

RESEARCH ARTICLE

Phenology of nesting marine turtles in the Cayman Islands

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Abstract

Climate-driven shifts in the phenology of species are altering ecosystems worldwide and have been documented in many species, including marine turtles. We present a 26 year analysis of population trends and nesting phenology for green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles in the Cayman Islands and show that although the onset of nesting has advanced for both species (by 0.6 days.yr⁻¹ for green turtles and 0.7 days.yr⁻¹ for loggerhead turtles), the peak of nesting has not significantly changed. The end of the nesting season for green turtles has been delayed by 1.0 days.yr⁻¹, extending the nesting season by 1.6 days.yr⁻¹, whereas no significant change in season duration was observed for loggerhead turtles. Over the study period, sea surface temperature (SST) at the nesting beach has increased significantly, with warmer temperatures correlating with earlier nesting for both species. The number of nests laid each year has also increased annually by 12.4% for green turtles and 8.1% for loggerheads but did not have a significant relationship with any phenological measures (onset, peak, end, or duration of nesting season). Our data suggest that marine turtles in the Cayman Islands are shifting the onset of nesting toward cooler periods outside peak summer months however there was no change to the peak of nesting for either species. Whether this shift mitigates the impacts of rising temperatures on clutch incubation and offspring sex ratios remains unclear.

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Introduction

Under conditions of climate change, species survival depends on their capacity to adapt [1,2]. While short-lived species may evolve rapidly, longer-lived species often rely on phenotypic plasticity or behavioural shifts [3]. For example, many species adjust by altering geographic ranges [4,5] whilst others may change their phenology—the timing of life-cycle events [6]. Such phenological shifts are

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widespread across ecosystems in a wide range of organisms [7–10], with rising temperatures linked to changes in the onset and duration of reproductive events [11–14]. One example of species phenology shifting with rising temperatures is the nesting season of marine turtles [15–17].

Marine turtles are particularly vulnerable to climate change due to the linkage between the thermal environment and critical physiological processes, including temperature-sex-determination [18]. Temperature plays a key role in the development of marine turtle embryos, hatching success and hatchling sex ratios [19]. Higher temperatures lead to female-skewed populations and have also been shown to influence the nesting phenology at locations worldwide [15] (e.g., loggerhead turtles (*Caretta caretta*) in Florida, United States [20], North Cyprus [21] and Brazil [22]; leatherback turtles (*Dermochelys coriacea*) in St. Croix, US Virgin Islands [23]; green turtles (*Chelonia mydas*) in North Cyprus [17] and in Florida [20]). Temperature is also likely to affect reproduction and the phenology of breeding (e.g., through potential cues for migration timing and effects on food availability) and nesting, and a critical issue is whether phenological shifts enable species to adapt to a changing climate [24] by nesting under different environmental conditions [25,26]. The Foraging Site Hypothesis [27] suggests that marine turtles likely use environmental cues at their foraging areas to initiate migration. Nesting phenology may also be influenced by population size or structure [28]. In leatherback turtles in Costa Rica and green turtles in Cyprus, older and/or more experienced individuals tend to arrive earlier to nest and lay more clutches [17,25], and consequently, population demographics might drive earlier and longer lasting nesting seasons [29].

Despite their strong fidelity to nesting sites, marine turtles can adapt to thermal changes across scales – from wide-scale oceanic migrations shaped by regional oceanographic patterns [21], to selecting finer nearshore microhabitats amid fluctuating local temperatures [30] – potentially affecting their energy allocation. These could consequently influence courtship timing [31] and nesting behaviour. Thermal conditions along migratory pathways and in localised inter-nesting areas have the potential to contribute to variations in the timing and length of nesting seasons. The duration of the inter-nesting interval [32,33], the time between two consecutive nesting attempts within a nesting season [34] is also influenced by the thermal environment.

Temperature plays a fundamental role in shaping multiple life-history traits of marine turtles across all life stages. Their metabolic rates, growth rates, and overall energy acquisition are directly linked to the thermal environment [35]. Warmer conditions at foraging grounds can enhance somatic growth and reduce the time to sexual maturity [36], however, warmer oceans often result in diminished primary productivity and prey abundance, which can impose time-lagged effects on the breeding capacity of marine turtles in subsequent years [37]. In the reproductive phase, temperature is a key factor in egg maturation, clutch frequency, and overall fecundity. However, excessive heat stress could also reduce clutch size and egg viability, as prolonged exposure to high temperatures during follicle development may impair reproductive output [38]. These spatial and environmental complexities underscore the challenges in drawing broad conclusions about the effects of climate change on marine turtle nesting patterns from relatively short-term studies [39].

Given the importance of temperatures on marine turtle population dynamics, we examined the nesting phenology in a Caribbean rookery: the tropical beaches of the Cayman Islands, which represent important nesting grounds for loggerhead turtles and green turtles. These populations have both shown signs of recovery following a history of overexploitation followed by long-term conservation efforts by the local Department of Environment [40] and a head-start programme for green turtles by the Cayman Turtle Centre [41]. Despite the two species being morphologically similar, using similar nesting habitats, and displaying analogous migratory and nesting behaviours (as described by [42]), their distinct trophic levels – green turtles, generally feed two or three trophic levels lower in the food chain than loggerhead turtles [43] – suggest that their responses to climate change are unlikely to be the same [44]. In this study, we analysed the temporal nesting patterns of green and loggerhead marine turtles in relationship to sea surface temperature (SST) and extended the previous analysis on population trends by Blumenthal et al., (2021) to allow us to control for the effects of nesting magnitude on phenology. We hypothesise that higher temperatures will mean that turtles receive their cue to migrate earlier in the year and thus arrive earlier at their nesting beaches.

Methods

Nesting data

The Cayman Islands consist of three small, inhabited islands in the Caribbean Sea: Grand Cayman, Little Cayman, and Cayman Brac (Fig 1). Beaches were monitored during the loggerhead and green turtle nesting seasons (April to November) in Grand Cayman from 1999 to 2024 and in Little Cayman and Cayman Brac intermittently from 1998 to 2024, with standardised annual monitoring taking place in Little Cayman from 2014 to 2024 and Cayman Brac from 2012 to 2024 [40]. Following methods by [40,45], nesting beaches were surveyed on foot at least twice weekly throughout the nesting

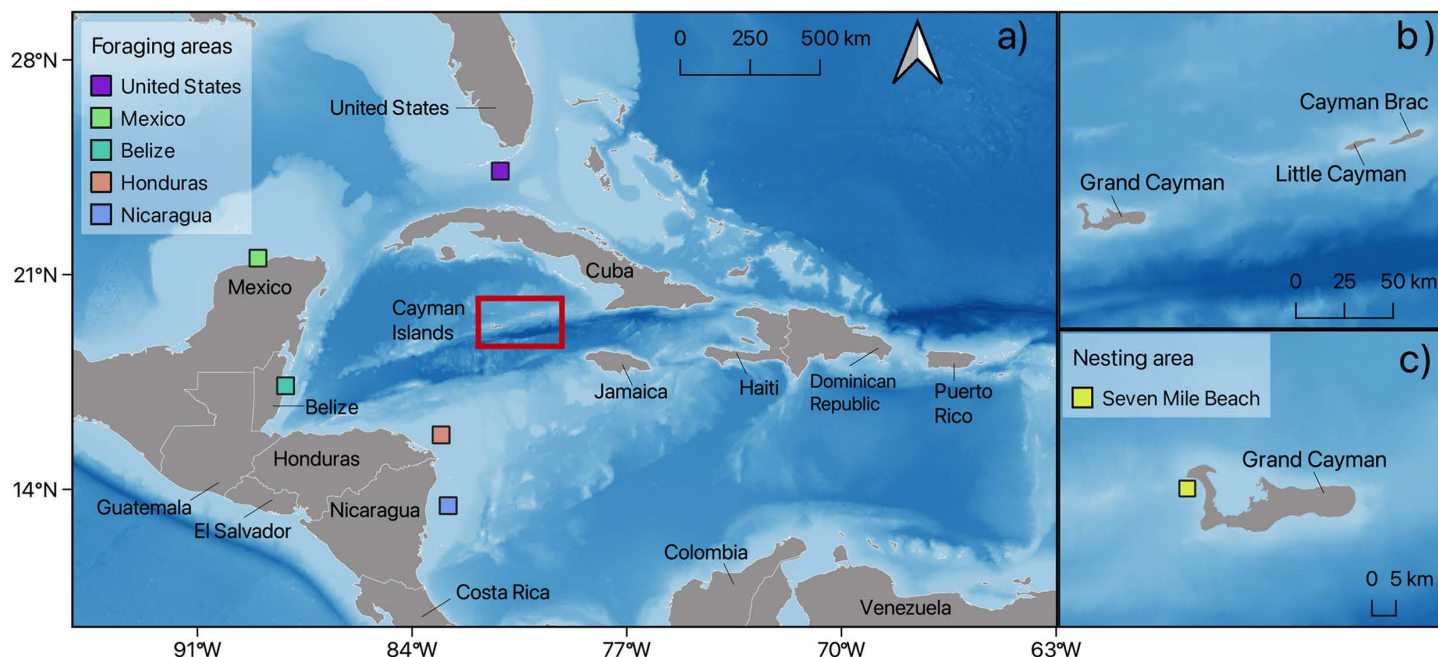


Fig 1. Map of study area and surrounding bathymetry (Global Bathymetric Chart of the Oceans (GEBCO) data) showing a) location of the Cayman Islands within the Caribbean Sea and foraging areas identified by previous satellite tracking [46], b) The three islands that comprise the Cayman Islands: Grand Cayman, Little Cayman and Cayman Brac, c) Grand Cayman showing the location of the sea surface temperature cell (SST) offshore from the nesting beach (Seven Mile Beach). Map produced using QGIS software. Administrative boundaries from OpenDataSoft World Administrative Boundaries dataset, licensed under OGL v3.0.

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season, and many beaches monitored daily. Only confirmed nests, where clutches were located or signs of hatching recorded, were used in nest counts. Nest monitoring was not carried out in Little Cayman in 2020 due to Covid-19 travel restrictions. All fieldwork was conducted by the Cayman Islands Department of Environment (DoE), under the mandate of National Conservation Act section 6 (subsections (g – i)) to “monitor the populations of indigenous or migratory species and identify endangered, threatened, endemic or other species and their critical habitats requiring protection” and “for the purposes of research, collect or obtain samples” of protected species. All research was subject to ethical approval by the University of Exeter Ethics Committee (Application ID: 491773).

Population trends

The trends in the annual number of green turtle nests across the three islands were analysed using generalized additive mixed models (GAMMs) with the ‘*gamm*’ function from the R package ‘*mgcv*’ [47]. A negative binomial distribution was applied to account for overdispersion in the nest counts (i.e., the observed variance in counts exceeding what would be expected under a Poisson distribution, often due to unmodeled heterogeneity such as variable environmental conditions or clustering of nesting events). To account for autocorrelation in the time series data, we tested several autoregressive moving average (ARMA) correlation structures using the *corARMA* function from the ‘*nlme*’ package [48]. The best-fitting model for each island was selected based on the lowest Akaike Information Criterion (AIC) value. The final models included a smooth term for year, with knot selection (*k*) adjusted for each location, and predictions were generated with associated confidence intervals. Model diagnostics were performed using autocorrelation (ACF) and partial autocorrelation (PACF) plots of the residuals to ensure model adequacy.

Determining nesting phenology

We conducted separate phenological analyses for each species. Owing to the shorter time series and lower magnitude of nesting in Little Cayman and Cayman Brac, the phenological analysis was conducted for Grand Cayman only. Due to small sample sizes (number of nests = 1, 18 and 2, respectively), we excluded years 1999–2001 for green turtles. We described the overall nesting phenology using a set of equations based on time series of nest counts [49,50] analysed using the R package ‘*phenology*’ [51]. This model applies a negative-binomial distribution to each ordinal day and incorporates seven parameters to describe nesting phenology: (1) the date of peak nesting, (2) the average number of nests at the peak, (3) the season’s duration, (4) the minimum number of nests laid outside the nesting season, (5) the duration from the season’s start to the peak, (6) the duration from the peak to the end (with the start and end estimated via parameter 4), and (7) a negative-binomial parameter that accounts for dispersion around the mean. The model used all recorded nests to estimate the start and end dates of nesting seasons (parameters 1, 5, and 6), which provided a more accurate representation of nesting phenology than relying on the first and last nesting attempts recorded, which may be sporadic events that do not accurately reflect the underlying seasonal nesting phenology [52]. The analysis assumes that nesting does not plateau at the peak, consistent with the bell-shaped distribution of nest counts observed at the study sites. To minimise constraints on parameters governing nesting phenology (e.g., start, peak, and end), the maximum nesting rate for each season was initially estimated while holding “shape” parameters constant. The maximum value was then fixed, and the shape parameters were estimated in a subsequent step. Parameters were first estimated using maximum likelihood, followed by Bayesian MCMC with the Metropolis–Hastings algorithm and an adaptive proposal distribution over 10,000 iterations, assuming Gaussian priors for parameter distributions. An example of phenology for each year and species on the same island (Grand Cayman) is shown in [S1](#) and [S2 Figs](#). For the overall temporal distribution of nests, we considered the most recent five years of the data (2020–2024) to represent current nesting patterns. However, in Little Cayman, we used data from 2019–2024, excluding 2020 due to a lack of monitoring that year.

Additionally, for comparison between methods and to allow comparison to other studies that use only one method, we used our raw data to conduct the same phenology analysis: with onset of nesting each year determined as the 5th

percentile of lay dates from clutches deposited at the rookery, while the end of the nesting season was defined as the 95th percentile of those dates. Annual metrics were calculated, including the median ordinal day of nesting and the duration of the nesting season, the latter being defined as the number of days between the 5th and 95th percentiles of clutches laid. Results for this analysis are presented in [S2 File](#) and Supporting Figures and Tables: [S8–S10 Figs](#), [S2](#) and [S3 Tables](#). An example of phenology for each year and species on the same island (Grand Cayman) is shown in [S3](#) and [S4 Figs](#).

Predictors of nesting phenology

Daily SST records were obtained from E.U. Copernicus Marine Service Information (<https://doi.org/10.48670/moi-00173>) and consisted of hourly measurements that were averaged to obtain a daily average temperature. They were spatially averaged using the ‘terra’ package [53] for five 0.25° x 0.25° grids: one adjacent to an important green and loggerhead turtle nesting beach in Grand Cayman (Seven Mile Beach) and four broadscale foraging areas, identified from satellite tracking of green turtles: north coast of Mexico, east coast of Belize (Belize/Guatemala feeding area), northeast Honduras, and southern Florida Keys (USA) and loggerhead turtles on the east coast of Nicaragua ([Fig 1](#) and [S5 Fig](#), [46]). We applied a sliding window approach using the R package ‘climwin’ [54] to identify the strongest predictor of nesting onset. The annual nesting onset dates were derived from the models using the R package ‘phenology’ described above. The SST adjacent to the nesting beach between the 1st March – 7th April for loggerhead turtles and the 13th April – 5th May for green turtles was found to be the strongest predictor of nesting onset (see [S1 File](#) for details). Thus, we used the mean temperatures recorded between the mentioned dates as a predictor variable to estimate the effects of sea surface temperature.

We quantified trends in the (1) nesting onset, (2) peak nesting date, (3) end and (4) duration of nesting seasons by performing linear regressions (F-test) against year, SST and magnitude of nesting. To consider the system in an integrative manner, we used generalized linear models (GLMs) with a Gaussian distribution with responses (1) nesting onset, (2) peak nesting date, (3) end, and (4) duration of nesting seasons for each species and SST, total number of nests laid in each year (magnitude), and year as predictors. We applied backward stepwise deletion based on Akaike Information Criterion (AIC) to select the most parsimonious model, retaining only significant predictors ($p < 0.05$). To test our hypothesis that higher SST will mean that turtles receive their cue to migrate earlier in the year and thus arrive earlier at their nesting beaches, we used a correlation test. This test assessed whether temperatures in the months associated with when turtles are likely leaving their foraging habitats correlate with the timing of the nesting season.

Results

Population trends

We estimated that between 1999 and 2024, 4670 green turtle clutches and 3696 loggerhead turtle clutches were laid across the Cayman Islands. The GAM regressions in [Fig 2](#) all showed a significant increasing trend in the annual number of nests for both species on all islands ([S1 Table](#)). The estimated mean annual rate of increase in nesting in Grand Cayman, based on the long-term dataset (1999–2024) was 12.4% for green turtles and 8.1% for loggerhead turtles. For the shorter period 2014–2024, when all three islands were monitored, the rates were 6.5% for green turtles and 2.6% for loggerhead turtles in Grand Cayman, 7.1% for green turtles and 2.1% for loggerhead turtles in Little Cayman, and 13.6% for green turtles and 5.7% for loggerhead turtles in Cayman Brac ([Fig 2](#)). Concurrently, the mean sea surface temperature (SST) has increased significantly over time ($p < 0.01$, $R^2 = 0.34$; [Fig 2c](#)).

Nesting phenology of green turtles

Using the ‘phenology’ package, we found that the nesting season for green turtles in the Cayman Islands starts at the end of May, peaks in August and ends by mid-October ([Fig 3](#) and [S6 Fig](#)). Over the past 23 years (2002–2024) there has

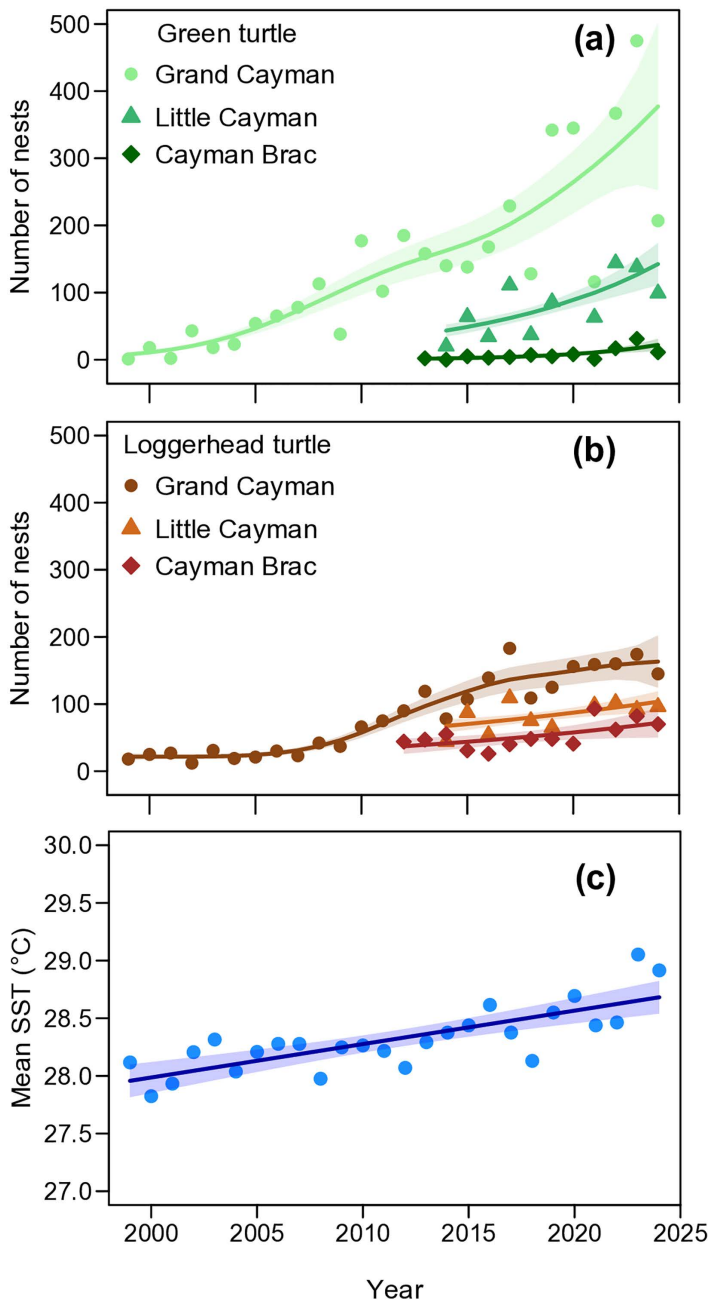


Fig 2. Annual number of green turtle (a) and loggerhead turtle (b) nests in the Cayman Islands, 1999–2024 (4670 green turtle clutches and 3696 loggerhead clutches in total). The annual number of nests in Grand Cayman is shown by filled dots, in Little Cayman by triangles and in Cayman Brac by diamonds. Solid curve: generalised additive model regression; shaded curves: approximate 0.95 pointwise confidence intervals. (c) Mean annual sea surface temperature (SST) recorded off the nesting beach in Grand Cayman, Cayman Islands, from 1999 to 2024. Each blue dot represents a mean annual SST measurement. The dark blue line indicates the overall temperature trend over time, fitted using a linear regression model. The grey shaded area represents the 95% confidence interval around the trendline.

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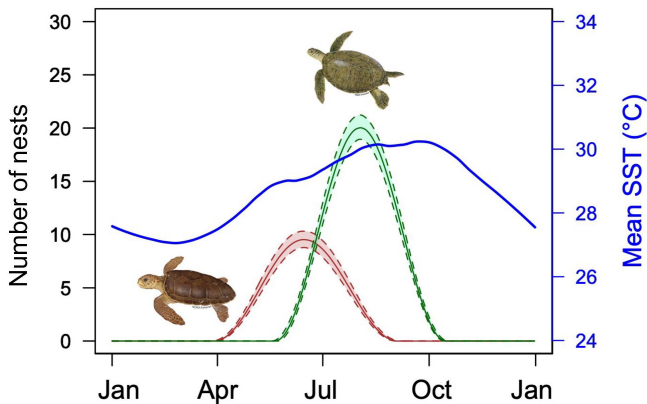


Fig 3. Phenology of green and loggerhead turtle nesting seasons in Grand Cayman from 2020-2024, based on nest counts. Solid lines: quantiles curve based on mcmc. Shaded area: credibility interval polygon based on MCMC. Green turtle shown in green and loggerhead turtle shown in brown. The trend in sea surface temperature during the same period is represented by the blue line.

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been a significant advancement in the onset of nesting at a rate of 0.6 days.yr^{-1} ($p=0.04$, $R^2=0.19$). This rate of advancement represents a total shift of approximately 14 days earlier in the onset of the nesting season. Additionally, a significant trend was observed for the end of the nesting season, which has been delayed by an average of 1.0 days.yr^{-1} ($p=0.04$, $R^2=0.19$). Consequently, the overall duration of the nesting season increased significantly, extending by 1.6 days per year ($p=0.01$, $R^2=0.31$), while the day of peak nesting showed no significant change over the period ($p=0.06$, $R^2=0.16$, Fig 4 and Table 1). SST was significantly related to the onset of the nesting season ($p=0.04$, $R^2=0.19$), duration of the nesting season ($p=0.04$, $R^2=0.19$), and magnitude of nesting ($p<0.01$, $R^2=0.35$), indicating that warmer conditions are associated with earlier onsets, longer durations, and increased nesting activity (Fig 5). SST was not significantly related to the peak of nesting ($p=0.14$, $R^2=0.10$). No significant relationships were found between magnitude of nesting and duration, end, or onset of nesting ($p>0.05$, Table 1 and S7 Fig).

GLMs with stepwise deletion revealed sea surface temperature (SST) significantly influenced nesting onset, but year and magnitude had no effect. For every 1°C increase in April SST, the onset of nesting advanced by 11.3 days. For nesting peak, no predictors were significant, including year, SST, or magnitude. Nesting duration increased significantly over time, while SST and magnitude were not significant. Similarly, nesting end occurred later over time, driven significantly by year, with no significant effects from SST or magnitude in the final model (Table 2).

Nesting phenology of loggerhead turtles

For loggerhead turtles, using the 'phenology' package, we found that the nesting season starts at the beginning of April, peaks in mid-June and ends by the end of August (Fig 3 and S6 Fig). Over the 26-year period (1999–2024), the onset of nesting has significantly advanced at a rate of 0.7 days.yr^{-1} ($p=0.03$, $R^2=0.18$). This rate of advancement represents a total shift of approximately 18 days earlier in the onset of the nesting season. No significant trends were observed for the end of the nesting season ($p=0.43$, $R^2=0.03$), the duration of the nesting season ($p=0.36$, $R^2=0.04$) or the peak of nesting over the period ($p=0.65$, $R^2=0.01$, Fig 4 and Table 1). SST was significantly related to the onset of the nesting season ($p=0.01$, $R^2=0.25$) and magnitude of nesting ($p<0.01$, $R^2=0.30$), indicating that warmer conditions are associated with earlier onsets and increased nesting activity (Fig 5), but SST was not significantly related to the peak of nesting ($p=0.46$, $R^2=0.02$). Additionally, a significant relationship was found between magnitude and onset of nesting ($p=0.03$, $R^2=0.19$) with larger nesting years starting earlier. No significant relationships were found between SST and duration or end of the nesting season, or between magnitude and duration or end of nesting ($p>0.05$, Table 1 and S7 Fig).

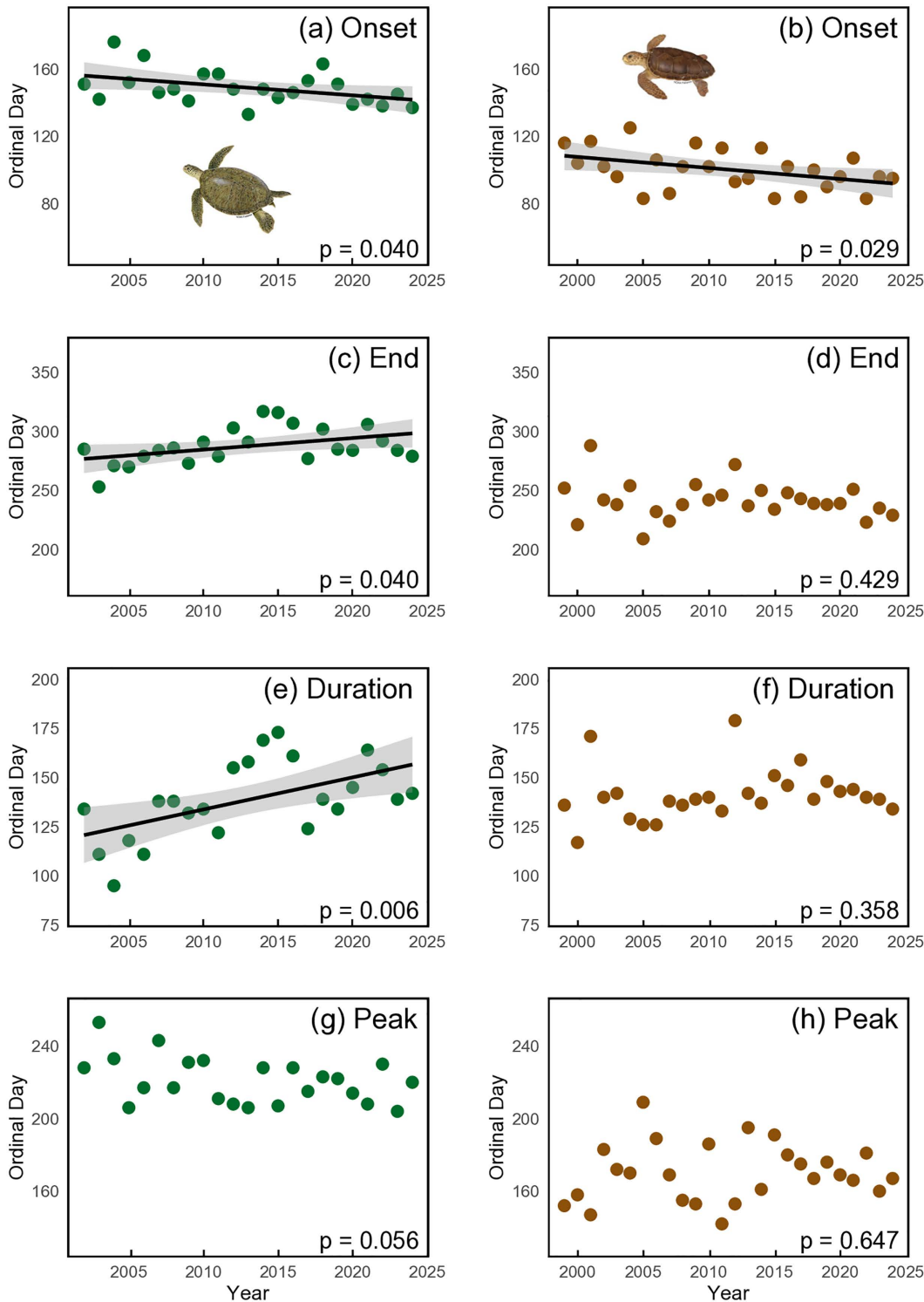


Fig 4. Phenology of green and loggerhead turtle nesting in Grand Cayman rookery. (a, b) nesting onset, (c, d) end of nesting season, (e, f) duration of nesting season and (g, h) peak day of nesting. Black lines in (a, b, e, f): linear regression according to season; shaded areas: 95% CI. Note that the trendline is shown only where linear regression was significant.

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Table 1. Summary of linear regression analysis between nesting parameters and SST for green (2002-2024) and loggerhead turtles (1999-2024) in Grand Cayman, Cayman Islands.

Pair	Green Turtle			Loggerhead		
	F	R ²	p-value	F	R ²	p-value
Year vs.						
Duration	9.52	0.31	0.01	0.88	0.04	0.36
End	4.79	0.19	0.04	0.65	0.03	0.43
Onset	4.77	0.19	0.04	5.36	0.18	0.03
Peak	4.09	0.16	0.06	0.22	0.01	0.65
SST vs.						
Magnitude	11.46	0.35	<0.01	10.40	0.30	<0.01
End	1.69	0.07	0.21	1.25	0.05	0.28
Onset	5.05	0.19	0.04	8.10	0.25	0.01
Duration	5.05	0.19	0.04	0.82	0.03	0.37
Peak	2.31	0.10	0.14	0.57	0.02	0.42
Magnitude vs.						
Duration	2.72	0.12	0.11	2.60	0.10	0.12
End	0.88	0.04	0.36	0.10	<0.01	0.76
Onset	2.98	0.12	0.10	5.48	0.19	0.03
Peak	2.89	0.12	0.10	0.14	0.01	0.71

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GLMs with stepwise deletion revealed sea surface temperature (SST) significantly influenced nesting onset, but year and magnitude had no effect. For every 1°C increase in March SST, the onset of nesting advanced by 13.4 days. For nesting peak, no predictors were significant, including year, or magnitude. Similarly, nesting duration was not significantly affected by magnitude, year, or SST. Nesting end also showed no significant effects of SST, magnitude, or year (Table 2).

Discussion

For marine turtles, shifts in phenology driven by warming conditions may represent the most effective short-term response to cope with climate change [52]. We observed that both marine turtle species nesting in Grand Cayman are advancing the onset of nesting, but only green turtles are increasing the duration of their nesting season, indicating interspecific variation in marine turtle response to increasing temperatures. In addition, we did not observe any shift in the peak nesting season, raising questions about what is driving earlier nesting. We discuss our key findings and provide recommendations for advancing this research to better understand the extent of population recovery, resilience and adaptive potential in response to climate change.

Nesting onset

After accounting for population growth, our analysis revealed significant advancements in the onset of nesting for both species. While some marine turtle populations show shifting nesting peaks [17,21], our study found no such associations. This discrepancy may be related to factors such as latitude and season length, which could influence phenological responses differently in our study region compared to other populations. Notably, the onset of nesting showed a strong negative correlation with SST, reinforcing its role as a key environmental driver of the start of the nesting season. The significant increase in the duration of the nesting season for green turtles could allow this species to maintain similar overall thermal conditions for embryonic development considering the predicted changes in temperature. Marine turtles in many regions predominantly nest during the warmest months of the year, typically aligning with summer or peak seasonal temperatures [52]. An extended nesting season could enable green turtles to experience a broader range of thermal

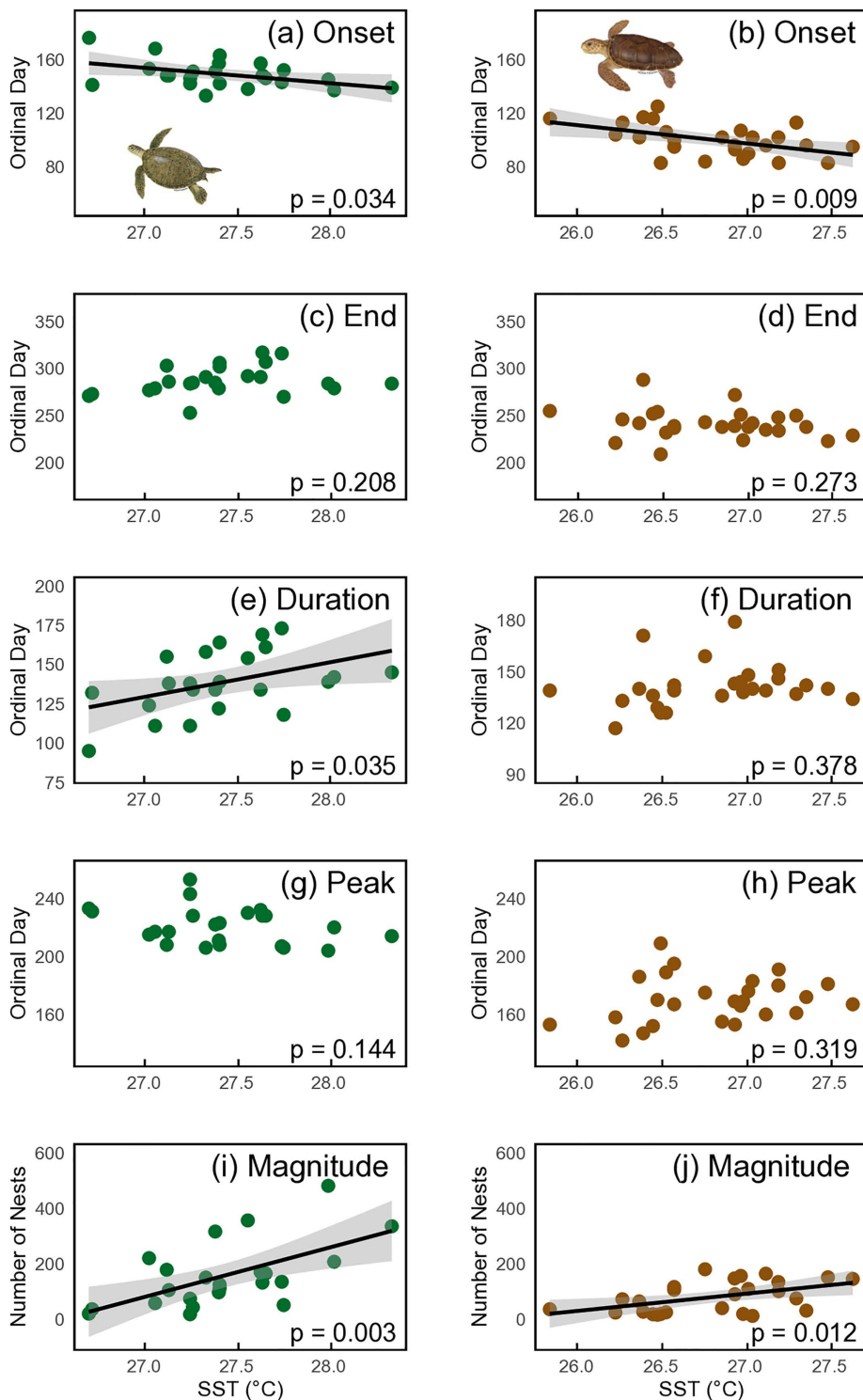


Fig 5. Relationship between the phenological parameters of green and loggerhead turtles nesting in the Grand Cayman rookery and sea surface temperature (SST). (a, b) nesting onset, (c, d) end of nesting season, (e, f) duration of nesting season, (g, h) peak day of nesting and (i, j) nesting magnitude. Black lines in (a, b, e, f): linear regression according to season; shaded areas: 95% CI. Note that the trendline is shown only where linear regression was significant.

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Table 2. Summary of stepwise Generalized Linear Model (GLM) results for predictors of nesting phenology in green and loggerhead turtles in Grand Cayman, Cayman Islands.

Species	Model	Year		SST		Magnitude	
		t-value	p-value	t-value	p-value	t-value	p-value
Green turtle	Onset	-0.95	0.35	-2.25	0.04	0.25	0.81
	Peak	-2.02	0.06	-1.52	0.14	-0.08	0.94
	Duration	3.09	0.01	1.10	0.29	-1.23	0.23
	End	2.19	0.04	1.30	0.21	-1.27	0.22
Loggerhead turtle	Onset	0.11	0.92	-2.85	0.01	-0.56	0.58
	Peak	0.12	0.91	0.76	0.46	-0.13	0.90
	Duration	-1.40	0.18	0.91	0.37	1.92	0.68
	End	-1.07	0.30	-1.12	0.28	1.12	0.28

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conditions, potentially buffering against extreme temperatures. If nesting is spread out over a longer period, some clutches may still develop under cooler conditions even if peak-season temperatures are rising, which could help mitigate the impacts of climate change on embryonic development.

Length of nesting season

While both species appeared to exhibit phenological shifts in response to SST, differences in their responses suggest species-specific adaptations. Green turtles demonstrated a greater extension of the nesting season compared to loggerhead turtles, potentially reflecting differences in their reproductive physiologies or resource use. Additionally, green turtles exhibited a greater increase in nesting over the study period, both in terms of magnitude and rate of increase which in turn may drive increased variation in arrival dates among females. The relationship between SST and nesting numbers was also much stronger in green turtles, suggesting that their reproductive patterns may be more closely linked to temperature fluctuations. For instance, higher SSTs have been associated with shorter inter-nesting intervals, which may enable green turtles to lay more clutches per season [32,55]. These findings are consistent with studies from other regions, such as in Australia, where earlier nesters exhibited higher clutch frequencies [38]. Loggerhead turtles, by contrast, displayed an advance in the onset of the nesting season by approximately 18 days over the study period, but with no significant increase in nesting duration or shift in the end of the season, despite earlier arrivals. This pattern could reflect their lower plasticity in reproductive timing overall, as well as distinct environmental drivers acting on different phenological parameters: Monsinjon et al. [22] found that the onset of nesting in loggerheads is primarily triggered by temperature cues at key foraging sites, whereas nesting duration is more closely tied to population size, allowing for independent responses to SST and demographic factors. As primary consumers feeding on seagrass, which is more directly impacted by environmental fluctuations, green turtles may exhibit earlier responses, such as initiating migration to reproductive areas in response to these changes.

Consistency with previous studies

Our findings are consistent with studies exploring phenological responses of marine turtles to climate change. Monsinjon et al. [56] found that loggerhead turtles in the Mediterranean exhibit significant advancements in nesting onset driven by rising SSTs, suggesting that earlier nesting may mitigate thermal stress on clutches, though it could increase exposure to suboptimal conditions later in the season. This aligns with our observed advancements in nesting onset for both green (0.6 days.yr⁻¹) and loggerhead turtles (0.7 days.yr⁻¹) in the Cayman Islands, although the lack of a shift in peak nesting dates indicates that thermal cues possibly primarily influence the initiation of nesting. Similarly, [16] demonstrated that phenological shifts, such as earlier nesting, may help marine turtles maintain their thermal niche in a warming climate, but

these adjustments may be limited in tropical regions where seasonal temperature variations are less pronounced. This supports our observation that, despite earlier nesting onsets and an extended nesting season for green turtles (1.6 days.yr⁻¹), the absence of significant peak nesting shifts in the Cayman Islands suggests that these populations may not fully counteract the impacts of rising temperatures on clutch incubation and sex ratios. These studies underscore the critical role of SST in driving phenological responses and highlight the challenges tropical populations face in adapting to rapid climate warming.

Role of sea surface temperature in nesting phenology

The sliding window analysis identified SST offshore from the nesting site as the most critical predictor of nesting onset for both species. While SSTs at the foraging areas were also significant, the stronger correlations observed for SSTs recorded weeks prior to nesting suggest a combination of influences on migration and reproductive timing. This supports the Foraging Site Hypothesis [27], indicating that marine turtles likely use environmental cues from their foraging areas to initiate migration, however conditions closer to the nesting site may further regulate the final stages of reproductive readiness and nesting. This underscores the importance of sea surface temperatures, often used as a proxy for the thermal environment experienced by turtles, as both a migratory cue and a physiological regulator, influencing the timing of nesting in ectothermic species such as marine turtles. However, as different individuals and species may forage or rest at various depths, future studies should explore how well surface temperatures correlate with the temperatures turtles encounter subsurface. Weishampel et al. [20] predicted that increases in Caribbean SSTs would result in earlier nesting and a change in duration of the nesting seasons of both green and loggerhead turtles, which, in part, aligns with our results, particularly for green turtles. In fact, SSTs in the Caribbean have been increasing over the past century, with studies reporting rises of 0.5 °C to 1 °C [57]. Our data, showing a 1°C increase from 1999 to 2024, suggest a relatively rapid warming trend in our study period. This warming trend has significant implications for marine ecosystems, including coral reefs and marine turtle nesting sites, which are highly sensitive to temperature changes.

Influence of analytical methods on phenological trends

The method chosen for the phenological analysis influences both the results and the interpretation of phenological trends. The '*phenology*' package, with its Bayesian model tailored for seasonal studies, provides biologically meaningful estimates of onset, peak, and end dates and captures uncertainty through credible intervals. In contrast, raw data percentiles describe general trends but may miss key phenological patterns. For green turtles, the '*phenology*' package identified significant trends in the onset (advancing 0.6 days.yr⁻¹), end (delaying 1.0 days.yr⁻¹), and duration (extending 1.6 days.yr⁻¹) of nesting seasons. In contrast, despite detecting the same advancement in the onset of nesting (0.6 days.yr⁻¹), the raw data approach did not detect a significant trend for the end of the nesting season, with the increase in nesting season duration slightly shorter (0.8 days.yr⁻¹). For loggerhead turtles, the '*phenology*' package detected a 0.7 days.yr⁻¹ advancement in onset, while the raw data showed a slower rate (0.4 days.yr⁻¹) and a significant increase in nesting season duration (0.6 days.yr⁻¹), which the '*phenology*' package did not detect. Overall, in this study, the '*phenology*' package better captured long-term phenological shifts, smoothed through noise, and reduced the risk of overfitting compared to the raw data approach. However, when high-quality count data are available, the necessity of the '*phenology*' package's modelled estimates versus the reliability of raw observations warrants consideration, raising questions about whether smoothed estimates or actual data best reflect true phenological patterns.

Population recovery and demographic shifts

The significant increase in nesting activity observed for both green and loggerhead turtles in the Cayman Islands aligns with previous reports of population recovery in these species at this site [40] and may reflect successful conservation efforts, such as egg and female protection, which have helped to mitigate historical exploitation [40]. A captive breeding

operation contributed to the increase in the Grand Cayman green turtle population [58,59], and loggerhead turtle populations began to increase following the cessation of a legal traditional turtle fishery in 2008, as they were never captive bred. Globally, green marine turtle populations are increasing, many after centuries of direct take [60–62]. Rising temperatures may further accelerate population recovery by increasing the speed of maturation and egg production. While many sites are reporting higher numbers of nesting females, a concurrent reduction in adult body size has been observed [63,64]. This raises questions about whether this reflects the recruitment of a larger number of smaller, younger females into the population or a genuine reduction in size at sexual maturity, which could have implications for their reproductive output and long-term population viability. Such demographic changes could drive variation in nesting phenology, as individual-level plasticity in response to environmental cues, such as advancing nesting dates with rising sea surface temperatures, and population-level shifts, like increasing proportions of less experienced breeders, influence timing and reproductive output [17]. For instance, younger turtles typically nest later in the season [25], so a decreasing mean age of nesters could counteract temperature-driven advancements and help explain the lack of a significant shift in mean peak nesting dates observed in our study. Similar demographic influences on phenology have been documented in leatherback turtles, where multidecadal trends in nesting timing were linked to changes in population age structure [23]. Investigating such individual variation in our population would provide valuable insights, however long-term individual-based data are not yet available.

Conservation implications

Our findings have significant conservation implications, particularly in the context of climate change. As SSTs continue to rise [57], if earlier nesting and longer seasons continue to occur, this will influence hatchling survival and sex ratios. Given the temperature-dependent sex determination in marine turtles and the thermal conditions needed for successful embryonic development, earlier nesting may be adaptive, offering cooler temperatures for some clutches than would be experienced otherwise. Our data suggest that marine turtles in the Cayman Islands may not be shifting nesting to a degree that will mitigate the impact of rising temperatures on clutch incubation and offspring sex ratios, particularly in the tropics where seasonal shifts are not as rapid as at higher latitudes [65] and turtles could show limited phenological responses to warming trends. This highlights the need to understand how individual females respond to rising temperatures in their timing of breeding [17] or whether they produce more clutches to compensate for thermal stress. Irrespective, conservation strategies should prioritise climate adaptation measures, such as protecting nesting beaches, particularly if they may be more male producing than others, and retaining natural vegetation cover at nesting sites [24].

Future research directions

This study represents a critical step in understanding phenological shifts of marine turtles in the Caribbean and underscores the need for long-term, multi-site studies that utilise standardised methodologies to disentangle site-specific factors from global trends. Investigating the interplay between environmental cues at foraging and nesting sites will provide deeper insights into the mechanisms driving these phenological shifts. Furthermore, exploring the broader ecological consequences of these shifts, such as changes in food availability, hatchling sex ratios and nesting success, will enhance our understanding of marine turtle resilience and adaptive capacity in a warming world.

Supporting information

S1 File. Methods.

(DOCX)

S2 File. Results.

(DOCX)

S1 Fig. Seasonality of green sea turtle *Chelonia mydas* nesting activity measured in Grand Cayman in the Cayman Islands during 2002–2024, using the ‘phenology’ package. Central plain line is the fitted Bayesian model, and dashed lines represent the 95% credible interval of the seasonality of nesting.

(DOCX)

S2 Fig. Seasonality of loggerhead sea turtle *Caretta caretta* nesting activity measured in Grand Cayman in the Cayman Islands during 2002–2024, using the ‘phenology’ package. Central plain line is the fitted Bayesian model and dashed lines represent the 95% credible interval of the seasonality of nesting.

(DOCX)

S3 Fig. Seasonality of green sea turtle (*Chelonia mydas*) nesting activity measured in Grand Cayman in the Cayman Islands during 2002–2024, using the raw data. The solid dark green line represents the fitted Generalized Additive Model (GAM) estimating the seasonal trend in nesting activity. Black dots indicate the actual daily nest counts recorded throughout the year. The shaded light green area shows the 95% confidence interval around the GAM fit, while the dashed dark green lines mark the upper and lower boundaries of this confidence interval.

(DOCX)

S4 Fig. Seasonality of loggerhead sea turtle (*Caretta caretta*) nesting activity measured in Grand Cayman in the Cayman Islands during 1999–2024, using raw data. The solid brown line represents the fitted Generalized Additive Model (GAM) estimating the seasonal trend in nesting activity. Black dots indicate the actual daily nest counts recorded throughout the year. The shaded light brown area shows the 95% confidence interval around the GAM fit, while the dashed brown lines mark the upper and lower boundaries of this confidence interval.

(DOCX)

S5 Fig. Foraging and nesting areas for green and loggerhead turtles used for Climwin analysis shown in detail. Foraging areas were previously identified from satellite tracking study (Blumenthal et al. 2006). Map produced using QGIS software. Administrative boundaries from OpenDataSoft World Administrative Boundaries dataset, licensed under OGL v3.0. Surrounding bathymetry from Global Bathymetric Chart of the Oceans (GEBCO) data.

(DOCX)

S6 Fig. Dynamics of green and loggerhead turtle nesting seasons, in Grand Cayman and Cayman Brac between 2020–2024, and in Little Cayman between 2019–2023, based on nest counts. Solid lines: quantiles curve based on MCMC. Shaded area: credibility interval polygon based on MCMC.

(DOCX)

S7 Fig. Relationships between nesting season parameters for *Chelonia mydas* (Cm) and *Caretta caretta* (Cc), using the phenology package. The plots illustrate the following correlations: (1) total number of nests (magnitude) vs. duration, (2) total number of nests (magnitude) vs. onset, (3) total number of nests (magnitude) vs. end, and (4) total number of nests (magnitude) vs. year. Solid lines represent linear regression fits, and text annotations display the Pearson correlation coefficients (r). Shaded areas indicate the 95% confidence interval (CI). Note that trendlines are shown only where linear regression was statistically significant. Titles above the plots specify the relationship depicted in each panel.

(DOCX)

S8 Fig. Phenology of green and loggerhead turtle nesting in Grand Cayman, Cayman Islands rookery, using raw data. (a, b) 5th percentile day of annual nesting onset, (c, d) 95th percentile day of annual nesting, (e, f) Duration of nesting season and (g, h) Annual median day of nesting. Black lines in (a, b, e, f): linear regression according to season; shaded areas: 95% CI. Note that the trendline is shown only where linear regression was significant.

(DOCX)

S9 Fig. Relationship between phenology parameters of green and loggerhead turtle nesting in Grand Cayman, Cayman Islands rookery, and sea surface temperature (SST), using raw data. (a, b) 5th percentile day of annual nesting onset, (c, d) 95th percentile day of annual nesting, (e, f) Duration of nesting season, (g, h) Annual median day of nesting and (i, j) Magnitude of nesting. Black lines in (a, b, e, f): linear regression according to season; shaded areas: 95% CI. Note that the trendline is shown only where linear regression was significant.

(DOCX)

S10 Fig. Relationships between nesting season parameters using raw data for *Chelonia mydas* (Cm) and *Caretta caretta* (Cc). The plots illustrate the following correlations: (1) total number of nests (magnitude) vs. duration, (2) total number of nests (magnitude) vs. onset, (3) total number of nests (magnitude) vs. end, and (4) total number of nests (magnitude) vs. year. Solid lines represent linear regression fits, and text annotations display the Pearson correlation coefficients (r). Shaded areas indicate the 95% confidence interval (CI). Note that trendlines are shown only where linear regression was statistically significant. Titles above the plots specify the relationship depicted in each panel.

(DOCX)

S1 Table. Summary of generalised additive model (GAM) analysis. The table shows the significance of smooth terms in explaining trends in annual nest counts for green turtles and loggerhead turtles across the Cayman Islands: Grand Cayman, Little Cayman, and Cayman Brac.

(DOCX)

S2 Table. Summary of linear regression analysis of nesting season parameters against year using raw data for green (2002–2024) and loggerhead turtles (1999–2024) in Grand Cayman, Cayman Islands.

(DOCX)

S3 Table. Summary of stepwise Generalized Linear Model (GLM) results for predictors of nesting phenology in green and loggerhead turtles in Grand Cayman, Cayman Islands, using raw data.

(DOCX)

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References

1. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 2003;421(6918):37–42. <https://doi.org/10.1038/nature01286> PMID: 12511946
2. Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. The velocity of climate change. *Nature*. 2009;462(7276):1052–5. <https://doi.org/10.1038/nature08649> PMID: 20033047
3. Hulin V, Delmas V, Girondot M, Godfrey MH, Guillon J-M. Temperature-dependent sex determination and global change: are some species at greater risk? *Oecologia*. 2009;160(3):493–506. <https://doi.org/10.1007/s00442-009-1313-1> PMID: 19277719
4. Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, et al. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*. 1999;399(6736):579–83. <https://doi.org/10.1038/21181>
5. Tingley MW, Monahan WB, Beissinger SR, Moritz C. Birds track their Grinnellian niche through a century of climate change. *Proc Natl Acad Sci U S A*. 2009;106 Suppl 2(Suppl 2):19637–43. <https://doi.org/10.1073/pnas.0901562106> PMID: 19805037
6. Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, et al. Ecological responses to recent climate change. *Nature*. 2002;416(6879):389–95. <https://doi.org/10.1038/416389a> PMID: 11919621
7. Crick HQP, Dudley C, Glue DE, Thomson DL. UK birds are laying eggs earlier. *Nature*. 1997;388(6642):526–526. <https://doi.org/10.1038/41453>
8. Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. Fingerprints of global warming on wild animals and plants. *Nature*. 2003;421(6918):57–60. <https://doi.org/10.1038/nature01333> PMID: 12511952
9. Dalleau M, Ciccione S, Mortimer JA, Garnier J, Benhamou S, Bourjea J. Nesting phenology of marine turtles: insights from a regional comparative analysis on green turtle (*Chelonia mydas*). *PLoS ONE*. 2012;7(10):e46920. <https://doi.org/10.1371/journal.pone.0046920>
10. Horton KG, La Sorte FA, Sheldon D, Lin T-Y, Winner K, Bernstein G, et al. Phenology of nocturnal avian migration has shifted at the continental scale. *Nat Clim Chang*. 2019;10(1):63–8. <https://doi.org/10.1038/s41558-019-0648-9>
11. Parmesan C. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*. 2007;13(9):1860–72. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
12. Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, et al. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Globa Change Biol*. 2010;16(12):3304–13. <https://doi.org/10.1111/j.1365-2486.2010.02165.x>
13. Brooks SJ, Self A, Powney GD, Pearse WD, Penn M, Paterson GLJ. The influence of life history traits on the phenological response of British butterflies to climate variability since the late-19th century. *Ecography*. 2016;40(10):1152–65. <https://doi.org/10.1111/ecog.02658>
14. Shipley JR, Twining CW, Taff CC, Vitousek MN, Flack A, Winkler DW. Birds advancing lay dates with warming springs face greater risk of chick mortality. *Proc Natl Acad Sci U S A*. 2020;117(41):25590–4. <https://doi.org/10.1073/pnas.2009864117> PMID: 32989166
15. Neeman N, Robinson NJ, Paladino FV, Spotila JR, O'Connor MP. Phenology shifts in leatherback turtles (*Dermochelys coriacea*) due to changes in sea surface temperature. *J Exp Mar Biol Ecol*. 2015;462:113–20.
16. Laloë J-O, Hays GC. Can a present-day thermal niche be preserved in a warming climate by a shift in phenology? A case study with sea turtles. *R Soc Open Sci*. 2023;10(2):221002. <https://doi.org/10.1098/rsos.221002> PMID: 36778962
17. Rickwood ML, Tucker E, Beton D, Davey S, Godley BJ, Snape RTE, et al. Individual plasticity in response to rising sea temperatures contributes to an advancement in green turtle nesting phenology. *Proc Biol Sci*. 2025;292(2041):20241809. <https://doi.org/10.1098/rspb.2024.1809> PMID: 39968614
18. Yntema CL, Mrosovsky N. Sexual Differentiation in Hatchling Loggerheads (*Caretta caretta*) Incubated at Different Controlled Temperatures. *Herpetologica*. 1980;36(1):33–6.
19. Hays GC, Mazaris AD, Schofield G, Laloë JO. Population viability at extreme sex-ratio skews produced by temperature-dependent sex determination. *Proc R Soc B Biol Sci*. 2017;284(1848):20162576. <https://doi.org/10.1098/rspb.2016.2576>

20. Weishampel J, Bagley D, Ehrhart L, Weishampel A. Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. *Endanger Species Res.* 2010;12(1):41–7.
21. Witt M, Beton D, Davey S, Fuller W, Godley B, Özkan M, et al. Phenological shift mitigates predicted impacts of climate change on sea turtle offspring. *Endanger Species Res.* 2025;56:41–51.
22. Monsinjon J, Lopez M, Lara P, Santos A, Dei Marcovaldi M, Girondot M, et al. Effects of temperature and demography on the phenology of loggerhead sea turtles in Brazil. *Marine Ecol Prog Ser.* 2019;623:209–19.
23. Robinson N, Valentine S, Tomillo P, Saba V, Spotila J, Paladino F. Multidecadal trends in the nesting phenology of Pacific and Atlantic leatherback turtles are associated with population demography. *Endang Species Res.* 2014;24(3):197–206. <https://doi.org/10.3354/esr00604>
24. Fuentes MMPB, Pike DA, Dimatteo A, Wallace BP. Resilience of marine turtle regional management units to climate change. *Glob Chang Biol.* 2013;19(5):1399–406. <https://doi.org/10.1111/gcb.12138> PMID: 23505145
25. Santidrián Tomillo P, Suss JS, Wallace BP, Magrini KD, Blanco G, Paladino FV, et al. Influence of emergence success on the annual reproductive output of leatherback turtles. *Mar Biol.* 2009;156(10):2021–31.
26. Valverde R, Wingard S, Gómez F, Tordoir M, Orrego C. Field lethal incubation temperature of olive ridley sea turtle *Lepidochelys olivacea* embryos at a mass nesting rookery. *Endang Species Res.* 2010;12(1):77–86. <https://doi.org/10.3354/esr00296>
27. Mazaris AD, Kallimanis AS, Sgardelis SP, Pantis JD. Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. *J Exp Mar Biol Ecol.* 2008;367(2):219–26.
28. Votier S, Hatchwell B, Mears M, Birkhead T. Changes in the timing of egg-laying of a colonial seabird in relation to population size and environmental conditions. *Mar Ecol Prog Ser.* 2009;393:225–33.
29. Ezard THG, Becker PH, Coulson T. Correlations between age, phenotype, and individual contribution to population growth in common terns. *Ecology.* 2007 Oct;88(10):2496–504.
30. Schofield G, Bishop CM, Katselidis KA, Dimopoulos P, Pantis JD, Hays GC. Microhabitat selection by sea turtles in a dynamic thermal marine environment. *J Anim Ecol.* 2009;78(1):14–21. <https://doi.org/10.1111/j.1365-2656.2008.01454.x> PMID: 18699794
31. Hamann M, Limpus C, Owens D. Reproductive cycles of males and females. In: *The biology of sea turtles (CRC marine biology series; vol. II)*. Boca Raton (Fla.): CRC press; 2003. p. 135–61.
32. Sato K, Matsuzawa Y, Tanaka H, Bando T, Minamikawa S, Sakamoto W, et al. Internesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are affected by temperature. *Can J Zool.* 1998;76(9):1651–62.
33. Robinson NJ, Sanfèlix MM, Blanco GS, Clyde-Brockway C, Hill JE, Paladino FV, et al. Effect of water temperature on the duration of the internesting interval across sea turtle species. *J Therm Biol.* 2022;110:103342. <https://doi.org/10.1016/j.jtherbio.2022.103342> PMID: 36462853
34. Alvarado J, Murphy TM. Nesting periodicity and internesting behaviour. In: *Research and Management Techniques for the Conservation of Sea Turtles*. 1990.
35. Wallace BP, Lewison RL, McDonald SL, McDonald RK, Kot CY, Kelez S, et al. Global patterns of marine turtle bycatch. *Conserv Lett.* 2010;3(3):131–42.
36. Bjørndal K, Bolten A, Chaloupka M. Green turtle somatic growth dynamics: distributional regression reveals effects of differential emigration. *Mar Ecol Prog Ser.* 2019;616:185–95.
37. Chaloupka M, Kamezaki N, Limpus C. Is climate change affecting the population dynamics of the endangered Pacific loggerhead sea turtle? *J Exp Mar Biol Ecol.* 2008;356(1–2):136–43.
38. Limpus C, Miller J, Parmenter C, Limpus D. The green turtle, *Chelonia mydas*, population of Raine Island and the northern Great Barrier Reef: 1843–2001. *Mem Qld Mus.* 2003;49(1):349–440.
39. Hawkes L, Broderick A, Godfrey M, Godley B. Climate change and marine turtles. *Endang Species Res.* 2009;7:137–54. <https://doi.org/10.3354/esr00198>
40. Blumenthal JM, Hardwick JL, Austin TJ, Broderick AC, Chin P, Collyer L, et al. Cayman Islands Sea Turtle Nesting Population Increases Over 22 Years of Monitoring. *Front Mar Sci.* 2021;8:663856. <https://doi.org/10.3389/fmars.2021.663856>
41. Barbanti A, Martin C, Blumenthal JM, Boyle J, Broderick AC, Collyer L, et al. How many came home? Evaluating ex situ conservation of green turtles in the Cayman Islands. *Mol Ecol.* 2019;28(7):1637–51. <https://doi.org/10.1111/mec.15017> PMID: 30636347
42. Pike DA. Do Green Turtles Modify Their Nesting Seasons in Response to Environmental Temperatures? *Chelonian Conserv Biol.* 2009;8(1):43–7. <https://doi.org/10.2744/ccb-0726.1>
43. Godley B, Thompson D, Waldron S, Furness R. The trophic status of marine turtles as determined by stable isotope analysis. *Mar Ecol Prog Ser.* 1998;166:277–84.
44. Edwards M, Richardson AJ. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature.* 2004;430(7002):881–4. <https://doi.org/10.1038/nature02808> PMID: 15318219
45. Bell CD, Solomon JL, Blumenthal JM, Austin TJ, Ebanks-Petrie G, Broderick AC, Godley BJ. Monitoring and conservation of critically reduced marine turtle nesting populations: lessons from the Cayman Islands. *Anim Conserv.* 2007;10(1):39–47.

46. Blumenthal J, Solomon J, Bell C, Austin T, Ebanks-Petrie G, Coyne M, et al. Satellite tracking highlights the need for international cooperation in marine turtle management. *Endang Species Res.* 2006;2:51–61. <https://doi.org/10.3354/esr002051>
47. Wood S. mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation [Internet]. 2000 [cited 2025 June 24]. p. 1.9–3. Available from: <https://CRAN.R-project.org/package=mgcv>
48. Pinheiro J, Bates D, R Core Team. nlme: Linear and Nonlinear Mixed Effects Models [Internet]. 1999 [cited 2025 June 24]. p. 3.1–168. Available from: <https://CRAN.R-project.org/package=nlme>
49. Girondot M. Estimating density of animals during migratory waves: a new model applied to marine turtles at nesting sites. *Endang Species Res.* 2010;12(2):95–105. <https://doi.org/10.3354/esr00292>
50. Girondot M. Optimizing sampling design to infer the number of marine turtles nesting on low and high density sea turtle rookeries using convolution of negative binomial distribution. *Ecol Indic.* 2017;81:83–9.
51. Girondot M. phenology: Tools to Manage a Parametric Function that Describes Phenology and More [Internet]. 2012 [cited 2025 June 24]. p. 10.3. Available from: <https://CRAN.R-project.org/package=phenology>
52. Fuentes MMPB, Santos AJB, Abreu-Grobois A, Briseño-Dueñas R, Al-Khayat J, Hamza S, et al. Adaptation of sea turtles to climate warming: Will phenological responses be sufficient to counteract changes in reproductive output? *Glob Chang Biol.* 2024;30(1):e16991. <https://doi.org/10.1111/gcb.16991> PMID: 37905464
53. Hijmans RJ. terra: Spatial Data Analysis [Internet]. 2020 [cited 2025 June 24]. p. 1.8–54. Available from: <https://CRAN.R-project.org/package=terra>
54. Bailey LD, van de Pol M. climwin: An R Toolbox for Climate Window Analysis. *PLoS One.* 2016;11(12):e0167980. <https://doi.org/10.1371/journal.pone.0167980> PMID: 27973534
55. Hays GC, Broderick AC, Glen F, Godley BJ, Houghton JDR, Metcalfe JD. Water temperature and internesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. *J Therm Biol.* 2002;27(5):429–32.
56. Monsinjon JR, Wyneken J, Rusenko K, López-Mendilaharsu M, Lara P, Santos A, et al. The climatic debt of loggerhead sea turtle populations in a warming world. *Ecol Indic.* 2019;107:105657.
57. Bove CB, Mudge L, Bruno JF. A century of warming on Caribbean reefs. *PLOS Clim.* 2022;1(3):e0000002.
58. Bell CDL, Parsons J, Austin TJ, Broderick AC, Ebanks-Petrie G, Godley BJ. Some of them came home: the Cayman Turtle Farm headstarting project for the green turtle *Chelonia mydas*. *Oryx.* 2005;39(2):137–48. <https://doi.org/10.1017/s0030605305000372>
59. Barbanti A, Blumenthal JM, Broderick AC, Godley BJ, Prat-Varela A, Turmo M, et al. The architecture of assisted colonisation in sea turtles: building new populations in a biodiversity crisis. *Nat Commun.* 2022;13(1):1580. <https://doi.org/10.1038/s41467-022-29232-5> PMID: 35332166
60. Weber SB, Weber N, Ellick J, Avery A, Frauenstein R, Godley BJ, et al. Recovery of the South Atlantic's largest green turtle nesting population. *Biodivers Conserv.* 2014;23(12).
61. Mazaris AD, Schofield G, Gkazinou C, Almpnidou V, Hays GC. Global sea turtle conservation successes. *Sci Adv.* 2017;3(9):e1600730. <https://doi.org/10.1126/sciadv.1600730> PMID: 28948215
62. Restrepo J, Webster E, Ramos I, Valverde R. Recent decline of green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica. *Endanger Species Res.* 2023;51:59–72.
63. Hays GC, Taxonera A, Renom B, Fairweather K, Lopes A, Cozens J, et al. Changes in mean body size in an expanding population of a threatened species. *Proc R Soc B Biol Sci.* 2022;289(1976):20220696. <https://doi.org/10.1098/rspb.2022.0696>
64. Hays GC, Rusli MU, Booth D, Laloë J-O. Global Decline in the Size of Sea Turtles. *Glob Chang Biol.* 2025;31(5):e70225. <https://doi.org/10.1111/gcb.70225> PMID: 40365694
65. Mazaris AD, Kallimanis AS, Pantis JD, Hays GC. Phenological response of sea turtles to environmental variation across a species' northern range. *Proc Biol Sci.* 2013;280(1751):20122397. <https://doi.org/10.1098/rspb.2012.2397> PMID: 23193130