

# Empirical evidence for the extent of spatial and temporal thermal variation on sea turtle nesting beaches

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## ABSTRACT

Recording sand temperatures has become routine at many sea turtle nesting sites across the world given the impacts of incubation temperatures on hatchling sex ratios. However, the extent of thermal variability found at a nesting site has previously received little attention. Here we examine empirical sand temperature records across five atolls extending 250 km in the Chagos archipelago, Indian Ocean, between October 2012 and July 2023 and quantify the extent of spatial and temporal thermal variability. Our results suggest that sand temperatures at our study site vary seasonally and inter-annually, between beaches in the archipelago, and within beaches in different nesting habitats. The biggest drivers of thermal variability were seasonal and inter-annual differences, which modulated sand temperatures by up to 3.00 °C and 1.03 °C, respectively. Intra-beach and inter-beach variability further modulated temperatures by up to 0.56 °C and 0.85 °C, respectively. In addition, mean monthly sand temperatures were relatively low, suggesting that hatchling sex ratios are fairly balanced. The wide range of sand temperatures recorded at this nesting site suggests that it is likely both male-biased and female-biased clutches are produced during the nesting season. Quantifying thermal variability from a long-term sand temperature time series offers valuable insight into a population with temperature-dependent sex determination and, when possible, should be considered when modelling temperature impacts on hatchling sex ratios.

## 1. Introduction

Sea turtles are a widely studied taxon that exhibit temperature-dependent sex determination (TSD), with females being produced at high incubation temperatures. Since the range of temperatures that produce both sexes is relatively narrow (Mrosovsky and Pieau, 1991), there are concerns that climate warming is raising incubation temperatures around the world and so biasing hatchling sex ratios towards females (Santidrián Tomillo and Spotila, 2020). Heightening this concern is the fact that highly female-biased hatchling sex ratios are already being observed around the world (Hays et al., 2014). A recent evaluation by researchers and managers in the Mediterranean concluded that climate change has the greatest impact on hatchling sex ratios (Mazaris et al., 2023). In light of these concerns, it has become routine to record sand temperatures at sea turtle nesting sites (e.g., Fuentes et al., 2010; Bentley et al., 2020) and gauge whether males are still being produced using theoretical models (Fuentes et al., 2017).

There are several factors that can influence incubation temperatures at a nesting site, which in turn can lead to a range of temperatures that

produce both sexes. First, within a nesting beach, the position where the clutch is laid can impact incubation temperature. For example, in French Polynesia the high abundance of tall vegetation at the back of the beach front provides shade that has the potential to cool incubating nests (Laloë et al., 2020). Similarly, shading due to trees fringing the beach decreased nest temperatures at the Mon Repos sea turtle rookery in eastern Australia (Wood et al., 2014). So, clutches that are laid near or within the vegetation incubate at temperatures lower than those laid in the open beach. Second, differences in abiotic factors between beaches can drive differences in incubation temperatures. For example, sand albedo was shown to be a main driver of incubation temperatures on two nesting beaches in Ascension Island, with a dark beach being >4 °C warmer than a light beach (Hays et al., 1995). Similarly, beach orientation affects temperature, and a windward facing Caribbean beach was almost 2 °C cooler than a leeward facing beach just 1 km away (Esteban et al., 2018). Third, seasonal variations in temperatures can lead to different incubation conditions throughout the nesting season. For example, low temperatures at the start and end of the loggerhead turtle (*Caretta caretta*) nesting season in the eastern USA were conducive to

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male production, while higher temperatures in the middle of the nesting season led to the production of females (Mrosovsky et al., 1984). Fourth, nest depth can influence incubation temperatures as findings from olive ridley nesting beaches in Guatemala showed lower sand temperatures at 50 cm depth compared to 30 cm depth (Ariano-Sánchez et al., 2023). Finally, differences in annual temperatures can also be a source of thermal variability at a site. For example, years that are exceptionally warm or cold can lead to the production of a cohort of mainly one sex for one nesting season (Hays et al., 2021).

The potential impacts of climate change, including rising air temperatures and the associated more intense and frequent rainfall, can influence sand temperatures. For example, increased air temperature will lead to rising sand temperatures, ultimately raising incubation temperatures and increasing the number of female hatchlings being produced (Laloë et al., 2016). Not only do rising temperatures impact sex ratios but if incubation temperatures exceed  $\sim 35^\circ\text{C}$ , successful embryonic development will not occur (Ackerman, 1997). On the other hand, increased and intense rainfall events can have an apparent cooling effect on sand and nest temperatures, that can fall in the range of male-producing incubation temperatures (Staines et al., 2020). However, increased precipitation may lead to higher clutch mortality if incubation temperatures fall below the lower thermal range of successful embryonic development ( $< \sim 27^\circ\text{C}$ ; Ackerman, 1997) or if intense rain and storms cause nest flooding.

Given the importance of incubation temperatures on sea turtle population dynamics, here we examine a decade of empirical sand temperatures recorded on nesting beaches in the Chagos Archipelago. We quantify the extent of thermal variability found within beaches, between beaches, within nesting seasons, and between years. In this way we inform on the factors that influence incubation temperatures at sea

turtle nesting sites and quantify the range of incubation temperatures experienced at this key nesting site. This work uncovers where the capacity for thermal variation lies not only for our study site, but likely also for other sea turtle nesting beaches across the world, and offers the possibility to consider thermal variability in a more informed way when modelling the impacts of incubation temperatures on hatchling production.

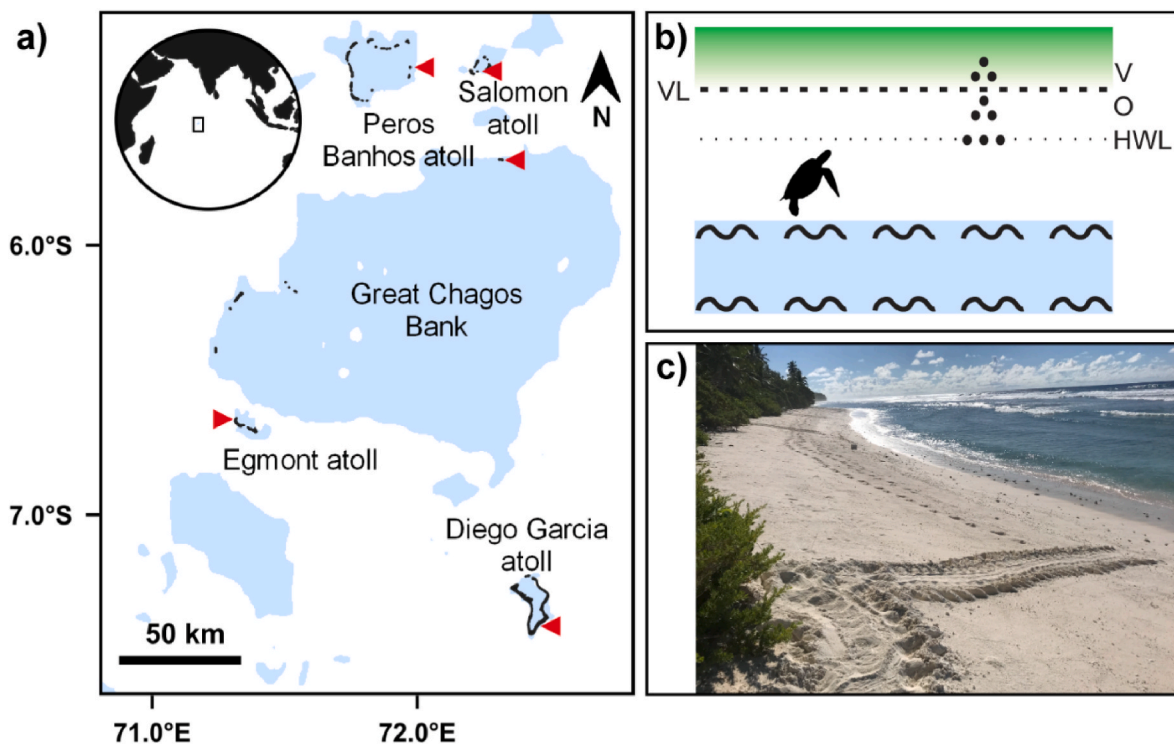
## 2. Methods

### 2.1. Field site

The Chagos Archipelago provides nesting beaches for both hawksbill (*Eretmochelys imbricata*) and green (*Chelonia mydas*) turtles and consists of five atolls comprising submerged banks and islands (Sheppard et al., 2012).

This study was conducted on five islands across all five islanded atolls in the archipelago (Fig. 1a): Diego Garcia (Diego Garcia atoll), Nelson's Island (Great Chagos Bank), Ile des Rats (Egmont atoll), Petite Ile Coquillage (Peros Banhos atoll), and Ile Jacobin (Salomon atoll). All islands have light-coloured beaches. Nesting beaches are narrow and bordered with a littoral hedge of shrub *Scaevola taccada* (Indo-Pacific native), *Suriana maritima* and trees including heliotrope, *Argusia argentea*, as well as scattered coconut palms, *Cocos nucifera* (Fig. 1c). Nest locations are mainly located under vegetation (90 %) and consequently subjected to partial or heavy shading (Stokes et al., 2023). However, some nests are also located in the open beach and receive little shading (Esteban et al., 2016; Stokes et al., 2023).

We recorded sand temperatures at sites known to be important nesting areas, as indicated by historic nesting activity (i.e., presence of



**Fig. 1.** a) The Chagos Archipelago. Islands where sand temperature was recorded are indicated by red triangles which span across all five atolls: Diego Garcia (Diego Garcia), Egmont (Ile des Rats), Great Chagos Bank (Nelson's Island), Peros Banhos (Petite Ile Coquillage) and Salomon (Ile Jacobin). The inset map shows the Chagos Archipelago (black rectangle) in relation to the wider Indian Ocean. b) Schematic showing the temperature logger survey design. Black filled circles represent where the temperature loggers were deployed at 30 cm, 50 cm and 70 cm depth within three nesting habitats: vegetation (V), in the open beach (O) and at the high water line (HWL; dotted line), which is typically less than a meter from the vegetation line. The dashed line represents the vegetation line (VL). Green shading indicates the decrease in vegetation cover and shading closer to the vegetation line. c) Nesting beach on Diego Garcia showing the available open beach in front of the vegetation and the vegetation line. A typical green turtle track is seen in the foreground and two more are seen in the distance. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

old body pits along the site; Esteban et al., 2016). To fully represent the extent of nest sites available to turtles and temperatures therein, we recorded temperatures along the beach in different habitats (e.g., in the open beach or in the vegetation) where turtles were observed to nest and at different depths. We collected sand temperature data using buried temperature loggers deployed across 11 years, to examine temporal, inter- and intra-beach thermal variability.

## 2.2. Deployment of long-term temperature loggers

Sand temperature was recorded using temperature loggers (Tinytag Plus 2 model TGP-4017, Gemini Data Loggers, UK, dimensions 34 x 51 x 80 mm and weighing 110 g, accurate to less than 0.5 °C) buried in the sand at nest depths on Diego Garcia (2.8 km Index Beach), Nelson's Island, Ile des Rats, Ile Jacobin, and Petite Ile Coquillage (Fig. 1a). When burying loggers, sand was excavated to the chosen depth using a sand core and then the same sand was replaced back on top of the logger. This process minimises the impact of logger deployment to the natural conditions (see full methods in Esteban et al., 2016). A total of 132 loggers were buried between October 2012 and July 2023 over the course of 9 research expeditions. Loggers were deployed at 30 cm, 50 cm, and 70 cm along the beach and in three different nesting habitats (i.e., in the vegetation, in the open beach and at the spring high water line (HWL), which is typically less than a meter from the vegetation). Loggers were only deployed at the spring HWL between 2012 and 2014. Loggers buried in the same nesting habitat but at different depths were 50 cm apart and buried in a line along the HWL and at points of a triangle (vegetation and open beach). In 2012, at all sites partially shaded in vegetation above the spring high water line one logger was buried at 80 cm to record sand temperatures near the maximum green turtle nest depth. Depths were initially chosen based on the range of nest depth recorded for hawksbills (30–45 cm; Hitchins et al., 2004; 45–70 cm; Mortimer & Day, 1999) and green turtles (70–85 cm; Fuentes et al., 2010). To check depth selection criteria, nest depths (from the surface to the top and bottom of nest chamber) were recorded during green turtle nest excavations in 2022. From nest excavations in 2022 we found nest depth to the top of the chamber ranged from 23 to 65 cm (mean = 50 cm, SD = 13, n = 16) and depth to the bottom of the chamber ranged from 33 to 82 cm (mean = 63, SD = 14, n = 16). Loggers were set to record every 4 h, except for loggers buried in 2019 and 2022 which were set to record every 1 h in order to examine diel thermal cycles in more detail. When processing the temperature data, the first 12 h of recordings were disregarded from analysis to remove potential thermal fluctuations due to logger deployment.

## 2.3. Statistical analyses

We used the long-term sand temperature records (i.e., data recorded between October 2012 and July 2023) to measure inter-annual, seasonal, inter-beach and intra-beach thermal variability. To describe seasonal thermal variation, we calculated mean monthly sand temperatures for each logger, excluding months for which any number of days of data were missing. To examine inter-annual thermal variation, we calculated mean annual sand temperatures from the aforementioned mean monthly sand temperatures. To study the relationship between sand temperature, island (i.e., Diego Garcia vs Nelson's Island vs Ile des Rats vs Ile Jacobin vs Petite Ile Coquillage), habitat (i.e., HWL vs open vs shaded), depth (i.e., 30 cm vs 50 cm vs 70 cm, vs 80 cm), year (i.e., 2012 to 2023) and month (i.e., January to December), we used generalized additive models (GAMs). We used the restricted maximum likelihood method to estimate smoothing parameters and assumed a Gaussian error distribution. Model convergence was verified and patterns in model residuals were checked using both diagnostic statistics (e.g., number of basis functions used for each smooth and estimated degrees of freedoms) and diagnostics plots (e.g., Q-Q plots and histograms). Additionally, we checked whether a smooth term should be included to the GAM by examining partial effects

plots for each variable. Finally, to examine the quality of our model, we measured concurvity in model variables, i.e., we checked that no variables were smooth curves of other variables. These analyses were done in R v. 4.4.1 and GAMs were implemented using the *mgcv* package.

We examined diel thermal variation using the long-term temperature loggers that recorded data every hour. In this subset of data, we had sand temperatures from 16 loggers that were buried at 30, 50, or 70 cm in the open habitat or in the vegetated habitat. For each day and each logger, we calculated the difference between the maximum daily temperature and the minimum daily temperature. We then calculated the mean of those differences, which gives an indication of the average diel thermal variation recorded by each logger and performed a two-way ANOVA to examine the effect of depth and habitat on sand temperature.

## 3. Results

Of the 132 temperature loggers deployed between 2012 and 2023, 18 are currently still active on the beach. As of July 2023, 90 loggers were recovered and 24 were lost. Of these loggers five were broken and recorded no data, two loggers were removed from the analysis due to beach erosion (e.g., loggers were brought to the surface and so did not record at the planned depth). This study examines sand temperatures for a total of 83 loggers. The longest period of data recorded by a single logger was 1465 days (mean = 548 days, SD = 223.0 days, n = 83 loggers). Across all loggers, a total of 36,689 days of sand temperature data were obtained (see published dataset, Stokes et al., 2024).

### 3.1. Temporal thermal variation

Results from the GAM suggest island, habitat, depth, year and month had an impact on sand temperatures (total deviance explained = 41.9%). The model obtained full convergence after 9 iterations. Visual observation of the residual plots suggested that model assumptions were met. We did not detect any obvious concurvity between variables.

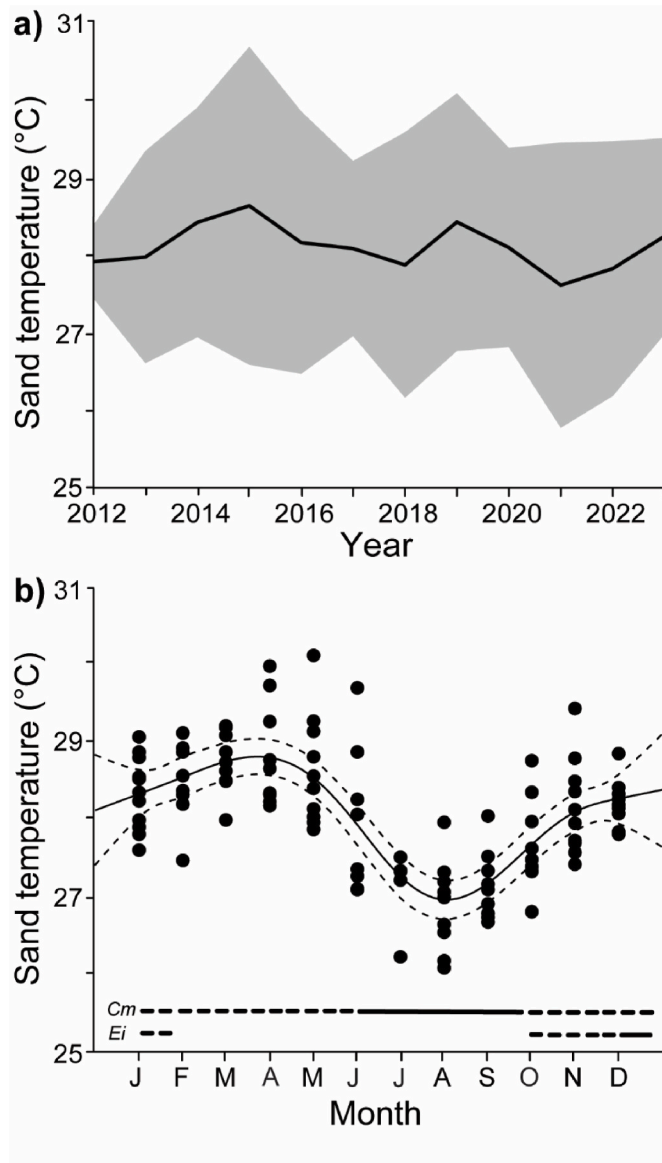
Inter-annual thermal variation was apparent in our sand temperature time series (approximate significance of the GAM smooth:  $F = 404.81$ ,  $edf = 7.0$ ,  $p < 0.05$ ; Fig. 2a). We recorded the coolest sand temperatures in 2021 (mean annual sand temperature = 27.60 °C) and the warmest ones in 2015 (mean annual sand temperature = 28.62 °C).

In addition to inter-annual variation, seasonal variation was clearly evident in our time series (approximate significance of the GAM smooth:  $F = 17.75$ ,  $edf = 5.9$ ,  $p < 0.05$ ), with sand temperatures increasing in the austral spring and summer and decreasing during the austral autumn and winter (Fig. 2b). Mean monthly sand temperatures were highest during March and April (mean = 28.77 °C, SD = 0.52 °C, n = 11 years), and lowest during August and September (mean = 27.02 °C, SD = 0.52 °C, n = 11 years). The maximum difference between the warmest month and the coolest month of a single year in our study was 3.00 °C. Across all years, the mean difference between the warmest month and the coolest month was 1.93 °C (SD = 0.48 °C, n = 11 years).

Diel cycles were also clearly visible in our data (Fig. 3). The range of daily temperatures (i.e., the maximum sand temperature - the minimum sand temperature recorded in one day) was generally larger at shallower depth ( $F_{1,13} = 3.681$ ,  $p > 0.05$ , n = 16 loggers). The mean daily range of sand temperatures was 0.6 °C (SD = 0.4 °C) at a depth of 30 cm, whereas it was 0.2 °C (SD = 0.1 °C) and 0.3 °C (SD = 0.3 °C) at depths of 50 cm and 70 cm, respectively. The range of daily temperatures was also larger in the open habitat (mean = 0.5 °C, SD = 0.4 °C) compared to the vegetated habitat (mean = 0.2 °C, SD = 0.1 °C;  $F_{1,13} = 3.914$ ,  $p > 0.05$ , n = 16 loggers).

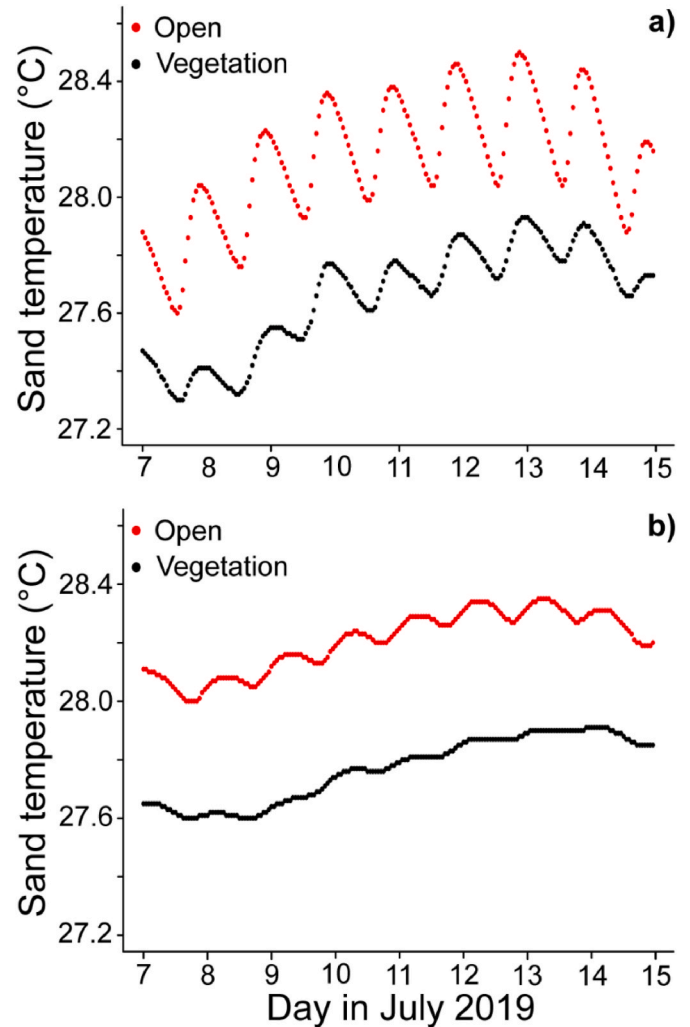
### 3.2. Inter-beach and intra-beach thermal variation

Sand temperatures were different between islands of the archipelago (t-value = 16.17,  $p < 0.05$ ), with the highest sand temperatures found on Ile des Rats and the lowest ones found on Petit Ile Coquillage. The



**Fig. 2.** a) Inter-annual variation in sand temperatures between 2012 and 2023 across the Chagos Archipelago. Sand temperature variation is shown between and within years. The solid line represents the mean sand temperature for each year and the grey shaded area represents the 95% confidence interval in where an individual temperature might lie. The warmest sand temperatures were recorded in 2015 and the coolest sand temperatures recorded in 2021. b) Seasonal variations in mean monthly sand temperatures between 2012 and 2023 across the Chagos Archipelago. Sand temperature showed seasonal cycles, with temperatures typically increasing between September and March and decreasing between April and August (approximate significance of the GAM smooth:  $F = 17.75$ ,  $edf = 5.9$ ,  $p < 0.05$ ). The solid line is the smoothing spline fitted using a GAM and the dashed lines represent the 95% confidence interval for the fitted line. Each point represents the mean monthly temperature recorded by all loggers in that year. Hawksbill (*Ei*) nesting season (indicated by the dashed horizontal line) occurs between October and February with a peak in December (horizontal line). Green sea turtles (*Cm*) nest year-round (dashed horizontal line) with a peak around austral winter (June to October; continuous horizontal line).

difference between sand temperatures found on these two islands was  $0.85\text{ }^{\circ}\text{C}$  ( $SE = 0.07\text{ }^{\circ}\text{C}$ ; Table 1). We also recorded different temperatures in the different nesting habitats (i.e., HWL vs open vs shaded;  $t$ -value =  $35.74$ ,  $p < 0.05$ ): lowest sand temperatures were recorded at the spring HWL and highest temperatures were recorded in the open, with the



**Fig. 3.** Diel variation patterns at two nesting habitats (vegetation and open) on the nesting beach in Diego Garcia, Chagos Archipelago. A point shows raw temperature data on the hour (starting at midnight) between July 07, 2019 and July 15, 2019 from one single logger in each habitat buried at a) 30 cm and b) 50 cm depth.

**Table 1**

Sources and extent of thermal variability recorded in sand temperature between October 2012 and July 2023. Values given in column “Extent of thermal variability” are extracted from the output of the GAM. The extent of inter-annual thermal variability is measured as the mean difference between the warmest year and the coolest year in our study. The extent of seasonal thermal variability is measured as the mean difference between the warmest month and the coolest month in a single year. The extent of inter-beach (island) variability is reported as the mean difference between the warmest island and the coolest island. The extent of intra-beach (nesting habitat) variability is reported as the mean difference between the warmest and coolest nesting habitat. The extent of depth variability is reported as the mean difference between the warmest and coolest depth.

Source of thermal variability	Extent of thermal variability
Inter-annual	$1.03\text{ }^{\circ}\text{C}$ ( $SE = 0.17\text{ }^{\circ}\text{C}$ )
Seasonal	$3.00\text{ }^{\circ}\text{C}$ ( $SE = 0.71\text{ }^{\circ}\text{C}$ )
Inter-beach: Island	$0.85\text{ }^{\circ}\text{C}$ ( $SE = 0.07\text{ }^{\circ}\text{C}$ )
Intra-beach: Nesting habitat	$0.56\text{ }^{\circ}\text{C}$ ( $SE = 0.03\text{ }^{\circ}\text{C}$ )
Depth	$0.08\text{ }^{\circ}\text{C}$ ( $SE = 0.01\text{ }^{\circ}\text{C}$ )

mean thermal difference between these two habitats being 0.56 °C (SE = 0.03 °C). Sand temperatures recorded in the vegetation were 0.24 °C (SE = 0.04 °C) lower than sand temperatures recorded in the open. Lastly, we found a significant but negligible effect of depth in our long-term sand temperature data (approximate significance of the GAM smooth:  $F = 19.16$ ,  $edf = 1.9$ ,  $p < 0.05$ ), with temperatures recorded at a depth of 80 cm being 0.08 °C (SE = 0.01 °C) higher than temperatures recorded at a depth of 30 cm.

#### 4. Discussion

Recording sand temperatures at sea turtle nesting sites has become a widespread conservation practice (e.g., Matsuzawa et al., 2002; Fuentes et al., 2010; Bentley et al., 2020) given the effect of incubation temperature on embryo survival and hatchling sex ratios (Howard et al., 2014; Santidrián Tomillo and Spotila, 2020) ultimately influencing population viability (Hays et al., 2017). Incubation temperature also influences hatchling locomotor performance (Booth, 2017). Here we describe one of the longest time series of sand temperatures recorded at a sea turtle nesting site to date, as to our knowledge the previous longest published time series was 6 years (Laloë et al., 2017). We also address a research topic that has previously received little attention, namely thermal variability. Our findings suggest that sand temperatures in the Chagos Archipelago varied inter-annually, seasonally, between beaches, and within beaches, thus providing a wide range of incubation temperatures for turtles nesting in the archipelago. Crucially, our recorded temperatures on nesting beaches in the archipelago all fall within the narrow window of incubation temperatures, notably lying at the lower end of the range previously reported in the literature, where successful development of sea turtle embryos occur (i.e., ~27–35 °C; Ackerman, 1997; Howard et al., 2014), making this site a thermal refuge for sea turtles.

Previous research showed that Diego Garcia had relatively low sand temperatures during the 2012 and 2013 nesting seasons (Esteban et al., 2016). Our current study extends this finding and shows that low sand temperatures are not anomalous at this site as they were recorded across the five atolls of the archipelago over a decade-long study period (2012–2023). This work also highlights the value of long-term sand temperature studies. Long-term sand temperature studies are critical to understanding inter-annual thermal variation and to capturing outlier years, which may play a significant role in the success of a sea turtle population. For example, a uniquely warm year can lead to female-biased sex ratios (Hays et al., 2021). In our time series, 2015 was the warmest year, which is likely linked to the ENSO-driven marine heatwave that impacted the archipelago in 2015/2016 (Sheppard et al., 2020). In consequence, it is likely that more female hatchlings were produced during the 2015–2016 hawksbill nesting season on Diego Garcia compared to any other year in the preceding 70-year period (Hays et al., 2021). On the other hand, a distinctively cold year facilitates the production of male hatchlings. Since male turtles can mate with multiple females in a breeding season, a predominantly male cohort produced one year could potentially sustain a population for decades. In contrast to our results, only small inter-annual differences in sand temperatures have previously been reported at other nesting sites (e.g., Hays et al., 1999; Matsuzawa et al., 2002). This may be due to shorter study periods (i.e., one or two nesting seasons), which limits the ability to identify temperature patterns over time as well as outlier years. So, when possible, we recommend long-term data collection, especially since deployment of loggers is relatively inexpensive and logistically uncomplicated (Staines et al., 2022).

Although, the pivotal temperature has not yet been identified for the green or hawksbill turtle populations in the archipelago, our temperature records reveal that sand temperatures straddle 29.0 °C, which is broadly representative of the pivotal temperature for TSD for all species of sea turtle (Ackerman, 1997; Davenport, 1997). The pivotal temperature of 29.0 °C was previously used to estimate primary sex ratios in the

Chagos Archipelago (Esteban et al., 2016), where it was estimated that the relatively cool temperatures would produce 63 % and 53 % male hatchlings for green and hawksbill turtles, respectively. Here we report similar sand temperatures as those reported in the 2016 study, suggesting that hatchling sex ratios have been slightly male-biased at this site for the past decade. Although relatively high proportions of male hatchlings have been reported in other parts of the world (e.g., loggerhead turtles at Fethiye beach in Turkey; Kaska et al., 2006), this finding is in stark contrast to many other sea turtle nesting sites around the world where high sand temperatures and female-skewed sex ratios are reported (Hays et al., 2014), such as on Ascension Island (central Atlantic; Godley et al., 2002), St Eustatius (Caribbean; Laloë et al., 2016), and Raine Island (Australia; Booth et al., 2020). In this sense, the Chagos Archipelago is a relatively unusual sea turtle rookery and likely one that will be resilient to warming sand temperatures predicted to occur with climate change (Esteban et al., 2016). Recently, Mortimer et al. (2020) highlighted the importance of the Chagos Archipelago to nesting turtles both regionally and globally. The review of nest numbers in the south-west Indian Ocean revealed that the Chagos Archipelago hosts 39–51 % of hawksbill nests and 14–20 % of green turtle reproduction for that region. In addition, nesting has increased 2–5 times for hawksbill turtles and 4–9 times for green turtles since 1996, with the most recent estimates of 6300 and 20,500 clutches laid annually, for hawksbill and green turtles, respectively (between 2011 and 2018; Mortimer et al., 2020). The size of the nesting populations add weight to the importance of our findings, since these populations that are very important regionally are likely to be resilient to sand warming.

Seasonal thermal variation was highlighted as an important driver of sand temperatures in some of the first studies reporting sea turtle sex ratios (Mrosovsky et al., 1984; Mrosovsky, 1994). In South Carolina and Georgia, seasonal changes were found to have a considerable impact on loggerhead (*Caretta caretta*) hatchling sex ratios, where clutches laid during the coolest period of the nesting season produced no females, and clutches laid in the warmer period produced 80 % females (Mrosovsky et al., 1984). Likewise, in Suriname a peak in male green turtle hatchlings was observed corresponding to the coolest period of the nesting season (Mrosovsky, 1994). Seasonality had the most influence on thermal variability in our study, modulating sand temperatures by up to 3.0 °C over a year. Since green sea turtles nest year-round in the Chagos Archipelago (Mortimer et al., 2020), the nesting period spans across this wide variation in sand temperatures. In addition, peak nesting season is between June to September (Mortimer et al., 2020), which spans the austral winter. Taken together, this suggests that 1) different sex ratios are produced throughout the nesting season, as seen in previous studies, and 2) over one nesting season it is likely that balanced, or slightly male-biased sex ratios are produced across the archipelago. On the other hand, the hawksbill turtle peak nesting window falls between October and February (Mortimer et al., 2020), which is during the austral summer when sand temperatures are at their highest, so hatchling sex ratios may not be as male-biased for this species. Variations in environmental parameters (e.g., temperature) can be linked to seasonal events for many animals (Sur and Sharma, 2024). The hawksbill turtle nesting season in the Chagos Archipelago corresponds to that of hawksbills in the Seychelles, which coincides with high precipitation due to the northwest monsoon (Mortimer and Bresson, 1999; Mortimer et al., 2020). Green turtle nesting season also corresponds with data from the region that nesting peaks in lower latitudes during the austral autumn and winter and higher latitudes during the austral summer, an indication that temperature is a key factor determining nesting seasonality (Dalleau et al., 2012; Mortimer, 2012; Mortimer et al., 2020). Further investigations may be required to understand the temporal separation in nesting seasons of these two species, but one possibility could be interspecific differences in pivotal temperatures being 28.26 °C for green turtles and 29.32 °C for hawksbill turtles (Ackerman, 1997). Another possible reason for the difference in nesting seasons could be to decrease interspecific spatial competition on nesting beaches. A temporal

separation in the start of the nesting season and low interspecific competition has also been reported for green, loggerhead and leatherback turtles (*Dermodochelys coriacea*) in Florida (Weishampel et al., 2003).

Our results revealed inter-beach thermal variation on different islands across the Chagos Archipelago, with the warmest beach being on average 0.85 °C warmer than the coolest beach. While we did not record variables that might explain these thermal differences, at other sites sand albedo is known to be a driver of inter-beach thermal variation (Hays et al., 2001). On Ascension Island, a 4 °C variation in sand temperature between 12 nesting beaches was strongly linked to beach albedo, with darker sand beaches being much warmer than light-coloured beaches (Hays et al., 1995, 1999). Similarly, in Cape Verde, sand temperatures recorded on dark-coloured beaches were 1.8 °C warmer than sand temperatures on light-coloured beaches (Laloë et al., 2014). All islands at our study site had light-coloured beaches largely contributing to the low sand temperatures we recorded. Furthermore, abiotic factors that are known to influence sand temperatures at sea turtle nesting sites include sand grain size, sand water content, sand conductivity (Speakman et al., 1998) and beach orientation (Esteban et al., 2018), which can influence sun and wind intensity on nesting beaches. So, there is a wide range of variables that can influence sand temperatures at a site, leading to different beaches presenting different thermal environments. It is therefore recommended to record sand temperatures at different beaches within a nesting site to provide a more holistic view of temperatures experienced at a site. This is particularly relevant in the Chagos Archipelago where nests are scattered across some 55 islands (Mortimer et al., 2020), and individuals are known to migrate from one nesting beach to another island during a single nesting season (personal observation), which has also been observed in the Caribbean (Esteban et al., 2015).

Our study also shows the importance of intra-beach thermal variation at our study site, and how different nesting habitats expose clutches to different thermal conditions. The islands of the Chagos Archipelago are densely vegetated, and vegetation assemblages differ along a single nesting beach, such that on Diego Garcia one section of the nesting beach is heavily vegetated with high canopy *Cocos nucifera* and another section with dense shrub *Scaevola* (Esteban et al., 2016). Although nests on Diego Garcia are predominantly in the vegetation, turtles also nest in the open where there is little shade (Stokes et al., 2023). Interestingly, we also recorded low sand temperatures in the open nesting habitat. This is possibly due to the cooling effect of over wash from spring tides or to the presence of a high water table. Water tables on low-lying islands are known to be dynamic, rising and falling with the tide, and raised during prolonged periods of heavy rainfall (Baillie et al., 2021). However, it is important to note that clutches laid too close to the high water line may be exposed to increased flooding, which can cause reduced hatchling success (Martins et al., 2022).

Like other studies around the world, including Malaysia (Reboul et al., 2021), Caribbean (Esteban et al., 2018) and Australia (Wood et al., 2014), our findings highlight the importance of natural shading on sea turtle nesting beaches. Preserving native vegetation and planting appropriate vegetation at the back of a nesting beach could be one of the most effective strategies to mitigate future warming sand temperatures (Kamel, 2013). However, despite the cooling benefits, negative impacts could occur, such as root growth into nests (Conrad et al., 2011), and so careful considerations must be taken. For warm nesting grounds with no natural vegetation, management strategies can be put in place to lower sand temperatures, such as nest irrigation (Smith et al., 2021; Gatto et al., 2023), nest relocation (Esteban et al., 2018) or artificial shading (Reboul et al., 2021; Wiggins et al., 2023).

Triaging threats to sea turtles is an important part of conservation planning (Fuentes et al., 2023) and in this regard it might be that sea level rise and the resulting habitat loss and nest inundation from coastal squeeze (Mazaris et al., 2009) is more of a threat in the region than warming sand temperatures. Islands in the Chagos Archipelago are low lying atolls and hence, in common with atolls around the world, at threat

from sea level rise (Bellard et al., 2013; Wu et al., 2021). Indeed, sea level rise is already driving threat mitigation measures in some parts of the world. For example, at Raine Island (northern Great Barrier Reef, Australia), sea water inundation of nests had led to a programme of importing sand to build up the nesting beaches (Hamann et al., 2022; Smithers and Dawson, 2023). Assessing this threat of inundation, and designing mitigation measures, is therefore an important conservation concern not only for the Chagos Archipelago but all other low-lying atolls around the world (Ware and Fuentes, 2018; Gammon et al., 2023).

Lastly, we found a minimal effect of nest depth on sand temperature across the range of depths considered. Previous studies around the world have also shown that nest depth has minimal impact on sand temperatures at nesting beaches (Carr and Hirth, 1962; Hays et al., 1999; Esteban et al., 2016). In our study, we recorded minimally higher temperatures at 80 cm compared to 30 cm (0.08 °C) which could be due to thermal conductivity properties of the sand at depth (Speakman et al., 1998). Warmer temperatures at depth have been reported on Heron Island, Australia. For example, during the warmest period, 100 cm depth was cooler than 70 cm depth but in the coldest months, 100 cm was warmer than 70 cm depth (Booth and Freeman, 2006). Daily fluctuations were also observed in sand temperature at 70 cm depth, contrary to expectation (Booth, 2018). One possible reason for the recorded fluctuation at depth is higher sand thermal conductivity on the islands but this is currently unknown for the Chagos Archipelago. We also recorded smaller daily sand temperature fluctuations in vegetation compared to open nesting habitat, likely because nest temperatures in vegetation are less affected by changes in air temperature (Spotila et al., 1987), and shading from trees reduces exposure of the sand surface to direct solar radiation (Wood et al., 2014). It has been suggested that sea turtles might be able to select different thermal microhabitats by laying their clutches at different depths in the sand (Marco et al., 2018). Such a strategy would help turtles adapt to varying sand temperatures, but unfortunately our study offers little evidence to support this hypothesis.

Previous research has used a variety of different models to describe sand temperatures at sea turtle nesting sites, including simple linear models to more complex linear mixed effects analyses and microclimate models (e.g., Hays et al., 1995; Esteban et al., 2016; Bentley et al., 2020). Here we used a GAM as it is a powerful statistical technique that is both flexible and easily interpretable and can be fit to complex, nonlinear relationships to help understand and explain the underlying structure of the data (Hastie and Tibshirani, 1987). However, as with other types of models, one caveat is that temporal autocorrelation may remain in our dataset, so our results should not be overinterpreted. In our study, autocorrelation might only be a minor issue as we use the GAM to describe our dataset rather than make predictions, so our conclusions that both temporal and thermal variation are present at our study site likely still hold.

## 5. Conclusion

Our study identifies different levels of sand temperature variability at a key sea turtle nesting site. We demonstrate how thermal variability can be captured using a handful of loggers strategically placed in the different turtle nesting habitats. Our results underline the need to consider thermal variability both temporally and spatially to capture the range of temperatures experienced at a beach. Furthermore, our work highlights the need to take potential sources of thermal variation into account when modelling sea turtle population dynamics such as sex ratios. Given the risks of increasing sand temperatures on population viability, the continued long-term monitoring of sand temperatures at sea turtle nesting sites is recommended, especially since temperature loggers are a relatively cheap and highly informative conservation tool.

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### CRedit authorship contribution statement

**Holly J. Stokes:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Jacques-Olivier Laloë:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nicole Esteban:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Graeme C. Hays:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

All data are available from Dryad: <https://doi.org/10.5061/dryad.f4qrj74k>.

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