Animal Behaviour 208 (2024) 59–68

Contents lists available at ScienceDirect

Animal Behaviour

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

Nest site selection in sea turtles shows consistencies across the globe in the face of climate change

Holly J. Stokes [a], Nicole Esteban [a,*], Graeme C. Hays [b]

[a] Department of Biosciences, Swansea University, Swansea, U.K.
[b] Deakin University, Geelong, VIC, Australia

ARTICLE INFO

Article history:
Received 8 June 2023
Initial acceptance 8 August 2023
Final acceptance 9 October 2023

MS. number: 23-00292

Keywords:
climate change
feminization
hatchling sex ratio
marine turtle
nest location
plastic pollution
sea level rise
temperature-dependent sex determination
trade-off

Sea turtles face a risk of extinction due to climate change causing warming of nests, which may increase both sex ratio skews, with fewer males being produced, and embryo mortality in nests. In theory, these threats could be mitigated by turtles switching their nest sites to cooler locations on beaches. We assessed nest positioning for green turtles, *Chelonia mydas*, in the Chagos Archipelago, a major nesting site in the Indian Ocean, and showed that nests were generally in vegetation at the back of the beach, where the risk of sea water inundation was lowest. The relatively few nests on the open beach were on average close to the vegetation. Sand temperatures at nest depths were similar across three beach zones (open sand, edge of vegetation, within the vegetation). Nest positioning was reviewed for 51 studies at 53 sites (including the current study) across the globe and across seven species: green turtles, hawksbills, *Eretmochelys imbricata*, loggerheads, *Caretta caretta*, leatherbacks, *Dermochelys coriacea*, olive ridleys, *Lepidochelys olivacea*, Kemp's ridleys, *Lepidochelys kempii*, and flatbacks, *Natator depressus*. Both in the Chagos Archipelago and across the globe studies show turtles generally tend to crawl a sufficient distance to minimize sea water overwash of nests, which can kill embryos. Hence maximizing embryo survival, rather than considerations of hatchling sex ratios, seems to be the main driver for nest positioning and so we conclude that sea turtles are, generally, unlikely to switch to select cooler beach sites to mitigate climate warming.

Across the globe the ability of animals and plants to mitigate climate warming impacts may be key to their future survival, through for example, range changes or phenological shifts in the timing of breeding and migrations (Charmantier & Gienapp, 2014). For oviparous species, including birds, reptiles and fish, the thermal environment eggs are exposed to, may have important implications for offspring survival (DuRant et al., 2019; Feiner et al., 2016; Martin et al., 2020) and so a potential avenue to mitigate climate warming in these taxa is through the selection of cooler sites for egg laying. For some species there is good empirical evidence that the egg-laying site may be selected based on their thermal environment, such as in some birds (Bison et al., 2020). However, for other taxa it is equivocal whether the likely thermal environment for developing eggs plays a role in the selection of sites for egg laying.

For sea turtles there are particular concerns about climate warming since the group has temperature-dependent sex determination, with female hatchlings being produced at warmer incubation temperatures and vice versa, with concerns that future warming may lead to increasingly female-skewed populations and, potentially, single-sex populations and then extinction (Booth et al., 2020; Godley et al., 2002; Hawkes et al., 2009; Hays et al., 2023; Jensen et al., 2018; Witt et al., 2010). Concern surrounding this scenario has been exasperated by the finding that the majority of nesting populations already produce heavily female-biased hatchling sex ratios (Booth & Freeman, 2006; Broderick et al., 2000; Fuentes et al., 2009; Laloë et al., 2016). With sea turtles, several studies have now suggested that phenological shifts in the nesting season will be insufficient to mitigate climate warming (Laloë & Hays, 2023; Monsinjon et al., 2019), which has reinvigorated studies of nest site selection as a possible means by which cooler incubation conditions at particular microhabitats might be selected (Heredero Saura et al., 2022; Kamel & Mrosovsky, 2006).

Given this interest in nest site selection, here we assessed the nest positions for green turtles, *Chelonia mydas*, at a major rookery in the Indian Ocean where a balanced hatchling sex ratio has previously been reported (Esteban et al., 2016). Further, we explored potential drivers of nest site selection based on the various

* Corresponding author.
E-mail address: n.esteban@swansea.ac.uk (N. Esteban).

https://doi.org/10.1016/j.anbehav.2023.12.001
0003-3472/

hypotheses that have been proposed, including that turtles might select sites close to vegetation behind beaches or at a certain distance or height above the water line or might simply randomly lay clutches across the width of beaches. We embedded our finding in a synthesis of the previous studies around the world to find a consensus for the key processes that seem to drive nest site selection for nesting populations across the globe.

METHODS

The study site is located on Diego Garcia which has 40 km of beach suitable for nesting turtles and is the largest atoll in the Chagos Archipelago, where an estimated 20 500 green and 6300 hawksbill turtle, *Eretmochelys imbricata*, clutches are laid annually (Mortimer et al., 2020). Green turtles nest year-round, mostly between June and October with a peak in August, and hawksbill turtles nest between October and February (Mortimer et al., 2020). A 2.8 km index beach (Fig. 1a) was selected for turtle nesting research as it hosts some of the highest densities of nesting activity identified, is partially located in the Diego Garcia Ramsar Site and is easily accessible (Mortimer et al., 2020). Foot patrols were conducted in 2021 and 2022 including daytime surveys (start time ranged from 0500 to 1500 hours) to count recent turtle activities (tracks, nests) and night-time surveys (dusk to dawn) in search of nesting females to directly observe nesting activity to record clutch counts, biometrics and nest measurements. The following measurements (using a flexible transect tape, m) to the nest were recorded: crawl distance (from sea to nest), high water line (HWL) to nest, HWL to vegetation line, sea to nest (straight distance), sea to vegetation line, vegetation line to nest (negative values are nests in front of the vegetation line towards the sea). The HWL was defined as the boundary between dry and wet sand and debris markings left by the last high tide. For some nests in 2022, crawl distances were measured at night from the water's edge as soon as the track was encountered, that is, within 2 h of the turtles emerging onto the beach. Not all measurements were recorded for all nests and so the sample sizes vary for each analysis. A straightness index (SI) was calculated from the straight distance to the nest from the sea divided by the total distance of the crawl from the sea to the nest.

In 2021, we measured heights of nests encountered in February and at nest sites recorded in 2018 and 2019 during peak nesting season (June–July) that were revisited using GPS coordinates. In 2022, we measured the height of recent nests that we encountered and marked between June and September.

We used a theodolite (Automatic Level AL8-26, Model 8926, David White, Lafayette, IN, U.S.A.), transit surveyor's tripod (model 1228, Lietz, Grand Rapids, MI, U.S.A.) and a 4 m pole marked at 0.5 cm intervals to measure the height of nests versus the recent neap HWL on the 19–20 February 2021 and 22 September 2022. Nest sites were recorded between February and September and the majority of sites were recorded during peak nesting season including June–July 2018, June–July 2019, February 2021 and June–September 2022. Nests located in 2018 and 2019 were measured in 2021 along with recent nests from February 2021 and recent nests in 2022. The tripod height was subtracted from the total height and the neap high tide height (from National Tidal and Sea Level Facility, 2021, 2022) was added to obtain nest height above chart datum. We calculated the mean high water (MHW) height across the months of February 2021 and September 2022 and subtracted values from our nest height above chart datum for each survey month to obtain nest height above MHW (Fig. 1b).

Sand temperature at 50 cm was measured at three locations along the nesting beach. We chose this depth because it covers both hawksbill and green turtle nest depths and allows comparison to previous sand temperature studies at this site where buried temperature loggers have been placed at 30 cm and 50 cm to estimate hawksbill conditions and at 50 cm and 70 cm to estimate green turtle conditions (Esteban et al., 2016). The three sampling zones (Fig. 1) were determined by observations of frequent green turtle nesting locations. At each location the sand temperature was measured several metres into the vegetated zone (where nesting occurred indicated by presence of body pits), at the edge of the vegetation zone and in the open beach zone a few metres from the vegetation and above recent HWL. Initial trials using a temperature probe and data logger (1 m long Compost Probe PB-5013-XM with a Tinytag View 2 TV-4020, Gemini Data Loggers, Chichester, U.K.)

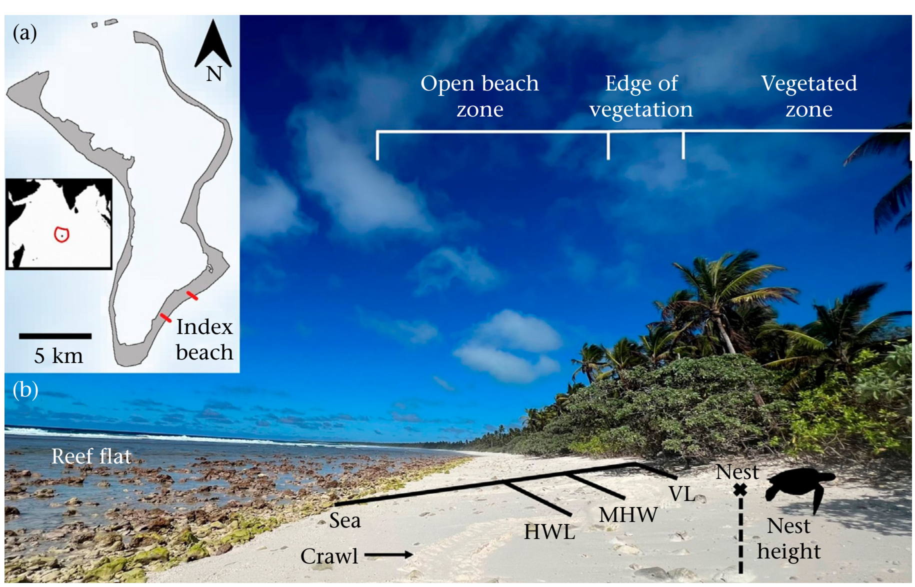

Figure 1. (a) Diego Garcia (land shaded grey) and the index beach (indicated by the red lines) with a map showing the location of the Chagos Archipelago in relation to the wider Indian Ocean (red boundary = Marine Protected Area). (b) Beach profile showing the measurements taken from the nest (VL: vegetation line; MHW: mean high water; HWL: high water line; sea to nest and vegetation distances; crawl distance; nest height). MHW was calculated (using National Tidal and Sea Level Facility, 2021, 2022) for estimation of nest height.

were conducted at 30, 50 and 70 cm depths to test stabilization time of the sand temperature at different depths.

Stable temperatures occurred quicker at deeper depths. At 50 cm depth the temperature stabilized within 3 min. For the study, the probe remained in the sand for 3 min before a reading was recorded. The probe was placed in cold water in an insulated bottle between each sample point and temperature was recorded for a calibration check. We took three measurements in each beach zone at each sampling location along the beach in March and September 2021 and in July and August 2022. In March 2021 and July 2022, repeat measurements were conducted over 3 consecutive days. We aimed to measure sand temperature as close to neap tides as possible and during dry periods to avoid overwash and heavy rainfall influencing measurements.

A literature search was conducted in March 2023 for papers on nest site selection of sea turtles. We conducted a search on Web of Science using the search term: ALL = (‘Sea turtle’) AND ALL = (‘Nest site selection’). For relevant papers, we made note of the species, location of study, nest zone preference (e.g. vegetation zone, in front of vegetation zone or in the open sand zone).

Ethical Note

The study was endorsed through research permits (0001SE21, 000XSE22) from the Commissioner's Representative for BIOT and research complied with all relevant local and national legislation. Protocols were approved by research ethics committee of Swansea University (Ethics Reference Number: STU_-BIOL_157334_011020182616_1; AWERB IP Reference Number: IP-2021-01). There were no experimental practices conducted on animals for this study.

RESULTS

Nest Positioning

Nest sites were generally in the vegetated zone that backed the nesting beach (Fig. 2a, for data see Supplementary Material 1a). For example, 43 of 48 nests (90%) were 0–9.55 m into the vegetation and only five of 48 nests (10%) were on the open beach zone before the vegetation. Even these few nests on the open beach were close (mean = −1.5 m) to the vegetation.

There were typically only a few metres between the HWL and vegetation line (mean = 2.56 m). When the distance from the HWL to the vegetation was further, nests tended to be further from the HWL as turtles needed to traverse more open sand before entering the vegetation zone (Fig. 2b, for data see Supplementary Material 1b). All nests were above the MHW (range 0.14–0.44 m; mode = 1.35 m; Fig. 2c, for data see Supplementary Material 1c).

As the crawl distance to a nest increased, nests tended to be further into the vegetation, although there were longer crawls where nests were on or just within the vegetation. Sometimes turtles encountered vegetation that was impenetrable, typically dense stands of native Indo-Pacific shrubs *Suriana maritima* or *Scaevola taccada*. In these cases, turtles then often crawled parallel to the vegetation until they found a break that allowed them to crawl further from the sea and into the vegetation zone (Fig. 3a and b). So often in these cases the total crawl distance could be very long (up to 76 m), even though these long crawls did not lead to nests being further into the vegetation (Fig. 3c, for data see Supplementary Material 2). Rather, these long crawls were simply due to the circuitous crawl path along the vegetation line, before the turtle was able to enter the vegetation and nest. Most (66%) nests had no preceding aborted digging attempts, but 24% and 10% of nests had one or two preceding aborted attempts, respectively.

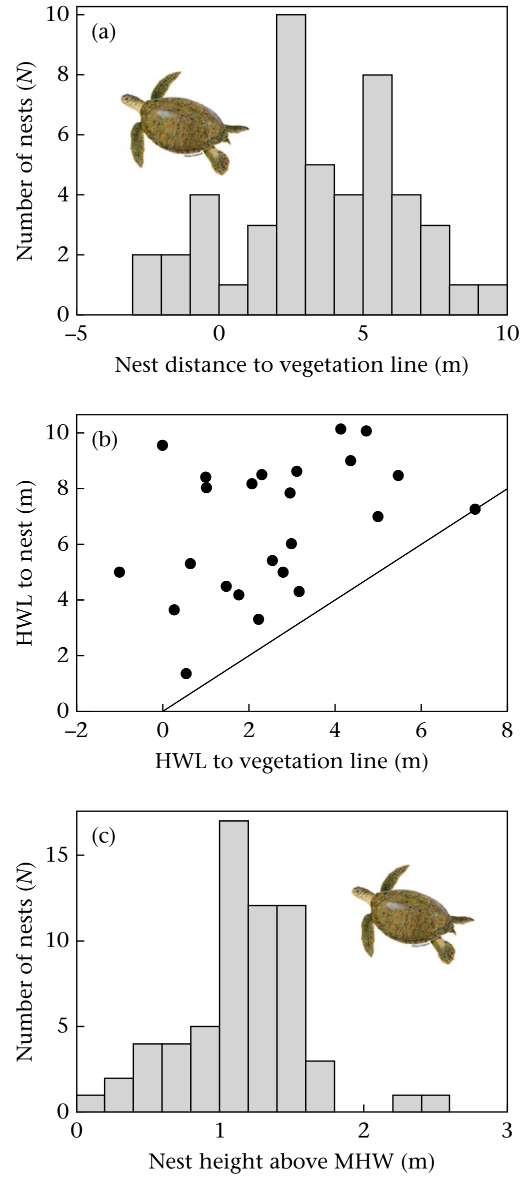

Figure 2. (a) The distribution of green turtle nests on Diego Garcia (Chagos Archipelago, Indian Ocean) with respect to the vegetation line ($N = 48$). (b) The distance from the high water line (HWL) to the nest in relation to the distance from the HWL to the vegetation line ($N = 25$). Black line = line of equivalence. (c) The frequency distribution of nest heights above the mean high water (MHW; calculated for the month the survey was conducted using National Tidal and Sea Level Facility, 2021, 2022; $N = 61$). Negative values are nests in front of the vegetation line towards the sea. Data sources: (a) and (b) in situ track surveys, (c) theodolite measurements from marked nest locations. For the full data set see Supplementary Material 1a, b, c. The turtle image was provided by NOAA Fisheries (www.fisheries.noaa.gov).

These nesting attempts were aborted because of material (typically roots or plastic macrodebris) impeding digging. These aborted digging attempts followed the same spatial distribution as nests, typically being within the vegetation zone.

Sand Temperatures and Nest Position

The mean daily sand temperature recorded at 50 cm depth at three sites in the vegetated zone was 26.87 °C (SD = 1.10 °C, range 25.70–28.60 °C, $N = 24$). Sand temperatures at 50 cm depth was similar across the three beach zones (open beach, edge of vegetation, vegetated zone) and not significantly different (ANOVA:

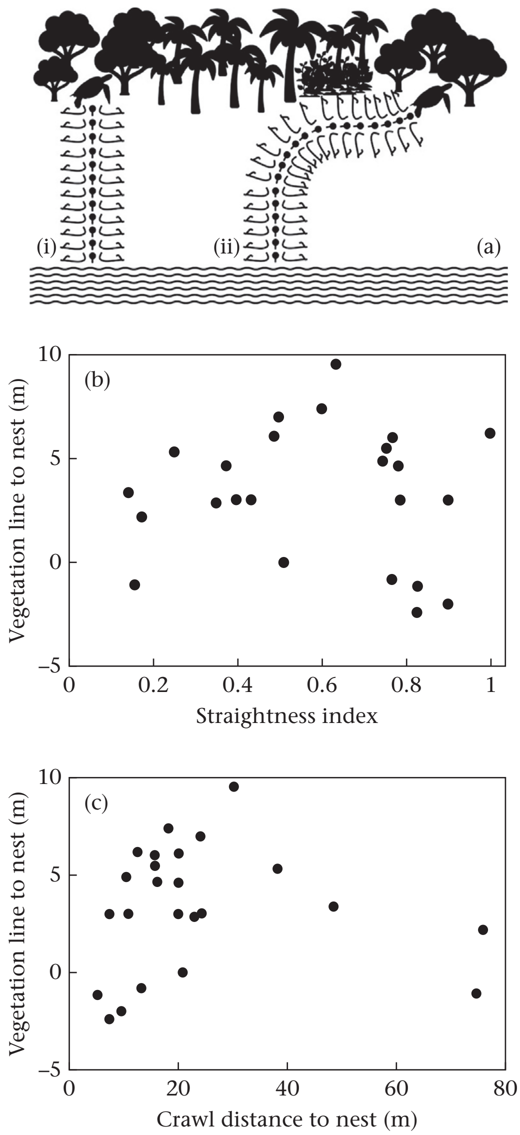

Figure 3. (a) Schematic of different crawls from the sea (see Supplementary Material 2 for data on crawl distances): (i) an example where a turtle crawled directly into the vegetation and (ii) an example where the turtle initially could not enter the vegetation as it was too dense and then crawled parallel to the vegetation line for some distance. (b) Relationship between the straightness of the crawl to the target (nest) and the distance of the nest to the vegetation. (c) Relationship between the crawl distance to the nest from the water's edge versus the distance of the nest to the vegetation line. Negative values are nests in front of the vegetation line towards the sea.

$F_{2,69} = 0.81$, $P = 0.45$). For example, the temperature at nest depth within the vegetated zone was, on average, only 0.48 °C cooler than on the edge of vegetation and 0.03 °C cooler than in the open beach zone (Fig. 4, for data see Supplementary Material 3).

Studies Across the World

We found 50 studies around the world (excluding the current study) that had reported nest site selection for sea turtles at 52 sites (Fig. 5, see Table A1). In general, studies found that nests tend to be distributed away from the sea and above the HWL. For some nesting beaches, where there was vegetation behind the beach, turtles tended to nest in the vegetation zone. In other cases, the vegetation tended to constrain the inland crawl distance, with turtles nesting in front of the vegetation. In other cases, where

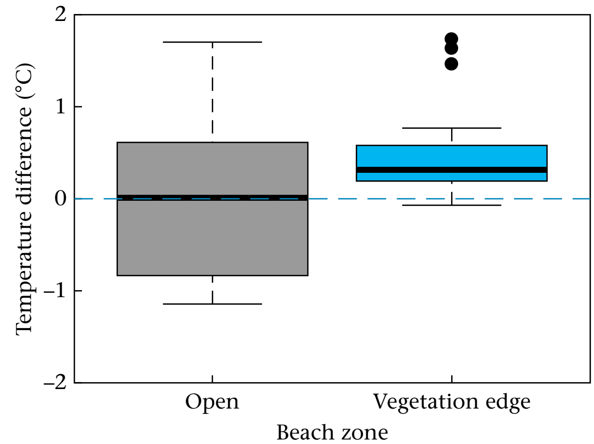

Figure 4. Temperature variation of the vegetation edge and open zones on the index beach, Diego Garcia, when compared to the vegetated zone as a reference. Bold horizontal lines indicate the median and boxes the 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers. See Supplementary Material 3 for the full data set.

there was no vegetation behind the beach or the vegetation was far from the sea, then crawl distances could be very long, and turtles seemed to position nests above the HWL but short of the vegetation. Across the studies, the consensus is that turtles position nests well away from the sea to reduce the risk of sea water inundation which could result in nesting in vegetation on narrow beaches.

DISCUSSION

For sea turtles the nest position may have important implications for survival and sex of embryos. Of concern across nesting beaches is the fact that repeated salt water inundation of nests will kill developing embryos due to both the osmotic impact of salt in the nest and the removal of oxygen spaces within the sand and the resulting drowning of embryos (Pike et al., 2015). Hence many studies have reported that hatching success (the proportion of eggs resulting in a hatchling emerging from the sand) tends to increase in nests further from the sea (Hays & Speakman, 1993; Martins et al., 2022; Patrício et al., 2018; Whitesell et al., 2022). Our key finding that green turtles tend to position their nests within the vegetation behind beaches, and hence as far from the sea as possible, even if this necessitates circuitous crawls to get to those nest positions, suggests these turtles are trying to minimize the likelihood of salt water inundation of their nests. The nesting beaches on Diego Garcia may be particularly prone to overwash as they are relatively narrow, with typically only a few metres between the HWL and the vegetation. So, at this site it may be particularly important for turtles to crawl into the vegetation to minimize nest inundation. A similar pattern of nesting in supralittoral vegetation far from the sea has also been reported for other green turtle nesting beaches around the world, for example Mexico (Zavaleta-Lizárraga & Morales-Mávil, 2013), Suriname (Whitmore & Dutton, 1985) and Costa Rica (Heredero Saura et al., 2022), as well as in hawksbill turtles nesting, for example, in Brazil (Serafini et al., 2009) and Guadeloupe (Kamel & Mrosovsky, 2005) and olive ridley turtles in Costa Rica (Ávila-Aguilar, 2015). In contrast, at some nesting beaches there may be a lack of supralittoral vegetation and so vegetation cannot be a constraint on the inland crawl distance. For example, at the major green turtle rookery on Ascension Island, supralittoral vegetation was historically very sparse or nonexistent and, there, green turtles have been shown to crawl long distances from the sea before nesting (up to many 10s of

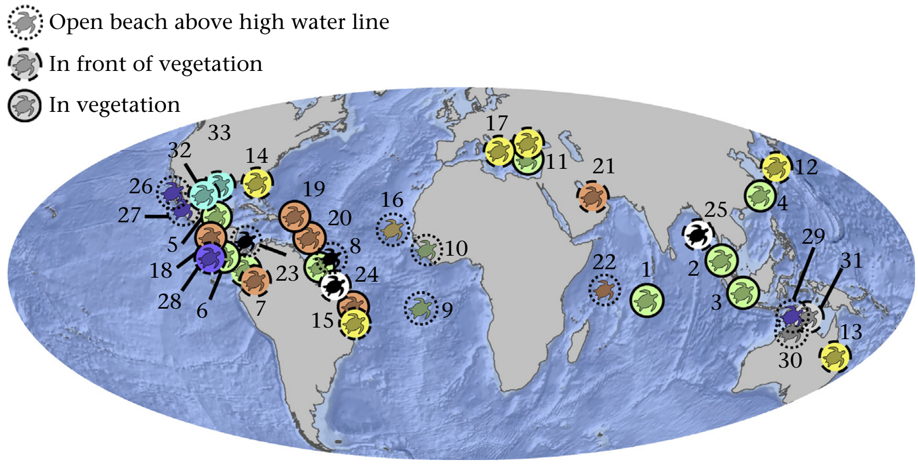

Figure 5. Studies around the world where the distribution of sea turtle nests has been recorded (see Table A1). Symbols show whether turtles nested mainly on the open beach above the high water line but short of vegetation, on the open beach close to the vegetation line or in the vegetation zone. Green = green turtle, yellow = loggerhead turtle, red = hawksbill turtle, purple = olive ridley, black = leatherback turtle, grey = flatback turtle, blue = Kemp's ridley turtle. Green turtles: 1 = this study, 2 = Malaysia (Mohd Salleh et al. 2018, 2021; Sarahaizad et al., 2012), 3 = Indonesia (Rumaida et al., 2021), 4 = Taiwan (Chen et al., 2007; Wang & Cheng, 1999), 5 = Mexico (Santos et al., 2017; Zavaleta-Lizárraga & Morales-Mávil, 2013), 6 = Costa Rica (East Pacific green turtles; Heredero Saura et al., 2022), 7 = Ecuador (Carpio Camargo et al., 2020), 8 = Suriname (Whitmore & Dutton, 1985), 9 = Ascension Island (Hays et al., 1995), 10 = Guinea-Bissau (Patrício et al., 2018), 11 = Turkey (Turkozan et al., 2011). Loggerhead turtles: 11 = Turkey (Kaska et al., 2010; Turkozan et al., 2011), 12 = Japan (Hatase & Omuta, 2018), 13 = Australia (Kelly et al., 2017), 14 = U.S.A. (Garmestani et al., 2000; Gravelle & Wyneken, 2022; Hays et al., 1995; Salmon et al., 1995), 15 = Brazil (Serafini et al., 2009), 16 = Cape Verde (Martins et al., 2022), 17 = Greece (Hays & Speakman, 1993; Karavas et al., 2005). Hawksbill turtles: 18 = El Salvador & Nicaragua (Liles et al., 2015), 7 = Ecuador (Carpio Camargo et al., 2020), 19 = Guadeloupe (Kamel & Mrosovsky, 2005), 20 = Barbados (Horrocks & Scott, 1991), 15 = Brazil (Santos et al., 2016; Serafini et al., 2009), 21 = Qatar & Iran (Ficetola, 2007; Nasiri et al., 2022; Zare et al., 2012), 22 = Seychelles (Gane et al., 2020). Leatherbacks: 23 = Costa Rica (Neeman et al., 2015; Spanier, 2010), 8 = Suriname (Whitmore & Dutton, 1985), 24 = French Guiana (Caut et al., 2006), 25 = India (Sivasunder & Devi Prasad, 1996). Olive ridley: 26 = Mexico (López-Castro et al., 2003), 27 = Mexico (Hart et al., 2014), 28 = Costa Rica (Ávila-Aguilar, 2015), 29 = Australia (Blamires & Guinea, 1998). Flatback turtle: 30 = Australia (Bannister et al., 2016; Blamires et al., 2003), 31 = Australia (Hope & Smit, 1998). Kemp's ridley: 32 = Mexico (Márquez, 1994), 33 = U.S.A. (Culver et al., 2020).

metres), crawling until they reach soft sand above the HWL (Hays et al., 1995). Similarly, on wide beaches in Guinea-Bissau, West Africa, green turtles crawl long distances from the water to nest either at the back of the beach or in supralittoral vegetation (Patrício et al., 2018). Additionally, a comparison of individual nesting beaches in Penghu Archipelago, Taiwan, found turtles nest in the open or interface zones when the vegetation was further inland, but when the open beach zone was narrower, nests were located more in the interface and vegetated zones (Chen et al., 2007).

Loggerhead turtles tend to show similarities to green turtles in that nests tend to be positioned far from the sea to minimize inundation, but at the same time loggerheads often tend to nest just in front of supralittoral vegetation rather than in the vegetation zone. This pattern of nest placement has been observed, for example, with loggerheads nesting in Brazil (Serafini et al., 2009), Greece (Hays & Speakman, 1993; Karavas et al., 2005) and Japan (Hatase & Omuta, 2018). Very few studies were found for Kemp's ridley turtles, but they are also known to nest far from the sea but in front of vegetation in Mexico (Márquez, 1994) and Texas, U.S.A. (Culver et al., 2020). This pattern of nesting just before reaching vegetation may be because roots impede digging with this species and may lead to nesting attempts being aborted (Hays et al., 1995). These nest positioning strategies seem to work well, with a dramatic increase in nesting numbers following the introduction of measures to reduce poaching of nests (Hays et al., 2022; Mazaris et al., 2017), that is, overwash of clutches does not impede population recoveries. Similarly, Gravelle and Wyneken (2022) showed nest location varied with microclimate: subtropical loggerhead nests were primarily in the mid-beach zone on flat and wide beaches which had high emergence and hatchling success compared to warm temperate nest sites situated on narrow beaches with nests clustered at high elevations by the base of the dune. For loggerheads nesting in Boa Vista (Cape Verde), Martins et al. (2022) reported that turtles crawled long distances away from the sea to nest, but preferentially nested in the middle of the beach, avoiding nesting both close to the tideline and close to the vegetation line; however, due to the low elevation profile at this study site and the fact that predation occurred across the whole beach profile, the risk of inundation and predation was high regardless of nest location.

Like loggerheads, olive ridley turtles nest in front of the vegetation line but they nest anywhere between the HWL and vegetation line. In Mexico, Hart et al. (2014) found turtles preferred nesting on the open beach from the berm to the vegetation line. Likewise, López-Castro et al. (2003) found nests from 3 to 41.5 m from the tide line with the majority (58%) 10–20 m above the tide line. In the South Pacific region of Costa Rica, turtles were found to nest between the HWL and vegetation line but showed a stronger preference for nesting as far from the tide line as possible, even if this meant closer to the vegetation where there was a higher risk of predation and a further crawl for the nesting female and hatchlings to reach the sea (Ávila-Aguilar, 2015).

While many studies, reviewed above, have examined nest positioning and the implications for embryo survival, fewer have considered the sensory processes that might drive nest site selection. Some earlier work suggested that turtles start digging when they perceive a decrease in surface sand temperature (Stoneburner & Richardson, 1981). However, several subsequent studies have cast doubt on this conclusion. On some beaches any perceived change in sand temperature at the sand surface is likely linked to the sand texture and a switch from compacted overwashed sand below the HWL to drier, 'fluffier' sand above the HWL where turtle flippers sink a little deeper as they crawl. So, sand texture might provide turtles with a cue to sense they have crawled above the HWL (Hays et al., 1995). This change in sand texture may occur, for example, with green turtles nesting on Ascension Island where crawl distance is linked to the distance from the water's edge to the HWL; turtles likely only attempt to nest when they perceive this discontinuity between overwashed compacted sand and dry uncompacted sand (Hays et al., 1995). Similarly, Wood and Bjorndal

(2000), working with loggerhead turtles in Florida, concluded that sand surface temperature alone was unlikely to be a cue to initiate nesting but might be used as one of several available when the crawl inland was far enough to reduce inundation. Through a process of simply perceiving when the HWL has been reached, and so a beach zone has been reached that has less chance of overwash, turtles might set the lower limit on the beach for where they nest. In contrast, where there is supralittoral vegetation behind beaches and the distance from the water to the vegetation line is relatively short, turtles might simply tend to crawl until they reach (loggerheads, olive ridleys, Kemp's ridley, flatbacks) or enter (green and hawksbill turtles) the vegetation zone before they start digging. So, again, on these types of nesting beach with supralittoral vegetation, a simple sensory process might be involved in nest site selection. Turtles might often follow simple rules: crawl a certain distance until you perceive (e.g. sand texture) that you are above the HWL and/or constrain your crawl and nest when/if you encounter vegetation. Such a simple decision-making process may explain why turtles sometimes nest on the open sand (i.e. they have crawled far enough to perceive they are above the HWL), sometimes nest just before vegetation (i.e. the vegetation constrains their inland crawl as in the case of loggerheads) or inside the vegetation (e.g. some green and hawksbill nesting sites). The outcome of this simple decision-making process would be that regardless of whether there is vegetation behind beaches or of the distance from the water to the vegetation line, turtles will minimize the risk of nest inundation. Through these processes of nest site selection, a tendency for turtles to nest a certain height above the sea level (e.g. this study but also widely reported for loggerhead and green turtles, Maurer & Johnson, 2017; Patrício et al., 2018; Wood & Bjorndal, 2000) might simply be an emerging property of other decisions driving nest site selection.

Our results for the drivers of nest site selection suggest that this process is unlikely to be an avenue that might help mitigate climate warming across populations. The picture emerging from studies around the world is that turtles tend to select nesting sites where the chances of sea inundation are low. At the same time, turtles do not continue to crawl indefinitely inland even if there is no vegetation to constrain their crawls, as then hatchlings emerging from nests further inland may have problems locating and reaching the sea (Kamel & Mrosovsky, 2004). There is also some evidence that experienced nesters may nest in beach zones less prone to inundation than first-time nesters (Pfaller et al., 2009), that is, as they nest more times turtles learn more about the physical make up of beaches and how far they can crawl inland. While generally turtles do not seem to select sites based on the likely incubation temperatures, there might be some sites where individual turtles differ in their selection of microhabitats and tendency to nest in cooler shaded areas versus warmer unshaded areas, as has been suggested for hawksbill turtles in the Caribbean (Kamel & Mrosovsky, 2005) and green turtles in West Africa (Patrício et al., 2018). In these cases, one possibility is that if nest site selection is a heritable trait, which is unknown, there might be future selection for females to nest in cooler sites. However, there is no evidence that this scenario might apply widely, with selection of nesting sites that minimize nest inundation seeming to dominate across the globe.

There was only a relatively small difference in sand temperature at nest depths between beach zones but even these small differences might impact hatchling sex ratios. For example, the mean temperature on the open beach zone was 0.45 °C cooler than that on the edge of the vegetation zone and the mean temperature on the vegetated zone was 0.48 °C cooler than that on the edge of the vegetation zone. A generic sand temperature versus hatchling sex ratio curve (Hays et al., 2017) shows that this difference in sand temperatures between zones might change the hatchling sex ratio (% females) by up to 15.7% for those nests close to the pivotal temperature where hatchlings of both sexes are produced.

While green, hawksbill, olive ridley, Kemp's ridley and loggerhead turtles seem to generally nest either in vegetation or high on the beach, often in front of vegetation, based on the presence or absence of vegetation and its distance from the sea, leatherback turtles have been suggested to position nests differently. Older reports suggested a strong tendency for leatherbacks to nest on the open sand and often below the HWL, reporting that around 30% of nests were below the HWL for leatherback nesting in French Guiana, Suriname and South Africa (Mrosovsky, 1983). It has been suggested that beach erosion and overwash on leatherback nesting beaches may be difficult to predict as they often nest on high-wave energy beaches and so there may be poor links between nest placement and embryo survival (Mrosovsky, 1983). However, Spanier (2010) and Neeman et al. (2015) found that for leatherbacks nesting on the Caribbean coast of Costa Rica, while nests tended to be laid on the open beach rather than in vegetation, turtles still avoided nesting below the HWL where the risk of inundation was highest, although nests were closer to the HWL than the vegetation line. Similarly, Caut et al. (2006) reported that for leatherbacks nesting in French Guiana, most nests were at the back of the beach in front of vegetation. It may be that other factors drive the tendency for leatherbacks not to nest within the vegetation zone, such as their softer carapace, compared with other species, which makes them less resistant to abrasions, or, like loggerhead turtles, they may struggle to dig nests in vegetated areas due to roots impeding their digging or due to their size making it difficult to carry themselves further up the beach.

Localized beach characteristics may also play a part in nest site selection for locations where leatherbacks nest. For example, dune scarps caused by beach erosion influence nest site selection in leatherbacks at Pacuare Nature Reserve, Caribbean Costa Rica, as Rivas et al. (2018) found dune scarps created a barrier on the nesting beach and around a quarter of the turtles, regardless of scarp height, would not crawl over them, consequently laying their eggs below the scarps in higher risk areas. This is also the case for flatback turtles at Fog Bay and Bare Sand Island in Northern Australia (Bannister et al., 2016; Blamires et al., 2003). Flatbacks on Bare Sand Island nest at the back of the wider beach on the western side of the island, where there is little to no vegetation, and it is the elevated sand dunes that constrain nesting (Bannister et al., 2016). Similarly, at Fog Bay, flatbacks nest mainly at the dune base and dune slope and very rarely nest on the dune crest (Blamires et al., 2003).

In summary, we have shown that at an important green turtle rookery in the Indian Ocean, as well as many other nesting sites around the world, sea turtles seem to select nesting sites away from the sea where the probability of nest inundation is minimized. These general findings suggest that maximizing hatching survival is the key determinant in nest site selection and so turtles might generally be unlikely to shift their nesting zones within beaches to mitigate climate warming. Even though turtles seem to generally crawl inland until the chances of nest inundation are low, a concern with climate change and sea level rise is that loss of nesting habitat, particularly for low-lying atolls, will mean turtles are unable to nest in safe beach zones (Rivas et al., 2023). How beaches respond to sea level change is therefore an important question and, in some cases, raising the beach by redistributing sand from higher beach areas to lower areas, as is already being implemented at some locations (e.g. Raine Island; Hamann et al., 2022; Smithers & Dawson, 2023), may be needed to improve egg survival.

Author Contributions

G.C.H. and N.E. conceived the project. H.S. and N.E. completed the fieldwork. H.S. led the data compilation and analysis. G.C.H. and H.S. led the writing with contributions from N.E.

Data Availability

Data are provided in the Supplementary Material.

Declaration of Interest

The authors declare no competing or financial interests.

Acknowledgments

We thank the many volunteers on Diego Garcia for logistical and fieldwork support. We are also grateful for logistical and fieldwork support from BF BIOT and Milly Fellows. This work was supported by the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science (projects 2017-4, 820633).

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2023.12.001.

References

Ávila-Aguilar, A. (2015). Selección de sitios de anidación de *Lepidochelys olivacea* (Testudines: Cheloniidae) en el Pacífico Sur de Costa Rica. *Revista de Biología Tropical, 63*, 375–381. https://doi.org/10.15517/rbt.v63i1.23116

Bannister, N., Holland, J., & Farrelly, T. (2016). Nest site fidelity of Flatback Turtles ('*Natator depressus*') on Bare Sand Island, Northern Territory, Australia. *Northern Territory Naturalist, 27*, 47–53. https://doi.org/10.5962/p.295467

Bison, M., Yoccoz, N. G., Carlson, B., Klein, G., Laigle, I., Van Reeth, C., Asse, D., & Delestrade, A. (2020). Best environmental predictors of breeding phenology differ with elevation in a common woodland bird species. *Ecology and Evolution, 10*, 10219–10229. https://doi.org/10.1002/ece3.6684

Blamires, S. J., & Guinea, M. L. (1998). Implications of nest site selection on egg predation at the sea turtle rookery at Fog Bay. In A. W. Kennet, G. Duff, M. L. Guinea, & G. Hill (Eds.), *Marine turtle conservation and management in Northern Australia* (pp. 20–24). Centre for Indigenous Natural and Cultural Resource Management & Centre for Tropical Wetlands Management, Northern Territory University, Darwin, Northern Territory University, Darwin.

Blamires, S. J., Guinea, M. L., & Prince, R. I. (2003). Influence of nest site selection on predation of flatback sea turtle (*Natator depressus*) eggs by varanid lizards in northern Australia. *Chelonian Conservation and Biology, 4*, 557–563.

Booth, D. T., Dunstan, A., Bell, I., Reina, R., & Tedeschi, J. (2020). Low male production at the world's largest green turtle rookery. *Marine Ecology Progress Series, 653*, 181–190. https://doi.org/10.3354/meps13500

Booth, D. T., & Freeman, C. (2006). Sand and nest temperatures and an estimate of hatchling sex ratio from the Heron Island green turtle (*Chelonia mydas*) rookery, Southern Great Barrier Reef. *Coral Reefs, 25*, 629–633. https://doi.org/10.1007/s00338-006-0135-4

Broderick, A. C., Godley, B. J., Reece, S., & Downie, J. R. (2000). Incubation periods and sex ratios of green turtles: Highly female biased hatchling production in the eastern Mediterranean. *Marine Ecology Progress Series, 202*, 273–281. https://doi.org/10.3354/meps202273

Carpio Camargo, A. J., Álvarez Gutiérrez, Y., Jaramillo Véliz, J., & Sánchez Tortosa, F. (2020). Nesting failure of sea turtles in Ecuador—causes of the loss of sea turtle nests: The role of the tide. *Journal of Coastal Conservation, 24*, 55. https://doi.org/10.1007/s11852-020-00775-3

Caut, S., Guirlet, E., Jouquet, P., & Girondot, M. (2006). Influence of nest location and yolkless eggs on the hatching success of leatherback turtle clutches in French Guiana. *Canadian Journal of Zoology, 84*, 908–915. https://doi.org/10.1139/z06-063

Charmantier, A., & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. *Evolutionary Applications, 7*, 15–28. https://doi.org/10.1111/eva.12126

Chen, H.-C., Cheng, I.-J., & Hong, E. (2007). The influence of the beach environment on the digging success and nest site distribution of the green turtle, *Chelonia mydas*, on Wan-an Island, Penghu Archipelago, Taiwan. *Journal of Coastal Research, 23*, 1277–1286. https://doi.org/10.2112/05-0455.1

Culver, M., Gibeaut, J. C., Shaver, D. J., Tissot, P., & Starek, M. (2020). Using lidar data to assess the relationship between beach geomorphology and Kemp's ridley (*Lepidochelys kempii*) nest site selection along Padre Island, TX, United States. *Frontiers in Marine Science, 7*, 214. https://doi.org/10.3389/fmars.2020.00214

DuRant, S. E., Willson, J. D., & Carroll, R. B. (2019). Parental effects and climate change: Will avian incubation behavior shield embryos from increasing environmental temperatures? *Integrative and Comparative Biology, 59*, 1068–1080. https://doi.org/10.1093/icb/icz083

Esteban, N., Laloë, J.-O., Mortimer, J. A., Guzman, A. N., & Hays, G. C. (2016). Male hatchling production in sea turtles from one of the world's largest marine protected areas, the Chagos Archipelago. *Scientific Reports, 6*, Article 20339. https://doi.org/10.1038/srep20339

Feiner, Z. S., Wang, H. Y., Einhouse, D. W., Jackson, J. R., Rutherford, E. S., Schelb, C., Vandergoot, C. S., Zorn, T. G., & Höök, T. O. (2016). Thermal environment and maternal effects shape egg size in a freshwater fish. *Ecosphere, 7*, Article e01304. https://doi.org/10.1002/ecs2.1304

Ficetola, G. F. (2007). The influence of beach features on nesting of the hawksbill turtle *Eretmochelys imbricata* in the Arabian Gulf. *Oryx, 41*, 402–405. https://doi.org/10.1017/s0030605307000543

Fuentes, M. M. P. B., Maynard, J. A., Guinea, M., Bell, I. P., Werdell, P. J., & Hamann, M. (2009). Proxy indicators of sand temperature help project impacts of global warming on sea turtles in northern Australia. *Endangered Species Research, 9*, 33–40. https://doi.org/10.3354/esr00224

Gane, J., Downs, C. T., Olivier, I., & Brown, M. (2020). Nesting ecology and hatching success of the hawksbill turtle (2004-2014) on Cousine Island, Seychelles. *African Journal of Marine Science, 42*, 53–65. https://doi.org/10.2989/1814232X.2020.1727952

Garmestani, A. S., Percival, H. F., Portier, K. M., & Rice, K. G. (2000). Nest-site selection by the loggerhead sea turtle in Florida's Ten Thousand Islands. *Journal of Herpetology, 34*, 504–510. https://doi.org/10.2307/1565263

Godley, B. J., Broderick, A. C., Glen, F., & Hays, G. C. (2002). Temperature-dependent sex determination of Ascension Island green turtles. *Marine Ecology Progress Series, 226*, 115–124. https://doi.org/10.3354/meps226115

Gravelle, J., & Wyneken, J. (2022). Resilient eggs: Highly successful loggerhead sea turtle nesting sites vary in their characteristics. *Frontiers in Ecology and Evolution, 10*, Article 853835. https://doi.org/10.3389/fevo.2022.853835

Hamann, M., Shimada, T., Duce, S., & Foster, A. (2022). Patterns of nesting behaviour and nesting success for green turtles at Raine Island, Australia. *Endangered Species Research, 47*, 217–229. https://doi.org/10.3354/esr01175

Hart, C. E., Ley-Quiñonez, C., Maldonado-Gasca, A., Zavala-Norzagaray, A., & Abreu-Grobois, F. A. (2014). Nesting characteristics of olive ridley turtles (*Lepidochelys olivacea*) on El Naranjo Beach, Nayarit, Mexico. *Herpetological Conservation and Biology, 9*, 524–534.

Hatase, H., & Omuta, K. (2018). Nest site selection in loggerhead sea turtles that use different foraging areas: Do less fecund oceanic foragers nest at safer sites? *Journal of Zoology, 305*, 232–239. https://doi.org/10.1111/jzo.12557

Hawkes, L. A., Broderick, A. C., Godfrey, M. H., & Godley, B. J. (2009). Climate change and marine turtles. *Endangered Species Research, 7*, 137–154. https://doi.org/10.3354/esr00198

Hays, G. C., Laloë, J.-O., Lee, P. L. M., & Schofield, G. (2023). Evidence of adult male scarcity associated with female-skewed offspring sex ratios in sea turtles. *Current Biology, 33*, R14–R15. https://doi.org/10.1016/j.cub.2022.11.035

Hays, G. C., Mackay, A., Adams, C. R., Mortimer, J. A., Speakman, J. R., & Boerema, M. (1995). Nest site selection by sea turtles. *Journal of the Marine Biological Association of the United Kingdom, 75*, 667–674. https://doi.org/10.1017/S0025315400039084

Hays, G. C., Mazaris, A. D., Schofield, G., & Laloë, J.-O. (2017). Populations viability at extreme sex-ratio skews produced by temperature-dependent sex determination. *Proceedings of the Royal Society B: Biological Sciences, 284*, Article 20162576. https://doi.org/10.1098/rspb.2016.2576

Hays, G. C., & Speakman, J. R. (1993). Nest placement by loggerhead turtles, *Caretta caretta*. *Animal Behaviour, 45*, 47–53. https://doi.org/10.1006/anbe.1993.1006

Hays, G. C., Taxonera, A., Renom, B., Fairweather, K., Lopes, A., Cozens, J., & Laloë, J.-O. (2022). Changes in mean body size in an expanding population of a threatened species. *Proceedings of the Royal Society B: Biological Sciences, 289*, Article 20220696. https://doi.org/10.1098/rspb.2022.0696

Heredero Saura, L., Jáñez-Escalada, L., López Navas, J., Cordero, K., & Santidrián Tomillo, P. (2022). Nest-site selection influences offspring sex ratio in green turtles, a species with temperature-dependent sex determination. *Climatic Change, 170*, 39. https://doi.org/10.1007/s10584-022-03325-y

Hope, R., & Smit, N. (1998). Marine turtle monitoring in Gurig National Park and Coburg Marine Park. In A. W. Kennett, G. Duff, M. Guinea, & G. Hill (Eds.), *Marine turtle conservation and management in Northern Australia* (pp. 53–62). Centre for Indigenous Natural and Cultural Resource Management & Centre for Tropical Wetlands Management, Northern Territory University, Darwin, Northern Territory University.

Horrocks, J. A., & Scott, N. M. (1991). Nest site location and nest success in the hawksbill turtle *Eretmochelys imbricata* in Barbados, West Indies. *Marine Ecology Progress Series, 69*, 1–8. https://doi.org/10.3354/meps069001

Jensen, M. P., Allen, C. D., Eguchi, T., Bell, I. P., Lacasella, E. L., Hilton, W. A., Hof, C. A. M., & Dutton, P. H. (2018). Environmental warming and feminization of one of the largest sea turtle populations in the world. *Current Biology, 28*, 154–159. https://doi.org/10.1016/j.cub.2017.11.057

Kamel, S. J., & Mrosovsky, N. (2004). Nest site selection in leatherbacks, *Dermochelys coriacea*: Individual patterns and their consequences. *Animal Behaviour, 68*, 357–366. https://doi.org/10.1016/j.anbehav.2003.07.021

Kamel, S. J., & Mrosovsky, N. (2005). Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences. *Animal Behaviour, 70*, 819–828. https://doi.org/10.1016/j.anbehav.2005.01.006

Kamel, S. J., & Mrosovsky, N. (2006). Inter-seasonal maintenance of individual nest site preferences in hawksbill sea turtles. *Ecology, 87*, 2947–2952. https://doi.org/10.1890/0012-9658(2006)87[2947:IMOINS]2.0.CO;2

Karavas, N., Georghiou, K., Arianoutsou, M., & Dimopoulos, D. (2005). Vegetation and sand characteristics influencing nesting activity of *Caretta caretta* on Sekania beach. *Biological Conservation, 121*, 177–188. https://doi.org/10.1016/j.biocon.2004.04.017

Kaska, Y., Başkale, E., Urhan, R., Katılmış, Y., Gidiş, M., Sarı, F., Sözbilen, D., Canbolat, A. F., Yılmaz, F., Barlas, M., Özdemir, N., & Özkul, M. (2010). Natural and anthropogenic factors affecting the nest-site selection of Loggerhead Turtles, *Caretta caretta*, on Dalaman-Sarıgerme beach in South-west Turkey. *Zoology in the Middle East, 50*, 47–58. https://doi.org/10.1080/09397140.2010.10638411

Kelly, I., Leon, J. X., Gilby, B. L., Olds, A. D., & Schlacher, T. A. (2017). Marine turtles are not fussy nesters: A novel test of small-scale nest site selection using structure from motion beach terrain information. *PeerJ, 5*, Article e2770. https://doi.org/10.7717/peerj.2770

Laloë, J.-O., Esteban, N., Berkel, J., & Hays, G. C. (2016). Sand temperatures for nesting sea turtles in the Caribbean: Implications for hatchling sex ratios in the face of climate change. *Journal of Experimental Marine Biology and Ecology, 474*, 92–99. https://doi.org/10.1016/j.jembe.2015.09.015

Laloë, J.-O., & Hays, G. C. (2023). Can a present-day thermal niche be preserved in a warming climate by a shift in phenology? A case study with sea turtles. *Royal Society Open Science, 10*, Article 221002. https://doi.org/10.1098/rsos.221002

Liles, M. J., Peterson, M. J., Seminoff, J. A., Altamirano, E., Henríquez, A. V., Gaos, A. R., Gadea, V., Urteaga, J., Torres, P., Wallace, B. P., & Peterson, T. R. (2015). One size does not fit all: Importance of adjusting conservation practices for endangered hawksbill turtles to address local nesting habitat needs in the eastern Pacific Ocean. *Biological Conservation, 184*, 405–413. https://doi.org/10.1016/j.biocon.2015.02.017

López-Castro, M. C., Carmona, R., & Nichols, W. J. (2003). Nesting characteristics of the olive ridley turtle (*Lepidochelys olivacea*) in Cabo Pulmo, southern Baja California. *Marine Biology, 145*, 811–820. https://doi.org/10.1007/s00227-004-1359-x

Márquez, R. (1994). *Synopsis of biological data on the Kemp's ridley turtle, Lepidochelys kempi (Garman, 1880)* (p. 152). US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center.

Martin, B. T., Dudley, P. N., Kashef, N. S., Stafford, D. M., Reeder, W. J., Tonina, D., Del Rio, A. M., Scott Foott, J., & Danner, E. M. (2020). The biophysical basis of thermal tolerance in fish eggs. *Proceedings of the Royal Society B: Biological Sciences, 287*, Article 20201550. https://doi.org/10.1098/rspb.2020.1550

Martins, S., Patrício, R., Clarke, L. J., de Santos Loureiro, N., & Marco, A. (2022). High variability in nest site selection in a loggerhead turtle rookery, in Boa Vista Island, Cabo Verde. *Journal of Experimental Marine Biology and Ecology, 556*, Article 151798. https://doi.org/10.1016/j.jembe.2022.151798

Maurer, A. S., & Johnson, M. W. (2017). Loggerhead nesting in the northern Gulf of Mexico: Importance of beach slope to nest site selection in the Mississippi barrier islands. *Chelonian Conservation and Biology, 16*, 250–254. https://doi.org/10.2744/ccb-1256.1

Mazaris, A. D., Schofield, G., Gkazinou, C., Almpanidou, V., & Hays, G. C. (2017). Global sea turtle conservation successes. *Science Advances, 3*, Article e1600730. https://doi.org/10.1126/sciadv.1600730

Mohd Salleh, S., Nishizawa, H., Ishihara, T., Sah, S. A. M., & Chowdhury, A. J. K. (2018). Importance of sand particle size and temperature for nesting success of green turtles in Penang Island, Malaysia. *Chelonian Conservation and Biology, 17*, 116–122. https://doi.org/10.2744/ccb-1266.1

Mohd Salleh, S., Nishizawa, H., Sah, S. A. M., Chowdhury, A. J. K., & Rusli, M. U. (2021). Sand particle size influences nest site selection of green turtles (*Chelonia mydas*) differently in east and west peninsular Malaysia. *Herpetological Conservation and Biology, 16*, 671–680.

Monsinjon, J. R., Wyneken, J., Rusenko, K., López-Mendilaharsu, M., Lara, P., Santos, A., dei Marcovaldi, M. A. G., Fuentes, M. M. P. B., Kaska, Y., Tucek, J., Nel, R., Williams, K. L., LeBlanc, A.-M., Rostal, D., Guillon, J.-M., & Girondot, M. (2019). The climatic debt of loggerhead sea turtle populations in a warming world. *Ecological Indicators, 107*, Article 105657. https://doi.org/10.1016/j.ecolind.2019.105657

Mortimer, J. A., Esteban, N., Guzman, A. N., & Hays, G. C. (2020). Estimates of marine turtle nesting populations in the south-west Indian Ocean indicate the importance of the Chagos Archipelago. *Oryx, 54*, 332–343. https://doi.org/10.1017/s0030605319001108

Mrosovsky, N. (1983). Ecology and nest-site selection of leatherback turtles *Dermochelys coriacea*. *Biological Conservation, 26*, 47–56. https://doi.org/10.1016/0006-3207(83)90047-2

Nasiri, Z., Gholamalifard, M., & Ghasempouri, S. M. (2022). Determining nest site selection by Hawksbill sea turtles in the Persian Gulf using unmanned aerial vehicles. *Chelonian Conservation and Biology, 21*, 256–265. https://doi.org/10.2744/ccb-1552.1

National Tidal and Sea Level Facility. (2021). *Tidal Predictions for British Overseas Territories, Diego Garica*. https://ntslf.org/tides/predictions-other. (Accessed 15 January 2022).

National Tidal and Sea Level Facility. (2022). *Tidal Predictions for British Overseas Territories, Diego Garcia*. https://ntslf.org/tides/predictions-other. (Accessed 15 January 2022).

Neeman, N., Harrison, E., Wehrtmann, I. S., & Bolaños, F. (2015). Nest site selection by individual leatherback turtles (*Dermochelys coriacea*, Testudines: Dermochelyidae) in Tortuguero, Caribbean coast of Costa Rica. *Revista de Biologia Tropical, 63*, 491–500. https://doi.org/10.15517/rbt.v63i2.14654

Patrício, A. R., Varela, M. R., Barbosa, C., Broderick, A. C., Ferreira Airaud, M. B., Godley, B. J., Regalla, A., Tilley, D., & Catry, P. (2018). Nest site selection repeatability of green turtles, *Chelonia mydas,* and consequences for offspring. *Animal Behaviour, 139*, 91–102. https://doi.org/10.1016/j.anbehav.2018.03.006

Pfaller, J. B., Limpus, C. J., & Bjorndal, K. A. (2009). Nest-site selection in individual loggerhead turtles and consequences for doomed-egg relocation. *Conservation Biology, 23*, 72–80. https://doi.org/10.1111/j.1523-1739.2008.01055.x

Pike, D. A., Roznik, E. A., & Bell, I. (2015). Nest inundation from sea-level rise threatens sea turtle population viability. *Royal Society Open Science, 2*, Article 150127. https://doi.org/10.1098/rsos.150127

Rivas, M. L., Rodríguez-Caballero, E., Esteban, N., Carpio, A. J., Barrera-Vilarmau, B., Fuentes, M. M. P. B., Robertson, K., Azanza, J., León, Y., & Ortega, Z. (2023). Uncertain future for global sea turtle populations in face of sea level rise. *Scientific Reports, 13*, 5277. https://doi.org/10.1038/s41598-023-31467-1

Rivas, M. L., Spínola, M., Arrieta, H., & Faife-Cabrera, M. (2018). Effect of extreme climatic events resulting in prolonged precipitation on the reproductive output of sea turtles. *Animal Conservation, 21*, 387–395. https://doi.org/10.1111/acv.12404

Rumaida, M. Y., Putra, S. A., Mulyadi, A., & Nasution, S. (2021). Nesting habitat characteristics of green sea turtle (*Chelonia mydas*) in the Tambelan archipelago, Indonesia. *Journal of Coastal Conservation, 25*, 6. https://doi.org/10.1007/s11852-021-00798-4

Salmon, M., Reiners, R., Lavin, C., & Wyneken, J. (1995). Behavior of loggerhead sea turtles on an urban beach. I. Correlates of nest placement. *Journal of Herpetology, 29*, 560–567. https://doi.org/10.2307/1564739

Santos, K. C., Livesey, M., Fish, M., & Lorences, A. C. (2017). Climate change implications for the nest site selection process and subsequent hatching success of a green turtle population. *Mitigation and Adaptation Strategies for Global Change, 22*, 121–135. https://doi.org/10.1007/s11027-015-9668-6

Santos, A. J. B., Neto, J. X. L., Vieira, D. H. G., Neto, L. D., Bellini, C., De Souza Albuquerque, N., Corso, G., & Soares, B. L. (2016). Individual nest site selection in hawksbill turtles within and between nesting seasons. *Chelonian Conservation and Biology, 15*, 109–114. https://doi.org/10.2744/ccb-1136.1

Sarahaizad, M. S., Shahrul Anuar, M. S., & Mansor, Y. (2012). Nest site selection and digging attempts of green turtles (*Chelonia mydas*, Fam. Cheloniidae) at Pantai Kerachut and Telok Kampi, Penang Island, Peninsular Malaysia. *Malaysian Applied Biology, 41*, 31–39.

Serafini, T. Z., Lopez, G. G., & Rocha, P. L. B. D. (2009). Seleção de locais de nidificação e sucesso de eclosão da tartaruga-de-pente e da tartaruga-cabeçuda (Testudines, Cheloniidae) na Praia de Arembepe, nordeste do Brasil. *Phyllomedusa: Journal of Herpetology, 8*, 3–17. https://doi.org/10.11606/issn.2316-9079.v8i1p03-17

Sivasunder, A., & Devi Prasad, K. (1996). Placement and predation of nest in leatherback sea turtles in the Andaman Islands, India. *Hamadryad Madras, 21*, 36–42.

Smithers, S. G., & Dawson, J. L. (2023). Beach reprofiling to improve reproductive output at the world's largest remaining green turtle rookery: Raine Island, northern Great Barrier Reef. *Ocean & Coastal Management, 231*, Article 106385. https://doi.org/10.1016/j.ocecoaman.2022.106385

Spanier, M. J. (2010). Beach erosion and nest site selection by the leatherback sea turtle *Dermochelys coriacea* (Testudines: Dermochelyidae) and implications for management practices at Playa Gandoca, Costa Rica. *Revista de Biología Tropical, 58*, 1237–1246.

Stoneburner, D. L., & Richardson, J. I. (1981). Observations on the role of temperature in loggerhead turtle nest site selection. *Copeia, 1981*, 238–241. https://doi.org/10.2307/1444068

Turkozan, O., Yamamoto, K., & Yılmaz, C. (2011). Nest site preference and hatching success of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles at Akyatan Beach, Turkey. *Chelonian Conservation and Biology, 10*, 270–275. https://doi.org/10.2744/ccb-0861.1

Wang, H.-C., & Cheng, I. J. (1999). Breeding biology of the green turtle, *Chelonia mydas* (Reptilia: Cheloniidae), on Wan-An Island, PengHu archipelago. II. Nest site selection. *Marine Biology, 133*, 603–609.

Whitesell, M. J., Hunter, E. A., Rostal, D. C., & Carroll, J. M. (2022). Direct and indirect pathways for environmental drivers of hatching success in the loggerhead sea turtle. *Marine Ecology Progress Series, 701*, 119–132. https://doi.org/10.3354/meps14197

Whitmore, C. P., & Dutton, P. H. (1985). Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname. *Biological Conservation, 34*, 251–272. https://doi.org/10.1016/0006-3207(85)90095-3

Witt, M. J., Hawkes, L. A., Godfrey, M. H., Godley, B. J., & Broderick, A. C. (2010). Predicting the impacts of climate change on globally distributed species: The case of the loggerhead turtle. *Journal of Experimental Biology, 213*, 901–911. https://doi.org/10.1242/jeb.038133

Wood, D. W., & Bjorndal, K. A. (2000). Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. *Copeia, 2000*, 119–128. https://doi.org/10.1643/0045-8511(2000)2000[0119:Rotmsa]2.0.Co;2

Zare, R., Vaghefi, M. E., & Kamel, S. J. (2012). Nest location and clutch success of the hawksbill sea turtle (*Eretmochelys imbricata*) at Shidvar Island, Iran. *Chelonian Conservation and Biology, 11*, 229–234. https://doi.org/10.2744/CCB-1003.1

Zavaleta-Lizárraga, L., & Morales-Mávil, J. E. (2013). Nest site selection by the green turtle (*Chelonia mydas*) in a beach of the north of Veracruz, Mexico. *Revista Mexicana de Biodiversidad, 84*, 927–937. https://doi.org/10.7550/RMB.31913

Appendix

Table A1
Sea turtle nest distribution studies around the world, including the general study location, sea turtle species and the beach zone where nests were predominantly found

Number	General location (list of study sites)	Sea turtle species	Beach zone	Source
1	Diego Garcia, Chagos Archipelago	Green, *Chelonia mydas*	In vegetation	Current study
2	Redang and Penang Island, Malaysia	Green, *Chelonia mydas*	In vegetation	Mohd Salleh et al. (2018); Mohd Salleh et al. (2021); Sarahaizad et al. (2012)
3	Tambelan Archipelago, Indonesia	Green, *Chelonia mydas*	In vegetation	Rumaida et al. (2021)
4	Penghu Archipelago, Taiwan	Green, *Chelonia mydas*	In vegetation	Chen et al. (2007); Wang and Cheng (1999)
5	Veracruz and Quintana Roo, Mexico	Green, *Chelonia mydas*	In vegetation	Santos et al. (2017); Zavaleta-Lizárraga & Morales-Mávil, 2013
6	Cabuyal, Costa Rica	Green, *Chelonia mydas*	In vegetation	Heredero Saura et al. (2022)
7	Manabí, Ecuador	Green, *Chelonia mydas*	In front of vegetation	Carpio Camargo et al. (2020)
8	Wia-Wia Nature Reserve, Suriname	Green, *Chelonia mydas*	In vegetation	Whitmore and Dutton (1985)
9	Ascension Island	Green, *Chelonia mydas*	Open beach above high water line	Hays et al. (1995)
10	Bijagós Archipelago, Guinea-Bissau	Green, *Chelonia mydas*	Open beach above high water line	Patrício et al. (2018)
11	Akyatan Beach, Turkey	Green, *Chelonia mydas*	In vegetation	Turkozan et al. (2011)
11	Akyatan Beach; Dalaman-Sarigerme beach Turkey	Loggerhead, *Caretta caretta*	In front of vegetation	Kaska et al. (2010); Turkozan et al. (2011)
12	Yakushima Island, Japan	Loggerhead, *Caretta caretta*	In front of vegetation	Hatase and Omuta (2018)
13	Sunshine coast, Australia	Loggerhead, *Caretta caretta*	In front of vegetation	Kelly et al. (2017)
14	Sanibel and Captiva Islands; Boca Raton; Ten Thousand Islands; Boca Raton, Juno Beach, Hutchinson Island, Archie Carr National Wildlife Refuge, and Canaveral National, Florida Seashore	Loggerhead, *Caretta caretta*	In front of vegetation	Garmestani et al. (2000); Gravelle and Wyneken (2022); Hays et al. (1995); Salmon et al. (1995)
15	Bahia, Brazil	Loggerhead, *Caretta caretta*	In front of vegetation	Santos et al. (2016); Serafini et al. (2009)
16	Boa Vista Island, Cape Verde	Loggerhead, *Caretta caretta*	Open beach above high water line	Martins et al. (2022)
17	Cephalonia Island and Zákynthos, Greece	Loggerhead, *Caretta caretta*	In front of vegetation	Hays and Speakman (1993); Karavas et al. (2005)
18	El Salvador and Estero Padre Ramos, Nicaragua	Hawksbill, *Eretmochelys imbricata*	In vegetation	Liles et al. (2015)
7	Manabí, Ecuador	Hawksbill, *Eretmochelys imbricata*	In front of vegetation	Carpio Camargo et al. (2020)
19	Trois Ilets and Folle Anse beaches, Guadeloupe	Hawksbill, *Eretmochelys imbricata*	In vegetation	Kamel and Mrosovsky (2005)
20	Barbados	Hawksbill, *Eretmochelys imbricata*	In vegetation	Horrocks and Scott (1991)
15	Bahia, Brazil	Hawksbill, *Eretmochelys imbricata*	In vegetation	Santos et al. (2016); Serafini et al. (2009)
21	Qatar; Shidvar Island, Iran; Nakhiloo, Ommolkaram and Nayband Bay in Bushehr Province, Persian Gulf	Hawksbill, *Eretmochelys imbricata*	In front of vegetation	Ficetola (2007); Nasiri et al. (2022); Zare et al. (2012)
22	Cousine Island, Seychelles	Hawksbill, *Eretmochelys imbricata*	Open beach above high water line	Gane et al. (2020)
23	Playa Gandoca; Tortuguero, Costa Rica	Leatherback, *Dermochelys coriacea*	Open beach above high water line	Neeman et al. (2015); Spanier (2010)
8	Wia-Wia Nature Reserve, Suriname	Leatherback, *Dermochelys coriacea*	Open beach above high water line	Whitmore and Dutton (1985)
24	Awala Yalimapo beach, French Guiana	Leatherback, *Dermochelys coriacea*	In front of vegetation	Caut et al. (2006)
25	Andaman Islands, India	Leatherback, *Dermochelys coriacea*	In front of vegetation	Sivasunder and Devi Prasad (1996)
26	Cabo Pulmo, Baja California peninsula, Mexico	Olive ridley, *Lepidochelys olivacea*	Open beach above high water line	López-Castro et al. (2003)
27	El Naranjo Beach, Nayarit, Mexico			Hart et al. (2014)

(*continued on next page*)

Table A1 (*continued*)

Number	General location (list of study sites)	Sea turtle species	Beach zone	Source
		Olive ridley, *Lepidochelys olivacea*	Open beach above high water line	
28	Piro and Pejeperro, Osa Peninsula, Costa Rica	Olive ridley, *Lepidochelys olivacea*	In front of vegetation	Ávila-Aguilar (2015)
29	Fog Bay, Northern Territory, Australia	Olive ridley, *Lepidochelys olivacea*	Open beach above high water line	Blamires and Guinea (1998)
30	Fog Bay; Bare Island, Northern Territory; Mundabullangana, Western Australia, Australia	Flatback, *Natator depressus*	Open beach above high water line	Bannister et al. (2016); Blamires et al. (2003)
31	Greenhill Island, Northern Territory, Australia	Flatback, *Natator depressus*	In front of vegetation	Hope and Smit (1998)
32	Rancho Nuevo, Mexico	Kemp's ridley, *Lepidochelys kempii*	In front of vegetation	Márquez (1994)
33	Padre Island, Texas, U.S.A.	Kemp's ridley, *Lepidochelys kempii*	In front of vegetation	Culver et al. (2020)

Numbers correspond to the numbers displayed in Fig. 5.