

Habitat use of the endangered iguana *Cyclura lewisi* in a human-modified landscape on Grand Cayman

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Abstract

Cyclura lewisi is an endangered rock iguana endemic to the island of Grand Cayman. Like many other animals, *C. lewisi* increasingly depends on modified landscapes for its survival. The remaining natural population is too small and fragmented to yield information on the natural history and population biology of this species. Therefore, we studied habitat use in a population of captive-bred, released iguanas in a botanic park. Compositional analysis was used to examine habitat selection and use by iguanas at two scales: selection of home range within the landscape and selection of locations within home ranges. At both scales and for all time periods examined, iguanas preferred modified habitat to natural habitat. Subhabitats were examined only at the scale of selection within the landscape, for which iguanas showed preference in some but not all time periods. Iguanas used artificial retreats more often than natural retreats and commonly occupied retreats in modified areas. Many female iguanas nested in artificial sites within the park. The use of modified habitats and artificial retreats and nests by reintroduced *C. lewisi* is encouraging, because this and other species of *Cyclura* may depend on these resources for future survival.

INTRODUCTION

Human modification and fragmentation of natural ecosystems are substantial and increasing worldwide (Vitousek *et al.*, 1997). Therefore, scientists cannot afford to focus research and conservation efforts solely on pristine habitats and must expand their efforts to include disturbed areas (Rosenzweig, 2003). Recently, many studies have examined the ecology and behaviour of species in urban and other anthropogenically-modified areas (Koenig, Shine & Shea, 2001; Wood & Pullin, 2002; Gehrt & Chelsvig, 2003; Godefroid & Koedam, 2003; Spinks *et al.*, 2003; Evelyn, Stiles & Young, 2004), with the increasing recognition that these areas may serve as reservoirs of biodiversity if managed properly (Marzluff & Ewing, 2001; Pickett *et al.*, 2001; Melles, Glenn & Martin, 2003; Zerbe *et al.*, 2003).

Certain taxa may depend largely on disturbed habitats for their survival. One such group is the largely threatened rock iguanas of the genus *Cyclura* which increasingly experience rapid encroachment by humans in their island habitats throughout the West Indies (Alberts, 2000). The Grand Cayman blue iguana, *Cyclura lewisi*, is endemic to the island and critically endangered, with only 7–25

wild iguanas remaining (Alberts, 2000; Burton, 2002). A captive breeding and release program, initiated in 1990 by the National Trust for the Cayman Islands, has produced a small population of reintroduced iguanas that were confirmed to be reproducing in 2001. No in-depth studies on the behaviour or ecology of this species have been published, and the remaining wild population is too small and fragmentary to yield useful data on natural history and population biology. Therefore, the reintroduced population serves as a valuable source of information that can be used for conservation planning.

To develop strategies for reintroducing and managing *C. lewisi* and other iguanas throughout the West Indies, it is important to understand how iguanas respond to the modified landscapes on which they increasingly depend. Therefore, we investigated the use of habitats and resources by *C. lewisi* in an area containing both natural and human-modified areas. The objectives of our study were (1) to determine if iguanas differentially used modified and natural habitats and subhabitats within each and (2) to determine the kinds of overnight retreats used most frequently by iguanas and the habitats in which those retreats were found. Habitat and retreat use were investigated by radiotracking, behavioural observation and regular monitoring of the reintroduced population of *C. lewisi*. In addition to examining which habitats were important to these iguanas, we qualitatively assessed the threats present in these habitats.

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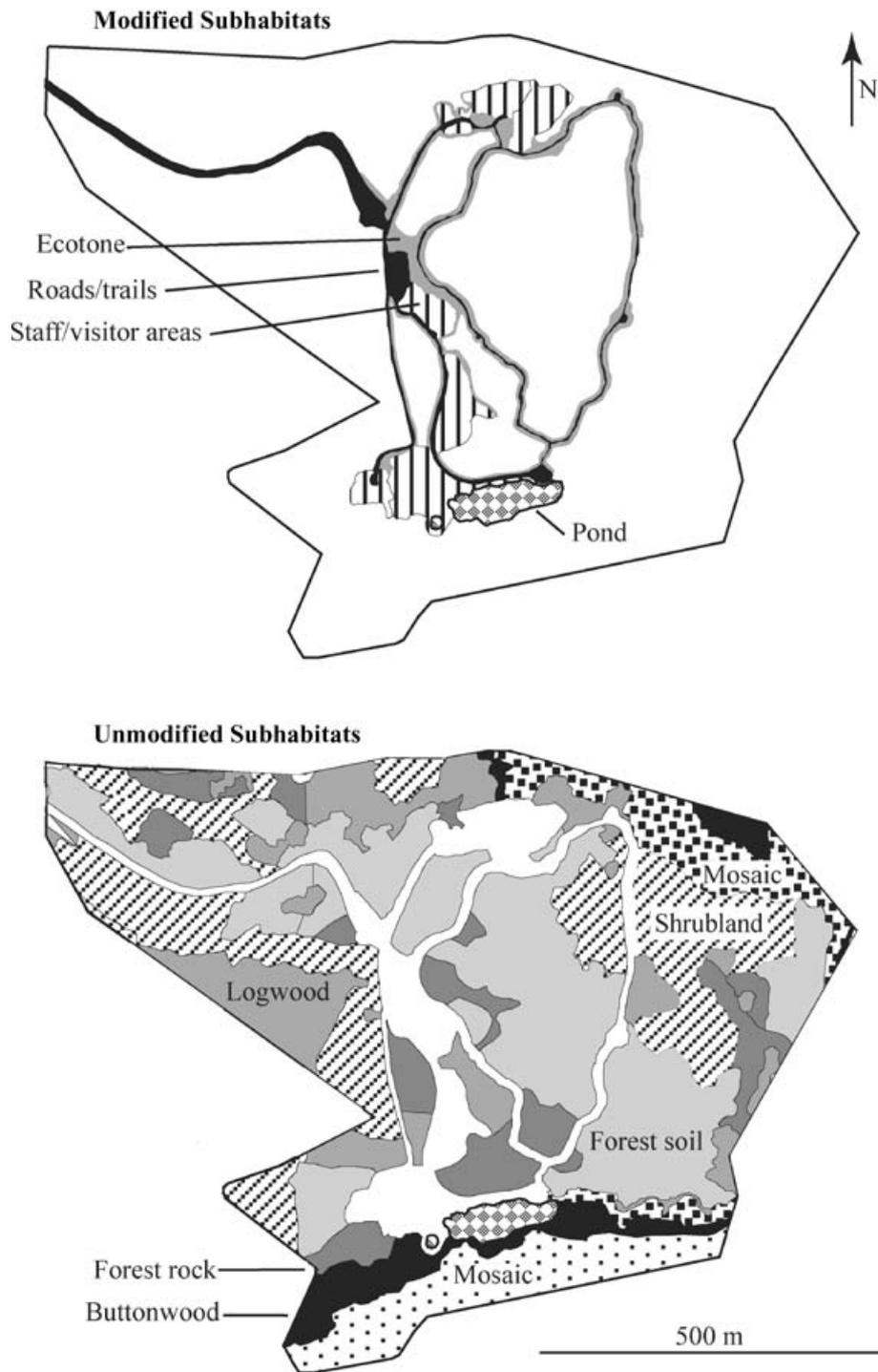


Fig. 1. Modified and natural subhabitats within the 55.2 ha study site at the Queen Elizabeth II Botanic Park on Grand Cayman. The outer boundary encloses the area within all minimum convex polygon (MCP) and kernel home ranges of the study population in 2002.

METHODS AND MATERIALS

Study site and population

Our study was based at the Queen Elizabeth II Botanic Park (24.3 ha), located at 19°19'N, 81°10'W and approximately 2m above sea level on Grand Cayman. The study site (total of 55.2 ha) includes surrounding area used by iguanas initially found in the park (Fig. 1).

The reintroduced population in our study site consisted of 15–20 iguanas during each season. The iguanas in this population were captive-bred on site and released at 2–3 years of age, when they are thought to be less vulnerable to predation (Alberts 2000). Our study population consisted of all iguanas in the park that were released at least 1 year prior to the initiation of this study. Therefore, study subjects ($n = 13$; all 3–7 years of age) were sexually mature adults.

Habitat mapping and description

We constructed a habitat map of the study site (Fig. 1) based on a 1990 aerial photograph of the area (Cayman Islands Government's Land Information System) and direct surveys. We first classed all land into major habitat categories defined as modified (heavily modified by humans during construction of the park) and natural (not recently modified as above, although may include land logged during the past century). We then further divided these habitat categories into subhabitats. Modified portions of the park were visited frequently during the study and were plainly visible in the aerial photograph. Modified habitat was divided into three subhabitats: ecotone (habitat bordering roads and trails that contains slightly modified natural habitats); roads and trails (roads, trails and parking lots); and staff and visitor areas (all remaining modified areas, including ornamental gardens, manicured lawns and buildings). During the course of the study, we discovered supplemental feeding by visitors and staff in the park which, although unquantified, appeared to be more frequent in modified habitats.

Ninety parcels of natural habitat were mapped on the basis of hue and heterogeneity of colour 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 distributed as evenly as possible within parcels. These points, located using a Garmin® GPS 12XL, were surveyed during Nov 2002. An additional 280 *ad hoc* locations were surveyed and marked with GPS coordinates en route to the original 200 locations. At each location, canopy height was estimated visually to the nearest metre and predominate substrates and trees were recorded. Subhabitats were described on the basis of a former botanic survey of the park (Burton, 1990) and on observations during surveying in the current study. Parcels of natural habitat were categorised into the following subhabitats: buttonwood swamp (*Conocarpus erectus*-dominated, flooded), logwood swamp (*Haematoxylum campechianum*-dominated, seasonally flooded), dry evergreen forest on rock substrate, dry evergreen forest on soil substrate, dry evergreen shrubland, and a mosaic of patches of swamp and evergreen forest. Descriptions of all subhabitats are given in Table 1 and in Goodman (2004).

Iguana capture and tracking

Iguanas were located during May–Nov of 2001 and 2002 by walking transects (consisting of trails and roads in the park) and surrounding areas. Iguanas were captured by hand or by using a landing net or Havahart® single door trap, sexed by probing, measured using a fold-out ruler and tagged in the nuchal crest with unique bead combinations as described by Rodda *et al.* (1998). Radio transmitters (Holohil Systems, Ltd. model AI-2, 35–40 g, 45 mm × 15 mm diameter cylinder with 23 cm whip antennae) were attached to large males (36–49 cm snout–vent length (SVL), 80–118 cm total length (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. Transmitters were attached to females (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. See Goodman (2005) for details on radio transmitters and attachment methods.

Iguanas (males $n = 5$, females $n = 6$) were tracked using radiotelemetry (Wildlife Materials, Inc. TRX-1000S tracking receiver and collapsible, hand-held yagi antenna) for 14–17 day periods during the summer (May–Jul) and autumn (Sep–Nov) of 2002. All iguanas were radio-located 3–8 times daily to ensure sampling of seldomly used habitats (Garshelis, 2000), with hours of tracking standardised to ensure an even distribution over the active hours of iguanas'. We omitted from our radiotelemetry data repeated locations of an iguana prior to the first movement of >10 m within a day. Autocorrelation still existed in location data (Schoener ratio (t^2/r^2) mean = 1.030, SD = 0.401 for both seasons: Schoener, 1981). However, because individuals and not locations were the sample units in analyses of habitat use, autocorrelation of successive locations was not problematic (Aebischer, Robertson & Kenward, 1993; Otis & White, 1999).

To estimate iguana locations when visual verification was not possible, 2–4 bearings were taken from known locations in the park with a 10-minute maximum period. 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 & 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 (CI) for triangulation error were 23–39 m and 20–34 m for two and three vectors, respectively.

Focal animal observations were performed during Sep–Nov 2001, May–Jul 2002, and Aug–Nov 2002. To offset a potential bias of locating iguanas in open areas, each iguana was followed for the remainder of the day of location, then from emergence the following day until the time of detection the previous day. A total of 357.5 hours of observations were collected ($n = 5$ males, $n = 8$ females), with an average total observation time per individual of 29.7 hours (SD = 16.8). Retreat use during focal animal observations and transect walks conducted 1–8 times daily over the entire study period was recorded.

Analysis of retreat use

We calculated percentages of retreat use for natural sinkholes, artificial retreats and trees, and percentages of retreat use in modified and natural habitats. These

Table 1. Descriptions of modified and natural subhabitats in the study site at Queen Elizabeth II Botanic Park, Grand Cayman, based on a former survey (Burton, 1990) and surveys during the current study

	Substrates	Canopy	Common vegetation	Other characteristics
Modified habitat 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 herbaceous 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; occasional human traffic
Staff/visitor areas	Gravel, cement, manicured lawn, bare soil	Highly variable, entirely open and entirely closed in patches	Highly diverse, both native and non-native herbaceous and woody plants	Buildings, cars and piles of construction materials and wastes present; frequent human traffic; never flooded
Unmodified habitat Buttonwood dominated, flooded swamp	Saturated peat, underlying limestone rock	Mostly closed canopy cover; canopy height of approx. 3 m	Dominant <i>Conocarpus erectus</i> ; some <i>Haematoxylum campechianum</i> , <i>Bursera simaruba</i> , <i>Hippomane mancinella</i> in transition zones	Regularly flooded
Logwood dominated, seasonally-flooded swamp	Limestone rock, soil, peat in some patches	Mostly closed canopy cover; canopy height of 5–7 m	Dominant <i>Haematoxylum campechianum</i> ; some <i>Bursera simaruba</i> , <i>Erythroxylum areolatum</i>	Seasonally flooded
Dry evergreen forest on rock	Limestone rock	Mostly closed canopy with gaps; canopy height of 6–8 m	Common <i>Bursera simaruba</i> , <i>Coccothrinax proctorii</i> , <i>Haematoxylum campechianum</i>	Infrequently flooded
Dry evergreen forest on soil	Soil	Mostly closed canopy with gaps, canopy height of 7–9 m	Common <i>Bursera simaruba</i> , <i>Clusia flava</i> , <i>Gyminda latifolia</i> , <i>Haematoxylum campechianum</i>	Infrequently flooded
Dry evergreen shrubland	Limestone rock, soil	Mostly closed canopy with gaps; canopy height of 3–5 m	Common <i>Coccothrinax proctorii</i> , <i>Myrcianthes fragrans</i> , <i>Agave sobolifera</i> , <i>Haematoxylum campechianum</i> , <i>Comocladia dentata</i>	Infrequently flooded
Mosaic of dry evergreen forest and swamps	Limestone rock, soil, peat	Mostly closed canopy; canopy height of 6–9 m	Common <i>Bursera simaruba</i> , <i>Hippomane mancinella</i> , <i>Conocarpus erectus</i> , <i>Haematoxylum campechianum</i>	Seasonally flooded in patches

percentages were calculated from data obtained using only focal animal observation and radiotracking, because transect walks were more likely to detect retreat use in modified habitats. We first examined repeated use of retreats by single or multiple iguanas based on all methods of observation and then based on only focal animal observation and radiotracking.

Analysis of habitat use

Home ranges were estimated for iguanas in each tracking session using the Animal Movement extension (Hooge & Eichenlaub, 1997) in Arcview[®] GIS version 3.2. Minimum convex polygon home ranges (MCP) containing all locations from radiotelemetry, transect walks and behavioural observations (mean = 244, range = 100–358 locations per iguana) were constructed for the entire 2002 study. The 95% contours of probabilistic, fixed kernels were used to estimate home ranges (kernel) for each season (mean = 80, range = 60–87 locations per iguana) and both seasons combined (mean = 146, range = 67–171 locations per iguana).

We used compositional analysis of habitat use in SAS version 9.0 (bycomp.sas: Ott & Hovey, 1997; SAS Institute Inc., 2002) to determine whether habitats and subhabitats were preferred (i.e. 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 because of (1) generation of preference rankings that are independent of habitat availability, (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, Gaines and Servheen, 2003). We chose to examine two scales of habitat selection: selection of home ranges within the defined study area and selection of locations within home ranges (i.e. second and third order selection, respectively, *sensu* Johnson, 1980).

To examine habitat selection by iguanas within the study site (second order analysis), kernel home ranges of iguanas were overlaid on the study site and overlap of each habitat was compared to availability of that habitat within the study site. For this analysis, available habitat (i.e. the study site) was defined as the total area encompassed in MCP and kernel home ranges of iguanas monitored and radiotracked in 2002. There is no universally agreed-upon definition for available habitat (McClellan *et al.*, 1998; Garshelis, 2000). We chose our definition to represent habitat that had been reached by iguanas that were released in the park. Kernel home ranges were chosen for this analysis because they better represent the actual area used by iguanas relative to MCPs, which are sensitive to outliers and include area never visited (Powell, 2000). We

Table 2. Retreat use by *Cyclura lewisi* in the Queen Elizabeth II Botanic Park on Grand Cayman

Iguana ID	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 instances of use		126	30	17

Numbers represent instances of retreat use confirmed during focal animal observations and radiotracking in 2001 and 2002. The number of retreats used by each iguana is given in parentheses.

examined second order selection at the levels of habitats and subhabitats.

To examine habitat selection by iguanas within home ranges (third order analysis), the proportion of radiotracking locations found in each habitat for an individual was compared to the availability of habitats within that individual's MCP home range for 2002. For this analysis, the MCP estimate was used because it better represents the total area potentially known and traversed by the animal relative to kernel estimates, which contain only area used commonly during a tracking period (Powell, 2000). Third-order analysis was performed only at the level of habitats because available areas (2002 MCP home ranges) differed for individuals and often lacked some subhabitats entirely.

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 autumn radiotracking periods first separately and then combined.

RESULTS

Retreat use

In 2001 and 2002, 489 uses of retreats by iguanas were verified. Of these, 173 instances were verified using the unbiased methods of radiotracking and focal animal observation and these are used in the following summary. Artificial retreats, which included piles of construction and waste material, cavities in rock piles and spaces under buildings, made up 72.8% (126 out of 173 incidents) of unbiased observations of retreat use (Table 2). Natural sinkholes in limestone and dolostone rock substrate comprised 17.3% (30 out of 173) of retreat use and the remaining 9.8% (17 of 173) consisted of iguanas spending

Table 3. Compositional analysis of habitat use of iguanas, *Cyclura lewisi*, within the study site (second order selection) and within home ranges (third order selection) on Grand Cayman

	<i>n</i>	Wilk's λ	F	df	<i>P</i>	Habitats, in order of preference
Habitats: within study site						
Summer	10	0.456	10.72	1,9	0.010	Modified, natural
Autumn	10	0.576	6.63	1,9	0.030	Modified, natural
Summer and autumn	11	0.216	29.07	1,8	0.001	Modified, natural
Habitats: within home ranges						
Summer	10	0.502	8.91	1,9	0.015	Modified, natural
Autumn	10	0.846	1.64	1,9	0.232	Modified, natural
Summer and autumn	9	0.508	7.76	1,8	0.024	Modified, natural

Sample size (*n*), Wilk's λ resulting from multivariate analysis of log-ratios of habitat use and availability, F-ratio (F) with associated degrees of freedom (df), and *P*-value (*P*) are shown for tests in each season separately and for both seasons combined in 2002.

Table 4. Compositional analysis of subhabitat use of iguanas, *Cyclura lewisi*, within the study site (second order selection) on Grand Cayman

	<i>n</i>	Wilk's λ	F	df	<i>P</i>	Subhabitats, in order of preference
Modified subhabitats: within study site						
Summer	10	0.404	5.89	2,8	0.027	Visitor/staff, ecotone, roads/trails
Autumn	10	0.851	0.70	2,8	0.525	Visitor/staff, roads/trails, ecotone
Summer and autumn	9	0.560	2.75	2,7	0.131	Visitor/staff, roads/trails, ecotone
Natural subhabitats: within study site						
Summer	9	0.163	4.12	5,4	0.097	Forest rock, forest soil, buttonwood, logwood, mosaic, shrubland
Autumn	8	0.078	7.08	5,3	0.069	Forest rock, forest soil, buttonwood, logwood, mosaic, shrubland
Summer and autumn	11	0.115	9.27	5,6	0.009	Forest rock, forest soil, buttonwood, logwood, mosaic, shrubland

Sample size (*n*), Wilk's λ resulting from multivariate analysis of log-ratios of habitat use and availability, F-ratio (F) with associated degrees of freedom (df), and *P*-value (*P*) are shown for tests in each season separately and for both seasons combined in 2002.

the night in tree hollows or exposed on tree limbs. Within artificial retreats (*n* = 16 retreats), 56.3% (9 out of 16 retreats) were cavities in piles of rock.

The majority of retreat uses (82.1%, 142 out of 173) were in modified habitat, with most (123 out of 173) occurring in staff and visitor areas, a minority (19 out of 173) occurring in the ecotone subhabitat and none occurring on roads and trails. Retreat use in natural habitat accounted for a minority (17.9%, 31 out of 173) of total use. Retreat reuse was greater for artificial retreats than for natural retreats (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 of observation, retreat use by multiple iguanas occurred more frequently for artificial than for natural retreats. Only one sinkhole was used by more than one iguana, whereas five artificial retreats were used multiple times, with one retreat used by four iguanas over time. No trees were used by more than one iguana. The trend was similar when examining only data obtained by 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

Kernel home ranges of iguanas revealed significant selection (second order) of habitats within the study site in the summer, autumn and overall (Table 3). In all time periods, home ranges were composed of a greater proportion of modified habitat than natural habitat, relative to availability.

Kernel home ranges showed selection of subhabitats in the summer within modified habitat in the study site, but not in the autumn or for summer and autumn combined (Table 4). Within modified habitat, subhabitats were significantly preferred during the summer in the following rank order: visitor and staff areas, ecotone, roads and trails (Table 4). Home ranges were composed of a greater proportion of the visitor and staff areas subhabitat relative to that available within modified habitat in each season, but this trend only approached statistical significance when the summer and autumn data were combined (Table 4).

Within natural habitat in the study site, subhabitats were preferred in the following ranked order for all time periods: forest rock, forest soil, buttonwood, logwood, mosaic, shrubland. Differences in preference approached statistical significance in the summer and autumn seasons alone, but were significant only when data from both seasons were combined (Table 4).

Within MCP home ranges (third order selection), iguanas preferred modified habitat to natural habitat in the summer and both seasons combined, but not in the autumn (Table 3).

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 & Berovides Alvarez, 1991; Alberts, 2000). However, *C. lewisi* most often used artificial retreats during our study. During this study, *C. lewisi* rarely slept in trees, as has been reported in a few species of *Cyclura* (Iverson, 1979). Retreats in our study site were reused by single and multiple iguanas, although not by multiple individuals simultaneously as has been found in some species of *Cyclura* (Wiewandt, 1977; Iverson, 1979; Cubillas Hernández & Berovides Alvarez, 1991).

During the majority of our observations, iguanas used and reused artificial retreats and used retreats in modified habitat. 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. During this study, we noted that natural sinkhole retreats often flooded during the wet season (May–Nov), whereas artificial retreats in modified areas did not because these areas were built on elevated foundations. Therefore, we suggest the construction of artificial retreats in areas not prone to flooding, using the limestone and dolostone rock that forms the natural sinkhole retreats preferred by iguanas in this study.

All but one population of *Cyclura* studied to date 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* as well. During the current study we observed that the majority of females in the park (4 out of 7 in 2001, 7 out of 10 in 2002) dug nest burrows in artificial sites, including garden beds and soil piles. We cannot present percentages for female *C. lewisi* that nested in modified versus natural sites because we did not radiotrack females during the nesting season. Also, the viability of artificial nests in our site has not been compared to that of nests in natural substrates. Nevertheless, the fact that artificial substrates are readily accepted as nest sites suggests a further management option which has been used in other reptiles (Webb & Shine, 2000; Nelson *et al.*, 2002; Milne, Bull & Hutchinson, 2003), especially since suitable natural nest substrates appear to be scarce in our study area.

Habitat use

Iguanas preferred modified habitats to natural habitats, both in terms of overall home range as well as individual locations within home ranges. 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 non-native plants and direct supplemental feeding by humans. Modified habitats in the botanic park also contain more open area with reduced or no canopy cover, a factor that may provide increased opportunities for basking and thermoregulation compared to natural habitats. Within modified habitats, the iguanas' preference for visitor and staff areas may be due to the frequent presence of humans and associated supplemental food or some other factor.

Within natural habitats, forest on rock substrate was the preferred subhabitat. The abundance of natural sinkhole retreats outside of periodic episodes of flooding may explain the 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 containing soil and sand are scarce or absent in forest rock.

The inland shrubland subhabitat was avoided by iguanas during this study. This result appears contradictory to reports of use of this habitat by closely related iguana species elsewhere in the Caribbean (for a review, see Alberts, 2000). 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 that is dominated by non-native logwood trees and occasionally floods. The pooling of various types of shrubland into one category based on vegetation structure alone, and not composition or diversity, warrants caution in extrapolating avoidance of shrubland by iguanas in this site to natural shrubland elsewhere.

Management implications

Because pristine habitats on Grand Cayman are limited, our finding that 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 nevertheless 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 because of small sample size. Although urban or disturbed areas may be used and even preferred by some animals, they may nevertheless result in increased parasitism, altered behaviour and reduced fitness (Boal & Mannan, 1999; Rubin *et al.*, 2002; Lacy & Martins, 2003). In the light of these possibilities, 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 *Cyclura*, they have been shown to decimate populations of these iguanas and even cause local extinctions (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, Fenton & Carmody, 1974; Ashley & Robinson, 1996; Carr & Fahrig, 2001; Koenig, Shine & Shea, 2002), including iguanas. During 2001 and 2002, three out of 15–20 resident iguanas were run over by vehicles, one fatally. In two of these instances, 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. 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 it is 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 risks. Uncontrolled feeding by humans may also lead to dependency and behavioural changes, including increased aggression towards humans (pers. obs.; Lacy & Martins, 2003; Iverson, Smith & Pieper, 2004).

Our study found that reintroduced *C. lewisi* in a botanic park on Grand Cayman preferentially occupied modified habitats and frequently used artificial retreats and nest sites. Because this and other species of iguanas face shrinking natural habitats, our results are encouraging. We suggest that *C. lewisi* and possibly other iguanas can successfully use modified habitats if managed so that safeguards are taken against unnatural predation, vehicular collisions and uncontrolled supplemental feeding.

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REFERENCES

- Aebischer, N. J., Robertson, P. A. & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**: 1313–1325.
- Alberts, A. C. (Ed.). (2000). *West Indian iguanas: status survey and conservation action plan*. Gland, Switzerland and Cambridge: IUCN/SSC West Indian Iguana Specialist Group, IUCN.
- Ashley, E. P. & Robinson, J. T. (1996). Road mortality of amphibians, reptiles and other wildlife on the long point causeway, Lake Erie, Ontario. *Can. Field Nat.* **110**: 403–412.
- Boal, C. W. & Mannan, R. W. (1999). Comparative breeding ecology of Cooper's hawks in urban and exurban areas of southeastern Arizona. *J. Wildl. Mgmt.* **63**: 77–84.
- Bond, B. T., Burger, L. W., Leopold, B. D., Jones, J. C. & Godwin, K. D. (2002). Habitat use by cottontail rabbits across multiple spatial scales in Mississippi. *J. Wildl. Mgmt.* **66**: 1171–1178.
- Burton, F. J. (1990). *General vegetation survey of the site for the National Trust Botanic Gardens Project, Block 59A, Parcel 216*. Grand Cayman: National Trust for the Cayman Islands (P.O. Box 31116 SMB, Grand Cayman, Cayman Islands, BWI).
- Burton, F. J. (2002). *Grand Cayman blue iguanas in the wild: a survey of the population status of Cyclura nubila lewisi*. Grand Cayman: Blue Iguana Conservation Project, National Trust for the Cayman Islands (P.O. Box 31116 SMB, Grand Cayman, Cayman Islands, BWI).
- Carey, W. M. (1966). Observations of the ground iguana *Cyclura macleayi caymanensis* on Cayman Brac, British West Indies. *Herpetologica* **22**: 265–268.
- Carey, W. M. (1975). The rock iguana, *Cyclura pinguis*, on Anegada, British Virgin Islands, with notes on *Cyclura ricordi* and *Cyclura cornuta*. *Bull. Florida State Mus., Biol. Sci.* **19**: 189–234.
- Carr, L. W. & Fahrig, L. (2001). Effect of road traffic on two amphibian species of differing vagility. *Conserv. Biol.* **15**: 1071–1078.
- Coleman, J. S. & Jones, A. B. I. (1988). *User's guide to TELEMS88: computer analysis system for radio-telemetry data*. Blacksburg, Virginia: Dept. of Fisheries and Wildlife, Virginia Polytechnic Institute and State University.
- Cubillas Hernández, S. O. & Berovides Alvarez, V. (1991). Características de los refugios de la iguana de Cuba, *Cyclura nubila*. *Rev. Biol.* **5**: 85–87.
- Evelyn, M. J., Stiles, D. A. & Young, R. A. (2004). Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. *Biol. Conserv.* **115**: 463–473.
- Garshelis, D. L. (2000). Delusions in habitat evaluation: measuring use, selection, and importance. In *Research techniques in animal ecology*: 111–164. Boitani, L. & Fuller, T. K. (Eds). New York: Columbia University Press.
- Gehrt, S. D. & Chelsvig, J. E. (2003). Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. *Ecol. Applic.* **13**: 939–950.
- Gicca, D. (1980). The status and distribution of *Cyclura r. rileyi* (Reptilia: Iguanidae), a Bahamian rock iguana. *Caribb. J. Sci.* **16**: 1–4.
- Godefroid, S. & Koedam, N. (2003). Distribution pattern of the flora in a peri-urban forest: an effect of the city-forest ecotone. *Lands. Urban Plan.* **65**: 169–185.
- Goodman, R. M. (2004). *Spatial ecology and habitat use of the endangered iguana, Cyclura lewisi, in an unnatural setting*. MSc thesis: University of Tennessee, Knoxville, Tennessee.
- Goodman, R. M. (2005). Attachment of radio transmitters in a rock iguana, *Cyclura lewisi*. *Herpetol. Rev.* **36**: 150–152.
- Grant, C. (1940). The herpetology of the Cayman islands. *Bull. Inst. Jamaica, Sci. Ser.* **2**: 1–65.

- Hooge, P. N. & Eichenlaub, B. (1997). *Animal movement extension to Arcview*. Anchorage, Alaska: Alaska Biological Science Center, U.S. Geological Survey.
- Iverson, J. B. (1978). The impact of feral cats and dogs on populations of the West Indian rock iguana, *Cyclura carinata*. *Biol. Conserv.* **14**: 63–73.
- Iverson, J. B. (1979). Behavior and ecology of the rock iguana, *Cyclura carinata*. *Bull. Florida State Mus., Biol. Sci.* **24**: 175–358.
- Iverson, J. B., Smith, G. R. & Pieper, L. (2004). Factors affecting long-term growth of the Allen Cays rock iguana in the Bahamas. In *Iguanas: biology and conservation*: 176–192. Alberts, A. C., Carter, R. L., Hayes, W. K. & Martins, E. P. (Eds). Berkeley, California: University of California Press.
- Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**: 65–71.
- Knapp, C. R., Buckner, S., Feldman, A. & Roth, L. (1999). Status update and empirical field observations of the Andros rock iguana, *Cyclura cychlura cychlura*. *Bahamas J. Sci.* **7**: 2–5.
- Koenig, J., Shine, R. & Shea, G. (2001). The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia? *Wildl. Res.* **28**: 215–227.
- Koenig, J., Shine, R. & Shea, G. (2002). The dangers of life in the city: patterns of activity, injury and mortality in suburban lizards (*Tiliqua scincoides*). *J. Herpetol.* **36**: 62–68.
- Lacy, K. E. & Martins, E. P. (2003). The effects of anthropogenic habitat usage on the social behaviour of a vulnerable species, *Cyclura nubila*. *Anim. Conserv.* **6**: 3–9.
- Lyons, A. L., Gaines, W. L. & Servheen, C. (2003). Black bear resource selection in the northeast Cascades, Washington. *Biol. Conserv.* **113**: 55–62.
- Marzluff, J. M. & Ewing, K. (2001). Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restor. Ecol.* **9**: 280–292.
- McClellan, S. A., Rumble, M. A., King, R. M. & Baker, W. L. (1998). Evaluation of resource selection methods with different definitions of availability. *J. Wildl. Mgmt.* **62**: 793–801.
- Melles, S., Glenn, S. & Martin, K. (2003). Urban bird diversity and landscape complexity: species–environment associations along a multiscale habitat gradient. *Conserv. Ecol.* **7**: Article No. 5.
- Milne, T., Bull, C. M. & Hutchinson, M. N. (2003). Fitness of the endangered pygmy blue tongued lizard *Tiliqua adelaidensis* in artificial burrows. *J. Herpetol.* **37**: 762–765.
- Nelson, N. J., Keall, S. N., Brown, D. & Daugherty, C. H. (2002). Establishing a new wild population of Tuatara (*Sphenodon guntheri*). *Conserv. Biol.* **16**: 887–894.
- Otis, D. L. & White, G. C. (1999). Autocorrelation of location estimates and the analysis of radiotracking data. *J. Wildl. Mgmt.* **63**: 1039–1044.
- Ott, P. & F. Hovey. (1997). *bycomp.sas*. British Columbia, Canada: British Columbia Forest Service.
- Oxley, D. J., Fenton, M. B. & Carmody, G. R. (1974). Effects of roads on populations of small mammals. *J. Appl. Ecol.* **11**: 51–59.
- Pickett, S. T. A., Cadenasso, M. L., Grove, J. M., Nilon, C. H., Pouyat, R. V., Zipperer, W. C. & Costanza, R. (2001). Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annu. Rev. Ecol. Syst.* **32**: 127–157.
- Powell, R. A. (2000). Animal home ranges and territories and home range estimators. In *Research techniques in animal Ecology*: 65–110. Boitani, L. & Fuller, T. K. (Eds). New York: Columbia University Press.
- Rodda, G. H., Bock, B. C., Burghardt, G. M. & Rand, A. S. (1988). Techniques for identifying individual lizards at a distance reveal influence of handling. *Copeia* **1988**: 905–913.
- Rodríguez Schettino, L. (1999). Systematic accounts of the species: genus *Cyclura*. In *The Iguanid lizards of Cuba*: 154–164. Rodríguez Schettino, L. (Ed.). Gainesville, Florida: University Press of Florida.
- Rosenzweig, M. L. (2003). *Win–win ecology: how the earth's species can survive in the midst of human enterprise*. Oxford and New York: Oxford University Press.
- Rubin, E. S., Boyce, W. M., Stermer, C. J. & Torres, S. G. (2002). Bighorn sheep habitat use and selection near an urban environment. *Biol. Conserv.* **104**: 251–263.
- SAS Institute Inc. (2002). *SAS System version 9.0*. Cary, North Carolina: SAS Institute Inc.
- Schoener, T. W. (1981). An empirically based estimate of home range. *Theoret. Pop. Biol.* **20**: 281–325.
- Spinks, P. Q., Pauly, G. B., Crayon, J. J. & Shaffer, H. B. (2003). Survival of the western pond turtle (*Emys marmorata*) in an urban California environment. *Biol. Conserv.* **113**: 257–267.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science* **277**: 494–499.
- Webb, J. K. & Shine, R. (2000). Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? *Biol. Conserv.* **92**: 93–99.
- Wiewandt, T. A. (1977). *Ecology, behavior, and management of the Mona Island ground iguana, Cyclura stejnegeri*. PhD thesis: Cornell University, Ithaca, New York.
- Wood, B. C. & Pullin, A. S. (2002). Persistence of species in a fragmented urban landscape: the importance of dispersal ability and habitat availability for grassland butterflies. *Biodivers. Conserv.* **11**: 1451–1468.
- Zerbe, S., Maurer, U., Schmitz, S. & Sukopp, H. (2003). Biodiversity in Berlin and its potential for nature conservation. *Landsc. Urban Plan.* **62**: 139–148.