



# Patterns of nesting behaviour and nesting success for green turtles at Raine Island, Australia

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**ABSTRACT:** To understand how turtles use the nesting habitat at Raine Island across a nesting season, and how the turtles respond to the restoration of the island's dune systems, we identified 534 nesting events for 39 green turtles *Chelonia mydas* across 2 breeding seasons using data derived from satellite tags. Tracked turtles laid between 4 and 10 clutches of eggs. Patterns of nesting success varied between individuals, within and between seasons. Nesting success was higher in 2018-19 (57%) than 2017-18 (45%), and in both years, nesting success was lowest between October and early January (<50%). In 2017-18, increased rainfall in January corresponded with increased nesting success (>50%). The density of female turtles ashore was lower in 2018-19, and likely explains higher nesting success in 2018-19 because competition for nest space was lower. In 2017-18, females had more attempts per clutch, and the attempts were around 90 min longer. Consequently, energy required to lay a clutch of eggs in 2017-18 was significantly higher than in 2018-19, highlighting potential costs of lower nesting success rates on reproductive output. The area of beach re-profiled as an intervention in 2014 and 2017 was a nesting hotspot in 2017-18. However, in 2018-19, the area was not used to the same extent, and the nesting hotspot occurred on the north-eastern unaltered beach. Collectively, the tracking of turtles across the whole nesting season enabled us to assess overall beach use and nesting site fidelity of green turtles at Raine Island. Results will aid future planning and management of beach restoration activities at turtle nesting sites.

**KEY WORDS:** *Chelonia mydas* · Reproduction · Marine turtle · Energetic costs · Fidelity · Fastloc GPS · Reproductive ecology · Restoration

## 1. INTRODUCTION

A ubiquitous issue for many threatened species of the world is the loss or alteration of their habitats. In particular, species reliant on coastal ecosystems are increasingly threatened by anthropogenic development, sea level rise or other biophysical changes (Wallace et al. 2011, Xu et al. 2019). Losses of, or changes to, these habitats are problematic for many long-lived migratory species because responses, such as the movement into peripheral habitats, may

be slow and occur across generational timescales. Increasingly, the restoration of altered habitats is being undertaken to reverse change, slow down the rates of change or restore adaptive capacity in the species affected (Hale et al. 2019, Hill et al. 2019). Hence it is important to understand both how species use their existing habitats and the extent to which they will respond to loss, change or restoration of breeding sites (Ikin et al. 2019).

Adult female marine turtles take decades to reach maturity, return to natal regions to breed and show

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long-term fidelity to nesting habitats (Limpus et al. 2003, Dethmers et al. 2006). Consequently, although across evolutionary time scales marine turtle species have coped throughout periods of significant habitat change, the rates of existing and predicted change to coastlines will challenge the way marine turtles can respond (Hamann et al. 2007). Hence, they are vulnerable to changes in their breeding habitats such as habitat loss/alterations due to coastal development, light pollution, sea level rise and coastal erosion. Alterations to nesting habitats are known to reduce available nesting space, which could lead to density-dependent impacts, increase disturbance to females, their ability to dig nest chambers and lay eggs, or influence the physical properties of the sand important for the incubation of eggs (Limpus et al. 2003). Each of these can act to reduce short-term (seasonal) or longer-term reproductive output from the rookery. In response to habitat loss and degradation, active interventions are increasingly being used as mitigation options (Fuentes et al. 2020). Examples, and their relevance to nesting marine turtles, include dune/beach modification (Nelson Sella et al. 2019), planting or replanting of vegetation along coastal habitats (including non-native) (de Vos et al. 2019), manipulation of clutches of eggs (e.g. shifting them to managed hatcheries and/or shading clutches) (Mrosovsky 2008, Pfaller et al. 2009), removing non-native predators, protecting nests from predators (Nordberg et al. 2019) and managing developments and their associated impacts such as beach access, beach use and light pollution. Fundamental to their development and to evaluating the success of these projects is knowledge on how turtles use the nesting beach within and across nesting seasons, including clutch number, factors that influence success and site fidelity (Hamann et al. 2010).

Quantifying nesting success at a beach or across a season is generally conducted by observing turtles on the beach or is determined after the nesting event by assessing the track and nest site for characteristics of successful versus unsuccessful attempts (Godley et al. 2001, Limpus et al. 2003, 2020, Chen et al. 2007, Ware & Fuentes 2020). These metrics most commonly provide data at a beach or rookery scale, but patterns of individual nesting success are less commonly reported, especially in remote or high-density rookeries, or rookeries with pro-longed breeding seasons (Weber et al. 2013, Rees et al. 2016, Pfaller et al. 2022). This is important because female turtles do not always lay a clutch of eggs on each attempt, and nesting success can be influenced by several factors such as the presence of obstacles, light pollution or

shadows, movement (including of other turtles) and the condition of the site such as dry sand or the presence of vegetation (e.g. Mortimer & Carr 1987, Godley et al. 2001, Chen et al. 2007). Importantly, nesting success data form a basis for the conversion between numbers of tracks and number of clutches/females or converting counts of the number of turtles on a beach to seasonal abundance and long-term trends (Godley et al. 2001, Weber et al. 2013, Esteban et al. 2017, Mortimer et al. 2020, Shimada et al. 2021a). These count data are now collected using drones and artificial intelligence (Schofield et al. 2019) as well as by conventional beach surveys for status assessments and thus require validation.

Raine Island is a small (32 ha) coral cay in the northern section of Australia's Great Barrier Reef that supports over 90% of the nesting activity for one of the world's largest green turtle *Chelonia mydas* populations, with an average of around 60 000 females breeding per year (Limpus et al. 2003). However, in the late 1990s and early 2000s, it became clear that while the island still supported a large number of nesting turtles and turtles tagged in previous years continued to return, the ability of females to lay eggs and have their eggs incubate successfully was being compromised by changes in both the distribution of beach sediments around the island and the bio-physical conditions of the nesting environments (Limpus et al. 2003, Dawson & Smithers 2010, 2020). In particular, there were areas of the beaches' swale section that either did not provide suitable sand depth for females to dig a nest, or the depth of clutches was close to the high-tide water table thus exposing clutches to inundation on higher tides (Dawson & Smithers 2010, 2020, Booth & Dunstan 2018). The consequences of these changes are long-term with at least 25 yr of reduced hatchling production and climate-related pressure believed to threaten the long-term viability of the green turtle population (Limpus et al. 2003, Fuentes et al. 2010a, Dunstan et al. 2020).

Due to the changes occurring at Raine Island, and concerns for the long-term viability of Raine Island as a location supporting successful nesting and incubation by green turtles, the Queensland Government initiated the Raine Island Recovery Project. This project was a 5 yr, AUD \$7.95 million collaboration between BHP Pty Ltd, the Queensland Government, the Great Barrier Reef Marine Park Authority, Wuthathi, Kemer Kemer Meriam Nation (Traditional Owners of Raine Island) and the Great Barrier Reef Foundation. The project support enabled management agencies to manually re-profile the dune sand

in 2 sections of the island, in order to restore the beach within these sections to a depth capable of supporting nest excavation by female turtles and the incubation of eggs. In both 2014 and 2017, approximately 100 by 150 m long sections of beach were re-profiled using machinery, by redistributing sand from the higher beach areas to the rest of the beach system to raise the height of the beach above the tidal inundation level.

The behaviour and biology of nesting turtles has been documented by beach-based research and monitoring for many decades. Despite significant effort, understanding of season-long behaviour such as reproductive output, habitat use and site fidelity of individuals often remains elusive for some species or populations, especially those breeding in remote areas such as Raine Island. Over the past decade, Fastloc GPS satellite trackers have increasingly been used by researchers to understand individual nesting attempts and associated behaviour of turtles throughout a nesting season, hence removing the reliance of in-person surveys to quantify life history traits (Weber et al. 2013, Esteban et al. 2017). Thus, to understand how the turtles use the nesting habitat at Raine Island and how the turtles respond in the short term to the restoration of the island's dune systems, we deployed Fastloc GPS tags on female green turtles throughout 2 nesting seasons to obtain data on each nesting attempt for tracked turtles across the nesting season. Our aim was to use the high-resolution location data from satellite telemetry to describe the reproductive behaviour of green turtles on Raine Island, including their nest site selection, site fidelity, nesting success and their use of areas of the Raine Island beach which were re-profiled by management agencies in 2014 and 2017.

## 2. MATERIALS AND METHODS

### 2.1. Study site

Raine Island (11° 35' 25" S, 144° 02' 05" E) is located on the outer edge of the northern Great Barrier Reef and is part of the Raine Island National Park (Scientific). The coral cay is situated on a detached reef lying outside of the Australian continental shelf, and its physical features have been described by Limpus et al. (2003). The circumference of the island is approximately 1800 m at the high tide level (Limpus et al. 2003, Dawson & Smithers 2010). The nesting habitat available to turtles lies between the island's berm (roughly equivalent to the mean high water

mark) and the phosphatic limestone cliff which surrounds an internal area that is largely inaccessible to turtles. The beach width between the berm and cliff ranges from around 15 m on the north-east side of the island to 90 m at the southern side (Limpus et al. 2003).

### 2.2. Data collection

At the beginning of the main nesting seasons, 19 (in 2017-18) and 20 (in 2018-19) green turtle females were randomly captured and fitted with Argos-linked Fastloc-GPS tags following the methods of Shimada et al. (2012). Turtles were located by walking around the circumference of the island. After a turtle had completed egg laying she was moved to a central location for application of the tag. Between 1 and 6 turtles were caught and tagged per night. Turtles were restrained in wooden-sided pens and tags were attached using Sika Anchorfix 3 and painted with 2 coats of Micron-66 anti-foul. Turtles were kept for 6 to 8 h while the epoxy set and released at the site of tag attachment. The tags were deployed between 31 October and 4 November 2017 and between 18 and 23 October 2018. For data analysis, we refer to October 18 as the start of the nesting season (Limpus et al. 2001, 2003). It is important to note that the turtles tracked in 2018 were tagged earlier than those tracked in 2017. Each of the tagged females was released on the morning after tags were attached. The higher resolution of locations received with the Fastloc-GPS (approximately 40 m) enabled us to understand fine-scale movement of green turtles on Raine Island (Dujon et al. 2014, Lopez et al. 2014, Shimada et al. 2016). The tags were set with a haul-out phase which started after the tag was dry for more than 10 min and recorded the duration of the haul-out event, ending when the tag was wet for 10 min. Each tag remained attached to the turtle until after she had completed the nesting season and had begun a migration towards her foraging area.

### 2.3. Data preparation

The satellite-derived location data were filtered to remove inaccurate positions by using the 'SDLfilter' package in R version 3.6.0 (Shimada 2018, R Core Team 2019). We removed locations generated by fewer than 5 GPS satellites, and biologically implausible positions according to time, distance and angle

between successive points (Shimada et al. 2012, 2016). Using ArcGIS version 10.6.1, the filtered locations were then plotted and separated into on-land data if the points were inside the berm (based on the berm locations surveyed using Real Time Kinematic GPS in 2017), and in-water if outside the berm. The on-land location data were extracted and combined with the haul-out data to classify each attempt and clutch for each female. The haul-out function on the tags is set to record the duration a tag is dry (out of the water). Nesting events for each of the turtles were classified as clutch (successful events) and attempt (unsuccessful events). The definition of an attempt was an event where the turtle returned to the beach within the same or following 7 nights, and clutch was an event where the turtle did not return to the beach, or a neighbouring island, for at least the following 8 nights, indicating a clutch was laid (Hamann et al. 2003). The duration of an event was determined from the tag's haul-out data and the duration between first and last on-land GPS location for each event. Because the frequency of locations per event varied between turtles and nights, we could not examine the distance a turtle travelled per event. To prepare data for analysis on the density of clutch and attempt location, the last location before midnight (or closest to midnight if she emerged after midnight) of each of event was selected and used to represent the clutch or attempt location.

We define the inter-nesting period as the duration (days) between the first clutch we observed (equal to the date of tag attachment) and the last clutch we recorded for each female. We define the re-nesting interval as the duration (days) between the date a female laid a clutch of eggs and the date of her next attempt, regardless of success (Limpus et al. 2001). We used 18 October as the start dates of the 2017 and 2018 seasons because this was the earliest date of our surveys. We acknowledge that some turtles may have laid an earlier clutch of eggs prior to the beginning of our monitoring. All parameters except total clutch number and clutch location exclude the data from clutch corresponding with tag attachment because we have no way of knowing their nesting activity prior to the night of tag attachment (such as the number of attempts or the duration of the attempt).

#### 2.4. Data analysis

The filtered GPS location data for each nesting event were mapped using ArcGIS for analysing clutch frequency, nesting success (successful or

unsuccessful nesting attempts), nest site fidelity, event duration and the beach site used (including the re-profiled areas). All data were projected to UTM Zone 55. To examine clutch density, a layer of 40 by 40 m grid cells was created across the study region (between the berm and the island cliff) using the 'Create Fishnet' tool, and the 'Spatial Join' tool was used to calculate the total number of successful clutches laid within each cell. This created a layer showing the density of nests and was displayed using a colour gradient. The 40 by 40 m size was applied because the accuracy distance of filtered GPS point averages ~40 m (Shimada et al. 2012). The same method was applied to create a layer showing the density of unsuccessful nests per 40 by 40 m cell. These nesting density layers were assessed using the 'Hotspot Analysis' (Getis Ord  $G_i^*$ ) tool in ArcGIS to identify statistically significant hotspot areas for both successful and unsuccessful nesting attempts (Evans et al. 2019; refer to <https://pro.arcgis.com/en/proapp/latest/tool-reference/spatial-statistics/hot-spot-analysis.htm> for further explanation). This tool compares the density values in a 'neighbourhood' with the average density across the entire study region to assess whether high-density areas are clustered together (hotspots) or dispersed (coldspots) beyond what would be expected given random chance (Getis & Ord 1992). The conceptualisation of spatial relationships was defined using first-order queen contiguity weighting (i.e. cells which share corners or edges were deemed part of each cell's 'neighbourhood'). False discovery rate correction was applied to account for multiple testing and spatial dependency (Caldas de Castro & Singer 2006). The cost of a nesting activity can be calculated as  $543 \text{ kJ h}^{-1}$  based on a mean maximum oxygen consumption of  $0.206 \text{ l O}_2 \text{ kg}^{-1} \text{ h}^{-1}$  for nesting green turtles (Prange & Jackson 1976), a mean weight of nesting green turtles at Raine Island of 126 kg (Limpus et al. 2003) and the assumption that the main energy source for nesting turtles is fat (Bjorndal 1982, Hamann et al. 2002). Summary statistics are provided as means  $\pm$  SD unless otherwise stated.

To analyse fine-scale nest site fidelity, we calculated the centroid location of Raine Island, and using a northern bearing from the centroid, we calculated the direction in degrees of each clutch location. The data in degrees were then converted into circular format using the 'circular' package in R (Agostinelli & Lund 2017). A Rayleigh test (Rtest) was used to determine the degree to which each individual turtle laid her clutches in a cluster, where Rayleigh Rtest values are between 0 and 1, with values closer 1 indicating

a higher degree of clustering. The distance between clutches was determined by calculating the distance in metres around the low tide circumference of Raine island between the north bearing and the position perpendicular to each clutch location. Distances between clutches for each individual turtle were then calculated. The circumference of the island was 2100 m and thus the maximum distance around the beach between clutches was 1050 m.

### 2.5. Nest density and rainfall data

Nightly turtle count data were collected following the methods of Limpus et al. (2003). In short, turtles on the beach were counted once in a night by at least 4 researchers walking a circuit of the island in a perpendicular line from the berm to cliff clockwise around the island and counting turtles between themselves and the person to the left. Daily rainfall was collected in 2017 by the Raine Island weather station, and no rainfall data were available in 2018. We used the 24 h accumulated rainfall totals for each day at 09:00 h. The unpublished turtle count and rainfall data were made available to us by the Queensland Government.

## 3. RESULTS

We satellite-tracked 19 and 20 turtles during 2017-18 and 2018-19 nesting seasons, respectively. Two turtles, one in each year, switched between laying clutches at Raine Island and a nearby rookery (Moulter Cay). In 2017 turtle QA75003 laid 5 clutches of eggs for the season: 3 on Raine Island and 2 on Moulter Cay, with a season-long nesting success of 33%. In 2018, turtle QA88237 laid 7 clutches of eggs for the season: 2 on Raine Island and 5 on Moulter Cay, with a season-long nesting success of 50%. We did not include their data in our analysis for Raine Island.

### 3.1. Nightly abundance of nesting turtles

The number of turtles nesting for the season was approximately 11 times larger in 2017-18 than 2018-19. For example, on 30 October in the 2017-18 season, 799 nesting turtles were recorded, compared to 70 turtles on the same date in 2018-19. Similarly, during the peak nesting season, the nightly tally counts were 5220 and 446 turtles on 9 December in 2017 and 2018, respectively.

### 3.2. Number of clutches

In 2017-18, the 18 turtles that remained at Raine Island for their entire breeding season laid 130 clutches, with individual females laying an average of 6.7 clutches each (range 4–10). The females had an average inter-nesting period of 88 d (range 51–100 d) and an average re-nesting interval of 11 d (9–22 d). In 2018, the 19 turtles that remained at Raine Island for their entire breeding season laid 140 clutches, with individual females laying an average of 7.3 clutches each (range 5–9). The females had an average inter-nesting period of 79 d (range 52–96) and an average re-nesting interval of 11 (9–16 d).

### 3.3. Patterns of nest site distribution

In 2017-18, the mean number of clutches laid by the tracked turtles per 40 × 40 m grid was  $0.76 \pm 1.12$  (range 0–6). Of all cells, 56% contained no clutches, 36% contained 1 or 2 clutches, 7% contained 3–5 clutches, and 6 cells contained >5 clutches (Fig. 1a). The hotspot analysis revealed that grid cells with significantly higher numbers of clutches were clustered on the south to south-eastern side of the island within the 2017 re-profiled zone (Fig. 1b). In 2018-19, the mean number of clutches laid by the tracked turtles per grid cell was  $0.83 \pm 1.35$  (range 0–8). Of all cells, 58% contained no clutches, 32% contained 1 or 2 clutches, 8% contained 3–5 clutches, and 3 cells contained >5 clutches (Fig. 1c). The hotspot analysis revealed that grid cells with significantly higher numbers of clutches predominantly occurred on the north-east of the island (Fig. 1d).

### 3.4. Nesting effort and nesting success

The patterns of nesting attempts around the island were generally similar in both years, and while in 2017-18 the hotspot analysis revealed a cluster of unsuccessful nesting on the south beach (Fig. 2b), in 2018-19 the unsuccessful attempts were spread randomly around the island (Fig. 2d). The overall mean seasonal nesting success for the tracked turtles, excluding their first recorded clutch, was 45.1% (130 clutches out of 288 nesting events) and 57.0% (140 clutches out of 246 nesting events) for 2017-18 and 2018-19, respectively. In both years, nesting success varied among individuals (2017-18 range  $15.9 \pm 5$  to  $82 \pm 31\%$ ; 2018-19 range  $38.3 \pm 35$  to  $90.4 \pm 25\%$ ) and across the season (Fig. 3). In both years, nesting



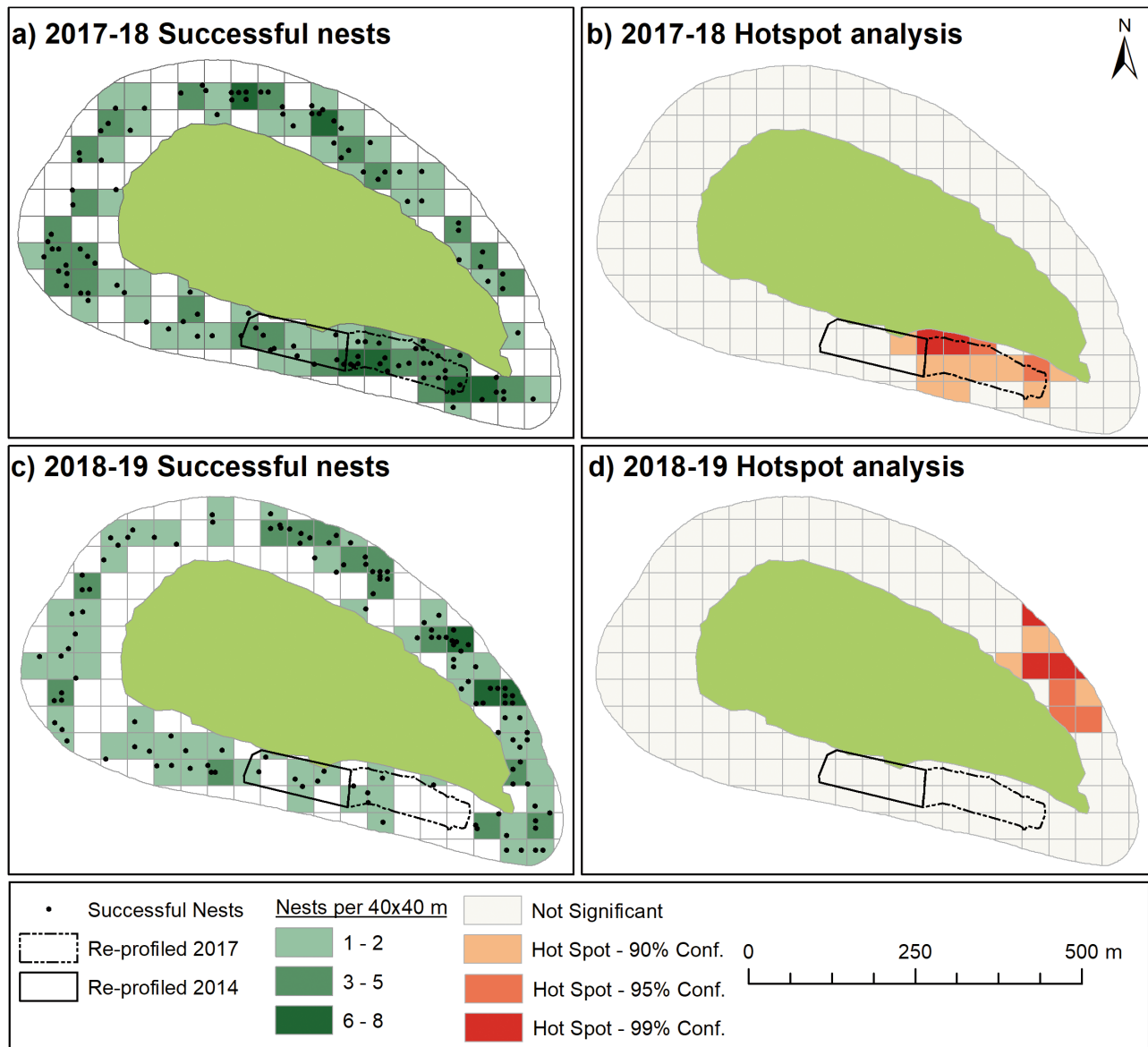


Fig. 1. (a,c) Clutch density and (b,d) hotspot analysis of clutches laid by tracked green turtles on Raine Island in 2017-18 ( $n = 124$ ; a,b) and 2018-19 ( $n = 135$ ; c,d) nesting seasons. Each grid =  $40\text{ m} \times 40\text{ m}$ . The outer edge of the polygon represents the berm and a cliff surrounds the outer edge of the central green polygon

success was lowest between early November and early January and highest from early January onwards (Day 75 onwards). Similarly, rainfall varied across the season, and 5 d accumulated rainfall was zero or low from 18 October until 6 January, with only one 24 h period prior to this experiencing  $>10\text{ mm}$  on 2–3 December (Fig. 4). After 5 January, the 5 d accumulated rainfall was generally above 50 mm, and corresponding nesting success exceeded 75% each week (Fig. 4).

The average number of attempts per clutch laid and the number of nights a female took to lay a

clutch of eggs varied both between individuals and across the season, especially in 2017. Collectively, the average number of attempts per clutch ranged from 1.0 to 6.1 and from 1.0 to 4.4 in 2017-18 and 2018-19, respectively. In general, in both years, the clutches laid between late November and early January took more attempts per female. We received durations from the haul out function for 92 and 80% of emergences in 2017-18 and 2018-19, respectively. The mean duration taken per unsuccessful nesting was significantly higher in 2017 ( $307 \pm 195\text{ min}$ ) than in 2018 ( $180 \pm 148\text{ min}$ )

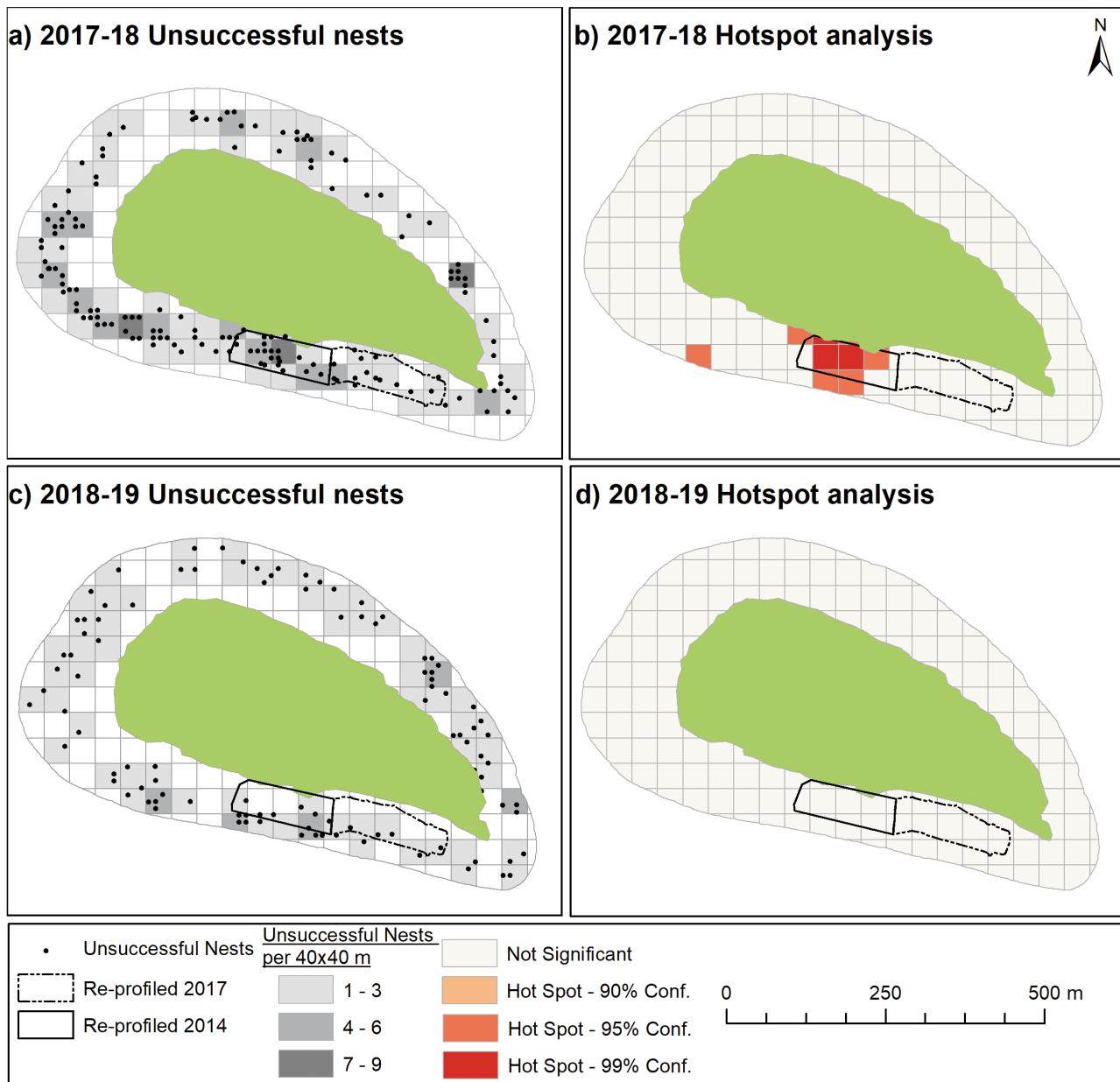


Fig. 2. (a,c) Unsuccessful nesting attempt density and (b,d) hotspot analysis of unsuccessful nesting attempts by tracked green turtles on Raine Island in 2017-18 ( $n = 174$ ; a,b) and 2018-19 ( $n = 105$ ; c,d) nesting seasons. Each grid = 40 m  $\times$  40 m

( $t = 4.16$ ,  $df = 207$ ,  $p$  [2-tailed]  $< 0.01$ ), and the mean duration of successful nesting attempts was similar in the 2 years (2017:  $371 \pm 160$  min; 2018:  $334 \pm 148$  min) ( $t = 0.74$ ,  $df = 209$ ,  $p$  [2-tailed] = 0.45).

However, although the duration of a successful nesting event was similar between years, the number of unsuccessful attempts, and the longer duration of unsuccessful nesting attempts, in 2017-18 compared to 2018-19 led to a significant difference in the cumulative duration a female spent ashore to lay each clutch of eggs between 2017-18 ( $782 \pm$

$435$  min) and 2018-19 ( $402 \pm 145$  min) ( $t = 3.585$ ,  $df = 21$ ,  $p$  [2-tailed]  $< 0.01$ ), and a significant difference in the cumulative duration a female spent ashore to lay her seasons' clutches between the 2 years (2017:  $4776$  min; 2018:  $2929$  min) ( $t = 4.19$ ,  $df = 29$ ,  $p$  [2-tailed]  $< 0.01$ ). Consequently, the energy cost per clutch was significantly higher in 2017 ( $7210 \pm 4005$  kJ per clutch, range 2701–18671 kJ) compared to 2018 ( $3836 \pm 1397$  kJ per clutch, range 1956–6786 kJ) ( $t = 5.12$ ,  $df = 145$ ,  $p$  [2-tailed]  $< 0.001$ ).

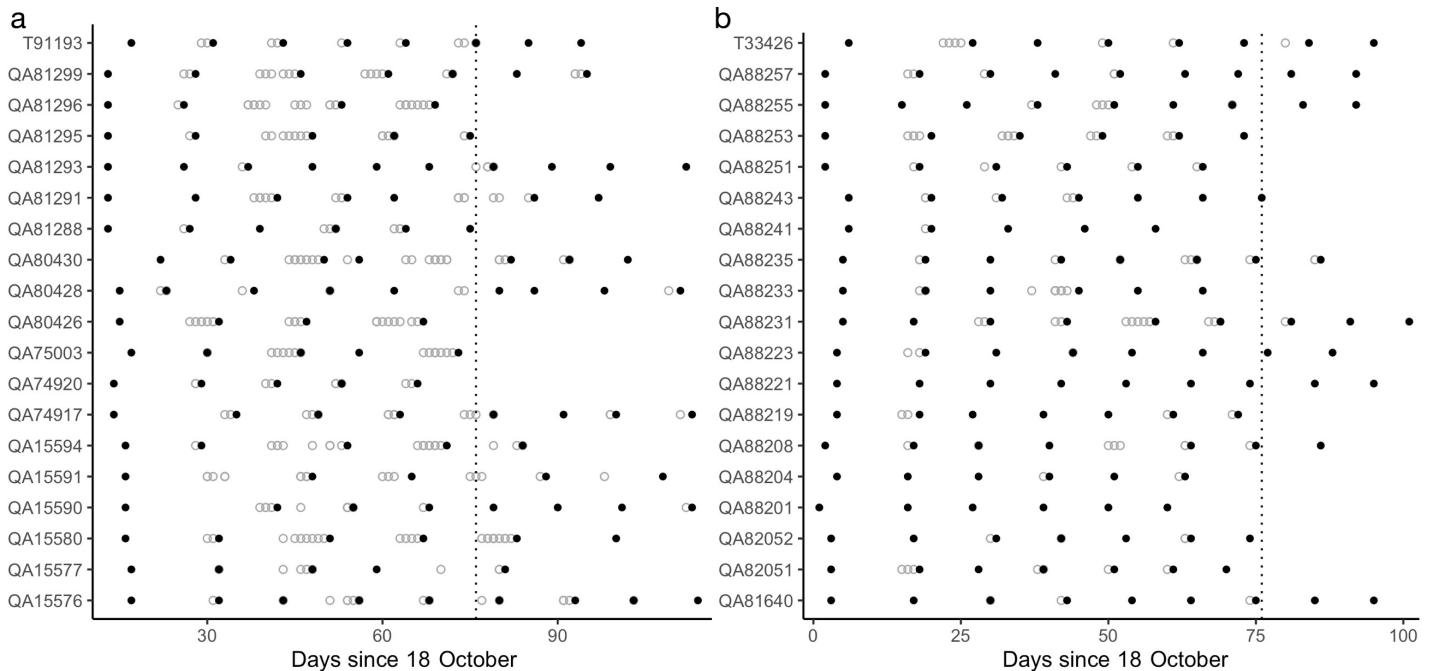


Fig. 3. Seasonal nesting profiles of individual tracked green turtles at Raine Island in (a) 2017-18 and (b) 2018-19. Black circles indicate a day with a successful nesting attempt (clutch laid) and open circles indicate a day with an unsuccessful nesting attempt (no clutch laid). Day 1 is 18 October in both years, and the dashed line indicates 1 January

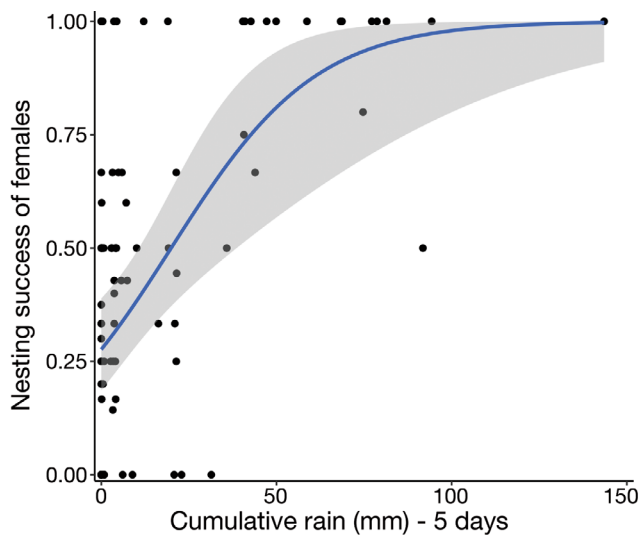


Fig. 4. Relationship between daily nesting success and accumulated rainfall (preceding 5 d) for turtle nesting events for each day during the 2017-18 nesting season (grey area refers to 95% CI). No rainfall data are available for the 2018-19 nesting season

### 3.5. Fine-scale nest site fidelity

In both nesting seasons, approximately half of the tracked turtles showed significant site fidelity, laying their clutches at localised areas on Raine Island (10 of 18 in 2017-18 and 10 of 19 in 2018-19). Of all turtles

tracked, 16 showed no significant fidelity among their seasons' clutch locations (all with Rayleigh Rtest values  $< 0.58$  and  $p > 0.05$ ) (Fig. 5a), and 21 females had significant fidelity to sections of Raine Island (Rtest values ranged from 0.63 to 0.97 and  $p < 0.05$ ); of these, 7 were clustered with no outliers (Rtest values 0.83 to 0.97, e.g. Fig. 5b), 5 were clustered bimodally (Rtest values 0.63 to 0.80, e.g. Fig. 5c), and 8 were clustered with a single outlier (Rtest values 0.69 to 0.88, e.g. Fig. 5d). The mean distance between successive clutches was significantly shorter in females showing site fidelity (mean 270 m between clutches) compared to females without fidelity (mean 461 m between clutches,  $t = 6.8$ ,  $df = 204$ ,  $p$  [2-tailed]  $< 0.001$ ). In both years, the distance between the turtles' first and second clutches did not significantly differ from the distances between subsequent clutches (1-way ANOVA  $F = 0.97$ ,  $df = 7$ ,  $p = 0.45$ ).

### 3.6. Use of the re-profiled sections of the beach

The area re-profiled in 2017 was a nesting hotspot area in 2017-18 and contained 28 out of 111 clutches laid by the tracked turtles. The turtles using the area had 70% nesting success, which was approximately 34% higher than the nesting success recorded for events in the remainder of the island (36%) including



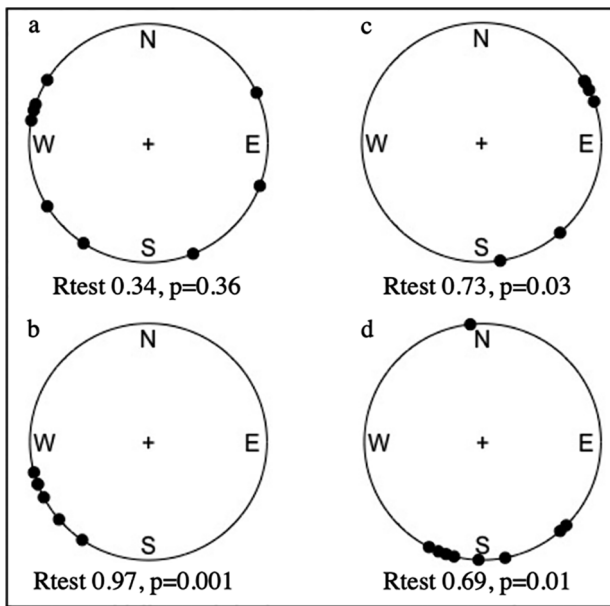


Fig. 5. Examples of circular clutch distribution plots assessing site fidelity in nesting green turtles tracked at Raine Island. Black dots represent clutch locations around Raine Island converted to degrees from north. Rayleigh Rtest values are between 0 and 1, with values closer 1 indicating a higher degree of clustering (see Section 2.4). Example of a female showing (a) no nest site fidelity, (b) significant fidelity to the SW region of the island, (c) significant bi-modal fidelity and (d) significant fidelity with a single outlier

the area re-profiled in 2014 ( $F = 11.01$ ,  $df = 267$ ,  $p < 0.001$ ). In 2018-19, the area re-profiled in 2017 was not a nesting hotspot and contained 6 of 121 clutches. Nesting success was similar between the areas re-profiled in 2017 (50%) and unaltered areas (60%) but was significantly lower in the areas re-profiled in 2014 (23%) ( $F = 5.54$ ,  $df = 242$ ,  $p < 0.004$ ).

#### 4. DISCUSSION

During the 2 breeding seasons, we tracked 39 nesting female green turtles throughout their nesting season. Of these, 37 remained to lay all subsequent clutches at Raine Island, and 2 females split their clutches between Raine Island and nearby Moulter Cay. Our results indicate that the tracked females laid between 4 and 10 clutches of eggs each and spent between 50 and 100 d in the vicinity of Raine Island before beginning a migration back to their foraging area. The nesting success of female turtles averaged 45% in 2017-18 and 57% in 2018-19 and varied among individuals, by location on the beach and with rainfall. Approximately half of the turtles demonstrated within-season site fidelity by cluster-

ing their clutches within a section of the island. Collectively, our results support the idea that nesting turtles demonstrate high fidelity to nesting sites (e.g. Godley et al. 2001, Weber et al. 2013), nesting behaviour is energetically costly (e.g. Bjorndal 1982), and cumulative unsuccessful nesting attempts, as were common early in the nesting season, could influence reproductive output of females (Hamann et al. 2002).

Satellite-tracking individuals enabled us to follow the nesting behaviour of each tracked animal throughout the whole nesting season and revealed that patterns of nesting success varied considerably among individuals, but also across and between seasons, with an average of around 50%. This is within the range of values reported for beaches at Ascension Island in the Southern Atlantic Ocean (Godley et al. 2001, Weber et al. 2013) and for previous seasons at Raine Island (Limpus et al. 2003), lower than the mean nesting success (63%) reported for green turtles nesting along the Red Sea coast of Saudi Arabia (Shimada et al. 2021b) and higher than nesting success reported in a long-term study of loggerhead turtles *Caretta caretta* in the Mediterranean (Margari-toulis 2005).

In both 2017-18 and 2018-19, our data indicate there were female turtles with consistently high or consistently low nesting success, and nesting success was lowest between the start of the season and early January. Nesting success in the drier part of the season was nearly 10% lower in the higher-density year (2017-18) than the lower-density year (2018-19). In addition, in 2017 nesting success was low up until the island received 5 d accumulations of rainfall above 50 mm. A similar response of greatly improved nesting success with increased sand moisture or rainfall has been reported later in the summer for green turtles at Bramble Cay, another nesting beach with a similar island type and sand characteristics to Raine Island (Fuentes et al. 2010b). This supports the idea that nesting success, and possibly the density of females ashore at night, is influenced by the moisture of the sand and the micro-habitat chosen by the turtle (Limpus et al. 2001).

Recognising this variability in the influence of rainfall is important because nesting success is not always recorded across a season, and thus sampling or monitoring could occur during periods with more, or less, favourable conditions for successful nesting. However, previous results of similar studies aiming to examine relationships between weather and nesting success have found a variety of relationships. Some, such as Godley et al. (2001) and Pike (2008), did not find relationships between nesting success

and rainfall patterns, while other studies have revealed relationships between nesting success and lower humidity and lower air temperature (Thums et al. 2020), nesting success with higher barometric pressure (Pike 2008) and lower nesting success with elevated daytime temperature (Shimada et al. 2021b). Given that all of these environmental variables are related to each other, previous studies plus our research highlight the need to collect site-specific weather and nesting success data across seasons. Doing so will enable improved understanding of how local climate and environmental and biophysical components influence turtle nesting patterns and subsequent estimates of abundance, especially when sub-season sampling for nesting success or surveys for abundance are completed.

The energetic cost of nesting in green turtles at Raine Island has been estimated at 543 kJ h<sup>-1</sup> (this study) and 510 kJ h<sup>-1</sup> (Bjørndal 1982). Our results indicate that the mean length of time a female spends on the beach at Raine Island to lay a clutch of eggs is 344 min, and the average duration of an unsuccessful attempt is 178 minutes. We found that it takes around 3000 kJ of energy to support the emergence, nest digging, laying, and concealing a clutch and 1600 kJ to support the physical exertion of an unsuccessful attempt. Hence, because green turtles are capital breeders and are not replenishing energy stores while they are at the nesting sites (Hamann et al. 2003), repeated unsuccessful nesting attempts can have important consequences for energy budgets over the nesting season. Indeed, based on our data, the physical act of digging associated with 2 unsuccessful nesting attempts would have a similar energy requirement as the physical act of digging, laying and concealing 1 clutch (based on our calculations of the energy to lay 1 clutch). Thus, while we found similar numbers of clutches being laid in the 2 study seasons, in 2017-18, the year with lower levels of nesting success, individuals with more attempts per clutch laid fewer clutches for the season. Our data suggest that cumulative unsuccessful nesting attempts leading to >3 attempts per clutch may lead to a compromised reproductive output through resorption of ovarian follicles through atresia, presumably to preserve energy stores for a return migration (Hamann et al. 2002). Indeed, in a year where nesting success was around 10%, the rates of ovarian atresia throughout the season were elevated and detectable in females in the peak of the nesting season (Limpus et al. 2005).

In the northern Great Barrier Reef, capture-mark-recapture of nesting turtles at Bramble Cay indicated that females laid an average of 6 clutches per year,

but also that turtles arriving for nesting earlier in the season tended to lay more clutches for the season than those arriving later (Limpus et al. 2001). Thus, knowing when in the season the turtles were tagged and recaptured is important. In our study, we found females laid between 4 and 10 clutches with an average of 6 clutches in 2017-18 and 7 clutches in 2018-19. This is around a clutch higher per season than the seasonal average for the population calculated from nearby Bramble Cay (Limpus et al. 2001). However, our results are very similar to the values for Bramble Cay if we use only the data derived from a subset of the Bramble Cay turtles that were initially tagged at a similar time of the season as the Raine Island nesters (i.e. 18–22 October and 29 October to 4 November, Limpus et al. 2001). Plus, there were already tracks on the beach when we arrived for both of our survey trips and when the research team arrived at Bramble Cay, so both studies may have missed the first clutch of the season for some individuals.

Clearly, the use of satellite GPS telemetry can provide detailed information on seasonal reproductive output, but it is important to also understand the relationship between arrival date of a female and the number of clutches she lays. Obtaining certainty about the nesting history (i.e. whether she has laid a clutch of eggs prior to tag attachment, or whether she is likely to lay a clutch after the date of tag attachment) or planning satellite telemetry studies at particular times throughout the season will require either comprehensive monitoring of the nesting beach(es) from before the first turtles arrive, or the use of ultra-sound or laparoscopic examination of females prior to tag attachment. Our data add further support to the conclusions of Tucker (2010), Weber et al. (2013) and Esteban et al. (2017), who all highlighted the value of satellite telemetry in the quantification of important life-history parameters where comprehensive, season-wide capture-mark-recapture cannot easily be conducted, or the density (high or low) precludes genetics-based population surveys (e.g. Shamblin et al. 2017, 2021).

As natural spaces are increasingly altered due to direct physical change or indirectly through changes to bio-physical processes, there is a need for discussion about the necessity for, and relevance of, restoration (Fuentes et al. 2020). Raine Island is an important nesting habitat for green turtles, and the nesting environment has changed in ways that have led to reductions in the ability of females to dig nests and the success of clutches (Dunstan & Robertson 2017). Restoration of the beach profile was undertaken as a restoration activity, and it was expected that turtles

would use the restored area and have higher levels of nesting success than elsewhere on the island. It is clear from our results that turtles continued to use the areas reprofiled in 2014 and 2017. However, the patterns and success of the use of these areas, and the rest of the island, differed across years. In both years, the tracked turtles laid clutches of eggs around most of the island. In 2017-18, close to 60% of clutches were laid on the southern beach and a third of all clutches were laid in the reprofiled areas at the southeastern end of the island (Fig. 1a). In comparison, in 2018-19, a lower-density year, the opposite pattern occurred, with 60% of clutches being laid on the northern side of the island, and a third of all clutches being laid on the northeastern side (Fig. 1c). Patterns of nesting success were similar on an island scale in both years; however, the nesting success of turtles attempting to nest in the 2014 reprofiled area was lower than the island average. Although patterns emerged in both years, these nesting success and clutch distribution data need to be considered in the context of overall seasonal nesting patterns, historically and among seasons. It could be that use of sections of the beach is random until good habitat is found, and a clutch is laid. Hence the use and fidelity to the different areas across years could be linked to a turtle's discovery of good habitat for her first clutch. However, we do not have data on individual behaviour prior to tag attachment to test this hypothesis. There are also no data from previous years that we can use to examine whether lower or higher proportions of turtles used the sections of beach prior to reprofiling, or to examine nesting patterns across seasons to determine whether the shift of activity from the southeast (2017-18) to the northeast (2018-19) reflects natural variation driven by local variation in wind direction, nearshore currents, proximity to inter-nesting habitat or other unknown factors.

One of the keys to understanding how turtles will respond to short- and long-term, acute or pervasive changes to their nesting habitat is understanding site fidelity. Based on studies elsewhere, the general pattern is that turtles return to their natal region to breed, and once they have completed their first breeding season, they will often, but not always (Pfaller et al. 2022), show long-term site fidelity to the same breeding site in subsequent breeding seasons (Meylan et al. 1990, Shimada et al. 2020, Shamblin et al. 2021). In addition, females could also lay each of their clutches in and across seasons in the same micro-habitats (Hays et al. 1995, Kamel & Mrosovsky 2006, Patrício et al. 2018), or between beaches on islands, or on the same sections of longer beaches

(Weber et al. 2013, Shamblin et al. 2017) and the selection and repeat use of micro-habitats could confer fitness benefits. Of the 39 turtles that we tracked, 2 females laid clutches on 2 different islands, moving between them throughout the season with similar nesting success on both, and of the remaining 37, approximately half showed significant clustering of all their clutches within 300 m of each other and half did not cluster clutches, with an average distance of ~500 m between clutches. Similar season-wide, beach-scale fidelity by nesting green turtles was observed at Ascension Island (Weber et al. 2013) and in the Red Sea (Shimada et al. 2021b). While site fidelity may function to enable clutches to be laid in areas that produce hatchlings, it also serves to delay any responses to longer-term changes to habitats, because (1) turtles may persist nesting in areas which change over time, or in unsuitable areas and/or (2) the responses could be driven by new recruits to the breeding population (Hamann et al. 2007, Pfaller et al. 2022). In addition, we are unable to determine whether the female is choosing the section of beach, or whether sections are more favourable in terms of access and/or sand conditions and thus receive a higher proportion of nesting because the micro-habitats are better or easier to access given the prevailing environmental conditions on a given night. Future studies coupling mark-recapture data, genetics, telemetry data, beach conditions, tides and wind direction could solve these uncertainties.

Given the current and predicted rates of change affecting coastal environments, targeted protection and conservation interventions are likely to become increasingly necessary. Thus, there is a corresponding need to understand how species may respond to changes to their habitats or interventions targeted at minimising impacts. The conclusions from our research highlight the effectiveness of using satellite telemetry to quantify key biological parameters for threatened marine species and demonstrates how tracking can be used to follow and assess turtles as they navigate changes to their habitats. Importantly, it also highlights the value of developing and implementing systems to collect environmental data concurrent with tagging mark-recapture programmes, census data or telemetry projects to enable behavioural changes to be linked to habitat and environmental change and to provide improved estimates of population abundance.

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