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Relative Importance of Thermal and Nonthermal Factors on the Incubation Period of Sea Turtle Eggs

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We indirectly estimated the time between hatching and emergence from the nest of loggerhead sea turtles (*Caretta caretta*) by comparing incubation rates of eggs incubated naturally on beaches and artificially in the laboratory (Godfrey and Mrosovsky, 1997). By measuring the difference in incubation duration of groups of eggs or nests that produced similar sex ratios in both laboratory and field conditions, we estimated that on average 4.1 days are spent by loggerheads in the sand before emerging onto the beach. Steyermark (1999) called into question the validity of our estimates. Using several examples from the literature on laboratory incubation of freshwater and loggerhead sea turtle eggs, Steyermark pointed out that differences in the water potential of the incubation medium (sand, vermiculite, etc.) were associated with differences in incubation period, even when ambient air temperatures were not varied (e.g., Morris et al., 1983; McGehee, 1990). The implication was that differences in moisture levels of the incubation medium may have affected the incubation periods, independent of differences in incubation temperature.

We agree that the incubation environment is composed of many nonthermal variables which may influence the incubation period, but we disagree with Steyermark's assertion that we implicitly assumed that "only incubation temperature (which affects sex ratio) affects incubation duration." This is not correct. For example, we recognized that changes in oxygen partial pressures can alter the incubation period, although our measurements suggested that they are not an important factor in our laboratory experiments (Godfrey and Mrosovsky, 1997). The main issue is not whether nonthermal factors can affect incubation duration, but rather what their importance is relative to temperature.

From our work, we have shown that there is a strong relationship between incubation duration and incubation temperature (Godfrey and Mrosovsky, 1997). Indeed, from our fitted curves, the coefficients of determination (r^2 values) suggest that temperature (as indicated by sex ratio) accounts for more than 75% of the variance in incubation duration. This has also been found for green sea turtle (*Chelonia mydas*) eggs (Broderick et al., 2000). Moreover, changes in temperature can produce large shifts in incubation duration, anywhere from around 45 days to over 70 days (e.g., Dodd, 1988). In contrast, the largest difference in incubation period as a result of changes in water potential as cited by Steyermark (1999) is of the order of 6 days. Hence, temperature plays a far more important role than water potential in terms of incubation period.

Furthermore, a potentially important methodological problem is often neglected in studies that appear to show changes in incubation duration resulting from differences in water potential. In studies of sea turtle eggs, it is well known that egg temperature is not always equivalent to ambient air temperature in the incubators. In the laboratory, we have found that egg temperature is lower than air ambient temperature, presumably as a result of evaporative cooling of the incubation medium (Mrosovsky, 1988; Mrosovsky et al., 1992; Godfrey, 1997; Marcovaldi et al., 1997; Godfrey et al., 1999). However, for most studies that measured hydric environment, the researchers reported only the ambient air temperature. It may be the case that wetter incubation conditions lead to longer incubation times of eggs partly because there is more evaporative cooling of the eggs, as compared to drier substrates. Indeed, in one study which actually measured evaporation of the substrate on which the eggs were incubating, the wettest substrates had the highest rates of evaporation (Appendix in Packard et al., 1987). Nevertheless, our estimate of hatching to emergence interval was based on sex ratios of the hatchlings produced by the eggs, not temperature, which helped us avoid the difficulties of differentiating between egg temperature and ambient incubation temperature.

Our interest in studying the hatching to emergence interval arose from the need of an appropriate value in our method of indirectly estimating sex ratios of hatchlings. Simply put, because incubation duration changes predictably with incubation temperature, we have developed a method by which incubation durations can be used to predict sex ratios of nests (e.g., Marcovaldi et al., 1997). Because incubation duration is easily monitored on nesting beaches and these data have already been collected for many years in some places, the method has the potential to rapidly increase our knowledge of hatchling sex ratios. If we had used an inappropriate value of the hatching to emergence interval, as Steyermark suggests, then our estimates of sex ratio should be wrong. However, a limited validation of the method to estimate sex ratios suggests that our value for the hatching to emergence interval is reliable (Mrosovsky et al., 1999).

These points reinforce our view that incubation temperature is more important than water potential in its effect on incubation duration and sex ratio in marine turtles. However, we also recognize that nonthermal factors may also play an important role. Our method of estimating sex ratio from incubation duration does not assume that nonthermal factors have no impact; indeed, there remains some 25% of the variance in incubation duration unaccounted for by our measure of incubation temperature. But we have assumed that these nonthermal factors are relatively similar for eggs incubating on the natural nesting beaches or in the laboratory, at least enough for us to derive first-order estimates on sex ratio of sea turtle hatchlings.

In this context, we welcome Steyermark's cautions about water potential and any ideas on deriving more accurate estimates on the hatching to emergence interval, a variable that has received relatively little attention. We also invite researchers to work together to develop standardized techniques in studies involving the incubation of turtle eggs, as a means to not only reduce the influence of confounding factors, but also to facilitate rigorous comparison among different studies (Girondot, 1999).

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