

Nesting Behavior and the Use of Termitaria by the Andros Iguana (*Cyclura cyclura cyclura*)

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ABSTRACT.—Nest-site selection and the behavioral mechanisms driving selection have received relatively little attention in nesting ecology studies despite their importance when establishing conservation and management programs for endangered taxa that have obligate habitat-specific nesting requirements. The nesting ecology of *Cyclura cyclura cyclura* was studied on Andros Island, Bahamas, from 2001 to 2004 to elucidate factors influencing nest site selection and address conservation and management implications. Female iguanas predominantly used active *Nasutitermes rippertii* (Termitidae: Isoptera) termite mounds as egg incubation chambers. Nesting females selected mounds with >5 cm surrounding soil depth and initiated excavation and oviposition in early May. There was no correlation between female body size and termite mound size. Tunnels were excavated into lateral sides of mounds and terminated in nest chambers. Eggs were deposited outside the mound and pushed into the chamber using thrusts of the forelimbs. Mean egg incubation length for the combined 2003 and 2004 seasons was 75.7 days. Temperatures inside the mound were warmer and less variable than corresponding ambient temperatures. Mean hatching success for clutches in monitored nests ranged from 69.9–100% from 2002 to 2004. The nesting behavior of *C. cyclura* on Andros most likely reflects the effects of local climatic history and topography on reproductive attributes such as nest success. Elucidating annual female nesting effort, as indicated by active nests, could be an extremely useful indicator to assess both the number of breeding females and, indirectly, the potential for hatchling recruitment.

The ecology of reproduction is a defining aspect of an organism's life-history strategy and has received substantial scientific interest focusing primarily on reproductive investment (e.g., Andrews and Rand, 1974; Vitt and Congdon, 1978; Seigel and Fitch, 1984), reproductive costs (e.g., Madsen and Shine, 2000; Olsson et al., 2001; Shine, 2003), physiological trade-offs between offspring size and number (e.g., Elgar and Heaphy, 1989; Sinervo, 1994), and functional and phylogenetic constraints on offspring size (e.g., Vitt and Congdon, 1978; Shine, 1992). However, nest-site selection and the behavioral mechanisms driving this selection have received considerably less attention, possibly because of the difficulty in observing nesting behavior in the wild (but see Madsen and Shine, 1999; Harlow and Taylor, 2000; Randriamahazo and Mori, 2001).

Nest-site selection and associated behavioral studies are important because they have demonstrated that female nesting choices can influence phenotype (e.g., Roosenburg, 1996;

Reinhold, 1998; Deeming, 2004) and survival probability of offspring (e.g., Burger, 1993). The study of nest-site selection and nesting behavior is also important when establishing conservation and management programs for endangered taxa that have obligate habitat-specific nesting requirements (e.g., Garcia et al., 2003; Troëng and Rankin, 2005). For example, iguanas of the genus *Cyclura*, considered the most endangered group of lizards (Alberts, 2000), are characterized by relatively uniform nesting strategies on the West Indian islands they inhabit. These strategies typically include migration from normal activity centers to limited areas suitable for oviposition, construction of nesting burrows, and nest site defense (Wiewandt, 1982; Iverson et al., 2004). Consequently, a critical aspect of conservation for *Cyclura* iguanas relies on knowledge of available nesting areas, migration patterns to nest sites, and behavioral mechanisms influencing nest site selection and nest success.

The Bahamian Andros Iguana (*Cyclura cyclura cyclura*) is the only iguana that reportedly deviates from the usual *Cyclura* nesting strategy of depositing eggs in subterranean chambers excavated in sand or organic soil (references in Alberts, 2000) by its use of termitaria as incubation chambers. Only anecd-

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total accounts exist regarding this behavior (Wiewandt, 1982; W. Auffenburg, unpubl. data), and nothing is known concerning the habitat and physical characteristics that influence nest site selection in this species. The Andros Iguana is classified as Endangered under 2004 IUCN Red List criteria and listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Consequently, understanding basic attributes of female reproductive ecology, such as the size of the female nesting population and the habitat and physical characteristics that influence distribution and selection of nest sites is necessary to facilitate informed conservation management decisions. The objectives of our study were to (1) monitor termitaria-specific environmental variables to elucidate factors influencing nest site selection, (2) examine the relationships among female body size and termitaria attributes, (3) monitor incubation and hatching rates, (4) describe, in detail, the unique nesting behavior of the Andros Iguana, and (5) address conservation and management implications.

MATERIALS AND METHODS

Study Site.—Andros is the largest island in the Bahamian archipelago encompassing an area of 5,959 km². This subtropical island is actually a composite of three main islands (North Andros, Mangrove Cay, and South Andros), along with dozens of associated cays, separated by saline tidal channels. The substrate consists of oolitic and bioclastic limestone, and from east to west, a thin coastal ridge (to 30 m elevation) gives way to a flat and pine-forested interior. Approximately halfway across the island in a westerly direction, forest grades into extensive shrubland, mudflats, and mangroves as the water table reaches the surface.

Fieldwork was conducted in a southerly cross-island zone on Andros between Mangrove Cay (24°10'15"N) and Sandy Cay (24°05'18"N). The majority of work was concentrated in three study locations: Sandy Cay (310 ha), Linder Cay (1,300 ha), and a trilobed peninsula (175 ha) extending from the south-southeast side of Mangrove Cay. The three main habitat types included pine woodland, evergreen shrubland, and mangrove shrubland. Knapp and Owens (2004) provide detailed descriptions of plant communities from each site.

Field Data Collection.—Preliminary field investigations began in May 2001 and April/May 2002. Based on observed courtship and oviposition dates from those two years, intensive fieldwork was concentrated in May/June and August/September 2003–2004. Termitaria used

by nesting females were located primarily by searching all habitat types and also while radio tracking females in conjunction with a concurrent home range study (for methods, see Knapp and Owens, 2005).

After a nest was discovered, attendant female iguanas were captured to record snout-vent length (SVL to the nearest millimeter) and body mass (BM in grams). Although female BM was recorded primarily postoviposition ($N = 27$), some females ($N = 11$) were weighed from 2–7 days prior to nesting. Therefore, gravid body mass (GBM) for females recorded after egg deposition was estimated as postoviposition BM + associated clutch mass and was used in statistical analyses to facilitate comparisons with other studies (e.g., Iverson et al., 2004).

For oviposition in termitaria, a general nesting pattern was documented based on a composite of observations from multiple females. Descriptions of oviposition behavior are derived from 12 observed females, whereas completed nest characteristics and defense behavior are from 37 females nesting in termitaria. After completion, we excavated nests to remove eggs, record clutch size, and map the internal three-dimensional structure of the mound. A StowAway[®] temperature logger was reburied with the eggs inside selected mounds to record hourly incubation temperatures. Other temperature loggers were hung 30 cm directly above mounds to record corresponding ambient air temperatures.

In 2003, we documented physical parameters and surrounding vegetation for each termite mound used ($N = 21$) as a nest as well as for mounds not used ($N = 22$) by nesting females. We recorded mound height (to the nearest centimeter) and circumference (to the nearest centimeter at the widest position). Skirt depth was recorded as the mean organic soil depth in front of the tunnel entrance at the base of the mound and at a 15-cm perpendicular distance (to the nearest 0.5 cm) to the base of the mound. A spherical densiometer was placed directly on top of mounds, and the mean of the four readings (at each cardinal direction) were taken to estimate percent canopy cover. Distance to the closest area with <50% canopy cover was estimated by sight, confirmed with the densiometer, and measured (to the nearest 0.5 m). The three nearest plant species also were identified and recorded.

We returned to nests approximately 72 days postoviposition to reexcavate and retrieve eggs or hatchlings. Eggs from partially hatched and unpipped clutches were placed in plastic containers containing surrounding soil and carton (i.e., a construction material created by termites from partly chewed or digested woody tissue,

salivary secretions, and feces) from the mound and incubated under ambient temperature and humidity conditions until hatching (1–7 days). Time to emergence from eggs after pipping (mean \pm SD = 1.9 ± 0.7 days, range 0–4, $N = 68$) and closure of the umbilical opening following emergence (mean \pm SD = 3.9 ± 0.9 days, range 3–6, $N = 70$) were used to estimate incubation times for nests found with hatchlings. When excavated, if neonates had already hatched and emerged from the nest, eggshells and failed eggs were counted to determine hatching success.

Statistical Analysis.—We used logistic regression to model the probability of termite mound usage by nesting female iguanas based on the five recorded parameters of mound height, circumference, soil skirt depth, canopy cover, and distance to nearest 50% canopy cover. We used stepwise selection with backward elimination to choose the best set of predictors. The dependent variable, mound usage, was a binomial response in all models. The final model was selected using likelihood ratio tests. Analyses of variance (ANOVA) and Student *t*-tests were used to test for temperature differences among years and locations in and above termitaria. Least-squares linear regression was used to test for relationships between body size and date of oviposition and termite mound characteristics. Iguana morphological data, tunnel entrance dimensions, and soil skirt depth were log transformed, whereas percent canopy cover was arcsine transformed to meet statistical assumptions prior to regression and mean-comparison statistical analyses. Means are presented \pm 1 SD. Statistical tests were performed using SAS (vers. 8, SAS Institute, Inc., Cary, NC).

RESULTS

Nesting Behavior.—Based on copulation and oviposition dates (see below), courtship presumably occurred from the first week of April until the first week of May. In a South Andros study area, characterized subjectively by extremely low iguana densities (<0.2 iguanas/ha), male mate-guarding was observed by us and our colleagues in April 2002–2005. One male was recorded following the same female continuously (as confirmed via radio telemetry) and sharing a nocturnal retreat. Although the nocturnal retreats changed between years, the guarding behavior of the same male to the same female during April remained consistent. Any approach by a rival male would cause the guarding attendant male to charge the intruder and give chase for long distances (recorded up to 150 m). In cases where males were of equal

size, we observed head-bobs and open-mouthed face-offs with lateral head pushing similar as reported for *Cyclura* elsewhere (Wiewandt, 1977; Iverson, 1979). Copulation events were observed on 24 April 2005 (P. Hartman, pers. comm.) and 25 April 2006 (A. Mitchell, pers. comm.).

Female Andros Iguanas primarily used active *Nasutitermes rippertii* (Termitidae: Isoptera) termite mounds. However, two of 45 iguana nests recorded in this study were discovered in coarse sand consisting primarily of gastropod (*Battilaria* sp.) shell fragments. Female iguanas initiated lateral digging into termitaria at ground level and often performed test digs on several mounds, or on the mound eventually used for oviposition. Loose carton and soil were kicked out of the tunnel with backward thrusts of the female's forelimbs and then with their back legs once the material was at the entrance opening. Carton and substrate material from termitaria were displaced in an apron around the tunnel entrance and frequently (39 of 43 nests) contained empty egg shells from previous years.

Female iguanas oviposited at the tunnel entrance and subsequently pushed eggs into the central mound chamber. Pushing was performed using alternating thrusts of the forelimbs and prodding with the snout. Loose soil and carton were pushed along with the eggs into the central chamber leaving a pocket of air above the eggs. While eggs were pushed into the mound, females intermittently packed the tunnel by bracing with their hind legs and thrusting their head and snout into the plug. When the eggs were no longer visible from the outside, females turned from the mound and scratched substrate toward the entrance using alternating movements of the forelimbs followed by reciprocal movements of the back legs.

Back-fill material consisted of carton from termitaria, associated soil, pine needles, twigs, leaf litter, palm fronds, and limestone fragments (ranging up to 14 cm in diameter) from the surrounding area. Back-filling continued for up to five hours until there was a large buttress of material piled against the side of the mound. Back-filling was always observed in the morning (as early as 0930 h) or early afternoon (before 1430 h). The affected termite colonies encapsulated the chamber and repaired the tunnel within one week. In 15 instances, the tunnel opening was not repaired by the colony but remained occluded with the nest back-fill.

Females were aggressive and protective of their mounds pre- and postoviposition, often charging and chasing female intruders if they ventured to within 10 m. Females remained in

TABLE 1. Termite mound parameter means (± 1 SD) for mounds used and unused for nesting by the Andros Iguana. Logistic regression final-model results (Nagelkerke $r^2 = 0.74$) of the relationship between termite mound use and mound parameters are presented with P -values. Logistic regression results are provided only for three parameters because, based on likelihood tests, only the parameters of height, circumference, and soil skirt depth were used in the final odds ratio model.

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

the nest area for a minimum of six weeks following oviposition and often would stay perched on top or within 3 m of the nest mound. Near the time of hatchling emergence, 23% (nine of 40) of nesting females were still in the immediate area of their nest and approached the termitarium while we investigated the mound. In these cases, aggression was normally subdued, although three females actively charged, perched atop the mound, and performed head-bob displays.

Termitarium Fidelity.—Eighty percent (12 of 15) of termitaria that were used for nesting from 2001 to 2003, and still supported active termite colonies, also were used in 2004. Fifty percent (six of 12) of these consecutive-year termitaria were used by the same female. The other mounds were used by different females in each year. Three nesting females from 2003 that nested in 2004 used different sites (up to 300 m away from previous sites). In these cases, the mounds were inactive, defended by a larger female, or damaged while excavating.

In 2004, there were 10 active termitaria (0.147 per ha) within our concentrated study area (68 ha) on north Sandy Cay, of which nine were used by nesting iguanas (90%). One mound was used twice after the defending female was forced from her mound. Three of the six active mounds (50%) observed on Sandy Cay in 2003 were used by the same females in 2004. The other two focal study areas on Linder and Mangrove Cays had termitaria concentrations of 0.875 and 0.292 per ha, respectively. Five of seven (71.4%) termitaria documented from the Linder Cay site (8 ha) were used by nesting females in 2003 and 2004. Two of the termitaria were used by the same female each year. At the Mangrove Cay site (65 ha), three of 19 (15.8%) mounds documented in 2004 were used with only one repeat nesting female using a different termite mound.

Timing of Oviposition and Nest Location.—Nesting females averaged 38.7 \pm 4.2 cm SVL (range 31.0–47.7 cm, $N = 32$) and 3,006 \pm 1,185 g GBM (range 1,279–6,657, $N = 31$). Iguanas initiated

nest excavation and deposited eggs in early May. The first nests discovered in 2001, 2002, 2003, and 2004 were on 12, 8, 10, and 8 May, respectively. We were able to remain on the island throughout the entire nesting season in 2003 and recorded nesting events from 10 May to 13 June (mean = 30 May, median = 3 June, $N = 9$). In 2004, we recorded nesting events from 8 May to 12 June (mean = 29 May, median = 31 May, $N = 21$) but are aware of one mound that was used for nesting after we left the island. Date of oviposition was not correlated with SVL in 2003 ($r = -0.08$, $P = 0.84$, $N = 9$) or 2004 ($r = -0.37$, $P = 0.27$, $N = 11$).

Nests were located primarily in open pine (46%) followed by dry evergreen shrubland (36%) and closed pine habitats (18%; habitat parameters defined in Knapp and Owens, 2005). These habitat data are similarly proportional to unused termitaria, which were discovered in open pine (50%), dry evergreen shrubland (32%), and closed pine habitats (18%). Twenty-two plant species were recorded <1 m from termitaria with the most frequent species being *Metopium toxiferum*, *Thrinax morrisii*, and *Savia bahamensis* (20, 13, and 12% of termitaria, respectively). The association of termitaria and vegetation was responsible for extremely high percentages of canopy cover over nests (mean = 72 \pm 20%, range = 28–96%, $N = 30$).

Termitarium and Internal Nest Characteristics.—The logistic regression results indicate that there was a significant relationship between termite mound usage and recorded parameters (Table 1). Based on likelihood tests, only height, circumference, and soil skirt depth were used in the final odds ratio model. Height and skirt depth had a significant effect on the probability of a mound being used by an iguana (Table 1). With the other factors fixed, a 1-cm increase in mound height decreased the estimated probability of mound usage by 0.855 (95% Wald Confidence Limits = 0.747, 0.979), whereas a 1-cm increase in soil depth increased the estimated probability of mound usage by 2.38 (95% Wald Confidence Limits = 1.061, 5.355).

TABLE 2. Yearly ambient and iguana nest temperatures ($^{\circ}\text{C}$) recorded from 6 June to 10 August on Andros Island. Means (± 1 SD) are followed by hourly ranges in parentheses. All nest temperatures were taken within termitaria. Mean temperature for the one 2004 nest in sand was $30.8 \pm 1.5^{\circ}\text{C}$. Mean temperature for a 2003 inactive mound was $29.1 \pm 1.4^{\circ}\text{C}$.

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

From 6 June to 10 August (Table 2), mean daily ambient air temperatures above termitaria were not significantly different between 2003 and 2004 ($t_{12} = 0.06$, $P = 0.96$). Likewise, mean daily nest temperatures were not significantly different among years 2002–2004 ($F_{2, 13} = 0.03$, $P = 0.97$). Mean nest temperatures for all years were significantly warmer than ambient air temperatures ($t_{28} = -10.78$, $P = < 0.0001$). Hourly nest temperatures also experienced less fluctuation than hourly ambient temperatures (Fig. 1), both within years and for all years combined (Levene homogeneity-of-variance test, $F > 5,150.2$, $P < 0.0001$). Nest temperatures were not correlated with percent cover ($r = -0.32$, $P = 0.40$, $N = 16$) or mound circumference ($r = 0.11$, $P = 0.77$, $N = 16$). Mean incubation temperature for the single recorded sand nest was $30.8 \pm 1.5^{\circ}\text{C}$.

Termitaria used as egg incubation chambers ranged in height from 23.0–71.0 cm ($N = 25$)

and in circumference from 55.0–214.0 cm ($N = 25$; Table 1). There was no correlation between iguana body size and termite mound circumference (for SVL, $r = -0.13$, $P = 0.50$, $N = 30$; for GBM, $r = -0.13$, $P = 0.51$, $N = 30$). Tunnel structure was highly variable and depended on the internal characteristics of the mound (Fig. 2). In some cases, limestone slabs, tree trunks, or branches obstructed tunnels, forcing females to excavate a diverse array of tunnel trajectories ranging from multiple lateral bends to upward pathways. The mean egg incubation period in termitaria for 2003 and 2004 was 75.7 ± 3.6 days (range 72–82 days, $N = 14$).

Hatching Success.—We documented hatching from 3 August to 2 September 2003 and from 4–30 August 2004. Mean hatching success for clutches was 100% ($N = 2$), 75.2% ($N = 15$), and 69.9% ($N = 17$) in 2002, 2003, and 2004, respectively, and did not differ significantly among years ($F_{2, 31} = 0.59$, $P = 0.56$). Egg

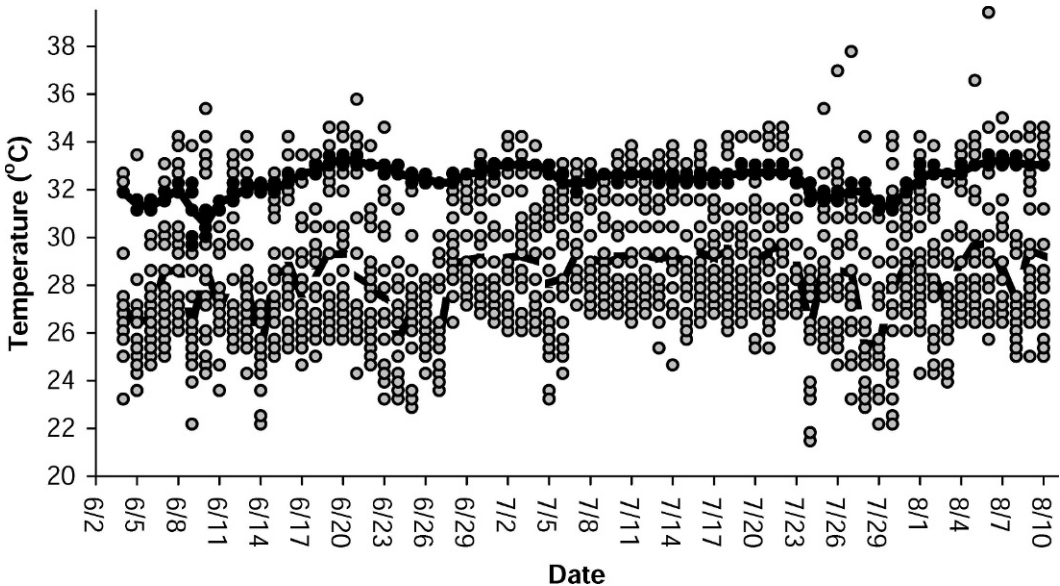


FIG. 1. Daily ambient air and nest temperatures from within a 2003 exemplar Andros Iguana nest oviposited in termitaria. Solid and broken lines represent mean nest and ambient air temperatures, respectively. Solid and shaded circles represent hourly recordings in and above nests, respectively.

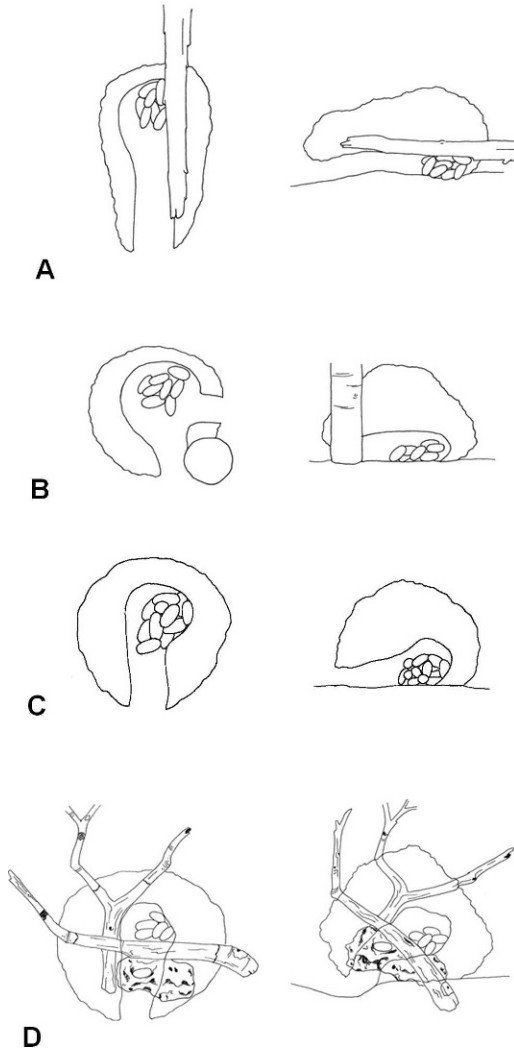


FIG. 2. Dorsal (left) and lateral (right) schematic views of representative termitaria used as oviposition sites by female Andros Iguanas in 2004. Vertical bar adjacent to mound A represents 12 cm.

mortality occurred because eggs were flaccid and died immediately after oviposition, desiccated during development, desiccated during development, ruptured by the nesting female, attacked by fungus, flooded (one mound nest located adjacent to a tidally flooded mangrove), depredated by crabs (*Cardisoma guanhumii*), or removed from their nests (presumably by crabs; Table 3).

DISCUSSION

Andros Iguanas selected nest sites nonrandomly with respect to termitarium height and soil skirt depth. Termitaria used as iguana nest sites were not as tall as those not used (Table 1);

TABLE 3. Causes of individual egg mortality in nests by year for Andros Iguanas. Total eggs in 2003 and 2004 were 144 and 165, respectively. Number lost by each cause is followed by the percent of total eggs lost to that cause.

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

however, this may be an artifact of use rather than a preference by iguanas. A typical defense position for females is resting on top of termitaria. The annual movement of iguanas on and off termitaria continually for up to 10 weeks postoviposition may reduce the height because of scratching involved when climbing up the side and while on top of the mound. Although not significant in the final logistic regression model, the circumference of used termitaria is also less relative to the unused mounds (Table 1), which may reflect the same artifact of iguana movement patterns.

Andros Iguanas selected termitaria that were associated with more surrounding soil relative to the unused mounds (Table 1). Soil is required to back-fill the nest tunnel and construct the buttress of material over the entrance. The overall lack of soil associated with Andros Island is evident; the mean soil depth surrounding termitaria used as oviposition sites, which are areas with the most soil accumulation, was <6 cm to the limestone substratum.

The propensity for using termitaria for oviposition sites appears to be well established for lizards in the genus *Varanus* (e.g., Cowles, 1928; King and Green, 1979; Ehmann et al., 1991; Auffenburg, 1994) but also occurs in other reptilian (see reviews in Riley et al., 1985) and avian taxa (e.g., Weaver, 1982; Reed and Tidemann, 1994). Purported benefits of using termitaria are the humidity and thermal advantages for brood incubation (see Riley et al., 1985) because termites are able to regulate the environmental conditions of their nests (Korb and Linsenmair, 2000). Although these benefits to reptilian eggs deposited within the regulated environmental conditions of termitaria are recognized, more studies should investigate the proximate or ultimate factors influencing the use of termitaria. This is especially intriguing in taxa where the behavior is facultative or specific to one population. For example, conspecifics of the Andros Iguana inhabiting the

small cays (< 50 ha) of the Exuma Islands (*Cyclura cychlura figginsi* and *Cyclura cychlura inornata*) deposit eggs only in sand areas despite the presence of termitaria on the islands (Iverson et al., 2004; Knapp et al., 2006). Because reciprocal transplant or common garden experiments (Conover and Schultz, 1995; Gotthard and Nylin, 1995) on large-bodied and endangered taxa are improbable, the conservation strategy of translocation (Knapp, 2001) may provide the opportunity to explore further the effects of proximate and ultimate causes on the nesting variation in this species.

West Indian iguanas inhabit areas of karst limestone with limited areas of sand/soil accumulation. Therefore, nest-site selection is constrained by the physical structure of the associated habitat, which has shaped generally uniform nesting tactics for *Cyclura* iguanas. The adaptive flexibility of nesting behavior for the Andros Iguana has facilitated their occupation of areas that would be unsuitable for the typical iguanine nesting strategy of depositing eggs in subterranean chambers excavated in sand or organic soil. The nesting behavior of *Cyclura cychlura* on Andros most likely reflects the effects of local climatic history and topography on reproductive attributes such as nest success. Andros offers little vertical relief, and the karst limestone provides few areas for soil accumulation (mean elevation above msl at study sites = 1.5 m). The island has a distinct wet season from May to October when heavy rainfall often results in a raised water table that continually breaches the limestone surface throughout the rainy season (pers. obs.). Therefore, the requirement for dry, well-drained oviposition sites and the use of termitaria by the Andros Iguana, when available, most likely reflects a history of selection favoring individuals nesting in mounds that remain dry and provide relatively high and constant internal temperatures for egg incubation.

Implications for Conservation and Management.—It is imperative that the use of termitaria by female iguanas for oviposition sites be addressed in conservation management planning. Although it appears that this behavior may be facultative in specific subpopulations, it is unknown how the general population would adapt to wide-spread environmental change such as the loss of termitaria. Furthermore, there are no ancillary nesting options for many subpopulations because of the lack of suitable areas that can support traditional nest burrow construction in sand or loose soil. Therefore, the monitoring and protecting of termitaria should be incorporated into management initiatives. Knowledge of nest-site characteristics preferred by females and the associated habitats where

termitaria are found also will assist managers in demarcating formal protected areas.

Annual female nesting effort, as indicated by active nests, could be an extremely useful indicator to assess both the number of breeding females and, indirectly, the potential for hatching recruitment into the population. Moreover, in the absence of labor-intensive monitoring programs, the capacity to assess annual activity and variation in nesting populations would provide managers with a simple strategy for identifying high-density populations and also improve the capacity to assess trends in the Andros Iguana population. Iguana nests are conspicuous and attendant females remain with the nest for weeks after oviposition. These factors make nest monitoring a cost-effective rapid survey technique.

Acknowledgments.—Financial support for this research was provided by Shedd Aquarium and grants from the Association of Zoos and Aquariums Conservation Endowment Fund, Disney Wildlife Conservation Fund, U.S. Fish and Wildlife Service International Conservation Fund, International Iguana Foundation, Chicago Zoological Society Board of Trade Endangered Species Fund, and the Chicago Herpetological Society. We thank the Bahamas Department of Agriculture for permission to conduct the study. Tiamo Resorts of South Andros provided crucial logistical support. R. Scheffrahn identified the termites from South Andros Island. We thank A. Alberts, K. Dodd Jr., M. Moulton, M. Sunquist, R. Franz, J. Iverson, and S. Buckner for their valuable comments on the manuscript.

LITERATURE CITED

- ALBERTS, A. C. 2000. West Indian Iguanas: Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland.
- ANDREWS, R., AND A. S. RAND. 1974. Reproductive effort in anoline lizards. *Ecology* 55:1317–1327.
- AUFFENBERG, W. 1994. *The Bengal Monitor*. University of Florida Press, Gainesville.
- BURGER, J. 1993. Colony and nest site selection in lava lizards *Tropidurus* spp. in the Galapagos islands. *Copeia* 1993:748–753.
- CONOVER, D. O., AND E. T. SCHULTZ. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology and Evolution* 10:248–252.
- COWLES, R. B. 1928. The life history of *Varanus niloticus*. *Science* 67:317–318.
- DEEMING, D. C. 2004. *Reptilian Incubation: Environment, Evolution and Behaviour*. Nottingham University Press, Nottingham, U.K.
- EHMANN, H., G. SWAN, G. SWAN, AND B. SMITH. 1991. Nesting, egg incubation and hatching by the heath monitor *Varanus rosenbergi* in a termite mound. *Herpetofauna* 21:17–24.

- ELGAR, M. A., AND L. J. HEAPHY. 1989. Covariation between clutch size, egg weight, and egg shape: comparative evidence for chelonians. *Journal of Zoology (London)* 219:137–152.
- GARCIA, A., G. CEBALLOS, AND R. ADAYA. 2003. Intensive beach management as an improved sea turtle conservation strategy in Mexico. *Biological Conservation* 111:253–261.
- GOTTHARD, K., AND S. NYLIN. 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* 74:3–17.
- HARLOW, P. S., AND J. E. TAYLOR. 2000. Reproductive ecology of the Jacky Dragon (*Amphibolurus muricatus*): an agamid lizard with temperature-dependent sex determination. *Austral Ecology* 25: 640–652.
- IVERSON, J. B. 1979. Behavior and ecology of the Rock Iguana *Cyclura carinata*. *Bulletin of the Florida State Museum, Biological Sciences* 24:175–358.
- IVERSON, J. B., K. N. HINES, AND J. M. VALIULIS. 2004. The nesting ecology of the Allen Cays Rock Iguana, *Cyclura cychlura inornata* in the Bahamas. *Herpetological Monographs* 18:1–36.
- KING, D., AND B. GREEN. 1979. Notes on diet and reproduction of the Sand Goanna, *Varanus gouldii rosenbergi*. *Copeia* 1979:64–70.
- KNAPP, C. R. 2001. Status of a translocated *Cyclura* iguana colony in the Bahamas. *Journal of Herpetology* 35:239–248.
- KNAPP, C. R., AND A. K. OWENS. 2004. Diurnal refugia and novel ecological attributes of the Bahamian Boa, *Epicrates striatus fowleri* (Boidae). *Caribbean Journal of Science* 40:265–270.
- . 2005. Home range and habitat associations of a Bahamian iguana: implications for conservation. *Animal Conservation* 8:269–278.
- KNAPP, C. R., J. B. IVERSON, AND A. K. OWENS. 2006. Geographic variation in nesting behavior and reproductive biology of an insular iguana (*Cyclura cychlura*). *Canadian Journal of Zoology* 84:1566–1575.
- KORB, J., AND K. E. LINSSENMAIR. 2000. Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? *Insectes Sociaux* 47:357–363.
- MADSEN, T., AND R. SHINE. 1999. Life history consequences of nest-site variation in tropical pythons (*Liasis fuscus*). *Ecology* 80:989–997.
- . 2000. Energy versus risk: costs of reproduction in free-ranging pythons in tropical Australia. *Austral Ecology* 25:670–675.
- OLSSON, M., R. SHINE, AND E. WAPSTRA. 2001. Costs of reproduction in a lizard species: a comparison of observational and experimental data. *Oikos* 93: 121–125.
- RANDRIAMHAZO, H. J. A. R., AND A. MORI. 2001. Egg-laying activities and reproductive traits in females of *Oplurus cuvieri cuvieri*. *Journal of Herpetology* 35:209–217.
- REED, M. A., AND S. C. TIDEMANN. 1994. Nesting sites of the hooded parrot *Psephotus dissimilis* in the Northern Territory. *Emu* 94:225–229.
- REINHOLD, K. 1998. Nest-site philopatry and selection for environmental sex determination. *Evolutionary Ecology* 12:245–250.
- RILEY, J., A. F. STIMSON, AND J. M. WINCH. 1985. A review of Squamata ovipositing in ant and termite nests. *Herpetological Review* 16:38–43.
- ROOSENBURG, W. H. 1996. Maternal condition and nest site choice: an alternative for the maintenance of environmental sex determination? *American Zoologist* 36:157–168.
- SEIGEL, R. A., AND H. S. FITCH. 1984. Ecological patterns of relative clutch mass in snakes. *Oecologia* 61:293–301.
- SHINE, R. 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? *Evolution* 46:828–833.
- . 2003. Locomotor speeds of gravid lizards: placing “costs of reproduction” within an ecological context. *Functional Ecology* 17:526–533.
- SINERVO, B. 1994. Experimental tests of reproductive allocation paradigms. *In* L. J. Vitt and E. R. Pianka (eds.), *Lizard Ecology: Historical and Experimental Perspectives*, pp. 73–90. Princeton University Press, Princeton, NJ.
- TROËNG, S., AND E. RANKIN. 2005. Long-term conservation efforts contribute to positive green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica. *Biological Conservation* 121:111–116.
- VITT, L. J., AND J. D. CONGDON. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *American Naturalist* 112:595–608.
- WEAVER, C. M. 1982. Breeding habitats and status of the golden-shouldered parrot *Psephotus chrysopterygius*, in Queensland. *Emu* 82:2–6.
- WIEWANDT, T. A. 1977. Ecology, Behavior, and Management of the Mona Island Ground Iguana, *Cyclura stejnegeri*. Unpubl. Ph.D. diss., Cornell University, Ithaca, NY.
- . 1982. Evolution of nesting patterns in Iguanine lizards. *In* G. M. Burghardt and A. S. Rand (eds.), *Iguanas of the World: Their Behavior, Ecology, and Conservation*, pp. 119–141. Noyes Publications, Park Ridge, NJ.

Accepted: 18 July 2007.