Science of the Total Environment 952 (2024) 175961

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

High thermal tolerance of egg clutches and potential adaptive capacity in green turtles

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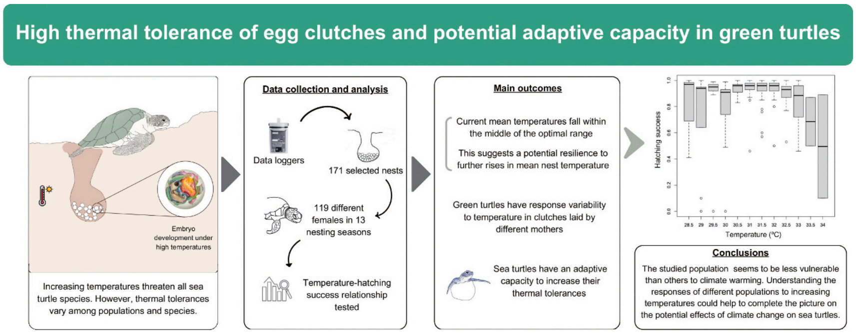
HIGHLIGHTS

- There is a high tolerance to temperature in green turtle clutches.
- Current temperatures fall within the optimal range that maximizes hatching success.
- There is variability in the response to temperature among clutches laid by different mothers.
- Sea turtle populations have an adaptive capacity to increase their thermal tolerances.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Rafael Mateo

Keywords:
Sea turtles
Hatching success
Nest temperature
Climate change
Resilience
Adaptation

ABSTRACT

Climate warming threatens sea turtles, among other effects, because high temperatures increase embryo mortality. However, not all species and populations are expected to respond the same way because they could have different thermal tolerances and capacities to adapt. We tested the effect of incubation temperature on egg mortality in a population of green turtles (*Chelonia mydas*) previously suggested to be less affected by extreme climatic events than others. We (1) assessed the relationship between temperature and hatching success, (2) defined an optimal range of temperatures that maximized hatching success and (3) assessed the variability in the response to temperature among clutches laid by different mothers, which could allow adaptation. Hatching success was consistently high in green turtle clutches with a skew toward high values, with 50 % of clutches having a success above 94 %. Yet, it was mildly affected by temperature, declining at both low and high temperatures. The optimal range of mean incubation temperatures was between ~30.5 °C and 32.5 °C. Current mean temperatures (31.3 °C) fall within the middle of the optimal range, indicating a potential resilience to further rises in mean nest temperature. Hatching success was best described by nest temperature and the interaction between female identity and temperature. This last predictor indicated a variability in thermal tolerance among clutches laid by different mothers and therefore, a capacity to adapt. The studied population of green turtles seems to be less vulnerable than others to climate warming. Understanding how different populations could

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https://doi.org/10.1016/j.scitotenv.2024.175961
Received 1 July 2024; Received in revised form 29 August 2024; Accepted 30 August 2024

respond to increasing temperatures could help complete the picture on the potential effects of climate change on sea turtles.

1. Introduction

Ongoing climate warming is a cause for concern as it threatens many species globally (Bellard et al., 2012; Harley, 2011). However, not all populations or species may respond the same way. Whereas some populations are likely to become extinct due to the severity of climatic conditions and/or because they have a lower capacity to respond, others will likely survive if they experience milder climatic conditions, are more resilient to high temperatures, or have a greater adaptive capacity (Bellard et al., 2012; Willis and Bhagwat, 2009).

Sea turtles are ectotherms that are threatened by climate change in several ways. Higher temperatures increase egg and hatchling mortality (Santidrián Tomillo et al., 2009; Valverde et al., 2010) and extremely biased sex ratios because they have temperature-dependent sex determination (Broderick et al., 2000; Tanner et al., 2019). Climate change could also cause a loss of nesting habitat due to changes in beach dynamics and sea level rise (Fuentes et al., 2010), as well as drive fluctuations in ocean productivity that in turn, condition the reproductive frequency of turtles (Saba et al., 2008). Their means of adaptation to changes in climate may imply shifts in spatial (Hochscheid et al., 2022) or temporal (Fuentes et al., 2024) distributions, or physiological adaptations toward increasing their thermal tolerance (Kynoch et al., 2024; Tedeschi et al., 2016). Some populations may, however, be favored by climate change if they nest in areas or at times that were previously suboptimal (Santidrián Tomillo et al., 2023), or be unaffected, if they have thermal limits that fall within the temperatures they encounter locally.

The two existent sea turtle families (*Cheloniidae* and *Dermochelydae*) originated in the Cretaceous period (Hirayama, 1997), a time characterized by rapid and severe climate changes (Hu et al., 2012). Consequently, they evolved over possibly >100 million years, surviving the mass extinction of the Cretaceous/Paleogene boundary (Sepkoski Jr., 1996), and through climatic conditions that were warmer and cooler than those encountered today (Crowley et al., 1986; Tajika, 1998). However, not all species or populations survived through drastic changes in climate and some went extinct, especially during the Cretaceous/Paleogene boundary (Hirayama, 1997). Consequently, we could expect a similar variability in the responses of modern sea turtles to the current warming period.

Incubation of eggs in sea turtle species can only occur within a viable range of temperatures, typically considered between 25–27 °C and 33–35 °C for the lower and upper thermal limits respectively (Ackerman, 1997; Howard et al., 2014). Within this viable range, there is a narrower optimal window over which, hatching success is maximum (Rutledge et al., 2024). The viable and optimal temperature ranges vary between species and populations, and it has been suggested that some populations, or at least some clutches, may have thermal tolerances that are above what is considered the upper thermal limit (33–35 °C) (Maulany et al., 2012a; Rutledge et al., 2024; Valverde et al., 2010).

On the other hand, variability in the response to temperature in clutches laid by different mothers has been recently reported for leatherback turtles (*Dermochelys coriacea*) (Kynoch et al., 2024). This indicates an inherent capacity of sea turtle populations to adapt, because mothers that produce hatchlings at detrimentally high temperatures have a greater chance of passing their genes to the following generations. As the warming trend continues, we could expect that the genotype of females that lay clutches of eggs with higher tolerance to high temperatures will become more abundant in the population, facilitating local adaptation.

We conducted an exhaustive analysis on the effect of nest temperatures on green turtle (*Chelonia mydas*) clutches over 13 nesting seasons in northwest Costa Rica. Nests of green turtles in this area were previously suggested to be more tolerant to high temperatures than those of other species, due to their milder response to the 2015 extreme El Niño event (Santidrián Tomillo et al., 2020). In particular, we wanted to assess the resilience and adaptive capacity of green turtles to ongoing climate warming by (1) analyzing the response of their clutches to current ranges of temperatures, (2) determining viable and optimal ranges of temperatures for egg development, and (3) assessing if different females exhibited different thermal tolerances that would allow adaptation. Understanding how populations that have high thermal tolerances may respond to currently ongoing climate warming, would help to draw a more complete picture about the overall effects of climate change on modern sea turtles.

2. Methods

Cabuyal (10°400 N, 85°390 W) is located in Northwest Costa Rica. It is a 1.4 km high-energy beach with frequent erosion and accretion dynamics surrounded by mangrove and dry forests (Yaney-Keller et al., 2019). Green turtles mainly nest on the upper vegetated area of the beach, where nests likely have a lower erosion/inundation risk (Heredero-Saura et al., 2022). The core of the nesting season extends from October to March (Santidrián Tomillo et al., 2015a). During this time, we patrol the beach every night to encounter nesting turtles and in the morning to count tracks and verify the nesting events from the previous night.

We marked every turtle with a Passive Integrated Transponder (PIT) tag that we injected in the right front flipper and with a metal INCONEL tag that we placed externally in the same flipper after the turtle had finished laying eggs (Santidrián Tomillo et al., 2015a). We measured the length and width of the turtle carapace, counted the number of eggs and marked the nest with a unique number. We located nests by triangulating them to the two nearest beach markers (to the North and South) that were separated by 25 m (Heredero-Saura et al., 2022).

We randomly selected a number of nests to deploy HOBO 8 K Pendant temperature data loggers (accuracy ±0.5 °C). Loggers were programed to collect data every hour throughout incubation. We deployed the logger in the middle of the clutch while the turtle was laying eggs and recovered it at the end of incubation, when the nest was excavated. All loggers were tested at the beginning of each season by comparing them against each other. Any loggers that were apart by more than the accuracy level from the mean value were excluded.

We waited two days to excavate nests after hatchling emergence was verified or 65 days if the emergence event was missed or if no hatchlings emerged. During the excavation, we counted the number of eggshells, classified dead eggs into four developmental stages, based on what can be identified correctly in the field, and counted any dead or live hatchlings if these were present. Any live hatchlings were released from the beach after dark. We estimated hatching success using the formula: $H = S / (S + U)$, where S corresponded to the number of eggshells (counted as one when >50 % of the shell remained, Miller, 1999) and U corresponded to the number of unhatched eggs. All remains were placed back into the emptied egg chamber and covered. We transformed the obtained ratio into a percentage.

We used data for 13 nesting seasons, from 2011/12 to 2023/24 and included nests for which we had both, nest temperature and hatching success data. We analyzed the effect of temperature on hatching success and tested if there were differences among mothers in the response of their clutches to temperature, as recently found in leatherback turtles (Kynoch et al., 2024).

2.1. Statistical analyses

We used a Shapiro-Wilk test to assess normality of the data. Temperature followed a normal distribution (Shapiro-Wilk test, $p = 0.482$) but hatching success did not ($p < 0.001$). Consequently, we used an ANOVA with a Tukey posthoc test to compare temperatures between seasons, and a Kruskall-Wallis to compare hatching success. To test the effect of different predictors on hatching success, we built a number of linear mixed effects models that included or excluded the following variables: temperature and year as fixed factors and female identity as a random factor. We also considered the potential effect of the interaction between temperature and female identity and between temperature and year. We considered a total of 13 models (Table 1). Models were evaluated using the corrected Akaike Information Criterion (AICc), with the lowest AICc values indicating the best models. Hatching success data were log-transformed prior to analysis. To better understand the relationship between temperature and hatching success and identify potential thresholds that could be used for conservation practices, we additionally looked at the effect of temperature on hatching success by 0.5 °C increments of temperature and ran a generalized additive model (GAM) to test the non-linear relationship between temperature and hatching success.

We used R version 4.1.2 to run all statistical analyses (R Core Team, 2023). We used the lmerTest R package for the linear mixed effect models (lmer function) (Kuznetsova et al., 2017), MuMIn library for the AICc (Bartoń, 2024) and mgcv library for the GAM function (Wood, 2017).

3. Results

We obtained nest temperature and hatching success data from 171 green turtle nests at Cabuyal over 13 nesting seasons, corresponding to 119 different females. For most turtles, we obtained information from a single clutch in a single season ($n = 86$). However, we had at least 2 clutches for 33 turtles, with 18 turtles laying clutches in one season, 12 turtles laying clutches in two different seasons and 3 turtles in three different seasons. The maximum number of clutches was six clutches for a female that nested in 2015 (2 nests) and 2019 (4 nests).

The model that best explained the variability in hatching success included temperature ($p < 0.05$) and the interaction between female identity and temperature ($p < 0.001$) (Table 1), indicating that clutches laid by different mothers could have different responses to temperature. The second best model included temperature, female identity and the interaction between temperature and female identity as predictors. However, in this model, only temperature ($p < 0.05$) and the interaction between temperature and female identity ($p < 0.001$) had a statistically significant effect. The third best model, only included temperature as a predictor. The first and second models were apart by 2.1 AICc points and the third model was 1.5 AICc points higher than the second one, indicating that the difference between the three models was small. All other models had AICc values that were 9 or more points higher and therefore, were considerably worse. Models that included the year as a fixed factor, were also worse than those models without it (Table 1).

Table 1
Models used to test the effect of different predictors on hatching success of green turtle nests. We considered temperature (Temp) and year as fixed factors, and identity of the mother (turtle ID) as a random factor. We also considered the interaction between turtle ID and temperature and between temperature and year as possible predictors. Best models are in bold.

Models tested (predictors)	df	AICc
Turtle ID	3	471.8
Temp + Turtle ID	4	473.0
Year + Turtle ID	15	490.6
Temp + Year + Turtle ID	16	492.7
Temp + Turtle ID + Turtle ID*Temp	**5**	**462.3**
Temp + Turtle ID*Temp	**4**	**460.3**
Temp + Year + Turtle ID + Turtle ID*Temp	17	485.1
Temp + turtle ID + Turtle ID* Temp + Temp*Year	17	569.0
Temp + Turtle ID + Temp*Year	16	576.5
Temp*Year + Turtle ID	16	576.5
Temp + Year	15	477.5
Year	14	478.8
Temp	**3**	**463.8**

Overall, hatching success was very high in green turtle nests (mean ± SD: 88 % ± 19 %, median: 94 %, $n = 171$) (Table 2), with 50 % of nests having a hatching success above 94 %, as indicated by the median. The skew value was negative (−3.01), also implying a skew toward high values, with most nests having a very high hatching success. Of the 171 nests, only 3 nests produced zero hatchlings, compared to 15 nests where all eggs hatched. Moreover, 14 and 12 nests respectively had 99 % and 98 % successes, generally implying that only 1 or 2 eggs in the clutch did not hatch. Only 9 nests had hatching successes below 50 %, and a total of 23 nests below 80 %, compared to the 76 nests that had a hatching success above 95 %.

As seen in the boxplot and GAM analysis (Fig. 1), the effect of temperature on hatching success was mild but statistically significant (GAM: deviance explained: 12.7 %, $p < 0.001$), declining at low and high temperatures. The figure generated from the GAM analysis showed that possible thermal thresholds occurred around mean nest temperatures of 30.5 °C and 32.5 °C (optimal range), with hatching success being highest between those two levels (Fig. 1). Interestingly, for the range of temperatures encountered, low temperatures seemed to have a generally greater negative effect on hatching success than that of high temperatures. Mean (±SD) nest temperatures ($n = 171$) were 31.3 °C ± 1.18 °C (median: 31.4 °C, range: 28.5 °C–34.2 °C). Noticeably, among the nests that had very high mean temperatures (≥33.0 °C or higher, $n = 14$), mean hatching success was still high (79 % ± 26 %). Only two nests had mean temperatures above 34.0 °C and both still produced hatchlings, with hatching successes of 10 % and 89 %. The number of days with temperatures above 35 °C in nests that had very high mean temperatures was on average (± SD) 13.8 ± 3.1 days (n = 14 nests, range = 7–19 days). Likewise, although hatching success declined at the lowest mean temperatures, there were still nests with low temperatures that had very high hatching success. There were only three nests with temperatures below 29.0 °C. Out of these, two of them had hatching successes above 95 % and the other one had 41 % hatching success. For nests with mean temperatures between 29.0 °C and 29.5°, there were six nests that had hatching successes above 90 %, and three nests with 0 %, 10 % and 64 % hatching successes.

We found statistically significant differences in nest temperatures between seasons (ANOVA, $p < 0.01$). However, the posthoc test only detected statistically significant differences between 2015/16 and 2020/21 (Fig. 2, Table 2). Although differences in temperatures between 2015/16 and 2017/18 were not statistically significant, the p-value was close to the significance level ($p = 0.06$). Highest nest temperatures were found in 2015/16, coinciding with the occurrence of an extreme El Niño event. We did not detect statistically significant differences in hatching success between seasons (Kruskal-Wallis, $p = 0.995$), which was consistently high every year (Fig. 2, Table 2), despite the variability in nest temperatures.

4. Discussion

Studies in sea turtle nests typically report mean or average values of hatching success (e.g. Bell et al., 2004; Ditmer and Stapleton, 2012; Martins et al., 2021; but see Brost et al., 2015). However, as indicated by our results, the median and the skewness (94 % and −3.01 in our case) can provide important information to characterize hatching success in a population. For example, pinpointing clutches that may have atypically high or low hatching success, could help focus conservation actions. Although the median is seldom mentioned, it has been included in a few studies on sea turtle hatching success (Perrault et al., 2011; Brost et al.,

Table 2

Number of nests (n) and mean, median, minimum (min) and maximum (max) values of hatching success and temperatures in green turtle nests per season.

		Hatching success				Temperature (°C)			
Season	n	Mean ± SD	Median	Min	Max	Mean ± SD	Median	Min	Max
2011/12	8	0.93 ± 0.07	0.96	0.78	0.99	30.8 ± 1.5	30.4	28.8	33.0
2012/13	14	0.87 ± 0.26	0.96	0.00	0.99	31.5 ± 0.8	31.6	29.6	32.6
2013/14	19	0.91 ± 0.14	0.94	0.41	1.00	31.1 ± 1.1	31.1	28.5	33.4
2014/15	16	0.90 ± 0.12	0.96	0.60	1.00	31.2 ± 0.8	31.0	29.9	32.6
2015/16	9	0.86 ± 0.20	0.97	0.50	1.00	32.4 ± 0.8	32.6	31.2	33.8
2016/17	2	0.95 ± 0.07	0.95	0.90	1.00	29.8 ± 1.5	29.8	28.8	30.9
2017/18	13	0.85 ± 0.28	0.94	0.00	0.99	30.8 ± 1.2	30.6	29.2	32.6
2018/19	13	0.90 ± 0.14	0.96	0.49	1.00	30.9 ± 1.1	31.0	29.1	32.8
2019/20	13	0.88 ± 0.17	0.92	0.46	1.00	31.7 ± 1.2	31.8	29.5	33.4
2020/21	5	0.75 ± 0.42	0.94	0.00	0.96	30.2 ± 1.0	29.8	29.0	31.6
2021/22	29	0.90 ± 0.16	0.93	0.10	1.00	31.3 ± 1.3	31.2	29.0	34.1
2022/23	7	0.88 ± 0.17	0.95	0.50	0.98	31.4 ± 0.6	31.4	30.7	32.3
2023/24	23	0.85 ± 0.22	0.95	0.10	1.00	31.8 ± 1.2	31.6	29.3	34.2

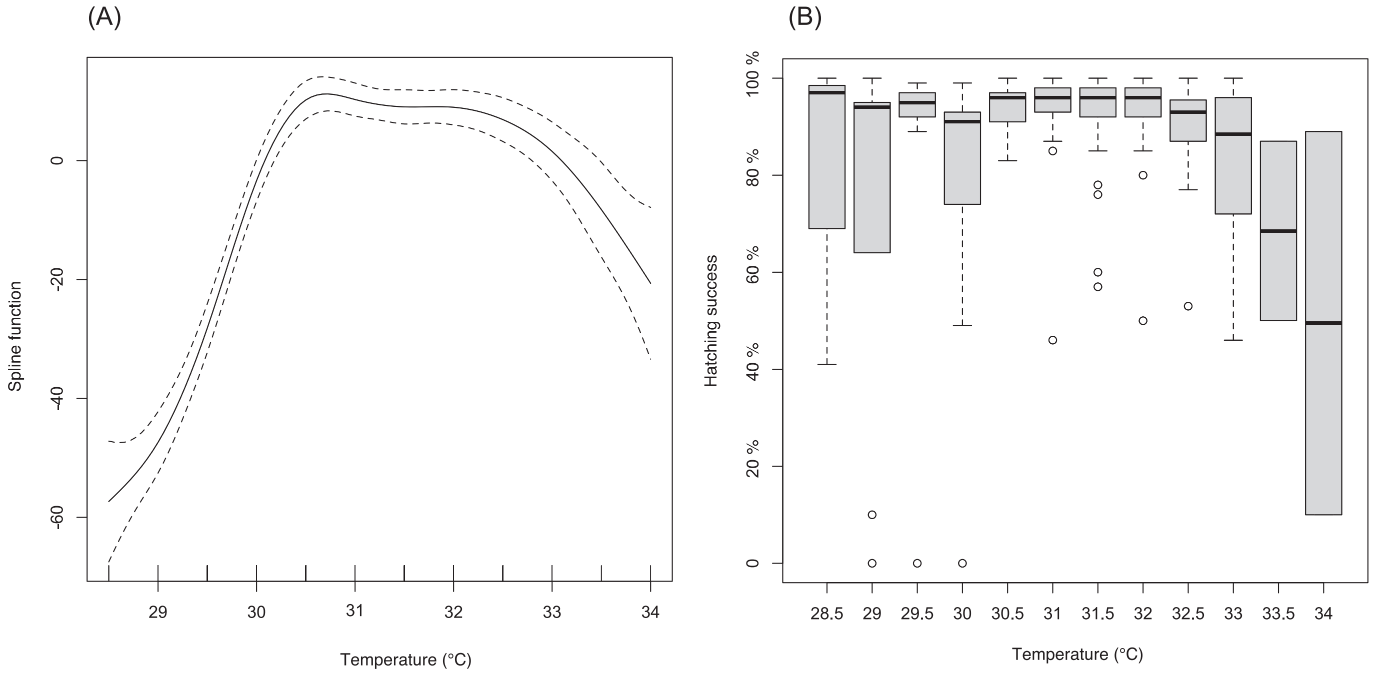

Fig. 1. Effect of nest temperature by 0.5 °C increments of temperature on hatching success of green turtle nests. A) GAM and B) boxplot. Optimal thermal range (maximum hatching success) was approximately at mean temperatures between 30.5 °C and 32.5 °C. The spline function (Y-axis) shows the additive effects of temperature (°C) on hatching success. Dash lines correspond to two standard errors around the main effect.

2015; Laloë et al., 2017). We found a hatching success that was consistently high (> 80 %) with most nests having a very high hatching success (>90–95 %), but with a few clutches that still had a low production of hatchlings, which lowered the mean. Low hatching success in these nests, although it was rare, could have been driven by unnoticed factors known to reduce the success of clutches, such as nest inundation (Pike et al., 2015), high presence of roots (Redding et al., 2024) or health of the mother (Perrault et al., 2012) among others. In addition, mean temperatures may not fully capture the effect of temperature on hatching success throughout incubation, because embryos at different stages of development often have different susceptibilities to high temperatures (Maulany et al., 2012b; Rutledge et al., 2024). For example, green turtle clutches at Rain and Heron Islands in the Great Coral Reef, Australia had similar mean incubation temperatures, but the temperature profiles were very different, as well as the time of greatest embryo death (Booth, 2023). A more focused analysis on the few nests that had low hatching success at Cabuyal could further infer information on the stage at which embryos died in relation to the specific temperature the eggs experienced, especially in those nests that had very low hatching success.

In comparison to other populations, relatively high mean hatching success (but lower than at Cabuyal) has also been reported for green turtles in Northern Cyprus (80–85 %, Broderick and Godley, 1996) and Taiwan (72.2 % and 80.7 % in two locations, Cheng et al., 2008). On the other hand, much lower hatching successes than that found at Cabuyal were reported in green turtles at the Galápagos Islands (46 %, Zárate et al., 2013) and the Arabian Gulf (38.8 %, Maneja et al., 2023). In Australia, hatching success in green turtles is also on the low side at Raine Island (20–60 %, Booth et al., 2021), despite being typically high in eastern Australian beaches (> 80 %, Limpus, 2008, Booth et al., 2021). In some instances, differences in the hatching success could be due to methodological differences. For example, the low hatching success at the Galápagos Islands was explained by high predation levels, nest density and tidal inundation (Zárate et al., 2013). At Raine Island, low hatching success is likely due to a very high nest-density (Booth et al., 2021). In our study, because our aim was to assess the effect of temperature on incubation, we excluded nests that were lost to erosion, inundated or predated, which could account for ~5–10 % of all nests

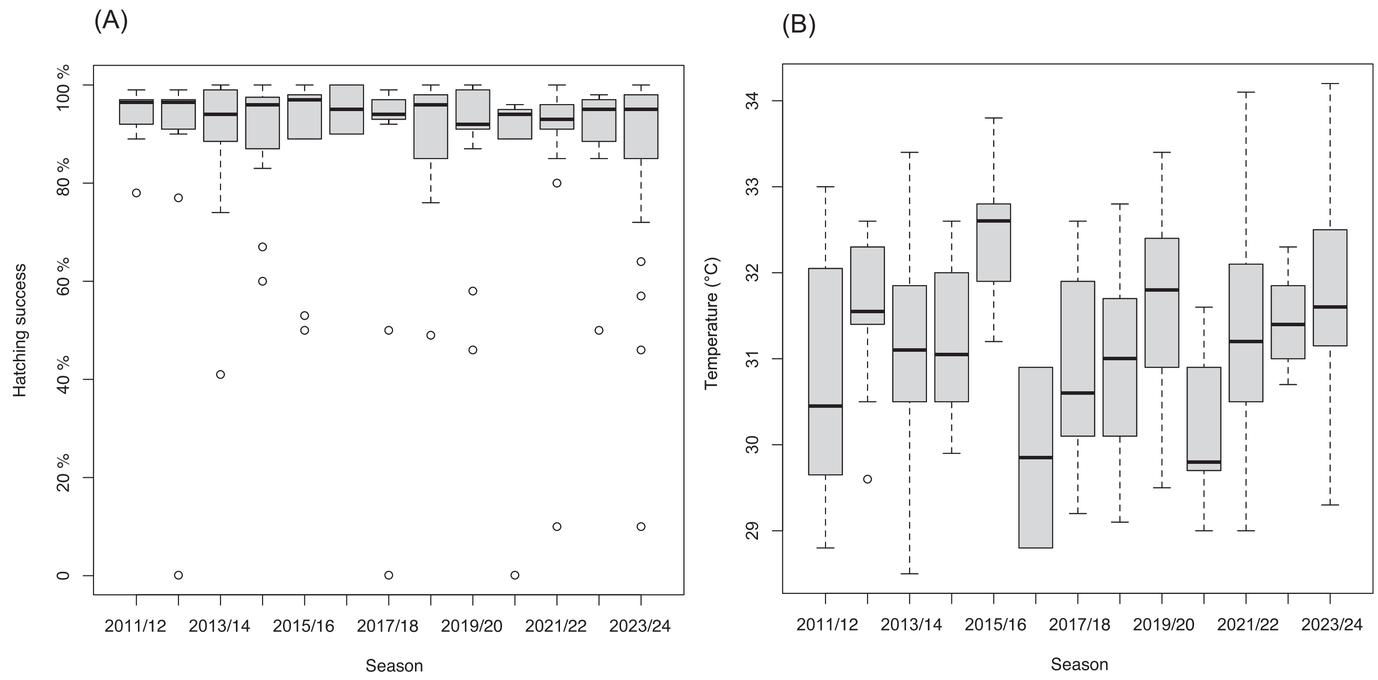

Fig. 2. Boxplot for A) hatching success and B) mean temperatures per nesting season in green turtle nests at Cabuyal, Costa Rica.

and that would lower the overall estimation of hatchlings produced if these nests had been included.

Hatching success at our study site declined at high temperatures but only mildly. Compared to Cabuyal, hatching success in green turtle nests was much lower at the Arabian Gulf due to the extremely high and dry conditions that nests experience there (Maneja et al., 2023). This population seems to encounter the most extreme climatic conditions of temperature and humidity on Earth, having mean temperatures during the middle third of incubation of 33.4 °C. Similarly than to Cabuyal, nests at the Arabian Gulf that encountered temperatures above 35 °C throughout extended periods of incubation still produced hatchlings and some nests had 60 % hatching success despite experiencing temperatures above 37 °C (Maneja et al., 2023). A few nests at Cabuyal also experienced very high mean incubation temperatures (as reported before, 14 nests had mean temperatures above 33 °C and two nests above 34 °C) and produced hatchlings. Consequently, it seems that the higher upper thermal limit for viable incubation is higher in sea turtles than previously thought, at least in some populations like the studied one. However, the temperatures in the nest during incubation can affect embryos differently at early or late developmental stages (Booth, 2023). Thus, mean nest temperatures should be used with caution.

Temperature, as expected, affected hatching success in green turtle nests at Cabuyal but its effect was mild. This lack of stronger effect, as seen in other species that nest in the area like leatherback turtles (Kynoch et al., 2024; Santidrián Tomillo et al., 2020), is possibly because the current range of temperatures they encounter are favorable for egg incubation in this population. Current mean incubation temperature at Cabuyal, was 31.3 °C, which is 1.2 °C lower than the temperature at which, hatching success slightly drops (32.5 °C) and possibly, 2 °C - 2.5 °C lower than the temperature at which, hatching success really starts declining (to or below 50 % hatching success). A similar relationship between temperature and hatching success was found in green turtles that nested in Turkey (also having a low adjusted $r^2 = 0.18$ in GAM), where hatching success started to decline at ~32 °C and had a mean nest temperature of 31.1 °C (Türkozan et al., 2023), a temperature only slightly lower than that recorded at Cabuyal. Interestingly, the authors also reported that the decline in hatching success at high temperatures was not evident in all nests, with some nests being highly tolerant to high temperatures (Türkozan et al., 2023). Declines in hatching success at temperatures above 32.5 °C have also been reported for flatback turtles in Australia (Van Lohuizen et al., 2016).

It is intuitive to think that sea turtles that nest in locations that experience higher temperatures also exhibit higher thermal tolerances, as it has been reported in some areas (Weber et al., 2012; Bentley et al., 2020). However, green turtles at Cabuyal, like those nesting in Turkey (Türkozan et al., 2023), seem to have thermal tolerances above the temperatures that they are currently encountering. Because Cabuyal green turtles tend to nest in the vegetation (Heredero-Saura et al., 2022), something that also occurs in other populations (Whitmore and Dutton, 1985), it is possible that their clutches have an increased resistance to the presence of roots. If the shells of green turtle eggs have developed an adaptation to resist the dry conditions generated by roots, this adaptation could have also increased the resistance of eggs to high temperatures. In addition, clutches that incubate underneath trees may be more climatically buffered than those incubating in the open beach, even if temperatures in shaded areas are also high.

Reconstructions of nest temperatures in leatherback turtles that nest in the same region of Costa Rica than the Cabuyal green turtles drew and estimate of 0.5 °C increase in nest temperatures throughout the 20th century (Santidrián Tomillo et al., 2015b). Similar per century increases in sand temperatures were estimated by Laloë et al. (2021) for other world regions. If the same warming in nest temperature occurred at Cabuyal and the trend continued throughout the 21st century, we could expect not to see an increase in egg mortality in this population by the end of the century. In fact, since sea turtles have temperature-dependent sex determination and females are produced at high temperatures (Standora and Spotila, 1985), the number of nesting females could increase with rising temperatures, due to an increase in the female-biased sex ratio (Laloë et al., 2014). This is expected when populations encounter temperatures that increase the female sex ratio but that do not yet increase egg mortality (Santidrián Tomillo et al., 2015b; Hays et al., 2017). Thus, the nesting population of green turtles at Cabuyal may be positively affected by current thermal conditions, until mean nest temperatures increase by ~2 °C–2.5 °C, when egg survival could decline.

Conversely, hatching success declined at low temperatures. Thus, climatic conditions could have negatively affected hatching success in the past. The optimal range of temperatures at Cabuyal was between 30.5 °C and 32.5 °C. If nests temperatures were ~1 °C lower during the

19th century, which seems feasible (Laloë et al., 2021; Santidrián Tomillo et al., 2015b), mean nest temperatures could have been at the lower end of the optimal range with many nests being incubated at suboptimal thermal conditions. Some nesting populations of green turtles around the world have increased and although, this is largely due to conservation actions (Broderick et al., 2006; Mortimer et al., 2011; Delgado-Trejo and Alvarado-Díaz, 2012), it is also possible that a switch toward more optimal incubation temperatures contributed to the positive trends.

The model that included temperature, and interaction between female identity and temperature explained most of the variability in hatching success. The influence of this interaction indicates variability in the response to temperature among clutches laid by different mothers and ultimately, a capacity to adapt. This effect was recently reported in leatherback turtles (Kynoch et al., 2024). Even if our dataset included a low number of turtles that laid multiple clutches, the model that included the interaction between females and temperature explained the variability in hatching success better than other models. However, the model that also included female identity alone and the one that only included temperature were also good models. A lack of larger differences between the best models, is possibly due to the fact that for many turtles, we had a single clutch and for those turtles with more than one clutch, we normally had two or three clutches. Leatherback turtles lay more clutches than green turtles (~7 clutches, Reina et al., 2002, vs. 4 clutches, Santidrián Tomillo et al., 2015a), and the leatherback study also included a much larger number of nests (Kynoch et al., 2024). Thus, it makes sense that Kynoch et al. (2024) detected a stronger effect of the interaction between female identity with temperature in leatherback hatching success than us. In any case, our best model included the effect of this interaction, confirming that there is also variability in the response of clutches laid by different mothers to temperature and a capacity to adapt in green turtles.

An adaptive capacity to increase thermal tolerance of clutches at the population level is likely present in all sea turtle species. However, chances of surviving the ongoing global warming are likely not equal for all populations. Some species, like leatherback turtles (Santidrián Tomillo et al., 2020; Kynoch et al., 2024) and olive ridley turtles that nest in *arribadas* (Valverde et al., 2010) are already suffering from high embryonic mortality and are therefore, more vulnerable to climate warming. Likewise, some populations are already severely depleted from other anthropogenic threats such as fishery bycath or egg harvest (Bjorndal et al., 1993; Tapilatu et al., 2013; The Laúd OPO network, 2020) and unlikely to resist the additional pressure from climate change. Throughout historical changes in climate, some species of sea turtles became extinct and others survived. We could expect similar responses in modern turtles to climate warming. Whereas those populations that are depleted and/or more heavily affected by high temperatures are at greater risk of extinction, those that are more tolerant to high temperatures and/or have larger numbers are more likely to survive. Studying the differences in the vulnerability to climate variability among sea turtle species and populations, and their capacities to adapt will help us understand how they may respond to climate warming and design appropriate ways to protect them.

CRediT authorship contribution statement

Pilar Santidrián Tomillo: Writing – review & editing, Writing – original draft, Supervision, Project administration, Formal analysis, Conceptualization. **Keilor Cordero-Umaña:** Writing – review & editing, Supervision. **Verónica Valverde-Cantillo:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors have no interests to declare.

Data availability

Data will be made available on request.

Acknowledgements

We thank all field assistants and volunteers that contributed to the data collection over the years. We thank Roger Blanco and the Guanacaste Conservation Area for granting the required research permits to conduct the study and for their overall support to research at Cabuyal. Funding to conduct the study over the years was provided by the Leatherback Trust, the National Fish and Wildlife Foundation of the USA, the AZA Sea Turtle SAFE Program, Virginia Aquarium & Marine Science Center, North Carolina Aquariums, South Carolina Aquarium and The Florida Aquarium, the Laúd OPO network and a Marie Curie Fellowship granted to PST.

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