside of the park, but not to the extent indicated by MCP usage areas (Figures 13, 14).

Table 5 shows the MCP and kernel estimates of usage areas and the movement rates for adults radio tracked during the summer and fall of 2002. Figures 13 and 14 illustrate usage areas in both seasons for males and females, respectively. Nearly all methods of examining space use in 2001 and 2002 showed that males use significantly larger areas than females during the summer (Table 6, Figure 15). There were no significant differences in home range or usage area sizes between the sexes during the fall. Comparisons between sexes of overall home range size for each year (summer and fall, all data combined) produced varying results based on different years and estimators (Table 6).

Based on 100% MCP's, males shifted usage area centers from the summer to the fall by a significantly greater distance than did females (average difference = 31.9 m; Mann-Whitney U test, S = 30.0, n = 9, p = 0.0159). However, there was no significant difference between sexes in shifts when usage area centers were calculated from fixed kernel estimators.

Movement rates

Males had significantly greater total and between location movements than females during the summer (total movements: average difference = 3,580 m, Mann-Whitney U test, S = 16.0, n = 10, p = 0.0159; between location movements: average difference = 45 m, S = 15.0, n = 10, p = 0.0079) (Table 2). Sexes did not exhibit significantly different movement rates during the fall tracking period (total movements: Mann-Whitney U test, S = 21.0, n = 10, p = 0.9143; between location movements:

Mann-Whitney U test, S = 18.0, n = 10, p = 0.4762).

DISCUSSION

Spatial ecology of *Cyclura lewisi*

Among iguanid lizards, males typically have larger home ranges than females of similar size, suggesting that social factors may affect home range size (reviewed in Perry and Garland 2002). Within the subfamily Iguaninae, there is variability in mating systems, with some males of some species traveling to and courting several females and males of other species defending small territories which several females visit (Wiewandt 1977, Dugan 1982, Werner 1982, Dugan and Wiewandt 1982, Rauch 1985). Male *C. lewisi* in this study used larger areas and had greater movement rates than did females during the summer, which coincides with the reproductive season, but not during the fall tracking period. Some estimators indicated that males also used larger areas than did females over the course of both years, a phenomenon probably attributable to the difference in home range size during summers. We observed males traveling to and courting several females during each summer. Polygyny and increased activity of males during the mating season characterize cycluran mating systems (Wiewandt 1977, Dugan and Wiewandt 1982) and probably increased home range size and movement rates during this period in our study population.

We found that males had larger home ranges and greater movement rates than females during the summer months. This conclusion was based on a number of results

which included radio tracking data and data collected during additional monitoring. We were unable to track females during active mating because of logistic constraints. However, the potential magnitude of this methodological bias is minimal because females were monitored during and outside of all radio tracking periods with transect walks of the park. During the active mating period, we observed all males traveling to mate, whereas females did not travel outside of their normal home ranges to mate. Moreover, home ranges estimated from all location data collected during the entire summer in both years show the trend of smaller home ranges in females than in males. Based on this evidence, we conclude that female *C. lewisi* have smaller home ranges and generally require less area than males, as has been noted for several species of *Cyclura* (Iverson 1979, Mitchell 1999, Knapp 2000).

The male with the smallest home range and usage area during the summer of 2002 (SLGR in Figures 12, 15) was affected by the presence of the iguana captive breeding facility which contained about ten sexually mature females. He entered the facility daily during the mating season and displayed dominant behavior and courtship behavior toward the caged females. This concentration of females probably contributed to a contraction of his home range. A similar pattern was evident the previous year with another, then-dominant iguana (PSYC in Figure 11). These anecdotal observations corroborate the suggestion that distribution of females heavily influences male movements and home range size during the mating season.

Males appeared to shift usage areas more than females between seasons based

on the MCP estimator, but this trend was not evident when using the probabilistic kernel method to calculate centers of usage area. Because MCP's are sensitive to outliers, male centers of usage areas were probably more affected by occasional forays outside of commonly used areas. Because locations in fixed kernels are weighted by frequency, these forays of males had a smaller effect on kernels and associated centers of usage areas.

Comparison of results with related studies

Considerable variation was measured in our estimates of home range and usage area size in this population, due to inter-individual variability, sex, season, and estimator method. Past studies of *Cyclura* populations have reported home range sizes varying by one order of magnitude among individuals (Carey 1975, Iverson 1979, Goodyear and Lazell 1994, Mitchell 1999, Knapp 2000), rather than the two orders of magnitude reported here. Our minimum home range estimates for adult iguanas (those radio tracked) cannot be explained by inadequate sampling as the four smallest home ranges estimated (<1,000 m^2) were based on 21, 25, 91, and 192 locations, which are comparable to other studies we reviewed.

This study did not attempt an intensive mark recapture program, but the entire study site was extensively monitored over two years and individuals were marked for identification. Therefore, we can use these data to approximate population density, for utility of comparison with other *Cyclura* populations. Within the park, an average of

16.7 iguanas were sighted in each season, including recently released iguanas which often disappeared after the season in which they were released. Using only the area within the park boundaries, since iguanas in outlying areas may not have been detected, we estimate a density of 0.64 iguanas per hectare (iguana/ha) in the park. This density is probably not an underestimate because of the inclusion of recently released iguanas, which often did not settle permanently in the park and therefore slightly inflated our estimate.

We reviewed 24 sources containing studies and surveys of 41 populations of *Cyclura* representing 11 subspecies, which yielded density estimates ranging from 0.3-128.3 iguana/ha (Table 1). Only three of 41 (7.3 %) populations had estimated densities below 1 iguana/ha; 19.5 % had estimated densities ranging from 1-10 iguana/ha; and the majority (73.2 %) had estimated densities ranging from 10-128.3 iguana/ha. Based on these ranges, our study population had a low population density when compared to other *Cyclura* populations in relatively natural settings. Of the three density estimates similar to that of our population (<1 iguana/ha), all three populations lived in degraded habitats with introduced predators or ungulates (Carey 1975, Wiewandt 1977, Goodyear and Lazell 1994, Mitchell 1999).

Home range sizes estimated in this study (MCP's) had higher maxima (eg. 376,010 m^2 and 186,370 m^2) than previously reported for any species of *Cyclura*. The closest maximum value of home range size previously reported in this genus, 90,000 m^2, was found in male *Cyclura pinguis* on Anegada, a disturbed island as noted

above (Mitchell 1999). The maximum home range size found in the current study may be indicative of larger home ranges in hypothetical natural populations of *C. lewisi*. Alternatively, large home ranges may be explained by a lower density of resources or females in the park which caused some males to roam more widely in order to fulfill their needs. Another explanation for larger home ranges is that the low population density in the park may allow for expansion of home ranges. Population density has been demonstrated to be inversely related to home range size in some iguanids (Schoener and Schoener 1980, Alberts 1993). Another possibility is that large home ranges may have been detected in this study and not in others because previous investigators of cycluran spatial ecology did not sample intensively enough, with radio telemetry, or over a long enough period of time to capture the full, shifting home ranges of these iguanas.

Home range sizes may have been influenced by supplemental feeding of iguanas, the magnitude of which was only discovered during the course of this study. However, supplemental feeding is expected to decrease home range size (Eifler 1996), whereas maximum home range sizes in this population were large compared to those of other *Cyclura* species. Food supplementation was shown to result in temporary reductions of home ranges in another iguana, *Conolophus pallidus* (subfamily Iguaninae); however, other resources were more important in determining the overall extent of home range over the course of a year (Christian 1981). An analogous situation might exist in the reintroduced population of *C. lewisi*, where the sporadic nature of

supplemental feeding and the distribution of other resources, including females, may result in home ranges that are not restricted by supplemental feeding. Although there did not appear to be any correlation between home range size and amount of supplemental feeding, our study could not directly address this question. Further studies, possibly conducted with controlled supplemental resources and variable densities of females, are needed to determine the factors which ultimately determine home range size for *C. lewisi*.

In the park, iguanas come into contact with humans on a regular basis and are heavily habituated, perhaps in part because of supplemental feeding. While one might argue that the captive origin of these iguanas, the disturbance level of the habitat, and the presence of supplemental food may limit the application of this study's findings to iguanas in more natural settings, few pristine settings remain for cycluran iguanas. Many populations are faced with frequent human interaction and habitat disturbance, and are increasingly managed with head-starting and captive breeding programs. There is little hope that *C. lewisi* will again exist in pristine settings, and this prediction applies to many other species as well. Therefore, the study of the spatial distribution and movements of captive-bred, released *C. lewisi* in a disturbed habitat is important to understanding and managing populations of *Cyclura*.

Implications for management and study of spatial ecology

Depending on the goals in a study of an animal's spatial ecology, different methods of estimating home range may be more or less suitable (reviewed in Powell, 2000). Fixed kernel home ranges, one estimator chosen for this study, are not as affected by sample size and outliers and are less sensitive to autocorrelation in location data sets, when compared to MCP's (Powell 2000). However, MCP's are important in the study of spatial ecology because they are easily compared with studies that are older or use varying methods, and because they always encompass all locations used by an animal. In providing baseline information on spatial distribution for reserve design, this study used kernel home ranges to estimate areas used frequently by iguanas that may be most important to their fitness. However, MCP estimates were also essential because they identified habitat used less frequently where iguanas might be vulnerable. In 2002, MCP home ranges showed that iguanas used areas outside of the park boundaries (Figure 12), which is important information because iguanas are potentially subject to increased predation, death by vehicle, and collecting or hunting by humans in these areas.

Whatever the goals of a monitoring program and the financial resources available, radio tracking of some individuals, ideally of different sexes and age classes, should be included. We were not able to track juvenile or hatchling iguanas because these were all head-started in captivity. However, the addition of radiotelemetry to monitoring in 2002 both expanded home range size estimates of tracked iguanas and

provided the crucial insight that iguanas were roaming outside of the park. We found considerable variability in home range size and movement estimates in this study, due to sex, season, and inter-individual variation, as well as monitoring method and home range estimator. The influences of these biological and methodological factors on analysis of spatial ecology demonstrate that intensive and extensive sampling is needed to accurately estimate the area used by an individual and that may be needed to ultimately support a population. Tracking animals in different seasons is recommended, especially in the case of large, herbivorous lizards such as *Cyclura lewisi*, which may shift home ranges in response to changing resources or mating season.

CHAPTER III:

HABITAT USE OF THE ENDANGERED IGUANA, *CYCLURA LEWISI*, IN AN UNNATURAL SETTING ON GRAND CAYMAN

This chapter is a modified version of a paper that will be submitted for publication. The use of "we" refers to myself and two co-authors, Frederic J. Burton and Arthur C. Echternacht. My contributions to this chapter include 1) the selection of the topic and development of the project, 2) the majority of the field work including all radio tracking, 3) the majority of the habitat mapping, 4) the data analysis, and 5) the writing of the manuscript.

INTRODUCTION

Human modification and fragmentation of the Earth's ecosystems are substantial and increasing worldwide (Vitousek et al. 1997). Therefore, scientists can no longer afford to focus research and conservation efforts solely on "pristine habitats," but instead must expand these efforts to include disturbed areas (Rosenzweig 2003). Recently, more studies have examined the ecology and behavior of species in urban and other human-modified areas (Koenig et al. 2001, Wood and Pullin 2002, Gehrt and Chelsvig 2003, Godefroid and Koedam 2003, Spinks et al. 2003, Evelyn et al. 2004), with the increasing recognition that these areas may be reservoirs of biodiversity if

managed properly (Marzluff and Ewing 2001, Pickett et al. 2001, Melles et al. 2003, Zerbe et al. 2003).

Certain taxa may depend largely on disturbed habitats for their survival in the future; one such group is the rock iguanas of the genus *Cyclura*, which face the rapid encroachment of humans onto their island habitats throughout the West Indies (reviewed in Alberts 2000). All nine species in this genus are threatened or endangered, including the blue iguana, *Cyclura lewisi,* which is endemic to Grand Cayman (Alberts 2000). This species faces an immediate threat of extinction; a recent census in 2002 estimated that only 7-25 wild iguanas remain (Burton 2002). A captive breeding and release program, initiated in 1990, has produced a small population of introduced iguanas in a botanic park which were confirmed to be reproducing in 2001. Because the remaining wild population of *C. lewisi* is too small and fragmentary to be the basis of any research, and because no studies on the behavior or ecology of this species have been published, the introduced population serves as a valuable source of information which can be used for management and conservation planning.

In order to develop a strategy for reintroducing and managing *C. lewisi* and other iguanas throughout the West Indies, it is important to know how iguanas respond to modified landscapes which they increasingly depend on. Much of Grand Cayman is developed, and beaches, which other rock iguanas commonly inhabit or utilize for nesting (Alberts 2000), are the most heavily developed areas on Grand Cayman. We investigated the habitat use of *C. lewisi* in an area containing both natural and human-

modified areas in order to examine whether iguanas would occupy human-modified habitat, and whether they would use artificial and natural retreats in modified habitat. Specifically, the objectives of this study were 1) to determine if iguanas differentially use modified and unmodified habitats, and those subhabitats within them, during the course of their daily activities, and 2) to determine what kind of overnight retreats were used most frequently by iguanas and in what habitats these retreats were found. These aspects of habitat and retreat use were investigated by radio tracking, focal animal observations, and regular monitoring of a population of reintroduced iguanas. In addition to examining which habitats were important to *C. lewisi*, we qualitatively assessed the dangers posed to them in these habitats.

METHODOLOGY

Study site and population

This study was conducted in the Queen Elizabeth II Botanic Park and surrounding area (19°19'N, 81°10'W, elevation 2 m) in Grand Cayman. The area of the botanic park is 24.3 ha. Additionally, the study site (55.2 ha) includes the surrounding area used by iguanas initially found in the park (Figure 2). The iguanas in this population were originally captive-bred on site and released at 2-3 years of age, when they were thought to be less vulnerable to predation. The study population consisted of all iguanas in the park that were released at least one year prior. Therefore, all study subjects (3-7 years of age) were adults and potentially sexually mature.

Habitat mapping and description

We constructed a habitat map of the study site (Figure 16) through interpretation of a scaled, orthorectified, digitized aerial photograph of the area (Cayman Islands Government's Land Information System, image date 1999) and extensive on-site inspection (ground-truthing). We first classed all land into the major habitat categories of modified (heavily modified by humans during construction of the botanic park) and unmodified (not modified as above, but including second growth vegetation on land logged during the past century). Modified habitat was further divided into the following subhabitats: ecotone (habitat bordering roads and trails wherein vegetation has been thinned to enhance viewing by visitors, and where iguanas are frequently within 6 m of humans passing by); roads, trails, and parking lots; and staff and visitor areas (all remaining modified areas, including cultivated gardens and buildings for visitors and staff). These subhabitats were all clearly defined on the aerial photograph.

Ninety distinguishable zones of unmodified habitat were mapped based upon hue and texture (scale-dependent heterogeneity of color) in the aerial photograph of the study site viewed at a scale of 1:2000 in Arcview® GIS version 3.2. On this map, 200 survey points were assigned as evenly as possible within mapped zones. These points, located using GPS units, were surveyed during November 2002. An additional 280 *ad hoc* locations were surveyed and marked with GPS coordinates, en route to the original 200 locations (see Figure 17 for distribution of survey locations). At each location, canopy height was estimated to the nearest meter, and predominate substrates and tree

species were recorded. The original ninety zones of land were grouped into subhabitats, based on a former botanic survey of the park (Burton 1990) and on habitat surveying conducted during this study (Table 7). Unmodified subhabitats were designated as buttonwood (*Conocarpus erectus* dominated, seasonally flooded swamp), logwood (*Haematoxylum campechianum* dominated, seasonally flooded swamp), forest rock (dry semi-deciduous forest on carbonate karst substrate), forest soil (dry semi-deciduous forest on soil substrate), shrubland (a complex mosaic of second-growth vegetation on soil and rock, mainly dominated by logwood, but also including small areas of primary xerophytic shrubland), and mosaic (mosaic of intergrading swamp and dry forest). Details and photographs of these habitats are in Table 7 and Figures 3-10.

Iguana location and tracking

Iguanas were located for this study in 2001 and 2002 through regular monitoring of the park, which consisted of 2-8 daily walks of trails, roads, and surrounding areas. Eleven iguanas (males n = 5, females n = 6) were tracked with radio telemetry for 14-17 day periods during the summer (May - July) and fall (September - November) of 2002. Iguanas were also located through regular monitoring and focal animal observations conducted from August - November of 2001 and May - November of 2002. Additional details of these methods are found in Chapter II.

During radio tracking, iguanas were located 3-8 times within days (at least one hour apart) in order to calculate movement rates and to sample seldomly used habitats.

Because individuals and not locations were the sample units in the habitat use analysis, autocorrelation of successive locations was not problematic (Aebischer et al. 1993). However, we excluded from our original data those points which represented repeated, consecutive sampling of a retreat location, or those which represented the same location before 10:00 prior to an iguana's first movement of >10 m for that day.

Analysis of retreat use

Instances of retreat use by iguanas observed during the course of radio tracking, monitoring, and focal animal observation in 2001 and 2002 were recorded. We calculated the percentages of retreat use for natural sinkholes, artificial retreats and trees, and the percentages of retreat use in modified and unmodified habitats. These percentages were calculated from the relatively unbiased methods of focal observation and radio tracking alone, because routine monitoring was more likely to detect retreat use in modified habitats. We examined repeated use of retreats by single or multiple iguanas based on all methods of observation.

Analysis of habitat use

Home ranges were created for males and females in each tracking session using the Animal Movement extension (Hooge and Eichenlaub 1997) in Arcview® GIS v. 3.2. Minimum convex polygons (MCP) containing all radio telemetry and additional monitoring locations were used to estimate home ranges for the entire 2002 study

season. The 95% contours of probabilistic, fixed kernels were used to estimate usage areas for each season (analogous to home range, but over a short time scale; Powell 2000) and home ranges for both seasons combined (see Chapter II for details).

We used compositional analysis of habitat use in SAS version 8.2 (bycomp.sas; Ott and Hovey 1997) to determine whether habitats and subhabitats were preferred, or used disproportionately relative to their availability. This method uses multivariate regression analysis to compare log ratios of used to available habitats (Aebischer et al. 1993). Compositional analysis was chosen for this study because of 1) generation of preference rankings that are independent of availability of habitats, 2) statistical testability of habitat preferences, 3) use of individuals rather than locations as samplings units, and 4) robustness when some habitats are rarely used (Aebischer et al. 1993). Studies of habitat use increasingly examine multiple spatial and temporal scales because animals may exercise different preferences at various scales (Johnson 1980, Garshelis 2000, Bond et al. 2002, Lyons et al. 2003). For this study, we chose to examine two scales of habitat selection: selection of home ranges within a defined study area and selection of locations within an animal's home range, or second and third order selection respectively (*sensu* Johnson 1980).

To examine second-order selection, the 95% kernel usage areas and home ranges of iguanas were overlain on the study site, and overlap of each habitat was compared to availability of that habitat within the entire study site. For this analysis, available habitat was defined as all area encompassed in MCP and kernel home ranges

of iguanas monitored and radio tracked in 2002. There is no universally agreed upon definition for available habitat (McClean et al. 1998, Garshelis 2000). We chose our definition to represent habitat that could be and apparently had been reached by iguanas that were initially released in the park. Fixed kernel usage areas and home ranges represented use in this analysis because they better represent the actual area used by iguanas relative to MCP's, which are sensitive to outliers and may include area never visited (Powell 2000). We examined second order selection at the levels of habitats and subhabitats.

To examine third-order selection, the proportion of tracking locations found in each habitat for an individual was compared to availability of habitats within that individual's MCP home range for 2002. For this analysis, the MCP estimate represented available habitat because it includes the total area potentially visited and known by an iguana, as contrasted by the kernel home range estimate which represents only the area used commonly during a tracking period (Powell 2000). Compositional analysis could not be used to examine third-order selection of subhabitats because available areas (2002 MCP home ranges) differed for individuals and often lacked some subhabitats entirely (Aebischer et al. 1993). Therefore, analysis of third-order selection was performed only at the level of habitats.

In all analyses, usage values of zero were replaced with the small value of 0.001 as suggested by Aebischer et al. (1993). All analyses of habitat use were performed for

the summer and fall radiotracking periods separately and combined. Sexes could not be analyzed separately and compared because of small sample sizes.

RESULTS

Retreat use

In the fall of 2001 and the summer and fall of 2002, 489 uses of retreats by iguanas were verified. Of these, 173 were verified during the relatively unbiased methods of radio tracking and focal animal observation, and are used in the following summary. Those instances which were excluded from analysis did not reveal any new types of retreats that were used or any patterns, other than that of bias in transect walks towards observing retreats in modified areas. Artificial retreats, which included piles of construction and waste material, holes in rock piles, and spaces under buildings, made up 72.8 % (n = 126 incidents) of unbiased observations of retreat use (Table 8). Natural sinkholes in limestone rock substrate made up 17.3 % (n = 30 incidents) of retreat use, and the remaining 9.8 % (n = 17 incidents) was made up of iguanas spending the night in tree hollows or exposed on tree limbs. Within artificial retreats (n = 16 retreats), 56.3 % (n = 9 retreats) were hollows in piles of the same limestone rock which forms natural sinkhole retreats. The majority of retreat uses (82.1%, n = 142) were in modified habitat, with most (n = 123) occurring in staff and visitor areas, a minority (n = 19) occurring in the ecotone subhabitat, and none occurring on roads and trails. Retreat use in unmodified habitat accounted for a minority (17.9 %, n = 31) of total use.

Retreat reuse was greater for artificial retreats than for natural retreats, based on unbiased observations only (Mann-Whitney U test, $n_1 = 17$, $n_2 = 19$, $S = 407.5$, $p = 0.0018$). Average reuse was 7.4 times (SD = 5.6) for artificial retreats and 2.5 times (SD = 2.7) for natural retreats (sinkholes and trees combined). Based on all methods, retreat use by multiple iguanas occurred more frequently in artificial than in natural retreats. Only one sinkhole was used by more than one iguana, whereas five artificial retreats were used multiply, with one retreat being used by four iguanas over time. No trees were used by more than one iguana. The trend was similar when only examining unbiased methods of observation with three artificial retreats, one sinkhole and no trees being used by multiple iguanas. For all types of retreats, reuse from one year to the next was observed. Multiple iguanas did not occupy the same retreat simultaneously.

Habitat use

A total of 2,686 locations were used in our analyses of habitat use of 11 iguanas in 2002. An average of 244 locations (range 100-358 locations), collected during monitoring, radio tracking, and individual observations, were used to estimate 2002 MCP home ranges for each iguana (Table 3; Figure 12). Two iguanas (one male, one female) with less than 200 locations were only located during one season. An average of 70.5 radio telemetry locations (range 54-82 locations) were used per iguana in each season to examine habitat use.

The habitat available to iguanas, defined by the area of MCP and fixed kernel home ranges of all iguanas in 2002, was 55.2 ha (Figure 2). Iguana home ranges and usage areas revealed selection of habitats within this available area in the summer (Wilks' $\lambda = 0.456$, $p = 0.010$), fall (Wilks' $\lambda = 0.576$, $p = .030$), and overall (Wilks' $\lambda = 0.216$, $p = 0.001$). In all time periods, home ranges and usage areas were composed of a greater proportion of modified habitat than that available in the landscape (Figure 18). Although sample sizes were too small to compare use and preference between males and females, they appeared to be similar at the level of habitats for the whole study period (Figure 18).

Within modified habitat, home ranges and usage areas showed selection of subhabitats in the summer (Wilks' $\lambda = 0.404$, $p = 0.027$), but not in the fall (Wilks' $\lambda = 0.851$, $p = 0.525$) or overall (Wilks' $\lambda = 0.560$, $p = 0.131$). Modified subhabitats were selected during the summer in the following order, from most to least selected: staff and visitor areas, ecotone, roads and trails (Figure 19). Within unmodified habitat, subhabitats were selected overall as indicated by home ranges and usage areas (Wilks' $\lambda = 0.115$, $p = 0.009$), but not in either season alone (summer: Wilks' $\lambda = 0.163$, $p = 0.097$, fall: Wilks' $\lambda = 0.078$, $p = 0.069$). Unmodified subhabitats were selected in the following order for both seasons combined: forest rock, forest soil, buttonwood, logwood, mosaic, shrubland (Figure 20).

Within 100% MCP home ranges, iguanas selected habitats in the summer (Wilks' $\lambda = 0.502$, $p = 0.015$), but not significantly in the fall (Wilks' $\lambda = 0.846$, $p =$

0.232) or overall (Wilks' $\lambda = 0.950$, $p = 0.487$). In all cases, however, there was a trend for greater use of modified habitat relative to the proportion present in iguanas' home ranges.

DISCUSSION

Retreat use

The reintroduced population of *Cyclura lewisi* commonly used natural sinkhole retreats, as reported for this species by Grant (1940) and for several other species of *Cyclura* (Carey 1966, 1975; Wiewandt 1977; Gicca 1980; Cubillas Hernández and Berovides Alvarez 1991; Alberts 2000). Unlike descriptions of some cycluran iguanas, *C. lewisi* in our study did not use burrows in the ground as retreats (Carey 1975, Iverson 1979, Gicca 1980, Cubillas Hernández and Berovides Alvarez 1991). One iguana in the botanic park had dug a burrow in crushed rock and soil prior to this study, although it was not known if the burrow was originally used for nesting. In a captive setting, *C. lewisi* has been reported to dig burrows that are used for sleeping and nesting (Crutchfield 1981; pers. obs.). *Cyclura lewisi* are capable of digging burrows for retreats but, according to the current study, this does not appear to be a preferred method when other retreats are available. During this study *C. lewisi* rarely slept in trees, as has been reported in few species of *Cyclura* (reviewed in Iverson 1979). We found that retreats were reused by single and multiple iguanas, though not used by multiple iguanas simultaneously as has been found in some cyclurans (Wiewandt 1977,

Iverson 1979, Cubillas Hernández and Berovides Alvarez 1991). *Cyclura lewisi* in our study used artificial retreats most commonly, and the use of such retreats has been noted for another species of *Cyclura* in disturbed areas (Iverson 1979).

Iguanas used and reused artificial retreats most commonly, and used retreats in modified habitat during the majority of our observations. During this study, we noted that natural sinkhole retreats often flooded during the wet season (May-November), whereas artificial retreats in modified areas did not because these areas were built on elevated foundations. One of the three iguanas who were observed to sleep in trees did so immediately after her home range became inundated with water and all previously used sinkhole retreats were flooded. Iguanas commonly vacated flooded sinkholes only to return and reuse them later in the year or during the next year.

We cannot discern whether iguanas used artificial retreats more commonly because they were present in already preferred modified habitat, or if iguanas preferred modified habitat because of the presence of artificial retreats. In either case, the common use of artificial retreats by *C. lewisi* suggests the option of supplementing this potentially limiting resource for conservation management. We suggest construction of artificial retreats in areas not prone to flooding, using the carbonate rocks which form their natural retreats and which they preferred among various artificial retreat materials in this study.

Supplemental artificial retreats have been used to assist in the management of some reptiles (Webb and Shine 2000, Nelson et al. 2002, Milne et al. 2003) and many

other animals (Caster et al. 1994, Twedt and Henne-Kerr 2001, Lindenmayer et al. 2003). All but one subspecies of *Cyclura* that have been studied dig nest burrows in sand or soil (Knapp et al. 1999, Rodríguez Schettino 1999, Alberts 2000), and this appears to be the case for *C. lewisi* also. We cannot present percentages for female *C. lewisi* that nested in modified versus natural sites because we did not radio track females during the nesting season. However, during our regular monitoring activities we observed that the majority of females in the park (four of seven in 2001, seven of ten in 2002) dug nest burrows in artificial sites, including garden beds and soil piles. Although the viability of nests in our study has not been compared to that of nests in natural substrates, the fact that artificial substrates are readily accepted as nest sites suggests a further conservation management option, especially since suitable natural nest substrates appear to be scarce in our study area.

Habitat use

Iguanas preferred modified habitats to unmodified habitats, according to both scales of our analyses and during all time periods examined in 2002. The preference for modified habitats may be explained in part by the greater abundance and diversity of food resources present, in the form of native and nonnative plants and direct supplemental feeding by humans which was discovered during this study. Modified habitats in the botanic park also contain more open area with reduced or no canopy cover as compared to unmodified habitats, and this may provide increased opportunities

for basking and thermoregulation. Within modified habitats, the iguanas' preference for visitor and staff areas may be due to the frequent presence of humans and related supplemental food or some other factor.

Within unmodified habitats, forest on rock substrate was the preferred subhabitat. The abundance of natural sinkhole retreats may explain the iguanas' frequent use of this subhabitat. Other factors may also contribute to the iguanas' preference, such as high plant diversity in this subhabitat which contains many areas that are historically undisturbed. However, potential nesting sites of soil or sand are scarce or absent in the forest rock subhabitat. Coastal shrubland and beach habitats are commonly used by cyclurans throughout the West Indies (Cooper 1958, Carey 1966, Rodríguez Schettino 1999, Alberts 2000), and anecdotal reports suggest that *C. lewisi* once inhabited these on Grand Cayman (Grant 1940, Lewis 1944). These habitats were not present in our study site, so we could not assess the reintroduced iguanas' preference for them.

The shrubland subhabitat was avoided by iguanas during this study, which appears contradictory to reports of closely related iguana species using this habitat throughout the Caribbean (reviewed in Alberts 2000). We note that the shrubland category in our study site is a heterogeneous mixture of natural xerophytic shrubland with a high diversity of plants, and second growth successional habitat dominated by the nonnative tree logwood. The combination of various types of shrubland into one category based on vegetational structure alone, and not composition or diversity,

warrants caution in extrapolating iguanas' avoidance of shrubland in this site to natural shrubland elsewhere.

Threats and management implications

Because pristine habitats on Grand Cayman are limited for potential reintroductions of *C. lewisi*, our finding that these iguanas will use modified habitat is encouraging. However, caution must be exercised in the extrapolation and application of our results. First, habitats that are used infrequently by animals may nonetheless be important to their survival and reproduction (Garshelis 2000). Second, preference of habitats is not necessarily correlated with fitness resulting from habitat use (Garshelis 2000). We could not investigate this relationship in our study of *C. lewisi* because of small sample size. Although urban or disturbed areas may be used and even preferred by some animals, they may nonetheless result in increased parasitism, altered behavior and reduced fitness (Boal and Mannan 1999, Rubin et al. 2002, Lacy and Martins 2003). With these possibilities in mind, we qualitatively examined the potential dangers posed to iguanas at this study site in their preferred modified habitat.

Non-native species of predators, specifically cats and dogs, were actively excluded from the park, and therefore did not pose a large threat to iguanas. However, where cats and dogs co-occur with cycluran iguanas, they have been shown to decimate populations of these lizards and even cause local extinctions on islands (Iverson 1978,

Alberts 2000). Therefore, if *C. lewisi* is to be introduced or managed in disturbed areas, active control of exotic predators is essential.

Vehicular collisions are a major source of mortality for many animals (Oxley et al. 1974, Ashley and Robinson 1996, Carr and Fahrig 2001, Koenig et al. 2002), and iguanas are no exception. In our study site, 15-20 iguanas including newly released iguanas were present at one time. During 2001 and 2002, three iguanas were run over by vehicles, one fatally. In two of these instances, the circumstances were known, and these iguanas were run over after seeking shade underneath parked vehicles. No iguanas were known to be run over by forward-moving vehicles, probably because of the slow speeds driven in the park and the staff's vigilance of iguanas on the roads and trails. Low speed limits and signs warning people of iguanas basking on roads or seeking shade under cars should be a critical component of reintroduction programs for these and other iguanas in modified areas with vehicular access.

Supplemental feeding of iguanas in the park was discovered during this study, although discouraged by the present management. Human foods, such as meats and rice which are not typically consumed by these primarily herbivorous lizards, pose unstudied potential health implications. Uncontrolled feeding by humans may also lead to dependency and undesirable behavioral changes, including increased aggression towards humans.

Our study found that reintroduced *C. lewisi* in a botanic park on Grand Cayman preferentially occupied modified habitats and frequently used artificial retreats.

Because this and other species of iguanas face shrinking natural habitats, our results are encouraging. We suggest that cycluran iguanas can successfully use modified habitats if managed so that safeguards are taken against unnatural predation, vehicular collisions, and uncontrolled supplemental feeding.

CHAPTER IV:

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The Grand Cayman blue iguana, *Cyclura lewisi*, is critically endangered, and the survival of this species may depend on the success of reintroduced populations in variously modified habitats on the heavily developed island. This study gathered information to improve the understanding and management of this species through examination of a reintroduced population of *C. lewisi* in the Queen Elizabeth II Botanic Park on Grand Cayman. Using radio tracking, routine monitoring, and focal animal observation, I investigated the spatial ecology of this population, specifically the spatial requirements in terms of home range size, and habitat use in this unnatural setting. Having determined that iguanas make heavy use of modified habitats, I also sought to qualitatively investigate dangers were posed to them in these habitats. The results concerning spatial requirements and habitat and retreat use demonstrated by iguanas in this study will be useful in managing this population and in future reserve design.

Home range sizes varied greatly among adult iguanas in this study, although males generally used larger areas than females during the summer. Because some iguanas moved large distances and used very large areas during the summer (up to 37 ha), future reserves should be large (size will depend on number of individuals desired in the population) and surrounded by buffer zones. Alternatively or additionally, fences are an option for dealing with widely roaming iguanas, and could also help address the issue or keeping feral cats and dogs out of reserves. Since only a few

scattered wild iguanas exist on Grand Cayman at present, eliminating gene flow by erecting fences is not a major issue. Factors affecting home range size of *C. lewisi* should be studied in greater detail in other species since no large populations of *C. lewisi* remain. Iguanas in our population had home range sizes that varied by two orders of magnitude, and this was not attributable to differences in sampling effort. This study provided indications that availability of food or females may affect home range size in males, as has been shown in other lizards. If the former influence is confirmed, supplemental resources could potentially contract home range sizes, thereby increasing the carrying capacity of a reserve. Similarly, limiting factors for female home range size should be determined, so that these resources can be supplemented if necessary.

The use of supplemental nests and retreats for management of *C. lewisi* is suggested by the positive response to these artificial resources in this study. Reintroduced iguanas in the park commonly used artificial retreats, and reused them more frequently than their common natural retreats in limestone sinkholes. Because the iguanas were commonly forced to vacate these natural retreats when flooded during the wet season, we recommended supplemental retreats be constructed to minimize flooding. Also, we recommend that artificial retreats be constructed from materials similar to the natural rock substrate, since this type of retreat was used most frequently among artificial retreats. Many females in both years nested in artificial substrates in

the park, which also suggests these may be supplemented in the park and other iguana reserves.

The iguanas in the park used retreats in modified habitat frequently, and generally preferred modified habitat, as indicated by their choice of home range location and by their choice of habitats within home ranges. Again, this result is encouraging because it indicates that iguanas can potentially coexist with humans and live in modified habitats. However, caution must be exercised in interpreting these results because we did not investigate the fitness of iguanas residing in modified versus unmodified habitat. It is possible that the use of modified habitats by iguanas may be detrimental to their health, despite their preference for them. Another possibility is that unmodified habitats are very important to fitness, but in smaller quantities than modified habitats, and thus do not appear to be preferred. Also, unmodified habitats may be important to iguanas in seasons which were not included in this study or in the hatchling or juvenile life stage, which I did not have the opportunity to study. In this case, absence of certain unmodified habitats in a reserve design may hinder survival and reproduction of introduced iguanas.

During this study, frequent supplemental feeding of iguanas by staff was discovered, although previously discouraged. This activity should be controlled in the botanic park and any future iguana reserves because of potential undesirable health and behavioral consequences. I also note that supplemental feeding may in part be responsible for the preference of iguanas for modified habitat in this study. Future

studies are needed to determine the effect of availability of food resources on size and location of home ranges in *C. lewisi* and related iguanas.

Iguanas only showed preference for subhabitats within unmodified habitat during one season in this study. Their apparent avoidance of shrubland in this study site during all seasons must be interpreted with caution since this shrubland type may be different from the natural undisturbed shrublands that cycluran iguanas typically inhabit.

Home range size estimates and preferences of subhabitats differed among the two seasons studied most intensively, the summer and fall of 2002. These results call attention to the importance of using long term studies to gather information on the spatial distribution of a population, including both the mating and post-mating season. Also, estimates of home range size differed when intensive radio tracking was added to routine monitoring of the park, indicating the need for continued radiotelemetry studies in this and other species. Especially if a park or reserve is being monitored, iguanas need to be radio tracked to determine if and how far out they roam outside of the protected area. In this study, radio tracking during 2002 exposed the fact that some iguanas in the population, especially males during the breeding season, traveled well outside the park into areas where they were vulnerable.

The heavy use of modified habitats and the shifting and sometimes large home ranges of *C. lewisi* in this study have several important implications for the management of this species in the Queen Elizabeth II Botanic Park and in future reserves. Generally,

the outlook is positive for this and other future reintroduced populations, which will probably not have access to pristine habitats historically inhabited by *C. lewisi*. However, safeguards must be taken to protect iguanas against potential threats in modified and human-occupied habitats, such as uncontrolled supplemental feeding, predation by nonnative predators, and vehicular collision, both with forward moving cars and parked cars under which iguanas seek shade. Hopefully, future research efforts will have access to larger populations of *C. lewisi* in which aspects of the behavior and ecology of this species can be examined in further detail. Until then, the best source of information we have for this species comes from inference from closely related iguanas and studies undertaken on captive bred, reintroduced populations of *Cyclura lewisi*, like that in the Queen Elizabeth II Botanic Park.

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APPENDICES

Appendix A:

Tables

Table 1. Estimates of population densities and home range sizes for populations of rock iguanas (*Cyclura* spp.), taken from all published studies and surveys of this group to date. Where repeat studies of the same site are boxed, the most recent population density estimate was taken from each population for analysis in Chapter II.

Species	Description of study location	Population density			Home range size (m2)			Reference
		iguanas /ha	kg/ha	Methods used	Males	Females	Methods used	
C. cychlura figginsi	Guana Cay in the Exumas, Bahamas; <2 ha island	47	x	research study conducted in winter and spring over two years; census and estimation methods not given; age classes unspecified	x	x	x	Coenen 1995 (data from 1970-1972)
C. cychlura figginsi	Guana Cay in the Exumas, Bahamas; <2 ha island	31.9	x	mark recapture; estimation method not given; all age classes	x	x	x	Windrow 1977
C. cychlura figginsi	Guana Cay in the Exumas, Bahamas; <2 ha island	34	39	one day census with eight people in June; Peterson mark-recapture method with estimator (Bailey 1952); all age classes	x	x	x	Knapp 1995
C. cychlura figginsi	Guana Cay in the Exumas, Bahamas; <2 ha island	42.6	x	1-2 week visit with census in June; methods not given; age classes unspecified	x	x	x	Carey 1976
C. cychlura inornata	Leaf Cay, Exumas, Bahamas	15.3-17.2 *	x	ten day visit with census in March; methods not given; age classes unspecified	x	x	x	Carey 1976
C. cychlura inornata	Leaf Cay in the Exumas, Bahamas; <5 ha island; supplemental feeding from passing boats	32	x	total population estimate from 17-year mark recapture study; all age classes	x	x	x	Iverson in Alberts 2000
C. cychlura inornata	U Cay, Exumas, Bahamas; 3 ha island	33	x	total population estimate from 17-year mark recapture study; all age classes	x	x	x	Iverson in Alberts 2000
C. cychlura inornata	Alligator Cay in the Exumas, Bahamas; 1.8 ha island	26.6-59.5 *	x	census with transect walks in Mar-Nov; modified Peterson estimator (Bailey 1952); all age classes	1,197-5,620	161-309	Minimum convex polygon (100% MCP) estimates; 4-22 sightings per individual; in Mar-Nov	Knapp 2000, 2001

* One asterisk indicates a range for the estimate in a single study site.

Table 1. (continued)

Species	Description of study location	Population density			Home range size (m2)			Reference
		iguanas /ha	kg/ha	Methods used	Males	Females	Methods used	
C. rileyi rileyi	Alligator Cay in the Exumas, Bahamas; 1.8 ha island	x	x	x	mean=439 (n=14)	mean=628 (n=24)	95% Fixed kernel home ranges with 10-26 locations per iguana	Hayes et al. 2004
C. rileyi rileyi	island in Hermitage Lake on San Salvador, Bahamas; 0.9 ha island	50.0-88.9[a]	x	one day exploration of island; not a research article; no methods given; age classes unspecified	x	x	x	Ostrander 1982
C. rileyi rileyi	Green Key, Man Head, Low Key, High Key; off San Salvador island, Bahamas; 5-15 ha islands	2.5, 7.3, 7.5[b] **	x	census with transect walks; 40 hours total for four cays in Dec; iguanas sighted/area; adults only	x	x	x	Gicca 1980
C. rileyi rileyi	Gaulin Cay, Goulding Cay, Green Cay, Guana Cay, Low Cay, Manhead Cay near San Salvador, Bahamas; 1.6-10.8 ha islands	4.5, 6.3, 24.0, 24.7, 30.0, 50.4[c] **	x	Jun-Jul censuses with mark recapture; Lincoln Peterson and observed iguanas x 3 estimate; all age classes	x	x	x	Hayes et al. 1995
C. rileyi rileyi	Goulding Cay, Green Cay, Guana Cay, Low Cay, Manhead Cay, Pigeon Cay near San Salvador, Bahamas; 1.6-10.8 ha islands	40.0, 25.5, 18.8, 3.9, 11.5, 9.0 **	22.5, 15.5, 12.5, 5.8, 3.1, 13.5 **	surveys over seven years; Lincold-Peterson mark recapture and iguanas sighted/area, modified; age classes unspecified	x	x	x	Hayes et al. 2004
C. rileyi cristata	White Cay, Bahamas; 14.9 ha	9.1	3.7	surveys over four years; Lincold-Peterson mark recapture and iguanas sighted/area, modified; age classes unspecified	x	x	x	Hayes et al. 2004

** Two asterisks indicate separate estimates for separate islands or study sites.
a The lower estimate was derived from the minimum number of iguanas evidenced in Ostrander's survey. The upper estimate is that given by Ostrander.
b These figures were not counted in overall density figures in Chapter II, since newer estimates are available.
c These figures (exception: Gaulin Cay) were not counted in overall density figures in Chapter II, since newer estimates are available.

Table 1. (continued)

Species	Description of study location	Population density			Home range size (m2)			Reference
		iguanas /ha	kg/ha	Methods used	Males	Females	Methods used	
C. rileyi nuchalis	North Cay, Bahamas	x	x	x	x	mean=1,222 (n=10)	95% Fixed kernel home ranges with 23-37 locations per iguana	Hayes et al. 2004
C. rileyi nuchalis	North Cay, Fish Cay, translocated population, Bahamas; 3.3-73.9 ha islands	128.3, 58.7, 95.2 **	58.9, 23.7, 104.4 **	surveys over four years; Lincold-Peterson mark recapture and iguanas sighted/area, modified; age classes unspecified	x	x	x	Hayes et al. 2004
C. carinata	12 islands of 0.05-0.7 ha each in the Chalk Sound, Bahamas	90.6, 78.0, 103.0, 117.4, 22.5, 63.3, 103.1, 27.8, 108.4, 126.6, 101.2, 44.4 **	x	Apr-Jun (mating season); iguanas sighted/area, modified for larger islands; age classes unspecified	x	x	x	Bissell and Martins 2004
C. carinata carinata	Pine Cay, Turks and Caicos; 350 ha island	42.9	22.2	flush transects; several density estimators; extrapolation from study sites to island; all age classes	700-2,480 (n=11)	780-1,180 (n=4)	100% MCP estimates; 34 days from Jun-Aug, no radio telemetry	Iverson 1979
C. carinata carinata	Water Cay, Turks and Caicos	x	x	x	2,330-3,790 (n=4)	x	no methods given	D. Auth in Iverson 1979
C. cornuta stejnegeri	Mona Island, Puerto Rico; several sites and transects on 5,500 ha island; feral ungulates and predators	0.3-0.5 *	x	census with transect walks in all seasons of two years; estimate given as iguanas sighted/area extrapolated to island; all age classes	x	x	x	Wiewandt 1977
C. cornuta	Ile Petite Ginave, Haiti; small island, size not given	13	x	no methods given; age classes unspecified	x	x	x	Meylan pers. comm. in Wiewandt 1977

* One asterisk indicates a range for the estimate in a single study site.
** Two asterisks indicate separate estimates for separate islands or study sites.

Table 1. (continued)

Species	Description of study location	Population density			Home range size (m2)			Reference
		iguanas /ha	kg/ha	Methods used	Males	Females	Methods used	
C. nubila nubila	Three cays off Cayo Largo del Sur, Cuba; 15-729 ha cays	4.4, 9.6, 25.0 **	x	transects, surveys, and estimation based on Iverson (1979); adults only	x	x	x	Perera 1985
C. nubila nubila	Guantanamo Bay, Cuba; 3 study sites of 0.5 ha each	50	x	census and estimation methods not given; age classes unspecified	x	x	x	Lacy and Martins 2003
C. nubila nubila	Guantanamo Bay, Cuba; 3 study sites of 1ha each; highly disturbed with frequent human interaction	25	x	census and estimation methods not given; age classes unspecified	x	x	x	Lacy and Martins 2003
C. nubila nubila	Guantanamo Bay, Cuba; study site size not given; site on naval base, close to firing range	7.8	x	census and estimation methods not given; age classes unspecified	274 (n=10)	390 (n=23)	100% MCP estimates; average 50 sightings per iguana per season; breeding season	Alberts et al. 2002
C. nubila nubila	Cayo Rosario, Cuba	11	x	census and estimation methods not given; age classes unspecified	x	x	x	Berovides in Alberts 2000
C. nubila nubila	Cayo Rosario, Cuba	9.6	x	census and estimation methods not given; age classes unspecified	x	x	x	Rodriguez-Schettino 1999
C. nubila nubila	Isla Magueyes, Puerto Rico; 7.2 ha island; population introduced in 1960's; iguanas fed by visitors at dock	23.2	x	census and estimation methods not given; all age classes	x	x	x	Christian et al. 1986

** Two asterisks indicate separate estimates for separate islands or study sites.

Table 1. (continued)

Species	Description of study location	Population density			Home range size (m2)			Reference
		iguanas /ha	kg/ha	Methods used	Males	Females	Methods used	
C. pinguis	Anegada; 3 study sites (~6 ha total) on 4,000 ha island; many feral ungulates and predators	2.03	x	40 day study in Mar-May, estimate given as iguanas sighted/area; all age classes	116-985 (n=5)	155-412 (n=5)	100% MCP estimates; 40 days Mar-May, 3-10 sightings per individual	Carey 1975
C. pinguis	Anegada Island, British Virgin Islands; 43 ha site on 4,000 ha island; many feral ungulates and predators	0.36	x	research study over 6 years, covering all seasons, mark-recapture and Schnabel (1938) estimation; all age classes	11,000-90,000 (n=7)	5,000-28,000 (n=2)	100% MCP; radiotracking for 6-30 days per iguana in different seasons	Mitchell 1999
C. pinguis	Guana Island, British Virgin Islands; 19 ha site on 300 ha island; population introduced only 6 yrs prior; resort area with few introduced sheep	0.5-0.7 *	x	one month mark-recapture study in Oct., Schnabel (1938) estimation; all age classes	73,000 (n=1)	9,000-35,000 (n=3)	100% MCP; limited radiotracking plus <2 years of sightings (dates not given); supplementally fed iguanas	Goodyear and Lazell 1994

* One asterisk indicates a range for the estimate in a single study site.

Table 2. Sex, age, and body size of all *Cyclura lewisi* observed in the study site during 2001and 2002. Body size was measured for all iguanas that were tracked with radio transmitters in 2002.

				Summer 2002		Fall 2002	
ID	Sex	Hatch Year	Release Date	SVL (cm)	Weight (kg)	SVL (cm)	Weight (kg)
PSYC	M	?	?				
GX2	M	1995	Sep 1997				
PU	F	1995	Sep 1997	30.3	1.1	28.9	1.4
PB	F	1995	Sep 1997				
Y	M	1995	Sep 1997	43.0	3.3	43.2	3.9
BTR	F	1996	Sep 1997	30.8	1.5	32.0	1.7
PI	M	1996	Sep 1997	36.5	2.4		
YB	F	1996	Fall 1999	34.0	1.6	34.6	2.3
R	F	1997	Fall 1999				
PIPB	F	1997	Fall 1999	37.0	2.1	37.5	2.5
PBX2	F	1997	Fall 1999	35.5	2.2	37.4	2.7
SLGR	M	1997	Fall 1999	43.0	4.0	48.9	5.1
SANT	M	1997	Fall 1999	41.2	2.7	43.0	3.9
G	?	1998	Jan 2001				
RB	F	1998	Jan 2001	26.9	0.9	28.8	1.1
TRAN	M	1998	Jan 2001	35.8	2.2		
WYW	F	1999	Mar 2002				
YX3	F	1999	Mar 2002				
GW	F	1999	Mar 2002				
WY	F	1999	Mar 2002				
YPU	F	1999	Mar 2002			32.3	1.5
PBY	M	1999	Mar 2002				
PUX3	M	1999	Mar 2002				
PBX3	M	1999	Mar 2002			28.9	1.0
YW	M	1999	Mar 2002			34.4	2.0
YX2	F	2000	*				
B	?	2000	*				

* These iguanas were found in the park in 2001. They are presumed to be the offspring of reintroduced iguanas in the park, since no naturally occurring iguanas have been found in this area for over a decade (Burton, pers. comm.).

Table 3. Estimates of home range size (100% minimum convex polygons) for all *Cyclura lewisi* located more than 10 times during 2001 and 2002. For 2002, estimates are given for data excluding and including radio telemetry data from 25-35 days of tracking during the summer (May-Jul) and fall (Aug-Nov).

			2001 without radiotracking			2002 without radiotracking			2002 with radiotracking		
ID	Sex	Hatching Year	Number locations	100% MCP (m^2)	100% MCP (ha)	Number locations	100% MCP (m^2)	100% MCP (ha)	Number locations	100% MCP (m^2)	100% MCP (ha)
PSYC	M	?	71	6323	0.632	0			0		
GX2	M	1999	4			0			0		
Y	M	1995	128	88342	8.834	170	26620	2.662	334	52165	5.216
PI	M	1995	18	8533	0.853	60	47629	4.763	220	376010	37.601
SLGR	M	1997	92	113513	11.351	188	6913	0.691	358	11435	1.144
SANT	M	1996	43	15374	1.537	60	23741	2.374	220	72428	7.243
PUW	M	1997	5			32	8171	0.817	100	186370	18.637
PBX3	M	1997	*			106	9365	0.937	134	9365	0.937
YW	M	1998	*			192	153	0.015	**		
PBY	M	1998	*			25	932	0.093	**		
G	M	1999	25	7351	0.735	0			0		
PUX3	M	1999	*			10	3118	0.312	**		
B	M	2000	21	47	0.005	0			0		
Yx2	?	2000	29	4325	0.432	0			0		
PU	F	1995	55	273	0.027	22	45848	4.585	122	81594	8.159
PB	F	1995	40	5199	0.520	0			0		
BITR	F	1996	97	1118	0.112	80	1365	0.136	327	4302	0.430
YB	F	1996	15	559	0.056	107	3757	0.376	273	5943	0.594
PIPB	F	1997	88	3353	0.335	94	7655	0.766	259	13807	1.381
PBX2	F	1997	*			112	2235	0.223	266	21128	2.113
R	F	1997	35	8497	0.850	0			0		
RB	F	1998	42	3018	0.302	64	1278	0.128	207	15303	1.530

* These iguanas had not yet been released into the park or tagged for identification during that season.

** These iguanas were not radio tracked during 2002 because they had been released less than one year prior. Two iguanas in this age class were radio tracked (PBX3, YPU) and were used in analyses comparing home range size with and without radio tracking, but not in home range size estimates for adult males and females.

Table 3. (continued)

			2001 without radiotracking			2002 without radiotracking			2002 with radiotracking		
ID	Sex	Hatching Year	Number locations	100% MCP (m^2)	100% MCP (ha)	Number locations	100% MCP (m^2)	100% MCP (ha)	Number locations	100% MCP (m^2)	100% MCP (ha)
YX3	F	1999	*			24	4408	0.441	**		
WYW	F	1999	*			16	13071	1.307	**		
GW	F	1999	*			91	422	0.042	**		
WY	F	1999	*			185	9419	0.942	**		

* These iguanas had not yet been released into the park or tagged for identification during that season.

** These iguanas were not radio tracked during 2002 because they had been released less than one year prior. Two iguanas in this age class were radio tracked (PBX3, YPU) and were used in analyses comparing home range size with and without radio tracking, but not in home range size estimates for adult males and females.

Table 4. Home range estimates (100% minimum convex polygons) of *Cyclura lewisi* for the summer and fall of 2001 and 2002. Estimates are based on data from all methods of observation (transect walks, focal animal observation, and radio telemetry).

			Summer 2001				Fall 2001			
ID	Sex	Hatch Year	locations	tracked[a]	100% MCP (m^2)	100% MCP (ha)	locations	tracked[a]	100% MCP (m^2)	100% MCP (ha)
PSYC	M	?	30		1813	0.181	41		5186	0.519
GX2	M	1995	2				2			
Y	M	1995	65	Y	76829	7.683	63	Y	14144	1.414
PI	M	1996	15		7165	0.716	3			
SLGR	M	1997	47	Y	86300	8.630	45	Y	66388	6.639
SANT	M	1997	4				39	Y	1955	0.195
PUW	M	1998	*				*			
G	M	1998	25		7359	0.736	0			
PBX3	M	1999	*				*			
YW	M	1997	*				*			
PBY	M	1999	*				*			
PUX3	M	1999	*				*			
B	M	2000	21		47	0.005	0			
YX2	?	2000	21		785	0.079	8		108	0.011
PU	F	1995	55	Y	263	0.026	0			
PB	F	1995	49		557	0.056	40	Y	2657	0.266
BITR	F	1996	37		542	0.054	60	Y	1017	0.102
YB	F	1996	9		301	0.030	6			
PIPB	F	1997	66	Y	2718	0.272	22		1336	0.134
PBX2	F	1997	*				5			
R	F	1997	32		5254	0.525	3			
RB	F	1998	8		782	0.078	38	Y	1666	0.167
YPU	F	1999	*				*			
YX3	F	1999	*				*			
WYW	F	1999	*				*			
GW	F	1999	*				*			
WY	F	1999	*				*			

a In 2001, some iguanas in the population were tracked and locations were recorded hourly during period of focal animal observation and testing of radio telemetry equipment (approximately 3-12 hours for 1-3 days).

* These iguanas had not yet been released into the park or tagged for identification during that season.

Table 4. (continued)

			Summer 2002				Fall 2002			
ID	Sex	Hatch Year	locations	radiotelemetry locations	100% MCP (m^2)	100% MCP (ha)	locations	radio tracking locations	100% MCP (m^2)	100% MCP (ha)
PSYC	M	?	0				0			
GX2	M	1995	0				0			
Y	M	1995	169	82	51546	5.155	165	82	23929	2.393
PI	M	1996	123	83	314837	31.484	97	75	51231	5.123
SLGR	M	1997	203	84	11261	1.126	155	87	4830	0.483
SANT	M	1997	109	76	95597	9.560	111	83	1577	0.158
TRAN	M	1998	100	67	186370	18.637	0			
G	M	1998	0				0			
PBX3	M	1999	89		3803	0.380	45	23	6294	0.629
YW	M	1997	54		84	0.008	138		76	0.008
PBY	M	1999	13		645	0.065	11		16	0.002
PUX3	M	1999	10		3118	0.312	0			
B	M	2000	0				0			
YX2	?	2000	0				0			
PU	F	1995	18		45859	4.586	104	87	24962	2.496
PB	F	1995	0				0			
BTR	F	1996	173	83	4311	0.431	154	88	457	0.046
YB	F	1996	142	87	5018	0.502	131	79	2545	0.255
PIPB	F	1997	139	86	8881	0.888	120	79	11423	1.142
PBX2	F	1997	145	79	9483	0.948	121	75	11873	1.187
R	F	1997	0				0			
RB	F	1998	143	83	11747	1.175	67	60	5444	0.544
YPU	F	1999	48		1545	0.155	170	80	1499	0.150
YX3	F	1999	23		4408	0.441	0			
WYW	F	1999	16		13071	1.307	0			
GW	F	1999	90		368	0.037	0			
WY	F	1999	104		9081	0.908	131		1045	0.104

Table 5. Size estimates for usage areas, based on 100% minimum convex polygons (100% MCP) and 95% fixed kernel contours (95% Kernel), and average core areas (50% Kernel) of *Cyclura lewisi*. Average estimates and movement rates, shown with sample sizes, standard deviations and ranges, were calculated from radio telemetry data collected during the summer and fall of 2002 (60-85 locations per iguana per season).

			Usage Area Estimator (m^2)			Movement (m)	
Sex	**Season**		**100% MCP**	**95% Kernel**	**50% Kernel**	**Ave between points**	**Overall**
		mean	**6,030**	**2,100**	**240**	**19.0**	**1,585**
	Summer	SD	± 3,018	± 1,809	± 201	± 6.4	± 519
Females	n=5	range	(2,430-9,470)	(480-4,580)	(90-580)	(14-27)	(1,158-2,254)
		mean	**8,570**	**4,680**	**450**	**25.8**	**1,961**
	Fall	SD	± 7,5461	± 4,868	± 441	± 14.0	± 1,176
Females	n=6	range	(240-20,810)	(70-11,800)	(10-1,190)	(4-44)	(415-3,754)
		mean	**127,670**	**45,630**	**6,820**	**64.0**	**5,165**
	Summer	SD	± 128,609	± 35,210	± 5,543	± 30.0	± 1,864
Males	n=5	range	(8,300-353,790)	(1,860-99,670)	(320-14,060)	(28-107)	(2,242-6,852)
		mean	**16,020**	**8,050**	**1,120**	**18.4**	**1,506**
	Fall	SD	± 16,573	± 11,034	± 1,451	± 8.9	± 723
Males	n=4	range	(470-36,280)	(180-24,390)	(30-3,260)	(6-27)	(485-2,186)

Table 6. Results of Mann-Whitney U tests comparing male and female estimated home range (100% MCP, 95% Kernel) and core area (50% Kernel) sizes in *Cyclura lewisi*. Estimates were constructed using data from sightings (from transect walks and focal animal observation) and radio telemetry of iguanas in the summer (May-Jul) and fall (Aug-Nov) of 2001 and 2002. Sample sizes (n), test statistic (S) and p-values (p) are shown for Mann-Whitney U tests, with significant results showing bolded p-values.

			Summer			Fall			Overall		
Year	**Method**	**Estimator**	**n**	**S**	**p**	**n**	**S**	**p**	**n**	**S**	**p**
2001	sightings	100% MCP	12	48	**0.0101**	8	25	0.0571	13	61	**0.0047**
2002	sightings and radiotelemetry	100% MCP	20	102	0.6027	15	55	0.9551	19	96	0.6607
2002	radiotelemetry data only	100% MCP	10	16	**0.0159**	10	25	0.6095	9	27	0.1111
2002	radiotelemetry data only	95% MCP	10	17	**0.0317**	10	24	0.7619	9	27	0.1111
2002	radiotelemetry data only	95% Kernel	10	17	**0.0317**	10	24	0.7619	9	28	0.0635
2002	radiotelemetry data only	50% Kernel	10	16	**0.0159**	10	25	0.6095	9	29	**0.0317**

Table 7. Descriptions of subhabitats found in the study site at the Queen Elizabeth II Botanic Park on Grand Cayman. Descriptions are based on Burton (1990) and surveying in the current study.

Modified habitat	Substrates	Canopy	Common flora	Other characteristics
Roads and Trails	gravel, asphalt	little to no canopy cover on roads; partially open canopy cover on trails with 7-9 m canopy height	few trees, mostly small herbacious weeds at edges of trails and roads	regular vehicular and human traffic; rarely flooded
Ecotone	limestone rock, soil	partially open canopy cover near trails; otherwise similar to forest and shrubland	same species found in forest and shrubland	includes portions of forest and shrubland with thinned vegetation; occassional human traffic
Staff/Visitor Areas	gravel, cement, manicured lawn, soil	highly variable, entirely open and entirely closed in patches	highly diverse, both native and nonative herbacious and woody plants	buildings, cars, and piles of construction materials and wastes present; frequent human traffic; never flooded

Table 7. (continued)

	Substrates	Canopy	Common flora	Other characteristics
Unmodified habitat				
Buttonwood dominated, seasonally-flooded swamp	saturated peat, underlying carbonate karst	mostly closed canopy cover; canopy height of approx. 3 m	dominant *Conocarpus erectus;* some *Haemotoxylum campechianum*, *Bursera simaruba*, *Hippomane mancinella* in transition zones	regularly flooded; no human traffic
Logwood dominated, seasonally-flooded swamp	carbonate karst, soil, peat in some patches	mostly closed canopy cover; canopy height of 5-7 m	dominant *Haematoxylum campechianum*; some *Bursera simaruba,* E*rythroxylum areolatum*	seasonally flooded; no human traffic
Dry semi-deciduous forest on rock	carbonate karst	mostly closed canopy with gaps; canopy height of 6-8 m	common *Bursera simaruba*, *Coccothrinax proctorii*, *Haematoxylum campechianum*	infrequently flooded; no human traffic
Dry semi-deciduous forest on soil	soil	mostly closed canopy with gaps, canopy height of 7-9 m	common *Bursera simaruba*, *Clusia flava, Gyminda latifolia, Haematoxylum campechianum*	infrequently flooded; no human traffic
Shrubland	carbonate karst, soil	mostly closed canopy with gaps; canopy height of 3-5 m	common *Coccothrinax proctorii*, *Myrcianthes fragrans*, A*gave sobolifera*, *Haematoxylum campechianum*, *Comocladia dentata*	mosaic of second-growth vegetation and primary xerophytic shrubland; infrequently flooded; no human traffic
Mosaic of forests and swamps	carbonate karst, soil, peat	mostly closed canopy; canopy height of 6-9 m	common *Bursera simaruba*, *Hippomane mancinella*, *Conocarpus erectus*, *Haematoxylum campechianum*	seasonally flooded in patches; no human traffic

Table 8. Instances of retreat use by *Cyclura lew*isi in the Queen Elizabeth II Botanic Park on Grand Cayman in 2001 and 2002. Figures presented here contain instances of retreat use confirmed during focal animal observations and radio tracking in 2001 and 2002. The number of retreats used by each iguana is in parentheses.

Iguana ID	Iguana sex	Artificial retreat	Natural sinkhole	Tree
SLGR	M	14 (3)	3 (2)	
PINK	M	6 (3)	3 (3)	
Y	M	22 (4)	1 (1)	1 (1)
SANT	M	14 (1)		
PUW	M	4 (2)		
BITR	F	21 (2)	2 (1)	
YB	F	8 (1)	8 (2)	
PURP	F			5 (1)
RB	F	12 (2)	7 (2)	
PIPB	F		3 (3)	11 (1)
PBX2	F	15 (1)		
YPU	F	10 (1)		
PB	F		3 (2)	
Total uses		126	30	17

Appendix B:

Figures

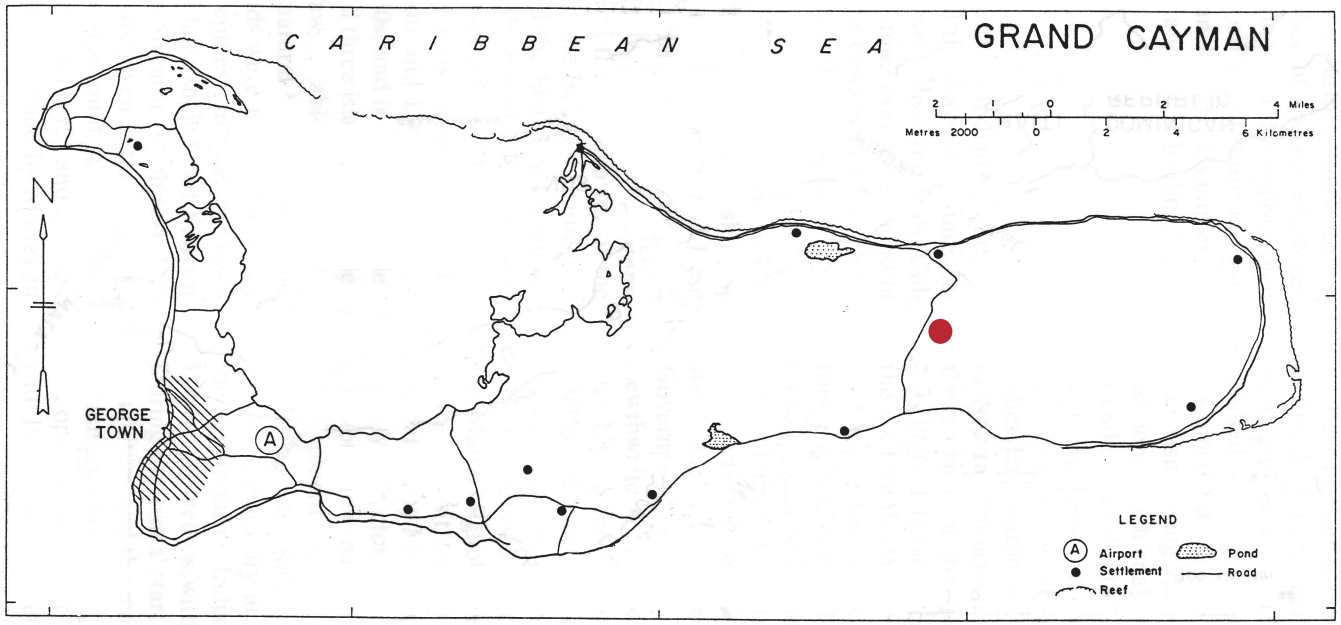

Figure 1. The Queen Elizabeth II Botanic Park, located in the east interior of Grand Cayman. The park is shown with a red circle (map modified from Brunt & Davies 1994).

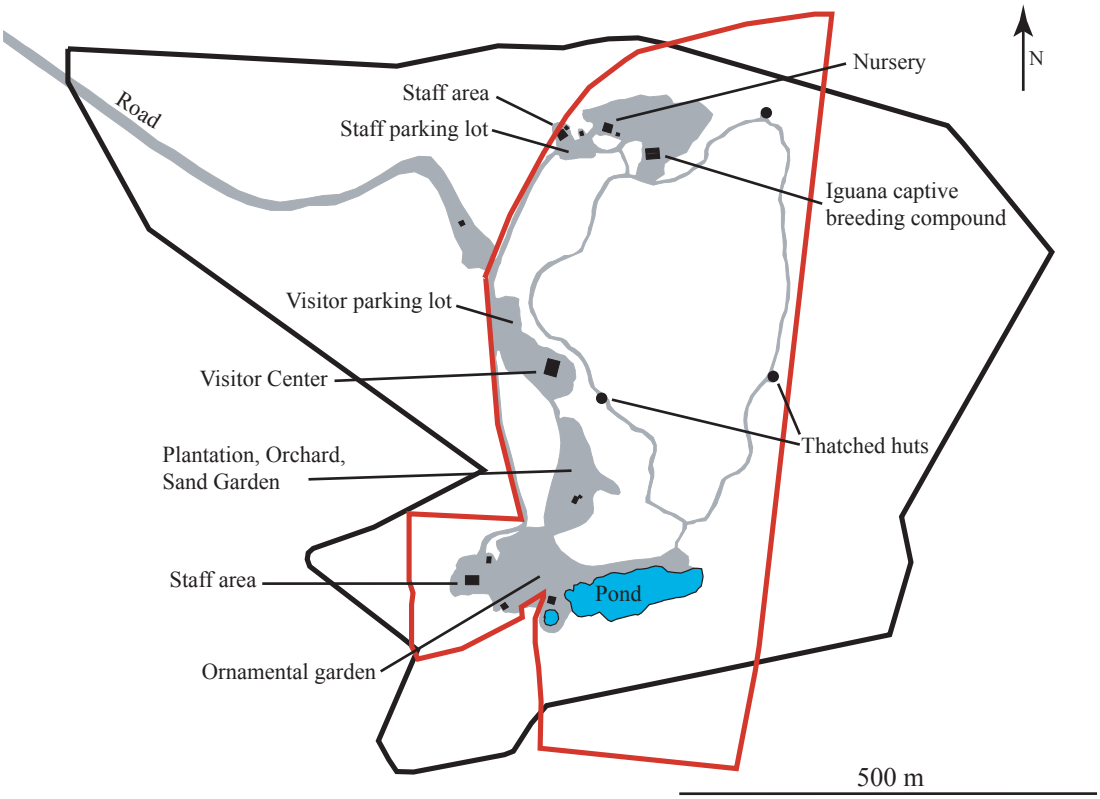

Figure 2. The study site includes the Queen Elizabeth II Botanic Park and surrounding undeveloped land. The smaller red polygon indicates the boundary of the botanic park, which encompasses 24.3 ha. The larger black polygon indicates the total area used by reintroduced iguanas, *Cyclura lewisi*, during the course of this study (55.2 ha). Trails, roads, and staff and visitor areas are shown shaded in gray. All major landmarks are labeled.

Figure 3. A modified subhabitat in the study site: roads, trails and parking lots. A. Above: main trail that loops through the botanic park. Below: parking lot and entrance to the botanic park.

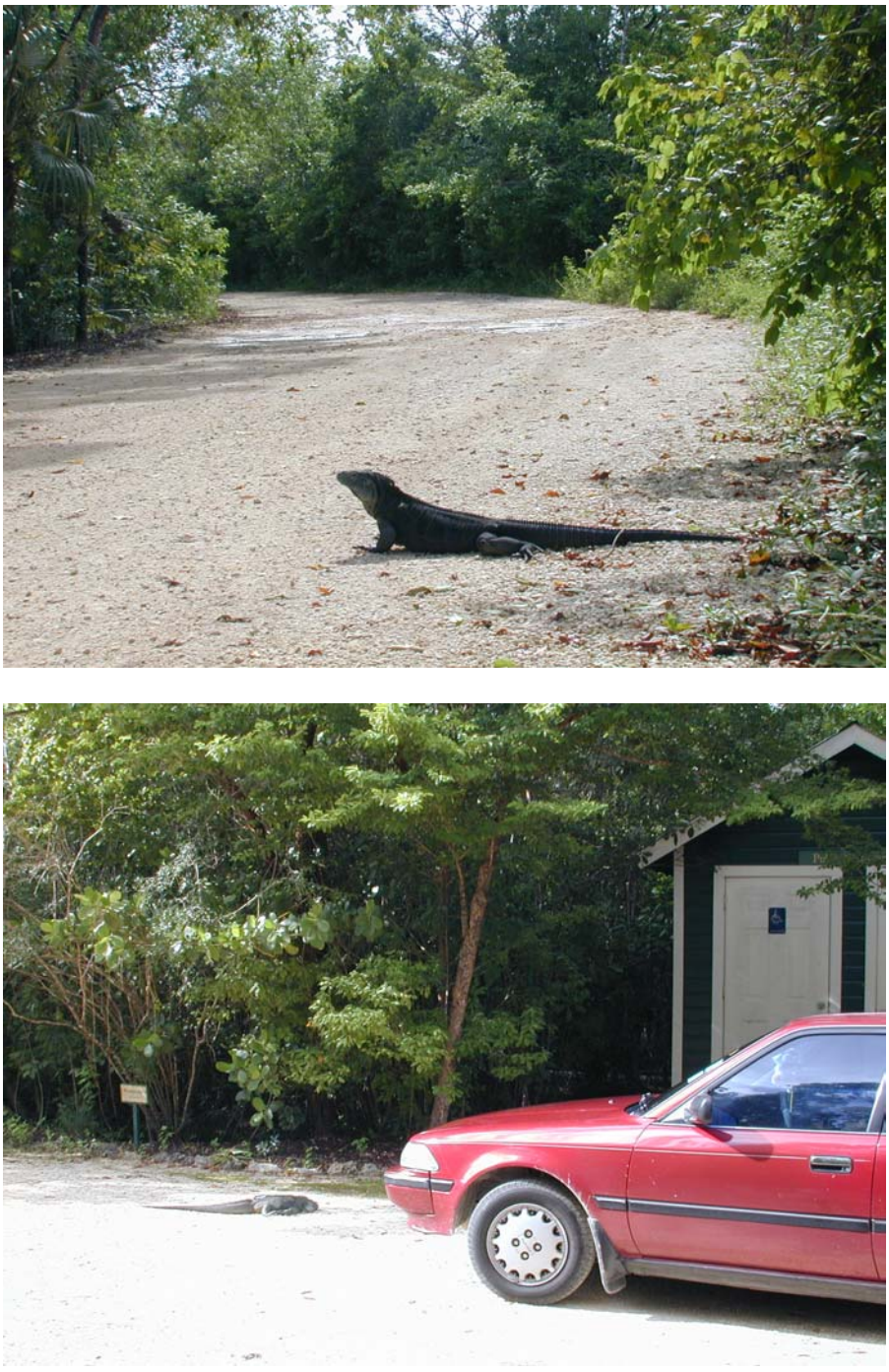

Figure 3. (continued) B. Above: iguana basking in sun on the side of a road within the park. Below: iguana basking in sun in front of a worker's car on the road.

Figure 4. A modified subhabitat in the study site: visitor and staff areas. A. Above: a manicured lawn and garden. Below: iguana resting in shade on porch of staff office building.

Figure 4. (continued) B. Above: nursery area. Below: plantation-style garden for visitors viewing.

Figure 5. A modified subhabitat in the study site: ecotone. Above: thinned vegetation in shrubland ecotone. Below: side of trail and thinned vegetation of forest ecotone.

Figure 6. An unmodified subhabitat in the study site: forest on rock. Above: view of forest on carbonate karst substrate, with *Bursera simaruba* tree in foreground. Below: close up view of rock substrate that forms natural sinkholes.

Figure 7. An unmodified subhabitat in the study site: forest on soil.

Figure 8. An unmodified subhabitat in the study site: buttonwood (*Conocarpus erectus*) dominated, seasonally flooded swamp.

Figure 9. An unmodified subhabitat in the study site: logwood (*Haematoxylum campechianum*) dominated, seasonally flooded swamp.

Figure 10. An unmodified subhabitat in the study site: shrubland. Above: primary xerophytic shrubland. Below: second-growth vegetation on soil and rock, mainly dominated by logwood, *Haematoxylum campechianum.*

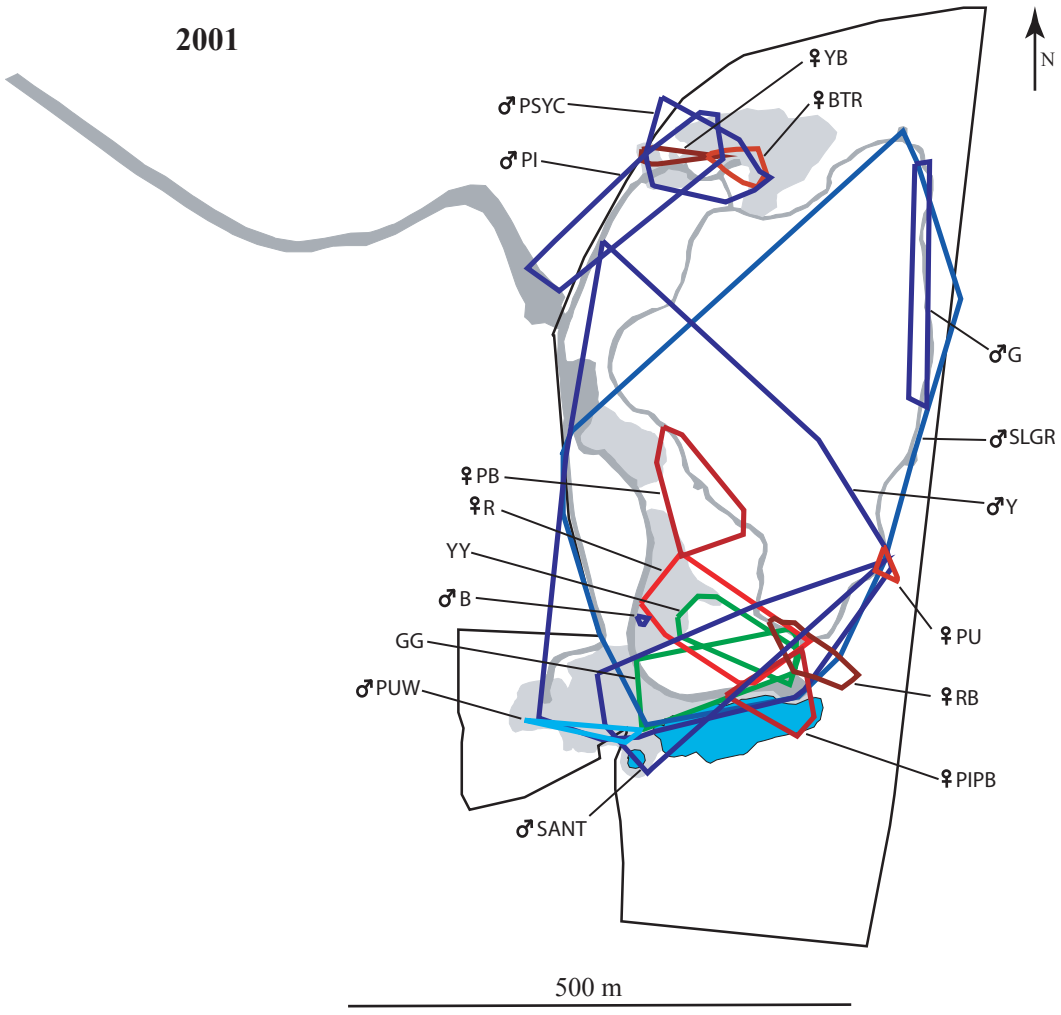

Figure 11. Home ranges (100% MCP's) of a reintroduced population of *Cyclura lewisi* on Grand Cayman constructed from locations collected during transect walks of the park and focal animal observation in 2001. Roads and trails are shaded in dark gray, and visitor and staff areas are shaded in light gray. Each home range is labeled with the respective iguana's name and sex (when known). Home ranges of males are shown in blue, those of females are in red, and those of iguanas of unknown sex are in green. Home ranges in 2002, which additionally included radio telemetry data, have larger maximum sizes and show more usage of area outside the park than those in 2001.

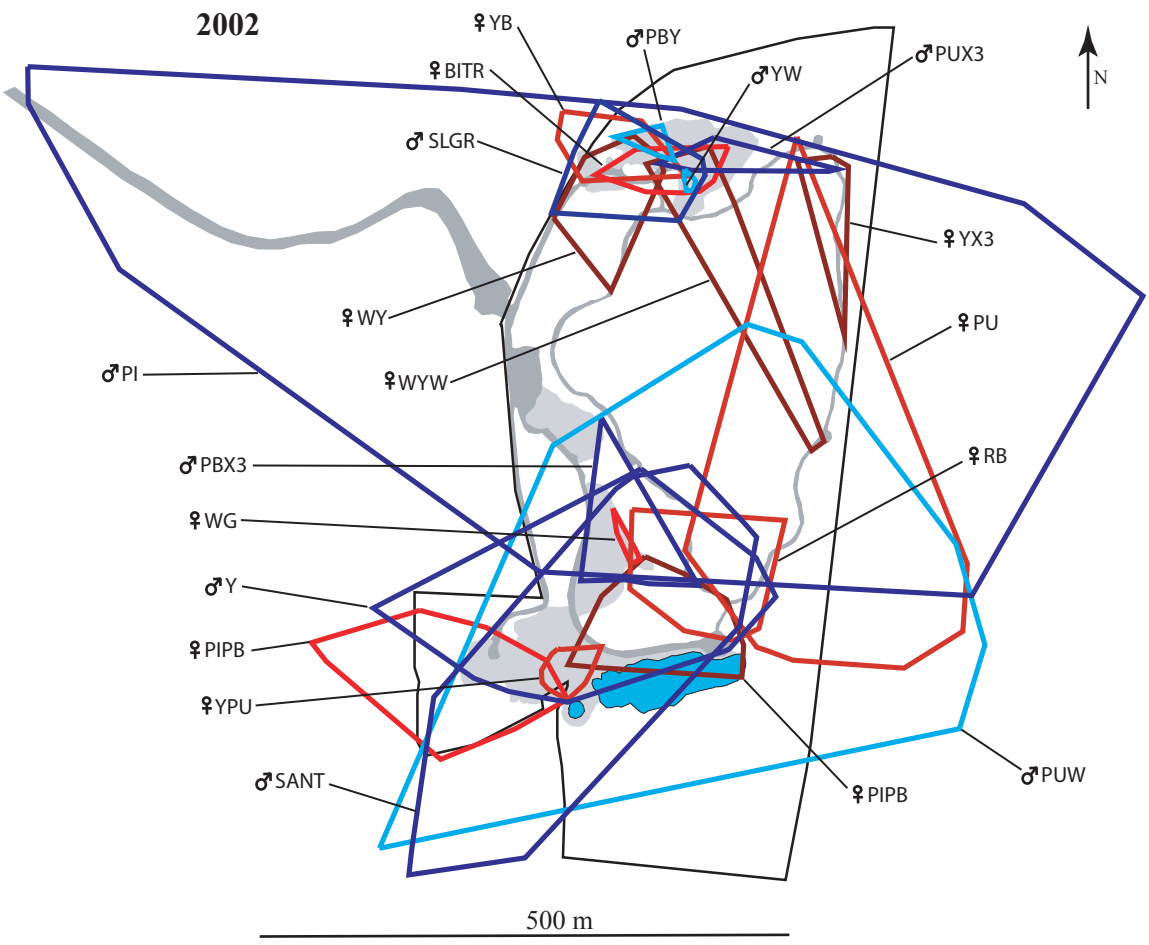

Figure 12. Home ranges (100% MCP's) of a reintroduced population of *Cyclura lewisi* on Grand Cayman constructed from locations collected during transect walks of the park and focal animal observation in 2002. Roads and trails are shaded in dark gray, and visitor and staff areas are shaded in light gray. Each home range is labeled with the respective iguana's name and sex. Home ranges of males are shown in blue, those of females are in red, and those of iguanas of unknown sex are in green. Home ranges in 2002 have larger maximum sizes and show more usage of area outside the park than those in 2001, which did not include radio telemetry data.

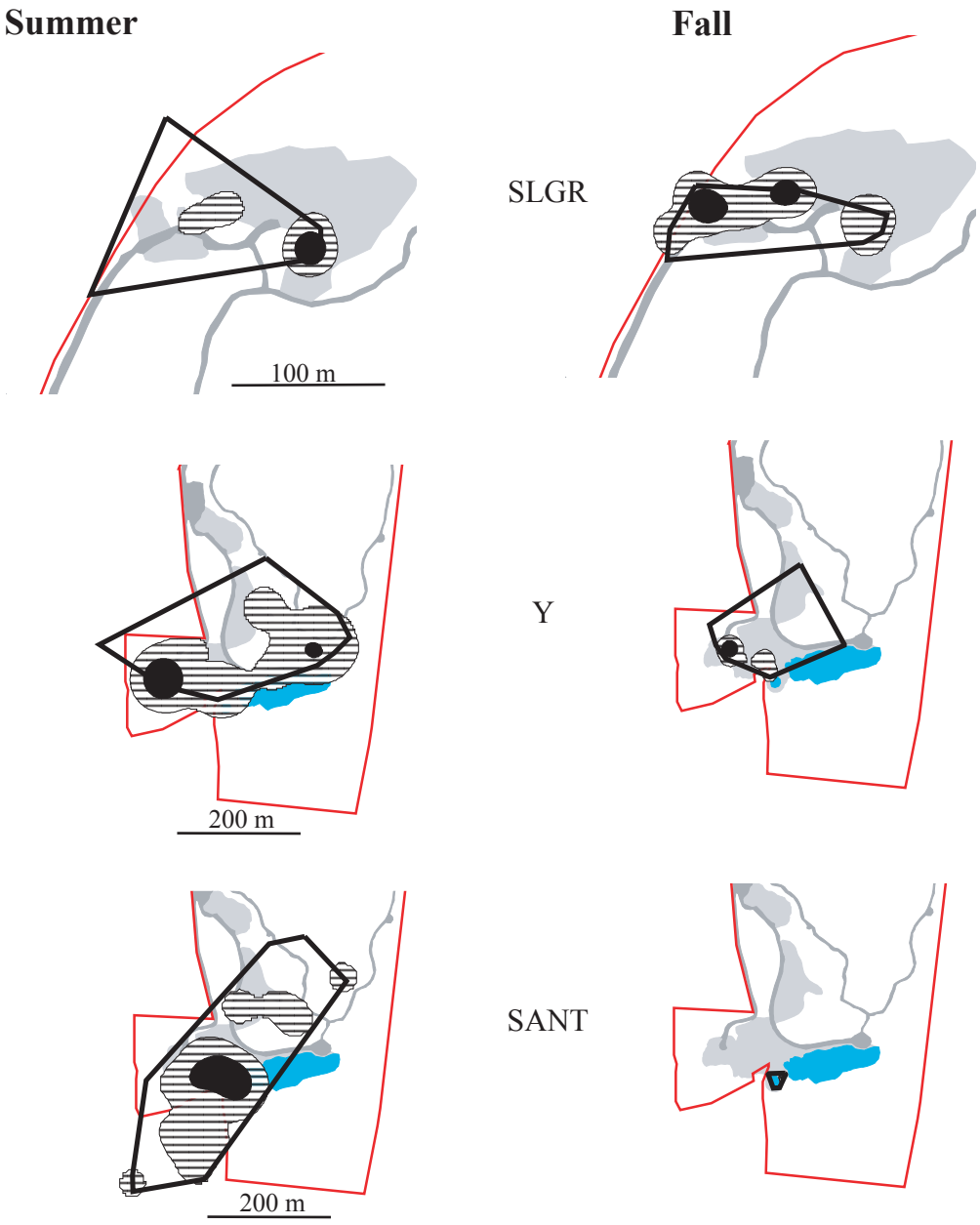

Figure 13. Usage areas, based on 60-85 locations per iguana, are shown for male *Cyclura lewisi* tracked for two week periods during the summer and fall of 2002. Minimum convex polygon (100% MCP) estimates are shown in the hollow polygon. Probabilistic kernel estimates are shown with 95% probability area as line-filled areas, and the 50% probability area (core area) as black-filled areas. Roads and trails are shaded in dark gray, and visitor and staff areas are shaded in light gray. The red line is the boundary of the botanic park.

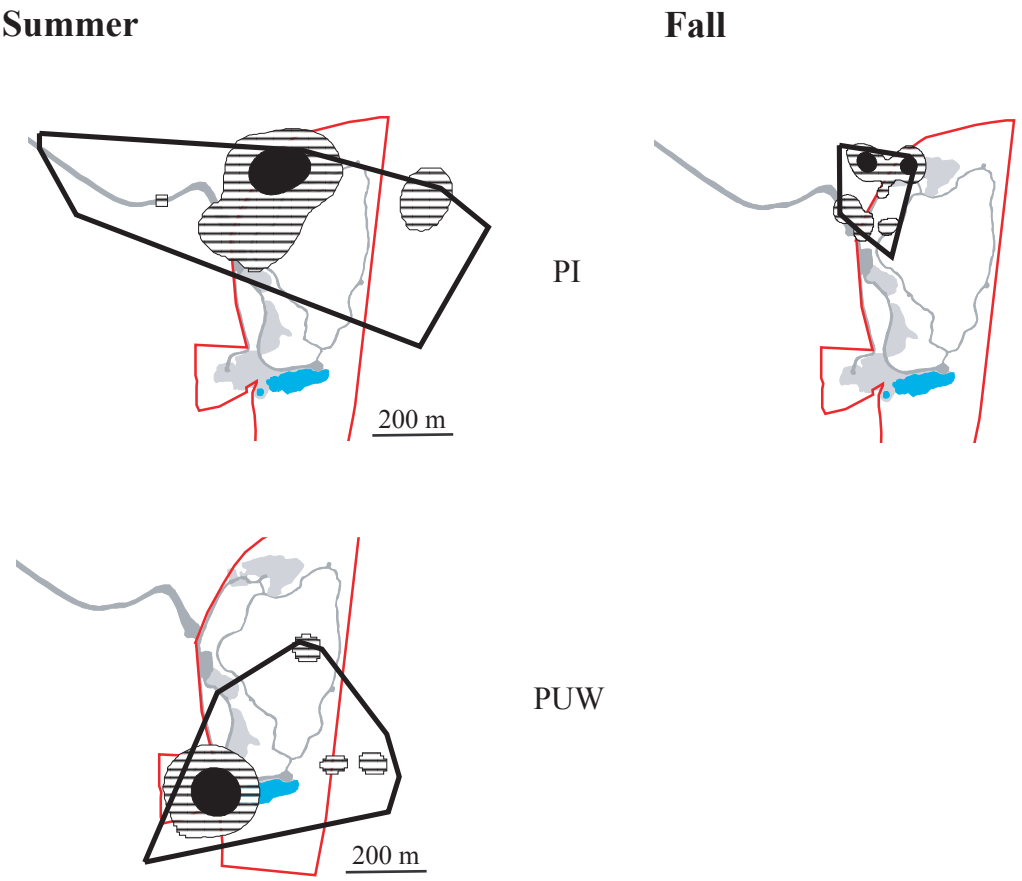

Figure 13. (continued)

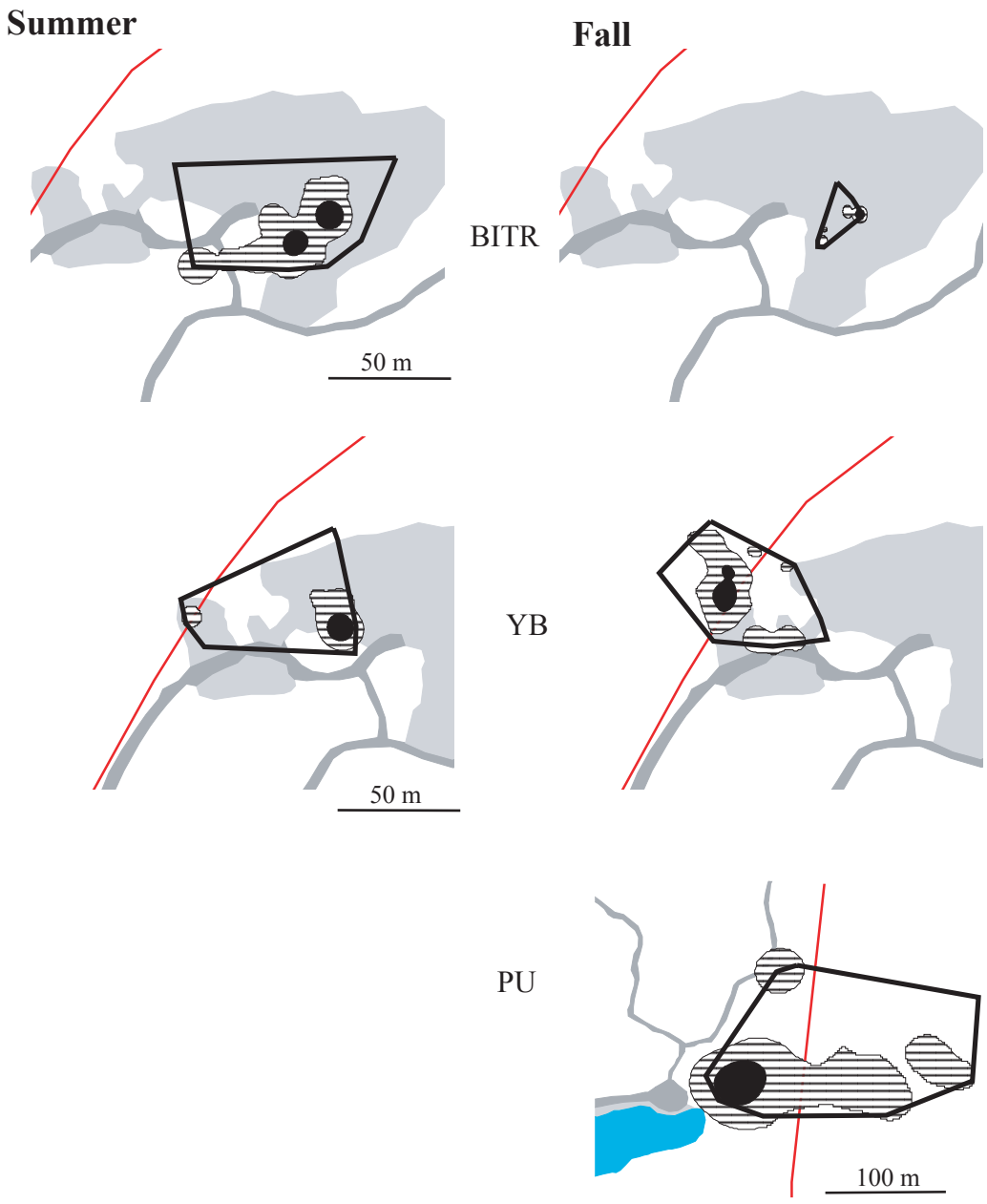

Figure 14. Usage areas, based on 60-85 locations per iguana, shown for female *Cyclura lewisi* tracked for two week periods during the summer and fall of 2002. Minimum convex polygon (100% MCP) estimates are shown in the hollow polygon. Probabilistic kernel estimates are shown with 95% probability area as line-filled areas, and the 50% probability area (core area) as black-filled areas. Roads and trails are shaded in dark gray, and visitor and staff areas are shaded in light gray. The red line is the boundary of the botanic park.

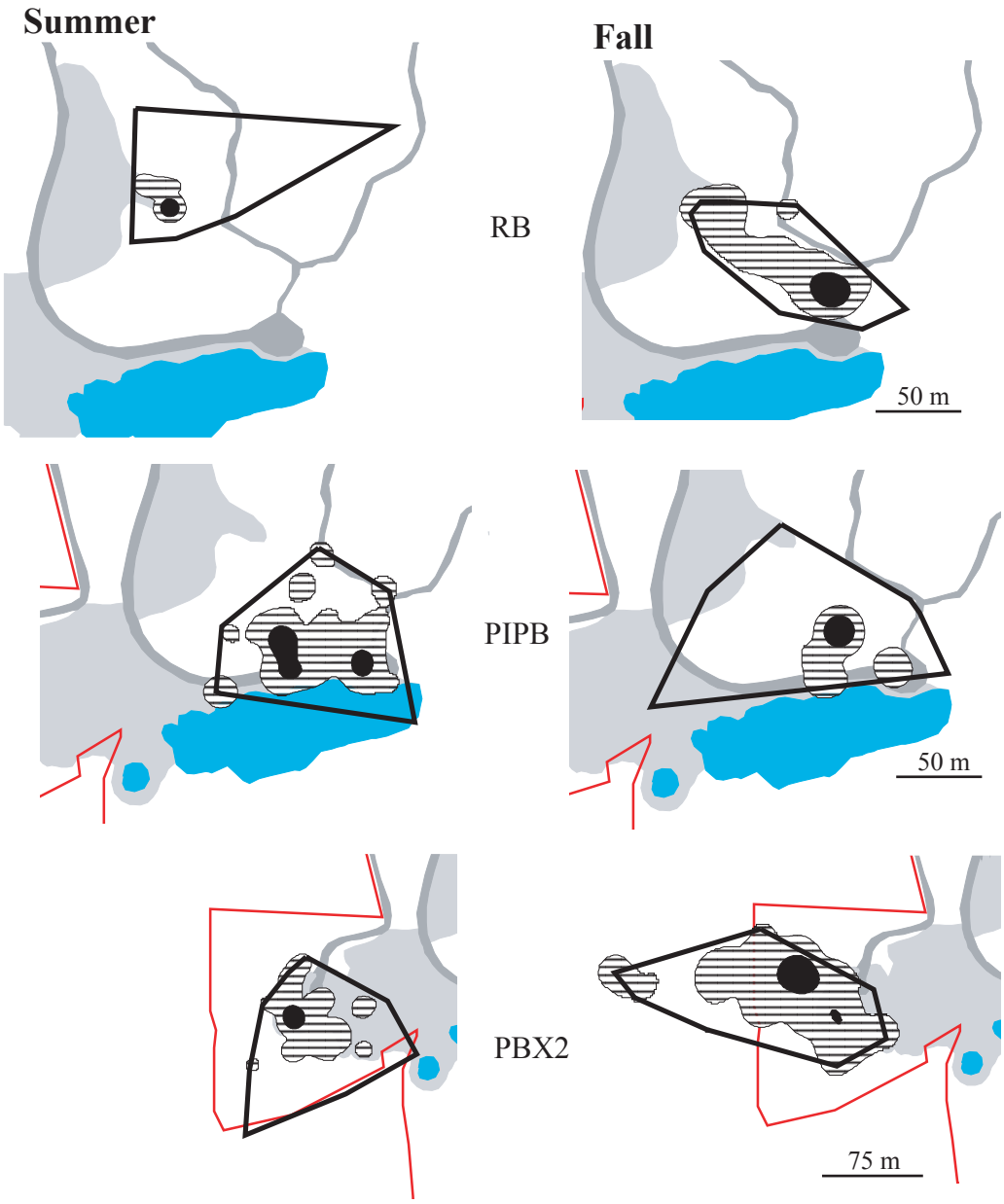

Figure 14. (continued)

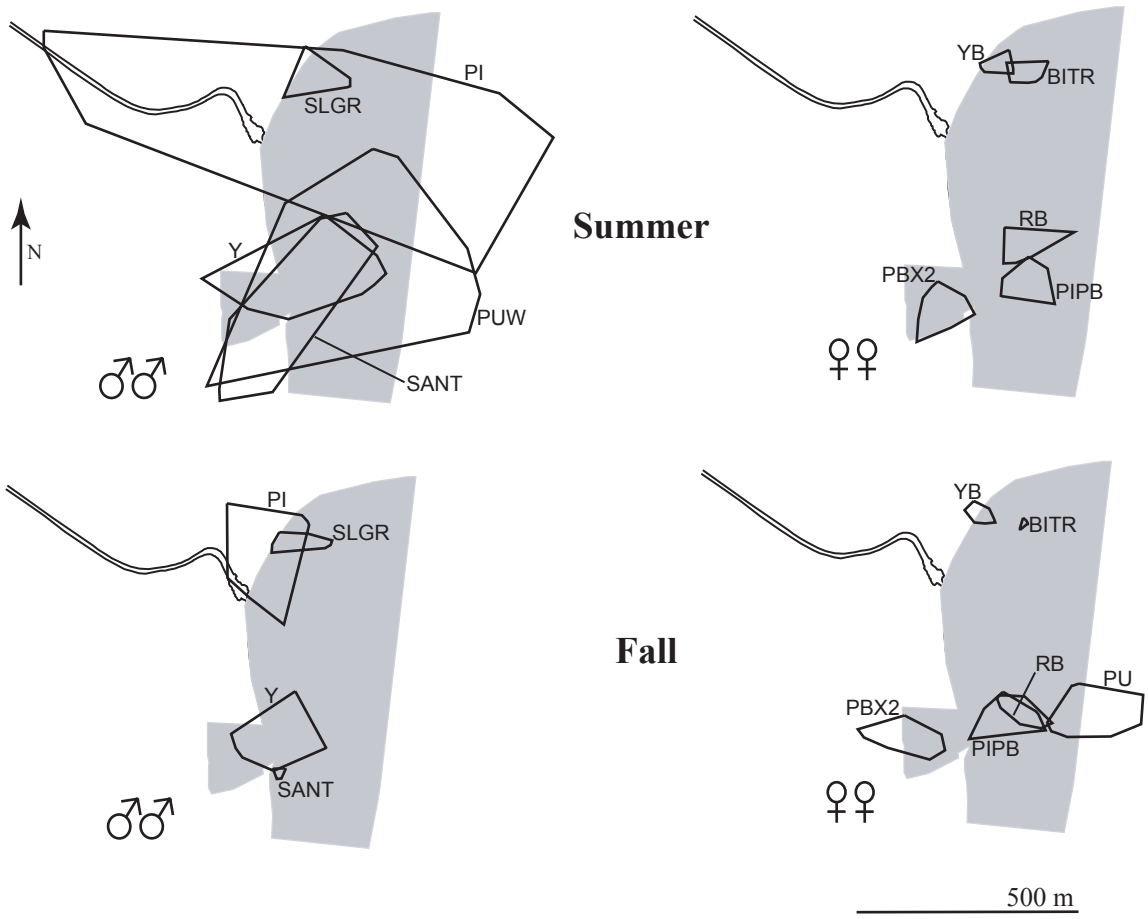

Figure 15. Minimum convex polygon (100% MCP) usage area estimates for *Cyclura lewisi* radio tracked during the summer and fall of 2002. Usage areas (constructed with 60-85 locations per iguana per period) of males are significantly larger than those of females in the summer, but not in the fall.

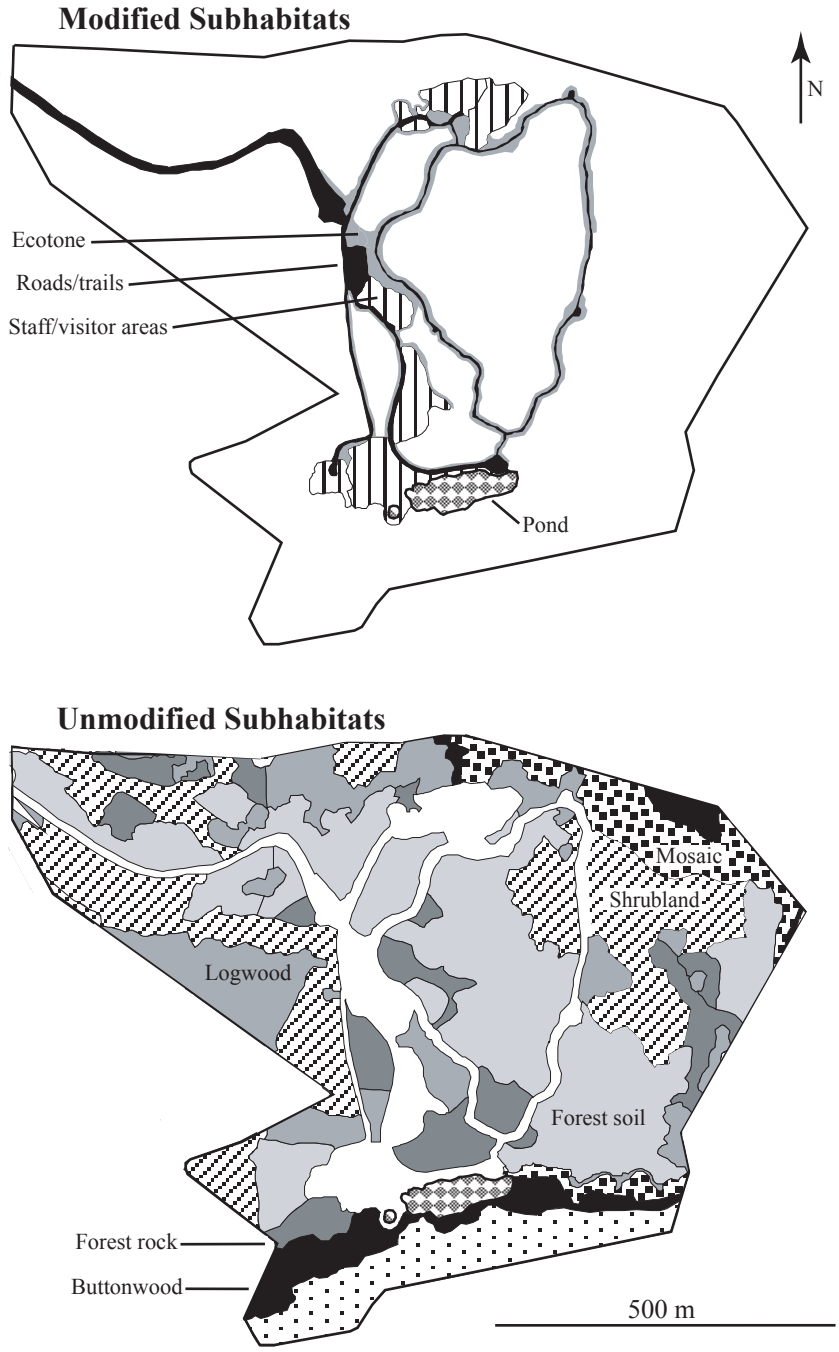

Figure 16. Modified and unmodified subhabitats within the study site. These subhabitats were designated through interpretation of a scaled, orthorectified, digitized aerial photograph of the area (Cayman Islands Government's Land Information System, image date 1999) and extensive ground-truthing.

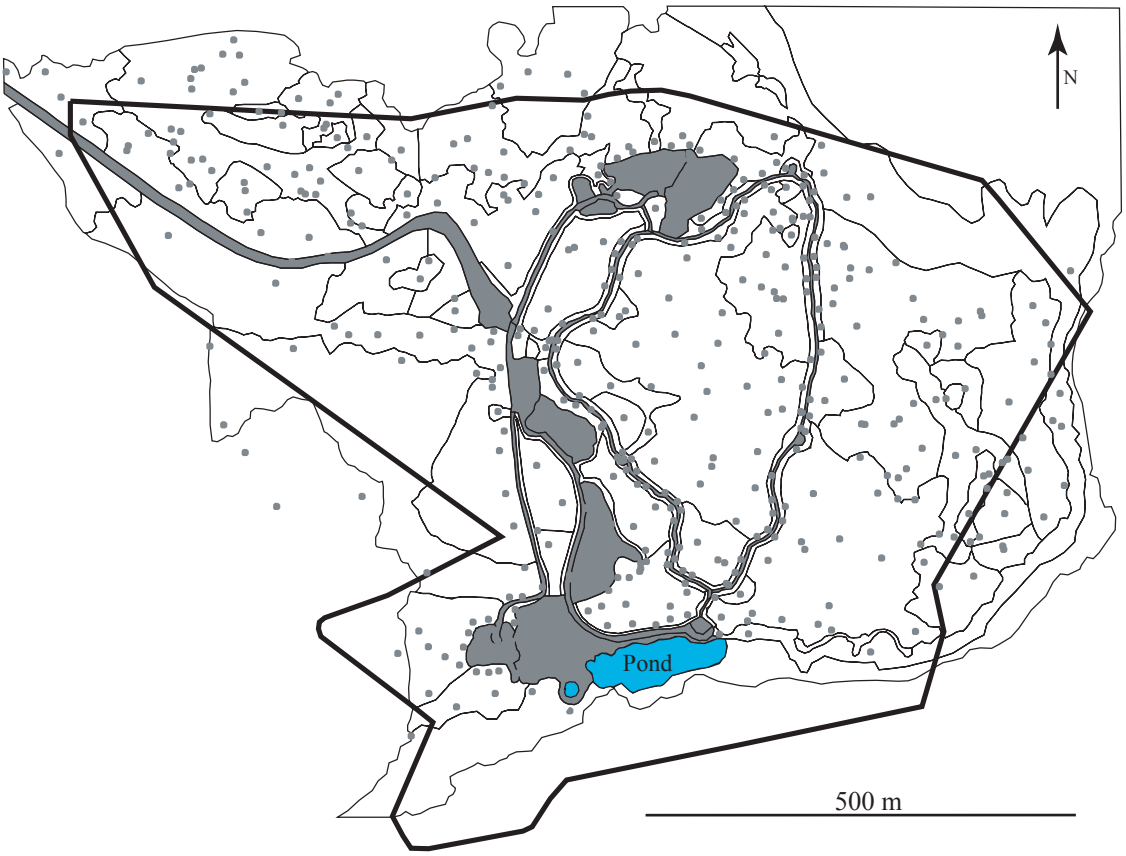

Figure 17. Locations for all 480 survey points in the study site visited during November of 2002. The ninety zones of unmodified habitat in the study site (outlined in thin black) were originally identified from aerial photography (see text for details) and later classed into subhabitats. The polygon outlined in thick black represents the available habitat for iguanas in this study (55.2 ha), determined afterward by enclosing all area included in iguanas' home ranges and usage areas during 2002. Modifed habitat in the study site is shaded in gray.

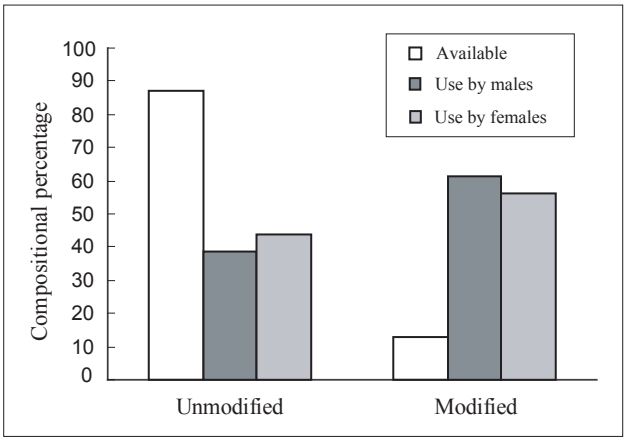

Figure 18. Compositional percentages of availability and average use of habitats for the summer and fall combined in 2002. Second-order habitat use for 11 iguanas, *Cyclura lewisi*, was determined with kernel home ranges created from radio telemetry data (see text for details).

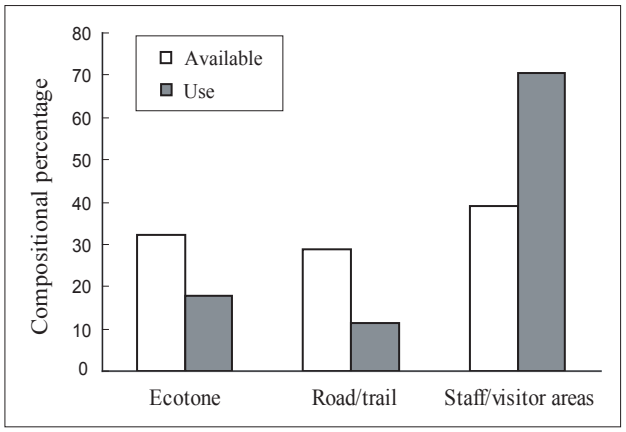

Figure 19. Compositional percentages of availability and average use of modified subhabitats for the summer of 2002. Second-order habitat use for 10 iguanas, *Cyclura lewisi*, was determined with kernel home ranges created from radio telemetry data (see text for details).

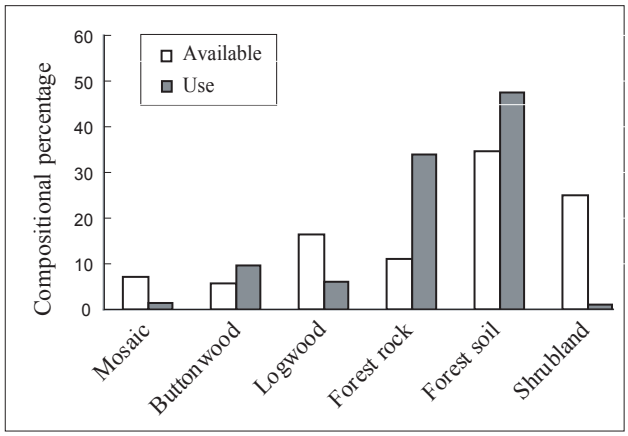

Figure 20. Compositional percentages of availability and average use of unmodified subhabitats for the summer and fall combined in 2002. Second-order habitat use for 11 iguanas, *Cyclura lewisi*, was determined with kernel home ranges created from radio telemetry data (see text for details).

VITA

Rachel Madeline Goodman was born in Storm Lake, Iowa on June 19, 1980. She lived with her family in Iowa until 1984, then in Colombia, South America from 1985-1987. She completed the majority of her primary and secondary education in El Paso, Texas, and graduated from high school in 1997. She then attended Columbia University and received her Bachelor of Arts degree in Environmental Biology in May, 2001. During this time, she traveled, attended field courses, and conducted research in the Biosphere 2 in Arizona, Spain, Costa Rica, and New York state. She joined the Department of Ecology and Evolutionary Biology at the University of Tennessee, Knoxville in August 2001 and received her Master of Science degree in May 2004.