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Received: 14 April 1996
Reviewed: 11 November 1996
Revised and Accepted: 12 September 1997

Chelonian Conservation and Biology, 1997, 2(4):576–581
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Growth of the Turtle, *Phrynops rufipes*, in Central Amazônia, Brazil

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Phrynops rufipes (see color cover photo) is a medium-sized chelid turtle (carapace length to ca. 240 mm) largely restricted to closed-canopy rainforest streams in the Amazon basin where it feeds mainly on invertebrates and palm fruits (Lamar and Medem, 1982). Known localities are tightly clustered close to Manaus and in southeastern Colombia. The ecology of the species is little known and it has been described as "one of the rarest of all turtles" (Pritchard, 1984). Information on growth is important for understanding population dynamics, and turtles may have ages at maturity that vary from 5 to 25 years (Shine and Iverson, 1995). However, there is no published account of the growth ecology of *P. rufipes*.

Growth in reptiles may follow any of a wide range of the Richards family of curves which describe most sigmoidal relationships between size and age (Brisbin et al, 1984), or may follow unusual empirical patterns (e.g., Webb et al., 1983; Magnusson and Sanaiotti, 1995), and it may be difficult to distinguish statistically between candidate curves even when the true relationship is known (Abercrombie, 1992). For most species and data-collection regimes, parametric tests should not be used (Rickard et al., 1989). There may also be large interannual variations in growth, so models based on short time series may be misleading (Tucker et al., 1995). These considerations impose severe restrictions on the construction and use of representative growth curves for a species and it is necessary to evaluate individual variability when descibing general growth patterns.

Variation among individuals may make it difficult to describe the mean growth pattern of a population. If variation in growth rate within individuals is as great as that among individuals, the mean age/size relationship for the population will be similar to that calculated for most individuals. In this case, growth may be adequately described by the population growth parameters. However, growth rates of individual reptiles may tend to follow parallel trajectories (e.g., Webb et al., 1983; Rickard et al., 1989; Congdon and van Loben Sels, 1993; Magnusson and Sanaiotti, 1995). When growth-rate-on-size trajectories tend to be parallel, curves of size on age for individuals tend to diverge, rather than converge, with time. Worse still, the "mean" growth curve constructed from the individual growth curves may not reflect the pattern in any of the population of curves it is meant to represent (Rickard et al., 1989). While it is unlikely that most age estimates of wild turtles have a precision of months or a few years, most methods of studying growth are probably capable of differentiating a species with an average age of maturity of 5 years from species with mean ages of maturity of 10 or 15 years.

In this paper, we analyze the growth of *P. rufipes* with the aim of answering the following questions: 1) do individuals tend to maintain parallel growth rate trajectories? 2) what is the approximate range of ages at maturity for *P. rufipes*? 3) can growth rings in scutes be used to age *P. rufipes*?

METHODS

The study was undertaken between 1981 and 1995 in Reserva Florestal Adolpho Ducke (03°08'S; 60°04'W) on the outskirts of the city of Manaus, Amazonas, Brazil. The reserve covers approximately 100 km^2 and the predominant vegetation is tropical rainforest. Most data were collected around a small stream, Igarapé Acará, in the interior of the reserve. The study site has been described in detail by Magnusson and Lima (1991).

Turtles were caught by hand while diving or in funnel traps with mesh leaders (fyke nets) baited with fresh chicken. Marking and recapture attempts were sporadic and were concentrated in the period 1990-95. At each capture, animals were measured (straight-line carapace length, CL), individually marked by drilling holes in the marginal scutes, and released at the site of capture. Attempts to measure growth rings in the field were unreliable so casts were made of the first costal scutes to record growth rings in 13 of the animals that were caught after 1992. The positions of the rings on the casts were all measured by WEM.

Growth rate was calculated as the size at recapture (CL_2) minus the size at initial capture (CL_1) divided by the time interval between captures (INT). Data are presented as the absolute growth rate [$(CL_2-CL_1)/INT$] plotted against the arithmetic mean size [$(CL_2+CL_1)/2$] because this is how growth rates have been conventionally presented (Andrews, 1982). However, absolute growth rate depends on the interval as growth models assume some form of decay in growth rate. Therefore, the exponential growth rate [$(\log_e CL_2-\log_e CL_1)/INT$] was plotted against the geometric mean size (square root of the product of CL_1 and CL_2) to verify that patterns in the absolute growth rates were not due to varying intervals between captures.

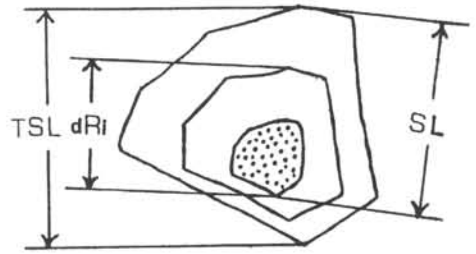

Figure 1. Points from which measurements were taken on the first costal scute (see methods). The stippled area represents the scute present at hatching.

Recapture rates were too low to evaluate growth rates of animals less than one year old using mark-recapture techniques. To estimate initial growth rates, animals less than 80 mm CL were attributed a hatching date of 1 July and a hatching CL of 54.6 mm. The mean hatching date was based on the seasonal size distribution of juveniles (see Results) and the sizes of hatchlings from a single clutch incubated in the laboratory ($n = 6$, range = 51–57 mm). We repeated analyses using mean hatching sizes of 50 mm or 60 mm but our conclusions were insensitive to variation in this parameter and we do not present individual results for these analyses. Failure to anchor the curve at smaller sizes potentially introduces far more error than does the lack of accuracy and precision in these estimates. The data for larger animals indicates a linear decline (monomolecular model) and initial growth rates of 60 mm/year, four times that observed for the two animals with recaptures at small sizes and that estimated from the size distributions of animals with CL < 80 mm.

Age/size curves were constructed using the Richards model (Brisbin et al., 1984) in the NONLIN module of SYSTAT (Wilkinson, 1990). These curves integrate the data on size at capture and recapture and the time interval between captures. Statistical evaluation of the fit of any integrated growth curve is problematic (Rickard et al., 1989) so we simply compared them to data for two known-age individuals.

Growth rates based on growth rings in scutes were estimated based on the assumption of deposition of one ring per year because recaptures of 14 individuals over known intervals indicated that known growth rates (KGR, in years) were linearly related to growth rates estimated from scutes (SGR, in years) ($KGR = -0.69 + 1.147SGR$, $r^2 = 0.44$, $F_{1,14} = 10.7$, $p = 0.005$), with an intercept not significantly different from zero and a slope not significantly different from one ($p > 0.4$ in both cases).

Early rings were lost due to erosion in most individuals, so the position of the posterior edge of the original first costal scute (original intersection of the first costal, second costal, and second vertebral scutes) was estimated by regression of the distance from the posterior edge of the ring marking the original scute to the leading edge (intersection of the first costal, and the second and third marginal scutes) of the scute (SL) against total scute length (TSL) for different-sized individuals (CL

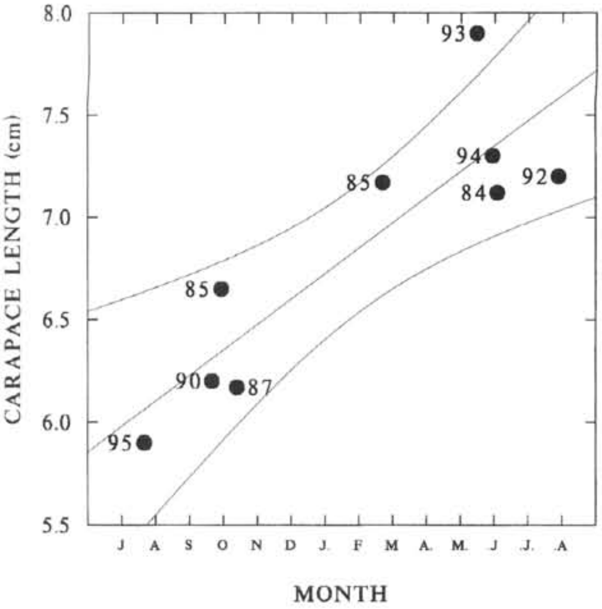

Figure 2. Carapace lengths and dates of capture of turtles with CL < 80 mm. Numbers indicate the year of capture.

range = 73–168 mm) which retained the first scute ($SL = 0.083 + 0.791TSL$, $r^2 = 0.92$, $F_{1,6} = 65.5$, $p < 0.001$). The CL at which each ring was formed (CLR_i) was calculated from the distance from the posterior edge of the first scute to the ring (dR_i) as $CLR_i = CL \times dR_i/SL$ (Fig. 1). Growth rates were calculated as $CLR_{i+1} - CLR_i$. As the interval is assumed to be one year, division is not necessary.

RESULTS

Initial Growth Rates. — Hatchlings from one clutch of 6 eggs incubated in the laboratory varied from 51 to 57 mm CL (mean = 54.6, SD = 2.13 mm). Captures of juveniles indicated that hatching occurs in a limited period each year (Fig. 2). Regression of size of juveniles (CL, in mm) on time since the previous 1 July (TI, in yrs) indicated a mean rate of growth in carapace length of 15 mm per year in the first year ($CL = 59 + 14.9TI$, $r^2 = 0.76$, $F_{1,7} = 21.9$, $p = 0.002$). This regression also indicated a mean size of individuals at the mean hatching date of about 59 mm. At that time, most animals would be only slightly larger than hatching size, which agrees with the size of the hatchlings in the laboratory. The inverse regression predicted a mean hatching date in the last week of June. Gravid females are found over an extended period (R. Vogt and W. Magnusson, unpubl. data). However, the data shown in Fig. 2 indicate that recruitment of hatchlings to the population occurs in a limited period each year. The nine juveniles were caught in eight different years so the pattern is not caused by an unusual recruitment year.

Growth rates estimated for first-year animals based on a mean hatching date of 1 July (Table 1) were within the range expected from the data for larger individuals (Fig. 3). We used this date because the regression analysis predicted a mean hatching date in the last week of June. The mean growth rate is lower than that which would be expected from the monomolecular (von Bertalanffy by length) model. However, it agrees with the data from the only animal with a mean CL < 100 mm during the growth period (Fig. 3), and with the estimate based on the size distribution of juveniles (Fig. 2).

Table 1. Carapace lengths (mm) of turtles at capture and recapture and the interval in years between captures. Asterisks indicate estimates based on presumed hatching on 1 July at 54.6 mm carapace length.

Turtle	Sex	Carapace Length 1	Carapace Length 2	Interval (yrs)
1	f	54.6*	71.7	0.644*
2	f	106.0	202.0	4.038
2	f	202.0	206.0	1.504
2	f	206.0	211.0	4.668
3	f	221.0	222.0	8.699
4	m	100.6	152.0	1.726
5	m	109.0	133.0	2.586
6	?	54.6*	66.5	0.244*
7	m	200.0	195.0	1.542
8	m	54.6*	71.2	1.005*
8	m	71.2	92.0	2.337
8	m	92.0	165.0	3.956
9	m	220.0	230.0	8.370
10	m	194.0	211.0	5.293
11	f	198.0	196.0	3.060
12	f	210.0	192.0	3.332
13	?	54.6*	61.7	0.279*
14	m	204.0	204.0	3.293
14	m	208.0	204.0	0.822
15	f	216.0	226.0	3.693
16	?	54.6*	62.0	0.219*
17	f	181.0	200.0	1.359
17	f	200.0	210.0	1.496
17	f	210.0	210.0	0.753
18	f	198.0	212.0	1.507
18	f	212.0	213.0	1.951
19	m	54.6*	79.0	0.868*
20	f	188.0	225.0	11.375
21	m	152.0	173.0	1.866
22	f	198.0	211.0	1.493
22	f	211.0	215.0	1.521
22	f	215.0	217.0	0.901
23	m	128.0	147.0	1.304
24	f	140.5	148.0	0.690
25	m	54.6*	72.0	1.074*
25	m	72.0	188.0	2.734
26	m	210.0	203.0	2.315
27	m	154.0	170.0	1.562
28	f	191.0	201.0	1.088
29	f	176.0	170.0	0.907
30	f	156.0	162.0	1.016
31	f	257.0	250.0	0.907
32	f	54.6*	73.0	0.910*
33	f	54.6*	59.0	0.055*
34	f	191.0	213.0	2.066
35	m	142.0	199.5	4.052
35	m	199.5	201.0	0.841
36	m	203.0	204.0	1.636

Growth-Rate Trajectories. — Growth rates were calculated from capture-recapture data for 36 individuals over periods of up to 10 years (Table 1). Growth trajectories of 5 large individuals with more than one recapture could be drawn for the growth rates spanning 0 to 1 cm/yr and for two juveniles spanning 1.5 to 2 cm/yr (Fig. 3). The probability of only two of the 7 lines intersecting if there was no tendency for the lines to be parallel can be calculated from the binomial probabilities as 0.001. As individual growth-rate-on-size trajectories tended to be parallel, integrated size-on-age-curves based on these data should tend to diverge. Also, individuals

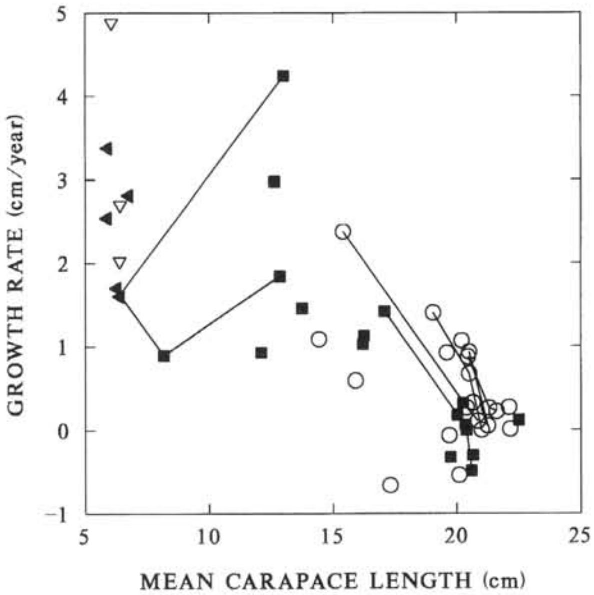

Figure 3. Relationship between growth rate and carapace length based on recaptures (see methods). Solid symbols represent males; open symbols females. Squares and circles indicate measured growth rates and triangles represent estimates of growth for individuals during the first year based on a presumed hatching date of 1 July (see methods). Lines connect data for individuals with multiple recaptures.

showed greater than four-fold differences in growth rates at a given size (Fig. 2). For both these reasons, "mean" age/size relationships must be treated with caution. Exponential growth rates plotted against geometric mean size showed the same pattern.

Males and females had very similar mean asymptotic sizes (215 and 217 mm, respectively) but large differences in growth rates (T = 12.4 and 11.4, respectively) and Richard's curve shape parameters (M = 0.84 and 1.41, respectively). Growth rates are too variable for valid statistical tests of growth parameters, but the distribution of sizes (Fig. 4) indicates that females generally reach larger sizes than males (Kolmogorov-Smirnov test, $D = 0.42$, $p = 0.007$).

We had difficulty attributing sex to animals less than 80 mm CL, though, with hindsight, we believe that males could have been identified without question whereas most observers have difficulty in sexing females. For analyses, we assumed that animals recorded without question as males were indeed males and animals registered as females or as unknown were probably females. Separation of juveniles was done solely to avoid the inclusion of the same animal twice in analyses. Randomly assigning sexes or artificially inflating sample sizes by including juveniles in analyses for both males and females gave qualitatively similar results, so any errors in sexing juveniles would not change any of our conclusions.

We estimated parameters for the Richards growth model for all females ($n = 18$), all males ($n = 15$), and the 7 fastest growing females (those with more than one recapture on Fig. 3 and the 3 fastest growing juveniles assumed to be females). The 95% confidence intervals of all parameters overlapped for all curves but we present them to show the probable range of variation in the "mean" curves (Fig. 5).

The size-age curves can be compared with data for two males for which we have good estimates of size and age (Fig. 5). They were captured at 71.2 and 72.0 mm CL which, based on Fig. 2, indicates ages of about 367 and 392 days respectively. The 95% confidence limit of these estimates is 116 days. Both turtles were recaptured when close to adulthood. Male no. 1 with three recaptures showed a growth trajectory parallel to, but lower than, the "mean" curve for males, indicating that it was a consistently slow grower and that its growth trajectory was little affected by short-term fluctuations in environmental conditions. Male no. 2 grew considerably faster than the curve estimated for fast-growing females (Fig. 5). Data for these two males span the three "mean" curves, indicating that, although large individual variation can be expected, the "mean" curves are in the right general region.

Growth Estimates Based on Scute Annuli. — The relationship between measured growth rate (MGR) and that estimated from the rings (SGR) for nine animals whose scute impressions were taken at capture and recapture showed an apparently linear, but highly variable relationship ($MGR = -0.069 + 1.147SGR$, $r^2 = 0.44$, $F_{1,14} = 10.7$, $p = 0.005$). It appears that the distances between rings reflect the growth rate of the carapace only if averaged over long periods of time.

Average linear growth rates estimated by the growth rings declined with size but approached zero only slowly. Attempts to use these data to estimate size-age relation-

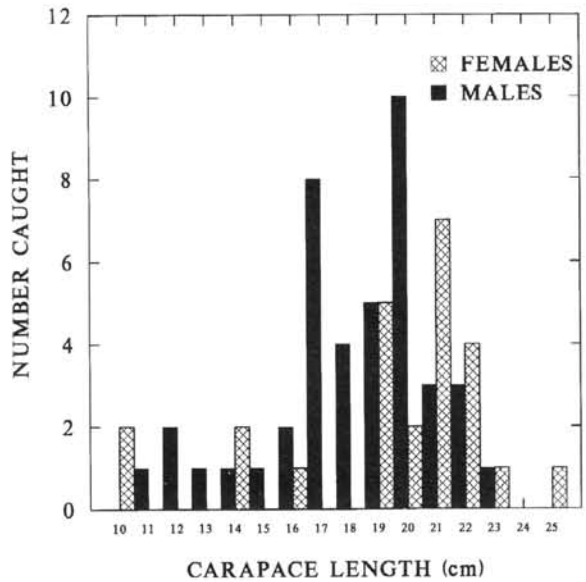

Figure 4. Frequency of different-sized male and female *P. rufipes* with CL > 80 mm in the study area. Data were included for only the first capture of each individual in the study.

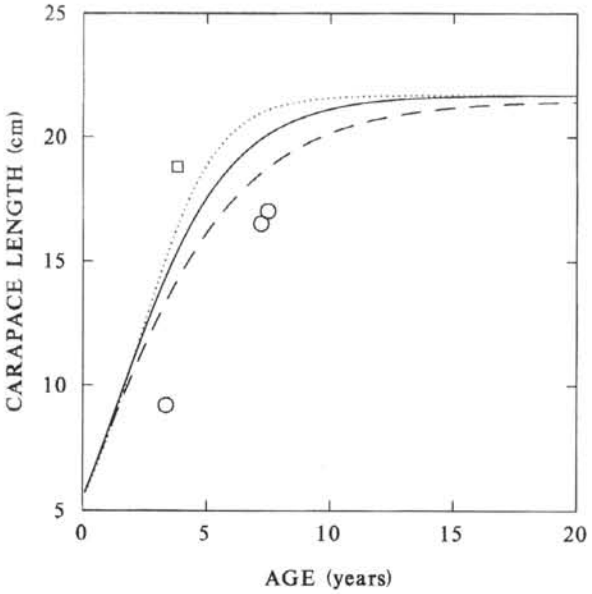

Figure 5. Estimated relationships between age and carapace length for males based on growth rates of 15 individuals (dashed line), females based on growth rates of 18 individuals (solid line), and fast-growing females based on growth rates of 7 individuals (dotted line). The differential form of the data used to generate these curves is shown in Fig. 3. The open symbols represent two separate males (circles = male no. 1; square = male no. 2) whose ages could be estimated with confidence because they were initially captured at small sizes and recaptured after long intervals.

ships using the Richards model or one of its simpler variants always resulted in biologically improbable parameter estimates (e.g., asymptotic CL > 300 mm). Any growth model requires accurate information on asymptotic size and information from scute annuli apparently does not provide this. We conclude that, although some aspects of the growth history are recorded in the scutes, the information is imprecise and probably inaccurate. Therefore, we based our description of growth in the species on direct measures of growth in CL.

DISCUSSION

Use of scute rings to estimate growth rates (e.g., Lambert, 1993; Rickard et al., 1989; Mushinsky et al., 1994) does not appear to be a viable strategy for *P. rufipes*. As with other larger reptiles (Webb et al. 1983; Rickard et al., 1989; Magnusson and Lima, 1991), individual variation in growth rates makes the construction of "mean" curves a potentially inaccurate procedure. Also, year-to-year variation can obscure long-term trends (Tucker et al., 1995). However, information from long-term recaptures, which covered many different series of years, gives us confidence in our ability to make at least rough estimates of age based on size.

The relationship between growth rate and size allows us to fairly confidently reject the von Bertalanffy by length (monomolecular) model for this species, even though it has been found, or assumed, to apply to many species of chelonians (Andrews, 1982; Frazer and Ehrhart, 1985; Rickard et al., 1989; Shine and Iverson, 1995) (for an exception, see Mushinsky et al., 1994). However, our general conclusions are not very sensitive to the estimate of the Richards shape parameter. Individual variation is so great that it swamps any slight differences introduced by variation in parameters in the Richards model.

The smallest gravid female we collected had CL = 204 mm. Integration of the growth rate data indicate that she would have been between 6.3 and 8.0 yrs old, depending on whether she was a fast or slow grower. The size of the smallest gravid female in a small sample almost certainly overestimates the mean age of females at sexual maturity. Shine and Iverson (1995) showed that most turtles reach sexual maturity at about 83% of mean asymptotic size. If that holds true for *P. rufipes*, females would reach maturity at between 4.5 and 5.3 years, depending on the individual growth trajectory. Therefore, all available evidence indicates that most individuals reach sexual maturity well before 10 years of age.

Phrynops rufipes is slightly sexually dimorphic in size (Lamar and Medem, 1982; this study). However, it is not clear what mechanism brings this about. In this study, males and females had similar estimated asymptotic sizes but different growth rate and growth-curve shape parameters. If the sexes have similar mortality rates, the slower growth rates of males would lead to a preponderance of females in the larger size classes independently of the potential of individuals to grow to large sizes (Dunham and Gibbons, 1990). However, no data are available on mortality rates.

One of the most unexpected aspects of this study was the indication that most hatching occurs in the early dry season from June to August. Year-to-year variation in growth rates of turtles can be high (Tucker et al., 1995). However, our data are based on 8 different years of observation, so the pattern appears to be general. Data from Colombia (Lamar and Medem, 1982) and our own unpublished data indicate the occurrence of gravid females throughout the dry season. Therefore, it appears that data on egg survival may be important to understand seasonality in recruitment in this species.

Acknowledgments. — Many people helped capture turtles but special mention is due to P. Harlow, J.-M. Hero, A. Lima, M. Janson, and P. Cohen. C.L. Abercrombie and R.C. Vogt provided equipment and advice. We are indebted to I.L. Brisbin, P. Bayliss, and T. Moulton for discussion of statistical analyses of growth models. Financial support for the study was provided by the Instituto Nacional de Pesquisas da Amazônia and grants from the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) to V. Costa and O. de Lima (Iniciação Científica), A. de Lima (Aperfeiçoamento), and W. Magnusson (Pesquisa and Auxílio a Pesquisa).

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Received: 16 May 1996
Reviewed: 12 November 1996
Revised and Accepted: 30 August 1997

Chelonian Conservation and Biology, 1997, 2(4):581–585

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Estimating the Time Between Hatching of Sea Turtles and Their Emergence From the Nest

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Sea turtles nest on tropical or temperate beaches. The eggs incubate in the sand, eventually producing hatchlings that emerge from the nest and scramble to the ocean. Several important physiological and behavioral events occur during incubation. These include temperature-dependent sexual differentiation during the middle third of incubation (Yntema and Mrosovsky, 1982; Raynaud and Pieau, 1985), and the typically nocturnal emergence of hatchlings from the nest, which appears to be gated by changes in sand temperature (Mrosovsky, 1968; Gyuris, 1993).

After hatching but before emerging, the hatchling turtles remain in the sand for a few days. This is an important stage for the hatchlings, allowing them time for improving behavioral synchrony in emergence from the nest, as well as for closing and straightening of the plastron and for absorbing the remnants of the yolk sac. Indeed, the greatest metabolism of residual yolk occurs while the hatchlings are still in the nest (Kraemer and Bennett, 1981). The interval between pipping from the egg and emerging from the nest has not been extensively studied and is not firmly established.

Investigation of the time between hatching and emergence has conservation and management implications. For instance, in some types of sand, sea turtles may have more difficulty digging to the surface after pipping. In the case of beach nourishment, a common technique used to stem beach erosion, sometimes the introduced sand is different from the naturally occurring sand and may initially be more compacted (Crain et al., 1995). This could lead to an increase in the emergence time, not only because the hatchlings must work harder to reach the surface, but also because greater exertion produces greater amounts of lactate in the body. High levels of lactate would be likely to require a longer resting period for the hatchlings just beneath the surface to allow for degradation of the lactate (Dial, 1987). The longer the period between hatching and emergence, the more residual yolk is likely to be used and the less yolk is left for the post-emergence period. This in turn might curtail the post-hatching frenzy, which is thought to be important in assisting the newly hatched turtles in moving away from a predator-filled shoreline towards a safer pelagic environment (Wyneken and Salmon, 1992).