

NESTING MIGRATIONS AND REPRODUCTIVE BIOLOGY OF THE MONA RHINOCEROS IGUANA, *CYCLURA STEJNEGERI*

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Abstract.—We studied the nesting migrations and reproductive ecology of the endangered Mona Rhinoceros Iguana *Cyclura stejnegeri* at three localities from 2003 to 2006. Female movements while seeking a nesting site ranged from 0.3 to 12.8 km, were mostly erratic. Time elapsed between mating and oviposition averaged 30 ± 5 days, while the nesting period lasted four weeks (July to early August). Nest site fidelity by females in consecutive years was 50%, although non-resident females at one study site used the same beach 72% of the time. Clutch size averaged 14 eggs and was positively correlated with female snout-vent length (SVL). Egg length was the only egg size variable correlated negatively with female size. Incubation temperatures averaged 32.8°C (2005) and 30.2°C (2006) and fluctuated up to 9°C . Overall hatching success from 2003–2005 was 75.9%. Some nests failed as a result of flooding of the nest chamber and in one case a nest was destroyed by feral pigs. Hatchling sex ratio was close to 1:1 for all individual nests and all hatchlings collected throughout the study. Hatchling morphometrics (SVL, body mass) were not related to female size. Egg predation by pigs was low compared to previous reports from the 1970s, which reached levels of up to 100% in some years. The dramatic increase in hatching success may be the result of fencing the most important iguana nesting areas in 1985, an initiative that is maintained until now, to prevent feral pig incursions.

Resumen.—Del 2003 al 2006 estudiamos la migraciones asociadas a la búsqueda de sitios para la anidación y la ecología reproductiva de la iguana *Cyclura stejnegeri* en tres localidades de Isla de Mona. Las distancias recorridas por las hembras durante la búsqueda de sitios para anidar fluctuaron entre 0.3 y 12.8 km con desplazamientos en su mayoría erráticos. El tiempo promedio entre el apareamiento y la ovoposición fue de 30 ± 5 días y la época de anidación duró cuatro semanas entre julio y agosto. Las hembras mostraron fidelidad al sitio de anidaje en un 50% de los casos, aunque el 72% de hembras no residentes en una playa retornaron a la misma en años consecutivos. El promedio de huevos por nidada fue de 14 y estuvo positivamente correlacionado con el tamaño (longitud hocico-cloaca, SVL) de la hembra. De las dimensiones de los huevos, solo el largo del huevo estuvo negativamente correlacionado con el tamaño de la hembra. Las temperaturas de incubación promedio fueron de 32.8°C (2005) y 30.2°C (2006) con fluctuaciones hasta de 9°C . Algunos nidos fueron destruidos debido a las fuertes lluvias que inundaron la cámara del nido y solo un nido fue destruido por cerdos silvestres. La proporción sexual de los neonatos fue de 1:1 para los nidos individuales y para todos los neonatos colectados en el estudio. La morfometría de los neonatos (SVL, peso) no estuvo relacionada con el tamaño de la madre. La depredación de nidos por cerdos fue baja comparada con los años setenta cuando podía alcanzar valores hasta del 100% en algunos años. El incremento sustancial en el éxito de eclosión puede ser el resultado de la instalación de cercas en 1985 en algunas áreas de anidaje para evitar la depredación de nidos por parte de cerdos silvestres.

Key Words.—Caribbean Iguanine; lizard; nesting ecology; reproductive success; rock iguana

INTRODUCTION

Caribbean Ground Rock Iguanas (11 species, eight subspecies; ITWG this volume) of the genus *Cyclura* are among the most endangered lizards in the world (Alberts 2000). Factors affecting most of the populations of these species include habitat degradation, illegal pet trade, and negative interactions with exotic animals (Alberts 2000). Current actions to augment some *Cyclura* populations include captive breeding and headstarting initiatives

(Alberts 2007; Pérez-Buitrago et al. 2008; Burton and Rivera-Milán 2014), translocations (Knapp 2000, 2001; Knapp and Hudson 2004; Wilson et al. 2004), and eradication/control of feral animal species (Mitchell et al. 2002; Donlan et al. 2003; Campbell et al. 2004; Hayes et al. 2004; Gerber 2007). However, knowledge of *Cyclura* biology is relatively poor due to the remoteness of islands on which some species live, and/or the lack of financial/logistic resources to study these long-lived lizards (Iverson et al. 2004).

Knowledge of the reproductive biology of the genus *Cyclura* is a critical component to the evaluation of their population trends, but studies addressing their reproduction have been limited to descriptions of basic aspects such as timing of nesting and hatching, clutch size, egg and hatchling dimensions, and hatching success based on relatively small sample sizes and over short periods of time (but see Iverson et al. 2004; Knapp et al. 2006). This information has been used to analyze life-history trait patterns among species/populations (Wiewandt 1982; Iverson et al. 2004), but its utility in developing population viability models that may be used to guide specific conservation actions is limited. Moreover, there are still several aspects of reproduction in *Cyclura* that are poorly documented, such as details of their nesting migrations. From a conservation perspective, knowledge of the factors that may be reducing the availability of nesting areas and/or reducing hatching success rates is critical.

In this study we document the reproductive biology of the Mona Rhinoceros Iguana (*Cyclura stejnegeri*) using radio-telemetry and mark-recapture techniques. During three reproductive seasons (2003–2005), we documented nest timing, clutch size, egg dimensions, hatchling size, reproductive effort, and the nesting migrations undertaken by females to reach nesting sites. In addition, we compared the spatial variation in clutch size and hatching success across study sites. We also evaluate the effect of management actions taken by the Department of Natural Resources of Puerto Rico (DRNA-PR) in 1982 on reproductive success. These actions included fencing some nesting areas to prevent feral pig incursions and creating areas free of vegetation to increase available nesting habitat.

MATERIALS AND METHODS

Study site.—Mona Island is located in the middle of the Mona channel, between the Dominican Republic and Puerto Rico. It is an oceanic island with a subtropical dry forest climate (Ewel and Whitmore 1973). Most of the island's perimeter is characterized by vertical cliffs 45 m in height that also delimit the largest habitat type of the island (93%), the relatively undisturbed limestone rocky "plateau". On Mona Island, there are three different types of iguana nesting habitat. First, on the plateau, a unique habitat type not extensively represented (1%) is the depressions called "bajuras". The "bajuras" are the only zones on the plateau with a relatively continuous accumulation of clay soil suitable for iguana nesting. Secondly, in the southwestern region of the island, there is a large sandy/limestone coastal plain that offers iguanas another area suitable for nesting (Wiewandt 1977; Haneke 1995). These coastal plain areas were fenced in 1985 by the DRNA-PR to minimize feral pig incursions and thus reduce egg predation.

However, a large part of the coastal plain was planted with exotic species such as *Casuarina equisetifolia* and *Swietenia mahogany* (Diaz 1984; Cintrón and Rogers 1991), thus reducing the availability of appropriate and contiguous nesting sites. Nonetheless, it still constitutes an estimated 74% of all nesting habitat available on the island. Currently, there are small sunny and sandy areas that apparently have not been affected by human activity recently, as well as areas that were cleared by the DRNA-PR in 1992 to provide additional suitable zones for nesting females. In addition to the nesting areas located in the southwestern coastal plain, there are a few narrow (< 150 m wide) beaches available that represent the third type of open area available for iguana nesting.

This study was conducted at three locations of Mona Island representing two of the three nesting habitats described above. The Lighthouse site is located near the eastern coast of Mona Island on its limestone plateau, lacks human disturbance and does not contain well-defined nesting areas (Fig. 1). The second area, Sardinera Beach, is located in the southwestern coastal plain near the site of the DRNA-PR facilities, and is a highly disturbed area close to the zones in which the native vegetation was replaced by exotic tree species. The third study site, Pájaros Beach, is a narrow but elongated beach in the southeast where the predominant vegetation type is "cliff forest" (Cintrón and Rogers 1991). This area has a small camping facility used by tourists approximately 30% of the year, and contains some open zones appropriate for nesting.

Field data collection.—From 2003 to 2005 we captured female iguanas at the three study sites using nets. Most capture effort was concentrated during April, June–July, and October–November. For each captured iguana, we recorded the snout-vent length (SVL) to the nearest 1 mm, body mass (BM) to the nearest 0.1 kg, tail length (TL) and tail breaks to the nearest 1 mm. If sex was externally unclear, we determined it by probing (Schaeffer 1934; Dellinger and Von Hegel 1990). We marked iguanas externally with a unique combination of color beads attached to the dorsal crest (Rodda et al. 1988) and internally with a passive integrated transponder (PIT) tag (AVID®).

We collected data on nesting ecology using two methods. First, we captured a subset of 21 females (nine in Sardinera, eight in Pájaros, and four in the Lighthouse) prior to the nesting seasons and outfitted them with 15 g collar radio transmitters (model R1-2D, Holohil Systems, Ltd., Ontario, Canada) with a battery life expectancy of 18 months (Goodman et al. 2009). We radio-tracked these females before the nesting season (April–March) to obtain information about their space use (i.e., home range) and activity patterns not associated with mating or nesting. We monitored females daily in June (mating period) to attempt to observe copulations and then we tracked them

during the nesting season (July–August) to document their movement patterns while seeking nesting sites (nesting migrations). During each monitoring session, we recorded the female’s position using WAAS enabled Magellan GPS units, the activity in which the animal was engaged as defined by Wiewandt (1977; i.e., seeking, digging, filling, and nest guarding), and the time of day. Battery life of some radio transmitters allowed us to

monitor some females for more than one nesting season. The second method we used to study nesting ecology involved capturing “unknown” females that arrived at our focal nesting sites at Pájaros and Sardinera from elsewhere. We captured and processed (as described above) these females either when they were gravid and seeking a place for nesting, or immediately after oviposition and were back-filling or guarding their nests.

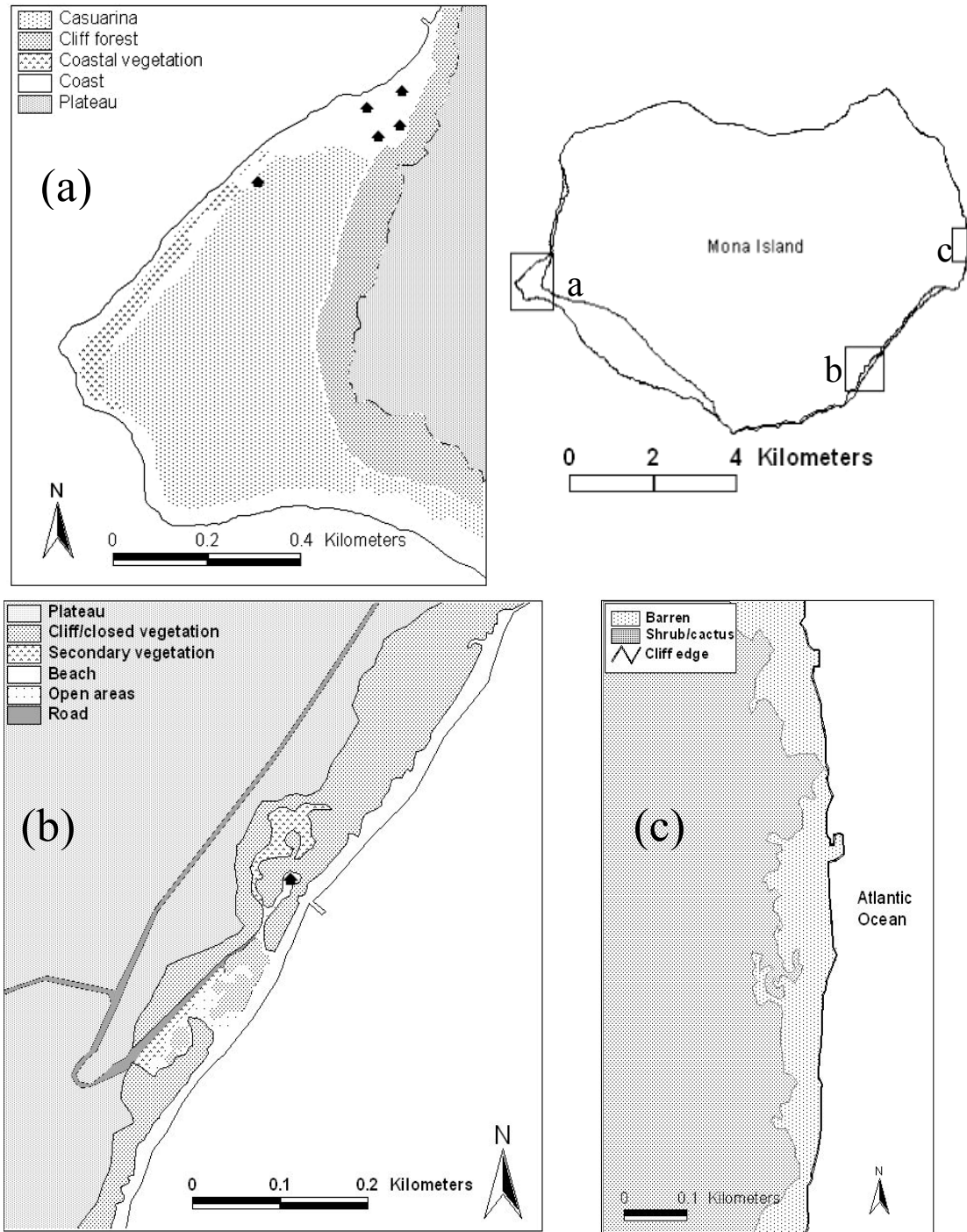


FIGURE 1. Schematic maps of Mona Island and the three study areas for *Cyclura stejnegeri*: (A) Sardinera [DRNA-PR facilities represented by up-right black arrows]; (B) Pájaros; and (C) the Lighthouse with major vegetation/terrain features shown for each.

To mark egg chamber locations, we drove away females engaged in filling the nest and we buried a piece of wood or rock tied to a nylon cord at the level of the first egg. The other end of the cord remained outside the nest, attached to a fixed item above the ground in a manner such that the nesting iguana could not remove it when she returned to continue back-filling and guarding the nest. This method allowed us to effectively locate nests during the hatching period in October–November and to document the hatching success of these nests.

During 2004 and 2005, we estimated the reproductive output of 15 gravid females that were seeking a nesting site or had just oviposited. We captured and measured (SVL, body mass) these females, and we counted and measured (length and width to the nearest 0.1 mm, mass to the nearest 0.1 g) their eggs within 24 h after being laid by temporarily removing them from the nest chambers. In addition, we noted egg aspect (collapsed, turgid) and numbered them with a marker pen. This protocol allowed us to estimate reproductive parameters and reproductive output following Iverson et al. (2004). Specifically, we calculated relative clutch size (RCS: the ratio of clutch size to body mass measured before nesting $\times 100$), relative egg mass (REM: the ratio of mean egg mass in the clutch to the female's body mass measured before nesting $\times 100$), and relative clutch mass (RCM: the ratio of total clutch mass to the female's body mass measured before nesting $\times 100$; Iverson et al. 2004). Sometimes, several iguanas construct nests within a small area, confounding nest chambers. To avoid this, we only used information from nests for which we were certain of the female's identity.

Approximately 75–78 days after nesting, when hatchling emergence was expected (Wiewandt 1977), we installed a circular aluminum fence (4 m diameter and 0.6 m height) using as the center point the estimated position of the nest chamber, to collect the hatchlings upon emergence. After 85 days we opened the nests using the nylon cord as a guide. If eggs were still inside of the nest, we refilled the nest, or we collected the individuals that had already hatched and left the remaining eggs buried. We removed and opened eggs that failed to complete the incubation process after 95 days of incubation to determine whether they contained embryos or were infertile (no visible embryo detected). We measured (SVL and tail length to the nearest 0.1 cm, body mass to the nearest 0.1 g) hatchlings obtained from each nest and determined sex by probing (Schaeffer 1934; Dellinger and Von Hegel 1990). In 2003 and 2004, we permanently marked 154 of the collected hatchlings with PIT tags placed in the lateral part of the tail, 3 cm behind the pelvic bone. Most of the PIT-tagged hatchlings were released into the wild after a month in captivity, but 30 individuals per year were retained in captivity at the Mona head-starting program facility.

In 2005 and 2006, we placed eight temperature data loggers (HOBO temp, Onset Computer Corporation, Bourne, Massachusetts, USA) each year in nest chambers. The data loggers were placed adjacent to the first eggs detected. In addition, we recorded environmental temperature at each site by placing temperature loggers 0.5 and 1.0 m above the ground near each nest, suspended in open areas exposed to direct sunlight.

During the 2006 hatching season (October–November), we conducted censuses every other day to record “escape holes” associated with nests (holes that hatchlings make to escape from the nest chamber) in all of the nesting areas in the southwestern coastal plain (including Sardinera) and in the small beaches located on the south and east sides of the island (sites not part of the three focal areas in this study). We identified potential nesting areas by inspecting satellite images (KONOS, 2 m pixel resolution, 2001) for open, vegetation-free sites followed by field corroboration of these areas. The sites surveyed comprised 74% of the total area available for nesting on the island, according to Haneke (1995).

Statistical analysis.—We made comparisons between reproductive parameters (clutch size and egg mass) only on data from Sardinera and Pájaros because the number of nests successfully monitored at the Lighthouse was low, and the number of eggs was sometimes impossible to measure in the Lighthouse area because nest chambers were located in deep rocky crevices. There were no differences in female size ($t = 0.91$, $P = 0.37$, $n = 29$), clutch size ($t = 1.92$, $P = 0.07$, $n = 26$), or hatchling morphometrics (SVL $t = -1.63$, $P = 0.11$, body mass $t = 1.23$, $P = 0.22$; $n = 34$ nests) between the Sardinera and Pájaros sites, so we pooled this information for all subsequent analyses. For females monitored for more than one year, we included only the first year's data on clutch size and egg morphometrics to avoid non-independent sampling. Means \pm one standard deviation (SD) are reported. We performed all statistical analyses using STATISTICA v5.5 (Kernel release 2000, StatSoft Inc., Tulsa, Oklahoma, USA) and we used $\alpha = 0.05$ to assign significance. For testing the directionality of a female's movements during the nesting period, we used the Rayleigh test (Batschelet 1981) as calculated in the Animal Movement extension analysis of ArcView v.3.2 (Hooge et al. 1999). For this analysis, we only included the locations recorded after radio-marked females moved out of the boundaries of their home ranges during the nesting season.

RESULTS

Mating activity and nesting frequency.—We observed four copulations of radio-collared females between 16 and 30 June, two in 2003, and two in 2004.

These females laid their eggs between 24 and 35 days (mean = 30 ± 5) after mating. The nesting seasons of 2004 and 2005 spanned from 5 July to 9 August, with a peak in nesting activity between 17 and 29 July (Fig. 2). Nesting females had a mean SVL = $48.5 \pm$ (SD) 4.4 cm (range, 34.4–57.7 cm; $n = 62$). The smallest nesting female detected (SVL of 34.4 cm, body mass of 2.3 kg) had been captive reared in the headstart facility for 2.7 years before release, and was 4.7 years old. Mid-size wild mature females (SVL < 45 cm) were scarce in the monitored areas, and when present they were very shy and avoided us. However, their relative rareness could also be because they are poorly represented in the population (e.g., see Fig. 3). The nine radio-collared or marked females resident at Pájaros or Sardinera that we monitored over two or more consecutive nesting seasons nested each year. However, of 25 non-resident females (i.e., females that probably lived on the plateau year-round and migrated for nesting) captured at the Pájaros nesting sites in 2004, only 18 (72%) were also detected nesting in 2005.

Nesting migrations and nest site fidelity.—Females were categorized into three groups based on their movements prior to nesting: (1) females that stayed in their home range and nested within it; (2) females that temporarily abandoned their usual home range but returned and nested within it; and (3) females that left their home range, returned, but left again to nest outside it.

Some of the females in this third category had areas that appeared suitable for nesting within their home ranges, but chose not to use them. Most females appeared to perform exploratory movements outside of their home ranges irrespective of where they nested (Table 1).

Radio-collared females nested in areas that were between 0 km (when females remained and nested inside their home ranges) to 930 m (mean = 279 ± 271 m, $n = 19$) from the center of their home ranges. However, actual movements taken to reach the final nesting site were variable and longer, with a maximum displacement of 12.8 km (mean = 2.4 ± 2.3 km, range = 0.3–12.8, $n = 21$). All females returned to their established home ranges after nesting, after having spent between 1 and 16 days (mean = 9 ± 9 days, $n = 18$) away.

Of the 11 radio-tracked females that we monitored for more than one nesting season, only four (two from the Lighthouse and two from Sardinera) moved in a specific direction to reach the same nesting spot used the previous year (all angle counts between 4–6, all angular concentration $R > 0.85$, all Rayleigh values $z > 4.2$, and all $P < 0.02$; $n = 4$). However, if the site was already occupied by another iguana, females started moving erratically. All other radio-tracked iguanas moved randomly, abandoning and returning to their home ranges at least once. The Rayleigh test of directionality failed to detect a specific bearing during the path (all angle counts between 4–9, all angular concentration $R > 0.23$, all Rayleigh values $z < 0.35$, and all $P > 0.27$; $n = 14$).

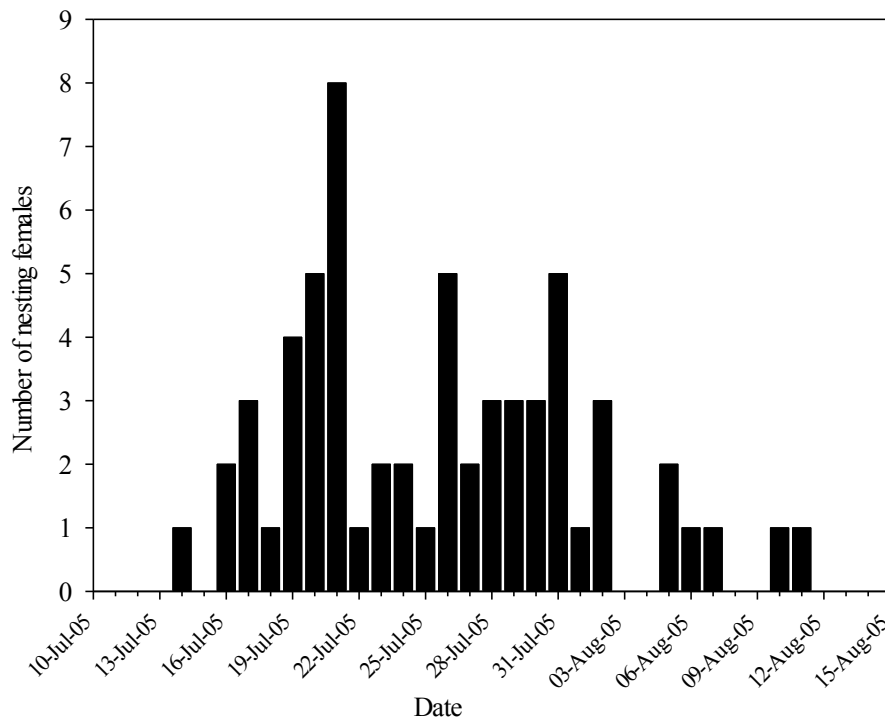


FIGURE 2. The number of nests of Mona Rhinoceros Iguanas recorded per day during the 2005 nesting season at Pájaros beach.

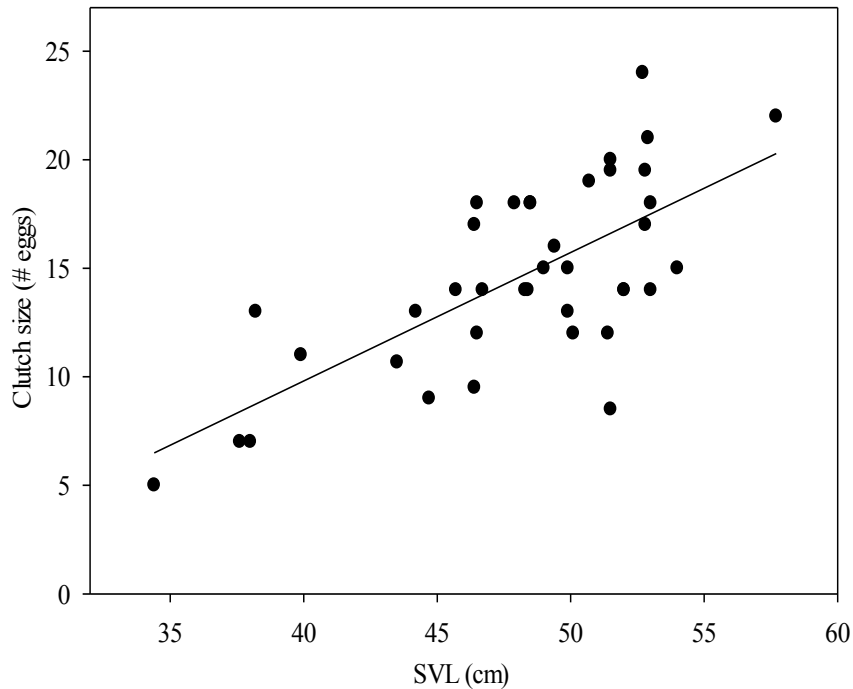


FIGURE 3. Relationship between female snout-vent length (SVL) and clutch size in the Mona Rhinoceros Iguana ($r^2 = 0.48$, $P < 0.001$, $n = 39$).

TABLE 1. Nest site availability and general movement patterns performed by Mona Rhinoceros Iguana females during the 2003–2005 nesting seasons. Note that although most of the females had potential nesting sites in their home range, most of them left and did not use those sites.

Behavior description	Radio-marked	Not radio-marked ¹
Never left the usual home range area and nested inside it.	5 (18.5%)	0 (n/a)
Left the usual home range but returned and nested inside it.	7 (25.9%)	6 (27.3%)
Left the home range, returned, and left again to nest outside of the usual home range.	15 (55.6%)	16 (72.7%)
% of females with available nest sites inside their home range.	19 (70.0%)	18 (80.0%)
Number of females.	27	22

¹Resident females in the study area that were never radio-collared but for which sporadic data were collected about their home range outside of the nesting season.

For females that we monitored more than one year (with or without a radio transmitter), nest site fidelity was variable. Thirteen (52%, $n = 25$) nested the second year within 7 m of their previous nest site, while the other 12 (48%, $n = 25$) nested in areas up to 400 m away. One of the females at the Lighthouse nested in the same spot (a limestone crevice) within her home range for three consecutive years.

Clutch size and egg size.—Clutch size (CS) varied from four to 24 eggs (mean = 14.1 ± 5.0 , $n = 61$; Table 2) and was positively related to female SVL ($r^2 = 0.48$, $P < 0.001$, $n = 39$; Fig. 3). Egg length (EL) averaged 76.4 ± 6.1 mm (range = 60.1–90.1, $n = 268$) and egg width (EW) 45.1 ± 3.1 mm (range = 35.4–

48.6, $n = 268$). Egg mass (EM) averaged 85.0 ± 16.6 g (range = 39.4–110.5, $n = 268$). EL and EW were positively correlated with egg mass ($r^2 = 0.61$, $P < 0.001$, $EM = 0.316(EL) + 49.16$, $n = 254$; and $r^2 = 0.42$, $P < 0.001$, $EM = 0.164(EW) + 31.225$, $n = 254$). In addition, EL and EW were positively correlated with each other ($r^2 = 0.21$, $EL = 0.73(EW) + 0.723$, $P = 0.001$, $n = 254$). Egg length was negatively correlated with female SVL ($r^2 = 0.31$, $P = 0.02$, $n = 17$; Fig. 4), although EW and EM were not ($r^2 = 0.41$, $P = 0.43$, $n = 17$; $r^2 = 0.15$, $P = 0.12$, $n = 17$, respectively; Fig. 4). Egg elongation (Mean clutch EL / mean clutch EW) averaged 1.68 ± 0.09 (range = 1.46–1.85, $n = 17$) and was not correlated with female SVL ($r^2 = 0.22$, $P > 0.40$, $n = 17$).

We found an atypical nest from a female (SVL = 54.1 cm) that contained eggs that were unusually small (EL = 60.1 ± 4.4 mm; EW = 41.1 ± 3.6 mm) and much lighter in mass (53.8 ± 12.2 g) compared with the average egg size. This nest had a hatching success of 64.7% (29.4% were infertile eggs and 5.9% embryos failed to complete development). Hatchlings from this nest were smaller in size (SVL mean = 10.4 ± 0.2 cm) and much lighter (body mass = 47.2 ± 3.6 g) than hatchlings that emerged from normal eggs (SVL mean = 11.6 ± 0.4 cm; hatchling body mass = 69.4 ± 0.1 g).

Reproductive output parameters.—Clutch mass (CM), which ranged from 470 to 1,700 g ($1,190 \pm 290$ g), was not significantly related to female size ($r^2 = 0.01$, $P = 0.07$, $n = 15$). Relative egg mass (REM) averaged 1.68 ± 0.51 (range = 0.59–2.44, $n = 15$) and was negatively related to female SVL ($r^2 = 0.39$, $P < 0.008$, $n = 15$) and clutch size ($r^2 = 0.70$, $P = 0.001$, $n = 14$). Relative clutch size (RCS) averaged 0.26 ± 0.04 (range = 0.18–0.35) and was not related to female size ($r^2 = 0.01$, $P = 0.67$, $n = 15$). Relative clutch mass (RCM) averaged 22.56 ± 5.47 (range = 7.16–29.29) and was not related to female size ($r^2 = 0.09$, $P = 0.23$, $n = 15$).

Incubation.—Incubation period (to emergence) averaged 82.7 ± 4.1 days (range = 74–93) and did not vary significantly among years (2003–2005; $F_{2,41} = 54$,

$P < 0.59$). We obtained only nine data sets (one Lighthouse, three in Pájaros, three in Sardinera, and two environmental) for temperature profiles during the incubation period. Mean temperatures in nest chambers from two nests in Pájaros and Sardinera in 2005 were $32.8 \pm 1.6^\circ\text{C}$ (maximum range = 25.9–36.5; Fig. 5A, 5B). The lowest temperatures recorded during the last four weeks of the incubation period were associated with heavy rains and cold days, with little sun that caused nest temperatures to drop. Temperatures from a nest located in a limestone crevice at the Lighthouse averaged $32.6 \pm 2.0^\circ\text{C}$ (range = 27.1–34.8; Fig. 5C) and were similar to temperatures in sand nests. However, hatching success for this nest was 0% due to flooding of the chamber that killed all embryos at a very late stage of development.

In 2006, temperatures from three data loggers were lower ($30.2 \pm 0.8^\circ\text{C}$, maximum range = 26.7–32.2) than in 2005. Two nests in 2006 always had temperatures above the mean air temperature during the incubation period (Fig. 5E, 5F), but one nest exhibited the lowest nest chamber temperature recorded, averaging $28.8 \pm 1.1^\circ\text{C}$ (range = 26.7–31.4). This nest was in a locality that experienced only between four and six hours of sun exposure daily (Fig. 5D). Despite the low solar exposure, hatching success was 79.2% in a clutch of 24 eggs, and was the longest incubation period recorded during the study (93 days).

TABLE 2. Comparison of nesting ecology parameters for the Mona Rhinoceros Iguana results from Wiewandt (1977) and this study.

Attribute	Wiewandt 1977	This study
Nesting period	Two weeks in July (most in a week); Earliest nesting date: July 25; Latest nesting date: 1 August.	Four weeks (peak between 18–30 July); Earliest nesting date: July 5; Latest nesting date: 10 August.
Nesting frequency	Indirect evidence that females nest every year (based on appearance of gravid females).	Females nest every year.
Females migrations	Reported up to 6.5 km. No further details given.	Described in detail (see text).
Nest architecture	Length: 1.1 m ($n = 7$, range = 0.6–1.5 m); Width: 21 x 15 cm; Depth: 54 cm ($n = 31$, range = 30–76).	Not documented.
Clutch parameters	Mean clutch size = 12, range = 5–12, $n = 37$.	Mean clutch size = 14.1 ± 5.0 , range = 4–24, $n = 61$.
Egg morphology	Mean length = 78 mm, range = 74–82; Mean width = 51 mm, range = 46–56; Mean mass = 88 g, range = 82–93; $n = 18$.	Mean length = 76.4 ± 6.1 mm, range = 60.1–90.1; Mean width = 45.1 ± 3.1 mm, range = 35.4–48.6; Mean mass = 85.0 ± 16.6 g, range = 39.4–110.5; $n = 268$.
Incubation temperatures	29–31°C. Two days monitoring.	2005: Mean = 32.8°C, range = 25.9–36.5; 2006: Mean = 30.2°C, range = 26.7–32.2.
Incubation period	Mean 83 days, range = 78–89 days, $n = 8$.	Mean 82.7 ± 4.1 days, range = 74–93, $n = 43$.
Hatching success	79% ($n = 451$ eggs)	Mean = $75.9 \pm 34.4\%$, range = 0–100, $n = 860$ eggs; 61 clutches (multi-year: 2003–2006).
Hatchling morphology	Mean SVL = 11.9 ± 0.5 cm, range = 10.5–12.7; Mean body mass = 70 g, range = 60–92; $n = 65$ hatchlings.	Mean SVL = 11.6 ± 0.5 cm, range = 10.0–12.9; Mean body mass = 68.9 ± 9.6 g, range = 41.6–97.2; $n = 423$ hatchlings from 36 nests; sex ratio 1:1.

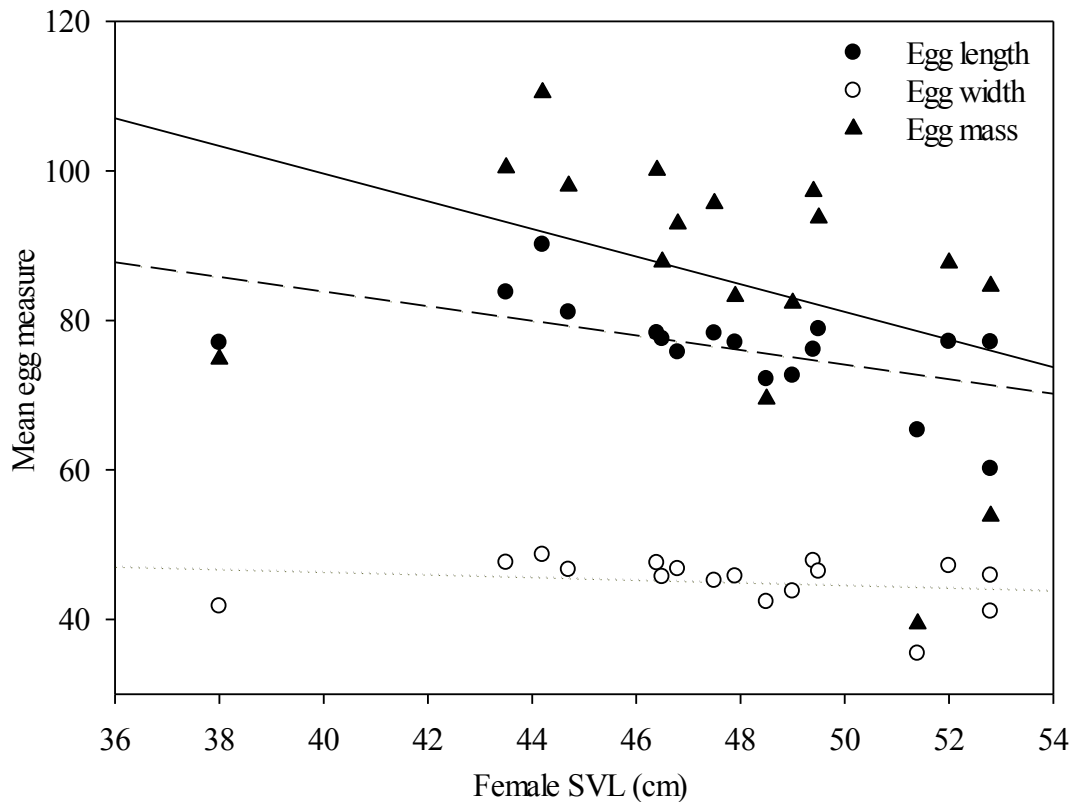


FIGURE 4. Relationship between female snout-vent length (SVL) and mean egg length, width, and egg mass in the Mona Rhinoceros Iguana. Mean egg length is measured in mm (solid circles), mean egg width measured in mm (open circles), and egg mass measured in g (triangles). Only egg length was negatively correlated with female SVL ($r^2 = 0.31$, $P = 0.02$, $n = 17$).

Hatching success.—Overall hatching success for the four years 2003 to 2006 fluctuated from 0 to 100% (mean = 75.9 ± 34.4 , $n = 61$). Neither hatching success nor the proportion of infertile eggs was related to female SVL ($r^2 = 0.11$, $P = 0.11$, $n = 22$; $r^2 = 0.11$, $P = 0.13$, $n = 22$; respectively). Hatching success within nests varied from 0–100% in 2004 and 2005, but in 2003 it varied from 40–100% and in 2006 from 70–100%. On average, the percentage of infertile eggs per nest was $8.6 \pm 18.5\%$ (range = 0–100%, $n = 61$) and the percentage of embryos that failed to complete development was $16.0 \pm 31.8\%$ (range = 0–100%, $n = 61$). Nests with zero hatching success and with embryos that failed to develop were nests that experienced chamber inundation due to heavy rains in 2004 and 2005. All four of these nests were from the Lighthouse area and they were located in limestone crevices. Of all the nests at the three study sites, feral pigs (*Sus scrofa*) depredated only one. This nest was located in a small depression (2 m in diameter) filled with soil in the Lighthouse area and the bottom of the egg chamber was only 25 cm below the surface.

Hatching morphometrics.—Hatchling SVL averaged 11.6 ± 0.5 cm and body mass averaged 68.9 ± 9.6 g ($n = 423$). There was a positive relationship between mean egg mass and mean hatchling mass per nest ($r^2 = 0.94$, $n = 8$, $P = 0.000057$). In addition, there was a positive relationship between mean egg length and mean hatchling SVL per nest ($r^2 = 0.79$, $n = 8$, $P = 0.002$). We also found a positive relationship between mean egg mass and hatchling SVL per nest ($r^2 = 0.91$, $n = 8$, $P = 0.0002$). Neither hatchling SVL nor body mass were related to the SVL of the female that laid them ($r^2 = 0.14$, $P = 0.26$, $n = 23$; $r^2 = 0.05$, $P = 0.49$, $n = 23$). The sex ratio of all hatchlings collected was not significantly different from 1:1 ($\chi^2 = 0.02$, $P = 0.88$, $n = 403$ hatchlings). Overall sex ratio in each clutch also did not differ significantly from 1:1 (all $\chi^2 < 0.25$, $P > 0.08$, $n = 22$).

Nest abundance in the coastal nesting sites.—The escape-hole surveys we conducted in 2006 yielded 680 nests along 8.6 ha of the southwestern coastal plain,

which included Pájaros beach and other small beaches in the south portion of the island, and resulted in a density of 0.007 nests/m². Eleven sites with a total area of 0.5 ha within the larger 8.6 ha monitored area exhibited nest densities that were much higher, averaging 0.107 ± 0.064 nests/m² (range = 0.026–0.232). Some of these sites correspond to managed areas within the *Casuarina* matrix that were cleared of vegetation, while others

correspond to natural, undisturbed nesting sites. We found no differences in nest densities between the high-density managed and natural nesting sites ($U = 12$, $z = -0.55$, $P = 0.58$, $n = 11$). We found 49% of the 680 nests with escape-holes in these 11 locations, despite that they only comprised 5.8% of the surveyed area. The other 51% of the nests we located in the remaining 94.2% of the surveyed area.

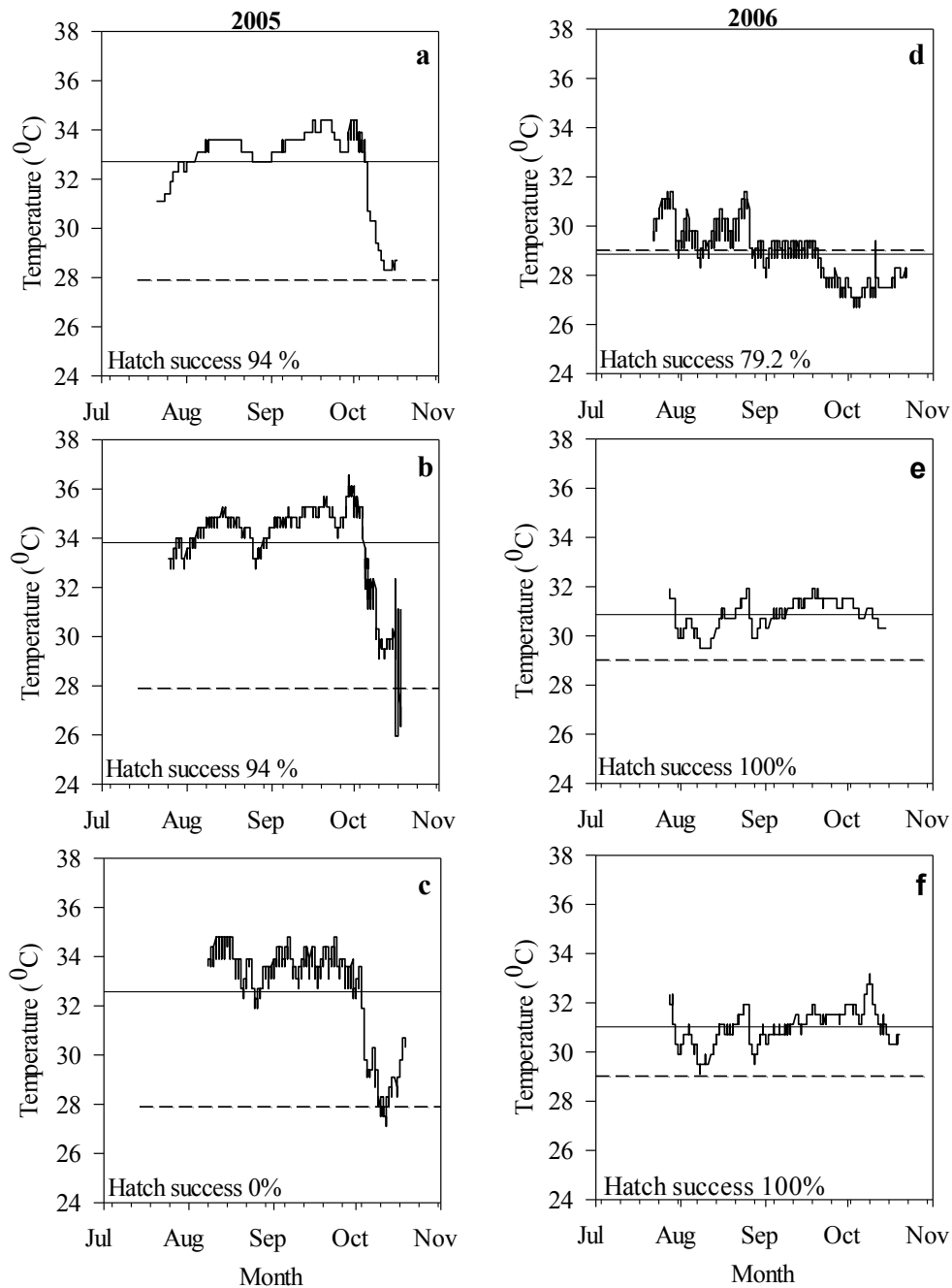


FIGURE 5. Nest chamber temperature profiles and hatching success of six nests for Mona Rhinoceros Iguanas monitored in 2005 or 2006. Dashed line represents the mean environmental temperature 0.5 m above the ground in an adjacent sunny and sandy exposed area during the incubation period. For more details see Results section. Horizontal solid lines are means across entire incubation period.

DISCUSSION

Wiewandt (1977) was the first to document the basic aspects of the nesting ecology of the Mona Rhinoceros Iguana. Wiewandt, however, did not capture iguanas, particularly breeding females, to avoid disrupting their nesting behavior. Thus, his findings were based on direct observations of aspects such as nesting phenology, clutch size, egg size, and hatch timing. In general, the major differences between Wiewandt's data and ours are for nesting period and clutch size (Table 2). Wiewandt recorded a nesting period of only two weeks in July, while we found that nesting can take place over a period of four weeks. Wiewandt measured a mean clutch size of 12 ± 3.9 eggs (range = 5–19), which is significantly lower than the mean clutch size of 14.1 ± 5.0 eggs (range = 4–24) we found in this study ($t = 2.23$, $P = 0.028$, $n = 98$). In addition, hatching success reported by Wiewandt (1977) in undisturbed nests was 79%, whereas in this study it was 75.9% over our four-year study period (Table 2).

Mating and nesting period.—Despite the limited number of mating observations, ours is the first study to record the time elapsed between mating and nesting for the Mona Rhinoceros Iguana (i.e., 30 ± 5 days). Although we cannot be sure whether the matings resulted in fertilizations of eggs and/or were the only copulation those females attained, females laid eggs a month after copulating, which is the expectation based on the mating-nesting timing for the species and has also been considered typical among *Cyclura* (Wiewandt 1982; Iverson et al. 2004).

For iguanas, the major determinants of nesting phenology (mating, nesting, and hatching) are related to climate (i.e., temperature and moisture). Climate may have strong effects on the seasonal activity patterns, incubation duration, hatchling emergence, and food abundance. Typically, iguanid species lay eggs during the period in which ambient temperatures are closer to the optimal incubation temperatures, and the hatch time coincides with the period of highest food availability for the hatchlings (Wiewandt 1982).

The only previous information on nesting frequency for this genus comes from *C. cyclura inornata* (Iverson et al. 2004). In that species, nesting frequency appears to be related to female size, with large females nesting on an annual basis but younger females only nesting every two or three years. In this study, we also found that large females nest on an annual basis, but the general lack of young adults in Mona precludes definitive conclusions about nesting frequency by smaller females. It has been suggested that nesting frequency in iguanines follows a latitudinal gradient (Wiewandt 1982). Species occurring at high latitudes have to confront a higher degree of environmental uncertainty that may compromise optimal

female conditions for successful reproduction (i.e., via low food availability prior to the reproductive season), and for at least some other species reproducing on an annual basis is not the rule, as occurs in *Sauromalus* from the Gulf of Mexico (Wiewandt 1982; Abts 1987).

In this study, we documented a 4.7 year-old headstarted female to have the smallest size (34.4 cm SVL and 2.3 kg) reported thus far for a nesting female in her first reproductive season, similar to captive female *C. cornuta* in the Dominican Republic (Ottenwalder 2000). Previously, the smallest breeding female had been an individual with a SVL of 38.0 cm and 2.1 kg, estimated to be six or seven years old (Wiewandt 1977). Captive-reared Mona Rhinoceros Iguanas grow at similar rates as their wild mid-sized counterparts (Pérez-Buitrago et al. 2008), so we believe that it is likely that wild females also mature at four or five years of age.

Nesting migrations.—Natal homing, the phenomenon by which a female returns to nest in the place where she hatched, has been widely documented for many reptiles, including marine and freshwater turtles (Bowen et al. 1994; Freedberg et al. 2005), some crocodylians, and some lizards (Hein and Whitaker 1997; Jenssen 2002; Russell et al. 2005). In theory, natural selection favors this behavior because it allows a female to nest in locations that have been previously successful for incubation (Freedberg and Wade 2001), but it requires the environment to be predictable and a net gain in fitness when natal homing is exhibited.

It is unclear if iguanas show natal homing, although nesting migrations from home ranges to the nest sites have been documented (see Iverson et al. 2004 and references therein). Reported distances traveled fluctuated between 30 m in *C. cyclura inornata* (Iverson et al. 2004) and 15 km in *Conolophus subcristatus* (Werner 1982) and appear to be dependent on island size. For the Mona Rhinoceros Iguana, the previous record for linear distance traveled by a female iguana was 6.5 km, based on a casual observation of a marked female (Wiewandt 1977). We found a large variation in the linear distances traveled by females before nesting (mean = 279 ± 271 m, range = 0–930 m, $n = 19$), and also in the length of the erratic and tortuous paths of females, which reached a maximum value of 12.8 km (mean = 2.4 ± 2.1 km). In this study, most females left (even those with available nesting sites in their home ranges), if only temporarily, shifting directions many times and passing by many potential nesting sites before ovipositing either within their home ranges or in other nesting areas outside their home ranges. Ignoring suitable nesting sites to nest far away from established centers of activity has been interpreted as a “sign” of natal homing (Wiewandt 1982). However, the irregular paths followed by most female Mona Rhinoceros Iguanas are not supportive of the natal homing hypothesis, which predicts that females would

move in a direct manner, such as in a straight line when the terrain allows. Specificity in travel directions has been documented for other reptile species showing natal homing, including turtles (Arens et al. 2003; Nagelkerken et al. 2003), and also seems to be the case for Galápagos Land Iguanas (*Conolophus subcristatus*), which migrate up to 10 km to an area located in a volcano caldera that appears to have the best conditions for nesting/incubation on the island (Werner 1983). Most females in this study moved erratically and only four radio-tracked females followed specific bearings. Additional indirect evidence of the lack of natal homing for the Mona Rhinoceros Iguana comes from captive-raised females that did not nest in the places where they were released or where they were hatched (García et al. 2007), as well as their erratic movement patterns, which differed from the constant bearings followed by hatchlings during the natal dispersal phase (Pérez-Buitrago and Sabat 2007).

Our observations suggest a high degree of behavioral plasticity, including the ability to navigate in a specific direction, but also the capacity to explore unfamiliar zones to find a suitable nesting site and then return to their usual centers of activity. The ability to find a suitable nesting site would be strongly selected for iguanas on Mona Island, where most sandy communal nesting sites are confined to the coastal plain, the “bajuras”, and to a much lower extent, very discrete crevices with soil on the plateau. In addition, the strong female-female competition in some communal nesting areas would be an additional factor prompting the development of optimal mechanisms for navigation that allow females to find less crowded nesting sites.

We also detected strong evidence of site fidelity on a coarse scale (i.e., regional, such as the southwestern beach) by re-capturing 72% of non-resident iguanas over two consecutive years on Pájaros beach. Once an iguana finds an optimal nesting beach she appears to be able to return to it in successive years. This is important for iguanas living in the interior of the island, far from the nesting areas located on the coastal plain or the “bajuras”. However, at a finer scale (within a local site), our data suggest low nest site fidelity, which perhaps only occurs incidentally, and/or is dependent on competition with other gravid/spent females. Competition may also be the reason why some females change nesting sites, particularly for young females, as was observed for one young female that traveled the longest distance (12.8 km; Fig. 6C). This female moved through many communal nesting areas where a high density of females could have prevented her from successfully acquiring a nesting site. For larger, stronger, more experienced females, tolerating competition in densely populated nesting aggregations may be related to benefits such as the soft sandy soils (due to the use of these sites in previous years) and vegetation-free areas that may facilitate digging and assure optimal incubation temperatures for eggs (Wiewandt 1982).

At the rocky Lighthouse study area, where good nesting sites were scarce and scattered, we detected females laying eggs inside their home ranges in limestone crevices where sufficient accumulation of reddish clay soil made nesting possible. One of these females used the same crevice within its home range for three consecutive years with an overall hatching success of 80%, while others migrated away from their usual home ranges following specific paths first, but eventually switching directions many times, perhaps because other females were already nesting there.

The extent of the importance of nesting in limestone crevices for the population as a whole is unclear, but should be considered in future studies. Moreover, hatching successes at these sites appeared to be highly dependent on the amount of rain during the incubation period, since flooding of the nest chamber can result in the embryo death. However, there are difficulties in identifying and gaining access to nests in limestone crevices for monitoring.

Clutch size and egg size.—We found that Mona Rhinoceros Iguanas laid a mean of 14 eggs, similar to what has been reported for *C. cornuta cornuta* (in captivity) from the Dominican Republic, but higher than the 12 eggs/clutch previously reported for the species (Wiewandt 1977). The discrepancy between Wiewandt’s (1977) data and our values may be due to the fact that in his nest surveys, he detected four nests with only six eggs and he did not detect any nests with as many eggs as we did (24 eggs/clutch). The difference in clutch size is likely due to the difference in body size between the studies. As documented for reptiles in general, larger individuals/species are generally able to produce larger clutches. We confirmed this pattern, one that also holds true across other species/populations of *Cyclura* (Iverson et al. 2004 and references therein). *Cyclura pinguis* and *C. stejnegeri* are the largest members of the genus and also have the largest clutch sizes, a character that has been considered ancestral (Iverson et al. 2004) based upon the currently accepted phylogeny for *Cyclura* iguanas (Malone et al. 2000).

Within iguanine species, egg mass (EM) is generally not related to female size as found in this study, although there is a reported positive relationship across species of *Cyclura* (Iverson et al. 2004). However, EM was highly variable on Mona Island with two females laying very small eggs. One case involved the smallest female detected in this study, whereas the other was a very old (perhaps unhealthy) female. For egg length (EL), we found that smaller females tended to produce longer eggs, a trait that allows small females (possibly constrained by a small pelvic opening) to produce eggs with a large mass (Iverson et al. 2004). However, egg elongation (Mean clutch EL / mean clutch EW) was not correlated with female size, which contrasted with what

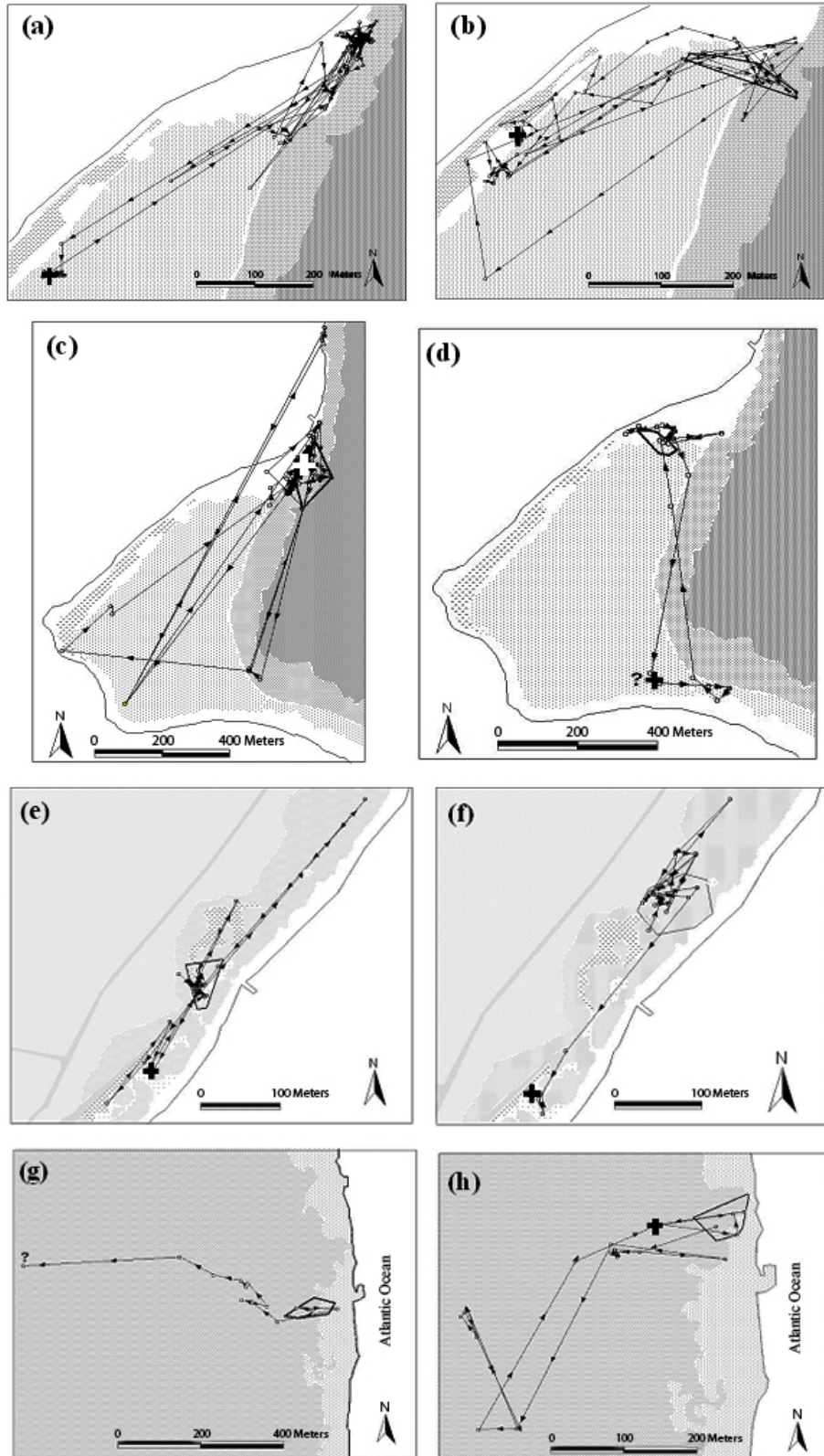


FIGURE 6. Nesting movements of four female Mona Rhinoceros Iguanas. Nesting locations were recorded at Sardinera (A, B, C, D), two at Pájaros (E, F), and two at the Lighthouse (G, H). Thick line polygons represent the home ranges of these females during the non-reproductive period. Nest sites, or suspected nest locations, are represented by a white (C) or black cross. Map legends for each study site are in Figure 1. The radio signal of the female represented in map G was lost at the position indicated by the question mark. All maps except F and G show the movements back to the home range after nesting.

was found in the smaller-sized *Cyclura cyclura inornata* (Iverson et al. 2004). *C. cyclura inornata* begins laying eggs at a SVL of only 26–27 cm and a body mass of 0.75 kg, while the Mona Rhinoceros Iguana first nests at 34.4 cm SVL and 2.3 kg. The smaller size and correspondingly constrained pelvic opening of *C. cyclura inornata* may explain why Iverson et al. (2004) found a negative relationship between egg elongation and female size, a relationship that does not exist in the Mona Rhinoceros Iguana.

Relative egg mass (REM) was lower ($1.68 \pm 0.50\%$) in this study than previously inferred (2.21%) from Wiewandt's data by Iverson et al. (2004). The discrepancy may be a result of the smaller clutch size reported by Wiewandt and the smaller egg mass data used for estimating REM by Iverson et al. (2004). The REM value we report here for the Mona Rhinoceros Iguana is the lowest for any *Cyclura* species. Given that the Mona Rhinoceros Iguana is one of the largest members of the genus, this suggests that having a large body size may result in a reduction in reproductive output per individual offspring. On the other hand, the lack of relationship between RCM and body size may imply that females are allocating a constant proportion of energy to their clutches, as reported for *C. cyclura inornata* (Iverson et al. 2004).

Consistent with reported patterns in lizards, including other iguanas and *Cyclura* specifically, we found that hatchling size (SVL and body mass) was positively related to egg size (Boylan 1984; Van Marken Lichtenbelt and Albers 1993; Alberts et al. 1997; Iverson et al. 2004; Knapp et al. 2006). The lack of a relationship between hatchling size and female size that we found has been previously documented for other *Cyclura* (Iverson et al. 2004; Knapp et al. 2006). The relationship between hatchling and egg size is in accordance with optimal egg size theory that postulates that both egg and hatchling sizes are maximized at a point at which there is not a reduction in fitness caused by a reduction in offspring number (Congdon and Gibbons 1987). Thus, hatchling size appears to be more "resilient" to environmental factors than other reproductive parameters such as clutch size and egg size. This can vary among populations of a single species across different environmental settings, including island size (Iverson et al. 2004; Knapp et al. 2006).

Incubation temperatures.—Despite the fact that the mean incubation temperature we report is similar to the previous records of incubation temperatures for other *Cyclura* (*C. cyclura inornata*: 31.4° C, Iverson et al. 2004; *C. cyclura cyclura*: 32.8° C, Knapp 2000; and *C. ricordii*: 30–31° C, Ottenwalder 2000), we found larger temperature fluctuations than previously reported – up to 9° C in one monitored nest and up to 6° C in others. This large variation was caused by consecutive

rainy or cloudy days that lowered nest chamber temperatures during the last weeks of the incubation period. Interestingly, despite these fluctuations, hatching success was high in the monitored nests (except in one case in which all full-term embryos died by drowning). This suggests that fertilized eggs are highly resilient to severe drops in temperature late in the incubation period and fluctuations in oxygen in nest chambers (Iverson et al. 2004). This is further corroborated by a nest (Fig. 5D) which exhibited mean temperatures that were lower than the environmental temperature through the incubation period, and only had temperatures higher than 30° C for short periods. In addition, the temperature recorded in the only nest located in a limestone crevice that was monitored did not differ from nests located in the more typical spots with a sandy substrate.

Hatching success.—The overall hatching success rate across the three years (76%) was similar to that reported by Wiewandt (1977) of 79% and other *Cyclura* species such as *C. carinata* (78%, Iverson 1979), *C. collei* (76%, Vogel 1994), *C. cyclura inornata* (81%, Iverson et al. 2004), *C. nubila caymanensis* (92%, Gerber 2000a), *C. nubila nubila* (85%, Christian 1986), and *C. pinguis* (84%, Gerber 2000b), as well as other island iguanid species such as *Conolophus* (87%, Snell and Tracy 1985) and *Amblyrhynchus* (88%, Rauch 1988). Complete failure of fertilized eggs to develop occurred only at the Lighthouse, and was the result of either flooding due to heavy rains, or predation by pigs (one nest). Neither of these factors caused mortality at the other two study sites located on the coast. Obviously, the sandy coastal plain offers more suitable areas for nesting, and if heavy rains occur, sand allows water to drain rapidly, preventing anoxic or high CO₂ conditions in the egg chamber. On the other hand, Wiewandt (1977) observed that hatching success in iguana nests could be dramatically affected by pig predation and hypothesized that the amount of rain in the 3–4 months before nesting could be a factor for the inter-annual variation in egg loss to pigs or flooding, which varied from 0–100% across four monitored localities. It is possible that years with heavy rains increase vegetation resources for pigs and thus reduces levels of egg predation during those years (Wiewandt 1977). However, pig access is restricted at Pájaros and Sardinera. At Pájaros, the beach is limited by vertical cliffs and has only one access trail that is used daily by the DRNA-PR staff and periodically by tourists, probably rendering the area unattractive to feral pigs. At Sardinera, and along the southwest coastal plain, the DRNA-PR installed a fence in 1985 (following one of the major recommendations made by Wiewandt 1977) that is still maintained to exclude pigs from the sandy areas that run parallel to the beach to reduce pig predation on turtle and iguana nests. Even though it has not been formally quantified, this

management action appears to have had a very strong positive impact on hatching success for turtles (Carlos Diez, pers. comm.) and as we report here, also for iguanas.

Nest abundance at coastal nesting sites.—The number of nests detected in the southwestern coastal plain and other beaches in 2006 was 680. In 1994, Haneke (1995) surveyed iguana nests in the same coastal localities and only found 159 nests with escape holes. In part, we attribute this dramatic increase in the number of nests between 1994 and 2006 to the management initiative conducted by the DRNA-PR in 1992 which cleared three 50m x 50m areas within the *Casuarina* matrix to increase the availability of suitable nesting areas. Other factors that may have contributed to the increase in nests in the coastal areas are that in 1998 the island was hit by Hurricane Georges which downed many *Casuarina* trees bordering the pine plantation, and also in 1998 the DRNA-PR initiated a non-systematic initiative of killing *Casuarina* trees in the same areas. These two factors have resulted in the creation of new open areas appropriate for nesting. We have shown that most females moved in erratic paths and thus they were probably able to discover these new areas and use them. We speculate that before these “new” nests sites were available, iguanas were forced to nest in suboptimal sites, such as the soils covered by *Casuarina* leaves or in the rocky sites on the plateau.

Wiewandt (1977) suggested that of the total surface area of Mona Island, only 1% (55.4 ha) was suitable for iguanas to nest. Of this area, only about 9 ha are located in the coastal portion of the island, which implies that most of the available nesting areas are located in the plateau depressions. However, hatching success in the plateau depressions is likely to be very low because dry years, although optimal for egg development, may induce high predation rates by pigs due to low resource abundance, whereas wet years, although bad for eggs due to the risk of nests flooding, apparently have low levels of pig predation (Wiewandt 1977). Nests in the sandy soils of the coastal plain do not flood even during wet years. Also, since 1982 the southwestern coastal plain has been fenced to prevent pig incursions, and the other beaches are not very accessible to pigs because vertical cliffs surround them. Thus, the coastal nesting sites account for most of the yearly hatchling production. Haneke (1995) suggested that in 1994 the bulk of the hatchlings were produced in the coastal sites and for that year, it represented the total hatchling production, since all 110 nests in the plateau depressions were completely depredated by pigs. The four-fold increase in the number of nests in the coastal area, followed by an increase in the area available for nesting, strongly suggests that good nest sites are limited on Mona and may therefore have been a potential factor constraining population growth. It also implies that removing the *Casuarina* plantation will

increase the number of iguanas that are able to nest in optimal sites and result in an increase in the overall reproductive output of the population.

Acknowledgments.—This research was funded by the Center for Applied Tropical Ecology and Conservation (grant NSF HRD-0206200) of the University of Puerto Rico, Rio Piedras Campus. Logistic support and research permits were provided by the Natural Resources Department of Puerto Rico (DRNA-PR) and we are particularly grateful to Alberto Álvarez, Carlos Diez, Miguel García, and the staff of the Endangered Species Division of the DRNA-PR. The DRNA-PR Mona Island staff (rangers, biologists, and technicians) helped us in many ways while conducting this project. Particularly, we are very grateful to Gaspar Pons, Miguel Nieves, Miltón Pérez, José Jimenez, Miguel Bonet, and Reynaldo Pagan. Many people helped us in the field, mainly Alberto Álvarez, Johanna Delgado, John Bendon, Stephany Boven, Raissa Menendez, Maria José Andrade, Jessica Castro, Carlos Toledo, Marcela Zalamea, Marina Rujas, Manuel Correa, and Keysa Rosas. We also want to thank Pilar Angulo-Sandoval and Brian C. Bock for reviewing early versions of this manuscript.

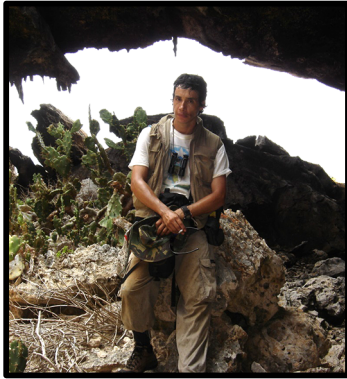
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