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TO BE OR NOT TO BE ON THE TOP: EXAMINING EGG SURVIVAL AT THE TOP OF THE CLUTCH FOR TWO SEA TURTLE SPECIES

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***Abstract*.—Rising temperatures due to climate change may increase embryonic mortality in oviparous ectotherms such as sea turtles, which develop within a narrow thermal range. Embryos at the top of the clutch are presumed to face greater thermal stress with rising temperatures due to closer proximity to the sand surface, yet *in situ* studies of vertical egg survival remain scarce. We tested whether higher top-of-clutch mortality occurs in Loggerhead Turtle (*Caretta caretta*) and Green Turtle (*Chelonia mydas*) nests along a 2-km stretch of the Archie Carr National Wildlife Refuge, Florida, USA, a key nesting site for both species. During the 2024 nesting season, we marked five to 15 top-positioned eggs per clutch (nine to 15 clutches per season third, per species) using India ink and compared top-of-clutch hatching success with the rest of the clutch. We found no differences in top-of-clutch survival across the season for Loggerhead Turtles (35 clutches). In Green Turtles (32 clutches), top eggs had lower survival during only the early season (odds ratio = 0.34, 95% HPD = 0.13–0.67). Inter-species comparisons during overlapping timeframes and high overall hatching success indicate that incubation temperature (indirectly inferred through incubation duration) may not explain the Green Turtle early season top-of-clutch mortality. We also showed that India ink had no adverse effect on egg survival and proved effective for tracking individual egg fate *in situ*. This minimally invasive method enables *in situ* monitoring of vertical egg survival in nests.**

Key Words.—*Caretta caretta; Chelonia mydas;* climate change; Green Turtle; India ink; Loggerhead Turtle; nest environment

INTRODUCTION

As oviparous ectotherms, sea turtle embryos are susceptible to temperature; as nest temperatures exceed the thermal tolerance limit, the mortality of embryos increases and hatching success decreases (Bladow and Milton 2019; Monsinjon et al. 2019). Therefore, understanding the effects of variation in the nest temperatures of oviparous species, both under current and projected climate conditions, and determining the lethal temperature limits for development are important factors to consider when predicting the vulnerability of species to climate change (Hulin et al. 2009; Howard et al. 2014; Laloë et al. 2017). For sea turtle eggs, incubation occurs within a narrow thermal range (Yntema and Mrosovsky 1980; Miller 1997; Howard et al. 2014). Sea turtle nesting seasons typically last several months; therefore, clutches experience a range of temperatures from the early season to the late season (e.g., Kobayashi et al. 2017). Additionally, the hatching success of individual clutches is highly variable both among and within beaches (Bowden et al. 2014; Patrício et al. 2017).

The lethal upper limit that embryos can withstand varies within and between species (possibly about 33° C and 35° C; reviewed by Howard et al. 2014). When the upper limits are surpassed, both the temperature and the duration of exposure to those temperatures have the largest effect on embryonic mortality (Valverde et al. 2010; Howard et al. 2014; Bladow and Milton 2019). Hatching success decreases when temperatures surpass the upper limits (Howard et al. 2014). Additionally, a myriad of biotic and abiotic factors can affect hatching success and egg survival, including genetics (Rafferty et al. 2011; Kynoch et al. 2024), rainfall and nest humidity (Lolavar and Wyneken 2015), inundation and wave/tidal wash over (Foley et al. 2006; Ware et al. 2021), sand type (Saito et al. 2019), oxygen and carbon dioxide levels (Ackerman 1981; Ralph et al. 2005; I-Jiunn et al. 2015), and disturbances experienced during incubation (e.g., predation and inundation; Lyons et al. 2022). Turtles have temperature-dependent sex determination (TSD), where higher temperatures within the thermosensitive range lead to production of females and lower temperatures produce males (Yntema and Mrosovsky 1980). Climate change projections indicate that future nest temperatures may exceed survivable thresholds (e.g., Santidrián Tomillo et al. 2015); therefore, embryonic mortality is a more immediate concern under rising thermal conditions (Hays et al. 2017).

Sea turtles lay relatively large clutches, with the mean number of eggs within a clutch ranging among populations and species (e.g., 122.8 ± [standard deviation] 3.6 eggs for Green Turtles, *Chelonia mydas*, and 112.4 ± 2.2 eggs for Loggerhead Turtles, *Caretta caretta*; see review Miller 1997), and egg position within the clutch can influence the thermal environment that eggs experience during incubation. Eggs located at the top of the clutch generally experience greater fluctuations in ambient temperature (e.g., Hanson et al. 1998) and may have a higher likelihood of exceeding the thermal tolerance limits, especially under projected climate warming scenarios. In addition to external conditions, metabolic heating also contributes to the thermal environment within the clutch, thus the center of the clutch can have significantly higher temperatures than both the top and the bottom of the clutch (Hanson et al. 1998; Booth and Astill 2001; Gammon et al. 2020). Therefore, in a warming climate, when clutches are at higher risk of exceeding the thermal limits, it remains unclear whether eggs at the top (which experience external fluctuations) or eggs in the center (which undergo sustained metabolic heating) are more vulnerable to mortality.

To investigate top-of-clutch mortality in sea turtle nests, we used Florida, USA, as a case study due to its high nesting density, warm incubation temperatures, and the potential for elevated egg mortality. Florida hosts one of the largest rookeries worldwide for Loggerhead Turtles (Ceriani et al. 2019) and an increasingly important Green Turtle rookery (Chaloupka et al. 2008; Seminoff et al. 2015; Valdivia et al. 2019). Loggerhead Turtles in Florida typically nest from April through August (peaking in June/July) and Green Turtles from June through late September (peaking in July/August; Weishampel et al. 2006; Florida Fish and Wildlife Conservation Commission [FWC], unpubl. data), although seasonal and peak timing for each species can vary among beaches/regions (FWC, unpubl. data). While phenological shifts in nesting season timing can occur within beaches (Weishampel et al. 2004, 2010; Pike et al. 2006), peak nesting coincides with summer of Peninsular Florida and the warmest months of June, July and August (Mirsa and Bhardwaj 2019). Loggerhead Turtle clutches in Florida have been modeled to be highly female-skewed (Hays et al. 2017) and therefore are likely experiencing temperatures at the upper thermal range. Going as far back as the late 1980s and in the 1990s, there was concern that nests in central east and southeast Florida were experiencing temperatures within the higher thermal range for Loggerhead Turtles. This was inferred from hatchling sex ratios (Mrosovsky and Provancha 1989, 1992), nest-depth sand temperatures (Mrosovsky and Provancha 1992), and recorded incubation temperatures (Hanson et al. 1998). Supporting this concern, temperature analyses in Florida have found significant increases in both average and extreme summer and autumn humid heat in both frequency and intensity (Wodzicki et al. 2024; Milrad et al. 2025). Under future forecasted temperature changes, Loggerhead Turtle clutches in southeast Florida (Boca Raton) laid in the middle and later parts of the nesting season are predicted to experience 100% mortality, even under optimistic warming scenarios (Monsinjon et al. 2019).

Assessment of differential mortality along the vertical position in the clutch could provide insights into how current temperature regimes affect incubating clutches; however, following the fate of eggs along the vertical position *in-situ* is challenging. Despite the potential importance of vertical egg position, only two studies have specifically investigated egg mortality within sea turtle nests based on vertical placement. Ralph et al. (2005) marked individual Leatherback Turtle (*Dermochelys coriacea*) eggs in relocated clutches and found that eggs on the periphery had higher hatching success than eggs in the center. Similarly, I-Jiunn et al. (2015) marked Green Turtle eggs in relocated nests and found no relationship between vertical position (upper, middle, lower) and embryonic development stage at failure. While these studies offer valuable insights,

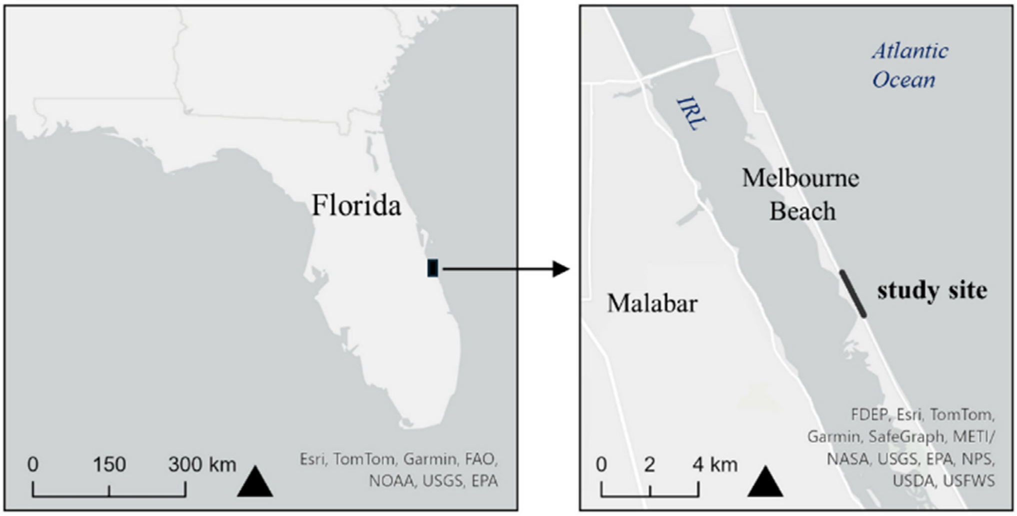

Figure 1. Study site (2-km) at Melbourne Beach, Florida USA, within the Archie Carr National Wildlife Refuge. The abbreviation IRL = Indian River Lagoon.

they remain some of the only published efforts to examine the vertical patterns of egg survival within sea turtle clutches, and there is a clear need to explore this topic further, particularly *in situ*. We aimed to examine whether egg mortality is higher at the top of *in situ* sea turtle clutches in central east Florida, where previous studies suggest that nest temperatures are already high (Mrosovsky and Provancha 1989, 1992). Specifically, the objective was to determine whether top-of-clutch embryonic mortality occurs, and if so, identify which part of the nesting season this mortality occurs in.

Materials and Methods

Study site and methods.—The Archie Carr National Wildlife Refuge (ACNWR) lies along the Florida, USA, central-east coast. The ACNWR is a hotspot for Loggerhead and Green Turtle nesting (about 20% and 35%, respectively, of nesting in Florida; Phillips et al. 2021), making it an ideal study site. We monitored Loggerhead Turtle and Green Turtle nests along 2 km (between 28.00866°N, -80.52847°W and 27.99272°N, -80.52031°W) during the 2024 nesting season (Fig. 1).

We partitioned the nesting season into thirds (early, middle, and late) based on a 3-y average of the number of nests recorded for the study area (2021–2023; Kate Mansfield and Erin Seney, unpubl. data). Season thirds for Loggerhead Turtles were April-May (early season), June to mid-July (mid-season), and mid-July through August (late season). Season thirds for Green Turtles were May to mid-July (early season), mid-July through August (mid-season), and September-November (late season). We encountered nests the morning after deposition by digging down and verifying the clutch following the Marine Turtle Conservation Handbook protocols of FWC (FWC 2016), and we manipulated the eggs in each nest to either assess a method to identify, at nest evaluation, where within the clutch individual eggs were incubating, or assess top-of-clutch egg survival. Surveyors recorded daily disturbances (e.g., predation) and washovers, then evaluated all nests following FWC protocols (FWC 2016).

For our first aim, to set up an identification method for eggs, we evaluated two criteria: the readability of marks after emergence of hatchlings from the nest (at evaluation); and the suitability of India ink for egg-marking (i.e., to determine whether marked eggs have similar egg survival to unmarked eggs). For the first criterion, we conducted a preliminary study using only one color (black) and a simple pattern (X) but could not see the marking on the eggs with confidence at time of evaluation. Consequently, we used three colors (in case one or two colors faded or blended in with naturally developing colors on the eggshell, i.e., colors produced by bacteria or fungi) and drew a more complicated pattern to increase our chances of recognizing marked eggs at the time of evaluation. In this study, we drew two overlapping Xs within a large circle on specific eggs using India ink Faber-Castell Pitt Artist Pen Big Brushes (Faber-Castell, Cleveland, Ohio, USA) colored with scarlet red 118, manganese violet 160, and phthalo blue 110 (Fig. 2). For the second criterion, we marked and monitored

Figure 2. Eggs marked with India ink the morning after the clutch of Loggerhead Turtles (*Caretta caretta*) and Green Turtles (*Chelonia mydas*) was laid (A) to assess top-of-clutch egg survival and (B) to assess if India ink can be used to identify egg position *in situ* after emergence of hatchlings; (C, D) differences in how the markings fared during evaluation > 50 d after the eggs were marked. Eggs in A, C, and D are from Loggerhead Turtle nests; eggs in B are from a Green Turtle nest. (Photographed by Cheryl L. Sanchez).

10 clutches laid during the middle of the season per species (Loggerhead Turtles: 10–20 June; Green Turtles: 21–25 July). The morning after deposition, we carefully removed all eggs from each nest and lined them up in the sand in the order of which we removed them (FWC 2016). We marked every other egg, then returned the eggs to their original location in the nest before 0900 (within 12 h after deposition), to avoid movement-induced mortality (Limpus et al. 1979; FWC 2016).

For our second and main aim to determine top-of-clutch egg survival, we targeted 15 nests per season third per species. We marked eggs that were exposed at the top of the clutch while verifying the location of the egg chamber. For this experiment, we did not lift or move eggs; we marked only the top eggs (and not eggs in other locations within the clutch) to minimize egg manipulation and handling. Therefore, the number of eggs marked in each clutch depended on the shape of the egg chamber; if the chamber was narrow and eggs were stacked directly on top of one another, then fewer eggs were seen directly on the top, and fewer eggs were marked. The wider the top of the egg chamber was, the more eggs were marked. We recorded the number of marked eggs within each clutch.

Surveyors conducted nest evaluations (excavations) 3 d after the first observed emergence of a hatchling or 70 d after deposition, if the emergence was not observed. Nest evaluations for both aims (evaluation of top-of-clutch egg survival and the suitability of India ink for egg-marking) included recording the depth (cm) between the top of the clutch and the surface of the sand, per clutch. Surveyors counted the number of hatched eggs (count of shell fragments > 50% of the egg size; Miller 1999), unhatched whole eggs, damaged eggs, pipped dead hatchlings, and pipped live hatchlings for both the marked eggs and unmarked eggs, following FWC (2016) protocols. Pipped hatchlings refer to when the turtle has broken through the eggshell (can range from having a small hole to a large tear), but the hatchling has not completely separated from the eggshell yet. Damaged eggs refer to eggs that are not whole eggs nor hatched, but to eggs that were damaged by a disturbance, including roots, predation, or ghost crabs (FWC 2016).

Analyses.—We performed data analyses separately for each turtle species in R (v4.3.3; R Core Team 2024) using RStudio (v2023.12.1.402; Posit team 2024). To assess the suitability of India ink for egg marking, we combined all clutches per species because there was no reason to believe that egg survival would differ at the individual clutch level based on the egg markings. Therefore, we assumed any potential influence of egg marking on egg survival was consistent across clutches. We classified pipped eggs as hatched. It was more difficult to see India ink markings on damaged eggs, depending on the extent of damage impacting the readability of the marking. Because India ink did not factor into egg damage, we excluded damaged eggs from the analysis. For each species, we tested if the proportion of hatched marked eggs (hatched marked eggs/unhatched marked eggs) was lower than the proportion of hatched unmarked eggs (hatched unmarked eggs/unhatched unmarked eggs) using a one-tailed Fisher's Exact Test, fisher.test (contingency_table, alternative = "less" and α of 0.05). The contingency table included marked hatched at evaluation (marked hatched + pipped), marked unhatched at evaluation (marked whole eggs), unmarked hatched at evaluation (hatched + pipped), and unmarked unhatched at evaluation (whole eggs).

For the top-of-clutch egg survival experiment analyses, the dataset only included clutches with the same number of marked eggs at deposition and evaluation, which allowed us to include damaged eggs. When calculating the hatching proportions, we classified pipped eggs as hatched (i.e., the embryo successfully completed its development during incubation). We tested if the position of eggs within the nest (Position; top-marked versus other-unmarked) and the timing of the nesting season (season_third; early, middle, late) affected egg survival using a Bayesian zero-inflated beta-binomial Generalized Linear Mixed Model (ZIB GLMM), per species, using the brms package in R (which interfaces with Stan for Bayesian inference; Bürkner 2017). The analysis modeled hatching proportion as the number of hatched eggs (Hatched) out of the total number of eggs (Hatched + Unhatched) using the trials() function, which is required in brms binomial models. The model included a zero-inflation component to account for excess zeros (i.e., nests with zero survival) and treated it as a constant (zi~1). The model included NestID as a random effect to account for repeated measures within nests. The full model was:

Hatched | trials (Hatched+Unhatched)-Position x season_third + (1 | nestID)

We fit the ZIB GLMM model with four chains of 4,000 iterations each (1,000 warm-up) using adapt_delta = 0.95 and max_treedepth = 15 to ensure convergence. Model diagnostics included evaluation of the R-hat values (< 1.01) and effective sample sizes (ESS; > 1,000) and posterior predictive checks (pp_check; observed values should fall within predicted simulations). We calculated the Bayesian R^2 to assess model fit, and a Bayesian *P*-value from the posterior predictive means. An acceptable *P*-value should be close to 0.5 (< 0.9 and > 0.1; Gelman et al. 2013).

To investigate specific differences in egg survival among egg-position and nesting season thirds, we used the emmeans package to calculate the estimated marginal means (EMMs) from the fitted ZIM GLMM. The analysis extracted EMMs on the response scale (type = response) to obtain the hatching proportion for each combination of egg-position and season third. We then conducted pairwise comparisons among factor levels using the contrast() function without adjustment for multiple comparisons. This allowed us to identify significant differences (α of 0.05) in survival between marked and unmarked eggs within each season category. The analysis visualized results using base plotting functions within emmeans.

We checked the data for normality (Shapiro-Wilk's Test) and conducted non-parametric analyses if data did not follow a normal distribution. First, we explored the associations between the proportions of hatched marked eggs and other possible predictors using Generalized Linear Models (GLMs), with the top-of-clutch hatching proportion (as the dependent, continuous variable) modeled against the following independent, continuous environmental variables: (1) distance to dune (m); (2) distance to high tide (m); and (3) depth (cm) to the top of the clutch at evaluation. Next, because temperature influences incubation duration (the number of days between the lay date, i.e., the morning after deposition, and hatchling emergence), the incubation duration can serve as a proxy for thermal conditions: clutches exposed to warmer temperatures tend to have shorter incubation durations, whereas clutches in cooler conditions have longer durations (Miller et al. 2017; Ware et al. 2025). To investigate if the incubation duration varied among the season thirds, we compared mean incubation duration (as the response variable) across season thirds using one-way Analysis of Variance (ANOVA) and Tukey HSD *post-hoc* Tests (car package; Fox and Weisberg 2019) because the data was normally distributed. Finally, to better understand why we observed a significant difference

Table 1. The number of India ink-marked and unmarked eggs for Loggerhead Turtles (*Caretta caretta*) and Green Turtles (*Chelonia mydas*) used in a Contingency Table analysis. Header abbreviations are H = hatched and UH = unhatched.

	Loggerhead turtle		Green Turtle	
	H	UH	H	UH
Marked eggs	329	140	484	87
Unmarked eggs	322	133	441	105

in top-of-clutch survival for one species but not the other during comparable time periods (see Results), we compared nest parameters between Loggerhead and Green Turtles. Specifically, the analysis applied *t*-tests (with α of 0.05) because the data was normally distributed, to evaluate the differences in mean top-of-clutch depth and nest distance to the high tide line, for nests laid during similar seasonal windows: Loggerhead Turtle mid-season (14–18 June) versus Green Turtle early season (25–30 June).

Results

Assessment of India ink for egg marking.—We marked 10 Loggerhead Turtle nests from 13–20 June 2024 and 10 Green Turtle nests from 21–25 July 2024 (Supplemental Information Tables S1 and S2). The mean clutch size at evaluation for Loggerhead and Green Turtle nests was 104.1 (median = 105.5; IQR = 12.25 eggs) and 121.4 (median = 123.5; IQR = 17 eggs), respectively. The mean number of marked eggs for Loggerhead and Green Turtle nests was 52.2 (median = 123.5; IQR = 6.5 eggs) and 61.1 (median = 123.5; IQR = 8.25 eggs). Marked eggs did not have a lower hatching proportion than the unmarked eggs for both species (Fisher's Exact Test; Loggerhead Turtles: $P = 0.447$; Green Turtles: $P = 0.968$; Table 1). For Loggerhead Turtle nests and Green Turtle nests, 98.3% and 99.5% of marked eggs, respectively, were recovered at evaluation. For Loggerhead Turtle nests, 70% of the marked eggs we found at evaluation hatched and 71% of the unmarked eggs hatched. For Green Turtle nests, 85% of the marked eggs we found at evaluation hatched and 81% of the unmarked eggs hatched (Supplemental Information Tables S1 and S2).

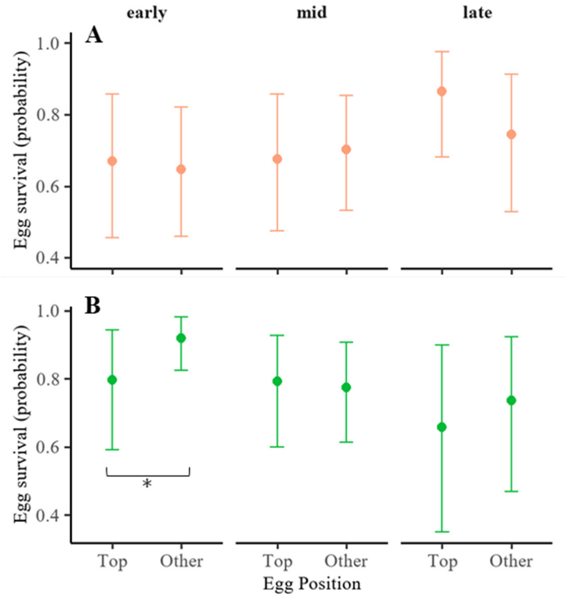

Figure 3. Estimated hatching probability (posterior medians ± 95% credible intervals) for top and other positioned eggs across nesting season thirds for (A) Loggerhead Turtles (*Caretta caretta*) and (B) Green Turtles (*Chelonia mydas*). The asterisk (*) indicates comparisons with significant differences ($P \leq 0.05$, one-tailed Fisher's exact test).

Top-of-clutch egg survival.—The number of eggs marked at deposition equaled the number of marked eggs found at evaluation for nine to 13 nests (detailed below) per season third (early, middle, late) per species. The ZI GLMM models for Loggerhead and Green Turtles had good explanatory power (Bayesian $R^2 = 0.83$, 95% confidence interval [CI] = 0.69–0.94; 0.95, 95% CI = 0.88–0.99, respectively), and the Bayesian *P*-values (0.27 and 0.34, respectively) suggested no major differences between the model predictions and observed data. The other diagnostic checks (Supplemental Information Table S3 and Fig. S1) confirmed that both models fit the data well.

The analysis included 35 Loggerhead Turtle nests: 12 early season (marked 15–22 May 2024), 13 mid-season (14–18 June 2024), and 10 late season (1–19 August 2024). Surveyors marked five to 15 eggs per clutch. Total marked eggs for the early, middle, and late seasons were 101, 123, and 96, and total unmarked eggs were 1,338, 1,276, and 1,083. For Loggerhead Turtle clutches, top-positioned eggs had similar hatching proportions to eggs positioned elsewhere in the clutch during the early, middle, and late season (Fig. 3).

The analysis included 32 Green Turtle nests: 10 early season (25–30 June 2024), 13 mid-season (21–25 July 2024), and nine late season (3–30 September 2024). Surveyors marked five to 13 eggs per clutch. Total marked eggs for early, middle, and late seasons were 71, 111, and 79, and total unmarked eggs were 1,248, 1,613, and 861. Other-positioned eggs had higher hatching proportions (EMMs = 0.92, 95% highest posterior density intervals [HPD] = 0.82–

Table 2. Estimated hatching probabilities, from Bayesian zero-inflated beta-binomial generalized linear mixed models, for Loggerhead Turtles (*Caretta caretta*) and Green Turtles (*Chelonia mydas*). Posterior mean probabilities (Prob) and 95% highest posterior density intervals (HPD) are shown by season third and egg position.

		Loggerhead Turtle		Green Turtle	
Season third	Position	Prob	HPD	Prob	HPD
Early	Top	0.67	0.46–0.86	0.80	0.59–0.94
	Other	0.65	0.46–0.82	0.92	0.82–0.98
Mid	Top	0.68	0.47–0.86	0.79	0.60–0.93
	Other	0.70	0.53–0.85	0.78	0.61–0.91
Late	Top	0.86	0.68–0.98	0.66	0.35–0.90
	Other	0.74	0.53–0.91	0.74	0.47–0.92

0.98) compared to the top-positioned eggs (EMMs = 0.80, 95% HPD = 0.59–0.94; Table 2) for the early season (pairwise contrasts, odds ratio = 0.34, 95% HPD = 0.13–0.67; Fig. 3). The Bayesian model suggests a significant effect of Position (credible interval not including zero), but the estimated differences on the response scale are modest, with overlapping credible intervals for marginal means. This indicates that while Position may influence the response, the practical magnitude of this effect is limited and may be subject to additional factors. Additionally, even though there was a lower hatching proportion for top-positioned eggs compared to the rest of the clutch in the early season, the hatching proportion for the top-positioned eggs in the early season remained similar for both top- and other-positioned eggs in middle and late seasons (Fig. 3, Table 2), and the pairwise comparisons showed no significant differences (Supplemental Information Table S4).

Because the proportion of top-of-clutch hatching differed significantly from that of other-positioned eggs in the early season for Green Turtle eggs, we explored the influence of additional variables. The GLMs revealed no significant main effects; however, the interaction effect for the mid-season distance to high tide and the proportion of hatched marked eggs was borderline insignificant ($P = 0.056$; Supplemental Information Table S5; distance to high tide boxplot, Supplemental Information Fig. S2). The mean incubation duration for Green Turtles differed significantly ($F_{2,24} = 28.11$, $P < 0.001$) with both the early (mean incubation duration = 48.9 d, 10 nests) and the middle season (50.8 d, 10 nests) showing shorter incubation durations than the late season (62.8 d, seven nests; Tukey HSD, late-early and mid-late, $P < 0.001$; Supplemental Information Fig. S3).

In comparison of the parameters for Green Turtle early season nests (25–30 June) and Loggerhead Turtle mid-season nests (14–18 June), Loggerhead Turtle nests had a shallower top-of-clutch depth (mean = 42.2 cm) than Green Turtle nests (mean = 59.3 cm; $t = -2.55$, df = 21, $P = 0.019$; Supplemental Information Fig. S4). When comparing the distance to high tide between the species, Loggerhead Turtles nested closer to the high tide line ($t = -2.86$, df = 21, $P = 0.009$) and had more variability in spread along the width of the beach than Green Turtles (Supplemental Information Fig. S5).

Discussion

Top-of-clutch egg survival varied between the two species. Specifically, the analysis detected no differences in egg survival for Loggerhead Turtle clutches; however, top-of-clutch egg survival was lower than the rest of the clutch for Green Turtle eggs in the early season. Overall, there was no consistent difference in egg survival between the top of the clutch and other-positioned eggs for the 2024 nesting season along our site. For Green Turtle nests, the hatching proportions for eggs in all positions were higher in the early season than in the middle and late seasons. Thus, under current conditions at our study site, we found no consistent evidence that eggs at the top of the clutch experience elevated mortality.

Although we did not directly test temperature, incubation duration is strongly influenced by the temperature within the nest; nests with higher incubation temperatures have shorter incubation durations (Ackerman 1997; Godfrey and Mrosovsky 1997; Godley et al. 2001). The higher incubation temperatures of the Green Turtle early and middle season, suggested by the shorter incubation duration of the early and middle season (compared to late season), may have had a minimal (if any) effect because the same was not seen for Loggerhead Turtles during the same timeframe. By comparing incubation durations, however, we are assuming the incubation duration is the same for all eggs, including the top and other positioned eggs. This comparison should be further explored in future studies.

The early nesting season of Green Turtles occurred around the same period as the Loggerhead Turtle mid-season (both in June), and the analysis detected no difference in top-of-clutch survival for Loggerhead Turtle nests. This is somewhat surprising because Loggerhead Turtle nests had significantly shallower egg chambers than the Green Turtle nests. Given their shallower egg chambers, we might expect Loggerhead Turtle nests to show lower top-of-clutch survival if high temperatures were the primary driver of differences in survival for the early season Green Turtle nests. It is also possible that the weak effect of position may only become evident when the potential survival is high (suggested in our study). Regardless, overall, the proportions of early season hatching for both top- and other-positioned eggs were high (74, 92%) and were high compared to the late season top-positioned eggs (top- and other-positioned: middle 78, 79%; late 66, 74%).

Nest site selection by females has a large influence on egg survival (Spencer 2002). For example, nesting further from the high tide line can decrease chances of nests being eroded or inundated (Wood and Bjorndal 2000; Stokes et al. 2024) while nesting near vegetation can in some cases decrease hatching (Redding et al. 2023). Overall, there is high variation in nest site selection among individuals, populations, and turtle species (Bjorndal and Bolten 1992; Kamel and Mrosovsky 2006; Kelly et al. 2017; Gravelle and Wyneken 2022). From our study, for the Green Turtle early season, seemingly less variability in nest site position on the beach width, coupled with shorter incubation times may have contributed to the lower top of the clutch egg survival. This should be explored with a larger dataset and supplemented with direct temperature measurements at different vertical locations within clutches. Additionally, this should be repeated over multiple seasons to see if there are seasonal differences in survival. Including other factors within the nest that can influence egg survival, not limited to but including nest humidity (Lolavar and Wyneken 2015), gas levels (I-Jiunn et al. 2015), and sand type (Saito et al. 2019), would also provide a more comprehensive analysis.

Although there are various ways in which turtles may adapt to rising temperatures, such as adjusting their nesting timing, as seen in central east Florida (Weishampel et al. 2004, 2010; Pike et al. 2006), and although there can be differences in temperatures/sex ratios within a season (Mrosovsky et al. 1984), turtles may not be able to adapt as quickly as needed to avoid nest failures (Fuentes et al. 2023). Even though we did not detect elevated mortality in this study, it leads us to wonder if an increase in embryonic mortality will be seen soon in central east Florida. Based on the present results (lack of differential mortality), there is no need to modify the monitoring programs, but we recommend periodic reassessment.

We were able to follow top-of-clutch egg survival and establish a method for following those specific eggs with India ink. India ink did not negatively impact egg survival (when comparing the proportions of hatched marked eggs to unmarked hatched eggs) and therefore offers a viable method for monitoring eggs within a nest. The whole-clutch experiment did not account for all marked eggs, with ink-markings observed mostly on hatched and unhatched eggs, and only limited observation of ink-markings on damaged eggs. At evaluation, eggs were several weeks old and damaged eggs often showed signs of more advanced decomposition, which may limit the detectability of the markings. The combination of the colors and design we used for the makings allowed us to identify ink-marked hatched and unhatched eggs, even when only slightly visible. It may be difficult, however, to extend this method to an entire clutch to distinguish between eggs at the periphery, top, and center because the designs did not always remain visible (due to the way the shell was torn by the hatchlings). We also did not examine whether the ink has any effects on hatchling fitness, although we have no reason to expect so. Other studies have used India ink to follow incubating eggs. One study followed sea turtle eggs using India ink, but in a laboratory setting (Bustard and Greenham 1968). India ink has also seen use on eggs of other species (e.g., birds; Grant 1982), but this is the first study we know of that showed no effect of India ink on sea turtle egg survival and applied India ink markings successfully on *in situ* nests.

Our results suggest that while Green Turtle nests had lower top-of-clutch survival during the early season, overall hatching success remained high. Coupled with the lack of a similar pattern in Loggerhead Turtle nests, despite their shallower nests and overlapping nesting period, our results do not support temperature-induced mortality (indirectly assessed through incubation duration) as the sole driver of egg survival and indicate the importance of other factors such as nest placement and beach microhabitat. Our findings demonstrate the utility of India ink as a minimally invasive tool to track egg fate within *in situ* sea turtle nests as a promising method for future *in situ* studies of intra-clutch survival. This type of monitoring may be useful for detecting any changes in egg survival at the top of the clutch. If changes in survival are detected, further detailed studies incorporating other clutch microclimate factors/measurements (e.g., direct temperature measurements) would be needed to make confident conclusions. Changes in egg survival will be important to detect if/as incubation temperatures rise, to help guide the long-term management of sea turtle rookeries in warming climates.

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