Activity patterns and foraging behavior of the endangered Grand Cayman blue iguana, *Cyclura lewisi*

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ABSTRACT.—The historic rarity of the critically endangered Grand Cayman blue iguana, *Cyclura lewisi*, has prevented detailed research on this species prior to this decade. This study primarily used focal animal observations, transect sweeps, and radio-telemetry to document the behavioral ecology of a captive-bred, reintroduced population of adult *C. lewisi* in a botanic park on Grand Cayman. Activity budgets and foraging budgets are presented for each sex in each season, and for all data combined. Distributions of basking time and active time differed between the two seasons. Iguanas both emerged earlier and retreated later in the summer than in the fall. Of the small percentage of time spent active, iguanas mostly foraged and engaged in locomotion. Iguanas spent little time in trees or bushes or inside of retreats during the day. Observations of extensive tongue-touching of retreats, substrates, and feces suggest an importance of chemosensory ability in *C. lewisi*. Iguanas primarily consumed plant matter, of which the majority was non-cultivated plants in the park and surrounding area. Limited geophagy, coprophagy, and consumption of invertebrates were observed. Supplemental feeding contributed little to the overall diet of iguanas, but appeared to make iguanas more aggressive towards humans. Iguanas were heavily habituated to human and vehicular disturbances, which were common occurrences. Aspects of the behavioral ecology of *C. lewisi* reported here will assist in the conservation of this and other endangered iguanas.

KEYWORDS.—lizard, disturbance, management, conservation, time budget, diet, herbivory

INTRODUCTION

Rock iguanas, genus Cyclura (Sauria: Iguanidae sensu Frost and Etheridge, 1989; but see discussion of taxonomy in Hollingsworth, 2004), are large, primarily herbivorous, ground-dwelling lizards found on islands in the Caribbean (Alberts, 2000; Alberts et al., 2004). All species are considered endangered or vulnerable (IUCN, 2004), and many have become the subject of scientific study, captive breeding, and intensive management in the last two decades. Until recently, however, little has been documented on the behavior and ecology of Cyclura lewisi, the Grand Cayman blue iguana. This was in large part due to the historic rarity of this critically endangered species (Grant, 1940; Alberts, 2000; Burton, 2002).

Cyclura lewisi is endemic to Grand Cayman, where less than 25 individuals are es-

timated to remain in the wild (Burton, 2002). Destruction and alteration of preferred habitats, predation by introduced cats and dogs, and hunting have probably contributed to the near extinction of *C. lewisi*. At present, all but hunting continue to threaten the persistence of the species (Grant, 1940; Lewis, 1944; Townson, 1980; Alberts, 2000). The persistence of *C. lewisi* on Grand Cayman will require reintroduction and management programs, which require knowledge of the basic ecology of this species.

The National Trust for the Cayman Islands began a captive breeding program for *C. lewisi* in 1990 and began releasing captive-bred, adult iguanas into the Queen Elizabeth II Botanic Park in eastern Grand Cayman in 1996. The small, reintroduced population provides an excellent opportunity to study *C. lewisi* and identify potential threats faced by populations in humanoccupied habitats. While the diverse natural and human-modified habitats found in

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this park may not reflect the original preferred habitat of *C. lewisi*, it is nonetheless important to study the iguanas in this setting. Little pristine habitat remains on Grand Cayman, and management and conservation of the species must occur under these circumstances. This study provides the first description of the activity patterns and foraging behavior of *C. lewisi*. Additionally, it assesses habituation to humans and the potential dangers encountered by iguanas in human-modified habitats.

MATERIALS AND METHODS

Study site and animal

The study site was located in and around the Queen Elizabeth II Botanic Park (QEIIBP) in the eastern interior of Grand Cayman (19°19'N, 81°10'W). The eastern part of the island has a warm wet season from May to November, a cool dry season from December to April, and receives mean annual rainfall of 111 cm (Burton, 1994). Iguanas initially found in the 24.3 ha park also used areas outside the park, resulting in a total of 55.2 ha used. Both natural and human-modified habitats are present and include xeric forests and shrublands, wetlands, manicured lawns, botanical gardens, buildings, and parking lots (details in Goodman, 2004; Goodman et al., 2005a). Tourism in the park was regularly on the order of tens of visitors daily (<100). Exceptions to this occurred when greater numbers of visitors came in the form of school group visits or infrequent special events. Approximately 10-20 staff members were on site during regular work hours, 0700-1700 every day. This activity resulted in overlap in both time and locations between humans and iguanas.

Iguanas in the study population were captive-bred on site and released at 2-3 years of age, when they are of a size thought to be less vulnerable to predation (Alberts, 2000). The reintroduced population in QEIIBP consisted of 15-20 iguanas during the study. Data were collected on all iguanas within the park that were released at least one year prior to the initiation of the study. All subjects (N = 5 males, 7 females;

all 3-7 years of age) were sexually mature adults. Mating was observed in May to June, and nesting and nest defense behaviors were observed in June to early July. Prior to initiation of this study, iguanas were measured and marked with colored bead tags on the nuchal crest (Goodman, 2004). Males (35.8-46.0 cm snout vent length (SVL), 2.20-4.55 kg) were generally larger than females (27.9-37.3 cm SVL; 0.95-2.45 kg).

Data Collection

Focal animal observations were performed in fall 2001 (4 Sep-14 Oct), summer 2002 (14 Jun-8 Jul), and fall 2002 (25 Sep-11 Nov). Iguanas either did not emerge or did not move far from their retreats on overcast and rainy days. Therefore, observations were made only on days with no precipitation and less than 75% cloud cover as estimated visually. In the summer, all females were observed at least nine days after the completion of nesting and after cessation of any nest defense. A total of 357.5 h observation time was analyzed: 106.9 h from summer 2002 and 250.6 h from fall 2001 and fall 2002 combined. Altogether, males were observed for 170.3 h and females were observed for 187.3 h. Total observation time per individual averaged 29.7 h (SD = 16.8; range = 8.6-33.9 h). To offset any potential bias in observed activity or location caused by the initial detection of an iguana (presumably more detectable in open areas), each iguana was followed for the remainder of the day on which it was detected. Each was then tracked from emergence the following day until the time of the previous day's detection. Iguanas moved through a variety of habitats and performed many activities during this observation period of 8.6-13.0 h, likely minimizing any bias incurred in locating iguanas. Focal animals were determined before the start of each session. Thus, animals were not chosen for observation based upon ease of detection.

Iguanas were mostly followed at a distance of 10-20 m because they were highly habituated to human disturbance (see Results). Occasionally iguanas moved towards the observer as a consequence of activities unrelated to the observer's presence. Unless the iguana approached to within less than 2 m, the observer remained motionless during these instances so as not to create distraction. All data wherein the focal animal approached the observer, incidentally or intentionally, to less than 2 m were noted as containing observer interference and excluded from analyses. The times of initiation and cessation of behaviors and movements (described in Table 1), including reactions of iguanas to human disturbances (described in Table 2), were recorded to the nearest second.

Seven female iguanas were radio-tracked for two weeks in both summer and fall 2002, while five males were radio-tracked for two weeks during the same seasons (details in Goodman et al., 2005b). Additionally, iguana locations were monitored through transect sweeps of the park performed 1-8 times daily during 26 Aug-7 Nov 2001, 9 May-2 Aug 2002, and 23 Sep-10 Nov 2002. Times of retreat and emergence and types of retreats used by iguanas were recorded during radio-tracking, transect sweeps, and focal animal observations.

Emergence and Retreat Times

Average times of emergence and retreat were calculated for each iguana in summer (2002) and fall (2001 and 2002 combined for all analyses) using 1-11 occurrences per iguana per season (emergence: mean ± $SD = 3.8 \pm 2.7$; retreat: 4.3 ± 3.8). In cases where an interval of 15-30 min was recorded instead of an exact time, the midpoint was used (e.g., if emergence was between 0630 and 0700, the time 0645 was used). Average emergence and retreat times of an individual were included in analyses only if available from both the summer and fall. Average times of emergence and retreat were each compared between the two seasons with paired t tests. Normality of differences was verified with omnibus normality tests. Unless noted otherwise, all statistical analyses in this study were performed in NCSS (Hintze, 2001) with α = 0.05. Means are given ± 1 *SD*.

Distribution of Basking Time and Activity

From focal observations only, percentage of total basking time for each iguana was calculated for each hour of the day. Percentage of basking time was also calculated for the periods 0600-1000, 1000-1300, 1300-1600, and 1600-1900 to compare basking time between seasons. Using the percentages for each iguana as sample units, the average percentage of basking time in the

| TABLE 1. Descriptions | of behaviors of iguanas, | Cyclura lewisi, | recorded durn | ng tocal anım | al observations. |
|-----------------------|--------------------------|-----------------|---------------|---------------|------------------|
| 1 | 0 , | , | | 0 | |
| | | | | | |

| | Description | | | | |
|---------------------------------|---|--|--|--|--|
| Behavior | | | | | |
| Foraging | Acquiring and consuming foods, including periods of locomotion and resting <15 continuous sec | | | | |
| Locomotion | Crawling, walking, or running for a distance of >0.5 m | | | | |
| Inspecting retreat or substrate | Tongue-touching a retreat or substrate more than three consecutive times (not during locomotion or foraging) | | | | |
| Displaying (no iguanas near) | Displaying when no other iguana is in visible proximity | | | | |
| Inactive categories | | | | | |
| Low alertness | Prostrate or neutral posture, with 1-2 head movements or shifts of body per min | | | | |
| Medium alertness | Neutral or raised posture, or with 3-6 head movements or shifts per min | | | | |
| High alertness | Raised or standing posture, or with >6 head movements or shifts per min | | | | |
| Basking | Any category of inactivity, with 75-100% of body in sunlight | | | | |
| Postures | | | | | |
| Prostrate | Bottom of chin, chest, and posterior ventor touching ground | | | | |
| Neutral | Head raised, chest and posterior ventor touching ground | | | | |
| Raised | Head and chest raised, posterior ventor touching ground | | | | |
| Standing | Body fully lifted off ground | | | | |

| | Description | | | | |
|------------------------------|--|--|--|--|--|
| Human disturbance levels | | | | | |
| Noise only | Person or people present >15 m away, with audible noise | | | | |
| Low | Person or people present 6-15 m away | | | | |
| Medium | Person or people present 1-5 m away | | | | |
| High | People <1 m away or 1-5 m away with extra noise or movement (e.g., yelling or running) | | | | |
| Vehicular disturbance levels | | | | | |
| Noise only | Vehicle passing or standing with engine running >15 m away | | | | |
| Low | Vehicle passing or standing with engine running 6-15 m away | | | | |
| Medium | Vehicle passing or standing with engine running 2-5 m away | | | | |
| High | Vehicle passing or standing with engine running <2 m away | | | | |
| Disturbance response level | | | | | |
| 0 | None | | | | |
| 1 | Freezing or moving head in response to disturbance | | | | |
| 2 | Walking away from or head-bob at disturbance | | | | |
| 3 | Running away from disturbance | | | | |

TABLE 2. Descriptions of types of human and vehicular disturbances and resulting reactions of iguanas, *Cyclura lewisi*, recorded during focal animal observations.

four time periods was compared between summer and fall with the Hotelling's two-sample T^2 test. Equality of variancecovariance structures between seasons was verified with the Bartlett-Box homogeneity of variance test. Multivariate normality was confirmed within each group by plotting Mahalanobis distances from the residuals in a chi-square probability plot (Johnson, 1980) in SAS (2002). Average percent of basking time was compared for each time period between seasons using two-sample t tests with a sequential Bonferonni correction. The Mann-Whitney U test was substituted when data contained violations of normality according to an omnibus normality test. The Aspin-Welch test was substituted when groups displayed unequal variance according to the modified Levene test. Identical analyses as those above were performed for percent of active time in the same hours with the exception of the first period, 0700-1000. This exception was made because iguanas were rarely active before 0700. For the above analyses, samples from the two seasons were treated as independent because not all iguanas were subjects of focal animal observation in both seasons. This violation of independence of samples makes these tests less powerful and more conservative but allows increased sampling of individuals, thereby increasing statistical power.

Time Budgets

Focal animal observation data were used to calculate the percentage of time spent by each iguana in a given activity, either within the total time between morning emergence and evening retreat or within the total time spent foraging (latter for types of foraging only). Averages of these percentages, using individuals as sample units, are presented separately for the most common activities for each sex in summer and fall and for all data combined (Tables 3 and 4). Formal statistical tests were not applied because small sample sizes and the large number of potential, correlated response variables would yield prohibitively low power.

Response to Disturbance

Human disturbances recorded during behavioral observations were grouped into the following classes: Noise only, Low, Medium, High (definitions in Table 2). Disturbances that involved vehicles, including dump trucks, cars, and golf carts, were grouped into the following classes: Noise only, Low, Medium, High. Reactions of iguanas to human and vehicular disturbances were placed on the following scale of increasing intensity: 0, 1, 2, 3 (Table 2). The Noise only category was excluded in

| TABLE 3. Percentages of time spent in categories of active and inactive behaviors by iguanas, <i>Cyclura lewisi</i> , within time spent out of retreats. Social situations were |
|---|
| defined by focal animals being within 15 m of another iguana and included ignoring, displaying, and chasing. Mean ± SD are shown separately for males and |
| females in each study season and for all data combined. Sample size (N) refers to number of iguanas observed. |

| | Ν | Social situations | Active | Active: Forage | Active: Locomotion | Active: Inspect retreat or substrate | Inactive: Low alertness | Inactive: Medium alertness | Inactive: High alertness | Inactive: Bask |
|-------------------|----|-------------------|----------------|-------------------|-----------------------|--|----------------------------|-------------------------------|-----------------------------|----------------|
| Males | | | | | | | | | | |
| Summer | 5 | 11.4 ± 21.1 | 20.3 ± 2.3 | 8.1 ± 4.8 | 8.3 ± 4.2 | 3.8 ± 2.6 | 37.5 ± 17.8 | 38.8 ± 17.9 | 1.7 ± 1.0 | 29.9 ± 9.2 |
| Fall | 4 | 1.9 ± 3.2 | 19.6 ± 3.0 | 10.2 ± 2.2 | 6.4 ± 2.5 | 2.1 ± 2.0 | 42.4 ± 20.0 | 35.8 ± 18.7 | 1.4 ± 0.8 | 23.5 ± 4.4 |
| Females | | | | | | | | | | |
| Summer | 5 | 20.7 ± 15.2 | 18.3 ± 1.7 | 9.0 ± 2.5 | 6.1 ± 1.4 | 1.3 ± 0.2 | 36.5 ± 10.8 | 44.2 ± 12.2 | 0.6 ± 0.2 | 23.5 ± 4.2 |
| Fall | 6 | 12.7 ± 20.3 | 16.9 ± 4.4 | 8.3 ± 3.4 | 5.7 ± 2.4 | 1.2 ± 1.4 | 42.9 ± 18.2 | 36.9 ± 15.6 | 1.5 ± 1.6 | 23.9 ± 9.3 |
| All data combined | 12 | 10.2 ± 1.47 | 18.4 ± 2.7 | 8.9 ± 2.7 | 6.6 ± 2.3 | 1.7 ± 1.5 | 39.6 ± 15.4 | 39.4 ± 14.9 | 1.4 ± 1.1 | 26.1 ± 7.6 |

TABLE 4. Percentages of time spent in foraging behaviors by iguanas, *Cyclura lewisi*, within all time spent foraging. Mean \pm *SD* are shown separately for males and females in each study season and for all data combined. Sample size (*N*) refers to number of iguanas observed.

| | Ν | Consume plant matter | Consume plant matter: Leaves, stems | Consume plant matter: Fruits, nuts | Consume plant matter: Flowers | Consume rocks/soil | Consume supplemental food | Consume unidentifiable matter | Carnivory |
|-------------------|----|-------------------------|---|--|-------------------------------------|-----------------------|------------------------------|-------------------------------------|---------------|
| Males | | | | | | | | | |
| Summer | 5 | 76.7 ± 18.9 | 66.4 ± 22.7 | 2.4 ± 4.3 | 7.9 ± 7.0 | 7.3 ± 8.4 | 0.0 ± 0.0 | 5.8 ± 6.2 | 2.4 ± 5.5 |
| Fall | 4 | 86.1 ± 8.2 | 72.0 ± 14.9 | 9.7 ± 9.9 | 4.5 ± 4.9 | 2.2 ± 1.9 | 4.4 ± 8.8 | 6.8 ± 6.2 | 0.8 ± 1.1 |
| Females | | | | | | | | | |
| Summer | 5 | 71.1 ± 27.5 | 70.0 ± 27.2 | 0.0 ± 0.0 | 1.2 ± 0.8 | 10.0 ± 11.5 | 6.3 ± 7.9 | 11.8 ± 12.2 | 0.5 ± 1.2 |
| Fall | 6 | 46.9 ± 41.0 | 40.2 ± 34.9 | 4.9 ± 10.5 | 1.8 ± 4.1 | 7.6 ± 9.4 | 7.6 ± 17.9 | 36.9 ± 35.5 | 0.2 ± 0.6 |
| All data combined | 12 | 67.8 ± 27.3 | 57.8 ± 24.3 | 5.7 ± 8.5 | 4.3 ± 5.9 | 5.7 ± 6.9 | 4.3 ± 7.7 | 19.8 ± 23.1 | 1.5 ± 3.5 |

the following calculations because reactions were difficult to detect and categorize due to the longer duration of these disturbances. Averages were compared between types and levels of disturbances. Formal statistical tests were not applied because of small sample sizes and the ordinal nature of the response variables.

RESULTS

Emergence and Retreat Times

With few exceptions, iguanas spent the night in retreats such as rock cavities or cavities under buildings. The exceptions consisted of iguanas spending the night on tree limbs, this occurring once with a male and on three consecutive nights with a female (also see Goodman et al., 2005a). Iguanas emerged from retreats significantly earlier in the summer (mean $\pm SD = 0715 \pm 0022$) than in the fall (0759 \pm 0037; paired t test, *T* = 6.05, *N* = 11, p < 0.001). They also retreated significantly later in the summer (1823 \pm 0029) than in the fall (1735 \pm 0019; paired t test, *T* = 5.37, *N* = 8, p = 0.001).

Distribution of Basking Time and Activity

Distribution of basking times throughout the day showed a bimodal pattern in both seasons (Fig.1). Distribution of basking in the four time periods was significantly different between summer and fall observations (Hotelling's T² test: $T^2 = 22.14$, df = 4, 20, p < 0.001). Iguanas basked more from 1000-1300 and less from 1600-1900 during fall compared to summer (two sample t test, *N* = 22, *T* = 4.07, p = 0.0013; Whitney U test, N = 22, Z = 3.22, p = 0.0006). Trends were evident for less basking from 0600-1000 and more basking from 1300-1600 during fall in comparison to summer, but there were no statistically significant differences (two sample t tests, N = 22, T = 1.92, p = 0.069; N = 22, T = 1.71, p = 0.102).

Unlike basking, distribution of activity throughout the day did not appear to be bimodal in either season (Fig. 2). Percent of active time in the four periods was significantly different between summer and fall observations ($T^2 = 27.31$, df = 4, 20, p <

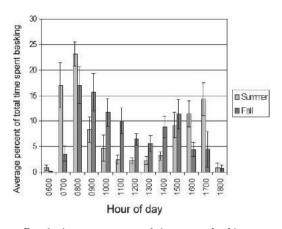


FIG. 1. Average percent of time spent basking per hour within the total time spent basking by iguanas, *Cyclura lewisi*. Individuals were the sample units in this analysis, taken from focal animal observations in the summer of 2002 (N = 9) and the fall of 2001 and 2002 combined (N = 13). Error bars show ± 1 *SE*.

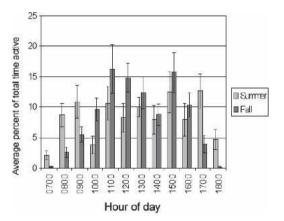


FIG. 2. Average percent of time active per hour within the total time spent active by iguanas, *Cyclura lewisi*. Individuals were the sample units in this analysis, taken from focal animal observations in the summer of 2002 (N = 9) and the fall of 2001 and 2002 combined (N = 13). Error bars show ± 1 *SE*.

0.004). Iguanas were significantly more active from 0700-1000 during summer than during fall (Aspin-Welch test, N = 22, T = 3.30, p = 0.0075). Iguanas tended to be more active from 1000-1300 and less active from 1600-1900 in fall than in summer, but these differences were not significant after the sequential Bonferonni correction (Mann-Whitney U test, N = 22, Z = 2.17, p = 0.030; two sample t test, N = 22, T = 2.34, p = 0.029). There was no significant difference

in activity between seasons for 1300-1600 (Mann-Whitney U test, N = 22, Z = 1.50, p = 0.133).

Time Budgets

Between morning emergence and evening retreat, iguanas spent the majority of their time inactive $(81.6 \pm 2.9\%)$ and most of that time in states of low and medium alertness (Table 3). During activity, iguanas primarily foraged, traveled, and inspected substrates, including retreats and feces (Table 3). While out of retreats, iguanas spent little time displaying when no other iguanas were nearby $(0.2 \pm 0.2\%)$. Iguanas also spent little time defecating $(0.1 \pm 0.1\%)$ and drinking water (<0.1%). Although permanent ponds and ephemeral bodies of standing water exist in the study area, no iguana was ever observed swimming. A large portion of each day was spent basking (Table 3, Fig. 1).

Focal animals were within 15 m of another iguana, including juvenile and captive iguanas not studied, 10.2% (SD = 14.7) of the time. In these instances, focal animals appeared to ignore other iguanas 90.6% (SD = 44.5) of the time, display 5.9% (SD =4.5) of the time, and perform other activities, including chasing, 3.5% (SD = 2.4) of the time. In both summer (including mating season) and fall, adult male iguanas rarely tolerated the presence of each other, but mostly chased and very rarely fought one another.

Iguanas spent very little time during the day (between initial emergence and final retreat) in any kind of retreat ($0.4 \pm 0.6\%$). Iguanas spent an average of 5.1% (SD = 7.4) of time outside retreats in trees or shrubs. This figure is heavily influenced by one female iguana that spent 25.2% of the time in trees and shrubs. Six out of twelve iguanas were never observed in trees or shrubs.

A previously unreported behavior observed 0.1% (SD = 0.1%) of time outside retreats was the turning of the head backwards and visual inspection and often tongue-touching of the hindquarters. Sometimes an iguana would lift a hind limb vertically in the air for several seconds during this process. Another behavior was observed only once, but merits mention. During the breeding season, a male iguana tongue-touched feces in a female's home range for several seconds and bobbed his head intermittently although no other iguanas were nearby. The iguana then dug at the ground with the front feet, kicked gravel about and over the feces, and then excreted a very small amount of fecal material next to the other feces. Finally, he walked around both feces, dragging his hind limbs and posterior ventor on the ground.

Iguanas mostly consumed plant matter, although carnivory and consumption of rocks, soil, ashes, and supplemental foods provided by humans comprised small portions of the overall foraging time budget (Table 4). Some iguanas returned repeatedly to certain piles of potting soil or spots of exposed natural red soil on different days to consume soil for several seconds. Consumption of agouti (Dasyprocta punc*tata*) feces was observed in one instance. Of the plant matter consumption that could be identified, the majority $(84.9 \pm 17.9\%)$ was of non-cultivated plants, while the remainder was of cultivated plants in the park. Within consumption of plant matter, leaves and stems were consumed most often, while fruits, nuts, and flowers were consumed less frequently (Table 4).

Carnivory included active predation on the slug, Veronicella sp. Iguanas lunged at, bit and shook the slugs, and sometimes dropped them to the ground and repeated these steps several times before swallowing them whole. Five iguanas were seen eating slugs on six occasions. On three occasions, consumption of five or six slugs occurred within 30 min. One of these iguanas and another iguana appeared to actively prey on items that could not be identified, lunging and shaking them before consumption. On at least two occasions, another iguana climbed into a tree and fed on larvae of the moth *Pseudosphinx tetrio* residing there. One iguana was observed to chase two lowflying butterflies for 5 m and then lunge in an unsuccessful attempt to capture one of them.

On two occasions, iguanas were observed eating bits of their own shedding skin. Additionally, iguanas were observed to eat or attempt to eat a plastic spoon, plastic bags containing food scraps, and a metal twist tie from a bread bag. Also, two iguanas on three occasions were seen attempting to climb into trash cans. The only observed aggregate feeding occurred when humans provided supplemental foods. On these occasions, which happened every 1-2 days, one male and one or more females and juveniles were observed feeding together. Adult males were never observed feeding together.

Response to Disturbance

During focal observations of iguanas, vehicular and human noises and disturbances were each present a small portion of the time (vehicular disturbance: $0.7 \pm 1.0\%$: human disturbance: $6.1 \pm 6.3\%$; vehicular and human noise only: $5.8 \pm 6.0\%$). However, all classes of noise and disturbance together were present during a substantial portion, 12.6% (SD = 9.1%), of all observations. Iguanas appeared to respond more intensely to increasing levels of human disturbance (Fig. 3) and to respond similarly to all levels of vehicular disturbance (Fig. 4). However, sample sizes for the latter were small because some iguanas never experienced a vehicle approach. On the imposed scale of 0-3, responses for all iguanas averaged 0.47 (SD = 0.59) for human disturbances and 0.37 (SD = 0.53) for vehicular disturbances.

DISCUSSION

Iguanas, *C. lewisi*, almost always spent the night in retreats. They emerged from their retreats earlier and retreated later in the summer relative to the fall. Thus, they were active for a longer daily period in the summer. This seasonal difference in activity may be due to longer day lengths, more available sunlight, and higher temperatures during the summer (Burton, 1994) as these factors allow iguanas to maintain optimal body temperatures for a longer period. Alternatively, iguanas may have been stimulated to be active for longer periods during the summer by elevated hormone

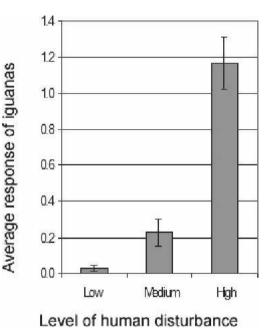


FIG. 3. Average responses of iguanas, *Cyclura lewisi*, to three levels of human disturbance observed during focal animal observations. Samples units are average responses from individuals over the entire study (N = 12 for all levels). Error bars show ± 1 *SE*.

levels associated with reproductive activities (Klukowski et al., 2004). Iverson (1979) found similar shifts in activity patterns for *C. carinata*, which emerged later and retreated earlier in the summer relative to the winter.

The distribution of basking times throughout the day was significantly different between the summer and fall. Iguanas basked most in the earliest and latest parts of the day in the summer, which may be due to greater sunlight in these times relative to the fall. Also, iguanas were out of retreats and awake for more of the day and so had more opportunity to bask in early and late hours. Iguanas basked less during the middle part of the day in the summer, perhaps because of higher peak temperatures during the summer (Burton, 1994). The general pattern of basking in *C*. lewisi was similar to those described qualitatively for C. nubila caymanensis (Carey, 1966) and C. pinguis (Carey, 1975), where most basking occurs in the morning, with a decrease during the day when tempera-

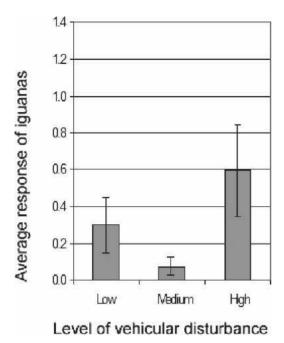


FIG. 4. Average responses of iguanas, *Cyclura lewisi*, to three levels of vehicular disturbance observed during focal animal observations. Samples units are average responses from individuals over the entire study (N = 6, 5, 8 for Low, Medium, and High, respectively). Error bars show ± 1 *SE*.

tures are hot and an increase in the late afternoon. The low amount of basking seen during the latest hours of the day in fall may be attributable to the earlier sunset during this season.

Iguanas were more active during the earliest and latest parts of the day in the summer than they were in the fall. This difference probably reflects warmer body temperatures associated with increased basking and warmer environmental temperatures during these times in the summer. During the breeding season, I often observed males moving from their retreats early in the day to enter the home range of a female to court and mate. This movement in the morning and return to retreats in the evening may have contributed to the increased activity during these time periods. Cyclura lewisi did not display a bimodal activity pattern in either season, as was reported for C. carinata (Iverson, 1979), C. rileyi nuchalis (Thornton, 2000), C. r. rileyi (Cyril, 2001), C. cychlura (Wilcox et al.,

1973), and *C. nubila caymanensis* (Carey, 1966). Iguanas in the current study concentrated activity in the mid-day during the fall and spread out activity over the entire day during the summer. The disparity in distribution of activity between studies may be due to differences among species, among methods of observation (surveys versus focal observations), or among dates of study.

Greater activity during the summer was noted in C. carinata (Iverson, 1979), but was not observed in C. lewisi in the current study. Time budgets for most behavior categories and foraging types appeared similar for both sexes and both seasons. However, future studies should investigate potential differences if larger sample sizes become available. Iguanas spent the majority of their time being inactive, characterized by states of low and medium alertness. Christian et al. (1986) reported that C. nubila nubila spent 14% of the day being active, which is close to my estimate of 18.4% for C. lewisi. During activity, iguanas primarily foraged and traveled. Auffenberg (1982) reported that searching and feeding comprised 15.6% of the daily time budget of C. carinata, whereas I found that C. lewisi only foraged 8.9% of time. Locomotion comprised an additional 6.6% of daily activity time for this species and some of this time, though probably not all, may have been directed toward food location. Some species of *Cyclura* may retreat into water if disturbed (references in Carey, 1975). Cyclua nubila nubila are reported to swim between islands in Cuba (Rodríguez Schettino, 1999). However, C. lewisi were never observed to enter water during this study.

Levels of social interaction among iguanas were low, possibly because iguanas were within 15 m of one another only 10.2% of the time. The population density of *C. lewisi* in the study site was low (0.64 iguana per ha) relative to that of other populations of *Cyclura* and may account for the infrequency of social behavior (Goodman, 2004). Iguanas sometimes displayed when no other iguanas were nearby, which could be interpreted as assertion displays (Carpenter, 1967). However, some of these instances included head-bobbing at nearby doves (various species), perhaps because the jerky walking motion of these birds simulated head-bobbing of an iguana. This suggestion is supported by the observation that iguanas rarely head-bobbed at larger birds such as moorhens (*Gallinula chloropus*) and West Indian whistling ducks (Dendrocygna arborea). Rats (Rattus sp.) and agoutis typically failed to arouse any reaction from iguanas. This habituation may be dangerous for iguanas if they react similarly when confronted with other mammals, such as cats, which prey on smaller iguanas, and dogs, which prey on most size classes of iguanas (Iverson, 1978; Christian, 1986). Although dogs and cats are actively excluded from the botanic park, such animals occasionally stray onto the property.

Inspection of retreats and substrates, including feces, comprised a substantial portion of activity in C. lewisi. Iguanas sometimes spent over a minute inspecting a fecal pellet or sinkhole in the ground. Individuals were observed to inspect both their own feces and those of other iguanas. Extensive tongue-touching of substrates has also been reported in C. carinata (Iverson, 1979) and C. pinguis (Carey, 1975). Self inspection, focused on the posterior of the body and often including tongue-touching, has not been reported previously in Cyclura, and its function is unknown. The previous behaviors, combined with the incident of a male inspecting and seemingly marking an area with feces and femoral and/or cloacal excretions, suggest an importance of chemical communication in C. lewisi.

In contrast to some rock iguanas (Wiewandt, 1977; Thornton, 2000), C. lewisi rarely entered retreats during the day, and typically did so only when frightened. The lack of time spent in day retreats may reflect both lack of predation pressure on adults and extreme habituation of C. lewisi to humans in the study population. Iguanas also spent little time in trees or shrubs. Half of the iguanas studied were never observed to climb into trees or shrubs. Other species of Cyclura climb into trees and bushes with varying frequency (references in Iverson, 1979; Wasilewski, 1998; Hayes et al., 2004). Thornton (2000) found that C. rileyi nuchalis, a smaller-bodied species, spent 14.2% of its time in trees and bushes. Hatchling *C. lewisi* have been observed to exhibit arboreal behavior (Goodman and Burton, 2005) and other young iguanas not included in this study were sometimes observed in trees (pers. obs.). The extent of arboreality in different size classes of *C. lewisi* should be studied further, as large body size in adults may constrain this suggested tendency of juveniles.

All rock iguanas examined to date are primarily herbivorous (Carey, 1966; Carey, 1975; Wiewandt, 1977; Iverson, 1979; Auffenberg, 1982; Iverson, 1982; Perera, 1985; Coenen, 1995; Knapp, 1995; Mitchell, 1999; Rodríguez Schettino, 1999; Alberts, 2000; Cyril, 2001; Knapp, 2001; Hayes et al., 2004). In this study, C. lewisi was found to be primarily herbivorous, as individuals only occasionally consumed animal matter and other items. Based upon volume analysis of feces and stomach contents, Auffenberg (1982) reported that plant matter comprised 94.8% of the diet of C. carinata *carinata*. The current study is not directly comparable to that of Auffenberg because I collected percent time spent in foraging food types rather than volume of food. Nonetheless, C. lewisi may consume less plant matter than C. c. carinata because the former was recorded to spend only 67.8% of total foraging time consuming plants. Still, iguanas consumed much matter from the ground that could not be identified. This consumption comprised 19.8% of foraging time and may have included some consumption of small berries or decaying plant matter. Additionally, the availability of supplemental foods to this population and the inclusion of rocks and soil consumption (these were not included as diet components in Auffenberg's study) may explain the observation of less plant consumption by C. lewisi. Among ingested plant matter, leaves and stems were consumed most frequently, while fruits, nuts, and flowers were consumed less frequently. People have complained that C. nubila caymanensis raided vegetable gardens, with favored foods being potato plant leaves, plums, mangoes, and papayas (Grant, 1940; Carey, 1966). However, in QEIIBP, most plant consumption by igua-

nas consisted of non-cultivated plants, including herbaceous weeds, tree leaves, and fruits.

Whether or not rock iguanas display intentional geophagy is an unsettled issue. Soil and rocks have been found in the feces of some species of Cyclura (Iverson, 1979; Cvril, 2001) and other iguanas (Sokol, 1971; Sylber, 1988). Iverson (1979) concluded that geophagy was not intentional in C. carinata because these iguanas were not directly observed consuming rocks or soil. The current study demonstrates that geophagy is intentional in C. lewisi, as iguanas were observed to ingest small rocks and soil, even returning to preferred sources for these materials. Consumption of soil was obvious to the observer when the source was barren land or a pile of potting soil. Consumption of rocks was confirmed by casual examination of feces. Instances where iguanas foraged small bits from the ground in sites containing fallen leaves, rocks, soil, and no vegetation were often recorded as consuming unidentifiable matter. Some of these instances may have included geophagy and, therefore, the overall frequency of geophagy in C. lewisi was probably underestimated.

One iguana consumed feces of an agouti and small amounts of conspecific feces may have been ingested by this individual during extended bouts of tongue-touching. Consumption of rat feces has been reported in *C. n. nubila* (Perera, 1985) and of bird feces in *C. cychlura figginsi* (Coenen, 1995). However, coprophagy in rock iguanas seems to be rare or may involve small amounts of feces that are difficult to detect.

Iguanas only engaged in carnivory during a small portion (1.5%) of foraging time. All such observed instances involved predation or attempted predation on invertebrates. When preying on slugs, iguanas used a different feeding behavior than that employed in consumption of plants and non-living foods. Most species of *Cyclura* are primarily herbivorous, but employ limited carnivory (typically 0-5% of diet) that is focused on slow-moving mollusks and insects (Carey, 1975; Wiewandt, 1977; Perera, 1985; Mitchell, 1999; Cyril, 2001; Knapp, 2001; Hayes et al., 2004). Exceptions include instances of rock iguanas preying on and consuming birds, conspecific hatchlings, carrion, land crabs, and hermit crabs (Iverson, 1979; Auffenberg, 1982; Perera, 1985; Knapp et al., 1999; Gerber et al., 2002; Hayes et al., 2004).

On two occasions, iguanas were observed eating bits of their own shedding skin. Iguana skin has been reported in the diet of other rock iguanas (Iverson, 1979; Perera, 1985; Mitchell, 1999; Knapp, 2001) and *C. carinata* has been observed to ingest shedding skin of other iguanas in captivity (Murphy, 1969).

Supplemental food consumption comprised a small portion (4.3%) of the feeding budget of C. lewisi. However, this had potentially substantial impact on both the health and behavior of iguanas. I observed that some iguanas routinely approached workers in the park when the latter gathered outside to eat at midday. Despite rules to the contrary, workers fed iguanas at close distances, often less than 2 m away. Iguanas that were not wary of humans would occasionally jump onto them and chase them (pers. obs.), which is undesirable in a tourism setting or otherwise. Resource availability impacts many aspects of animal behavior (Stamps and Tanaka, 1981; Dunbrack et al., 1996; Hidalgo-Mihart et al., 2004; Kolluru and Grether, 2005) and supplemental feeding is thought to have altered the spatial distribution and behavior of at least one rock iguana, C. cychlura inornata (Iverson et al., 2004). The supplemental foods consumed by C. lewisi, including rice, bread, beans, meats, and cheeses, may also be nutritionally detrimental to primarily herbivorous iguanas. Additionally, if consumed, plastic silverware and bags and other non-food items that contain discarded food present potential choking hazards and dangers to the gastrointestinal tract of iguanas. For these reasons, human food and refuse need to be restricted and disposed of properly when in the vicinity of iguanas. Also, trash cans must be constructed to keep iguanas out, both to prevent consumption of improper foods and to prevent iguanas from becoming trapped inside the receptacles.

Responses of iguanas to human distur-

bances seemed to increase with the level of disturbance. However, the average quantitative response to even the highest level of disturbance was lower than 1, which represented cessation of current activity or moving the head in response to the disturbance. Responses to vehicular disturbances were similar across levels of severity, and were generally the same as or lower than responses to humans. This level of habituation is encouraging in one respect, in that C. lewisi can coexist with humans and serve as a potential tourist attraction in parks or nature reserves. However, a total lack of response to moving vehicles is worrisome particularly because iguanas sometimes roam outside the boundaries of OEIIBP, an area partially encircled by roads (Goodman, 2004). During 2001-2002, one iguana in the population was killed by a vehicle and another was injured. Iguanas are vulnerable to vehicles because they both rest in the shade of parked cars (and may be hidden from motorists) and bask on the edges of roads. Both situations make iguanas vulnerable to being run over by vehicles. Therefore, low speed limits and signs warning visitors of the potential presence of iguanas on roads and beneath parked cars are essential in any current and future sites containing C. lewisi. Lack of wariness may make iguanas better spectacles for the viewing public. However, this comes at the price of increased aggressiveness towards humans. Consequently, supplemental feeding of iguanas by humans must be restricted.

Undoubtedly, the unnatural habitats in the park and habituation to humans and vehicles have affected the behavioral ecology of Cyclura lewisi in the study population (Lacy and Martins, 2003). However, no alternate study population exists nor has existed in recent times. In addition, it is unlikely that future populations of this species will ever exist in pristine settings. Therefore, the findings of this study represent the closest possible representation of the natural behavior and ecology of this species. Moreover, this representation is one that will be useful in the management of this and future reintroduced populations of C. lewisi. Other species of Cyclura face similar situations in that they also have small population sizes and are subject to increasing human influence (Alberts, 2000). Therefore, future research will need to address the ecology of these unique and endangered iguanas as they interface with disturbed and human-occupied regions.

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