



JOHN BINNS

Ctenosaura bakeri basking in Utila's mangroves.

Population Structure and Reproduction in *Ctenosaura bakeri* on Isla de Utila¹

Alexander Gutsche

Institute of Biology, Department of Sensory Biology, Humboldt University, Berlin, Germany

Photographs by the author except where indicated.

Field studies occurred mainly in two phases, from 27 June 1999 until 17 July 2000 and 1 January to 31 December 2001, allowing examination of distribution, abundance, and population structures within a complete annual cycle.

Population Structure: Biometric Data

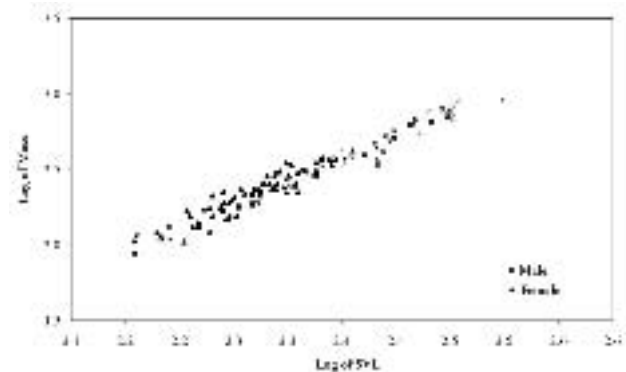
Data for *Ctenosaura bakeri* captured during the study at various sites and for which sex could be clearly determined are included. As in most iguanas, males were longer and heavier than females. The total length (TL) of the largest animal captured, a male with a partial tail, was 781 mm. Adding the snout-vent length (SVL, 315 mm) and the mean tail length/SVL suggest a possible TL of about 828 mm. Males attain a larger size (mean 230.9 mm and 460.6 g) than females (mean 188.0 mm and 237.4 g), with females averaging 81.4% of SVL and 51.5% of body weight of males. Mean tail length for males (337.0 mm) was 11.9% longer than that of females (296.9 mm). Differences in relative tail length (tail length/SVL) of both sexes did not differ significantly.

Growth and Development

I examined growth of captive juveniles maintained in outdoor enclosures for periods usually lasting one year, at which point the sex of the animals could not yet be clearly determined. Some individuals were raised and measured for up to 2.3 years,

Biometric values for male and female *Ctenosaura bakeri* from Isla de Utila (mean values \pm 1 standard deviation, range, sample size). Lengths are in mm and mass in g.

Character	Males	Females	Total
SVL (mm)	230.9 \pm 42.2 145–315 n = 76	188.0 \pm 18.6 151–229 n = 80	208.9 \pm 38.7 145–315 n = 156
Tail length/SVL	1.60 \pm 0.09 1.40–1.74 n = 38	1.57 \pm 0.09 1.32–1.79 n = 48	1.58 \pm 0.09 1.32–1.79 n = 86
M (g)	460.6 \pm 231.5 100–923 n = 76	237.4 \pm 79.9 105–424 n = 80	339.9 \pm 200.6 105–923 n = 156

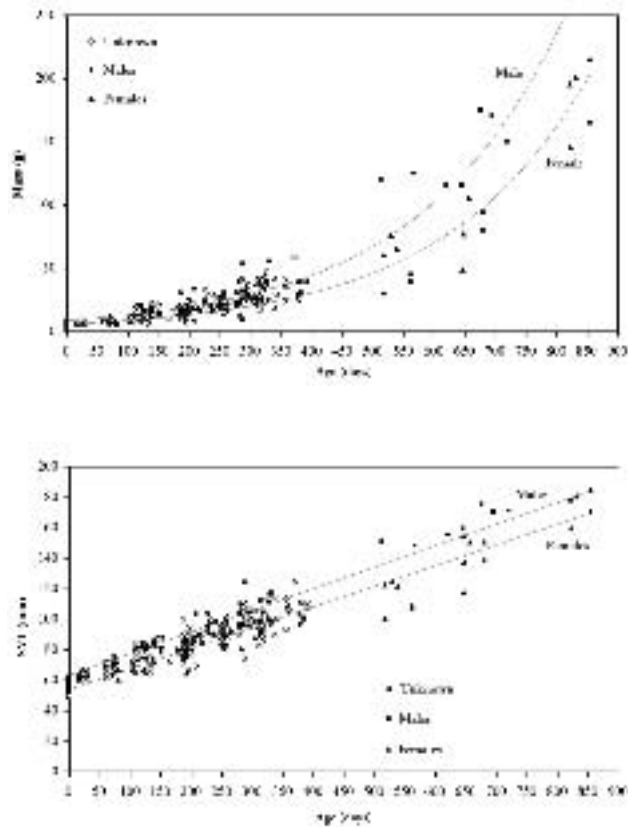


Relationship between mass (g) and snout-vent length (SVL, mm) of adult *Ctenosaura bakeri*. Because of a suspected allometric relationship, \log_e -transformed variables were used.

enabling collection of sex-specific growth data. Increases in length were predominantly linear, whereas weight increased exponentially. Juveniles (sex unknown) attained 1.7 times initial SVL and 4.9 times initial weight at 300 days. Development was sex-specific. Males were 5.1% larger and 8.6% heavier than females at hatching, 17.9% larger and 48.6% heavier at 300 days, and 9.1% larger and 27.9% heavier at 650 days. No comparisons were made beyond 800 days as only one (small) male remained. When I compared growth rates of captive-held and wild-caught animals, rates of growth were essentially similar for captive and wild caught animals of both sexes.

The proportional growth of SVL and tail length was examined for 145 wild caught animals with intact tails. Relative tail length decreased with increasing SVL, from longer tails in juveniles to relatively shorter tails in adults. The relative tail length of juveniles was significantly greater than that of adults. Sex-specific differences for relative tail length were not evident, although males had longer tails than females.

¹ This is a continuation of a series that began in Iguana 12(3):142. See that article for an introduction to the series and for maps and detailed descriptions of the study sites. All articles are based on the dissertation research of the author. Translation by AJ Gutman.



Snout-vent length (SVL) and mass of captive *Crenosaura bakeri*.

Sexual Maturity

In order to clarify the issue of age and size of *C. bakeri* at onset of sexual maturity, I compared body weights of 87 wild-caught gravid females with those of individually marked iguanas that were raised under controlled conditions. The smallest wild-caught gravid female had an SVL of 150 mm, likely the lower limit of sexual maturity for this species. Among captive-raised animals, three of five females had attained an SVL of 150–154 mm at an age of about 650 days, and at an age of about 840 days, all females had attained an SVL > 150 mm.

By the end of 2001, mating activity had not been observed among the captive-raised animals. Only in the following spring (2002), during the regular mating season, was mating activity first noted in this group (S. Knapinski, pers. comm., 2002). At that time, animals were approximately 2.5 years old, likely the earliest age at which mating would be initiated in the wild.

Population and Age Structure

The following data are based on the capture-recapture study. Based on growth data from captive animals, I roughly evaluated age structure. When comparing the individual study sites, the proportion of subadult iguanas (< 150 mm SVL) in Iron Bound was higher than that at Blue Bayou and Big Bight Pond. At Big Bight Pond and Iron Bound, the proportion of both adult iguanas and large iguanas was higher than at Blue Bayou.

Of the 24 iguanas captured at Blue Bayou, four animals (16.7%) were subadults and 20 animals (83.3%) were adults. Subadults (50–130 mm SVL) ranged in age from about 0.5–1.5



Nesting area at Iron Bound.



JOHN BINNS

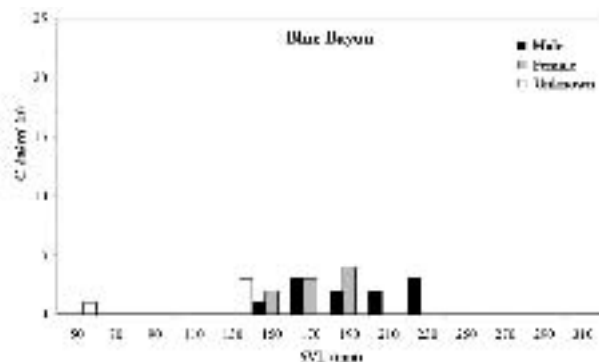
Ctenosaura bakeri in copula.

years. Five females (150–170 mm SVL) were about 2.5 years old, and four females (190 mm SVL) were more than 2.5 years old. Four males (150–170 mm SVL) were about 2–2.5 years old, and seven males (190–230 mm SVL) were more than 2.5 years old.

Of 40 iguanas taken at Big Bight Pond, two animals (5%) were subadults and 35 animals (95%) were adults. The subadults (50, 70 mm SVL) were about 0.5 years old. Of the 18 females, one female (150 mm SVL) was about 2.5 years old and 17 (190–210 mm SVL) were older than 2.5 years. Five males (150–170 mm SVL) were about 2–2.5 years old and 15 males (190–310 mm) were more than 2.5 years old.

Of the 107 captured iguanas collected at Iron Bound, 40 (37.3%) were subadults and 67 (62.7%) were adults. Subadults (50–130 mm SVL) were about 0.5–1.5 years old. Thirty females (150–170 mm SVL) were about 2.5 years old, and 11 females (190–210 mm) were older. Of the 26 males, four males were about 2.5 years old, and 22 males (190–270 mm SVL) were more than 2.5 years old.

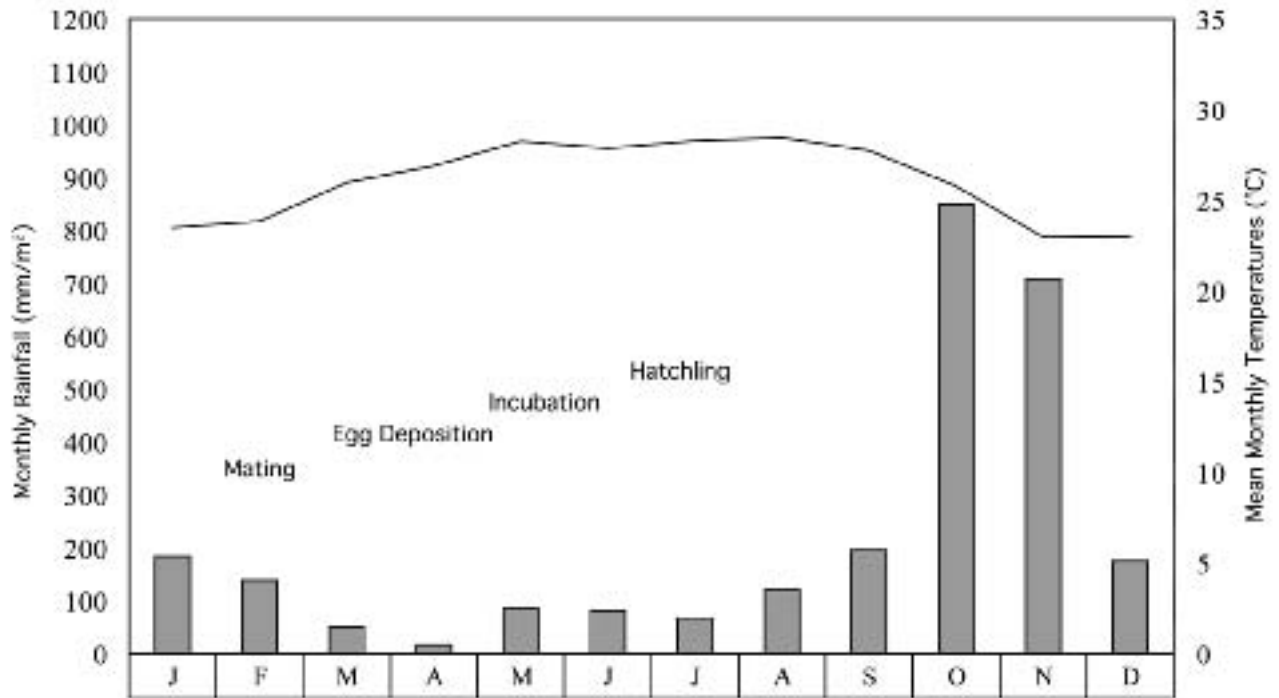
The ratios of males to females at Blue Bayou (11:9) and Big Bight Pond (20:18) were closely balanced, but that at Iron Bound (26:41) was conspicuously female-biased. The latter probably results from the polygynous mating system in the species, rather than a real demographic skew.



Frequency distribution of *Ctenosaura bakeri* by snout-vent length (SVL) for various size classes, differentiated by sex and study site. Data are based on the capture-recapture study.

Reproduction

The reproductive cycle occurs during the dry season, roughly from mid-January to early August. Mating begins when both the quantity and frequency of precipitation decreases in comparison with the heavy rainfall of previous months. In 2000, the first mating was observed on 17 January. Mating activity reached the highest intensity by about mid-February; the last mating of the year was observed on 24 March. Egg-laying began about mid-March at all study sites and during all three years of the study. The most intense nesting activity was observed from the beginning until the middle of April. Egg-laying ended in early May at all sites. Hatching began during the latter half of June, with the earliest observed hatch occurring on 20 June 2000 at Iron Bound. The latest observed hatching date was 10 August 2001.



Reproductive cycle of *Ctenosaura bakeri* comparing the amount of precipitation (bars) and air temperature (line) throughout the year. Climatic data represent mean monthly values from 1999–2001 (at Big Bight Pond); the reproductive phases are averaged from observational data.



Female digging a nest burrow.

No reproductive activities occurred outside this time period in this or other years.

Nesting Areas

Female *Ctenosaura bakeri* exclusively use a small number of sandy coastal areas as nesting grounds. All are adjacent to the mangrove areas where iguanas spend the bulk of their time. More distant sandy coastal areas (e.g., at Pumpkin Hill on the northeastern coast or between Big Rock and David Beach on the southern coast) were not used, nor were inland sandy areas bordering mangroves. The total extent of the nesting areas amounted to roughly 109 ha. Vegetation consists largely of plants characteristic of Caribbean coasts (e.g., *Ipomoea pres-caprae*, *Cocos nucifera*, *Coccoloba uvifera*). Nesting burrows were invariably located in the vegetation-free areas. Iguanas avoided even those open areas where the surface of the ground was covered with fallen leaves.

Erstwhile vegetation-free nesting sites used for many years at Iron Bound and Rock Harbor were gradually colonized after 2001 by an invasive creeping vine. In 2002, nest burrows were restricted to the remaining open areas; by 2003, these areas had also become overgrown. Within a few days of the growth being manually removed, the first test excavations were observed.

I noted a clear preference for sunny locations. Of 110 excavations, 55.5% (test and nest burrows) were situated where they received full sunshine throughout the day or were subject to light shade for only a few minutes. Such conditions were present primarily in sandy areas where short periods of shade occurred only in the vicinity of isolated trees. Partly sunny locations subject to shade at particular times of the day were also utilized (49 excavations; 44.6%). These locations were close to or within adjacent beach forest.

Burrows were preferentially selected in areas with sandy substrate and few coarse coral fragments. Larger coral fragments or pieces of driftwood were often (61.8%) incorporated into nesting burrows, with entrances located directly beneath these surface structures.

Depths of nest chambers were occasionally influenced by various environmental factors. Chambers in areas with well-developed root networks were directly beneath the root system. These nests were generally deeper (mean 345.0 mm) than those in sandy areas without root networks (mean 242.9 mm). Surface



Beginning of a nest excavation (test dig).



Opened nesting chamber with temperature logger.

substrates (to 170 mm) were dry. Nesting chambers, however, were discernibly damp.

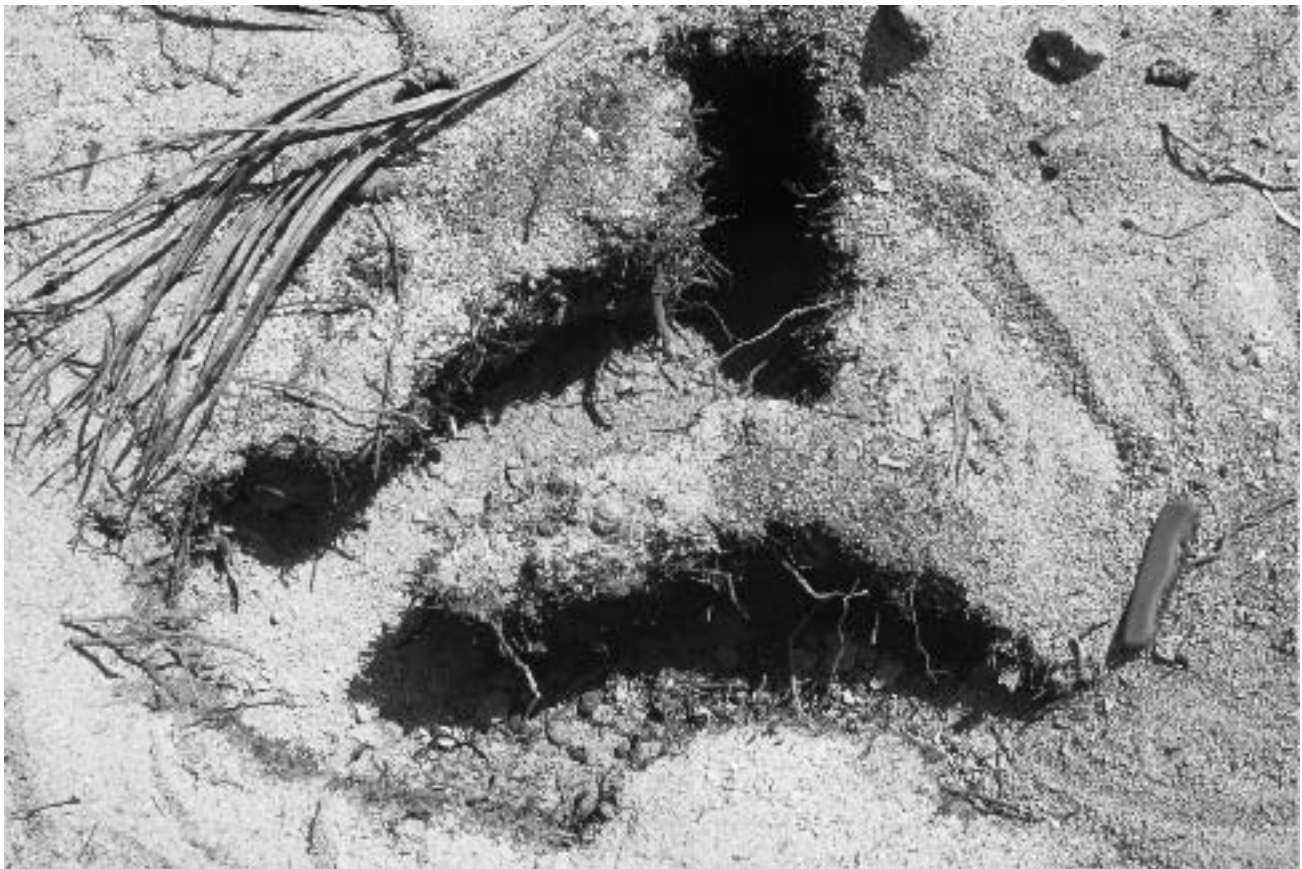
Temperature loggers buried at depths of 200 and 400 mm (representing upper and lower limits where nests were typically found) recorded mean temperatures between 29.7 °C (200 mm) and 30.3 °C (400 mm).

Migration of Females to Nesting Areas

Five females marked in the mangroves were recaptured in various nesting areas. Two were from Blue Bayou and the other three from Iron Bound. Distances between the original capture site and the nesting areas were 158.1–880.0 m. Four of the females were recaptured in nesting areas bordering their home mangrove areas. The fifth female was marked at Iron Bound and recaptured 880 m away on the beach at Rock Harbor. The return journey was documented for two of the females at Iron Bound, with both recaptured at their home trees.

Nesting Burrows

Females dig individual nesting burrows in sandy beach substrate in order to deposit eggs. Burrows are dug anew each breeding season. Females will usually dig a number of test burrows in various locations before selecting a final nesting site. Test burrows are abandoned in various stages of completion. The actual nest burrow is backfilled with substrate following successful oviposition.

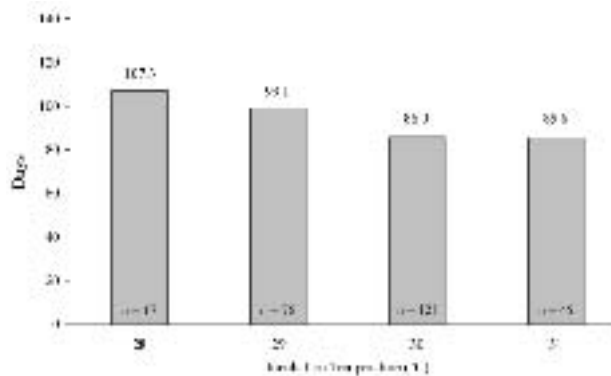


Opened nest burrow; the knife marks the entrance.

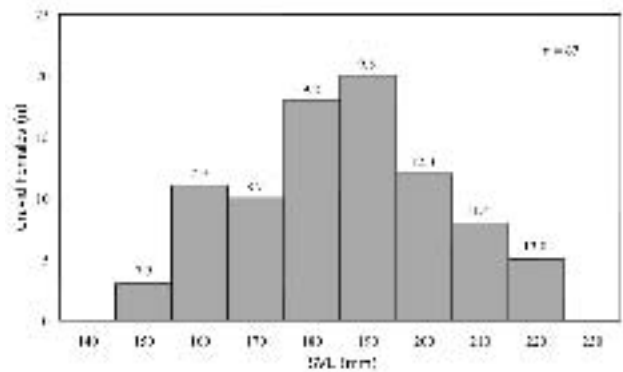
Nest burrows consist of an entrance, a tunnel, and a connecting egg-laying chamber. Openings were uniformly oval. The smallest measured entrance was 60 x 30 mm, the largest 100 x 70 mm. Tunnels were roughly circular in cross-section with diameters of 50–70 mm and lengths of 510–1240 mm from the entrance to the end of the nest chamber. Nest chambers were fist-shapes, measuring on average 112 x 73 mm (width x height). Depths, measured from the surface of the ground to the bottom of the nest, were about 300 mm (160–450 mm). Of 22 nest chambers excavated, five had approximately 1-cm air pockets above the eggs, all others were filled with loose sand.

Incubation

Data on natural incubation temperatures were collected for four clutches in 2000 and four clutches in 2001. Data loggers were placed directly next to the eggs either on the day they were deposited or on the day following and removed 95 days (13 weeks) later. Temperature fluctuations were generally small and varied, despite differing locations, times of day, and depths, on average between 29.1–30.8 °C with a total mean of 30.1 ± 0.2 °C. Deeper nests varied less (only by about 1.0 °C around the mean value) than shallower nests. Observations on last oviposition and first hatch indicated incubation periods in the wild that



Incubation periods for *Ctenosaura bakeri* at various temperatures under artificial conditions.



Distribution of gravid *Ctenosaura bakeri* females by size class. Numbers above the bars are mean clutch size for that size class.

ranged from 91–99 days. Also, all eggs in nests ($n = 22$) excavated after 95 days had hatched. Under artificial conditions, incubation period decreased with increasing temperature.

Hatching Rates

Seventeen clutches from 2000 consisted of 204 eggs with clutch sizes of 6–16 eggs. Hatching rate was 94.1%. One clutch of 12 eggs all died. One day following oviposition, an inspection of the nest, which had not been sealed by the female, revealed that hard root tips had pierced the shells of two eggs and the yolk had run out. The nest was full of tiny black ants feeding on the damaged as well as undamaged eggs. All eggs had been fertile.

Five clutches from 2001 contained a total of 57 eggs with clutch sizes of 9–14 eggs. Hatching rate was 86.0%. One clutch of 14 eggs produced only six hatchlings; the other eight eggs died. Of these, seven contained dark, hardened yolk remnants, and one egg contained remnants of vertebrae. Fly pupae (family Sarcophagidae) were on and in all of the dead eggs.

Clutch Data

Clutch data were obtained from free-living females ($n = 87$) that were caught at various nesting sites and others housed in outdoor enclosures at the “Iguana Station” until oviposition. The SVL of



Female with collapsed flanks following oviposition.



Gravid female on the trunk of a Coconut Palm. Eggs are clearly visible along the flanks.

captured gravid females ranged from 150–229 mm. Mean body weight before egg-laying (body weight including clutch) was 224.5 g (118–435 g). Whereas clutches averaged 27.5% of female body weight before egg-laying, the average loss of body weight due to egg-laying was about 33%. The difference of roughly 5.5% might reflect water released during ovipositioning. Mean clutch weight was 55.3 g (30.6–107.3 g) and varied significantly according to the number of eggs per clutch. Mean egg weight was 6.2 g (4.8–8.4 g). The mean number of eggs laid was 9.8 (5–16). Mean egg dimensions were 30.5 x 18.7 mm (27–35 x 18–19 mm).

Larger females produced significantly more eggs per clutch, but only very slightly larger eggs. The relationship of body weight before and after egg-laying was strongly linear. Egg and hatchling masses were significantly correlated, but clutch size had no apparent effect on hatchling mass.

Using number of adult females captured, mean clutch sizes for each size class, and the natural hatching rate (92.3%), I calculated birth rates for females at each study site for the year 2000. Using census and distribution data for each area, hypothetical birth rates were 79.9 (Blue Bayou), 184.0 (Big Bight Pond), and 346.0 (Iron Bound) hatchlings per hectare.