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Effects of Incubation Temperature and Water Potential on Growth and Thermoregulatory Behavior of Hatchling Cuban Rock Iguanas (*Cyclura nubila*)

ALLISON C. ALBERTS, ANDREW M. PERRY, JEFFREY M. LEMM, AND JOHN A. PHILLIPS

To examine the effects of incubation temperature and moisture levels on embryonic development and posthatching growth and behavior, we incubated a total of 123 eggs collected from 18 wild female Cuban rock iguanas at 28.0, 29.5, or 31.0 C on wet (-150 kPa), moist (-550 kPa), or dry (-1100 kPa) substrates. Although there was no effect of incubation temperature or water availability on egg survival, larger females exhibited higher infertility and greater mortality of initially viable eggs, suggesting that reproductive senescence may occur in this long-lived species. Incubation temperature, although it had little influence on size at hatching, significantly affected several measures of growth, including changes in body length, mass, and head dimensions. In general, hatchlings from higher incubation temperatures grew faster during their first year. However, by 16 months of age, growth rates no longer varied among hatchlings incubated at different temperatures. Incubation temperature had no detectable effect on thermal selection by hatchlings at 14 to 16 months of age, as there was no tendency for hatchlings incubated at higher temperatures to preferentially select higher basking temperatures. Moisture levels during incubation did not significantly affect size, growth, or thermoregulatory behavior of hatchlings. These results have important implications for understanding how environmental conditions experienced during embryonic development may affect future fitness and survivorship.

THE West Indian rock iguanas of the genus *Cyclura* form a unique group of eight species inhabiting tropical dry forests throughout the Greater Antilles and the Bahamas (Schwartz and Henderson, 1991). They are among the most endangered lizards in the world, primarily because much of their natural habitat has been eliminated by human development or degraded by exotic species (Case et al., 1992). Mongooses, dogs, and feral cats prey heavily on juvenile iguanas, resulting in scant to nonexistent recruitment in severely impacted populations (Iverson, 1978; Vogel, 1994). Because the smallest age classes appear to be the most vulnerable (Iverson, 1979), the rate at which juveniles grow to a less susceptible body size may critically influence their probability of survival.

The physical conditions under which reptile eggs are incubated can profoundly affect hatching success and hatchling morphology, physiology, and behavior. Through its influence on embryonic metabolism, the incubation environment affects hatchling body size in a variety of species (for review, see Packard and Phillips, 1995). Even in species for which incubation conditions have a negligible influence on morphology at hatching, subsequent growth of juveniles can be significantly affected (Hutton,

1987; Joanen et al., 1987). Several aspects of hatchling behavior, including locomotion (Miller et al., 1987; Burger, 1989; Van Damme et al., 1992), thermoregulation (Lang, 1987), prey handling efficiency and escape tactics (Burger, 1990), can also be influenced by incubation conditions.

Larger body size may benefit hatchling reptiles by enhancing their ability to utilize a diversity of food resources (Wiewandt, 1977), dominate conspecifics (Ferguson and Bohlen, 1978; McKnight and Gutzke, 1993), and successfully evade predators (Ferguson and Fox, 1984; Vleck, 1988). Given the apparently high loss rate of *Cyclura* hatchlings to introduced predators, large body size may significantly affect juvenile survivorship in the wild. To investigate the effects of incubation temperature and water availability on morphology of hatchlings, we experimentally incubated eggs of Cuban rock iguanas, *Cyclura nubila*, under controlled conditions and studied juvenile growth through 16 months of age. Because both juvenile growth rates and the ability to escape predation appear to be closely tied to thermoregulatory behavior in other lizards (Christian and Tracy, 1981; Sinnero and Adolph, 1989), we also evaluated the influence of incubation conditions on thermal selection by hatchlings.

MATERIALS AND METHODS

Study animals.—Between 29 April and 30 May 1993, we captured 22 adult female Cuban rock iguanas at nine different locations on the US Naval Station, Guantánamo Bay, Cuba. At the time of capture, we weighed all females (± 1 g) and measured snout-vent length (SVL; ± 0.1 cm). Females were immediately transported to a large outdoor holding pen (100 m²) at the Army Veterinary Clinic, which contained 20 artificial nest sites constructed by digging an angled tunnel 1.5 m in length covered with a rounded plastic top that had an entrance hole cut into the front end. Within two weeks of capture, we radiographed each female to assess the presence of eggs (Alberts, 1995). Four females showed no visible signs of egg development and were released at the site of capture.

Although all females presumably had ample opportunity to mate prior to capture, we placed two adult males sequentially into the holding pen for two weeks each to ensure that all captured females were inseminated. Subsequent to introduction of the males, we observed several matings. We kept loose soil within each nest site hydrated to a water potential of approximately -550 kPa throughout the nesting period. Although appetite appeared to decrease prior to laying, we provided the females with food and water daily. The first female began to lay eggs on 23 June, and laying continued until 23 July when the last female deposited her clutch. We checked nest sites twice daily, collected eggs as they were laid, and immediately transported eggs to indoor incubators and weighed them. Females were allowed to guard the empty nest chamber for 1–2 days and then released at the site of capture.

Incubation procedure.—We modified three 100-quart plastic coolers filled with water for use as field incubators. Small air holes drilled into the lids of the coolers ensured adequate oxygen exchange during incubation. In each cooler, we placed a thermostatically controlled aquarium heater, with the thermostat sensor mounted centrally. We calibrated each thermostat control with a mercury thermometer (± 0.1 C) and adjusted the controller units until the three coolers maintained temperatures of 28.0, 29.5, and 31.0 C. We placed three covered plastic boxes containing eggs half buried in moistened vermiculite in each cooler such that the bottom of each box was in contact with surface of the heated water. A water retention curve constructed in previous studies was used to determine the amount of distilled water required for hydration

of dry grade-three vermiculite to water potentials of -150 , -550 , and -1100 kPa (Packard and Phillips, 1995; Phillips et al., 1990). One box representing each water potential was placed in each of the three incubators to create a three-temperature \times three-water potential design. Eggs from each female were as uniformly distributed as possible among the nine incubation treatments.

Every 10 days throughout incubation, we weighed the eggs, rotated the boxes within the coolers, and rehydrated the vermiculite to maintain the desired water potentials. We immediately removed eggs that showed molding or discoloration. The first lizard hatched after 89 days and the last after 136 days of incubation. After complete emergence from the egg, we weighed (± 0.1 g) and measured (± 0.01 mm, digital caliper) the SVL of each hatchling. For the first month after hatching, we maintained the hatchlings in four 1.5 m² enclosures equipped with infrared heat lamps and hiding areas. We provided the hatchlings daily with water and mixed greens supplemented with a commercial cereal product (Hill's Product #6920).

Hatchling measurements.—At approximately one month of age, we transported the hatchlings to the Center for Reproduction of Endangered Species at the San Diego Zoo for developmental studies. Hatchlings were housed indoors as a group in a large enclosure (48 m²) where they had access to natural sunlight through UV-transmitting plastic roofing. The enclosure had rocks and wood structures that simulated natural terrain. Ceramic infrared heating elements provided several localized basking sites with surface temperatures up to 45 C. We maintained hatchlings on a diet similar to that provided during their first month, with the addition of *Hibiscus* leaves and flowers and fresh fruit. For the first 16 months of life, we weighed and measured hatchlings every four months. In addition to mass and SVL, we measured head width (lateral distance across the top of the head centered over the parietal eye) and head length (distance from the tip of the snout to the edge of the occipital). At four months of age, we sexed the hatchlings with probes.

Thermoregulation studies.—To examine potential effects of incubation conditions on thermoregulatory behavior of hatchlings, we examined thermal preferences between 14 and 16 months of age. On 30 different days, we took middorsal body surface temperatures on 41 hatchlings with a Raytek Raynger PM noncontact thermometer equipped with an FDA class-IIIa laser

sighting device (accuracy rated to ± 1 C; Raytek, Inc., Santa Cruz, CA). All temperature measurements were at a distance of approximately 1 m. We measured temperatures between 1200 h and 1300 h each day, after daily feeding was complete and hatchlings had been basking for at least 30 min.

Use of the noncontact thermometer allowed us to make temperature measurements under ambient enclosure conditions with no disturbance to daily behavior patterns of the lizards. However, because lizards are poikilothermic, skin surface temperatures are not necessarily indicative of internal body temperatures (Garrick, 1979). To assess the relationship between body mass, skin surface temperature, and internal body temperature, we also measured temperatures of nine representative hatchlings ranging in mass from 210–1450 g (Alberts and Grant, 1997). We placed each hatchling in a restraint directly under a ceramic infrared heating element that had been turned off and cooled to the ambient enclosure temperature of 27 C. We turned the heating element on, and once per minute for the next 35 min, we measured internal body temperature with a thermistor probe (accurate to $\pm 1\%$ of reading) inserted into the cloaca while simultaneously measuring skin surface temperature using the noncontact thermometer.

Using regression analysis, we examined the relationship between skin surface temperature and internal body temperature for nine hatchlings of differing body size for the period of linear temperature increase (mean $R^2 = 0.678 \pm 0.053$, $df = 34$, all $P < 0.0001$). Based on how the slope of this relationship changed with body mass, we determined the expected relationships between skin surface temperature and internal body temperature for the original 41 hatchlings (see Alberts and Grant, 1997). Using these regression equations, we then estimated internal body temperatures for the 41 hatchlings from measured skin surface temperatures ($R^2 = 0.852$, $df = 40$, $P = 0.0001$).

Statistics.—All variables were normally distributed with the exception of female mass, which was natural-log transformed to meet the assumptions of normality. We examined relationships between female SVL, clutch size, egg size, clutch mass, fertility, and egg viability using regression analyses. To facilitate comparisons of egg mass changes during incubation periods of varying length, we standardized the initial mass of eggs in each treatment to the mean mass for all eggs to compensate for differences in egg mass at laying. We then calculated masses of individual

eggs at each 10th percentile of development (10–90%) and compared them across treatment conditions. We tested effects of incubation temperature and water potential on survival of eggs using chi-square contingency tables.

Because of variation among females in number of viable eggs produced, not every female was ultimately represented in each of the nine temperature/water potential conditions. This precluded use of a three-factor design in statistical testing of clutch effects and the influence of temperature and moisture regime on length of incubation and hatchling mass, SVL, head width, head length, and subsequent growth. Instead, we examined clutch effects separately in single-factor ANOVAs, and we examined treatment effects in two-factor ANOVAs with temperature and water potential as independent variables. Because the eggs of individual females were as uniformly distributed as possible among the nine experimental treatments, it is unlikely that random clutch effects would be confounded with fixed effects arising from the experimental conditions.

Hartley's test (Hartley, 1950) revealed no significant heterogeneity of variance among treatment groups for any measures of hatchling size or growth. We adjusted data for mass and SVL at hatching for initial differences in egg size prior to conducting statistical analyses. To compare growth in mass, SVL, head width, and head length of hatchlings incubated under different temperature and moisture conditions, we determined the slopes of the regression lines of hatchling age on each of these variables at four-month intervals for each hatchling using linear regression (Van Damme et al., 1992). Relationships between age and mass (mean $R^2 = 0.958 \pm 0.006$), age and SVL (mean $R^2 = 0.957 \pm 0.004$), age and head width (mean $R^2 = 0.925 \pm 0.008$), and age and head length (mean $R^2 = 0.925 \pm 0.029$) were linear for all hatchlings. We used single- and two-factor ANOVAs to assess the effects of clutch, incubation temperature, and moisture regime on rates of change in these morphological variables over time. We assessed differences between treatment conditions a posteriori using Fisher's protected least significant difference test, PLSD (Dunnett, 1970).

For the thermoregulation studies, we compared skin surface and estimated core body temperatures among hatchlings incubated at 28.0, 29.5, and 31.0 C and at -150 , -550 , and -1100 kPa using two-factor ANOVA. We used single-factor ANOVA to assess the effect of clutch on thermoregulatory patterns. All variables were normally distributed, and Hartley's

TABLE 1. INCUBATION TIME, PERCENTAGE FEMALES, AND HATCHLING BODY SIZE FOR CUBAN IGUANA EGGS INCUBATED UNDER THREE TEMPERATURE AND WATER POTENTIAL TREATMENTS. Only fertile eggs are included. Standard errors are given in parentheses.

| Temperature (C) | Water potential (kPa) | n | Initial egg mass (g) | Days of incubation | % Female | Hatch mass (g) | Hatch SVL (cm) |
|-----------------|-----------------------|----|----------------------|--------------------|----------|----------------|----------------|
| 28.0 | -150 | 9 | 74.5 (2.6) | 127 | 25 | 46.5 (4.2) | 9.43 (0.25) |
| 28.0 | -550 | 8 | 75.5 (2.7) | 130 | 33 | 54.5 (0.6) | 9.96 (0.18) |
| 28.0 | -1100 | 8 | 72.9 (1.5) | 128 | 67 | 46.6 (4.1) | 9.98 (0.30) |
| 29.5 | -150 | 9 | 72.6 (3.7) | 107 | 57 | 47.5 (2.0) | 10.04 (0.17) |
| 29.5 | -550 | 10 | 72.0 (3.2) | 109 | 50 | 45.6 (2.8) | 9.82 (0.18) |
| 29.5 | -1100 | 8 | 73.5 (2.2) | 109 | 50 | 51.3 (2.7) | 10.18 (0.10) |
| 31.0 | -150 | 9 | 74.6 (3.0) | 93 | 43 | 51.1 (1.2) | 10.11 (0.11) |
| 31.0 | -550 | 9 | 77.6 (2.0) | 94 | 40 | 47.1 (4.7) | 10.02 (0.28) |
| 31.0 | -1100 | 9 | 74.3 (2.2) | 94 | 17 | 43.4 (8.3) | 9.60 (0.43) |

test revealed no significant heterogeneity of variance among treatment groups. Because there were no significant differences between the sexes in thermoregulatory preferences, we pooled data for males and females prior to statistical analysis. We carried out all statistical analyses using Statview[®] statistical software (Abacus Concepts, Inc., Berkeley, CA).

RESULTS

Egg viability.—Mean clutch size was 6.8 ± 0.6 (range 2–13). Larger females produced larger clutches ($R^2 = 0.311$, $df = 17$, $P = 0.02$), but although there was a large variation in egg mass at oviposition (range 51.6–98.6 g), there was no association between size of the female and either individual egg mass ($R^2 = 0.023$, $df = 17$, $P = 0.55$) or total clutch mass ($R^2 = 0.128$, $df = 17$, $P = 0.14$). A total of 45 of 123 eggs appeared to be infertile, because they failed to gain mass and molded within the first two weeks after laying. Of the 78 eggs that were viable at oviposition, 54 survived to hatching. There was a significant negative relationship between female SVL and fertility ($R^2 = 0.230$, $df = 17$, $P = 0.04$), with larger females producing a higher percentage of infertile eggs. In addition, the initially viable eggs of larger females tended not to survive the incubation period as well as those of smaller females ($R^2 = 0.250$, $df = 14$, $P = 0.06$). These differences were not the result of differing incubation regimes, because neither temperature ($\chi^2 = 2.28$, $df = 2$, $P = 0.32$) nor water potential ($\chi^2 = 3.57$, $df = 2$, $P = 0.17$) had a significant effect on survivorship of eggs to hatching.

Egg incubation.—Incubation temperature had pronounced effects on length of incubation (F

$= 221.97$, $df = 2$, 32 , $P = 0.0001$), but water potential did not ($F = 1.67$, $df = 2$, 32 , $P = 0.20$; Table 1). Clutch had no effect on incubation length ($F = 0.037$, $df = 1$, 40 , $P = 0.85$), and there was no significant interaction between temperature and water potential ($F = 1.24$, $df = 4$, 32 , $P = 0.31$). Incubation was approximately 34 days longer at 28.0 C (128.5 ± 1.5) than at 31.0 C (93.9 ± 1.0), whereas eggs held at 29.5 C exhibited an incubation period of intermediate length (108.4 ± 0.9). Early-hatching individuals tended to have small amounts of external yolk that were absorbed within a few days after hatching, whereas those hatching later emerged with fully internalized yolk sacs. The masses of eggs with viable embryos generally increased through the first half of incubation and then decreased over the remainder of the incubation period. Within each temperature treatment, eggs incubated on wet substrates (-150 kPa) peaked at higher masses and exhibited greater net gains in mass during incubation than those on either moist (-550 kPa) or dry (-1100 kPa) substrates (Fig. 1).

Hatchling growth and morphology.—Of the 41 hatchlings that survived to 16 months of age, 24 were male and 17 were female. Because there were no significant differences between the sexes in mass and SVL at hatching, or in growth in mass, SVL, head width, or head length over the first 16 months of life, we pooled data for male and female hatchlings to determine the effects of clutch, incubation temperature, and incubation moisture regime on these hatchling characteristics.

Although clutch explained significant variation in SVL ($F = 12.62$, $df = 9$, 40 , $P = 0.0001$) and marginally significant variation in mass ($F = 2.14$, $df = 9$, 40 , $P = 0.06$) at hatching, it did

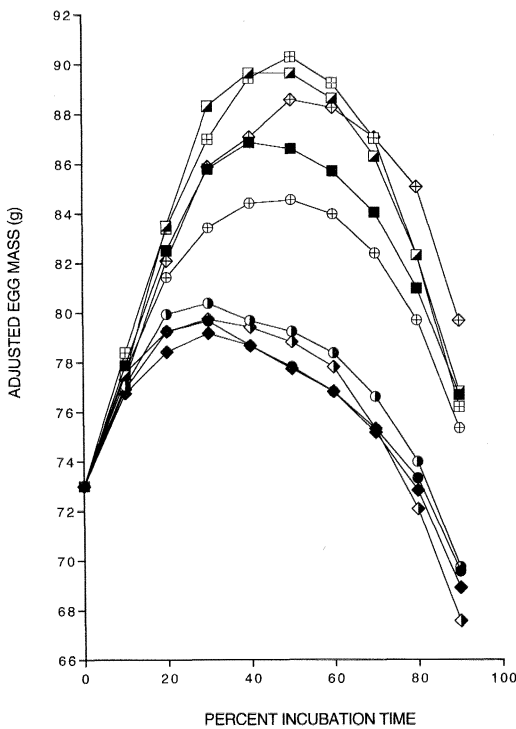
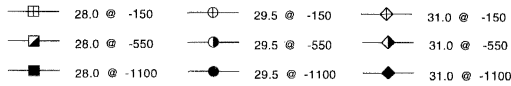


Fig. 1. Temporal changes in mass of viable Cuban iguana eggs incubated on vermiculite at different temperatures and water potentials. Closed symbols represent -1100 kPa, half-filled symbols represent -550 kPa, and cross-hatched symbols represent -150 kPa. Squares represent 28.0 C, circles symbols represent 29.5 C, and diamonds represent 31.0 C. Initial mass of eggs in each treatment were standardized to the mean mass for all eggs to compensate for differences in egg mass at laying.

not influence any subsequent measures of hatchling mass, SVL, head width, head length, or growth. Incubation temperature, although it did not influence size at hatching (Table 1), affected several measures of hatchling growth, including changes in mass at 4 months ($F = 4.23$, $df = 2$, 38 , $P = 0.02$), 8 months ($F = 4.10$, $df = 2$, 38 , $P = 0.02$), and 12 months ($F = 3.36$, $df = 2$, 38 , $P = 0.05$); changes in SVL at 4 months ($F = 5.61$, $df = 2$, 38 , $P = 0.008$) and 8 months ($F = 3.46$, $df = 2$, 38 , $P = 0.04$); changes in head width at 4 months ($F = 3.75$, $df = 2$, 38 , $P = 0.03$), 8 months ($F = 3.99$, $df = 2$, 38 , $P = 0.03$), and 12 months ($F = 2.45$, $df = 2$, 38 , $P = 0.05$); and changes in head length at 4 months ($F = 4.26$, $df = 2$, 38 , $P =$

0.02) and 8 months ($F = 4.64$, $df = 2$, 38 , $P = 0.02$) (Table 2).

Through four months of age, hatchlings emerging from eggs incubated at 31.0 and 29.5 C, although not initially larger, apparently grew faster in mass (PLSD = 0.155 and 0.142 , $P < 0.05$ for each), SVL (PLSD = 0.007 and 0.008 , $P < 0.05$ for each), head width (PLSD = 0.008 and 0.009 , $P < 0.05$ for each), and head length (PLSD = 0.022 and 0.019 , $P < 0.05$ for each) than those incubated at 28.0 C. At eight months of age, hatchlings incubated at 31.0 C were still growing faster than those incubated at 28.0 C in mass (PLSD = 0.264 , $P < 0.05$), SVL (PLSD = 0.007 , $P < 0.05$), head width (PLSD = 0.006 , $P < 0.05$), and head length (PLSD = 0.012 , $P < 0.05$), although growth of hatchlings incubated at 29.5 C was no longer significantly different from those incubated at 28.0 C for any of the measured variables. At 12 months, hatchlings incubated at 31.0 C continued to grow faster than those incubated at 28.0 C in mass (PLSD = 0.292 , $P < 0.05$) and head width (PLSD = 0.0005 , $P < 0.05$) but not SVL and head length. By 16 months of age, growth rates for mass, SVL, head width, and head length were no longer significantly different among hatchlings incubated at 28.0 , 29.5 , and 31.0 C.

Although similarly sized at hatching, because of their faster growth rates, hatchlings from eggs incubated at higher temperatures were larger than those from eggs incubated at lower temperatures in mass ($F = 7.25$, $df = 2$, 38 , $P = 0.0002$), SVL ($F = 13.65$, $df = 2$, 38 , $P = 0.001$), head width ($F = 13.13$, $df = 2$, 38 , $P = 0.0001$), and head length ($F = 8.31$, $df = 2$, 38 , $P = 0.001$) by four months of age. Differences in SVL persisted throughout 16 months of age ($F = 3.53$, $df = 2$, 38 , $P = 0.04$), with hatchlings incubated at 31.0 and 29.5 C still exceeding those incubated at 28.0 C (PLSD = 2.503 and 2.044 , $P < 0.05$ for each) despite the convergence in growth rates across temperature treatments which had occurred by that time. In contrast, differences in mass among hatchlings incubated at different temperatures were no longer evident by 16 months of age ($F = 2.08$, $df = 2$, 38 , $P = 0.14$). Differences in head width ($F = 4.50$, $df = 2$, 38 , $P = 0.02$) and head length ($F = 3.89$, $df = 2$, 38 , $P = 0.03$) persisted through 16 months of age but were only significantly different for hatchlings incubated at 31.0 and 28.0 C (PLSD = 2.516 and 4.030 , $P < 0.05$ for each).

In contrast to the results for incubation temperature, water potential experienced by eggs during incubation did not influence the mass ($F = 0.22$, $df = 2$, 32 , $P = 0.80$) or SVL (0.63 ,

df = 2, 32, $P = 0.54$) of animals at hatching (Table 1) or their subsequent growth at any stage. There were no significant interactions between temperature and water potential.

Thermoregulatory behavior.—Because there were no effects of clutch on measured skin surface ($F = 0.76$, df = 9, 40, $P = 0.65$) or estimated internal ($F = 1.21$, df = 9, 40, $P = 0.34$) body temperatures, we pooled data to examine the influence of incubation conditions on thermal selection by hatchlings. Incubation temperature did not significantly affect either skin surface ($F = 0.22$, df = 2, 38, $P = 0.80$) or estimated internal ($F = 0.26$, df = 2, 38, $P = 0.77$) body temperatures of hatchlings at 14 to 16 months of age (Table 3). Water potential experienced by eggs during incubation also did not affect skin surface ($F = 0.56$, df = 2, 38, $P = 0.57$) or estimated internal ($F = 0.33$, df = 2, 38, $P = 0.72$) body temperatures at this age.

DISCUSSION

In this study, maternal body size was positively correlated with clutch size but not with individual egg size. These results concur with those of previous studies on lizards suggesting a stronger genetic association of female size with the number of eggs produced than with egg size (Ferguson et al., 1991). As has been hypothesized for fish, direct effects of the food supply available to individual females during vitellogenesis may outweigh any indirect effects on egg size resulting from differences in maternal body size (Mire and Millett, 1994).

Survival of fertile *C. nubila* eggs in the present study (69.2%) was comparable to that observed in previous artificial incubation studies (75.8%; R. Ehrig, pers. comm.) and slightly less than that recorded for natural nests of this (88.0–90.2%; Christian, 1986; Christian and Lawrence, 1991) and two closely related species, *C. carinata* (78.3%; Iverson, 1979) and *C. stejnegeri* (86.0%; Wiewandt, 1977). However, larger females tended to produce a greater percentage of infertile eggs and exhibit a higher mortality rate for fertile eggs than did smaller females, suggesting that reproductive senescence may occur in this long-lived species. Like other species of *Cyclura*, the lifespan of *C. nubila* may exceed 40 years (Schwartz and Henderson, 1991). As indeterminate growers, larger individuals are probably older than smaller ones. In birds, reproductive capability deteriorates with age, resulting in decreased reproductive behavior, ovarian dysfunction, and erratic egg laying (Ottinger, 1993; vom Saal et al., 1994). Alligators, which live up to 60

TABLE 2. MEAN GROWTH RATES FOR MASS (g/DAY), SNOUT-VENT LENGTH (cm/DAY), HEAD WIDTH (mm/DAY), AND HEAD LENGTH (mm/DAY) OF CUBAN IGUANA HATCHLINGS EMERGING FROM EGGS INCUBATED AT 28.0, 29.5, OR 31.0 °C AT 4, 8, 12, AND 16 MONTHS POSTHATCHING AS DETERMINED FROM REGRESSION EQUATIONS. Standard errors are given in parentheses. Asterisk indicates a significant difference among temperature treatments.

| | 4 months | | | 8 months | | | 12 months | | | 16 months | | |
|-------------|------------------|------------------|-------------------|------------------|------------------|-------------------|------------------|------------------|-------------------|------------------|------------------|------------------|
| | 28.0 | 29.5 | 31.0 | 28.0 | 29.5 | 31.0 | 28.0 | 29.5 | 31.0 | 28.0 | 29.5 | 31.0 |
| Mass | 0.208 (0.047) | 0.349 (0.043) | 0.363* (0.035) | 0.438 (0.073) | 0.602 (0.071) | 0.702* (0.044) | 0.638 (0.091) | 0.883 (0.106) | 0.930* (0.063) | 0.657 (0.082) | 0.897 (0.113) | 0.932 (0.070) |
| SVL | 0.014 (0.001) | 0.022 (0.002) | 0.021* (0.002) | 0.021 (0.002) | 0.026 (0.002) | 0.027* (0.001) | 0.023 (0.002) | 0.027 (0.002) | 0.028 (0.001) | 0.021 (0.002) | 0.024 (0.002) | 0.025 (0.001) |
| Head width | 0.013 (0.002) | 0.022 (0.002) | 0.021* (0.002) | 0.017 (0.002) | 0.021 (0.002) | 0.023* (0.001) | 0.017 (0.002) | 0.020 (0.002) | 0.022* (0.001) | 0.015 (0.001) | 0.018 (0.001) | 0.019 (0.001) |
| Head length | 0.014 (0.004) | 0.033 (0.004) | 0.035* (0.007) | 0.033 (0.004) | 0.043 (0.003) | 0.046* (0.002) | 0.036 (0.003) | 0.042 (0.003) | 0.044 (0.002) | 0.032 (0.003) | 0.037 (0.003) | 0.038 (0.002) |

TABLE 3. MEAN SKIN SURFACE AND ESTIMATED INTERNAL BODY TEMPERATURES FOR 41 CUBAN IGUANAS EMERGING FROM EGGS INCUBATED AT 28.0, 29.5, OR 31.0 C AND -150, -550, OR -1100 kPa BETWEEN 14 AND 16 MONTHS OF AGE. Standard errors are given in parentheses. See text for further description of measured variables.

| Incubation temp (C) | Incubation water potential (kPa) | Surface temp (C) | Internal temp (C) |
|---------------------|----------------------------------|------------------|-------------------|
| 28.0 | -150 | 35.4 (0.2) | 34.1 (0.2) |
| 28.0 | -550 | 35.2 (0.3) | 34.1 (0.4) |
| 28.0 | -1100 | 35.0 (0.5) | 33.7 (0.6) |
| 29.5 | -150 | 34.9 (0.6) | 33.8 (0.5) |
| 29.5 | -550 | 35.0 (0.5) | 33.6 (0.4) |
| 29.5 | -1100 | 35.8 (0.3) | 33.8 (0.6) |
| 31.0 | -150 | 35.0 (0.5) | 33.2 (0.3) |
| 31.0 | -550 | 35.6 (0.3) | 34.2 (0.2) |
| 31.0 | -1100 | 35.9 (1.7) | 34.2 (0.9) |

years, show maximum fertility at 15–20 years of age, but dramatic declines occur in egg production after 30 years (Finch, 1990). If similar processes occur among rock iguanas, then it may be important to adjust estimates of effective population size accordingly when planning for conservation management purposes. Further studies are needed to document temporal changes in ovarian function and egg viability in wild female *Cyclura*. In particular, more data on how the aging process affects rates of population growth will be valuable for islands on which introduced predators have unnaturally skewed the age structure of local populations toward older adults (Vogel et al., 1996; N. Mitchell, pers. comm.).

In the present study, there was no effect of incubation temperature or water potential on survival of *C. nubila* eggs to hatching, probably because the incubation conditions employed closely paralleled those observed in natural nests and were well within the range of tolerance for this species (Christian and Lawrence, 1991). However, higher incubation temperatures did accelerate time to hatching, as has been observed in numerous other species (Packard and Phillips, 1995). Patterns of water absorption by eggs during incubation were similar to previous studies indicating greater net mass increases for eggs incubated on wetter substrates (Gutzke et al., 1987; Phillips et al., 1990; Phillips and Packard, 1994).

As has been observed in turtles, initial egg mass explained significant variation in size of *C. nubila* at hatching but had no appreciable influ-

ence on subsequent hatchling growth (Brooks et al., 1991; McKnight and Gutzke, 1993; Bobyn and Brooks, 1994). Clutch effects on hatchling size were also evident in *C. nubila* but, in contrast to results for turtles (Brooks et al., 1991; McKnight and Gutzke, 1993), had no influence on growth through 16 months of age. In addition, no significant interactions between clutch and either incubation temperature or water potential were detected, suggesting that genetically unrelated *C. nubila* hatchlings respond more uniformly to incubation conditions than do some other species (Bobyn and Brooks, 1994).

Although water availability during incubation can affect hatchling morphology (Tracy and Snell, 1985; Gutzke et al., 1987; Werner, 1988), growth (Overall, 1994), and certain measures of performance (Miller et al., 1987; Miller, 1993), these effects are usually less dramatic than those produced by variation in incubation temperature (Webb and Cooper-Preston, 1989; Brooks et al., 1991; McKnight and Gutzke, 1993). For *C. nubila*, water potential experienced during incubation, although it influenced the pattern of water uptake by developing embryos, ultimately had no effect on size at hatching or any measure of hatchling growth. These results are concordant with data from wild populations, indicating that water potential in natural nests, although it varies with vegetation type, depth, aspect, slope, and soil texture, has no effect on SVL or mass of hatchlings (Christian et al., 1991).

In many species of reptiles, incubation temperature affects hatchling size, with eggs incubated at lower temperatures usually exhibiting a longer developmental period and ultimately producing larger hatchlings (Packard and Phillips, 1995). However, not all species respond in this manner. That high or intermediate temperatures produce larger hatchlings in some alligators and snakes (Gutzke and Packard, 1987; Allsteadt and Lang, 1995) whereas incubation temperature has little effect on hatchling size in other species (Joanen et al., 1987) indicates that the relationship between reptilian embryonic growth and incubation temperature is complex and likely species specific. Although temperatures of natural *C. nubila* nests appear to be fairly thermally stable, ranging over not more than 5 C throughout incubation (Christian and Lawrence, 1991), studies on other species have found increased hatchling body mass for eggs incubated under variable temperature treatments (Overall, 1994). Further studies are needed to determine how changing thermal conditions experienced by *C. nubila* nests in the wild potentially affect hatchling size and growth.

Although incubation temperature had no effect on either mass or SVL of *C. nubila* at hatching, it did have significant effects on long-term growth of hatchlings. As has been shown in alligators, these results indicate that incubation temperature can ultimately affect mass and SVL of juveniles even when it has no detectable effect on body size at hatching (Joanen et al., 1987). Where they have been measured, effects of incubation temperature on hatchling growth appear somewhat contradictory. Low (Van Damme et al., 1992; Bobyne and Brooks, 1994), intermediate (Joanen et al., 1987; Brooks et al., 1991; Spotila et al., 1994), and high (Hutton, 1987) incubation temperatures have all been shown to maximize hatchling growth, depending on the species studied and the range of incubation temperatures employed. Apparently, growth rates are optimized at different incubation temperatures for different species, depending on the range of tolerance. Hatchlings reared in isolation sometimes grow faster than those in groups (McKnight and Gutzke, 1993), suggesting that social conditions may be a confounding factor affecting growth rates. Although these considerations make generalizations difficult, it is clear that incubation temperature has significant effects on long-term growth for diverse reptiles and that size at hatching is not always a reliable indicator of the potential for future growth.

In *C. nubila*, higher incubation temperatures resulted in faster growth during the first year of life. This effect was temporary, however, with growth rates for all morphological measurements becoming approximately equal across incubation temperature treatments by 16 months posthatching. Such transitory effects have also been observed in species for which hatchlings incubated at lower temperatures initially grow faster than those incubated at higher temperatures. In snapping turtles, McKnight and Gutzke (1993) found that hatchlings incubated at 22 C grew faster than those from 31 C at first; yet eventually growth in the 31 C hatchlings accelerated to the point where the two groups no longer differed in size. These results indicate that long-term studies of hatchlings throughout the juvenile period to sexual maturation, in which social conditions are carefully controlled, may be necessary to understand the ultimate fitness effects of differences in incubation temperature for various species.

Lang (1987) found that *Crocodylus siamensis* incubated at higher incubation temperatures selected consistently higher basking temperatures as hatchlings than those incubated at lower temperatures. Because higher basking temperatures

may accelerate food passage (Sinervo and Adolph, 1989), speed protein absorption (Lang, 1987), increase enzymatic activity (Regal, 1966), and improve digestive efficiency (Harlow et al., 1976), they have the potential to accelerate hatchling growth. In the present study, thermal selection by hatchling *C. nubila* at 14–16 months of age was unaffected by incubation temperature, suggesting that the initially faster growth rates of individuals incubated at higher temperatures may not have resulted from differences in thermal selectivity. However, future studies are critical to assess whether thermal selectivity could be manifested at earlier stages of development and, if so, the degree to which it may be associated with incubation conditions and juvenile growth rates. If the lack of correlation between incubation temperature and thermoregulatory behavior holds throughout the neonatal period, this would be consistent with studies on viviparous snakes, in which the temperature experienced by females during gestation had little effect on body temperatures selected by their offspring (Arnold et al., 1995). Similarly, Spotila et al. (1994) found no effect of incubation temperatures on temperatures selected by hatchling desert tortoises.

In addition to the possibility that thermal selection affects growth in juvenile *C. nubila* at an earlier age than that examined here, there are several possible reasons why observed growth rates in *C. nubila* were unrelated to tested temperature preferences in the present study. Growth in reptiles may be more closely tied to length of access to a radiant heat source than to basking temperature (Sinervo and Adolph, 1989). Lang's (1987) observations that hatchling alligators selecting a wide range of basking temperatures in response to periods of feeding and fasting grew faster than those that thermoregulated within a narrow range also suggest that the association between temperature preferences and hatchling growth may not be a simple positive relationship. As in other iguanids, dominance interactions among hatchling *C. nubila* are intense, and the ability of dominant individuals to exclude subordinate individuals from preferred heat resources in captivity at a young age may prevent expression of any thermoregulatory preferences resulting from differences in incubation temperature (Phillips et al., 1993). Finally, other factors to which thermal behavior in reptiles is sensitive, such as nutritional status and general health, may obscure more subtle effects of incubation temperature on thermal selection.

Despite its transient nature, the larger body and head size and faster growth rates of *C. nu-*

bila hatchlings incubated at higher temperatures may enhance their ability to escape predation and survive their first year. Larger body size, and especially head size, may also allow hatchlings to exploit a wider variety of food resources (Phillips and Packard, 1994). As has been suggested for green iguanas, large body size in young males may enhance social status and increase the probability of future mating, whereas in females, it may decrease the age of first reproduction and allow for larger clutch sizes (Pratt et al., 1994). However, larger body size may not be advantageous under all environmental conditions. For some reptiles, smaller hatchlings with more extensive yolk reserves may survive better than their larger counterparts when food and water are limited or unpredictable (Gutzke et al., 1987; Werner, 1988; Allsteadt and Lang, 1995).

Historically, flexibility in patterns of embryonic and juvenile growth in *C. nubila* in relation to varying incubation temperature may have represented an adaptive response to an environment in which either larger or smaller body size could be selectively favored depending on local conditions. However, for the majority of *Cyclura* populations which are currently heavily impacted by introduced mammalian predators, faster growth rates resulting from higher incubation temperatures are likely to outweigh any advantages normally associated with smaller body size. Consideration of the nesting environment and its potential influence on hatchling viability and survivorship should be an important component of any habitat preservation and restoration efforts on behalf of these endangered lizards.

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