



# **Nesting habitat characteristics of flatback**  *Natator depressus***, green** *Chelonia mydas* **and loggerhead** *Caretta caretta* **turtles in eastern Queensland, Australia**

**Lauren Heddle1,2,\*, Katharina J. Peters3 , Mark Hamann4 , Guido J. Parra2**

**1 School of Biological Sciences, University of Western Australia, Crawley, WA 6009, Australia 2 Cetacean Ecology, Behaviour and Evolution Lab, College of Science and Engineering, Flinders University, Adelaide, SA 5042, Australia** 

**3 Marine Vertebrate Ecology Lab, Environmental Futures, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW 2522, Australia** 

**4 College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia**

ABSTRACT: Coastal areas provide essential habitats for marine turtle nesting and hatching, but they are under increasing threat due to climate change and other anthropogenic impacts. Very little is known about the nesting habitat characteristics of flatback *Natator depressus*, green *Chelonia mydas* and loggerhead *Caretta caretta* turtles in eastern Queensland, which limits our ability to evaluate which nesting beaches are at risk due to anthropogenic and environmental disturbances and prioritise conservation and monitoring actions. Here, we used generalised linear models to investigate the relationship between the presence/absence of flatback, green and loggerhead turtle nests and environmental and topographic characteristics of 237 potential nesting sites along the central and southern coasts of Queensland. The presence of nesting flatback turtles was strongly correlated with the mainland and non-coral cay islands with decreasing latitude, as there is an interaction between site type and latitude. In contrast, green turtles preferred to nest on coral cays rather than mainland and island beaches. Loggerhead turtles were more likely to nest on coral cays, the mainland, then islands, with presence increasing with latitude. Among these site types and higher latitudes, presence was stronger on sheltered than on semi-exposed beaches. Identifying environmental and topographical features influencing the presence of nesting flatback, green and loggerhead turtles is an important first step to improve the conservation of these species by prioritising sites for monitoring and managing threats to important beaches.

KEY WORDS: Sea turtles · Habitat changes · Nesting distribution · Habitat degradation · Spatial ecology · Reproduction

# **1. INTRODUCTION**

Nesting and breeding habitats are critical for species to reproduce and survive (Carbonell et al. 2003, FitzSimmons et al. 2020). A species will likely thrive if its habitat meets specific environmental requirements (Tellería 2016). Thus, understanding where

\*Corresponding author: lauren.heddle@gmail.com

species nest and the characteristics of their nesting sites is fundamental for their conservation. Nesting beach selection, the process by which female sea turtles choose a specific beach on which to lay their eggs, is widely regarded as a key process, as the nesting environment can strongly influence reproductive success (Kikukawa et al. 1999), and there is an adap-

Publisher: Inter-Research · www.int-res.com

<sup>©</sup> The authors 2024. Open Access under Creative Commons by Attribution Licence. Use, distribution and reproduction are unrestricted. Authors and original publication must be credited.

tive trade-off between the cost of searching for a site (increased energy expenditure and the risk of predation) and the reproductive benefits of selecting a site appropriate for successful incubation (Miller et al. 2003, Katselidis et al. 2012). Overall, for marine turtle reproduction to be successful, a beach must be chosen to provide the environmental conditions necessary for adult emergence onto the shore, nest building, oviposition, incubation and hatchling dispersal (Miller 2017).

The environmental drivers of beach selection for marine turtles are not well understood (Hamann et al. 2011). Marine turtles exhibit natal homing and longterm nesting site fidelity, and females are believed to select nesting locations to minimise predation risk and their energy expenditure and maximise reproductive success and the ease with which they can return to sea (Lohmann et al. 1996). Adult female turtles deposit their eggs in shallow nests (approximately 45–75 cm deep) on the dunes of sandy beaches (Limpus 1971, Loop et al. 1995), and since they provide no parental care, they cannot compensate for poorly selected nesting beaches or changes to the environment near the nest after oviposition (Fuentes et al. 2016). Thus, selecting suitable nesting beaches and establishing rookeries is important for the species' reproductive fitness (Hamann et al. 2011), and the environmental attributes of nesting beaches play a critical role in determining marine turtle hatchling fitness and survival (Lohmann et al. 1996). However, many coastal areas currently used by turtles are experiencing accelerating human use and urbanisation, resulting in increased light and noise pollution, habitat degradation, beach compaction, pollution and beach stabilisation (Kamrowski et al. 2012, Fuentes et al. 2016, 2020). These pressures on marine turtle habitat jeopardise the quality of nesting sites and can change the behaviour of the nesting females and their hatchlings and have population-scale consequences (Koch & Guinea 2006). Thus, understanding the environmental drivers of beach selection is key for their conservation and management.

Marine turtles select nesting beaches across various spatial scales according to environmental and topographic factors (Kikukawa et al. 1999). At re gional scales (10s of km), the choice of nesting beach is thought to be primarily determined by variations in weather, coastal features and oceanographic conditions as well as the natal homing behaviour of the nesting females (philopatry) (Bannister et al. 2016, FitzSimmons et al. 2020). At the beach scale (100s of m), it has been hypothesised that nesting beach selection by adult females may be influenced by local environmental conditions, including beach morphology,

dune vegetation and sediment attributes (grain size and sand temperature) (Pike 2013).

The habitat of the nesting beach must allow egg laying and, once laid, embryonic development and survival of embryos and hatchlings by being well drained and aerated and having low salinity, high humidity and an appropriate temperature fluctuation (Miller et al. 2003, Laloë et al. 2014). This indicates that besides vegetation, shoreline characteristics are an important predictor of nesting beach selection. Nesting beach selection is also important for hatchlings, as the character of the beach, including elevation, moisture and temperature, can change with distance from the ocean (Miller et al. 2003). Therefore, understanding the information individuals use to determine their choice of nesting beach is important to understand the species' vulnerability to habitat changes, the evolution of nesting beach selection and the conservation of the species.

In Australia, marine turtles are known to nest along most of the northern coastline (Queensland across the north and west to central Western Australia) (Queensland Government 2022). Considering that many of the nesting beaches across this range are isolated, large and remote, acquiring fine-scale environmental, topographic and abundance data to understand beach selection is challenging.

Although general patterns of the nesting beach selection of marine turtles are known from presence/ absence surveys, there are many gaps in the distribution of monitoring efforts by species and nesting beach location (Queensland Government 2022). This information is required to obtain research goals listed under Action Area A2 of the Australian Government's Marine Turtle Recovery Plan (Queensland Government 2022). Such information is particularly important for threatened species such as flatback *Natator depressus* and green *Chelonia mydas* turtles, which are listed as vulnerable, and loggerhead *Caretta caretta* turtles, which are listed as endangered in Queensland due to various threats, such as habitat degradation, sea level rise, beach stabilisation and light and noise pollution (Queensland Government 2022).

The few studies investigating nest site selection (nesting suitability within beaches) in Australian marine turtles have been conducted in Western Australia and the Northern Territory (Garcon et al. 2010, Bannister et al. 2016, Thums et al. 2020). These studies have not examined nesting beach selection (nesting suitability at a coastal scale) specifically. However, they have found attributes influencing beach selection, such as beach topography (beach slope, dune elevation, wind and wave exposure). Previous studies outside of Australia have found species-specific patterns with marine turtle beach selection preferences, such as green turtles preferring low-lying coral cays that are highly vegetated (shade) and sheltered (Fuentes et al. 2010b, Ferreira 2019, Heredero Saura et al. 2022) and loggerhead turtles preferring beaches with a low slope, higher exposure to wind and wave action, high vegetation and high elevation (Varela et al. 2019, Siqueira-Silva et al. 2020, Patino-Martinez et al. 2023). While it is important to understand the nesting characteristics of marine turtles to assess the species' vulnerability to changes in their habitat, very little is known about inter- and intra-species variation in nesting beach characteristics across spatial scales used by populations.

This study aims to identify the environmental and topographic attributes of the beaches along the east coast of Queensland that may be associated with flatback, green and loggerhead turtle nesting beach selection. Specifically, we (1) collated available data on the presence/absence of flatback, green and loggerhead turtles along the east coast of Queensland; (2) characterised each of these nesting beaches according to environmental and topographic features thought to influence nesting beach selection; and (3) assessed the relationship between the presence/absence of flatback, green and loggerhead turtle nests and the environmental and topographic features of these beaches using generalised linear models (GLMs).

## **2. METHODS**

#### **2.1. Study area**

The study area included the southern and central Queensland coastline, covering the latitudinal range of the eastern Australian flatback turtle population, the southern Great Barrier Reef (GBR) green turtle population and the Queensland loggerhead population (Fig. 1). The coastline has a subtropical humid climate with both a wet season (Dec–Mar) and a relatively dry season (Apr–Nov) (Butt et al. 2016), and the turtle nesting season for all species occurs between October and March.

## **2.2. Data collection**

## 2.2.1. Marine turtle nesting beaches

We accessed turtle nesting distribution data from the Queensland Government database (Queensland Government 2022). The Queensland Government's Department of Environment and Science has had an ongoing marine turtle monitoring project since 1968 across the study area, and turtle nesting sites are well known for each species (Queensland Government 2022). Survey effort differs across sites



Fig. 1. Study area along the eastern Queensland coastline. Coloured symbols indicate nesting beaches for flatback, green, loggerhead and mixed (more than 1 species present) turtles. Data are provided by the Queensland Government turtle nesting distribution monitoring program (Queensland Government 2022). Bathymetry is indicated by different shades of blue; inset map indicates location study area in relation to Australia

and years, as data were collected by various methods over 50 yr. Surveys to count clutches of turtles are not done on most turtle nesting beaches. Regular annual monitoring, including surveys every day for the entire nesting season, for flatback, green and loggerhead turtles only occurs on approximately 10 to 15 of their approximately 100 nesting beaches. We therefore used presence/absence as our response/predictor variable rather than abundance data in this study. The response variable was defined as 1 for a beach if the species was recorded to be present at an abundance of at least 1 to 10 females per year at a beach in the Queensland Government database and as 0 if the species was recorded as absent. Although the presence/ absence data are based on different methods, marine turtles have high site fidelity and have likely nested on the same beach for hundreds of years (Lettrich et al. 2020). We acknowledge that absence scores for a beach, especially mainland beaches, may not always represent an absolute absence, as turtle presence may be undetectable due to female nesting attempts occurring at such a low density and frequency to be detected by any surveys. We also acknowledge that some presence beaches might be from infrequent nesting records.

## 2.2.2. Environmental and topographic variables

We collected environmental and topographic variables known to influence nesting beach selection by turtles from a range of platforms for each turtle nesting beach in the study area. The selection of these variables depended on their availability over the temporal and spatial scale of the turtle nesting monitoring data (Table 1) (Kikukawa et al. 1999, Fuentes et al. 2011, Katselidis et al. 2012, Patrício et al. 2019, Thums et al. 2020). These variables in clude exposure (sheltered, semi-exposed or exposed), site type (mainland, island or coral cay), shoreline characteristics (sand, rocky reef and sand, rock, mixed fines, gravel or fringing coral reef), elevation (m) and latitude.

#### **2.3. Data analysis**

Through visual inspection of boxplots and histograms of shoreline characteristics, slope, elevation, vegetation, exposure, latitude, site type and beach orientation (Figs. S1 & S2 in the Supplement at [www.](https://www.int-res.com/articles/suppl/n054p353_supp.pdf) [int-res.com/articles/suppl/n054p353\\_supp.pdf\)](https://www.int-res.com/articles/suppl/n054p353_supp.pdf), we identified site type (mainland, island or coral cay),

shoreline characteristics, elevation, exposure (sheltered, semi-exposed or exposed) and latitude as strong proxies of flatback, green and loggerhead turtle nesting beach selection (see Section 3). Be cause of their flexibility to incorporate multiple quantitative and qualitative independent variables (Laloë et al. 2017, Williams et al. 2017), we used GLMs (Agresti 2015) to assess the simultaneous effects of exposure (wind and waves), site type, shoreline characteristics and elevation on the presence/absence of nesting female flatback, green and loggerhead turtles (Text S1).

We assessed spatial autocorrelation for all nesting beaches and each variable using the Mantel test (Table S1, Legendre et al. 2015), and we assessed multicollinearity among the explanatory variables with Cramer's *V*-test (Shishkina et al. 2018) for categorical variables (site type, exposure and beach type) and the point biserial correlation test to test for correlation between the numerical variables (elevation and latitude) (Kornbrot 2014). The variable shoreline characteristics was removed from the analysis, given its strong correlation with site type (Fig. S3, see Section 3) (Mansfield & Helms 1982).

To determine which explanatory variables best predict flatback, green and loggerhead turtle presence, we built 16 models with binomial distribution with a logit link function using all possible combinations of the remaining 4 variables. We ranked them based on Akaike's information criterion corrected for small sample size (AICc) (Burnham et al. 2011) (Tables S2– S4). We checked the top-ranked models (within 3 AICc of each other) for interactions between variables and over-dispersion, normality and apparent patterns in the residuals. Where the top-ranked model had at least 2 non-interacting variables, we evaluated the relative importance of each explanatory variable by calculating the change in goodness of fit (i.e. the adjusted amount of deviance accounted for by the GLM) when the respective variable was left out of the full model (Weisberg 2005). This method is equivalent to a sensitivity analysis for the final model, allowing us to quantify and rank the relative importance of each explanatory variable for the full model. All analyses were conducted using R version 4.2.1 (R Core Team 2022).

# **3. RESULTS**

We collated data on flatback, green and loggerhead turtle nesting locations along 194 beaches along the central and southern Queensland coast of Australia



Table 1. Environmental and topographic variables used to model the presence of flatback, green and loggerhead turtle nesting beaches across the east coast of Queensland, Australia

(Fig. 1). Loggerhead turtles nest from southeastern Queensland north to Agnes Waters, green turtles nest from southeastern Queensland north to the Townsville region, and flatback turtles nest between the Bundaberg region and the Townsville region. We acknowledge that there are green turtle nesting sites further north than the Townsville region in Queensland, but these northern sites contribute to the northern GBR genetic stock, and our study is limited to the southern GBR genetic stock. The nesting range where mixed species occurred was broad, encompassing much of the coast and islands between southeastern Queensland north to Townsville. The main

nesting sites for loggerhead turtles were the Woongarra coast, the islands of the Capricorn–Bunker groups and Swains reefs on the southern GBR. The main nesting sites for green turtles included rookeries within the Capricorn–Bunker groups, and for flatback turtles, the main nesting rookeries included Wild Duck Island, Avoid Island and Peak Island in eastern Queensland.

Nesting flatback turtles were present on 107 and absent on 125 beaches, nesting greens were present on 51 and absent on 143 beaches, and nesting loggerheads were present on 73 and absent on 121 beaches along the east coast of Queensland (Fig. 1). The total

presence and absence of nesting beaches is not the same between each species because we truncated the dataset based on knowledge of the respective distribution of each species (Limpus 1971, Williams et al. 2017, Jensen et al. 2018, Queensland Government 2022).

The top-ranked GLM explaining the presence/ absence of flatback turtle nesting beaches along the east coast of Queensland retained the variable site type interacting with latitude, which explained 41% of the deviance (Table 2, Table S2). Flatback turtles predominately nested on island and mainland beaches but not on coral cays, with a more substantial presence on mainland beaches (Fig. 2). There is a latitude effect, with the likelihood of presence decreasing with lower latitude (i.e. further north) and very few sites further south than 24° S (Table 3, Fig. 2, Fig. S2). Those nesting beaches located further north where flatback nesting occurs were more likely to be mainland beaches than islands. Flatback turtle nesting is generally absent south of Bargara. For green turtles, the top-ranked model retained only the variable site type, and this explained 22% of the deviance (Table 2, Table S3). Green turtles nested on coral cays over islands and mainland beaches (Table 3) across a broad latitudinal range (19°–27° S). The top-ranked model for loggerhead turtles retained the variables site type and exposure interacting with latitude, explaining 61% of the deviance (Table 2, Table S4). Of these variables, the interaction between exposure and latitude contributed more to the overall model fit than site type (Fig. S4). Loggerhead turtles were more likely to nest on coral cays, the mainland, then islands, with presence decreasing with decreasing lati-

Table 2. Generalised linear models (GLMs) for flatback, green and loggerhead nesting beach selection across the east coast of Queensland, Australia. **Bold**: best model; LL: log likelihood; %DE: deviance explained; ΔAICc: difference in Akaike's information criterion corrected for small sample size (AICc); *w*AICc: AICc weigh; *k*: number of parameters per model

<b>Species</b>	Model	Variable	LL	%DE	$\triangle$ AICc	wAICc.	k
Flatback		Site type × latitude	$-78.7$	41	$\bf{0}$	0.98	6
		Site type + latitude	$-84.9$	36	8.06	0.02	
	3	Site type $+$ elevation $+$ latitude	$-84.9$	36	10.16	0.01	
Green		Site type	$-87.4$	22	$\bf{0}$	0.43	3
		Site type $+$ latitude	$-86.5$	23	0.21	0.38	4
	3	Site type $+$ elevation	$-87.2$	22	1.60	0.19	4
Loggerhead		Site type $+$ exposure $\times$ latitude	$-50.5$	61	$\bf{0}$	0.81	8
	∩	Site type $\times$ latitude $+$ exposure	$-52.1$	59	3.04	0.18	8
	3	Site type $+$ exposure $+$ latitude	$-56.9$	56	8.40	0.01	6

Table 3. Results of the top generalised linear models (GLMs) for flatback, green and loggerhead turtles across the east coast of Queensland, Australia, including estimate, SE, statistic and p-value for each variable. Variables include site type (island), site type (mainland), exposure (semi-exposed), exposure (sheltered) and latitude. The GLM uses the first (alphabetically) variable to compare against, meaning that coral cay and exposed were used to compare against the other site and exposure types



tude and nesting sites occurring south into southern Queensland. This effect was stronger on sheltered than on semi-exposed beaches (Table 3, Fig. 2).

# **4. DISCUSSION**

Nesting beach selection is important for the survival and reproduction of marine turtle populations (Kikukawa et al. 1999), but data on the environmental and topological drivers of nesting beach selection have been lacking for vulnerable and data-deficient species such as the flatback, green and loggerhead turtles in eastern Australia. In this study, we evaluated the influence of a suite of environmental (exposure) and topographic (site type, latitude and elevation) factors on nesting beach selection by flatback, green and loggerhead turtles along the east coast of Queensland. Our results highlight the importance of site type for predicting the presence of all 3 turtle species as well as latitude for both flatback and loggerhead turtles and exposure for loggerhead turtles. This is important new information which will support future research and monitoring efforts to mitigate the effect of anthropogenic impacts, including climate change, on the habitat of flatback, green and loggerhead turtles, aiding the conservation and management of these vulnerable species along the east coast of Queensland.

The tendency for flatback turtles to nest on beaches on the mainland and islands, instead of on coral cays, is supported by previous studies which looked at nest site selection in eastern Queensland, the Gulf of Carpentaria, northern Australia, Western Australia and the GBR region (Hamann et al. 2011, Howard et al. 2015, Bustard 2017, Thums et al. 2020, Gammon et al. 2021). However, these studies were conducted over smaller spatial scales and did not specifically focus on beach selection. The focus of site selection includes influencing factors after a beach has been chosen. A study has found that one of the largest rookeries for flatback turtles has been discovered on a small coral cay, Crab Island, in the Gulf of Carpentaria (Bustard 2017). This finding differs from our results, as we found the eastern Queensland population does not nest on coral cays. This highlights the need to run these types of studies at population scales over their geographical range. Similarly, previous studies on the nesting beach selection of green and loggerhead turtles support our findings, as they have been found using coastal reef habitats, islands, coral cays and mainland beaches across Australia, the Mediterranean, Asia, coastal East Africa, the Gulf of California and the Mesoamerican Reef (Booth & Freeman 2006,



Fig. 2. Interaction between site type ([a] mainland, [b] island) and latitude (*x*-axis) for flatback turtles (shaded in blue) and between exposure types ([c] exposed, [d] semi-exposed, [e] sheltered) and latitude (*x*-axis) for loggerhead turtles (shaded in green) across the east coast of Queensland, Australia. An unsmoothed regression line was used for the final models, with shading representing the SE of the estimated smooth function

Chaloupka et al. 2008, Fuentes et al. 2010b, Mazor et al. 2013, Williams et al. 2017).

Our findings suggest that flatback turtles are found to nest at locations with different environmental and topographic features (site type and latitude) compared to loggerhead and green turtles nesting within a similar latitudinal area. This demonstrates the difference in the nesting ecology and behaviour of flatback turtles in eastern Queensland. One driver of this difference could be the hydrodynamic environment adjacent to nesting beaches, which influences hatchling dispersal. Unlike other species, flatback turtles remain within the GBR region during their post-hatchling phase (Walker & Parmenter 1990), and thus nesting sites are presumably in areas where the currents enable hatchlings to be entrained within coastal waters (e.g. Wildermann et al. 2017). In particular, the beaches south of Bundaberg are likely adjacent to unfavourable currents for flatback turtle dispersal.

Some studies report a relationship between hatching success and temperature changes at different latitudes in marine turtles but not how latitude affects beach selection (Limpus 1971, Bentley et al. 2020). All beaches in our study region are likely to be warm enough during the austral summer to allow eggs to incubate. It is possible that the effect of latitude in our results for flatback turtles is due to our study site being located at the southern end of the species' latitudinal range, which means that there may naturally be more variation in where the turtles have chosen to nest. The border of a species range generally represents the area in which their populations are not within the optimal part of the range as the suitability of their environments decreases (Carbonell et al. 2003). For flatbacks, while we are uncertain what limits the northern extent of nesting, it is likely a combination of beach availability and exposure of beaches to cyclones (Fuentes & Abbs 2010, Garcon et al. 2010). The southern extent, however, is likely constrained by oceanographic processes, and the coast south of Bundaberg does not provide a favourable habitat to allow retainment of hatchlings within nearshore environments (Hamann et al. 2024).

Furthermore, because marine turtles demonstrate long-term (decades) site fidelity (Lohmann et al. 1996) and take over 20 yr to reach maturity (Miller 2017), the latitudinal range and sites used by the flatback, green and loggerhead turtles are likely to have been established decades ago (Bannister et al. 2016, Thums et al. 2020). However, it has been suggested in the literature that a possible adaption for marine turtles in response to climate change is to gradually shift their nesting sites into cooler latitudes (Fuentes et al.

2011, Pike 2013, Rivas et al. 2016, Patrício et al. 2021). However, this is unlikely for flatback turtles in eastern Queensland because any southward shift in nesting sites, especially south of K'gari (Fraser Island), will correspond with oceanographic features that do not allow hatchlings to remain within continental waters as they disperse. Thus, our study's results are important to enable predictions about possible site shifts in different climate or coastal change scenarios.

The exposure variable was present in the top model for loggerhead turtles, indicating that they are found on both sheltered and semi-exposed beaches and not on exposed beaches. Although data visualisation identified loggerheads to nest on exposed beaches, this involved only assessing 1 variable at a time and therefore does not allow for the inclusion of multiple variables (see Text S1). These nesting beach selection characteristics are also consistent with findings where loggerhead turtle nests were found on the side of the island that was semi-exposed to wind and wave action (Garcon et al. 2010). However, loggerhead turtles nesting on Maio Island, Cabo Verde, were found to choose nesting beaches with greater exposure to wind and wave action and other relative exposure index values (Patino-Martinez et al. 2023). These differences in our findings could be due to a variation of traits among different genetic stocks of this species (Garcon et al. 2010) and availability of habitats in particular areas. Nesting sites for loggerhead turtles occur along the exposed coast of southern Queensland, and there are predictions that nesting will become more prevalent in this region in response to increased beach temperatures (Hamann et al. 2024).

In general, our results indicate that within the GBR region, loggerhead and green turtles (southern GBR population) predominately nest within the same latitudinal range as the flatback turtles, but they have a southward expansion of minor nesting sites.

The elevation variable was also not retained in the top model, suggesting that it may not be an important factor in the nesting beach selection of any of the 3 species. This could be because all sites provided enough dune habitat above the high tide levels for nesting (Fish et al. 2005). However, elevation and latitude were retained in one of the top 3 models (all almost equal rating) for green turtles, suggesting they have higher importance for this species. The majority of green turtle nesting sites were found on low-lying coral cays, and sites were across a broader latitudinal range (19°–27° S). A study on loggerhead turtles in Okinawajima and adjacent islands of the central Ryukyus, Japan, suggested that beach height is an influential variable but was also not chosen as the top

variable, although sand softness was (Kikukawa et al. 1999). In addition, some beaches are likely to be more vulnerable under projected sea level rise increases, either because they are low lying or because natural or anthropogenic barriers cannot retreat (Blechschmidt et al. 2020, Patrício et al. 2021).

The deviance explained for green turtles is lower than that for the other species, suggesting that other factors which have not been measured could be influencing their nesting beach selection. Previous studies have suggested additional factors that could influence nesting beach selection such as oceanography and wind direction. We could not model these factors, as there is insufficient fine-scale data on wind direction, and the analysis of data on oceanography would have been outside the scope of this study (Pike 2013, Thums et al. 2020). However, oceanic data are important to consider when looking into nesting beach selection, as oceanic currents adjacent to nesting beaches play a part in the dispersal of hatchlings (Hamann et al. 2011, Barbour et al. 2020, Hoover et al. 2020). Studies have suggested that loggerhead turtles have been found to nest on the more exposed beaches, as they are adjacent to favourable currents which presumably enable them to escape rapidly from predator-rich coastal areas and, therefore, are of greater value for nesting (Putman et al. 2010, Scott-Hayward et al. 2014). Onshore wind directions may cool down sand temperatures and thus could also be an important factor in nesting beach selection, as the temperature of the sand affects their development, sex ratio and hatchling emergence (Booth & Astill 2001, Garcon et al. 2010, Fuentes et al. 2024). This could be an important relationship that remains to be tested.

# **4.1. Implications for future conservation and research**

The results from this study have implications for flatback, green and loggerhead turtle conservation and management in eastern Australia, as they provide information on what beach characteristics females are found nesting on. We can use this knowledge to help understand if flatback, green and loggerhead turtles could be threatened by habitat changes and what natural responses might be. This can be achieved by identifying the important nesting beaches for each species according to the characteristics determined from our results and then increasing the monitoring of these nesting beaches to prioritise the threat management of habitat changes in the future. Flatback turtles nesting on the mainland and islands, and

green and loggerhead turtles nesting on islands, including coral cays and mainland beaches, are at risk due to sea level rise. Sea level rise will be exacerbated by future climate change, causing nesting beaches in Australia with low dune structures or beaches with development behind the dunes and therefore nowhere to retreat to become completely inundated with water (Fish et al. 2005, Fuentes et al. 2010a). Female turtles may have to move to less favourable locations to nest in these cases, meaning that those beaches that are currently not highly favourable could become more favourable. Due to the higher temperatures predicted for the future due to climate change, marine turtles in Australia may expand their latitudinal range and shift nesting to sites where the sand temperatures are cooler or start to nest earlier in the year when the temperature is lower (Butt et al. 2016, Laloë & Hays 2023, Fuentes et al. 2024). Therefore, increased spatial and temporal monitoring of the species into the future is essential to determine how, and if, they can adapt to these climatic pressures.

In the future, using knowledge from this study, increased monitoring of beaches with potential turtle nesting could provide a better understanding of the current and predicted distribution of flatback, green and loggerhead turtle populations in eastern Queensland and to further identify which beaches are likely to continue to enable successful nesting and hatchling dispersal. For future turtle management to be effective, we will need to foster an increase in the resilience of populations to climate change (Patrício et al. 2019). Within-beach site selection could potentially ameliorate broad-scale changes in environmental conditions; therefore, other existing or newly established beaches will become critical for the persistence of turtle populations.

## **4.2. Conclusions**

We have assessed the nesting beach characteristics of flatback, green and loggerhead turtles in eastern Queensland. This fills knowledge gaps regarding the optimal conditions for nesting turtles, contributing to meeting the research goals listed under Action Area A2 of the Australian Government Marine Turtle Recovery Plan (Queensland Government 2022). Along the east coast of Queensland, the most significant habitat characteristics of flatback nesting beaches were the mainland and non-coral cay islands in higher latitudes. The significant indicators of nesting beaches for green turtles were coral cays. Loggerhead turtles were also found predominately nesting on coral cays in high latitudes when the beaches were semi-exposed and sheltered. Our results provide an important baseline for aiding the assessment of the vulnerability of each species to habitat changes, with future studies in this area needed to provide additional insights to further characterise important nesting beaches considering likely future changes due to climate and anthropogenic effects.

*Acknowledgements*. We are very grateful to the Queensland Government turtle nesting distribution and abundance monitoring program, Queensland Globe and Queensland Spatial for the use of their data for this study. We are thankful for the access to their data for the nesting distribution of marine turtles and for all the environmental and topographic variables used in this study.

#### LITERATURE CITED

- Agresti A (2015) Foundations of linear and generalized linear models. John Wiley & Sons, Hoboken, NJ
- Bannister N, Holland J, Farrelly T (2016) Nest site fidelity of flatback turtles (*Natator depressus*) on Bare Sand Island, Northern Territory, Australia. North Territ Nat 27: 47– 53
- [Barbour N, Shillinger GL, Hoover AL, Williamson SA and](https://doi.org/10.3389/fmars.2020.582933)  others (2020) Environmental and biological factors influencing dispersal of neonate leatherback turtles (*Dermochelys coriacea*) from an endangered Costa Rican nesting population. Front Mar Sci 7:582933
- [Bentley BP, Stubbs JL, Whiting SD, Mitchell NJ \(2020\) Vari](https://doi.org/10.1111/1365-2435.13645)ation in thermal traits describing sex determination and development in Western Australian sea turtle populations. Funct Ecol 34: 2302– 2314
- Blechschmidt J, Wittmann M, Blüml C (2020) Climate change and green sea turtle sex ratio — preventing possible extinction. Genes (Basel) 11:588
- $\blacktriangleright$  Booth D, Astill K (2001) Incubation temperature, energy expenditure and hatchling size in the green turtle (*Chelonia mydas*), a species with temperature-sensitive sex determination. Aust J Zool 49:389-396
	- Booth D, 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
- [Burnham KP, Anderson DR, Huyvaert KP \(2011\) AIC model](https://doi.org/10.1007/s00265-010-1029-6)  selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol 65:23-35
- [Bustard R \(2017\) Rediscovery of the flatback turtle \(](http://www.britishcheloniagroup.org.uk/sites/default/files/u8/v8n4Bustard.pdf)*Natator depressus* [Garman]) and its conservation. Testudo 8:4. www.britishcheloniagroup.org.uk/sites/default/files/u8/ v8n4Bustard.pdf
- $\blacktriangleright$  Butt N, Whiting S, Dethmers K (2016) Identifying future sea turtle conservation areas under climate change. Biol Conserv 204: 189– 196
- [Carbonell R, Pérez-Tris J, Tellería JL \(2003\) Effects of habitat](https://doi.org/10.1046/j.0024-4066.2002.00156.x)  heterogeneity and local adaptation on the body condition of a forest passerine at the edge of its distributional range. Biol J Linn Soc 78: 479– 488
- [Chaloupka M, Kamezaki N, Limpus C \(2008\) Is climate](https://doi.org/10.1016/j.jembe.2007.12.009)  change affecting the population dynamics of the endangered Pacific loggerhead sea turtle? J Exp Mar Biol Ecol 356: 136– 143
- ESRI (2022) ArcGIS Pro Desktop. Environmental Systems Research Institute, Redlands, CA
- Ferreira RL (2019) Hawksbill (*Eretmochelys imbricata*) and green turtle (*Chelonia mydas*) nesting and beach selection at Príncipe Island, West Africa. Arquipélago Ciênc Biol Mar 1:61-78
- [Fish M, Cote I, Gill J, Jones A, Renshoff S, Watkinson A](https://doi.org/10.1111/j.1523-1739.2005.00146.x)  (2005) Predicting the impact of sea-level rise on Caribbean sea turtle nesting habitat. Conserv Biol 19:482-491
- [FitzSimmons N, Pittard S, McIntyre N, Jensen M and others](https://doi.org/10.1002/aqc.3270)  (2020) Phylogeography, genetic stocks, and conservation implications for an Australian endemic marine turtle. Aquat Conserv 30:440-460
- Fuentes MMPB, Abbs D (2010) Effects of projected changes in tropical cyclone frequency on sea turtles. Mar Ecol Prog Ser 412:283-292
- [Fuentes MMPB, Limpus CJ, Hamann M, Dawson J \(2010a\)](https://doi.org/10.1002/aqc.1088)  Potential impacts of projected sea-level rise on sea turtle rookeries. Aquat Conserv 20: 132– 139
- [Fuentes MMPB, Hamann M, Limpus CJ \(2010b\) Past, cur](https://doi.org/10.1016/j.jembe.2009.11.003)rent and future thermal profiles of green turtle nesting grounds: implications from climate change. J Exp Mar Biol Ecol 383: 56– 64
- [Fuentes MMPB, Bateman BL, Hamann M \(2011\) Relation](https://doi.org/10.1111/j.1365-2699.2011.02541.x)ship between tropical cyclones and the distribution of sea turtle nesting grounds. J Biogeogr 38: 1886– 1896
- [Fuentes MMPB, Gredzens C, Bateman BL, Boettcher R and](https://doi.org/10.1002/eap.1386)  others (2016) Conservation hotspots for marine turtle nesting in the United States based on coastal development. Ecol Appl 26:2706-2717
- [Fuentes MMPB, Allstadt AJ, Ceriani SA, Godfrey MH and](https://doi.org/10.1007/s10113-020-01689-4)  others (2020) Potential adaptability of marine turtles to climate change may be hindered by coastal development in the USA. Reg Environ Change 20: 1– 14
- [Fuentes MMPB, Santos AJB, Abreu-Grobois A, Briseño-](https://doi.org/10.1111/gcb.16991)Dueñas R and others (2024) Adaptation of sea turtles to climate warming: Will phenological responses be sufficient to counteract changes in reproductive output? Glob Change Biol 30:e16991
- [Gammon M, Bentley B, Fossette S, Mitchell N \(2021\) Meta](https://doi.org/10.1086/716848)bolic rates and thermal thresholds of embryonic flatback turtles (*Natator depressus*) from the North West Shelf of Australia. Physiol Biochem Zool 94: 429– 442
- [Garcon S, Grech A, Moloney J, Hamann M \(2010\) Relative](https://doi.org/10.1002/aqc.1057)  exposure index: an important factor in sea turtle nesting distribution. Aquat Conserv 20:140-149
- [Hamann M, Grech A, Wolanski E, Lambrechts J \(2011\) Mod](https://doi.org/10.1016/j.ecolmodel.2011.02.003)elling the fate of marine turtle hatchlings. Ecol Modell 222: 1515– 1521
	- Hamann M, Limpus CJ, Kophamel S (2024) Dispersal and connectivity of marine turtles in the Great Barrier Reef and links to the South Pacific Ocean. In: Wolanski E, Kingsford MJ (eds) Oceanographic processes of coral reefs. CRC Press, Boca Raton, FL, p 254– 259
- [Heredero Saura L, Jáñez-Escalada L, López Navas J, Cordero K,](https://doi.org/10.1007/s10584-022-03325-y)  Santidrián Tomillo P (2022) Nest-site selection influences offspring sex ratio in green turtles, a species with temperature-dependent sex determination. Clim Change 170:39
- [Hoover AL, Shillinger GL, Williamson SA, Reina RD, Bailey](https://doi.org/10.1038/s41598-020-75769-0)  H (2020) Nearshore neonate dispersal of Atlantic leatherback turtles (*Dermochelys coriacea*) from a non-recovering subpopulation. Sci Rep 10: 18748
- [Howard R, Bell I, Pike D \(2015\) Tropical flatback turtle](https://pubmed.ncbi.nlm.nih.gov/26347558)  (*Natator depressus*) embryos are resilient to the heat of climate change. J Exp Biol 218:3330-3335
- [Jensen MP, Allen CD, Eguchi T, Bell IP and others \(2018\) Envi](https://doi.org/10.1016/j.cub.2017.11.057)ronmental warming and feminization of one of the largest sea turtle populations in the world. Curr Biol 28:154-159.e4
- [Kamrowski RL, Limpus C, Moloney J, Hamann M \(2012\)](https://doi.org/10.3354/esr00462)  Coastal light pollution and marine turtles: assessing the magnitude of the problem. Endang Species Res 19:85–98
- [Katselidis KA, Schofield G, Stamou G, Dimopoulos P, Pantis](https://doi.org/10.1111/j.1469-1795.2012.00543.x)  JD (2012) Females first? Past, present and future variability in offspring sex ratio at a temperate sea turtle breeding area. Anim Conserv 15:508-518
- [Kikukawa A, Kamezaki N, Ota H \(1999\) Factors affecting nest](https://doi.org/10.1111/j.1469-7998.1999.tb01214.x)ing beach selection by loggerhead turtles (*Caretta caretta*): a multiple regression approach. J Zool 249: 447– 454
	- Koch AU, Guinea ML (2006) Lower nesting success of flatback turtles caused by disorientation. Mar Turtle Newsl 114: 16
- [Kornbrot D \(2014\) Point biserial correlation. Wiley StatsRef](https://doi.org/10.1002/9781118445112.stat06227)  Stat Ref Online, https://doi.org/10.1002/9781118445112. stat06227
- [Laloë JO, Hays GC \(2023\) Can a present-day thermal niche](https://doi.org/10.1098/rsos.221002)  be preserved in a warming climate by a shift in phenology? A case study with sea turtles. R Soc Open Sci 10: 221002
- [Laloë JO, Cozens J, Renom B, Taxonera A, Hays G \(2014\)](https://doi.org/10.1038/nclimate2236)  Effects of rising temperature on the viability of an important sea turtle rookery. Nat Clim Chang 4:513-518
- [Laloë JO, Cozens J, Renom B, Taxonera A, Hays G \(2017\)](https://doi.org/10.1111/gcb.13765)  Climate change and temperature-linked hatchling mortality at a globally important sea turtle nesting site. Glob Change Biol 23: 4922– 4931
- $\blacktriangleright$  Legendre P, Fortin MJ, Borcard D (2015) Should the Mantel test be used in spatial analysis? Methods Ecol Evol 6: 1239–1247
	- Lettrich MD, Dick DM, Fahy CC, Griffis RB and others (2020) A method for assessing the vulnerability of sea turtles to a changing climate. NOAA Tech Memo NMFS-F/SPO-211
	- Limpus CJ (1971) The flatback turtle, *Chelonia depressa* Garman in southeast Queensland, Australia. Herpetologica 27: 431– 446
	- Lohmann KJ, Witherington B, Lohmann CMF, Salmon M (1996) Orientation, navigation, and natal beach homing in sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 107-135
- [Loop K, Miller J, Limpus C \(1995\) Nesting by the hawksbill](https://doi.org/10.1071/WR9950241)  turtle (*Eretmochelys imbricata*) on Milman Island, Great Barrier Reef, Australia. Aust Wildl Res 22:241-251
	- Mansfield ER, Helms BP (1982) Detecting multicollinearity. Am Stat 36: 158– 160
- [Mazor T, Levin N, Possingham HP, Levy Y, Rocchini D, Rich](https://doi.org/10.1016/j.biocon.2012.11.004)ardson AJ, Kark S (2013) Can satellite-based night lights be used for conservation? The case of nesting sea turtles in the Mediterranean. Biol Conserv 159:63-72
	- Miller JD (2017) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 51-81
	- Miller J, Limpus C, Godfrey M (2003) Nest site selection, oviposition, eggs, development, hatching, and emergence of loggerhead turtles. In: Bolton AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Institution, Washington, DC, p 125-143
- [Patino-Martinez J, Dos Passos L, Amador R, Teixidor A and](https://doi.org/10.1017/S0030605321001496)  others (2023) Strategic nest site selection in one of the world's largest loggerhead turtle nesting colonies, on Maio Island, Cabo Verde. Oryx 57:152-159

*Editorial responsibility: Bryan P. Wallace, Fort Collins, Colorado, USA Reviewed by: S. A. Williamson and 1 anonymous referee* 

- [Patrício AR, Varela MR, Barbosa C, Broderick AC and others](https://doi.org/10.1111/gcb.14520)  (2019) Climate change resilience of a globally important sea turtle nesting population. Glob Change Biol 25:522-535
- [Patrício AR, Hawkes LA, Monsinjon JR, Godley BJ, Fuentes](https://doi.org/10.3354/esr01110)  MMPB (2021) Climate change and marine turtles: recent advances and future directions. Endang Species Res 44: 363– 395
- [Pike D \(2013\) Climate influences the global distribution of](https://doi.org/10.1111/geb.12025)  sea turtle nesting. Glob Ecol Biogeogr 22: 555– 566
- [Putman NF, Bane JM, Lohmann KJ \(2010\) Sea turtle nesting](https://pubmed.ncbi.nlm.nih.gov/20573619)  distributions and oceanographic constraints on hatchling migration. Proc Biol Sci 277: 3631– 3637
- Queensland Government (2022) Turtle nesting distribution abundance and migration. https://apps.information.qld. gov.au/TurtleDistribution/
	- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- [Rivas ML, Santidrián Tomillo P, Diéguez-Uribeondo J,](https://doi.org/10.3354/meps11748)  Marco A (2016) Potential effects of dune scarps caused by beach erosion on the nesting behavior of leatherback turtles. Mar Ecol Prog Ser 551:239-248
	- Scott-Hayward LAS, Borchers DL, Burt ML, Barco S, Haas HL, Sasso CR, Smolowitz RJ (2014) Use of zero- and oneinflated beta regression to model availability of loggerhead turtles off the east coast of the United States. Final report prepared for US Fleet Forces Command. Submitted to Naval Facilities Engineering Command Atlantic, Norfolk, VA, under contract no. N62470-10-D-3011, task order 40, issued to HDR, Norfolk, VA. Prepared by the Centre for Research into Ecological and Environmental Modelling, University of St. Andrews
- [Shishkina T, Farmus L, Cribbie RA \(2018\) Testing for a lack](https://doi.org/10.20982/tqmp.14.3.p167)  of relationship among categorical variables. Quant Methods Psychol 14: 167– 179
- [Siqueira-Silva IS, Arantes MO, Hackradt CW, Schiavetti A](https://doi.org/10.1016/j.marenvres.2020.105090)  (2020) Environmental and anthropogenic factors affecting nesting site selection by sea turtles. Mar Environ Res 162: 105090
	- Tellería JL (2016) Wildlife habitat requirements: concepts and research approaches. In: Mateo R, Arroyo B, Garcia JT (eds) Current trends in wildlife research. Springer, Cham, p 79– 95
- [Thums M, Rossendell J, Fisher R, Guinea M \(2020\) Nesting](https://doi.org/10.1071/MF19022)  ecology of flatback sea turtles *Natator depressus* from Delambre Island, Western Australia. Mar Freshw Res 71: 443– 451
- [Varela MR, Patrício AR, Anderson K, Broderick AC and](https://doi.org/10.1111/gcb.14526)  others (2019) Assessing climate change associated sealevel rise impacts on sea turtle nesting beaches using drones, photogrammetry and a novel GPS system. Glob Change Biol 25: 753– 762
- [Walker T, Parmenter C \(1990\) Absence of a pelagic phase](https://doi.org/10.2307/2845123)  in the life cycle of the flatback turtle, *Natator depressa* (Garman). J Biogeogr 17:275–278
	- Weisberg S (2005) Applied linear regression, 3rd edn. John Wiley & Sons, Hoboken, NJ
- [Wildermann N, Critchell K, Fuentes MMPB, Limpus CJ,](https://doi.org/10.1098/rsos.170164)  Wolanski E, Hamann M (2017) Does behaviour affect the dispersal of flatback post-hatchlings in the Great Barrier Reef? R Soc Open Sci 4: 170164
- [Williams JL, Pierce SJ, Rohner CA, Fuentes MMPB,](https://doi.org/10.3389/fmars.2016.00288)  Hamann M (2017) Spatial distribution and residency of green and loggerhead sea turtles using coastal reef habitats in southern Mozambique. Front Mar Sci 3:288

*Submitted: November 30, 2023 Accepted: June 14, 2024 Proofs received from author(s): July 24, 2024*