

THE NESTING ECOLOGY OF THE ALLEN CAYS ROCK IGUANA, *CYCLURA CYCHLURA INORNATA* IN THE BAHAMAS

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ABSTRACT: The nesting ecology of the Allen Cays rock iguana was studied on Leaf Cay and Southwest Allen's Cay (= U Cay) in the northern Exuma Islands, Bahamas, during 2001 and 2002. Mating occurred in mid-May, and females migrated 30–173 m to potential nest sites in mid to late June. Females often abandoned initial attempts at digging nest burrows, and average time from initiation of the final burrow to completion of a covered nest was six days. At least some females completely buried themselves within the burrow during the final stages of burrow construction and oviposition. Females defended the burrow site during the entire time of construction, and most continued that defense for at least three to four weeks after nest completion. Nests were completed between mid-June and mid-July, but for unknown reasons timing was seven days earlier on U Cay than on Leaf Cay. Nest burrows averaged 149 cm in length and terminal nest chambers usually angled off the main burrow. Depth to the bottom of the egg chamber averaged 28 cm, and was inversely correlated with shadiness of the site, suggesting that females may select depths with preferred temperatures (mean, 31.4 C in this study). Overall, only about one in three females nested each year, although nesting frequency increased with female size such that the largest females usually nest annually. Nest fidelity was common, despite the potential for observer effects; seven of 13 two-year nesters placed nests within 0.7 m of that constructed the previous year.

Nesting females averaged 32 cm snout-vent length (SVL) and 1336 g body mass, and larger, older females nested earlier than smaller, younger ones. Sexual maturity is reached at 26–27 cm SVL, about 750 g body mass, and twelve years of age (nearly twice as old as any previously studied lizard). Longevity of females apparently exceeds 40 years. Clutch size ranged from 1–10 eggs (mean 4.6) and was correlated with female body size and age. Eggs averaged 66 mm in length, 35 mm in width, and 49 g in mass. Egg mass was not correlated with female body size, although egg length was negatively correlated, and egg width was positively correlated with female size. The production of elongate eggs in the smaller females allowed them to invest the same total mass in each egg as a larger female, while being constrained by the limits of the pelvic opening. No trade-off existed between standardized clutch size versus egg size. Relative clutch mass (clutch mass/gravid female body mass × 100) averaged 16.5 and did not vary with female size or age. Hatching apparently occurs in late September and early October after about 80–85 days incubation, with emergence within just a few days. Hatchlings averaged 9.5 cm SVL and 33 g body mass. Survivorship to emergence was 78.9%, and was inversely correlated with soil moisture.

The reproductive ecology of other iguanids (*sensu strictu*) is reviewed for comparison with that of the Allen Cays rock iguana. Comparisons of these data with those available for other rock iguanas of the genus *Cyclura* suggest that colonization of smaller islands has produced reductions in adult female body size, clutch size, clutch mass, and relative clutch mass, but no change in egg or hatchling mass. Because this pattern is also demonstrated by a population of Cuban iguanas introduced to a small island only 40 years ago, it may primarily be a proximal response to decreased resource availability and/or physiological processability on small islands rather than an evolved response to reduced predation rates or other factors affecting survivorship.

Key words: Iguana; Nesting; Nest defense; Nest fidelity; Nest burrows; Egg size; Clutch size; Survivorship; Exuma Islands.

THE LIZARD FAMILY IGUANIDAE includes eight genera (~35 species) of large, herbivorous iguanas distributed primarily in the New World tropics and subtropics, but also the Fiji Islands (Etheridge, 1982; Pough et al., 1998). The West Indian rock iguanas of the genus *Cyclura* include many of the largest, most

impressive, and most endangered lizards in the world. Only eight species of rock iguanas still exist (APPENDIX); populations on Puerto Rico and St. Thomas (Miller, 1918; Barbour, 1919; Pregill, 1981) were apparently extirpated by pre-Columbian humans and that on Navassa Island (Thomas, 1966; Powell, 1999) by post-Columbians. Remaining species have relict distributions on Caribbean Islands and all are considered Vulnerable to Extinction,

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Endangered, or Critically Endangered (Alberts, 2000). Most taxa (including subspecies) number less than 5000 total individuals, and two, the Jamaican iguana (*Cyclura collei*) and the Grand Cayman iguana (*Cyclura nubila lewisi*), with fewer than 100 individuals in the wild, are perhaps the rarest lizards in the world (Alberts, 2000; Burton, 2000, 2002). All are (or were) highly adapted to xeric, rocky islands lacking large predators, making them particularly vulnerable to humans and the feral animals that accompany us (Iverson, 1978; Henderson, 1992; Mitchell, 1999; Tolson, 2000).

Our knowledge of the life histories of West Indian iguanas is surprisingly rudimentary. This is in part because of declining populations and in part because their long lives make long-term field studies necessary to obtain baseline data. In addition, funding for long-term field work in the West Indies and long-term commitments by researchers have been inadequate. As a result, even a preliminary suite of most life history traits (including fecundity, survivorship, age and size at maturity, etc.) is available for only one species in this genus (*C. carinata*; Iverson, 1979), and growth rates in the field have been estimated only for that species, for *C. cychlura* (Iverson and Mamula, 1989; Iverson et al., 2004), and for *C. nubila* (Gerber, 2000a). Although some aspects of the nesting ecology of all eight species have been elucidated (*C. carinata*, Iverson, 1979; Gerber, unpublished; *C. collei*, Vogel, 1994, 2000; *C. cychlura*, Coenen, 1995; Knapp, 1995; Iverson, 2000; *C. nubila*, Christian, 1986; Christian and Lawrence, 1991; Alberts, 1995; Gerber, 1994, 2000a; *C. pinguis*, Gerber, 2000b; *C. ricordii*, Ottenwalder, 2000b; *C. rileyi*; Thornton, 2000; Cyril, 2001; Hayes et al., 2004; *C. stejnegeri* [= *C. cornuta*], Wiewandt, 1977; Wiewandt and Garcia, 2000), important features of nesting strategies (including variation related to female age and size, nest site fidelity, and annual reproductive frequency) have not been well studied.

We have studied the life history of the Allen Cays iguana, *C. cychlura inornata* since 1980 when a nearly annual mark-recapture program was initiated on the only two islands known to harbor natural populations. Our study represents the second longest continuous field study of any lizard, after that of the Galapagos land

iguana begun in 1979 (Snell and Tracy, 1985). Growth (Iverson and Mamula, 1989; Iverson et al., 2004) and survivorship (Iverson, 2000; Iverson et al., in preparation) data were collected during the subsequent 21 years in preparation for our studies of the reproductive biology of this species. Of particular interest to us was the determination of age-specific effects on reproductive traits, since those data are unavailable for any other species of iguana. Our nesting studies commenced during the summers of 2001 and 2002, and the results form the basis of this report.

METHODS

Study Islands

As diagnosed by Schwartz and Carey (1977) *Cyclura cychlura inornata* occurs naturally only in the Allen Cays (24° 45' N, 76° 50.5' W; Fig. 1) of the northern Exuma Islands in the Commonwealth of the Bahamas (but see Malone et al., 2000, 2003 for recent controversy about this taxonomy based on genetic work). This is the most northerly occurrence of any member of the genus. The core of the population of this taxon occurs on Leaf Cay (ca. 4 ha; ~600 individuals excluding young of the year) and Southwest Allen's Cay (also called U Cay; 3 ha; ~300 excluding young of the year), both private islands. However, 11 to 15 individuals, believed to have been introduced by humans in the 1980's, are now known to inhabit Allen Cay (7 ha); at least one was originally marked on Leaf Cay. One additional population of 80–100 individuals also now exists on a small cay in the Exuma Cays Land and Sea Park (ECLSP; managed by the Bahamas National Trust), the result of the intentional introduction of eight iguanas from Leaf Cay in 1988–1990 for the purpose of establishing an "insurance" population in a nearby area where access can be monitored directly by the wardens of the ECLSP (Knapp, 1999, 2000a, 2001a; Knapp and Malone, 2003).

This subspecies is strictly protected by the Bahamas government; it is formally listed as Endangered on the 1996 IUCN Red List; and its international trade is prevented under the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES). The primary threats to its existence are poaching (for the illegal pet trade and for

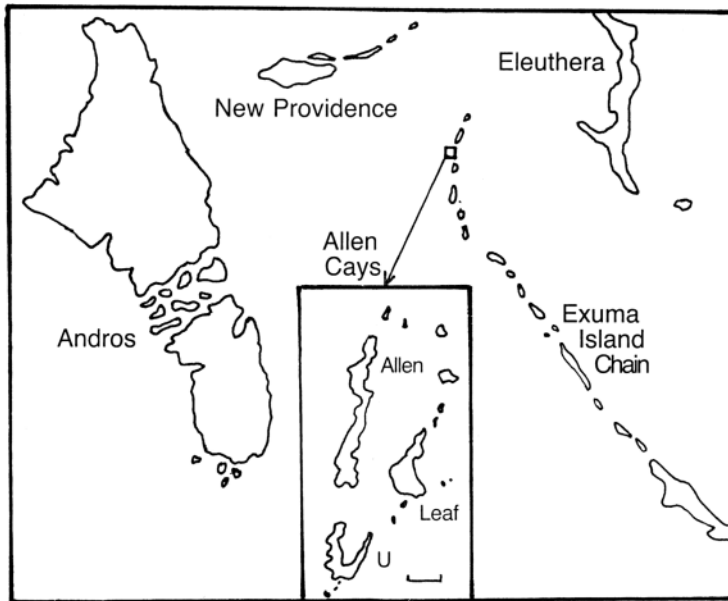


FIG. 1.—Map of the Allen Cays, northern Exuma Islands, Bahamas. Scale in inset = 200 m.

consumption by local Bahamians), the potential effects of supplemental feeding (sometimes of inappropriate foods) by tourists (up to 150 per day), the increasing probability of the introduction of feral mammals (either rats, cats, or dogs), and the vulnerability of the low, tiny islands to hurricane damage.

Maximum elevation on Leaf Cay is 4 m (above mean sea level), and approximately 70% of the perimeter is exposed honey-comb limestone, including all of the northern peninsula (Fig. 2). Above the splash zone, these rocky areas are covered with xeric coppice vegetation dominated by *Bumelia americana*, *Casasia clusiifolia*, *Conocarpus erectus*, *Erithalis fruticosa*, *Jacquinia keyensis*, *Rhachicallis americana*, *Reynosa septentrionalis*, *Sophora tomentosa*, and *Suriana maritima*. Four separate small, sandy beaches occur along the western and southern coastlines. One of these beaches (Big Beach; Fig. 3) on the western coast is the site of most of the tourist visitation (and feeding). Most of the eastern coastline is lined with a mosaic of sandy beach and exposed, weathered, limestone slabs. This beach lies parallel to a high (3 to 3.5 m above msl), sandy ridge, dominated by low (generally <1 m) strand species such as

Antirhea myrtifolia, *Casasia clusiifolia*, *Coccothrinax argentata*, *Erithalis fruticosa*, *Ernodea littoralis*, *Pithecellobium* sp., *Savia bahamensis*, *Sophora tomentosa*, *Suriana maritima*, and *Uniola paniculata*. The interior of Leaf Cay is primarily low sand (1 to 2 m above msl). In the lee (west) of the east ridge, the vegetation reaches its greatest diversity and stature (to nearly 4 m). The most common plants include *Acacia choriophylla*, *Antirhea myrtifolia*, *Bumelia americana*, *Ernodea littoralis*, *Guaiacum sanctum*, *Guapira discolor*, *Manilkara bahamensis*, *Pithecellobium* sp., and *Reynosa septentrionalis*. Most of the interior is covered in thatch palm forest (*Coccothrinax argentata* and some *Thrinax morrisii*), and is more sparsely vegetated toward the east (i.e., with numerous areas of exposed sand), but with extremely dense palm thickets to the west. At least 48 plant species have been identified on Leaf Cay (Moyroud and Ehrig, 1996; S. Buckner, personal communication). Potential nesting areas are nearly continuous along the east ridge and in open areas inland from the southern beaches and across the eastern half of the interior (Fig. 3).

U Cay consists of two northern rocky peninsulas of honeycomb limestone with low



FIG. 2.—Aerial photos of the study islands. Top: looking NW across Leaf Cay (Allen Cay in background); bottom: looking NW across U Cay. Photos courtesy Sandra Buckner.

rocky coppice vegetation (species as for Leaf Cay). Most of the area of these peninsulas is less than 4.5 m above msl, although the western ridge rises to a maximum elevation of 9.5 m at its southern extreme. A low (1 to 2 m above msl) southern isthmus of sand links the two peninsulas. Despite being ~40% open sand, the vegetation on the isthmus is relatively diverse, ranging from low strand vegetation (e.g., *Antirhea myrtifolia*, *Erithalis fruticosa*, *Jacquinia keyensis*, *Sophora tomentosa*, and

Uniola paniculata) inland from the northern sandy beach to a mixture of palms (*Coccothrinax argentata*) and low trees (to 3 m; including *Bumelia americana*, *Casasia clusifolia*, *Eugenia foetida*, *Manilkara bahamensis*, *Reynosa septentrionalis*) further inland. The vegetation increases in diversity, density, and stature (to 4 m) near the interface between the sandy isthmus and the edges of the rocky peninsulas (especially the east), and includes *Bumelia americana*, *Casasia clusifolia*, *Coc-*

coloba wifera (including one 5 m tall), *Eugenia axillaris*, *Guapira discolor*, and *Reynosia septentrionalis*. Nesting on U Cay is possible only on the southern sandy isthmus.

Long-term climate records are unavailable for the Allen Cays, but the general pattern is probably similar to that for Nassau (35 miles northwest; Ruffner and Bain, 1987), which experiences hot, rainy summers (May–Oct.; shaded daily mean maximum and minimum air temperatures for July, 31 C and 24 C) in which 78% of the annual 118 cm of rain falls, and warm dry winters (Nov.–April; mean max/min for January, 25 C and 18 C). Despite experiencing the same general weather pattern, precipitation on these cays may be as little as half that at Nassau (personal observation). On average Nassau receives 15.5 cm of rain from mid-June to mid-July. Rainfall there was above average during our field work (Sandra Buckner, personal communication); but we recorded only 6.15 cm of rainfall on Leaf Cay each year during that period. Measurable rain fell on 8 days in 2001 and 2002, and 62.0% and 74.4% of that rain fell during a single storm in the respective years. The only standing water on either cay is that which collects temporarily in small rocky depressions after rain events, and in an old open cistern on Leaf Cay.

Soil temperature was recorded every 12 min from May 2002 to Oct 2002 by three Tidbit™ data loggers at 20 cm depth in open sandy (i.e., potential nesting) areas and showed no difference between Leaf and U Cay (e.g., for August 2002, mean temperature at two sites on Leaf Cay was 31.1 and 32.2 C, and at one site on U Cay it was 31.5 C).

Field Protocols

Nearly annual trips have been made to the Allen Cays since 1980 (Table 1) during which we (at least one of us and five to 12 assistants) captured and processed as many iguanas as possible. From 1980 to 2000, we spent one to five (usually) days in mid-March in the cays, but recently shifted our survey work to mid-May, so that lizards were processed and visibly marked immediately before nesting season to avoid disturbing nesting females a month later.

During our surveys most iguanas were captured in dipnets by baiting them onto areas of open sand using food items (e.g., orange

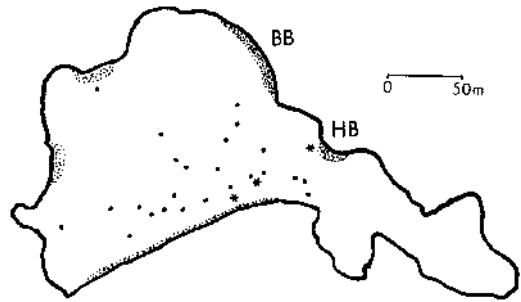


FIG. 3.—Nest sites of Allen Cay iguanas on Leaf Cay in 2002. Beaches are stippled. Dots indicate females that were captured on or near Big Beach (BB) in May; asterisks mark those captured on House Beach (HB) in May. Due north is to the right.

peels or parts of natural fruits) or red objects tied to a string. Others were noosed using fish leaders attached via swivels to extendable golf ball retrievers or captured by hand. Captured lizards were placed in pillow cases to calm them until processing (always within 24 hours, usually within a few hours). Snout–vent length (SVL to the nearest mm), tail length (TL to the nearest mm), and body mass (BM in grams) were measured on each capture (4227 total to date; Table 1). Sex was determined by cloacal probing (Schaefer, 1934; Dellinger and von Hegel, 1990). Age at first capture was estimated using the appropriate growth equations in Iverson et al. (2004). Captured iguanas were individually marked by a unique combination of toe clips (three maximum), marked temporarily on the dorsolateral mid-body with fingernail polish or touch-up paint, and released as soon after capture as possible. Paint-marked lizards could then be clearly avoided during our capture of other iguanas. In 1993, we began injecting PIT (passive integrated transponder) tags under the skin of many iguanas on the left side just anterior to the pelvis; 440 have been implanted to date as time and PIT tag funding have been available.

In May 2001, we painted the lizard's identification number on one side (left for males; right for females) to permit identification of individuals (and sex) from a distance without disturbance during our June–July field work. This was repeated in May 2002, although only females were paint-numbered. In May 2002, radiotransmitters were attached with silicone sealer and duct tape to the dorsal base

TABLE 1.—Recapture information by year for Allen Cays iguanas. Abbreviations are caps (captures), recaps (recaptures), and Cum (cumulative). Total number of captures for U Cay is 1581 (463 + 1118) lizards, and for Leaf Cay it is 2646 (945 + 1701). All trips for 1980 through 2000 were in mid-March (1–5 days each). Trips in 2001 and 2002 were in mid-May (6 days) and mid-June to mid-July (26 and 28 days).

Year	U Cay					Leaf Cay				
	Total caps	Total recaps	% recaps	Cum. # w/marks	Cum. # recaps	Total caps	Total recaps	% recaps	Cum. # w/marks	Cum. # recaps
1980	30	0	0	30	0	14	0	0	14	0
1982	43	9	21	64	9	50	3	6	61	3
1983	48	25	52	87	34	51	26	51	86	29
1986	75	37	49	125	71	79	19	24	146	48
1988	111	58	52	178	129	109	59	54	196	107
1990	113	83	74	208	212	136	81	60	251	188
1992	124	89	72	243	301	148	102	69	297	290
1993	34	33	97	244	334	94	73	78	316	363
1994	150	94	63	300	428	204	110	54	410	473
1995	123	106	86	317	534	150	125	83	435	598
1996	113	86	76	344	620	177	126	71	486	724
1998	95	79	83	360	699	205	150	73	541	874
2000	169	124	73	405	823	254	175	69	620	1049
2001	140	110	79	435	933	284	220	77	679	1274
2001	40	34	85	441	967	209	89	43	799	1363
2002	143	118	83	460	1085	350	266	76	880	1629
2002	37	34	92	463	1118	147	72	49	945	1701

of the tail of 15 randomly selected adult-sized females (including some that had nested in 2001 and some that had not). Seven of these females retained their transmitters until our return in mid-June and were located regularly as a test of our ability to be certain which females did or did not nest.

We spent the nights on all March and May trips aboard a support vessel anchored near Leaf Cay, but we camped on Leaf Cay from 15 June to 11 July 2001 and 15 June to 13 July 2002. During these periods we searched both Leaf and U Cay at least every other day, noting locations of burrows (and flagging them), associated females, and nests. We also continued to capture unpainted iguanas (i.e., those missed during the May survey) as time permitted. A few females that nested lacked painted numbers (i.e., had not been captured in May or had faded paint numbers). They were captured as they defended the nest site, their numbers checked (all were recaptures), and released within one minute of capture. All returned immediately to guard their nests.

In 2001 we flagged, numbered, and took a GPS reading for each freshly constructed burrow that exceeded about 20 cm in length; in 2002, we flagged virtually every fresh burrow no matter how extensive. Therefore, the data seem to suggest that iguanas dug fewer

burrows in 2001 than 2002, but that was not necessarily the case.

Once a female completely covered her nest burrow and began defending the site, we excavated and mapped (in three dimensions) the nest burrow, counted, weighed (nearest g), and measured (nearest 0.1 cm) the eggs, replaced the eggs in the original egg chamber, and re-covered the nest burrow. During excavation we attempted not to remove the soil from above the last 40 cm of the burrow (i.e., approximately an arm's length), so as to leave the nest chamber as intact as possible. We also placed Tidbit™ miniature digital temperature loggers (recording every 5–6.5 min) among the eggs in four nests in 2001 and 13 nests in 2002, and retrieved those when we returned to the cays to excavate each nest (18–21 October 2001; 2–6 October 2002). All lateral chambers in burrow systems were completely excavated in 2001 (i.e., to locate old nests), but not always in 2002. Digital temperature loggers were deployed at several sites (representing a variety of microhabitats) on each island from March 2000 to October 2002.

At least one egg in 14 nests (of 75 total nests) was flaccid, weighing about half of a fully turgid egg of the same dimensions. In 2001, we removed and discarded these eggs from each nest (eight total eggs in six nests) because they

were unlikely to hatch (Boylan, 1984; van Marken Lichtenbelt and Albers, 1993). However, in 2002, we left all flaccid eggs in the nests (nine eggs in six clutches) to evaluate the effects of their presence on the survivorship of the remaining eggs. All flaccid eggs found in 2002 died early in development.

Two soil samples (ca. 2 cc) were collected from within each nest during excavation in October of 2002. These samples were stored in sealed vials until they were weighed several days later, then dried to a constant mass at 60 C, and reweighed. Soil moisture was calculated as $(\text{wet mass} - \text{dry mass}) \times 100 / \text{dry mass}$. Given the general uniformity of the sandy soils in the nesting areas, we assume this method provided accurate soil moisture estimates.

A spherical densiometer was placed on the ground directly above each egg chamber and four readings (from the four main compass points) were taken to estimate percent canopy cover (i.e., an index of shadiness). We also recorded the three nearest plant species.

Because nesting is a prolonged process and burrows were long, we could not witness actual oviposition. We therefore estimated the actual oviposition date by assuming that nest covering was continuous and lasted less than a day (as it did for nests we monitored very closely). Generally the oviposition date was assumed to be the day before nest covering was completed. This was somewhat complicated when we could not fully survey an island every day. Thus, if a burrow was open one day, and completely covered and being defended two days later when first rechecked, we assumed that oviposition occurred on the first day (i.e., not yesterday).

Based on the lack of covered nests and defending females, and the extent of preliminary digging observed, we are confident that no nesting occurred before our arrival either year. We believe that no additional nesting occurred on U Cay after our departure, because no active burrows remained and no females exhibited digging behavior for at least five days before we left. We are certain that a few nests were completed on Leaf Cay after we departed in July in both years, because a few partial burrows were still active when we left, but in October were found covered, and contained eggs on excavation. For calculations of nesting frequency, we were

able to identify females that probably would have nested after our departure (those that had migrated away from their May capture locations, were seen near [but not inside] partially excavated burrows, remained in that general area, and were bold [i.e., not quick to retreat on our approach]) and those that almost certainly did nest after we left (the above criteria, plus they were actually seen digging in a burrow and/or were seen defending the area of an incomplete burrow [i.e., chasing away other iguanas or at least bobbing aggressively while holding their ground near the burrow]).

For estimates of reproductive output, we calculated relative clutch size (RCS; the ratio of clutch size to body mass measured in May \times 100), relative egg mass (REM; the ratio of mean egg mass in the clutch to body mass measured in May \times 100), and relative clutch mass (RCM; the ratio of total clutch mass to body mass measured in May \times 100). We used Statview (Abacus Concepts) for all statistical analyses. Means are reported \pm one standard deviation. Analyses of island and year effects on individual parameters were done via two-way ANOVA as well as multiple *t*-tests (two-tailed). Because the statistical conclusions based on the results of the two approaches were the same, only the latter are reported.

Phylogenetic bias in interspecific analyses (Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Hansen, 1997; Martins and Lamont, 1998) was reduced by calculating phylogenetic independent contrasts using COMPARE (Martins, 2003). Calculations were based on the phylogenetic relationships presented by Malone et al. (2000; including the introduced population of *C. nubila* off Puerto Rico as sister to *C. nubila* on Cuba), assuming equal branch lengths.

RESULTS

Nesting Behavior

Mating apparently occurs in mid-May, based on our observations of copulations on 18 May on U Cay (0900 h) and 20 May (1500 h) in 2002 on Leaf Cay, and that of Chuck Knapp (personal communication) on Leaf Cay on 26 May 2000 (0920 h). In mid- to late June females move from their usual activity centers to sites with areas of open sand (e.g., Fig. 3, for

2002 captures on Leaf Cay). Some females crossed the length of Leaf Cay (ca. 173 m), passing many seemingly adequate nesting areas, before beginning to dig trial nesting burrows. Mean distance between female capture site in May of 2002 and her eventual nest site was 88 ± 32 m (range 30–173 m; $n = 27$). Distance was not correlated with body size (e.g., for SVL, $r = 0.03$, $P = 0.87$), nesting date ($r = 0.13$, $P = 0.55$), nor any measured reproductive parameter. The time between mating and nesting could be determined for only one female (#188) that mated on 20 May and completed her nest on 24 June (35 days later).

The general nesting pattern was evident from a composite of observations of many females at differing times, and could be divided into four phases (see also Rand, 1968, and Wiewandt, 1977): 1) digging; 2) oviposition; 3) covering; and 4) defense [A Quicktime™ movie of these phases is available for download at www.earlham.edu/~johni/iguana.mov]. The entire process was as short as 30 h in one large female (SVL 34.5 cm) that dug a relatively short burrow (54 cm), but usually required several days. For 19 burrows flagged the day construction began, and which became completed nests on known days, the interval averaged 6.1 ± 3.2 day (range 1.5 to 12 day). Because we tried not to disturb females while they were excavating or even when they were near their nest burrows, we were unable to time the individual phases of nesting.

Digging.—Even before digging at a site, females exhibited defensive behavior toward other iguanas (e.g., vigorous head-bobbing, aggressive charging with open mouth, open-mouthed face-offs, etc.), and the intensity of these displays increased as the nesting process continued. Although some females eventually nested in the first and only burrow they excavated, others initiated two or more. Initial burrows were sometimes abandoned for obvious reasons (e.g., plant roots precluded digging; the site was too dry or loose and the burrow kept collapsing; or the site was too close to that of another defending female), but in other cases it was not clear why the burrow was abandoned. Abandoned burrows were usually less than 0.3 m long, although some were at least twice that long.

Excavation of the initial 50 cm of the burrow was only observed during the day. We checked a few burrows at night (to avoid frightening the females), and in each case the female was inactive within the burrow, with her head oriented toward the burrow mouth. We cannot say that excavation deep within the burrow does not sometimes occur at night.

Initially, soil from burrow excavations is kicked out of the burrow entrance by backward thrusts of the female's arms and legs. The freshly ejected soil forms an apron outside the burrow entrance. At some point females shift from tunnel excavation to excavation of the nest chamber. That chamber is usually constructed at a bend or curve off the initial nest tunnel, resulting in the burrow mouth (i.e., daylight) not being visible by the female in the nest chamber (Fig. 4; but note burrow #152). The female then simply pushes newly excavated soil behind her in the burrow. The result is that most females apparently fill the tunnel behind them with soil during the final stages of nest construction. Thus, the amount of soil deposited outside the burrow entrance is nearly always much less than the total volume of soil excavated by the female.

Oviposition.—Because of the female's burying behavior, we have no data on the timing of final nest chamber construction nor oviposition itself. However, once the eggs are laid, some soil is apparently kicked over the eggs, although the eggs typically remain at most only half buried in soil. There is always a large open cavity remaining above the clutch.

Covering.—After oviposition, the female kicks soil backward in the burrow (i.e., toward the nest chamber), partially covering the eggs, and blocking off the nest chamber. The burrow is then completely and tightly filled, suggesting that females pack the soil with their head or forelimbs. The female continues filling the burrow by alternating between kicking sand backward into the burrow and turning around, entering the burrow head-first, and either inspecting the plugged burrow, rearranging the soil just kicked in, or perhaps packing the soil.

Once the female has filled the burrow to near its entrance, she no longer enters it, but simply kicks sand backward as she walks away from the burrow entrance. She continues this covering behavior in a wide fan-shaped area

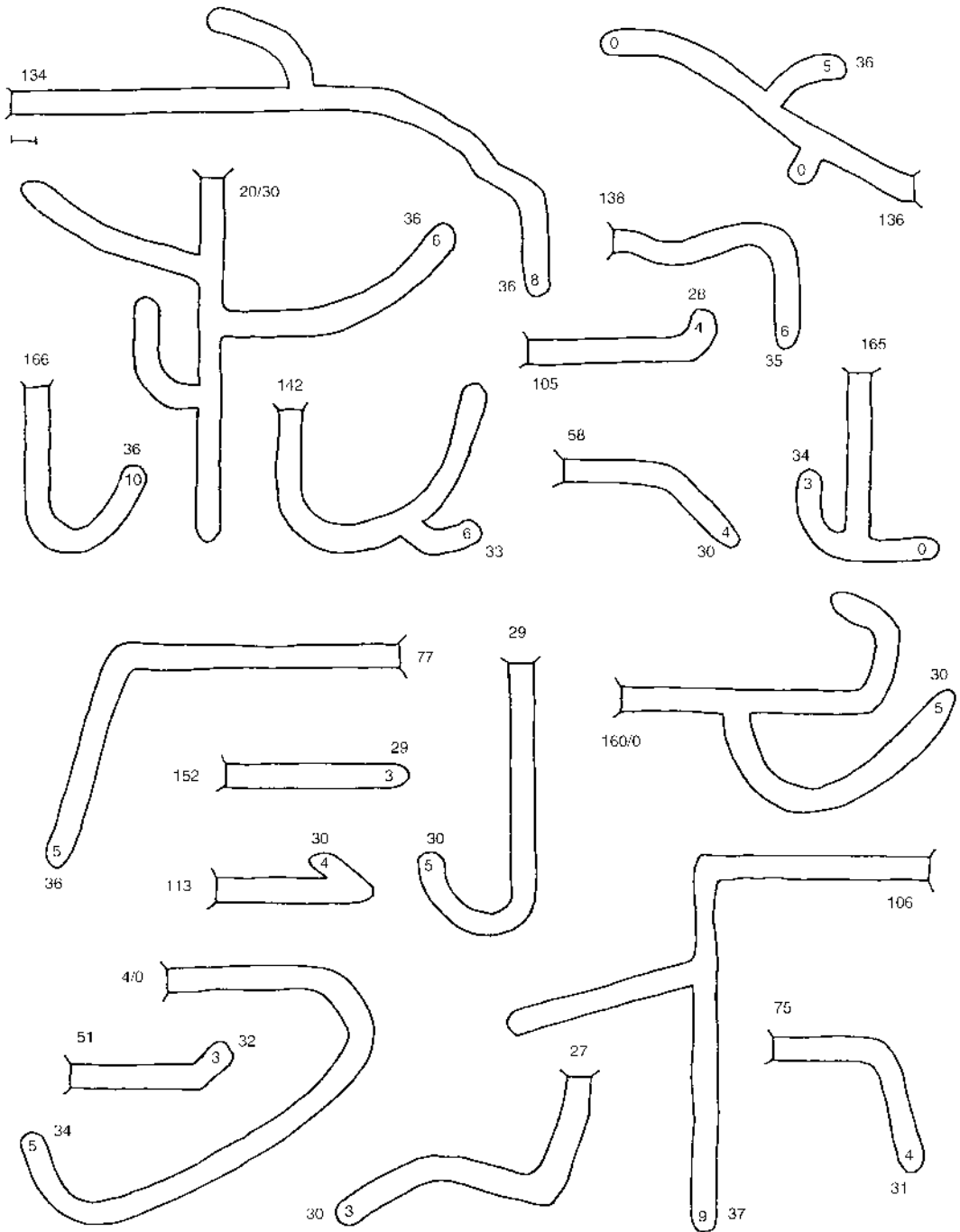


FIG. 4.—Sample configurations of nesting burrows from excavations made in 2001. Numbers in burrow terminus are clutch sizes (zeros indicate presence of egg complements from previous years); adjacent numbers are depth to bottom of nest chamber. Numbers adjacent to burrow entrances are female identification numbers. All burrows are to the same scale (10 cm, near burrow #134). Compass orientations are not actual directions.

around the burrow entrance until a mound of sand and surface debris (up to 10 cm high) is deposited over the former entrance. The exposed sandy apron adjacent to a mound of sand covered with plant debris makes recently completed nests apparent to the trained eye. The presence of a nearby defending female makes these sites unmistakable.

Defense.—Both during covering and after completion, females are extremely aggressive as they defend their nest sites against other iguanas (both females and males). Any iguana approaching a nest site is met with vigorous head-bobbing and aggressive charges. If that does not drive away the interloper, the female will actually attack the intruder, in some cases accompanied by vicious biting of the intruder's head, neck and shoulder region. On occasion defending females physically attacked other females twice their mass, and drove away males four or more times their mass. Females that nest near another female (see below), spend considerable time defending the nesting area against the adjacent female. Vigorous defense of the nest site (including an area of about 8 meters diameter) was maintained by most females at least until we departed in mid-July. It was our subjective sense that late-nesting females seemed less intense in their defense than earlier nesters, although this was not quantified. Some females were still in the area of their nests in October 2002, rather than near their May 2002 capture sites; they appeared curious about our nest excavations, but did not show any aggressive behavior (not even head-bobbing).

Nests.—Nests were completed (i.e., covered) between 17 June and 10 July on U Cay, and from 20 June to at least 11 July on Leaf Cay (Fig. 5). Mean nest dates were not significantly different between years on U Cay (25 June in 2001; 27 June in 2002) or Leaf Cay (4 July in 2001; 3 July in 2002), but the start, finish, and mean nesting dates were earlier on U Cay than Leaf Cay (Fig. 5; mean date 26.1 June on U Cay, 3.5 July on Leaf Cay; $t = 5.7$, $P < 0.0001$; Mann-Whitney $U = 211.5$, $P < 0.0001$). This week-long difference is actually an underestimate of the real difference since some females on Leaf Cay completed nests after our departure in July. Individual females that were observed nesting both in 2001 and 2002 finished their nests from

up to 6 days earlier to 9 days later in 2002 (mean change = +0.5 days; $n = 13$). This change in date was not related to any factor we could identify (e.g., location, timing, female size, burrow structure, etc.).

Nest burrows averaged 149 ± 55 cm in total length ($n = 74$; range, 54 to 330 cm) from entrance to end of egg chamber. No significant difference in burrow length existed between years on either island, or between islands in 2002 (mean 150 vs. 147 cm); however, in 2001, burrows on U Cay were significantly longer ($\bar{x} = 188 \pm 80$ cm; $n = 11$) than on Leaf Cay ($\bar{x} = 136 \pm 48$ cm; $n = 29$; $t = 2.52$; $P = 0.016$) as was female size (see below). Although body size was not correlated to burrow length in 2002 (for SVL, $r = 0.21$; $P = 0.23$; $n = 33$), they were correlated in 2001 ($r = 0.42$; $P = 0.008$; $n = 39$). For the combined years, differences in burrow length approached significance between islands ($t = 1.8$; $P = 0.07$), but SVL was not correlated with burrow length ($r = 0.17$; $P = 0.16$). Burrow length was weakly negatively correlated with nest date for the combined data ($r = -0.23$, $P = 0.049$), the combined 2001 data ($r = -0.45$, $P = 0.004$), and the 2001 U Cay data alone ($r = -0.37$; $P = 0.05$), but not for other samples ($|r| < 0.28$, $P > 0.22$). We were initially concerned that our activities might explain the differences between the two years, but it seems unlikely that our presence in 2002 would cause an increase in burrow length on Leaf Cay yet decreases on U Cay. Age was not correlated with burrow length ($|r| < 0.24$, $P > 0.22$) for any sample except the combined 2002 data ($r = 0.38$, $P = 0.04$).

The depth to the bottom of egg chamber averaged 27.7 ± 8.2 cm ($n = 75$; range, 11 to 59 cm), and no differences existed between islands or years (for all comparisons, $t < 1.5$; $P > 0.15$). In addition, neither female body size ($r < 0.44$; $P > 0.16$) nor age ($r < 0.31$; $P > 0.08$) were related to nest depth for either years or islands, or for the combined data. Nest depth did not vary with nest date for any island-year sample ($|r| < 0.23$, $P > 0.21$) except for the combined 2001 data ($r = -0.34$, $P = 0.029$). Given the lack of statistical significance for other samples (including within islands for 2001), the latter was likely a sampling artifact.

Burrow structure was highly variable, but egg chambers were usually off the main

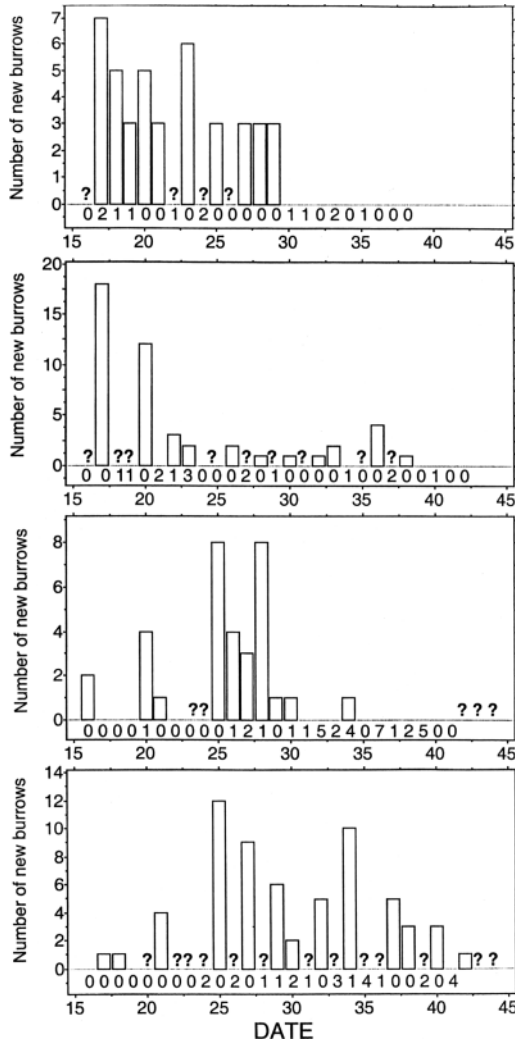


FIG. 5.—Nesting phenology of Allen Cays iguanas by year and island (top to bottom: U Cay 2001, 2002, Leaf Cay 2001, 2002). Bars represent the number of burrow starts on a given day, and the numbers below the bars represent the number of burrows completed on that day. Date is the number of days after 31 May (e.g., day 35 equals 5 July). Question marks in place of bars indicate that the island was not sampled for burrow starts on that day.

burrow in a J-shaped configuration (Fig. 4). Because nesting areas are used year after year, digging females often burrowed into filled nesting burrows from previous years, sometimes completely excavating the older nest and depositing the empty eggshells on the apron of the burrow entrance. Other females bypassed old egg chambers to construct their own (e.g., #136 in Fig. 4).

Orientation of the initial opening of nest burrows was apparently random ($\bar{x} = 174 \pm$

104, range 1° to 355°). Burrows were not associated with a particular plant species, but they did tend to be in open areas with considerable direct sun exposure (see below). Nest burrows were often constructed within 5–10 m of other nests. The shortest inter-nest distances were 1.0 m, 5.3 m, 6.1 m, 6.9 m (two), 7.2 m (two), and 7.6 m (two). Six others were 9.1 to 10.7 m distant. In two instances, one female apparently usurped the burrow of another female that had already oviposited,

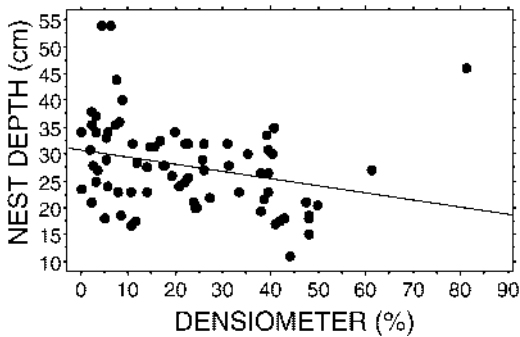


FIG. 6.—Relationship between densiometer reading (a measure of shadiness in percent) and nest depth (cm) for nests of Allen Cays iguanas. Least squares regression is plotted (Nest depth = $-0.13\text{Den} + 30.68$; $r = -0.28$, $P = 0.017$).

unearthed (and ruptured) the eggs of the latter, and then oviposited and covered her own clutch. In one of the cases, the first female was actually buried in the nest burrow by the second, and we discovered her, trapped among roots in the sand as she was trying to dig out.

Densiometer readings averaged $22 \pm 17\%$ (range 0 to 81%), and only two values exceeded 50%. No differences between years or islands were significant and densiometer readings were not related to SVL ($r < 0.25$, $P > 0.12$ for all island-year samples) or age ($r < 0.28$, $P > 0.21$ for all samples). For all data combined, nests dug in shadier areas tended to be shallower than those dug in more open areas (Fig. 6; $r = -0.28$; $P = 0.017$). That relationship was also significant for all 2001 data ($r = -0.58$; $P < 0.0001$) and all Leaf Cay data ($r = -0.56$; $P < 0.0001$), but not for all 2002 data ($r = +0.1$; $P = 0.58$), or for all U Cay data ($r = +0.21$; $P = 0.31$). The lack of statistical significance for the latter is in part due to the inclusion of nests (five on U Cay in 2002) deposited under sea oats (*Uniola*), which had high densiometer readings but were actually much hotter environments than those with similar readings under taller vegetation. For example, the highest densiometer reading (81% on U Cay in 2002) was amid sea oats, and the nest below was the third deepest nest (46 cm) recorded in the study.

Densiometer readings were inversely correlated with burrow length (Fig. 6) for the combined data as well as for the combined Leaf Cay data, the combined 2001 data, and

the Leaf Cay data from 2002 ($r > 0.29$, $P < 0.025$), but not for any other sample subsets ($|r| < 0.35$, $P > 0.13$). Densiometer readings did not vary with nest date ($r < 0.23$, $P > 0.14$ for all samples).

Mean incubation temperatures for 13 nests over the 85 days following deployment of the loggers in 2002 ranged from 30.6 C to 32.7 C, and averaged 31.1 C for six U Cay nests and 31.7 C for seven Leaf Cay nests (overall mean, 31.4 C). The difference in mean incubation temperatures between U and Leaf Cay was not significant ($t = 2.0$; $P = 0.07$). Four nests from U Cay that were similarly logged in 2001 averaged 31.1 C (range of means: 30.8 to 31.8 C). Average nest temperature was not correlated with densiometer readings ($r = 0.29$; $P = 0.33$). Although average temperatures were quite uniform among nests, and nest depth was not correlated with nest temperature ($r = 0.37$; $P = 0.15$), deeper nests experienced much less fluctuation in temperature (e.g., compare top and bottom of Fig. 7; Levene homogeneity-of-variance test = 14280.8, $P < 0.0001$). The temperature profiles demonstrated that rain events significantly reduced soil temperatures (see also Wiewandt, 1977). For example, 46 mm fell during one hour on 6 July 2002 followed by 9 mm more the next morning, and nest temperatures were reduced for the next five days (Fig. 7).

Nesting Frequency

To determine nesting frequency we tallied all females captured both during 2001 and 2002 (i.e., known to be alive through the period) and for which we were quite certain whether or not they nested. These females were then scored as two-time nesters, one-time nesters, or non-nesters. We also did a second tally including females that were probable nesters in one or both years (see Methods for definition of probable). These data (Table 2) suggest that about one in five small females (26–30 cm SVL) nested each year, that 40 to 50% of medium-sized females (30–36 cm SVL) nested each year, and that large females (36–38 cm SVL) nested every year. A weighted average across all size classes indicates that about one in three females nested each year (Table 2).

For 13 females that nested in both 2001 and 2002, almost half nested at precisely the

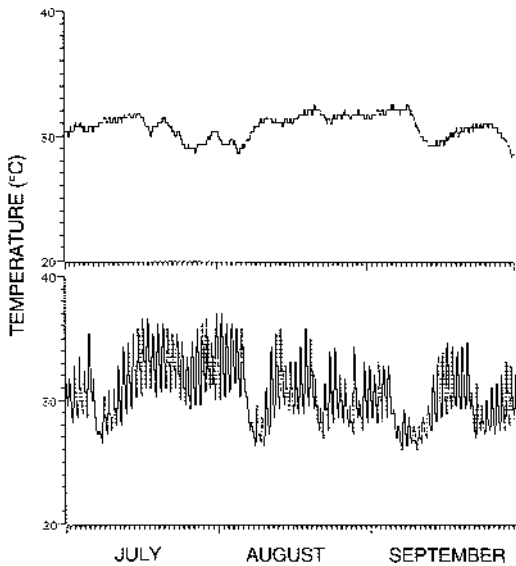


FIG. 7.—Temperature profiles of typical nests on U Cay with 100% survivorship from 1 July to 1 October in 2001 (top) and 2002 (bottom). Recording interval was 6.5 minutes in 2001 and 5 minutes in 2002. 2001 nest (#20/30) was laid 22 June at a depth of 44 cm, and mean temperature for the first 85 days of incubation was 30.8 C; 2002 nest (#25) was laid 23 June at a depth of 21 cm, and averaged 30.7 C for the first 85 days. Note impact of rain event on 6 July 2002 (see text); other obvious temperature drops probably also indicate rain events.

same site each year (two on U Cay; four on Leaf Cay). Nest sites for two others from U Cay were 0.7 m and 8.1 m distant, and for five others from Leaf Cay, distances averaged 49.8 ± 20.5 m apart (range, 22.0 to 76.7 m).

Female Size and Age

Nesting females averaged 32.0 cm SVL and 1336 g BM ($n = 80$ and 70 , respectively; Table 3), and did not vary by year, but females were significantly larger on U Cay ($\bar{x} = 33.6 \pm 3.1$ cm SVL, $n = 25$; 1564 g BM; $n = 20$) than on Leaf Cay ($\bar{x} = 31.3 \pm 3.1$ cm SVL, $n = 55$, $t = 3.15$, $P = 0.002$; 1245 g BM, $n = 50$, $t = 2.87$, $P = 0.005$). The size ($r = -0.55$; $P < 0.0001$ for all data; $|r| > 0.51$ for all data subsets, except for the combined U Cay data and the 2001 U Cay data: $|r| < 0.35$, $P > 0.08$) and age ($r = -0.40$; $P = 0.0005$ for all data; $|r| > 0.39$, $P < 0.019$ for all data subsets except for the combined, the 2001 and the 2002 U Cay data: $|r| < 0.25$, $P > 0.31$) of nesting females decreased as the nesting season progressed. The lack of significance for some U Cay samples is likely an artifact of small sample size.

The smallest nesting females were between 26.5 and 28.0 cm SVL and 749 and 835 g BM (Table 3). Several of these females had been reliably aged during our long-term mark-recapture studies and were 13.8 (four females) or 14.8 years post-hatching when they nested. Based on long-term growth rates (Iverson et al., 2004), females reach 26.5 cm SVL on average between 11 and 12 years. These data suggest that maturity in some females is reached by 12 years of age, at sizes of 26 to 27 cm SVL and about 750 g BM.

The oldest nesting females with reliable age estimates (i.e., first marked as juveniles or young adults and hence initially aged with an accuracy $\pm 1-2$ yr) were 31.8, 33.8., 35.8, and 39.8 years post-hatching and 32 to 36.5 cm

TABLE 2.—Nesting frequency by size class for female Allen Cays iguanas captured both in 2001 and 2002. Females allocated to size class by mean SVL for captures in 2001 and 2002. Size class 26–27 cm includes mean SVLs from 26.0 to 27.9 cm. Data are tallied for females for which we were certain about their nesting, as well as (in parentheses) including females which probably nested (see Methods for criteria), but for which we did not find their nest. For both islands combined, 63 of 200 (31.5%) possible nests (assuming a maximum of one nest per year) were produced among females known to have nested; for all females (including probable nesters), 81 of 224 (36.2%) were produced.

SVL class	U Cay				Leaf Cay			
	Both years	1 of 2 years	neither year	proportion of possible nests	Both years	1 of 2 years	neither year	proportion of possible nests
26–27 cm	0	3	5	3/16	0	4 (5)	8	4/24 (5/26)
28–29 cm	0	1	5	1/12	1 (3)	8 (9)	18	10/54 (15/60)
30–31 cm	0	2 (3)	3	2/10 (3/12)	3 (6)	9 (10)	8	15/40 (22/48)
32–33 cm	1	4	2	6/14	2 (3)	1	1	5/8 (7/10)
34–35 cm	0 (1)	3	1 (2)	3/8 (5/12)	0	0	0	—
36–38 cm	4	0	0	8/8	3	0	0	6/6 —
All classes	5 (6)	13 (14)	14 (15)	23/68 (26/74)	9 (15)	22 (25)	35	40/132 (55/150)

TABLE 3.—Mean reproductive parameters for female Allen Cays iguanas by island and year. Sample size appears in parenthesis after mean \pm 1 SD, and above range in brackets. All lengths are in cm, mass in grams. RCS = clutch size/body mass in May \times 100; REM = mean egg mass/body mass in May \times 100; RCM = clutch mass/body mass in May \times 100. Mean egg size parameters are averages of clutch means.

Parameter	Leaf Cay		U Cay		All data
	2001	2002	2001	2002	
SVL	31.5 \pm 2.9 (32) [26.5–38.9]	30.9 \pm 3.2 (23) [27.0–38.7]	34.7 \pm 2.1 (11) [31.8–38.2]	32.7 \pm 3.5 (14) [27.0–38.9]	32.0 \pm 3.2 (80) [26.5–38.9]
Body mass	1250 \pm 406 (27) [790–2370]	1239 \pm 447 (23) [749–2595]	1761 \pm 337 (9) [1325–2273]	1403 \pm 418 (11) [835–2075]	1336 \pm 441 (70) [749–2595]
Clutch size	4.4 \pm 1.6 (31) [2–10]	3.8 \pm 1.5 (22) [1–6]	5.7 \pm 1.6 (12) [3–9]	5.4 \pm 2.0 (13) [2–8]	4.6 \pm 1.7 (78) [1–10]
Egg length	68.1 \pm 3.8 (21) [61.6–76.9]	68.8 \pm 5.0 (21) [60.0–80.0]	64.4 \pm 3.8 (11) [57.7–70.6]	64.6 \pm 4.6 (12) [57.5–74.5]	67.2 \pm 4.6 (74) [57.5–80.0]
Egg width	34.1 \pm 1.8 (30) [30.2–38.2]	34.9 \pm 1.5 (21) [32.9–37.8]	35.4 \pm 1.7 (11) [31.2–37.1]	36.6 \pm 1.8 (12) [33.2–40.6]	34.9 \pm 1.9 (74) [30.2–40.6]
Egg mass	48.6 \pm 4.4 (30) [37.2–55.7]	49.9 \pm 4.2 (21) [43.1–57.5]	48.0 \pm 5.6 (11) [32.6–54.8]	49.7 \pm 3.2 (12) [46.5–57.3]	49.1 \pm 4.3 [32.6–57.5]
Clutch mass	215 \pm 52 (30) [74.4–399.8]	191 \pm 71 (21) [56.6–324.9]	279 \pm 88 (11) [97.7–426.1]	261 \pm 106 (13) [57.5–458.0]	226 \pm 85 (75) [56.6–458.0]
RCS	0.37 \pm 0.06 (25) [0.24–0.52]	0.31 \pm 0.10 (21) [0.12–0.44]	0.34 \pm 0.08 (9) [0.22–0.43]	0.34 \pm 0.07 (9) [0.24–0.43]	0.34 \pm 0.08 (64) [0.12–0.52]
REM	4.1 \pm 1.0 (24) [1.7–5.6]	4.4 \pm 1.4 (20) [2.1–6.7]	2.8 \pm 0.5 (9) [2.1–3.5]	3.4 \pm 1.1 (9) [2.5–5.4]	3.9 \pm 1.2 (62) [1.7–6.7]
RCM	17.4 \pm 2.9 (24) [9.4–22.1]	15.7 \pm 4.0 (20) [6.7–19.8]	16.4 \pm 4.8 (9) [7.4–21.1]	15.9 \pm 4.2 (9) [6.9–21.5]	16.5 \pm 3.7 (62) [6.7–22.1]
Hatchling SVL	—	9.4 \pm 0.3 (21) [8.8–9.9]	—	9.5 \pm 0.2 (16) [9.1–9.9]	9.5 \pm 0.27 (37) [8.8–9.9]
Hatchling BM	—	35.1 \pm 3.9 (21) [28.0–42.9]	—	34.1 \pm 2.1 (16) [30.3–38.2]	34.7 \pm 3.2 (37) [28.0–42.9]

SVL. Other females captured initially as adults and hence less reliably aged could have been 42.5 and 43.5 years old when they nested. The two oldest females were adults when first captured in 1986 on Leaf Cay (initial SVL = 35.6 cm) and 1988 on U Cay (initial SVL = 38.7 cm), respectively, estimated then to be 38.5 and 41.5 years of age, and therefore possibly as old as 54.8 and 61.5 yr when they nested in 2002.

Clutch Parameters

Clutch size.—Counts of egg shells in 11 nests from previous years (found while excavating active nests) averaged 4.1 ± 1.9 (range 2–8). Clutch size (CS) for fresh nests averaged 4.6 (Table 3), and did not differ between years on either island ($t < 1.4$; $P > 0.17$). CS was greater on U Cay than Leaf Cay both within year and for the combined years ($t > 2.3$; $P < 0.01$). This difference is a direct consequence of the positive relationship between CS and body size (Fig. 8). ANCOVA to remove the effects of body size (SVL) revealed no

difference in adjusted CS between years or islands (for both slopes and intercepts, $P > 0.22$). CS was highly correlated with age for the combined data ($r = -0.55$, $P < 0.0001$; Fig. 9), as well as for all other island-year combinations ($r > 0.38$; $P < 0.05$) except for the 2001 Leaf Cay data, the 2001 U Cay data, and the 2002 U Cay data ($r < 0.45$; $P > 0.17$). ANCOVA revealed a significant difference in the intercepts of the relationship between age and CS ($F = 5.8$, $P = 0.019$) between islands, suggesting that U Cay females produce about one more egg per clutch than Leaf Cay females of the same age (Fig. 9), even though the former are smaller (Iverson et al., 2004). The same analysis revealed no difference in this relationship between 2001 and 2002.

All but one female that nested both in 2001 and 2002 produced from two fewer eggs to two more eggs in 2002 than they did in 2001 (mean change = -0.2 ± 1.3 egg; $n = 13$); the exception was the largest nesting female (38.9 cm SVL) and she produced 10 eggs (the maximum we recorded) in 2001 and only four

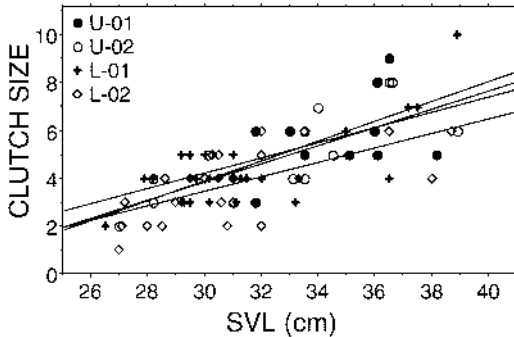


Fig. 8.—Relationship between female body size (snout-vent length; SVL in cm) and clutch size (CS) for Allen Cays iguanas by year (01 or 02) and by island (U or Leaf). Overall regression equation for both years and islands combined is $CS = 0.38SVL - 7.53$ ($n = 74$; $r = 0.73$; $P < 0.0001$). All individual regressions are significant except that for U Cay in 2001 ($r = 0.41$; $P = 0.21$).

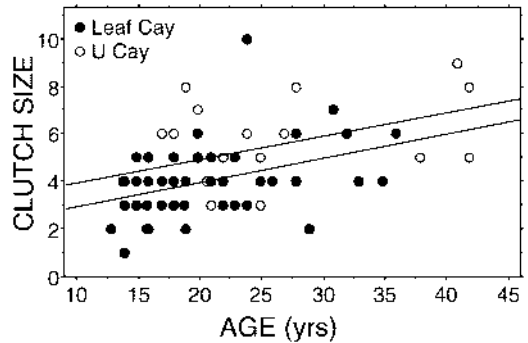


Fig. 9.—Relationship between age (in years) and clutch size (CS) for Allen Cays iguanas, plotted by island (U or Leaf). Overall regression equation is $CS = 0.11Age + 2.06$ ($r = 0.45$, $P = 0.0002$). Y-intercepts for separate island regressions are significantly different (greater in U Cay; see text).

in 2002. Surprisingly, she weighed less in May of 2001 (2370 g) than in May of 2002 (2595 g). Most double nesters differed by one ($n = 9$) or no eggs ($n = 1$) between years.

Because the average size of nesting females decreased during the nesting season (see above), and because of the strong correlation between body size and CS, the latter also decreased through the season ($CS = -0.142 * Date + 9.038$; $r = -0.54$; $P < 0.0001$), by about one egg for each seven days. That relationship was significant for all data subsets ($|r| > 0.39$, $P < 0.02$) except for the small 2001 U Cay sample ($r = -0.32$, $P = 0.32$). CS was also weakly correlated with burrow length for the combined data ($r = 0.26$; $P = 0.027$), and for the combined 2001 data ($r = 0.44$; $P = 0.005$), but not for the combined 2002 data or for any individual island-year data set ($r = 0.42$ to 0.07 , $P = 0.08$ to 0.96). CS was not related to nest depth for any data subset ($|r| < 0.49$, $P > 0.09$) except for the combined 2001 data ($r = 0.44$, $P = 0.004$).

Relative clutch size (RCS; CS/May body mass $\times 100$) averaged 0.34 (Table 3), suggesting that on average one egg is produced for each 293 g BM. RCS did not differ significantly between islands or years (Table 3), and was not correlated with SVL ($r = -0.06$, $P = 0.62$). There was no relationship between RCS and date during the nesting season ($r = 0.1$; $P = 0.93$).

Egg size.—The leathery-shelled eggs averaged 66.0 ± 4.9 mm in length (EL; $n = 326$; range, 50.0–82.4), 35.4 ± 2.1 mm in width (EW; $n = 326$; range, 29.9–43.2), and 49.4 ± 4.1 g in mass (EM; $n = 326$; range, 37.9–60.0). EL and EW were each correlated with EM (EM = $0.38EL + 24.08$, $r = 0.45$, $P < 0.0001$; EM = $0.97EW + 15.07$, $r = 0.50$; $P < 0.0001$); however, EL and EW were inversely related (EL = $-0.16EW + 45.64$; $r = -0.36$; $P < 0.0001$). EL and EW were related to EM by the multiple regression equation EM = $0.61EL + 1.48EW - 43.40$ ($r = 0.84$; $P < 0.0001$).

Flaccid eggs (i.e., eggs with nearly typical shell dimensions but with much reduced contents) were found in 6 of 34 clutches in 2001 (three on each Cay; 9 total eggs) and 6 of 41 clutches in 2002 (three on each Cay; 8 total eggs). These eggs averaged 63.3 ± 5.06 mm EL and 31.2 ± 2.8 mm EW, but only 31.1 ± 4.1 g EM (ca. 63% of normal egg mass; see above). The presence of these eggs in nests could be related to no other measured variable (e.g., body size, age, timing, burrow characteristics, etc). None of these flaccid eggs developed (see below).

Mean EL per clutch did not differ between years on the same island ($t < 0.6$; $P > 0.55$); however, eggs were longer on Leaf Cay than U Cay (Table 3), both within years ($t = 2.4$ to 2.8 ; $P = 0.02$ to 0.008) and with both years' data combined ($t = 3.64$; $P = 0.005$). Mean EW also did not differ between years on the same

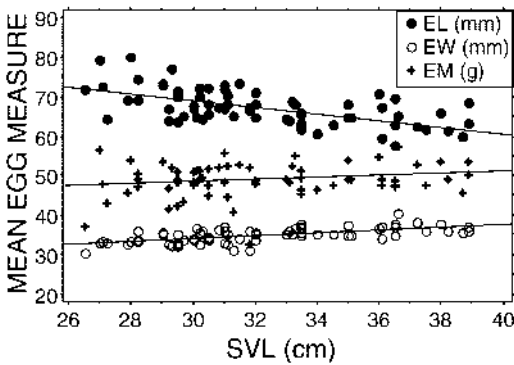


FIG. 10.—Relationship between female body size (snout-vent length; SVL in cm) and egg size (egg length in cm; egg width in cm; egg mass in g) in Allen Cays iguanas. Plotted regression equations are $EL = -0.85SVL + 94.73$ ($r = -0.61$; $P < 0.0001$), and $EW = 0.38SVL + 22.83$ ($r = 0.65$; $P < 0.0001$). Regression line for egg mass is not significant ($r = 0.02$; $P = 0.09$).

island ($t < 1.8$; $P > 0.07$); however, eggs on U Cay were wider than those on Leaf Cay (Table 3), both within year ($t = 2.2$ to 2.8 ; $P = 0.03$ to 0.008) and with both years combined ($t = 3.7$; $P = 0.0005$). These differences are explained (at least in part) by the relationship between egg size and body size (see below). Mean EM did not differ between islands or years ($t < 1.3$; $P > 0.18$ for all comparisons; Table 3).

EL was negatively correlated with body size (SVL or BM; Fig. 10) and age for all data combined ($r < -0.50$; $P < 0.0001$ for all three analyses), as well as for data from separate years and islands ($r < -0.45$; $P < 0.047$ for all comparisons). For separate island-year samples egg length was negatively correlated with SVL for Leaf Cay samples ($r < -0.56$, $P < 0.002$), but not for the smaller U Cay samples ($r = -0.40$ and -0.52 , but $P = 0.10$ and 0.22). The same statistical pattern was found for the relationship between EL and age.

EW was positively correlated with body size (SVL or BM; $r > 0.65$; $P < 0.0001$; Fig. 10) for all data combined, as well as for data from separate years and islands ($r > 0.42$; $P < 0.05$ for all comparisons). Individual island-year samples showed the same pattern, but only those from Leaf Cay were statistically significant (for SVL, $r = > 0.73$, $P < 0.0003$; $r < 0.57$, $P = 0.07$ to 0.15 for U Cay). EW was also positively correlated (though less strongly) with age ($r = 0.30$; $P = 0.018$ for all data;

$r > 0.38$, $P < 0.028$ for 2001 and Leaf Cay data; $r < 0.29$, $P > 0.14$ for 2002 and U Cay data). Of the individual island-year samples, only that for Leaf Cay in 2001 was significant ($r = 0.55$, $P = 0.005$).

Egg elongation (mean clutch EL/ mean clutch EW) averaged 1.93 ± 0.20 (range 1.54–2.40; $n = 74$), but was highly negatively correlated with body size (Fig. 11). EM was not correlated with body size or age for all data combined nor for any subset of the data by year and/or island ($|r| < 0.40$; $P > 0.05$ for all comparisons; Fig. 10). ANCOVA to remove the effects of body size (SVL) revealed no differences in adjusted egg length, egg width, or egg mass between years or islands (for all slopes and intercepts, $P > 0.08$), except egg width was greater in 2002 than 2001 (for intercept, $F = 19.2$, $P < 0.0001$).

During the course of the nesting season, EL tended to increase ($r = 0.41$, $P = 0.0003$ for all data; $r > 0.36$, $P < 0.02$ for data by year; but $r < 0.59$, $P > 0.05$ for data by island or island-year). EW tended to decrease during the season ($r = -0.57$, $P < 0.0001$ for all data; $r < -0.49$, $P < 0.001$ for all data subsets except for the combined U Cay data and the 2001 U Cay data: $r > -0.37$, $P > 0.08$). There was no change in EM through the season (e.g., for all data, $r = 0.17$, $P = 0.15$; $P > 0.05$ for all other island and/or year samples). These patterns reflect the seasonal changes in female body size, and its relationship to egg dimensions (see above).

Relative egg mass (REM; mean egg mass of clutch / May body mass $\times 100$) averaged 3.9 (Table 3), and did not differ between years on the same island ($t < 1.03$; $P > 0.12$). However, REM did differ between islands for both years combined ($t = 3.6$; $P = 0.0006$) and for the 2001 data ($t = 3.8$; $P = 0.0007$), but not for the 2002 data ($t = 1.8$; $P = 0.089$).

REM was strongly negatively correlated with body size (SVL; $r = -0.90$, $P < 0.0001$ for all data; $r = -0.67$ to -0.92 , $P < 0.048$ for all island-year comparisons; Fig. 12) and with age ($r = -0.62$; $P < 0.0001$ for all data; $r = -0.42$ to -0.72 , $P = 0.0001$ to 0.0013 for all other data subsets, except for the small [$n = 15, 7$ and 8] U Cay, 2001 U Cay, and 2002 U Cay data sets: $r = -0.36$ to -0.55 , $P = 0.16$ to 0.35). REM also increased through the nesting season (for all data, $r = 0.59$, $P < 0.0001$; $r >$

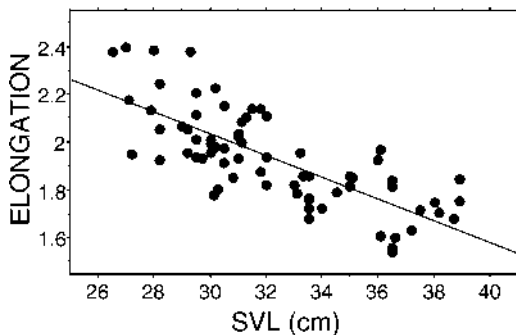


FIG. 11.—Relationship between female body size (snout-vent length; SVL in cm) and egg elongation (EE, mean clutch egg length/mean clutch egg width) in Allen Cays iguanas. Least squares regression is plotted ($EE = -0.045SVL + 3.392$; $r = -0.75$; $P < 0.0001$).

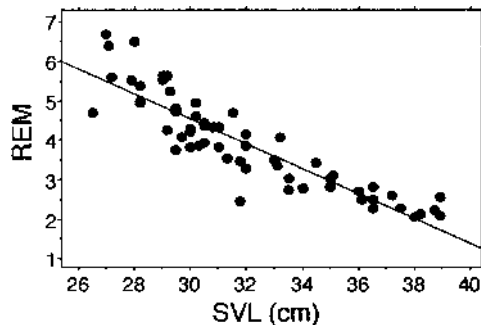


FIG. 12.—Relationship between female body size (snout-vent length; SVL in cm) and relative egg mass (REM, mean clutch egg mass/body mass in May $\times 100$) in Allen Cays iguanas. Least squares regression is plotted ($REM = -0.31SVL + 3.62$; $r = -0.87$, $P < 0.0001$).

0.45, $P < 0.03$ for all other island-year data sets except for 2001 on U Cay: $r = 0.10$, $P = 0.80$).

Raw clutch size was not correlated with mean egg mass of clutch ($r = 0.06$; $P = 0.61$). Partial correlation analyses to remove the effects of body size (SVL) revealed no tradeoff between CS and EM ($r = -0.12$, $P = 0.33$) or EW ($r = 0.20$, $P = 0.09$), but that standardized clutch size and EL were inversely correlated ($r = -0.49$, $P < 0.0001$).

Clutch mass.—Clutch mass averaged 226 ± 85 g (Table 3), and did not differ significantly between years ($t < 1.18$, $P > 0.24$, for all data or data by island). CM was positively correlated with body size (for SVL, $r > 0.68$, $P < 0.002$ for all island-year samples except for U Cay in 2001: $r = 0.42$, $P = 0.19$), and generally so with age ($r = 0.46$; $P = 0.0002$ for all data; $r > 0.35$, $P < 0.04$ for the 2001, 2002, combined Leaf Cay, and 2002 Leaf Cay data, but not significant for the other subsamples: $r < 0.37$, $P > 0.14$). Because of this relationship (and the larger size of U Cay females; see above), CM was significantly greater on U Cay than on Leaf Cay ($t > 2.32$, $P < 0.03$ for all data or data by year) and it decreased through the nesting season ($r = -0.57$, $P < 0.0001$ for all data; $r < -0.46$, $P < 0.01$ for all subsamples except for U Cay in 2001: $r = -0.26$, $P = 0.44$). ANCOVA to remove the effects of body size (SVL) revealed no difference in adjusted clutch mass between years or islands (for both slopes and intercepts, $P > 0.30$).

Clutch mass was much more strongly correlated with clutch size ($r = 0.97$, $P <$

0.0001) than egg mass ($r = 0.26$, $P = 0.023$). Furthermore, partial correlation to eliminate the body size effect on these variables revealed that clutch size was still highly correlated with clutch mass ($r = 0.92$, $P < 0.0001$), but that egg mass was not ($r = 0.19$, $P = 0.12$). Thus, increases in clutch mass are primarily the result of increases in clutch size rather than egg mass.

Relative clutch mass (clutch mass/May body mass $\times 100$) averaged 16.5 ± 3.7 (Table 3) and did not differ significantly between islands or years ($t < 1.5$; $P > 0.14$ for all island-year comparisons). It also was not significantly related to body size (for SVL, $|r| < 0.35$, $P > 0.36$ for all data or any subset) or to age ($|r| < 0.51$, $P > 0.15$ for all data or any subset), and did not vary by nest date ($|r| < 0.33$, $P > 0.27$ for all data or any subset).

Nest Success

Hatching apparently occurs in late September to early October, after which the hatchlings dig out of the nest and begin feeding independently. All hatchlings had left the nests in 2001 by our arrival on 18 October. Nests excavated the first week of October 2002 that contained live hatchlings (i.e., not yet emerged) had been completed 85, 86, 88 (two nests), or 89 (two) days earlier. Four nests under construction on Leaf Cay when we left on 13 July had hatched by our return in October after maximum incubation times (i.e., since 13 July) of 82, 83, and 84 days (two); the latter three nests contained live hatchlings (the

last in the act of hatching), but hatchlings had already emerged from the first. Only one nest (in a very shady location on Leaf Cay) was unhatched on 2 October, 85 days after it was completed. Hatchlings had emerged from most nests by our arrival on 1 October, the shortest intervals since nest construction being 84, 85, 87, 88, and 89 days. Hatchlings had emerged from every successful nest ($n = 19$) older than 89 days. These data suggest that incubation must require about 80 to 85 days, although we cannot be certain that incubation does not take fewer than 80 days in some nests. Emergence apparently occurs within just a few days after hatching.

Hatchlings ($n = 37$) captured in nest chambers in early October 2002 (i.e., before they had exited the nest) averaged 9.5 ± 0.27 cm SVL, and 32.8 ± 3.2 g BM ($n = 37$; Table 3), and did not differ between cays ($t < 1.27$; $P > 0.21$). Mean hatchling mass per clutch was correlated with mean egg mass for that clutch ($r = 0.89$; $P = 0.007$; $n = 7$), although mean hatchling SVL was not ($r = 0.32$; $P = 0.49$). Neither mean hatchling SVL nor BM was correlated with female SVL or BM ($r < 0.35$; $P > 0.50$ for all comparisons).

Survivorship to emergence of eggs in individual nests ranged from 0% to 100% and averaged $75.2 \pm 34.5\%$ ($n = 86$). For Leaf Cay it did not differ significantly (Mann-Whitney $U = 1.0$; $P = 0.29$) between 2001 (79.0 ± 26.9) and 2002 (83.0 ± 32.5). Similarly, it did not differ significantly ($U = 0.59$; $P = 0.55$) for U Cay between 2001 (66.4 ± 40.5) and 2002 (58.0 ± 43.5). However, it was significantly higher on Leaf Cay than on U Cay for the 2002 data ($U = 2.0$; $P = 0.05$), though not for the combined 2001–2002 data (81.0 ± 29.5 vs. 61.9 ± 49.5 ; $U = 1.9$; $P = 0.059$), nor for the 2001 data ($t = 1.2$; $P = 0.24$).

We also calculated survivorship to hatching based on 11 clutches of eggs from previous years that were unearthed in well-defined (i.e., otherwise undisturbed) nest chambers while we were excavating recently deposited nests. Survivorship in these nests ranged from 40 to 100% across nests (mean 91.5% ; $n = 11$), and 41 of 45 total eggs in those nests hatched (91.1% success). This may be an overestimate of survivorship since undeveloped eggs (and their shells) decompose much more rapidly than hatched egg shells.

Of 106 total eggs deposited on Leaf Cay in 2002, 91 (85.8%) hatched and emerged successfully (counting those captured alive in their nests as emerged), compared to 111 of 137 eggs (81.0%) in 2001. Of 73 eggs deposited on U Cay in 2002, only 37 (50.7%) were successful, compared to 49 of 68 (72.1%) in 2001. For all 384 eggs, 303 (78.9%) hatched and emerged. Individual egg mortality occurred because of rupture by the nesting female, the eggs laid were flaccid and died immediately, during early development (apparently from desiccation), during mid to late development (again apparently from desiccation), were depredated by insects or crabs during development, as full-term embryos still in the egg, during pipping of the egg, as hatchlings in the nest, or because eggs were completely removed from their nests (presumably by crabs) (Table 4).

The production of flaccid eggs by some females was not related to any biotic or abiotic factor that we recorded. Five of 14 females that nested in both 2001 and 2002 produced one or more flaccid eggs in their clutches, but only in one of the two years. All flaccid eggs died early in development, and although survivorship among the non-flaccid eggs in these clutches (67.3 ± 38.7) was less than that among nests without flaccid eggs (82.3 ± 30.2), the difference was not significant ($U = 1.4$; $P = 0.15$; one-tailed $t = 1.56$; $P = 0.06$). Nests with flaccid eggs had significantly lower RCM ($\bar{x} = 0.13 \pm 0.05$ vs. 0.17 ± 0.03 ; $t = 3.4$; $P = 0.0012$) and RCS (0.30 ± 0.08 vs. 0.35 ± 0.08 ; $t = 2.1$; $P = 0.04$) than nests without flaccid eggs; however, they differed for no other abiotic or biotic variable we measured.

Soil moisture (wet mass – dry mass/dry mass in %) in 23 nests on Leaf Cay and 14 nests on U Cay excavated in October 2002 averaged $6.35 \pm 3.14\%$ (range 1.9 to 12.9), and was significantly wetter ($U = 6.25$; $P < 0.0001$) on U Cay (9.2 ± 2.8) than Leaf Cay (4.6 ± 1.7). The driest nests were on the eastern (windward) sandy ridge on Leaf Cay, and the wettest were from the eastern and western edges of the sandy isthmus on U Cay. Survivorship to emergence of eggs in the nest was significantly lower in nests with moistures greater than 10% ($\bar{x} = 53 \pm 42\%$) than for those with moistures less than 10% ($89 \pm 24\%$; $U = 2.93$; $P = 0.003$). It was

TABLE 4.—Causes of individual egg mortality in nests by year for Allen Cay iguanas. Total eggs in 2001 and 2002 were 205 and 179, respectively. Number lost by each cause is followed by the percent of total eggs lost to that cause.

Cause	2001	2002
Rupture by female	5 (2.4)	2 (1.1)
Flaccid eggs	8 (3.9)	12 (6.7)
Early in development	10 (4.9)	6 (3.4)
Mid to late development	7 (3.4)	9 (5.1)
Depredated	3 (1.5)	1 (0.6)
Full term embryos	4 (2.0)	11 (6.1)
While pipping	2 (1.0)	4 (2.2)
In nest	1 (0.5)	5 (2.8)
Eggs gone	4 (2.0)	1 (0.6)

inversely correlated with soil moisture (Spearman Rank $Z = -1.93$; $P = 0.05$), positively correlated with nest date ($Z = 1.91$; $P = 0.056$), nest depth ($Z = 2.74$; $P = 0.006$; Fig. 13), and relative clutch mass ($Z = 2.15$; $P = 0.03$), but not correlated with any other abiotic or biotic parameter we measured.

DISCUSSION

Nesting Behavior

The reproductive behavior of *Cyclura cythlura inornata* is similar to that of most other iguanids, with females migrating to nest sites 3–7 weeks after mating, excavating a new burrow for oviposition, refilling that burrow after egg-laying, and defending that nest site (e.g., reviews in Iverson, 1979, and Wiewandt, 1982). Copulation has been observed in the field for *Cyclura nubila caymanensis* (April to early May; Gerber, 2000a), *C. cythlura inornata* (18–26 May; this study), *C. r. rileyi* (26–30 May; Hayes et al., 2004), *C. r. nuchalis* (21 May–9 June; Hayes et al., 2004), and *C. cornuta stejnegeri* (16–29 June; Wiewandt, 1977), as well as for captive *C. carinata* caught in early April (24 April–9 May; Iverson, 1979). Although the interval between mating and nesting ranges from three to seven weeks across all iguanids (Wiewandt, 1982; Gerber, 2000a; Hayes et al., 2004), our data (including our observation of one individual female seen mating and nesting) suggest that five weeks is typical for *C. c. inornata*. Furthermore, that same interval is also suggested by the general

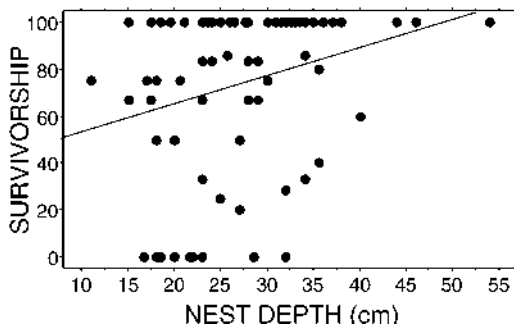


FIG. 13.—Relationship between survivorship of eggs in nest (in percent emergence) and nest depth for Allen Cays iguanas. Least squares regression is plotted (NS = $1.20ND + 41.46$; $r = 0.28$; $P = 0.012$); Spearman Rank $Z = 2.74$, $P = 0.006$.

reproductive phenologies of other *Cyclura*: *C. carinata* (Iverson, 1979), *C. cornuta stejnegeri* (Wiewandt, 1977), *C. n. caymanensis* (Gerber, 2000), and *C. rileyi* (Hayes et al., 2004).

Migration of females from normal activity centers to distant nesting sites is also typical of iguanids, and has been documented in *Cyclura collei* (Lewis, 1944; Vogel, 1994), *C. cornuta stejnegeri* (up to 6.5 km; Wiewandt, 1977, 1982), *C. cythlura inornata* (30–173 m; this study), *C. c. figginsi* (up to 500 m; Coenen, 1995), *C. n. nubila* (Street, 1952; Christian, 1986), *C. n. caymanensis* (Lewis, 1944; Gerber, 1997); *C. n. lewisi* (Lewis, 1944; Burton, 2000), and *C. rileyi nuchalis* (145–1000 m; Hayes et al., 2004), as well as in *Amblyrhynchus cristatus* (up to 3 km; Carpenter, 1966; Eibl-Eibesfeldt, 1984; Rauch, 1988; Rodda and Grajal, 1990), *Conolophus subcristatus* (up to 15 km; Werner, 1982, 1983), *C. pallidus* (up to 1 km; Christian and Tracy, 1982), *Ctenosaura similis* (Hackforth-Jones, in Iverson, 1979; Mora, 1989), *Iguana iguana* (up to 3 km; Rand, 1968; Montgomery et al., 1973; Bock, 1989), and *I. delicatissima* (up to 900 m; Day et al., 2000). However, female *Cyclura carinata* (Iverson, 1979), *Dipsosaurus dorsalis* (Norris, 1953), and *Sauromalus obesus* (Johnson, 1965) apparently do not migrate beyond normal activity ranges to nest. The fact that most iguanas migrate to open areas to nest, many passing through areas that seem to offer suitable nesting sites (review in Wiewandt, 1982; Hayes et al., 2004; this study), suggests some

females may be returning to the area where they were hatched. Natal homing has not yet been clearly demonstrated for an iguanid, but is suspected (Wiewandt, 1982).

Females of all species of rock iguanas except one apparently dig a separate burrow in which to nest, and then cover it completely following oviposition (references in Tables 5, 6). However, for *Cyclura carinata* in the Turks and Caicos Islands, Iverson (1979) found nest chambers in side tunnels off what appeared to be active retreat burrows. That species could be unique in its nesting behavior, or those observations could have been biased by high rates of predation by feral cats and dogs on nest-guarding females (i.e., depredated before they completely filled and covered their nesting burrows).

Although the actual nesting sequence (including digging, laying, covering, and defense) is similar across most iguanid species (Wiewandt, 1982), conspicuous variation occurs in at least four aspects: 1) the timing of nesting; 2) the occurrence of pre-nesting defense; 3) whether or not the female closes herself completely inside the nest burrow during oviposition, and 4) the length and intensity of post-oviposition nest defense.

Most species of rock iguanas nest from early June to mid-July (including *C. c. inornata*); however, *C. cornuta stejnegeri* nests after this period, and *C. ricordii* and *C. n. caymanensis* nest as early as late May (Table 5). In addition, despite being conspecific with *C. c. inornata*, *C. c. cyclura* nests as early as mid-May (Table 5). This variation may relate to varied sensitivity to photoperiod (rather than rainfall), the factor Wiewandt (1982) identified as the probable cue for nesting in iguanas. His hypothesis has been supported by a nearly six month shift in the reproductive cycle of captive *Cyclura cornuta* moved to Sydney, Australia (Table 5; Boylan, 1984, 1985). However, data from *Amblyrhynchus cristatus* (Rubenstein and Wikelski, 2003) suggest that sea surface temperatures affect food quality, and the latter provides the proximate cue for the timing of mating (and indirectly, perhaps nesting as well).

The ultimate explanation for variation in nest timing also remains unclear. The timing of nesting probably represents a local adaptive compromise among selective pressures oper-

ating on females (from physiological constraints to social pressures), eggs (via nest temperature, moisture, and respiratory gas concentrations), and hatchlings (through food availability and risk of predation) (van Marken Lichtenbelt and Albers, 1993; Hayes et al., 2003). Determining the relative importance of these factors to reproductive phenology of single populations is difficult. For example, it is not clear why *C. c. cyclura* on Andros begins nesting three weeks before *C. c. figginsi* in the Exumas, and four weeks earlier than *C. c. inornata* in the Allen Cays, when the three have been geographically isolated by rising sea levels for less than 18,000 years (Malone et al., 2000). Even more remarkable, given their geographic and genetic proximity, is the consistent one-week difference in nest timing of Allen Cays iguanas on U Cay versus Leaf Cay, which cannot be explained by any selective pressure previously applied to iguanids. Perhaps because the majority of adult females on Leaf Cay remain (unnaturally) near the primary feeding (by humans) beaches when not nesting (Fig. 3), their ability to select optimal basking sites (via competition for space) is compromised and the result is a delay in nesting on that island. Likewise, local thermal conditions might also explain the early nesting of the Andros iguana.

Nest defense prior to oviposition occurs in at least *Cyclura cornuta stejnegeri* (Wiewandt, 1977), *C. c. figginsi* (Coenen, 1995), and *C. c. inornata* (this study), as well as for *Amblyrhynchus cristatus* (Bartholomew, 1966; Carpenter, 1966; Eibl-Eibesfeldt, 1966, 1984; Rauch, 1988), *Brachylophus fasciatus* and *B. vitiensis* (Gibbons and Watkins, 1982), *Conolophus pallidus* (Christian and Tracy, 1982), and *Iguana iguana* (Rand, 1968). However, it is apparently rare in an introduced population of *Cyclura nubila* off Puerto Rico (Christian, 1986).

Nearly all *Cyclura* defend their completed nests (*C. carinata*, Iverson, 1979; *C. collei*, Vogel, 1994; *C. cornuta stejnegeri*, Wiewandt, 1977; *C. c. cyclura*, Knapp et al., 1999; *C. c. inornata*, this study; *C. n. nubila*, Christian, 1986; *C. n. caymanensis*, Gerber, 2000a; *C. pinguis*, Gerber, 2002b; *C. rileyi*, Hayes et al., 2003), as do at least six other iguanids (Rand, 1968; Alvarez del Toro, 1972; Trillmich, 1979; Werner, 1982; Christian and Tracy, 1982;

TABLE 5.—Reproductive phenology of rock iguanas of the genus *Cyclura*. Species are listed in order of their approximate north to south distribution. Incubation period is reported to hatching (^H) or to emergence (^E).

Taxon	Nesting season	Incubation period (days)	Emergence season	Source
<i>cyclura inornata</i>	mid-June to early July	80–85 ^H	late September to early October	This paper
<i>cyclura cyclura</i>	mid-May to late June	—	—	Knapp et al., 1999; Knapp, 2001b
<i>cyclura figginsi</i>	early to mid-June	—	—	Coenen, 1995; Knapp, 1995
<i>rileji rileji</i>	early July to late July	91–92 ^E	late September–early October	Cyril, 2001; Hayes et al., 2004
<i>rileji nuchalis</i>	late June to early July	—	—	Thornton, 2000; Hayes et al., 2004
<i>carinata carinata</i>	early June	ca. 90 ^E	September	Iverson, 1979
<i>nubila nubila</i>	14 June to 23 July ^a	94 ± 1 @ 31 C ^{Ha}	October?	Alberts, 1995; Alberts et al., 1997
<i>nubila nubila</i>	—	83–85 @ 30.5 C ^a	—	Rehak and Velensky, 1997
<i>nubila nubila</i>	—	93–119 ^a	—	Street, 1952; Shaw, 1954
<i>nubila lewisi</i>	late June to early July	80–91 ^E	late September	Burton, personal communication
<i>nubila caymanensis</i>	late May to mid-June	63–80 ^E	early August to early September	Gerber, 2000a
<i>collei</i>	mid to late June	85–87 ^E 86–90 @ 30 C ^{Ha}	September	Vogel, 1994, 2000
<i>cornuta cornuta</i>	June ^a	ca. 85 ^H 81–87 @ 31 C ^{Ha}	8–15 September ^a	Ottenwalder, 1978, 2000a
<i>cornuta cornuta</i>	—	106–125 ^a	—	Shaw, 1969; Haast, 1969
<i>cornuta cornuta</i>	December–February ^a (Australia)	87–109 ^{Ha}	April–May ^a	Boylan, 1984, 1985
<i>cornuta stejnegeri</i>	mid-July to early August	78–89 ^{H²}	mid- to late October	Wiewandt, 1977; Wiewandt and Garcia, 2000
<i>ricordii</i>	May–June	95–100 ^{H²}	September to October	Ottenwalder, 2000b
<i>pinguis</i>	mid-June to mid-July	87–94 ^E	mid-September to mid-October	Gerber, 2000b
<i>nubila nubila</i> ^b	early June	70–78 ^H	late August to early September	Christian, 1986

^a Captive data.^b Introduced population from Cuba to island off Puerto Rico.

Gibbons and Watkins, 1982; Rauch, 1988). However, Coenen (1995) and Knapp (2000b) reported that female *C. c. figginsi* do not defend their covered nests. This observation is surprising given the near genetic identity of *C. c. figginsi* and *C. c. inornata*, and their sister relationship with *C. c. cyclura* (Malone et al., 2000). Gerber (1997) noted protracted nest defense in female *C. n. caymanensis* that nested in rocky areas, but not in females nesting in sandy areas. Likewise, at least three populations of *Amblyrhynchus cristatus* in the Galapagos Islands clearly exhibit nest defense (Eibl-Eibesfeldt, 1966; Trillmich, 1979; Rauch, 1988), whereas a fourth population may (Boersma, 1983) or may not (Carpenter, 1966; Eibl-Eibesfeldt, 1966).

Length of nest defense in iguanids is also quite variable. *Cyclura carinata* in the Caicos

Islands defends for several days to at least a month (Iverson, 1979). *C. collei* on Jamaica defends for 9–17 days (mean, 13.4; Vogel, 1994). Most female *C. c. inornata* in the Allen Cays were still defending their nest sites after three to four weeks (this study). Three of sixteen female *C. cornuta stejnegeri* on Mona Island did not defend, but the others defended from one to ten days (mean 3.4 days for defenders; Wiewandt, 1977). Similarly, defense by individual female *C. n. nubila* introduced off Puerto Rico ranged from none to at least 20 days of defense (Christian, 1986). In captivity, one female *C. n. nubila* defended her nest site for three months in each of three consecutive years (Ehrig, 1993). In the Galapagos Islands, 25% of female *Conolophus pallidus* defend the nest site for as long as a month (but some exhibit no guarding;

TABLE 6.—Nest burrow dimensions among species of the genus *Cyclura*. Nest depth is from the soil surface to the bottom of the nest chamber. Species are listed in order of their approximate north to south distribution.

Species	Burrow length (cm)		Nest depth (cm)		Source
	Mean \pm 1 SD	Range	Mean \pm 1 SD	Range	
<i>cyclura inornata</i>	149 \pm 55	54–330	27.7 \pm 8.2	11–59	This paper
<i>cyclura figginsi</i>	61	—	—	8–13 ^a	Knapp, 2000b
<i>rileyi rileyi</i>	53	30–116	22	18–28	Hayes et al., 2004
<i>rileyi nuchalis</i>	129	69–235	22	14–40	Hayes et al., 2004
<i>nubila caymanensis</i>	—	—	—	10–50 ^a	Gerber, 2000a
<i>collei</i>	—	90	—	50	Vogel, 1994
<i>cornuta cornuta</i>	—	40 ^b	—	—	Haast, 1969
<i>cornuta stejnegeri</i>	110	60–115	54	30–76	Wiewandt, 1977
<i>ricordii</i>	—	—	—	40	Ottewalder, 2000b
<i>pinguis</i>	186 \pm 105	65–320	67 \pm 19	38–90	Gerber, 2000b
<i>nubila nubila</i> ^c	153	95–310	43	26–70	Christian, 1986

^a To top of egg chamber.

^b Captive data.

^c Introduced population from Cuba to island off Puerto Rico.

Christian and Tracy, 1982), whereas female *Amblyrhynchus cristatus* defended nests from zero to 16 days (Rauch, 1988). Finally, nest defense in *Iguana iguana* in Panama apparently lasts only up to four days (Rand, in Wiewandt, 1982), but in Chiapas, Mexico, it apparently continues for up to 15 days (Alvarez del Toro, 1972).

This variation in nest defense across and within populations suggests that given the appropriate social stimuli (e.g., as a result of high female density in limited and/or optimal nesting sites), all iguanids may have the potential to respond to them by protracted nest defense. In cases where these stimuli are absent or reduced (or where the animals are disturbed by humans), iguanas may exhibit less nest defense or forgo it altogether. Rauch's (1988) observations for the marine iguana *Amblyrhynchus cristatus* of longer defense by earlier nesters supports this hypothesis. The importance of age as a factor influencing nest defense also deserves attention.

Some females of three species of rock iguanas have been observed to close the nesting burrow behind them during the final stages of nest construction and oviposition (*C. n. nubila*, Christian, 1986; *C. n. caymanensis*, Gerber, 1997; *C. rileyi*, Hayes et al., 2004; and *C. cyclura*, this study). This burrow-closing behavior has also been noted for the Galapagos land iguana *Conolophus pallidus* (Christian and Tracy, 1982), but for no other iguanid. Not only does this behavior make it more difficult for the female to be disturbed during actual

oviposition, but much less energy is expended by the female than if she removed all the soil to the surface. We suspect that this behavior is exhibited by other iguanids but has not been noticed because it happens deep in the nesting burrow.

Typical nest sites for all but one population of *Cyclura* are in open soil areas (reviews in Wiewandt, 1982, and Alberts, 2000); however, *C. c. cyclura* regularly nests in termite mounds, apparently because exposed soil is limited (Auffenberg, in Iverson, 1979; Knapp et al., 1999; Knapp, 2002). Estimates of canopy cover of nest sites are available only for our study populations of *C. c. inornata* (22%) and that of *C. r. rileyi* off San Salvador (19%; Hayes et al., 2004), and demonstrate the pattern of choosing an open, sunny site. For *C. c. inornata* shadier nests tended to be shallower and shorter, but to have average nest temperatures similar to those of sunnier sites. Although shading is only one of several determinants of soil temperatures at our sites (along with wind speed and direction, proximity to coastline, etc.), these patterns suggest that females are constructing nest chambers at depths providing preferred temperatures, and that females nesting in more open areas may have to dig longer burrows in order to find depths with appropriate temperatures.

Although there was no relationship between female body size and nest depth within our populations, Hayes et al. (2004) found that larger female *C. r. nuchalis* dug deeper burrows. That pattern is also evident across

species of *Cyclura* (Table 6; $r = 0.92$; $P = 0.0035$; $n = 7$). There was only a weak tendency for larger female *C. c. inornata* (see Results) and larger female *C. r. nuchalis* ($r = 0.79$; $P = 0.06$; Hayes et al., 2004) to dig longer nest burrows. No relationship ($r = 0.49$; $P = 0.26$) exists between body size and nest burrow length across species of *Cyclura* (Table 6).

Distances between the closest nests are similar among various species of *Cyclura*. We observed at least eight pairs of nests separated by 5–8 m, Gerber (2000b) reported distances of 5.1 and 8.1 m for *C. pinguis*, and Hayes et al. (2004) found up to 3.6 nests in a 10 m radius (estimated internest distance, 10.5 m) in *C. rileyi*. In the Allen Cays we also observed one instance of the construction of a nest only 1.0 m from another, and two cases where a second female used exactly the same burrow as an earlier female (destroying the earlier eggs in the process). The latter observation was also made for *C. rileyi* by Hayes et al. (2004). These data (see also Rand, 1968; Rand and Dugan, 1980, 1983; Rodda and Grajal, 1990) suggest that optimal nest sites may frequently be limiting in iguanids, resulting in communal nesting (review in Wiewandt, 1982; Eibl-Eibesfeldt, 1984; Mora, 1989; review in Alberts, 2000). One consequence of concentrated nesting is that females often dig up nests of other females (e.g., Rand, 1968; Sexton, 1975; Rand and Dugan, 1980, 1983; Werner, 1982; Rauch, 1988). Furthermore, this competition for sites may even result in the death of females from burrow collapse, as may have happened for *C. cyclura inornata* (this study), and has been noted for *Amblyrhynchus cristatus* (Carpenter, 1966; Boersma, 1983; Rauch in Eibl-Eibesfeldt, 1984; Rauch, 1988; Laurie and Brown, 1990) and *Iguana iguana* (Rand, 1968).

Average incubation temperatures for *C. c. inornata* (31.4 C; this study) were similar to those of other rock iguanas: *C. c. cyclura* (32.8 C, in termitaria; Knapp, 2000b), *C. r. nuchalis* (ca. 30 C; Thornton, 2000), *C. cornuta stejnegeri* (30–32 C for two days of incubation; Wiewandt, 1977), *C. ricordii* (30–31 C; Ottenwalder, 2000b), *C. nubila* (32.2 C for one day of incubation; Christian and Lawrence, 1991), and *C. pinguis* (30.8 C; Gerber, 2000b). The consistency of these incubation temperatures across species and

environments further supports our earlier hypothesis that females may be selecting nest sites offering conditions optimal for incubation temperatures. For example, Licht and Moberly (1965) determined that optimal incubation temperature for *Iguana iguana* in Colombia was 30 C, and Rand (1972) demonstrated that temperatures in natural nests of the same species in Panama were 31–32 C.

Nesting Frequency

On average only one in three female *C. c. inornata* of adult size nested each year during our study, and interannual nest frequency tended to increase with female size (and presumably age). Similarly, Abts (1987) found that the annual frequency of reproduction in female chuckwallas (*Sauromalus obesus*) ranged from 0% to 95% (mean 52%; see also Berry, 1974, and Case, 1982). In addition, Laurie (1990) found that 1.0 to 87.9% (mean, 51.1%) female *Amblyrhynchus cristatus* nested each year. These data suggest that less than annual reproduction may be common in iguanas. However, Bock et al. (1985) believed that females of *Iguana iguana* in Panama nest every year (though their return rates to the communal nesting site from year to year were only 30–45%) and all adult females sampled during the reproductive season there by Rand (1984) were gravid.

Seven of 13 female *C. c. inornata* that nested two years in a row constructed nests in 2002 within 1 m of the nest deposited in 2001. The other six produced nests from 8 to 77 m apart. These data provide some evidence for nest site fidelity, particularly considering the possibility that our regular nesting patrols may have disturbed nest site selection by some females. Some degree of nest site fidelity apparently occurs in *Amblyrhynchus cristatus* and *Iguana iguana*, with 37% and 30 to 45% of females, respectively, from one year returning to the communal nesting area to nest the following year (Rauch, 1988; Bock et al., 1985).

Female Age and Size

Female *C. c. inornata* require at least 12 years to reach maturity, longer than any other lizard for which data are available (Table 7; Wiewandt, 1982; Shine and Charnov, 1992, and references therein). Juvenile growth rates are slower than those of any

TABLE 7.—Maturity in female rock iguanas of the genus *Cyclura*. Species are listed in order of their approximate north to south distribution.

Species	Age (yr)	SVL (cm)	Body mass (g)	Source
<i>cyclura inornata</i>	12	26–27	750	This paper
<i>rileyi rileyi</i>	—	21.5	340	Hayes et al., 2004
<i>rileyi nuchalis</i>	—	19.5	260	Hayes et al., 2004
<i>carinata carinata</i>	6–7	18.5–20	200–300	Iverson, 1979
<i>nubila nubila</i>	2–3	—	—	Perera, 2000
<i>nubila caymanensis</i>	2–3	30.8	1141 ^a	Gerber, 2000a
<i>collei</i>	7–8	—	—	Hudson, personal communication (captive)
<i>cornuta cornuta</i>	3–4	—	—	Ottenwalder 2000a; Boylan, 1984, 1985 (captive data)
<i>cornuta stejnegeri</i>	6–7	38.0	2119 ^a	Wiewandt, 1977; Wiewandt and Garcia, 2000
<i>ricordii</i>	2–3	—	—	Ottenwalder, 2000b
<i>pinguis</i>	7–9	35–40	—	Carey, 1975
<i>pinguis</i>	4–7	37.8	2086 ^a	Gerber, 2000b
<i>nubila nubila</i> ^b	—	29.3 ^a	983	Christian, 1986

^a Estimated from body mass-snout-vent length regression in Iverson et al. (2004): $BM = 0.04665SVL^{2.948}$.

^b Introduced population from Cuba to island off Puerto Rico.

other species of iguana except *C. carinata* (Iverson and Mamula, 1989; Iverson et al., 2004). It seems likely that this delay in maturity is related to its northern location, although there is no evidence for a latitudinal increase in age at maturity among other rock iguanas (Table 7).

Larger female *C. c. inornata* tend to nest earlier in the season than smaller females, a pattern also found in captive *Cyclura n. nubila* from Cuba (Alberts, 1995; Alberts et al., 1997), wild *C. n. caymanensis* on Little Cayman (Gerber, 1997), and wild *C. r. rileyi* on Green Cay off San Salvador in the Bahamas (Cyril, 2001; Hayes et al., 2004). The opposite pattern was observed for *C. r. nuchalis* on North Cay in the Bahamas (Thornton, 2000; Hayes et al., 2004). Earlier nesting of larger females could be related to their possible earlier insemination (via sexual selection), their hypothesized increased ability to obtain food to support vitellogenesis, their better capacity for thermoregulation during egg development (e.g., via their greater thermal inertia), and their presumed enhanced ability to locate, construct and defend a nest burrow. Which of these reasons are of primary importance in explaining the general pattern will require further field and laboratory study.

Clutch Parameters

Clutch size.—Clutch size in *C. c. inornata* is among the smallest of all the rock iguanas (Table 8). Within that subspecies, clutch size is positively correlated with body size, as it is for every other population of *Cyclura* previously studied (*C. carinata*, Iverson, 1979; apparently in *C. cornuta stejnegeri*, Wiewandt, 1977; *C. n. nubila*, Alberts et al., 1997; *C. pinguis*, Gerber, 2000b; *C. r. rileyi* and *C. r. nuchalis*, Hayes et al., 2004) as well as that of every other studied iguanid: *Amblyrhynchus cristatus* (Trillmich, 1979; Rauch, 1988), *Conolophus subcristatus* (Werner, 1983), *Iguana iguana* (Fitch and Henderson, 1977; Rand, 1984; van Marken Lichtenbelt and Albers, 1993), and *Sauromalus obesus* (Berry, 1974; Case, 1982; Abts, 1987). CS is also related to body size across species of *Cyclura* ($CS = 0.43SVL - 6.34$; $r = 0.74$; $P = 0.004$; $n = 13$; for independent contrasts, $r = 0.76$). The interspecific data suggest that *C. cyclura* and *C. n. nubila* (particularly the introduced population off Puerto Rico) tend to produce relatively fewer eggs than expected based on their body size, and that *C. collei* and *C. n. caymanensis* tend to produce relatively more.

Egg size.—The eggs of *C. c. inornata* fall in the middle of the range of variation among other rock iguanas (Table 8). A comparison of

TABLE 8.—Reproductive parameters for rock iguanas of the genus *Cyclura*. Species are listed in approximate north to south order. REM = mean clutch egg mass/mean female body mass $\times 100$; RCM = mean clutch mass/mean female body mass $\times 100$. See review in Iverson (1979) for additional anecdotal reports.

Species subspecies	Mean adult female size		Clutch size	Mean egg size			Clutch mass	REM	RCM	Hatchling mass (g)	Source
	SVL (cm)	BM (g)		length	width	mass					
<i>cyclura inornata</i>	32.0	1336	4.6	66.0	35.4	49.4	227	3.7	17.0	32.8	This paper
<i>cyclura cyclura</i>	36.2	2080	8.8	71.6	40.1	68.0	351	3.27	16.9	45	Knapp, 2002;
<i>cyclura figginsi</i>	28.5	960	3	85	40	51	153	5.31	15.9	—	Coenen, 1995,
<i>rileyi rileyi</i>	~24.3	567 ^a	4.4	53.4	29.5	27.7	122.9	4.89	21.5	21.5	Knapp, 1995
<i>rileyi nuchalis</i>	21.7	358	3.1	55.4	30.2	27.1	86.1	7.57	24.1	—	Cyril, 2001;
<i>carinata carinata</i>	22.5	476	4.65	51.8	31.1	25.9	120.4	5.44	25.3	14.6	Hayes et al., 2004
<i>nubila nubila</i>	37.9	2102 ^a	8.6	43.5 ^b	32.1 ^b	75.2	646.7	3.58	30.8	—	Thornton, 2000;
<i>nubila nubila</i>	—	—	10	73.3	—	79.4	—	—	—	—	Hayes et al., 2004
<i>nubila caymanensis</i>	38.5	2202 ^a	15	—	—	—	—	—	—	50	Thornton, 2000;
<i>collei</i>	38.9	2270 ^a	17.3	55.8	38.9	39.9	690.3	1.76	30.4	32.8	Hayes et al., 2004
<i>cornuta cornuta</i>	—	—	17.4	68.6	45.9	77.7	1352	—	—	—	Iverson, 1979
<i>cornuta cornuta</i>	—	—	14.3	74.7	46.9	78.2	1118	—	—	60.5	Alberts, 1985,
<i>cornuta stejnegeri</i>	47.5	4700	12.0	80.3	50.9	104.0	1248	2.21	26.6	74.0	personal communication
<i>ricordii</i>	34.0	1526 ^a	11.1	—	—	—	—	—	—	30	Rodríguez Schettino, 1999
<i>pinguis</i>	46.8	4750	14	—	—	—	—	—	—	—	Schettino, 1999
<i>pinguis</i>	43.8	3021	11.4	64.8	45.0	62.7 ^c	715	2.08	23.7	46.6	Gerber, 2000a
<i>nubila nubila</i> ^d	36.3 ^a	1845	5.6	—	—	49.9	279	2.70	15.1	46.4	Gerber, 2000b

^a Estimated from body mass-snout-vent length regression in Iverson et al. (2004: BM = 0.04665SVL^{2.948}).

^b From radiographs.

^c Estimated from egg length-egg width-egg mass regression in this paper.

^d Introduced population off Puerto Rico.

egg dimensions of *C. c. cyclura*, *C. c. inornata*, and *C. c. figginsi* (Table 7) suggests that the data for the latter (particularly EL; Coenen, 1995) should be considered suspect. Based on the EL-EW-EM regression for *C. c. inornata* eggs, an egg of 40 mm width and a mass of 51 grams should have a length of only 57.7 mm (much shorter than the reported 80 mm; Table 8).

The production of flaccid eggs by iguanids has been previously reported for captive female *Cyclura cornuta* from Hispaniola (Shaw, 1969; Boylan, 1984) and for both wild and captive *Iguana iguana* from Curacao (van Marken Lichtenbelt and Albers, 1993). Al-

though in all cases these eggs failed to develop, it remains to be proven that they are unfertilized eggs (e.g., Boylan, 1984).

Generally, egg size in *Cyclura* is not related to female body size within a population (Wiewandt, 1982; Hayes et al., 2003; this study; but see Alberts, 1995, and Alberts et al., 1997), nor is there such a relationship for the eggs of *Conolophus subcristatus* or *Sauromalus obesus* (Werner, 1983; Abts, 1989). There is a relationship for at least three different populations of *Iguana iguana* (Fitch and Henderson, 1977; Rand, 1984; van Marken Lichtenbelt and Albers, 1993). Average egg size is positively related to body

size across populations of rock iguanas ($EM = 2.34SVL - 25.80$; $r = 0.84$; $P = 0.001$; $n = 11$; for independent contrasts, $r = 0.80$), although *C. collei* and *C. pinguis* apparently produce relatively smaller eggs than expected.

Although there was no relationship between egg mass and body size in *C. c. inornata*, smaller females produced longer and narrower eggs than larger females, presumably an adaptation to produce the largest eggs possible given the constraints of the size of the pelvic opening (e.g., Sinervo and Licht, 1991). This same pattern was observed in Galapagos marine iguanas (Rauch, 1988), but has not been noted for other iguanids.

We found a positive relationship between initial egg mass and hatching body mass, as did Alberts et al. (1997) for *C. n. nubila* incubated in the laboratory. This relationship is also known for *Iguana iguana* in the field (van Marken Lichtenbelt and Albers, 1993) and *Cyclura c. cornuta* in captivity (Boylan, 1985), and has been hypothesized for lizards in general (Tracy, 1982).

Relative egg mass for populations of *C. cychlura* lies in the middle of the range of values for other rock iguanas (1.8 to 7.6%). *C. collei*, *C. cornuta*, and *C. pinguis* have the lowest relative egg masses, and *C. carinata* and *C. rileyi* have the highest values (Table 8).

Raw mean clutch egg mass and clutch size were inversely correlated in *C. r. rileyi* and *C. r. nuchalis* (Hayes et al., 2004), but were unrelated in *C. c. inornata* (this study). Ours is the only study to correct for body size in this relationship, and we found no evidence of a trade-off between clutch size and egg size after standardization. Thus, egg mass stays the same as body size increases, although eggs get shorter and wider, and clutch size increases, a pattern predicted by optimal egg size theory (Smith and Fretwell, 1974; Brockelman, 1975; Roff, 1992). For example, the elongate eggs produced by small females appear to be a response to selection to produce an optimal egg size under the constraints of the size of the pelvic opening (Sinervo and Licht, 1991).

Clutch size and egg size are both positively correlated with body size across species (see above), but clutch and egg size are not correlated ($r = 0.44$; $P = 0.17$; $n = 11$). On

the other hand, partial correlation of those data to remove the effect of body size (mean SVL) suggested a trend toward a trade-off between clutch size and egg size ($r = 0.59$; $P = 0.06$); however, those data were skewed by the values for *C. collei*, without which there was no correlation whatsoever ($r = -0.05$; $P = 0.89$; $n = 10$).

Clutch mass.—Clutch mass is strongly correlated with body size both within and across ($CM = 38.09SVL - 857.91$; $r = 0.90$; $P = 0.0002$; $n = 11$; for independent contrasts, $r = 0.93$) populations of *Cyclura* that have been studied. For *C. c. inornata*, relative clutch mass (RCM) does not vary with body size, suggesting that females are allocating a constant proportion of their energy to their clutches. In contrast, in *Iguana iguana* (the only other iguana for which variation in RCM has been examined; Rand, 1984) RCM increases with female body size. More data on variation in RCM in iguanas is needed before any pattern can be elucidated. Estimates of average values of RCM for other populations of iguanas (Tables 8, 9) reveal that *C. cychlura* has the lowest values of all iguanas except for the introduced population of *C. nubila* off Puerto Rico (Table 8).

Across all *Cyclura* populations for which data could be estimated (Table 8; $n = 11$), RCM averaged 22.5, with most estimates between 22 and 31. These values are on average slightly lower than those for most other iguanas (Table 9), although the values for the Galapagos iguanas (*Amblyrhynchus* and *Conolophus*) are similar to those found in *C. cychlura*. In comparison, RCM for iguanian lizards (i.e., those lizards most closely related to iguanids, but including many species that produce multiple clutches per year; Pough et al., 1998) average from 27.7 (Vitt and Congdon, 1978; 20 populations of 16 species) to 25.6 (Vitt and Price, 1982; 62 populations of 28 species) to 26.0 (Shine, 1992; six species), similar to that for the most populations of *Cyclura*. Unlike some iguanas (e.g., *I. iguana* and *C. cornuta*; with high RCM), which have been described as being emaciated after nesting (Rand and Rand, 1976; Wiewandt, 1977), post-nesting *C. cychlura* (with a much lower RCM) never appear to be so physically challenged.

TABLE 9.—Reproductive output for iguanas other than of those in the genus *Cyclura*. REM = mean clutch egg mass per clutch/mean female body mass \times 100; RCM = mean clutch mass/mean female body mass \times 100. Species are listed in approximate phylogenetic order of genus (from oldest to newest lineage; Malone et al., 2000); *Cyclura* (Table 7) would appear after *Dipsosaurus*.

Species	Location	REM	RCM	Source
<i>Brachylophus fasciatus</i>	Fiji Islands	7.7	27.0	Gibbons, 1981, personal communication
<i>Brachylophus vitiensis</i>	Fiji Islands	5.4	21.4	Gibbons, 1981, personal communication
<i>Dipsosaurus dorsalis</i>	California	8.7	38.6	Shaw, 1952; Mayhew, 1971; Muth, 1977
<i>Iguana iguana</i>	Nicaragua	0.8	24.8	Fitch and Henderson, 1977
	Panama	0.7	30.3	Rand, 1984
	Curacao	1.9	32.0	van Marken Lichtenbelt and Albers, 1993
<i>Sauromalus obesus</i>	Michoacan, Mexico	1.3	35.6	Alvarado et al., 1995
	Arizona	5.0	34.0	Abts, 1987
	California	—	35–40	Case, 1982
<i>Sauromalus hispidus</i>	Baja California	—	35.0	Case, 1982
<i>Sauromalus varius</i>	Baja California	—	37.0	Case, 1982
<i>Amblyrhynchus cristatus</i>	Galapagos Islands	9.7	22.6	Carpenter, 1966
	Galapagos Islands	~9.0	18.0	Boersma, 1983
	Galapagos Islands	8.8	20.0	Rauch, 1988
<i>Conolophus subcristatus</i>	Galapagos islands	1.5	19.9	Werner, 1983
<i>Ctenosaura acanthura</i>	Tamaulipas, Mexico	1.4	23.8	Iverson, unpublished
<i>Ctenosaura macrolopha</i>	Sonora, Mexico	2.2	32.6	Iverson, unpublished
<i>Ctenosaura pectinata</i>	Morelos, Mexico	<0.6	<29.0	Evans, 1951

Phylogenetic Patterns

Phylogenetic analyses of iguanid lizards based on morphology identify the genera *Cyclura* and *Iguana* as relatively recently divergent sister taxa (Wiens and Hollingsworth, 2000). However, subsequent analyses of molecular data suggest that the genus *Cyclura* is an ancient, distinctive lineage that is sister to all other iguanas, excluding *Brachylophus* and *Dipsosaurus* (Sites et al., 1996; Malone et al., 2000). In a preliminary attempt to understand the reproductive adaptations that have occurred during the evolution of rock iguanas, we plotted the major shifts in body mass, hatchling mass, relative clutch mass, and relative egg mass on the cladogram generated by Malone et al. (2000) for the genus *Cyclura* (Fig. 14).

Character mapping suggests that small adult body size, small hatchling size, small clutch size, increased relative egg mass, and reduced relative clutch mass may have evolved during each of three separate radiations onto small islands (*C. carinata*, *C. rileyi*, and *C. cyclura*). However, the introduced population of *C. nubiola* on a small island off Puerto Rico

only 40 years ago also exhibits this same pattern of change (Table 8), suggesting an environmental component to the pattern. Eight *C. c. inornata* introduced from Leaf Cay to previously uninhabited Alligator Cay in the Exumas in 1988 and 1990 have grown significantly faster than those on Leaf Cay over the same period (Knapp, 2001a; Iverson et al., 2004). Furthermore, four females on Allen Cay (Fig. 1), presumably introduced from Leaf or U Cay in the 1980's, now measure 49.2 to 57.0 cm SVL (mean, 53.7) and weigh 4965 to 6875 g (mean, 6195), averaging 68% longer than females on Leaf or U Cay, and more than twice the mass of the largest Leaf or U Cay females (Table 3). Unfortunately, the lack of nesting habitat on Allen Cay precluded our examination of reproductive traits for that population. Nevertheless, these data suggest significant plasticity in at least body size in these lizards, apparently in response to environmental conditions such as resource abundance. Immediate initiation and long-term study of the reproductive biology of these introduced populations could provide detailed information on the magnitude of density-

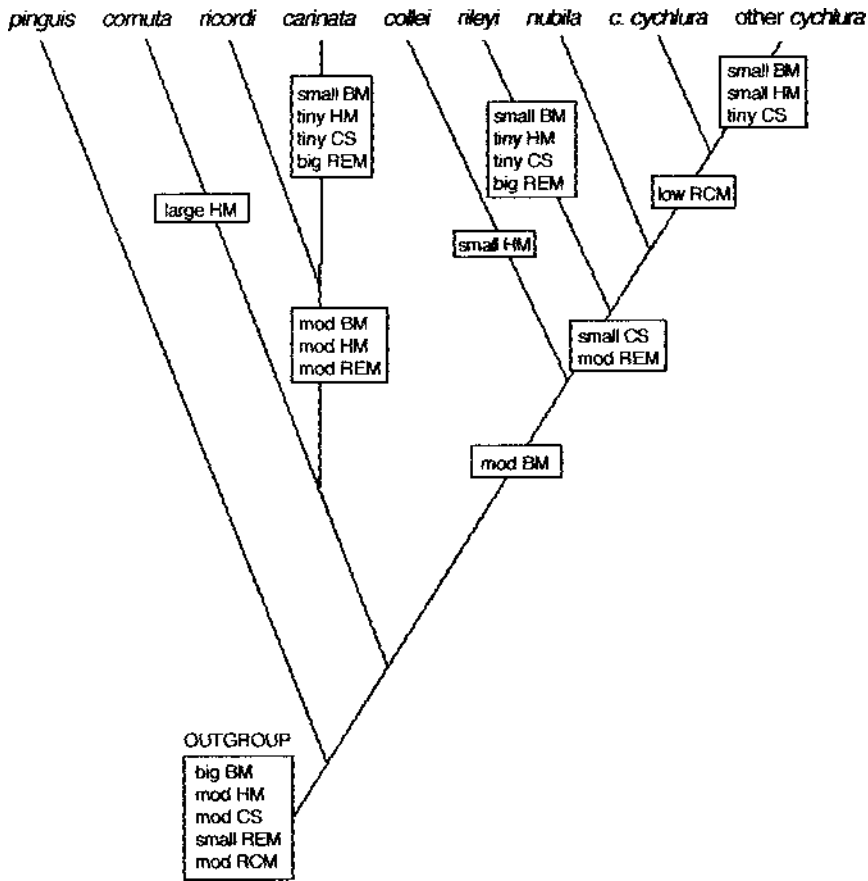


FIG. 14.—Character cladogram of life history traits for the genus *Cyclura* based on the molecular phylogeny of Malone et al. (2000; see also Sites et al., 1996). Traits are body mass (BM: big = >2.5 kg; moderate = 1.5–2.5 kg; small = <1.5 kg), hatchling mass (HM: big = >50 mm SVL; moderate = 40–50 mm; small = 25–40 mm; tiny = 15–25 mm), clutch size (CS: moderate = 10–18; small = 6–9; tiny = 3–5), relative clutch mass (RCM: moderate = 20–30; small = 15–20), and relative egg mass (REM: big = >4; moderate = 3–4; small = 1.5–3).

dependent effects on life history traits in these lizards.

In general, iguanid lizard body size is larger on islands than on the mainland (Case, 1976, 1978), although the precise relationship between body size and island size has not been examined. Furthermore, body size in chuckwallas (*Sauromalus*) varies significantly among populations, tends to be larger in more productive environments, and has a significant genetic basis (Tracy, 1999; but see Case and Schwaner, 1993). Given the general phylogenetic pattern of smaller *Cyclura* on smaller islands, we explored the relationship between

reproductive parameters and current island area in the genus *Cyclura* (realizing that current surface area may not reflect the selective history of a particular population, given Pleistocene sea level changes). For the raw mean population data for the various species of *Cyclura* (Table 8), female body size (SVL) and clutch mass were nearly significantly correlated with the natural log of island area ($r = 0.53$, $P = 0.06$; $r = 0.59$, $P = 0.06$; assumes a paleo-island size for *C. ricordi* of 10,000 ha, Ottenwalder, 2000b, and references in Seidel and Inchaustegui, 1984); clutch size (Fig. 15) and relative clutch mass ($r = 0.67$, P

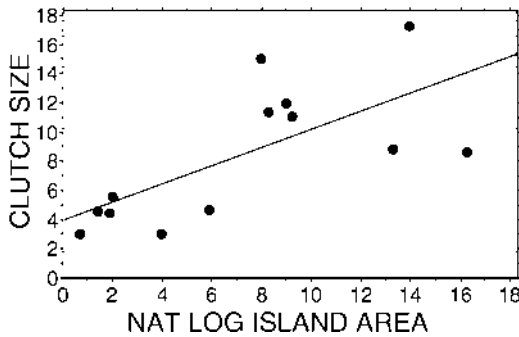


FIG. 15.—Relationship between the natural logarithm of island area (in ha) and clutch size for 13 rock iguana populations. Least squares regression is plotted ($CS = 0.63\ln area + 3.93$; $r = 0.69$; $P = 0.009$).

= 0.02) were positively correlated with \ln island area; and egg mass, relative egg mass, and mean hatchling mass were not correlated with \ln island area ($r = 0.46$, $P = 0.16$; $r = -0.48$, $P = 0.14$; $r = 0.26$, $P = 0.47$). Thus, clutch size and relative clutch mass (and perhaps also body mass and clutch mass) appear to be reduced on small islands, but offspring size is not. When phylogenetic bias was reduced by calculating independent contrasts, clutch size ($r = 0.64$; $P < 0.05$; $n = 13$), clutch mass ($r = 0.72$; $P < 0.01$; $n = 11$), and relative clutch mass ($r = 0.62$; $P < 0.05$; $n = 11$) were correlated with island area, but body size (BM or SVL) and offspring size (egg or hatchling mass or relative egg mass) were not (for all other comparisons, $|r| < 0.43$ and $P > 0.05$).

Unfortunately, the ultimate explanation of this hypothesized pattern (e.g., decreases in food abundance and diversity; cooler, windier environments; and/or reduced predation on smaller islands) is still not clear. However, we speculate that the reductions in at least clutch size, clutch mass, and relative clutch mass on small islands are proximal responses to reduced resource availability and/or reduced resource processability (see Iverson, 1982), whereas egg and hatchling size have a much greater genetic basis and are the products of much more intense selection for optimal offspring size.

Nest Success

Survivorship to hatching for rock iguana eggs in the field consistently exceeds 75%

TABLE 10.—Survivorship of eggs to hatching (^H) or emergence (^E) for rock iguanas of the genus *Cyclura*.

Taxon	n	Survivorship	Source
<i>C. carinata</i>	23	78% ^H	Iverson, 1979
<i>C. collei</i>	53	76% ^H	Vogel, 1994
<i>C. c. stejnegeri</i>	451	79% ^H	Wiewandt, 1977
<i>C. c. inornata</i>	384	81% ^H	This study
	384	79% ^E	
<i>C. n. caymanensis</i>	—	92% ^E	Gerber, 2000a
<i>C. n. nubila</i> ^a	82	85% ^H	Christian, 1986
<i>C. pinguis</i>	57	84% ^H	Gerber, 2000b

^a Introduced population from Cuba to island off Puerto Rico.

(Table 10), although success under captive conditions is generally lower (76% and 6%: Shaw, 1954, 1969; 90%: Haast, 1969; 5%: Duval and Christie, 1990; 69%: Vogel, 1994; 44%: Alberts et al., 1997). Natural rates of survivorship in eggs of *Cyclura* are comparable to those found for *Conolophus* (87%; Snell and Tracy, 1985) and *Amblyrhynchus* (87.5%; Rauch, 1988) in the Galapagos, but higher than those found for iguanas on the mainland where predators are more abundant (e.g., see Rand and Robinson, 1969; Sexton, 1975). In Panama for example, females of *Iguana iguana* laid 823 eggs, of which the fate of 168 could not be determined, but 489 of the remaining 655 (75%) hatched (Rand and Dugan, 1980). Thus, survivorship must have been between a maximum of 80% (657/823) and a minimum of 59% (489/823). In a later study the same authors (Bock and Rand, 1989) found survivorship to hatching to vary from 1.7% in a wet year to 41–50% in three normal years. Survivorship to emergence in that study ranged from only 1.4% to 27–46%. Abts (1987) reported no data on nest survivorship, but estimated survivorship through the first year of life (i.e., including nest and neonatal survivorship) at only 38%. These mainland values are more like those for other lizards (means: 53% and 36% for *Sceloporus undulatus*, Tinkle and Ballinger, 1972, and Parker, 1994; 58% for *Sceloporus merriami*, Dunham, 1981; 73% for *Lacerta vivipara*, Heulin et al., 1994; and 33% for *Anolis limifrons*, Chalcraft and Andrews, 1999).

Egg survivorship in individual nests was not related to female body size in *C. c. inornata* (this study), but was positively correlated with size in six *C. collei* (though one of the clutches was artificially incubated and the eggs in two

others were assumed to have died even though the nests were never found; Vogel, 1994), and negatively correlated with body size in artificially incubated clutches from Cuban *C. nubila* (Alberts et al., 1997). Reproductive senescence in larger (presumably older) rock iguanas was suggested by the latter study, but not by ours. Only additional field studies can explain these discrepancies.

For *C. c. inornata*, we also found higher nest survivorship in nests laid later in the season, in deeper nests, in nests of relatively heavy clutches (i.e., from high RCM females), and in drier nests. We can only speculate on the reasons for these. It is logical that nests laid early in the season have a greater chance of being disturbed by females that nest subsequently. In addition, the complete failure of two early nests on U Cay (see below) may also have unduly skewed the data. Similarly, the failure of several nests of small females with very low RCM values (6.9, 7.4, 8.2, 10.7% compared to the overall mean of 16.5%) strongly influenced the relationship. At least three of these were likely primiparous females, and lower survivorship in their nests is perhaps not surprising.

The relationship between egg depth and nest survivorship was clearly influenced by seven nests laid between 17 and 23 cm deep (overall sample mean = 27.7; Fig. 13) that completely failed. Although we found no relationship between mean nest temperature and nest depth, perhaps the greater diurnal fluctuation in nest temperature at shallow depths contributes to higher mortality there.

Our preliminary data suggest that excess soil moisture (particularly late in development) may cause nests to fail. For example, a heavy rain event occurring near or at the time of hatching may occlude the soil (particularly if the site is close to the water table as it is on U Cay), retarding the diffusion of oxygen into and carbon dioxide out of the nest cavity (Christian and Lawrence, 1991). The high metabolic demands of late embryos and/or neonates (especially in large clutches) may result in their suffocation under these conditions. Indeed, the offspring in two large clutches (each of eight eggs) in two of the five wettest nests on U Cay all died in the nests near (i.e., full term in the egg), at (i.e., as they pipped their eggs), or immediately following hatching. Our temperature loggers indicated

that a major rain event occurred on 6 September 2002 (i.e., nest temperature dropped 2 C on that day; Fig. 7, bottom), and that event likely led to the failure of those nests. In addition, the generally higher soil moisture levels on U Cay compared to those on Leaf Cay likely explains the lower nest success on the former. Our observations thus corroborate those of Bock and Rand (1989), who also found a reduction in hatching rates (from 41–50% to 1.7%) in nests of *Iguana iguana* as a result of heavy rain events late in development.

Interestingly, Snell and Tracy (1985) found the opposite situation with soil moisture in *Conolophus subcristatus* in the Galapagos; hatching success was positively correlated with water potential in the nest, and even opening the nest to examine the clutch resulted in a reduction in survivorship across nests from 87% to 35%. At their site rainfall during the entire incubation period ranged only from about 2.5 cm to 13.5 cm in the years during which they excavated nests, whereas we experienced over 6 cm of rain during the first month of incubation alone at our site.

Conservation Implications

Although the population of *C. c. inornata* on Leaf Cay is heavily supplemented with food by tourists, we did not find substantial differences in the reproductive ecology (or average growth rates; Iverson et al., 2004) between that cay and U Cay (which receives much less supplemental feeding). However, it does appear that most of the food provided by people is eaten by the more aggressive males on the feeding beaches (personal observations). Thus, females may be little impacted nutritionally by this feeding. Fortunately, most visitors to the islands remain on the beaches, and there is so far no evidence of human trampling of nests.

More comprehensive data are now available on long-term growth (Iverson et al., 2004) and reproduction (this study) of *C. c. inornata* than any other species of iguana. Our long-term recapture data are currently being analyzed to provide the first age-specific survivorship data for an iguana. With those data, demographic analyses will finally be possible (e.g., Heppell, 1998; Caswell, 2001). It is our hope that these data and that those analyses will be useful in making management decisions that will reverse the precipitous declines presently oc-

curing in most populations of rock iguanas (Alberts, 2000).

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APPENDIX

Scientific and Common Names of Extant West Indian Iguanas of the Genus Cyclura (After Alberts, 2000).

Scientific name	Common name	Distribution
<i>C. carinata carinata</i>	Turks and Caicos Iguana	Turks and Caicos Islands
<i>C. c. bartschi</i>	Bartsch's Iguana	near Mayaguana, Bahamas
<i>C. collei</i>	Jamaican Iguana	southeastern Jamaica
<i>C. cornuta cornuta</i>	Rhinoceros Iguana	Hispaniola
<i>C. c. stejnegeri</i>	Mona Island Iguana	Mona Island
<i>C. cyclura cyclura</i>	Andros Island Iguana	Andros Island, Bahamas
<i>C. c. fggginsi</i>	Exuma Island Iguana	central and southern Exumas, Bahamas
<i>C. c. inornata</i>	Allen Cays Iguana	Allen Cays, Bahamas
<i>C. nubila nubila</i>	Cuban Iguana	Cuba
<i>C. n. caymanensis</i>	Lesser Caymans Iguana	Little Cayman and Cayman Brac
<i>C. n. lewisi</i>	Grand Cayman Iguana	Grand Cayman Island
<i>C. pinguis</i>	Anegada Island Iguana	Anegada, British Virgin Islands
<i>C. ricordi</i>	Ricord's Iguana	southern Dominican Republic
<i>C. rileyi rileyi</i>	San Salvador Iguana	San Salvador, Bahamas
<i>C. r. cristata</i>	White Cay Iguana	White Cay, southern Exumas, Bahamas
<i>C. r. nuchalis</i>	Acklins Iguana	Acklin Islands, Bahamas