



## Effect of water temperature on the duration of the internesting interval across sea turtle species

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### ABSTRACT

Sea turtles generally lay several clutches of eggs in a single nesting season. While a negative correlation between water temperatures and the time required between constitutive nesting events (termed the internesting interval) has been previously reported in loggerhead *Caretta caretta* and green turtles *Chelonia mydas*, it is not understood whether this relationship remains constant across other sea turtle species. Here, we expanded upon these previous studies on loggerhead and green turtles by using larger sample sizes and including data from species with a wider range of body-sizes; specifically: hawksbill *Eretmochelys imbricata*, leatherback *Dermochelys coriacea*, and olive ridley turtles *Lepidochelys olivacea*. In total, we compiled temperature data from biologgers deployed over internesting intervals on 23 loggerhead, 22 green, 7 hawksbill, 26 leatherback and 11 olive ridley turtles from nesting sites in 8 different countries. The relationship between the duration of the internesting interval and water temperatures in green and loggerhead turtles were statistically similar yet it differed between all other turtle species. Specifically, hawksbill turtles had much longer internesting intervals than green or loggerhead turtles even after controlling for temperature. In addition, both olive ridley and leatherback turtles exhibited thermal independence of internesting intervals presumably due to the large body-size of leatherback turtles and the unique capacity of ridley turtles to delay oviposition. The observed interspecific differences in the relationship between the length of the internesting interval and water temperatures indicate the complex and variable responses that each sea turtle species may exhibit due to environmental fluctuations and climate change.

### 1. Introduction

Sea turtles are predominantly capital breeders, building an energy reserve over several months to years before dedicating it towards a specific nesting season (Plot et al., 2013; Perrault and Stacy 2018). The length of the nesting season for an individual turtle is determined by the number of nesting events and the time elapsed between each consecutive nesting event (termed the internesting interval). Several studies have revealed a negative correlation between the length of the

internesting interval and the water temperatures inhabited by gravid green turtles *Chelonia mydas* and loggerhead turtles *Caretta caretta* (Sato et al., 1998, Hays et al., 2002); however, relatively little information has been published on this relationship in the other sea turtle species. Considering that the timing of the nesting season has implications for hatching success (Santidrián Tomillo et al., 2012) and the dispersal of hatchlings (Shillinger et al., 2012), this lack of knowledge represents a “blind spot” in our understanding of how different sea turtle species may respond to the shifting environmental regimes caused by climate

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change.

Interesting intervals vary by sea turtle species, ranging from one to several weeks (Dornfeld et al., 2015; Robinson et al., 2017). It might be presumed *a priori* that the length of the interesting interval is determined by the time required for yolk formation for the succeeding clutch of eggs; however, this has been proven to not be the case as vitellogenesis for the entire nesting season is completed before the turtle arrives at the nesting beach (Rostal et al., 1996; Limpus et al., 2003). Nor is the interesting interval essential for further copulation or egg fertilization, as sea turtles can store sperm over the nesting period (Owens 1980) and potentially even between nesting seasons (Phillips et al., 2014). Instead, the interesting interval appears to be used for follicular maturation, specifically the formation of albumin and shells, for the subsequent clutch (Aitken and Solomon 1976).

While the physiological processes limiting the rate of albumin and shell formation in sea turtles are not well understood (Price et al., 2019), a negative correlation between the length of the interesting interval and water temperatures has been observed in green and loggerhead turtles (Sato et al., 1998; Hays et al., 2002). Such a correlation may be expected considering the relationship between body-temperatures and the rate of many metabolic and physiological processes in poikilothermic species (Penick et al., 1996; Standora et al., 1982), and it is also possible that this relationship would vary with turtles' body size. For example, the large body-size of adult turtles can provide them with notable thermal-inertia (= degree of slowness with which the temperature of a body approaches that of its surroundings) also known as gigantothermy (Paladino et al., 1990; Sato et al., 1995). To this extent, the reverse may also be true for smaller turtles such as olive ridley *Lepidochelys olivacea* or Kemp's ridley turtles *Lepidochelys kempii*, while more comparably sized turtles such as green, loggerhead, and hawksbill turtles *Eretmochelys imbricata* may all exhibit relationships between water temperature and the duration of the interesting interval.

Considering the role of body-size on thermal-inertia in sea turtles, it is possible to generate predictions as to how the length of the interesting interval in differently sized sea turtles will be influenced by water temperatures. Specifically, we predict that water temperature will have a stronger negative correlation with interesting intervals in smaller species rather than larger species. To test this prediction, we compared the relationship between water temperatures and the length of the interesting interval using data generated by biologgers deployed on green, loggerhead, leatherback, olive ridley, and hawksbill turtles.

## 2. Materials and methods

We deployed temperature-depth biologgers, either MK10 satellite transmitters (Wildlife Computers, USA) or LAT 1100 data loggers (Lotek, Canada), on nesting green, hawksbill, and leatherback turtles at several locations worldwide. Green turtles were sampled on Cabuyal and Nombre de Jesús beaches in northwest Costa Rica (10.67 N, 85.66 W), hawksbill turtles on St. Croix in the US Virgin Islands (17.69 N, 64.89 W), and leatherback turtles in the iSimangaliso Wetland Park in northeast South Africa (27.01 S, 32.86 E). In all instances, loggers were deployed immediately after oviposition and only on females that still had vitellogenic follicles, as confirmed via ultrasonography (Blanco et al., 2012), and thus likely to nest again that season. Biologgers were attached to nesting turtles by creating a small hole at the posterior end of the carapace to which the device was anchored via crimps and fishing line – detailed descriptions of the attachment process for green turtles can be found in Blanco et al. (2013) and Clyde-Brockway et al. (2019), for leatherback turtles in Robinson et al. (2017), and for hawksbill turtles in Hill et al. (2017). The biologgers recorded temperature and depth every 10 s for green and leatherback turtles but only every 60 s for hawksbill turtles. We also measured the Curved Carapace Length (CCL) of each turtle using a flexible tape measure. We checked each turtle for either internal Passive Integrated Transponder (PIT) tags or external flipper tags and applied them to untagged animals. After processing, the

turtle was allowed to return to the sea. The nesting beaches were patrolled nightly following the deployment of a temperature logger to reencounter the turtle and retrieve the logger.

We defined an interesting interval as the number of days between a successful nesting event and the next attempted nesting event even when it did not result in egg-laying. This is because sea turtles may emerge onto nesting beaches with presumably fully developed and shelled eggs yet may still delay nesting if suitable nesting conditions are not encountered (Blanco et al., 2012). We therefore reviewed the temperature and depth data recorded by the data logger to identify any periods of time when the depth of the data logger was at depth shallower than 0.5 m for >1 h as this would presumably indicate that the turtle had left the water and had attempted to nest. This period was also generally accompanied by a noticeable change in temperature due to continual exposure of the logger to air temperatures instead of water temperatures. Mean temperature was then calculated across each interesting interval.

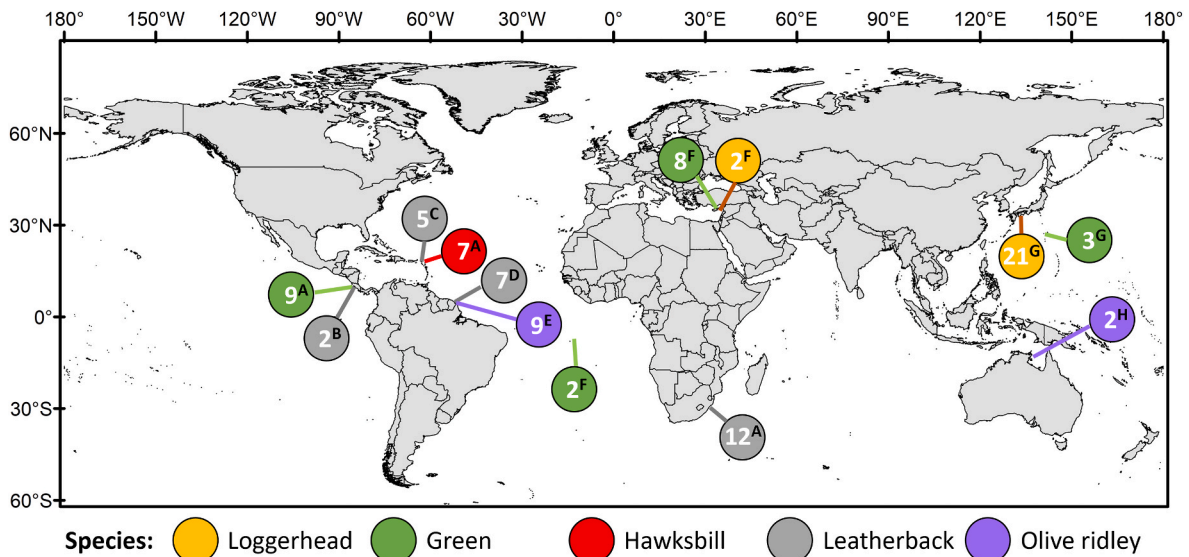
In total, we recorded 7 interesting intervals from hawksbill turtles, 9 intervals from green turtles, and 12 intervals from leatherback turtles. These data were further supplemented by additional data from the published scientific literature that reported on interesting intervals and mean water temperatures from other sea turtle populations that had been tagged using temperature loggers. The authors in these previous studies also stated that they confirmed that no other nesting attempts had taken place between each specified interesting interval by reviewing the temperature and depth data provided by the biologgers. These studies were found via a thorough yet unstructured literature search in Google Scholar. This included 23 interesting intervals from loggerhead turtles (Sato et al., 1998, Clyde-Brockway et al., 2019; Hays et al., 2002), 13 intervals from green turtles (Sato et al., 1998, Hays et al., 2002), 14 intervals from leatherback turtles (Southwood et al., 2005; Fossette et al., 2009), and 11 intervals from olive ridley turtles (Hamel et al., 2008; Plot et al., 2012). We were unable to find suitable data in the literature for Kemp's ridley *Lepidochelys kempii* or flatback turtles *Natator depressus*.

To examine the effect of water temperatures on the interesting interval, and to determine how this differed between species, we used an ANCOVA with species as the fixed factor, mean water temperature as the covariate, and interesting interval as the dependent variable. As the ANCOVA revealed that the correlation between mean water temperatures and interesting intervals differed per species, we used post-hoc Tukey tests to look for pair-wise difference between species. Finally, we assessed the relationship between mean water temperatures and interesting interval for each species independently using linear regression analyses. All statistics were run in JASP (v.0.14.1) using  $p = 0.05$ .

## 3. Results

By combining data collected in the field with data from the published literature, we calculated the duration of and mean water temperature over interesting interval for 22 loggerhead, 21 green, 7 hawksbill, 26 leatherback, and 11 olive ridley turtles from nesting sites in 8 different countries worldwide (Fig. 1).

Among these five species, leatherback turtles had the shortest mean interesting interval of 9.7 d (range: 8.0–12.1) and experienced an intermediate mean water temperature of 26.2 °C (range: 24.1–28.1). Green turtles had the second shortest mean interesting interval of 12.6 d (range: 8.3–23.0) and experienced a similar mean water temperature to leatherback turtles of 26.7 °C (range: 21.7–28.9). Hawksbill turtles had intermediate mean intervals of 14.9 d (range: 12.9–16.2) and experienced the highest mean water temperature of 29.1 °C (range: 28.8–29.4). Loggerhead turtles had the second longest mean interesting interval of 16.8 d (range: 12.0–25.1) and experienced the lowest mean water temperatures of 24.0 °C (range: 22.0–27.4). Olive ridley turtles had the longest mean interesting interval of 26.3 d (range:

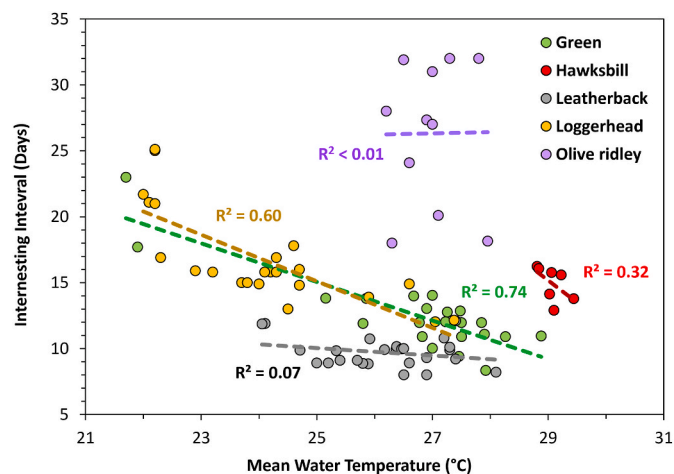


**Fig. 1.** Geographic distribution of the data collected on mean temperatures during interesting intervals for loggerhead, green, hawksbill, leatherback, and olive ridley turtles. The lines protruding from each circle highlight the sampling location while the color of the circle represents the species. In addition, the white number represents that number of interesting intervals recorded at that location while the superscript black letter represents the data source: <sup>A</sup>This study, <sup>B</sup>Southwood et al., 2005, <sup>C</sup>Casey et al. 2010, <sup>D</sup>Fossette et al., 2009, <sup>E</sup>Plot et al., 2012, <sup>F</sup>Hays et al., 2002, <sup>G</sup>Sato et al., 1998, and <sup>H</sup>Hamel et al., 2008.

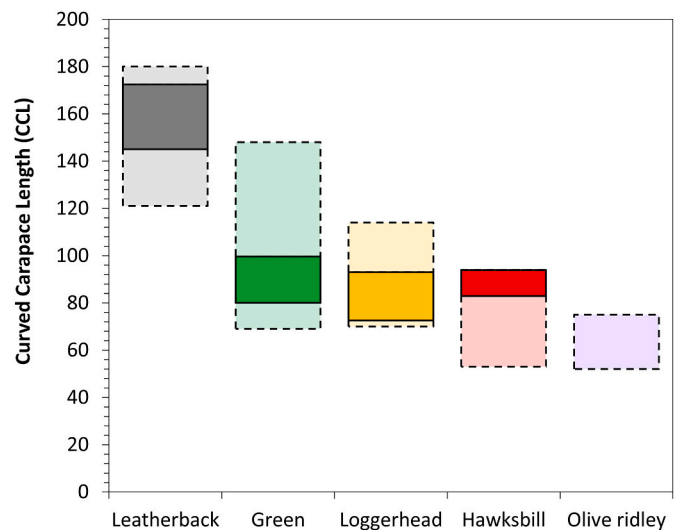
18.0–32.0) and experienced a similar mean water temperature to leatherback and green turtles of 27.0 (range: 26.2–28.0). Body-sizes of turtles with biologists, as well as general trends for each species, were measured as CCL and are presented in Fig. 2. While we accept that CCL is not an exact proxy of body-size, we used it as a standardized approximation that remained relevant across the different sea turtle taxa in this study.

Our results confirmed that temperature had a significant effect on duration of the interesting interval ( $F = 40.92$ ,  $df = 1, 83$ ,  $p < 0.01$ ). It also showed a statistically significant difference between the duration of the interesting intervals for the different sea turtle species when controlling for temperature ( $F = 92.08$ ,  $df = 4, 83$ ,  $p < 0.01$ ) (Fig. 3). Post-hoc tests confirmed that all species were statistically different ( $p < 0.05$ ) except for the green and loggerhead turtles ( $t = 0.707$ ,  $p = 0.95$ ).

Regression analyses indicated that there was a significant negative regression between the duration of the interesting intervals and temperature in loggerhead ( $R^2 = 0.60$ ,  $F = 31.34$ ,  $p < 0.001$ ) and green



**Fig. 2.** Relationships between the duration of the interesting interval and mean water temperatures experienced by green, hawksbill, leatherback, loggerhead, and olive ridley turtles. Each circle represents a unique interesting interval and the species is denoted by the color of the circle.



**Fig. 3.** Ranges for Curved Carapace Length (CCL) for nesting sea turtles. Darker colors inside the solid borders represent the CCL range for the sea turtles with biologists from Fig. 1, except for turtles from Hays et al. (2002), Hamel et al. (2008), and Plot et al. (2012) as these studies did not report CCL. The lighter colors inside dashed border represent the global CCL for that species as reported in Hirth (1980).

turtles ( $R^2 = 0.74$ ,  $F = 26.90$ ,  $p < 0.01$ ) (Fig. 3). In contrast, no statistically significant regression was observed for hawksbill ( $R^2 = 0.32$ ,  $F = 2.30$ ,  $p = 0.19$ ), leatherback ( $R^2 = 0.07$ ,  $F = 1.2$ ,  $p = 0.18$ ) and olive ridley turtles ( $R^2 < 0.01$ ,  $F < 0.001$ ,  $p = 0.977$ ).

#### 4. Discussion

Our results indicate that not all sea turtle species exhibit a correlation between mean water temperature and the duration of the interesting interval. Moreover, the differences in this correlation between species cannot be explained entirely by differences in body-size and likely indicate other key physiological, behavioral, or ecological differences.

Supporting our original prediction that leatherback turtles would be

the least sensitive to changes in temperature due to their large body size, we observed no statistically significant effect of mean water temperature on the interesting intervals of leatherback turtles. Such a result may be expected considering that leatherback turtles exhibit notable thermal inertia (Paladino et al., 1990; Sato 2014). Furthermore, the leatherback turtle is unique amongst other sea turtle taxa in that its muscle tissue metabolism appears unaffected by typical temperature variation (Penick et al., 1998) and capable of some level of physiological thermoregulation (Bostrom et al., 2010).

Also adhering to our original prediction, green and loggerhead turtles, which are notably smaller than leatherback turtles, exhibited a negative correlation between the duration of the interesting interval and water temperature. Much like Hays et al. (2002), we confirmed that there was no statistical difference in this relationship between the two species. This adheres to our predictions as both species have largely overlapping body-sizes as nesting adults (Fig. 2). The relatively long interesting intervals often reported for loggerhead turtles when compared to green turtles, even when nesting at similar sites (e.g., Cyprus: Broderick et al., 2002), therefore likely do not represent a key physiological difference. Instead, the differences in interesting intervals may be largely driven by differences in the thermal habitats occupied by each species during the interesting interval.

While the hawksbill turtles with biologgers had similar body-sizes to those of green and loggerhead turtles in this study (Fig. 2), they did not exhibit a correlation between the duration of the interesting interval and water temperatures. That said, the reasonably high  $R^2$  value of 0.32 suggests that perhaps we were unable to identify a significant correlation due to a low sample size ( $n = 7$ ). In addition, the range of mean water temperatures experienced by hawksbill turtles in this study was notably smaller than for the other sea turtle species (Fig. 3). As such, we cannot unequivocally confirm that hawksbill turtles do not exhibit a correlation between the length of the interesting interval and water temperatures. We recommend that data for hawksbill turtles from areas with a great variation in water temperatures are collected in future studies to confirm the relationship between the length of the interesting interval and water temperature for this species.

Interestingly, even though all the loggerhead, green, and hawksbill turtles in this study were of comparable body-sizes, the interesting intervals for hawksbill turtles were much longer than those for green and loggerhead turtles at water temperatures above 25 °C. This finding may undermine the “water-limitation” hypothesis proposed by Price et al. (2019) that posited that interspecific variation in duration of the interesting interval was determined primarily by body-size through allometric scaling of the salt glands and its impact on desalinization. However, it could be that interspecific variation in the effect of water temperatures on metabolic rates could also be a key factor here. Considering that the metabolic rates in “hard-shelled” turtles are tied to water temperature (Hochscheid et al., 2005), this may suggest that hawksbill turtles might have lower metabolic rates than green and loggerhead turtles at comparable temperatures. While there is presently a distinct lack of data on direct measurements of in situ metabolic rates in hawksbill turtles (Wallace and Jones, 2008), future studies could test this hypothesis by investigating interspecific differences in maximum dive durations under different temperature regimes. Specifically, if we accept that the maximum dive duration in air-breathing sea turtles is limited by the rate at which metabolic processes deplete internal oxygen stores then we could predict that hawksbill turtles would exhibit longer maximum dive durations than loggerhead and green turtles at water temperatures above 25 °C.

The turtle species in this study that most strongly contradicted the predicted relationship between body-size, water temperature, and the duration of the interesting interval was the olive ridley turtle. Being the smallest sea turtle, it is unlikely that like the leatherback turtle the lack of a correlation can be explained by gigantothermy associated thermal inertia. Instead, it appears that there is likely a key physiological difference between olive ridleys and the other turtles in this study. This

could be because while all sea turtles have some capacity to retain fertilized eggs in their oviducts for several days, this period likely extends far longer in olive ridley turtles (Williamson et al., 2019) and presumably in the Kemp’s ridley turtles. Indeed, olive ridley turtles have been observed delaying oviposition for up to 63 d (Plotkin et al., 1997). This adaptation may facilitate synchronization during the mass nesting events (called arribadas) that are only observed in ridley species (Rostal 2007) and the strong connection between moon phase and tides in the nesting patterns of solitary nesting olive ridley turtles (Tomás et al., 2001; Dornfeld et al., 2015).

The lack of a uniform relationship between the length of the interesting interval and water temperature experienced during this period in the sea turtle taxa highlight the complexity of predicting how these species will respond to changing thermal regimes due to climate change. As such, there remains a need to collect and compare temperature data from biologgers on gravid flatback and Kemp’s ridley turtles, for which we were unable to find any appropriate data in the published literature, and to build upon current sample sizes for hawksbill turtles. Future studies should also aim to collect data over wider temperature ranges as the negative linear correlation observed in green and loggerhead turtles could theoretically plateau at high temperatures if the processes governing the rate of albumin and shell formation have physiological limits. Finally, there is a need to understand how changes, or a lack of them, in the length of the interesting interval in response to higher temperature regimes will influence key measures of reproductive success, namely the number of nests that can be laid per season as well as their hatching success.

#### Credit author statement

NJR, PST: Conceptualization; NJR, MMS: Data curation; NJR, MMS: Formal analysis; NJR, GSB, CCB, JEH, JT, FVP, PST: Funding acquisition; NJR, GSB, CCB, JEH: Investigation; NJR, GSB, CCB, JEH: Methodology; FVP, JT, PST: Supervision; NJR: Roles/Writing - original draft; All authors: Writing – review & editing.

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#### Declaration of competing interest

The authors declare no conflicts of interest.

#### Data availability

Data will be made available on request.

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