

Estimation of Age in Nesting Female *Iguana iguana*: Testing Skeletochronology in a Tropical Lizard

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Abstract. Skeletal elements of female *Iguana iguana* nesting in Panama show a distinct pattern of periosteal rings or marks of skeletal growth (MSGs), thereby indicating a pattern of cyclic growth. The numbers of MSGs, assuming one MSG is formed each year, slightly underestimate the known ages of a small sample of female iguanas. Based on the estimated age data, female iguanas probably reach sexual maturity in their fourth or fifth years. Age estimates and size are poorly correlated, and females nesting for the first time on Slothia are 292-415 mm in body length (SVL) and range in estimated minimum age from 3-8 yr.

Introduction

Each February and March, gravid female *Iguana iguana* migrate from the forest of Barro Colorado Island (Lake Gatun, Panama) to a small, adjacent islet, Slothia, to nest (Rand, 1968). Nesting females have been marked since 1980 and some hatchlings since 1965. Even with this regular marking program, the age distribution of the nesting females has remained unknown, because only a fraction of each year's nesting females have been previously marked, and most marked individuals were marked as adults, not as hatchlings. Thus, even relative ages are unknown for the majority of the nesting females and actual ages are available only for a few individuals. These few females marked as hatchlings and those marked upon first nesting and recaptured later provide an opportunity to test the technique of skeletochronology on a tropical reptile. If confirmed, this technique provides a means to age individuals captured as adults.

Skeletochronology is a technique for aging animals based on the presence of periodic markers in skeletal tissue (Castanet et al., 1977). The use of this technique in vertebrates follows from three major assumptions. 1) Regular cyclic growth occurs in

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the skeleton or elements thereof. As corollaries of this assumption, each cycle consists of a period of active growth and a period of arrested or no growth, and this cyclic growth leaves visible permanent markers in the bone. The arrested growth appears as darkly staining lines (Lines of Arrested Growth, LAG) and each LAG and an adjacent broader lighter staining band of bone represents one cycle of growth (Mark of Skeletal Growth, MSG). 2) The growth markers represent a repeatable and specific period of time (typically one year) in the life of an individual; hence, the total number of growth markers (MSGs) provides a direct and accurate estimate of the individual's age. 3) Where growth markers are lost, through bone remodeling, the number of lost markers can be estimated from the number and size of markers remaining.

These assumptions have been variously tested. Cyclic growth in skeletal elements has been demonstrated in numerous temperate-zone vertebrates through the presence of distinct periosteal or dental layers and vital dye experiments. However, the one MSG-one year hypothesis has been less rigorously and less often tested. Such tests require known-aged animals, either through long term captive or mark-recapture studies. Such data have been largely lacking, particularly for amphibians and reptiles. The annual hypothesis has been tested and confirmed in a few amphibians and reptiles: *Triturus cristatus* (Francillon, 1979), *Bufo bufo* (Hemelaar and van Gelder, 1980), *Rana temporaria* (Gibbons and McCarthy, 1983), *Cophosaurus texanus* (Nouira et al., 1982), *Lacerta lepida* and *L. viridis* (Castanet, 1978), *Lacerta vivipara* (Pilorge and Castanet, 1981), *Crocodylus siamensis* (Buffrenil, 1980), and *Testudo hermanni* (Castanet and Cheylan, 1979). Because all but one of these taxa are temperate-zone in distribution, the immediate questions are whether periosteal growth layers (MSGs) develop in tropical species and whether the MSGs correlate with predictable time intervals, e.g., years. The marked female iguanas returning to Slothia offer an ideal sample to investigate these two questions. If MSGs occur in iguanas and if the MSGs prove to be reliable estimators of age, demographic parameters can be examined. Herein, we address the two former questions and then use the estimated age data to investigate some demographic parameter, i.e., relation of size and age, age at first reproduction, and age structure of the nesting population.

Materials and Methods

In 1982 and 1983, the ultimate and penultimate phalanges of one digit were removed from a forefoot of each female nesting on Slothia and some females trapped at nearby nesting sites ($n = 107$ and 57 , respectively). In both 1982 and 1983, iguanas were captured at the Slothia/Growing House, Pepper/Salt, DeLesseps, and Mosca/Guindilla nesting sites (see Bock et al., 1985, for a map of the nesting sites). In 1983, iguanas were also captured on the Barbour and Buena Vista peninsulas. All localities are on the edge of Gatun Lake in the Barro Colorado Nature Monument and the furthest are less than 7 km apart. An attempt was made to capture all of the females nesting on Slothia. At the other sites only a small portion of the females were caught.

The removed phalanges were preserved in formalin. The penultimate phalanx of each digit was removed from its epidermal sheath and partially stripped of connective tissue, decalcified (formic and hydrochloric acid solution), dehydrated in alcohol and xylene, imbedded in paraffin, sectioned (10 μm), and stained with Harris's haematoxylin and eosin.

The 1982 sample was examined and counted independently by two individuals (Addison Wynn and George Zug; these data sets are identified as WYN82 and ZUG82/1) under a blind test protocol, i.e., sections identified by field number only. Once the age estimates were obtained by the skeletochronological method, the estimates were compared to the known age sample. The 1983 sample was similarly examined to obtain age estimates independently of the size and known age data, but by a single individual (data set designated ZUG83/1). The 1982 and 1983 samples were re-examined after an interval of 6-9 months (these data are designated ZUG82/2 and ZUG83/2). These procedures were used to test the reliability and consistency of our skeletochronological technique.

Our skeletochronological procedure involves the examination of whole cross-sections of the phalanges; identification of the individual marks of skeletal growth (MSGs), counting the MSGs dorsally, laterally and ventrally; determining whether any MSGs had been lost through bone remodeling by comparing the size of the marrow cavity to phalangeal diameters of a hatchling and 1 yr old juvenile; and estimation of age using maximum number of MSGs as equivalent to iguana's age in years. Cross-sections with extensive remodeling and/or loss of initial MSGs, with faint or no LAGs, or with numerous accessory LAGs were noted; some such specimens were impossible to score and were eliminated from the following analyses.

Results

Presence and Nature of Growth Marks

Of the 107 females captured during the 1982 nesting season, the majority (90) possessed one or more distinct periosteal MSGs (Fig. 2A). Most of the remainder (17) also showed growth marks in the phalanges, but the number of extant MSGs was difficult to determine owing to extensive remodeling for the repair of earlier injuries or to inadequate staining of the LAGs. The 1983 sample is smaller (57 females) and again, some distinct MSGs were present in the majority of the phalanges examined (43). Thus, these iguanas show a cyclic growth pattern.

There is no evidence (Fig. 1A&C) of lines of arrested growth (LAGs) forming at the time of hatching/birth as occurs in the lizards *Cophosaurus texanus* (Nouira et al., 1982) and *Lacerta vivipara* (Pilorge and Castanet, 1981). Absence of a hatching LAG is shared with the lizard *Podarcis muralis* (Castanet and Roche, 1981) and is not unique to *Iguana*. The first LAG appears to mark the end of the first period of growth in *Iguana*.

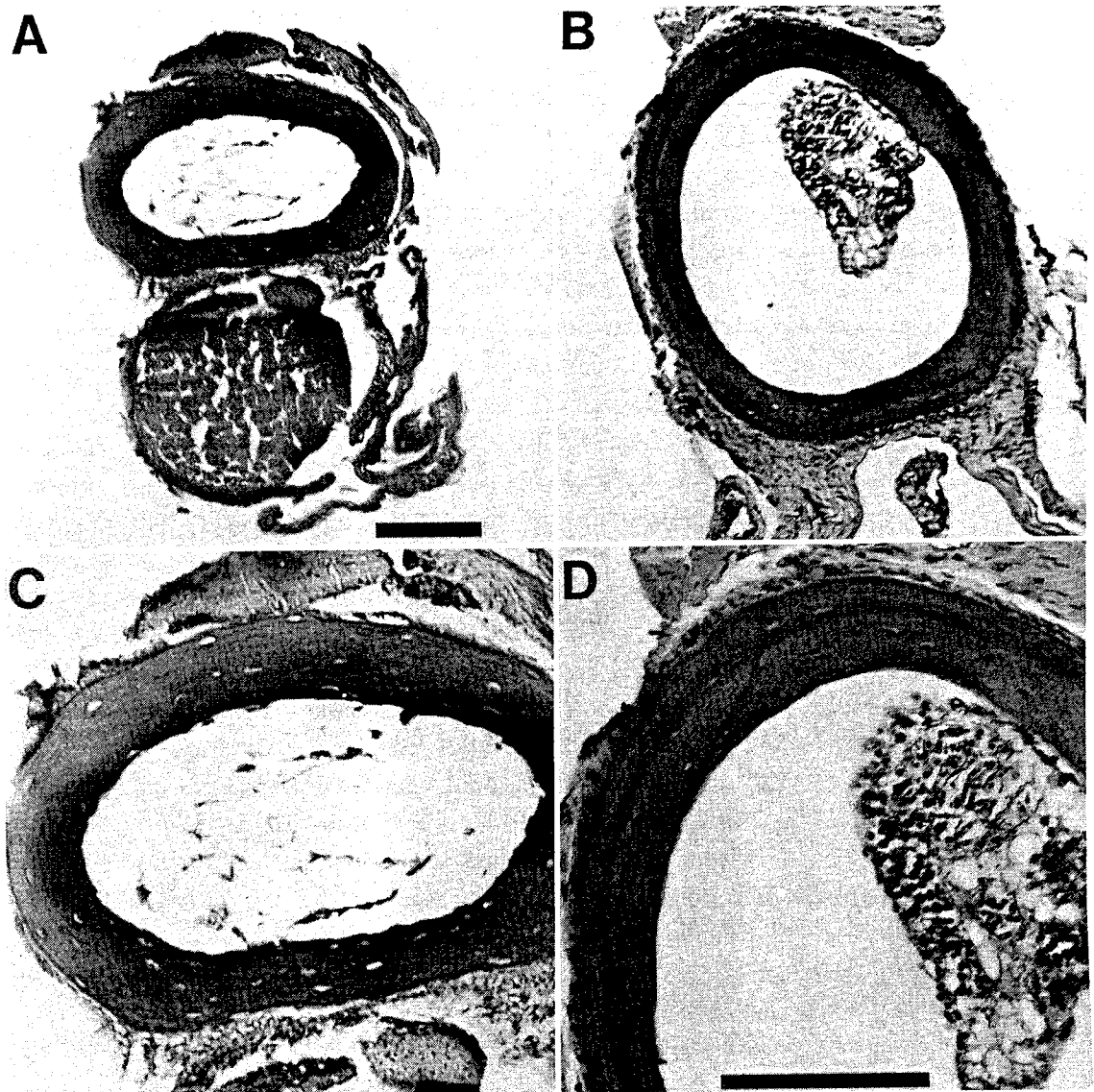


Figure 1. Cross sections of penultimate phalanges of juvenile *Iguana iguana*. A&C. No LAG in a post-hatchling (USNM 31587, 57 mm SVL). B&D. One LAG indicating an animal in its second year of growth (USNM 219868, 87 mm SVL). Insets equal 0.1 mm; A&B and C&D to same scale.

Although MSGs were present in most phalanges, they were not always easy to count and this difficulty leads to the differences in counts and estimation of age. All histological sections showed some resorption/remodeling around the periphery of the marrow cavity (Fig. 2A), although a portion of the first or second MSG often remained dorsally in the cavity; growth and resorption are concentrated ventrally and ventrolaterally. However, the major difficulty was not the loss of earlier MSGs, rather it was the indistinct (Fig. 2C) and/or supernumerary (Fig. 2D) LAGs, upon which the observer must depend to delimit the MSGs.

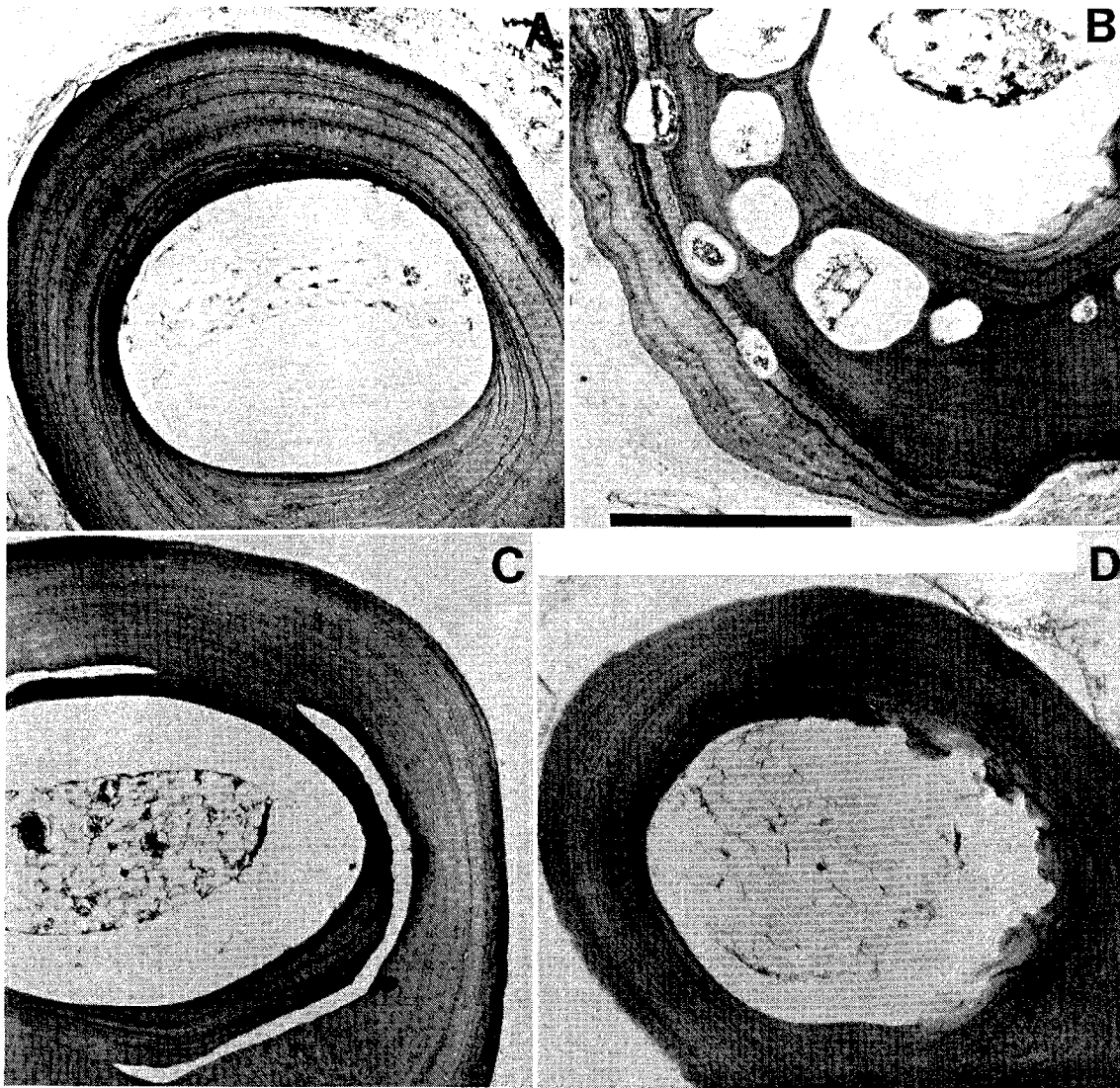


Figure 2. Cross sections of penultimate phalanges of adult female *Iguana iguana*. A. Distinct MSGs (field number 227, 301 mm SVL). B. Extensive remodeling (\neq 11, 415 mm SVL). C. Indistinct MSHs (\neq 233, 315 mm SVL). D. Supernumerary LAGs (\neq 239, 359 mm SVL). Inset equals 1.0 mm; all photographs at same magnification.

These difficulties caused counting errors and inconsistencies, and require scrutiny. We used the Wilcoxon matched-pairs signed rank test (Siegel, 1956) to compare the differences between the two observers' (WYN82 & ZUG82/1) counts on the 1982 sample and the difference between the counts of the 1982 and 1983 samples (ZUG82-83/1) contrasted to ZUG82-83/2; Fig. 3) taken 6-9 months apart by a single observer. With two observers, the null hypothesis that the two 1982 data sets were not different was rejected ($Z = -6.068$, $P < 0.001$); these data sets had 15 matches and 17 differences of ± 1 ($n = 80$, sample size differences from those in the appendix result from one observer being unable to score all sections scored by other observer). The data sets

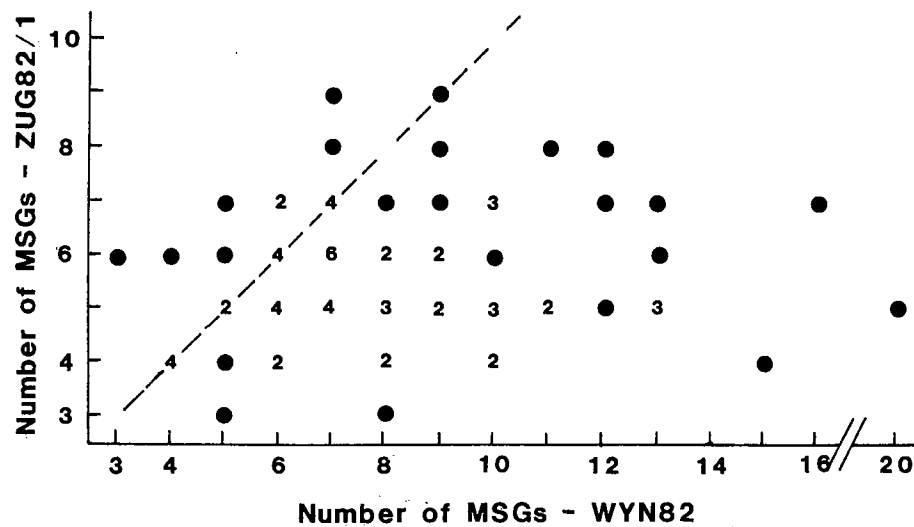


Figure 3. Comparison of MSG counts by two observers (WYN82 & ZUG82/1). A spot denotes a single datum point, the integers indicate the number of identical data at the same point, and the dashed line indicates matching MSG counts.

(ZUG/1 vs ZUG/2) of the single observer were significantly different for the 1982 sample ($Z = -3.543$, $P < 0.001$) but not for the 1983 sample ($Z = 0.592$, $P > 0.28$). Replicate estimates by a single observer yielded 25 matches and 34 differences of ± 1 for the 1982 sets ($n = 87$) and 18 matches and 20 differences of ± 1 for the 1983 sets ($n = 43$).

The differences between the two observers derived from differences in both counting technique and interpretation. One observer (Wynn) examined the entire bone section, but used only the MSGs that were delineated by the LAGs in the dorsal quadrant of the section to estimate age. The other (Zug) examined the entire bone section, selected the most distinct LAGs and attempted to connect them throughout the circumference of the section. The latter technique yields lower counts (e.g., 1982 sample, $\bar{X}_{zug} = 5.7$ and $\bar{X}_{wyn} = 8.2$, $t = 7.308$, $df = 168$, $P < 0.01$), because it tends to eliminate indistinct, frequently interrupted LAGs.

Periodicity of Growth Marks

Is the growth cycle an annual one? Barro Colorado Island experiences a distinct dry season, usually from mid December to April and a distinct rainy season usually from mid April through mid December (Rand and Rand, 1982), so environmental variation exists that can potentially enhance or retard growth. Data from specimens of known age, although few, suggest an annual growth cycle (Table 1). The number of MSGs is equal to or less than the known age in most specimens, so our estimates, assuming one year for each MSG, are underestimates.

Table 1. A comparison of ages, actual and estimated from the number of MSGs, in iguanas nesting in 1982. Estimated age data are significantly different from actual ages (sign test, $p = 0.25, 0.25, 0.125$, respectively for WYN, ZUG1, ZUG2).

Specimens	Actual Age	Estimated Age		
		WYN82	ZUG82/1	ZUG82/2
11S	8	>5	>5	5
82S	6	—6	—7	4
187S	7	6	6	4
204S	7	7	>4	—

Ideally, the examination of bone samples removed from the same animal in successive years should show additional MSGs, and the number of additional MSGs would match the number of years between the collection of the samples. Our data do not show this pattern. Of the seven iguanas captured in both 1982 and 1983, MSGs can be scored for only three from 1983: 7 vs >5, >8 vs 6 and 4 vs 7 yr, for 1982 vs 1983 counts. This mismatch and absence of MSG counts result from the removal of bone samples from the same digit in successive years and, in most cases, the first year's sampling caused major remodeling in the more proximal phalanx.

Demographic Parameters

The preceding results illustrate the major problem areas in our skeletochronological data for *Iguana iguana*. They do not, however, negate the usefulness of the data for examining age-related aspects of *Iguana* life history. Since the ages are estimates and are predominantly underestimates, our extrapolation of demographic parameters must be considered as tentative hypotheses. We certainly do not claim that MSG data represent actual ages.

The estimated age data discussed subsequently are from the ZUG82-83/1 sets; the first examination sets were selected because these MSG counts most closely matched the ages of the known-aged animals (Table 1). Each age estimate (in yr) derives directly from the number of MSGs observed in the histological preparation. The estimates are not adjusted to account for the possible loss of the original/earlier MSGs, because such adjustments would likely compound the observer's error owing to the uncertainty of determining the number of MSGs lost and the possible presence of a portion of the first MGS in some specimens.

Size and age. — Within these samples, body size and estimated age are poorly correlated, i.e., larger animals do not have more MSGs and are not necessarily older animals (Fig. 4). Regression analysis supports this observation; coefficients of determination are not or only marginally significant (e.g., ZUG82/1 $r^2 = 0.14$, ZUG 83/1 $r^2 = 0.46$). The disassociation of age and size is reinforced by a regression analysis of

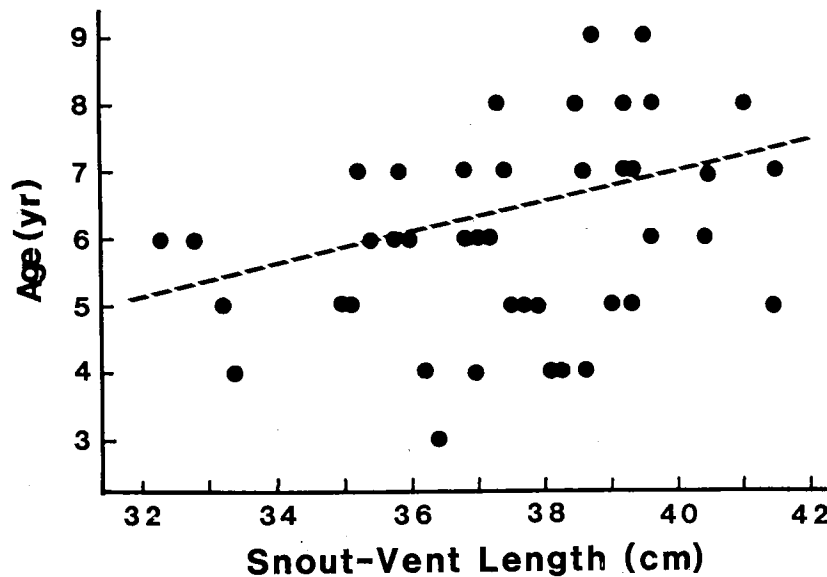


Figure 4. The relation of snout-vent length to estimated age (Appendix: Table A) in the female inguanas nesting on Slothia in 1982. $Y = -2.573 + 0.024 X$, $r = 0.38$, $n = 37$.

the small sample ($n = 11$) of known-aged females recaptured in 1982 ($r^2 = 0.005$); the youngest was 3 yr old and 384 mm SVL, the oldest 8 yr and 359 mm. These observations are contrary to the hypothesis of Fitch and Henderson (1977) that females can be divided into age classes on the basis of body length. The disassociation of size and age is reinforced by the smallest gravid females (Table 2) not being the youngest mature females. Size may be more important than age in determining when an female iguana first breeds.

Age distribution. — Age estimates allow an examination of several characteristics of the nesting female population. The average age of the 1982 and 1983 samples are similar 5.7 yr ($s = 1.30$, $n = 90$) and 5.3 yr ($s = 1.08$, $n = 43$), and not significantly different from one another ($t = 1.688$, $df\ 131$, $0.10 > P > 0.05$). The age distributions between the iguanas nesting in different areas do not appear different, nonetheless we confine our examination of demographic parameters largely to the Slothia females because of the larger sample sizes.

The age composition (based on number of MSGs) of 1982 and 1983 nesting populations on Slothia are similar. The youngest female to nest on Slothia in 1982 and 1983 was at least three years old. This age represents the minimum estimate for the attainment of sexual maturity. The preponderance of Slothia females were older (4-7 yr) whether nesting for the first, second or third time (Table 3). A similar age structure is observed in the DeLesseps sample ($n = 38$); Appendix Table A); the age estimates range from 3-8 yr with most individuals in the 4-7 yr classes. The distribution in the six age classes is 1, 6, 16, 8, 6, 1 from 3-8 yr, respectively; this distribution approaches a normal curve with median and mode skewed to the 5 yr olds. The much smaller Mosca

Table 2. Estimated ages of the smallest gravid female iguanas (< 310 mm snout-vent length) captured during the 1982 and 1983 nesting seasons. A "R" following the identification number indicates that the animal was marked as an adult in 1981.

Specimen	SVL	Age WYN82	Estimates ZUG82-83/1
81R	274	4	4
91R	307	6	5
218	303	6	5
227	301	7	7
276	295	-	4

Table 3. Distribution of age estimates for female iguanas nesting on Slothia in different years. The age estimates derive from the ZUG82/1 sample and the new individuals in the ZUG83/1 sample (respectively, Table A and B in Appendix).

Year of First Capture	Age (years) in 1982						
	3	4	5	6	7	8	9
1980			2	2	1	4	2
1981		1	6	4	3		
1982	1	3	1	5	4	1	
Total Nesting Population	1	4	9	11	8	5	2
	Age (years) in 1983						
	3	4	5	6	7	8	9
1980			1	1		1	
1981				1	2		
1982					1		
1983		6	8	3	2		
Total Nesting Population	0	6	9	5	5	1	0

sample ($n = 10$; Table A) also shows the nesting females clustered at 4-7 yr with a frequency of 3, 2, 3, 2 in the four age classes. The samples from the other localities are too small to indicate age structures for these populations; however, the age ranges and median/modal ages are the same.

Discussion

The presence of MSGs denotes a cyclic growth pattern and suggests a seasonal environment in which growth is alternately promoted and retarded. *Iguana* in Panama are exposed to an alternation of a wet and a dry season each year. Hence, our initial assumption was that each MSG represented one year of growth. The similarity of our age estimates to the actual (true) age of lizards marked as hatchlings supports the pro-

duction of one MSG each year in the Barro Colorado population of iguanas. Likewise, in other species of lizards (*Lacerta lepida*, *L. viridis*, *L. vivipara*, and *Cophosaurus texanus*; op. cit.), one MSG is produced each year. These data do not, however, guarantee that MSGs will be present or always denote an annual growth cycle in other lizards. Castanet (1978) found no MSGs in the gecko *Tarentola mauritanica* or the sand skink *Chalcides ocellatus*. Were these animals growing continuously and were no LAGs produced? Similarly, do the homogeneous sections from some of the BCI iguanas indicate that some members of the population feed and grow year around? Do supplementary LAGs reflect local or brief food shortages or other demands on energy? Our data cannot address the question or discern whether homogeneous sections result from a different form of osteogenesis or from abnormal preservation and histological preparation. Although we advocate the assumption of the annual production of each periosteal MSG, we caution against the treatment of skeletochronological age estimates as actual ages. The difficulties and inconsistencies outlined in the Results Section argue for the statistical interpretation of skeletochronologically determined ages. In spite of the inconsistencies, this technique has great potential for the investigation of marked populations of amphibians and reptiles, because the clipped toes can provide an estimate of age for each individual marked.

It is important to note that our age estimates were not corrected for the absence of MSGs resulting from resorption and remodeling. Furthermore comparison of our estimates with the known ages showed the estimates to be the same or less. Thus, our estimated ages are commonly underestimates, particularly for the larger and older individuals (see Table 1). An attempt to correct for this bias in our data would likely increase the inaccuracy of our age estimates.

Although we noted earlier (Table 2) that the correlation between estimated age and body size (SVL) is weak to nonexistent, comparison of the average size of the age classes of first-time nesting females (Table 4) shows a general trend of increasing average body size, but a trend that is not statistically significant or even convincing with these small sample sizes. The range of body sizes is commonly 100 mm or more for each age class. This variability likely derives from three major sources: 1) errors of our age estimates, 2) natural variation in growth rates, and 3) errors in size measurement. Our data cannot differentiate between these aspects.

Are the older females actually nesting for the first time, have they nested elsewhere previously, or were they not marked during earlier nesting seasons? Bock et al. (1985) in an analysis of the 1980-1984 capture data for Slothia and nearby sites concluded that female iguanas usually nest every year upon reaching sexual maturity and return year after year to the same nesting area. The middorsal row of the spines show differential wear in nesting females (B. Bock, A.S. Rand & K. Troyer, unpubl. data) and may provide a method for determining first-time-nesting females. The age distributions for each year approximately normal curves and the age distributions of adjacent years are not greatly different. As would be expected, the females known to have nested on Slothia in previous years average older than those nesting there for the first time

Table 4. Size of females nesting for the first time on Slothia in 1982 and 1983. The same age data were used as in Table 2.

Estimated Age	Range	\bar{X}	Snout-vent Length s	N
3		364.0		1
4	295-381	344.8	24.84	9
5	331-390	361.1	20.21	10
6	335-411	375.4	25.04	8
7	358-415	385.3	22.30	6
8		373.0		1

(Table 3). The large numbers of older females nesting for the first time was not expected.

Nesting females (all study sites) for the 1982 and 1983 seasons ranged in size (SVL) from 274-425 mm and in estimated age from 3-9 yr. These ranges are nearly identical to those nesting for the first time on Slothia (Table 4). Three years appears to be the minimum age for sexual maturity and, questionably, eight years is the maximum age for sexual maturity. Since not all nesting females were marked prior to 1980, the five year and older individuals may have nested previously on Slothia and were not marked. The preponderance of 4-7 yr olds nesting for the first time (Table 3) seems to indicate that most of the females require 4-7 yr before they are ready to lay their first clutch. These ages for maturity are consistent with those for other iguanines, 2-9 yr (see Table 7.1 in Wiewandt, 1977).

Slothia iguanas hatch at 60-70 mm (SVL) and are 140-170 mm at the end of their first year of growth (Rand and Greene, 1982: fig. 8.3); growth in captivity may be faster (Kline and Cullum, 1984) or slower (Braunwalder, 1979). Projection of Rand's and Greene's growth rate to three years would yield individuals at the minimum size observed in nesting females. Thus, growth data independently support three years as the minimum age of maturity and 4-5 yr as the more common age for maturation in this population.

The widths (e.g., thickness) of MSGs provide some insights into growth patterns. The second and thirds MSGs are typically the widest bands (note that a portion of the first or innermost MSG is always resorbed) and are frequently of equivalent widths. The fifth MSG is occasionally as wide as the third and fourth, but more external ones are commonly very narrow. This pattern of growth conforms to the rapid growth of juveniles and the reduced growth upon or shortly after maturation. Infrequently a narrow MSG occurs within the juvenile series, and it may represent reduced growth in response to injury, disease, or low food supply.

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APPENDIX

Table A. Age estimates (in years; ZUG82/1) for females nesting in 1982 (n = 90). An asterisk beside an estimate denotes high reliability, i.e., distinct LAGs in histological preparation. Identification (ID) integers are the field numbers assigned to each iguana upon first capture when nesting. Letters are the sites of capture: B, Barbour; D, DeLesseps; M, Mosca/Guindilla; P, Pepper/Salt; S, Slothia; V, Buena Vista.

ID	Age	ID	Age	ID	Age	ID	Age	ID	Age
9S	5	115S	5*	196D	5*	220D	4	242D	5
10S	6*	117M	6*	197D	5	221D	7	243D	4
11S	≥5	120M	6	198S	7	222D	6	244D	6*
15S	9*	124S	5	199D	7	223D	7	246S	4
27S	7*	127S	7*	200D	7*	224D	8	247D	4
28S	≥8	141M	5	201S	7	225D	6	248D	5
33S	6*	146S	4	202S	6	226S	7	250M	5
34S	8*	148S	7	203S	6*	227P	7	252M	6
36S	≥9*	149S	5	204S	≥4	228D	6	253M	4
42S	8	164S	5	210S	6	230D	3	254D	4
58S	8	178S	5	211M	7	231D	5	255S	6
72S	6*	184P	5*	212M	7*	232D	5	256S	7
79S	6	187S	6	213S	8	234D	5	257S	5
81D	4	188S	4	214D	7	235D	4	259D	5*
82S	7	189D	6*	215D	6*	236D	6		
91D	5	190D	5	216D	5	237D	5*		
100S	6*	192D	5*	217D	6	239S	3		
101S	5*	194D	5	218D	5	240M	4		
114S	6	195D	5*	219D	7	241M	4		

Table B. Age estimates (in years; ZUG83/1) for females nesting in 1983 (n = 43). Other information is the same as in Table A.

ID	Age	ID	Age	ID	Age	ID	Age	ID	Age
11S	5	261S	7*	273B	7	283P	5	294B	7
28S	6	263M	5	274B	4	284P	4	295S	5
46B	8	265P	5	275D	6	285S	4	296P	4
112S	7	266B	5	276S	4	286P	5	297V	4
120M	5	267S	4*	277S	6*	287S	5*	298V	5
168S	7	268S	5	279S	6*	290P	5	300V	5
183S	6*	269S	5*	280S	4	291S	5	302S	4
187S	7	270S	5	281S	6*	292S	5*		
260S	7*	271S	5	282S	4	293B	5		