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Sand Particle Size Influences Nest Site Selection of Green Turtles (*Chelonia mydas*) Differently in East and West Peninsular Malaysia

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Abstract.—**Understanding the environmental characteristics influencing nest site selection of Green Turtles (*Chelonia mydas*) is important for preserving suitable nesting habitats. By comparing successful nest sites and aborted nest sites (i.e., nest chambers discarded without egg laying) during the same nesting event, we identified the factors associated with nest site selection of Green Turtles at Redang Island off the east coast of Peninsular Malaysia. We compared the results with those reported for Penang Island off the west coast of the peninsula. While the sand temperature and distance from high tide line are potential factors contributing to nest site selection at Redang Island, the most important factor was sand particle size. Successful nest sites contained less coarse sand (< 19.6% of sand ≥ 1 mm; mean ± standard deviation = 10.4 ± 13.3%) than aborted nest sites (52.9 ± 24.0%). This result is in contrast with Penang Island where successful nest sites contained more coarse sand. The difference between locations indicates that the effect of sand particle size on nest site selection of Green Turtles may change in combination with other effects such as sand moisture.**

Key Words.—animal behavior; conservation; endangered species; nesting ecology; sea turtles

Introduction

Sea turtles are marine-adapted reptiles that only come ashore to lay eggs. Because six out of the seven sea turtle species are listed as either Critically Endangered, Endangered, or Vulnerable in the Red List of the International Union for Conservation of Nature (IUCN; 2020), the preservation of nesting beaches has garnered considerable attention. Maintaining specific characteristics of the nesting environment is important for sea turtles because they lack parental care and the nest site selected by the mother will determine the fitness and survival of the hatchlings. Environmental factors within the nest, such as temperature and moisture, influence embryogenesis, phenotype, performance, and survivability of hatchlings (Booth 2017; Gatto and Reina 2020; Lolavar and Wyneken 2021). Furthermore, because sea turtles exhibit temperature-dependent sex determination, alterations to the nesting environment may result in skewedness of sex ratios (Booth et al. 2020; Chatting et al. 2021). For these reasons, understanding the environmental characteristics that influence nest site selection in sea turtles is important for preserving suitable nesting habitats and formulating management strategies for sea turtle nesting beaches.

There are several approaches for understanding the relationship between nest site selection and environmental characteristics. One common approach involves evaluating the relationship between nest density and environmental characteristics of different beaches or beach zones (Horrocks and Scott 1991; Cuevas et al. 2010; Price et al. 2018). A second approach involves measuring the environmental characteristics of available nest sites along the beach profile (Kolbe and Janzen 2002; Flitz and Mulin 2006; Mitchell et al. 2013), as well as along nesting turtle crawls (Wood and Bjorndal 2000; López-Castro et al. 2004) and comparing the microhabitat characteristics of chosen nest sites against other possible nest sites that were either avoided or not chosen. This also includes comparing the environmental characteristics of nesting versus non-nesting events (Yalçin-Özdilek et al. 2007).

A third approach focuses on comparing successful nest sites and aborted nest sites (i.e., nest chambers discarded without egg laying) during the same nesting event (Mohd Salleh et al. 2018). Using these approaches, several environmental characteristics have been shown to influence nest site selection in sea turtles, including artificial lights (Price et al. 2018), beach slope (Horrocks and Scott 1991; Wood and Bjorndal 2000; Cuevas et al. 2010), sand temperature, sand moisture (López-Castro et al. 2004; Yalçin-Özdilek et al. 2007), and sand particle size (Mohd Salleh et al. 2018).

Green Turtles (*Chelonia mydas*) nest on various beaches in the tropical and subtropical regions (Seminoff et al. 2015) and the environmental characteristics influencing their nest site selection may vary among populations or rookeries (Mortimer 1990; Hays et al. 1995). In Peninsular Malaysia, there are rookeries of Green Turtles on the west coast (Mohd Salleh et al. 2018, 2020) and east coast (Van de Merwe et al. 2006; Chan 2010, 2013; Aini Hasanah et al. 2014) that experience different environmental characteristics at their nesting beaches. Mohd Salleh et al. (2018) found that Green Turtles nesting on Penang Island, west coast of Peninsular Malaysia, selected nest sites with larger sand particle sizes (i.e., coarser sand) over nest sites with smaller sand particle sizes (i.e., finer sand). Because the nesting habitats are different on the east coast, however, the environmental characteristics influencing nest site selection of Green Turtles on the east coast might also be different. In fact, the strength of wind and waves, as well as precipitation, especially during the monsoon season, are different between the west and east coasts (Kubota and Ahmad 2006; Wong et al. 2009; Mohd Fauzi et al. 2014). Moreover, the west coast is experiencing greater beach-front development (i.e., reclamation), while nesting grounds on the east coast remain relatively undisturbed.

In this study, we first investigated the environmental characteristics influencing nest site selection of Green Turtles on Redang Island (east coast of Peninsular Malaysia) by comparing successful nest sites and aborted nest sites encountered during the same nesting event. We then compared these results with similar data previously obtained from Penang Island on the west coast (Mohd Salleh et al. 2018). Because Green Turtles nesting on the east and west coasts of Malaysia not only have different nest site preferences but are also part of two separate subpopulations or Regional Management Units (Wallace et al. 2010), we believe that different management actions might be required to maintain the suitability of nesting beaches.

Materials and Methods

Study site.—We performed fieldwork at Chagar Hutang Turtle Sanctuary (5°48’45”N, 103°0’24”E), located at the north end of Redang Island, Terengganu, in the northeast region of Peninsular Malaysia (Fig. 1). Chagar Hutang (length = 350 m; mean width = 40 m) is one of the major nesting beaches for Green Turtle in Malaysia and was designated as a Turtle Sanctuary by the State Government of Terengganu in 2005 (Chan 2013). In Chagar Hutang, the sand particle size composition varies within the beach with both coarse sand sites (dominated by sand particle size ≥ 0.710 mm) and fine sand sites (dominated by sand particle size ≤ 0.500 mm; Stewart et al. 2019). Various species of woody and shrub vegetation are observed at Chagar Hutang: Sea Lettuce Tree (*Scaevola taccada*), Whistling Pine Tree (*Casuarina equisetifolia*), Sea Almond (*Terminalia catappa*), Coconut Tree (*Cocos nucifera*), Nipa Palm (*Nypa fruticans*), Fragrant Screw Pine (*Pandanus odoratissimus*), and Pandan (*Pandanus amaryllifolius*), while grass vegetation Beach Morning Glory (*Ipomoea pes-caprae*) is distributed in patches along the beach.

We compared results from Chagar Hutang beach on Redang Island (East Malaysia) with similar data from Kerachut and Teluk Kampi beaches on Penang Island

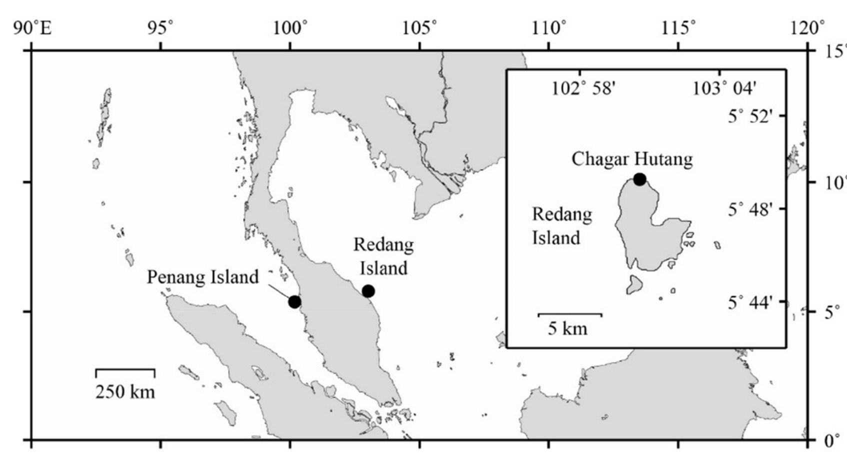

Figure 1. Map of Redang Island and Penang Island, located off the east coast and west coast of the Peninsular Malaysia, respectively.

(West Malaysia) published by Mohd Salleh et al. (2018; Fig. 1). The width of the beaches surveyed on Penang Island ranged from 29.5 to 45.6 m, slightly narrower than those surveyed on Redang Island. In contrast with Redang Island, grassy vegetation as well as shrub vegetation, dominated by *Scaevola taccada*, are observed at Penang Island. The overall distribution of sand particle size at Penang Island is unknown, but these beaches are likely dominated by coarser sand because the proportion of sand size ≤ 0.425 mm was small for both successful and aborted nest sites (Mohd Salleh et al. 2018).

Nocturnal surveys.—We conducted beach patrols from 2000–0600 on nine consecutive nights from 8–17 August 2020 with help from field rangers, research assistants, volunteers, and university interns that were assigned to three time periods (2000–0000, 0001–0300, and 0301–0600). During surveys, we restricted the use of light to the minimal amount and covered flashlights with red transparent film to reduce the disturbance on sea turtles. We monitored nesting activities of turtles from approximately 5–20 m away until egg laying commenced because turtles are more easily disturbed prior to nesting (Miller et al. 2003). When females finished oviposition, we checked each turtle for individualized flipper tags and attached new tags when tags were absent. We also measured curved carapace length (CCL) and curved carapace width (CCW) using 2.0 m flexible measuring tape (± 0.1 m).

In this study, we monitored only nesting emergences in which eggs were laid. We did not tag and identify the individuals that returned to the sea without nesting successfully; therefore, we excluded non-nesting emergences from the analysis, regardless of whether digging attempts were made, to avoid biasing the results by including repeated measures of the same individuals. Along each nesting emergence, we categorized each nest site as either successful or aborted. Successful nest sites involved oviposition, while aborted nest sites involved digging attempts without oviposition. If there was more than one aborted nest site along a given nesting emergence, we focused on the aborted nest site nearest to the successful nest site (typically the last aborted nest site). Nesting success ratio was calculated by dividing the number of successful nest sites by the total number of nest sites (successful nest sites plus aborted nest sites).

Environmental characteristics of nest sites.—To evaluate microhabitat characteristics associated with nest site selection, we first measured sand temperature and distance from tidal line both at successful and aborted nest sites. We measured sand temperature using a digital soil thermometer (± 0.1° C; range, -50° to 150° C; Dial Thermometer 392050, Extech Instruments, Waltham, Massachusetts, USA). Just after the turtle finished oviposition, the temperature was measured at four points around the nest chamber at a depth of 5 cm (López-Castro et al. 2004) and averaged. Distance from tidal line was measured using 30 m measuring tape (± 0.1 m). We categorized nest sites (successful and aborted) into one of four habitat types: (1) woody or shrub vegetation area, (2) grassy or herbaceous vegetation area, (3) open sand area with no vegetation, or (4) riverbank with no vegetation (approximately < 2 m from river stream). We also identified plant species.

Next, we collected sand samples to determine the size composition of sand particles. We collected approximately 100–200 g of sand at the depth of 10 cm around the nest chamber area. The sand sample was tightly sealed in a plastic bag and transported to the laboratory. In the laboratory, we dried the sand samples in an oven for 24 h at 105° C according to Foley et al. (2006) using a Universal Oven U (Memmert GmbH & Co. KG, Schwabach, Germany). We weighted the sand samples using the electronic weighing balance (± 0.1 g; A&D Weighing, FX-3000i precision digital scale, A&D Co., LTD., Tokyo, Japan). We then separated each sand sample into particle size classes by sieving the sample through the following series of six sieves: 2.0, 1.0, 0.425, 0.250, 0.125, and 0.063 mm for 20 min using an Endecotts test sieve shaker EFL 2000/2 (Endecotts Ltd, London, UK). We weighed sand from each particle size class to the nearest 1 g using a balance and divided the weight by the total dried weight of the sample. Hereafter, we treated sand particle size as a ratio by weight of sand ≥ 1 mm that was calculated by summing the weights of two size classes (≥ 2 mm and 1–2 mm) according to Mohd Salleh et al. (2018). During inclement weather events (e.g., heavy rain), we did not measure sand temperature and we treated it as missing data, but we still collected all other data and samples.

Data analysis.—We performed statistical analyses using R ver. 4.00 (R Core Team 2020) and averages are shown as ± 1 standard deviation (SD). Environmental characteristics were compared between successful nest sites and aborted nest sites at Redang Island. For this comparison, we excluded nesting events that did not include aborted nest sites or that contained missing data, resulting in a paired dataset. Distance from high tide line and temperature were compared using paired *t*-tests, while sand particle size was compared using Wilcoxon Signed Rank Test because of its deviation from normality.

We then compared data from Redang Island collected in this study with data from Penang Island obtained from Mohd Salleh et al. (2018). We compared environmental characteristics of nest sites among four categories: (1) successful nest sites at Redang Island, (2) aborted nest sites at Redang Island, (3) successful nest sites at Penang

Island, and (4) aborted nest sites at Penang Island. For these analyses, we used all environmental data obtained at Redang Island. The distance to the high tide line and sand temperature was compared using pairwise *t*-tests that assume heterogeneity in SD among categories. The sand particle size composition was also compared among these categories using pairwise Wilcoxon Rank Sum Tests implemented in rstatix package (Kassambara 2020). The difference in the distribution of nest sites in relation to vegetation types was tested using pairwise comparisons using Fisher's Exact Test implemented in the RVAideMemoire package (Herve 2020). For all tests $\alpha = 0.05$, but all pairwise comparisons incorporated corrections for multiple testing using false discovery rate (FDR).

We estimated the effects of the environmental characteristics on nest site selection at Redang Island using Logistic Regression. Explanatory variables as candidate factors were sand particle size, temperature, distance from the high-tide line, and vegetation type. Vegetation type was considered as a binary variable that represents whether the site was vegetated (wood/shrub and grass/herbaceous) or not vegetated (open sand and riverbank). We selected the best model using Akaike Information Criterion (AIC) values. In addition, we constructed a decision tree model from the same candidate environmental characteristics using the rpart package (Therneau and Atkinson 2019). The constructed decision tree was visualized using the partykit package (Hothorn and Zeileis 2015).

Results

Within the nine nights of our study period, there were 4–10 Green Turtle nests per night (6.33 ± 1.89 nests/night) at Redang Island. We observed 87 digging attempts that resulted in 58 successful nest sites and 29 aborted nest sites. The nesting success ratio was 66.7% (58 successful nests of 87 digging attempts). We measured body size for 53 of the 58 female Green Turtles: mean CCL = 91.9 ± 5.1 cm (range, 86.0–113.0 cm); mean CCW = 86.0 ± 5.1 cm (range, 71.5–98.0 cm).

Environmental characteristics of nest sites were measured at 48 successful nest sites and 20 aborted nest sites, of which temperature was not measured in 10 successful nest sites (Fig 2). At Redang Island, successful nest sites were significantly lower in sand temperature ($t = 6.68$, df = 16, $P < 0.001$), closer to the

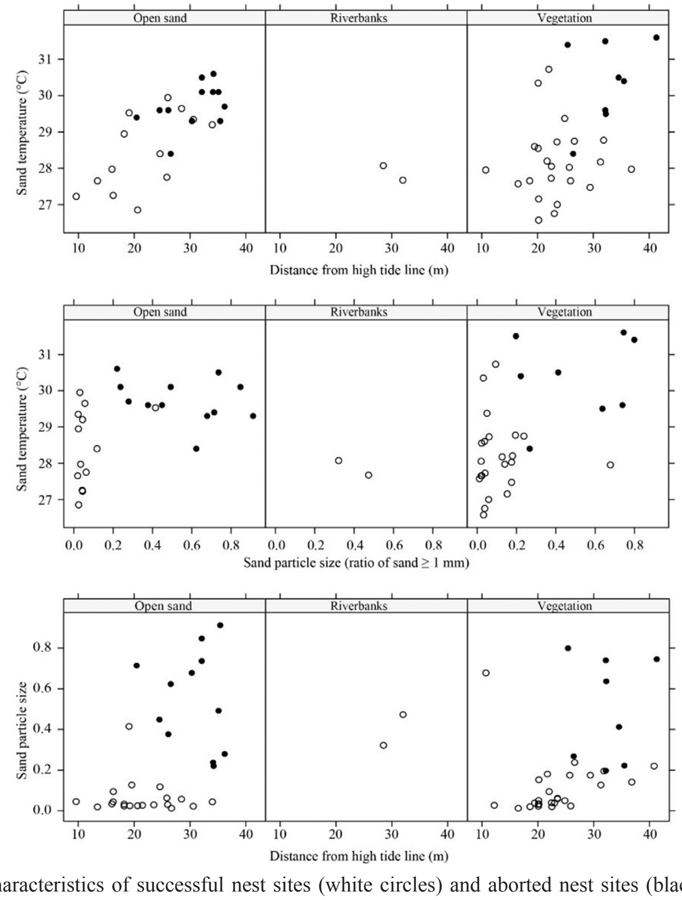

Figure 2. Microhabitat characteristics of successful nest sites (white circles) and aborted nest sites (black circles) for Green Turtles (*Chelonia mydas*) nesting on Redang Island, Peninsular Malaysia. Vegetation area includes woody, shrub, grassy vegetation areas.

Table 1. Summary of environmental factors influencing nest site selection in Green Turtles (*Chelonia mydas*) at Redang Island (this study) and Penang Island (Mohd Salleh et al. 2018), Peninsular Malaysia. Different superscript letters indicate significant differences after false discovery rate adjustment.

	Redang Island		Penang Island	
	Successful nest sites	Aborted nest sites	Successful nest sites	Aborted nest sites
Sand temperature (°C)	28.2 ± 1.0^{a} (n = 38)	30.0 ± 0.9^{c} (n = 20)	28.7 ± 2.2^{ab} (n = 36)	29.1 ± 2.7^{b} (n = 106)
Distance from tide line (m)	22.9 ± 6.5^{a} (n = 48)	31.3 ± 5.0^{b} (n = 20)	22.7 ± 10.3^{a} (n = 43)	22.6 ± 8.2^{a} (n = 106)
Sand particle size (weight % ≥ 1 mm)	10.4 ± 13.3^{a} (n = 48)	52.9 ± 24.0^{bc} (n = 20)	64.7 ± 14.3^{c} (n = 43)	38.8 ± 7.0^{b} (n = 42)

high tide line ($t = 7.50$, df = 19, $P < 0.001$), and finer in sand particle size ($Z = 3.81$, $P < 0.001$) compared to aborted nest sites (Table 1). We found that sand temperature and distance from high tide line at successful nest sites were not significantly different between Redang Island and Penang Island ($t = 1.10$, df = 49, $P = 0.335$ and $t = 0.10$, df = 69, 0.950, respectively); however, we found that the sand particle size of successful nest sites on Redang Island was significantly finer than successful nest sites on Penang ($W = 2032$, $P < 0.001$; Table 1). We also found that aborted nest sites on Redang Island were significantly warmer ($t = 2.63$, df = 93, $P = 0.02$) and further from the high tide line ($t = 6.39$, df = 41, $P < 0.001$) than aborted nest sites on Penang Island but were not significantly different in sand particle size compared to both successful and aborted nest sites on Penang Island ($W = 545$, $P = 0.09$ and $W = 295$, $P = 0.07$, respectively; Table 1; Fig. 3).

We recorded the location of nest sites in relation to vegetation type in 57 successful nest sites and 25 aborted nest sites at Redang Island. Nesting attempts were mainly within the vegetation area (woody and shrub vegetation) or the open sand area (Table 2). There were only two nesting attempts on the riverbank at Redang Island, in contrast with Penang Island where no nests were observed on the riverbank. There were no significant differences in the distribution of nest sites in relation to vegetation types among all pairs of the sites (i.e., successful nest sites and aborted nest sites at Redang Island and Penang Island) after the FDR adjustment (Fisher's Exact Test, $P > 0.05$). There were only two cases that the nesting turtle changed the vegetation types from the aborted nest site and successful nest site during the same nesting event at Redang Island.

Logistic Regression resulted in two best-fitting models based on AIC (difference < 2), one that contained all explanatory variables (temperature, distance from high tide line, sand particle size, and vegetation type) and one that included all variables except vegetation type (Table 3). Models that did not include vegetation type and that included sand particle size mostly improved the model. However, the decision tree model selected only sand particle size. Successful nest sites exhibited less sand (< 19.6%) within larger particle size classes (≥ 1 mm), while aborted nest sites exhibited more sand (≥ 19.6%) within larger particle size classes (Fig. 4), meaning sand at aborted nest sites was coarser than sand at successful nest sites at Redang Island. This preference pattern was in contrast with that of Penang Island where successful nest sites exhibited more sand (≥ 50.3%) within large particle size classes (≥ 1 mm), while aborted nest sites

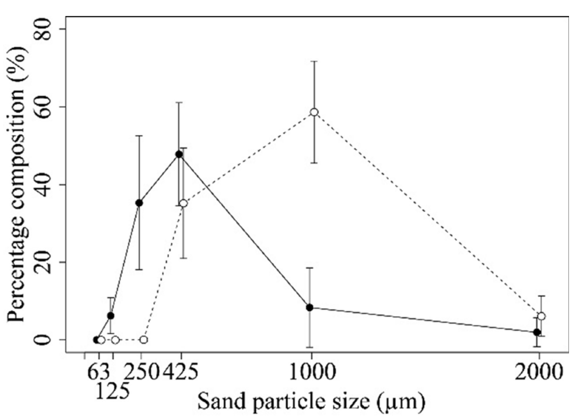

Figure 3. Percentage composition of sand particle size of successful nest sites of Green Turtles (*Chelonia mydas*) at Redang Island (black circles) and Penang Island, Peninsular Malaysia, obtained by Mohd Salleh et al. (2018; white circles). The symbols are means and the vertical lines are ± one standard deviation.

Table 2. Distribution of Green Turtle (*Chelonia mydas*) nests at Redang Island (this study) and Penang Island (Mohd Salleh et al. 2018), Peninsular Malaysia, in relation to vegetation type.

	Redang Island		Penang Island	
	Successful nest sites	Aborted nest sites	Successful nest sites	Aborted nest sites
Grassy vegetation	1	0	6	7
Open Sand	25	17	18	62
Woody/shrub vegetation	29	8	19	37
Riverbank	2	0	0	0
Total	57	25	43	106

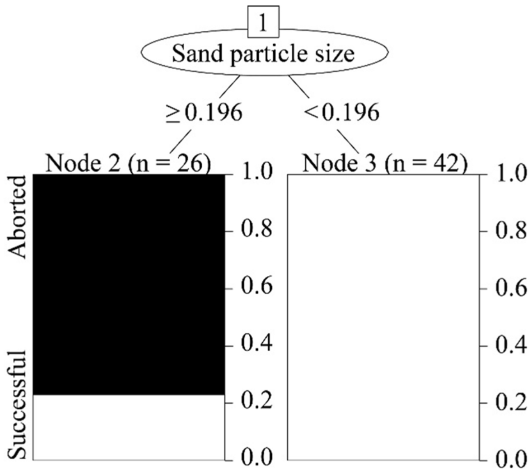

Figure 4. Decision tree for factors influencing nest site selection in Green Turtles (*Chelonia mydas*) nesting on Redang Island, Peninsular Malaysia. Sand particle size is represented as the ratio of sand ≥ 1 mm. Nodes 2 and 3 indicate the ratio of successful nest sites (white bars) and aborted nest sites (black bar).

exhibited less sand (< 50.3%) within larger particle size classes (Mohd Salleh et al. 2018).

Discussion

This study indicates that the sand particle size is a major factor involved in nest site selection by Green Turtles on Redang Island. Sand particle size was also found to influence Green Turtles nesting on Penang Island (Mohd Salleh et al. 2018), but the direction that sand particle size influences nest site selection was different between Redang Island and Penang Island. Because the sand particle size distribution at Redang Island beach (Stewart et al. 2019) is more varied and less disturbed than the one in Penang beach, nesting Green Turtles might choose the nest sites more naturally at Redang Island. On Redang Island, Green Turtles aborted nest sites with large sand grain sizes (≥ 20% of sand particles > 1 mm; mean = 53%) in favor of nest sites with smaller sand grain sizes (< 20% of sand particles > 1 mm; mean = 10%). Conversely, Green Turtle nesting on Penang Island aborted nests with smaller sand grain size (< 50% of sand particles > 1 mm; mean = 39%) in favor of nest sites with larger sand grain sizes (> 50% of sand particles > 1 mm; mean = 65%; Mohd Salleh et al. 2018). The composition of beach sand must support nest construction and facilitate gas exchange necessary for embryonic development (Mortimer 1995), but the effect of sand particle size on nesting success may change in combination with other factors such as moisture. In general, coarse sand has a higher angle of repose than fine sand (Vangla and Latha 2015), which indicates higher resistance to collapsing nest chambers. On the other hand, wet sand has resulted in higher angle of repose and sand clustering than dry sand (Hornbaker et al. 1997). Higher precipitation on the east coast of Peninsular Malaysia versus the west coast (Kubota and Ahmad 2006; Wong et al. 2009) may result in high nesting success at finer sand area at Redang Island.

Table 3. Selection of Logistic Regression models for nesting success of Green Turtles (*Chelonia mydas*) at Redang Island, Peninsular Malaysia, based on Akaike Information Criterion (AIC) values. Distance indicates distance from high tide line, Sand indicates sand particle size, and Vegetation indicates vegetation type as binary (vegetated site or not). The letter k = the number of parameters.

Model	Explanatory variables	AIC	ΔAIC	k
1	Temperature + Distance + Sand	19.8	0.0	3
2	Temperature + Distance + Sand + Vegetation	20.3	0.5	4
3	Temperature + Sand	25.8	6.0	2
4	Distance + Sand	29.6	9.8	2
5	Temperature + Distance	43.1	23.3	2

Sand particle size may influence conditions for hatchling development and survival. In freshwater turtles, finer particle size has been shown to provide cooler nest temperatures (Mitchell and Janzen 2019). Green Turtle nests at Redang Island deposited in finer sand, however, were hotter than nests deposited in coarser sand (Stewart et al. 2019). This is consistent with the observation from the nests of Loggerhead Turtles (*Caretta caretta*) that smaller sand grains may correlate with higher conductivity that results in higher temperature (Speakman et al. 1998). If the heating results in incubation conditions that are too hot, then hatching success and hatchling performance can both decrease (Booth 2017). In addition, coarser sand may be preferred to increase gas exchange of incubating eggs (Ackerman 1980; Foley et al. 2006); however, these effects are possibly offset by precipitation that cools nests and facilitates gas exchange (Prange and Ackerman 1974), given the relatively high precipitation in Redang Island. In fact, a recent study at Redang Island indicated that neither hatchling morphology nor locomotor performance were influenced by sand particle size composition (Stewart et al. 2019). Therefore, the preference to finer sand particle size may not have negative effects on hatchling survival at Redang Island.

Sand temperature and distance from high tide line were not selected as important factors influencing nest site selection in the decision tree but did improve model fits. Nevertheless, these factors, particularly sand temperature, may still be important for nest site selection, as suggested by previous studies (López-Castro et al. 2004; Mohd Salleh et al. 2018). The lack of a significant difference in these factors between the successful nest sites between Redang Island and Penang Island may indicate that these variables are generally important for nesting site selection and hatchling success in Green Turtles. The importance of temperature in nest site selection has not always been supported in studies of sea turtles (Horrocks and Scott 1991; Wood and Bjorndal 2000), but it is reasonable to consider that nesting females might select nesting sites where the sand temperature does not get too high, thereby avoiding nest temperatures that cause metabolic alterations in the developing embryos (López-Castro et al. 2004). Selecting nest sites with certain sand temperature may also be important for avoiding skewing of sex ratio in species with temperature dependent sex determination (Doody et al. 2006), like Green Turtles.

Distance from the high tide line is important for sea turtle nests to avoid flooding and reduce predation risk. In general, long distance from high tide line reduces mortality of nests, but hatchlings must take long distance movement to the sea during which the predation risk is high (Delaney and Janzen 2018). The tradeoff between the risk and benefit may result in nests approximately 23 m from high tide line both at Redang Island and Penang Island. Aborted nests in Redang Island were located further from the high tide line than successful nests and aborted nests in Penang Island. The difference between Redang Island and Penang Island may be attributable to the fact that the beach width of Redang Island is slightly greater than that of Penang Island. During observations, Green Turtles sometimes moved to higher areas of the beach, aborted nesting, and then moved back towards the high tide line for successful nests. Aborted nests at higher areas might be partly due to difficulty in digging at roots of dune trees, but possibly nesting turtles selected nest sites for improving survivability of their hatchlings. Crawling up to the beaches may pose a predation risk to nesting females, but this is not a case in Malaysia because there are no large carnivorous animals such as Jaguars (*Panthera onca*) and Malaysian people have generally consumed only sea turtle eggs, not sea turtle meat.

On the other hand, the effect of vegetation type on nest site selection was not supported in all the analyses in this study. Vegetation areas may be preferable for sea turtle nesting as higher digging success of Green Turtles was reported at grassy vegetation zone composed of Bermuda Grass (*Cynodon dactylon*) and Mission Grass (*Pennisetum setosum*; Wang and Cheng 1999). The number of successful nest sites at vegetation areas was not significantly higher than aborted nests either in Redang Island and Penang Island, however. Thus, improvement in digging success at vegetation was not supported in Malaysia. Vegetation at Chagar Hutang beach in Redang Island is characterized mainly by shrub and woody vegetation; therefore, benefits of vegetation roots such as sand stability and moistures may not be apparent. Nonetheless, the effects of vegetation on nest site selection should be further studied by correlating the number of nests with available areas of each habitat type (area % cover of each habitat) or considering confounding between habitat types and other factors such as temperature and distance from high tide line. In fact, some measurements at the vegetation area unexpectedly showed high temperature in this study, possibly resulting from variations in vegetation areas (e.g., some vegetation areas might not be shaded in the evening and might not be cooled at night).

The nesting success ratio was higher in Redang Island (66.7%) than Penang Island (28.9%, 43 successful nests/149 digging attempts; Mohd Salleh et al. 2018). It must be kept in mind that the nests in Redang Island were monitored only in August in this study, whereas the nests were monitored over an entire year in Penang Island (Mohd Salleh et al. 2018). The difference in nesting success may be one of the factors that resulted in the difference in the annual number of nests between Redang Island (221–687 nests; Chan 2010) and Penang Island (43–61 nests; Mohd Salleh et al. 2020). The beach in Redang Island may have more suitable microhabitats (e.g., sand particle size composition in relation to moisture) for nesting than Penang Island, in addition to less severe anthropogenic effects (beaches near the civilization in Penang Island vs highly protected area in Redang Island). In fact, it is concerning that the beach areas suitable for sea turtles have been reduced by reclamation projects in Penang Island (Ministry of Entrepreneur Development and Cooperatives. 2021. On The Penang South Reclamation Project. Available from https://www.medac.gov.my/index.php?id=11&page_id=28 [Accessed 12 June 2021]).

In conclusion, we found that a difference in the effects of sand particle size on nesting success of Green Turtles between the Redang Island and Penang Island located on the east and west coast of Peninsular Malaysia, respectively. On the other hand, the sand temperature and distance from high tide line of successful nests were similar at both islands, possibly indicating that these factors are commonly important. Considering that nesting Green Turtles at the east coast of Peninsular Malaysia are genetically differentiated from the west coast (Nishizawa et al. 2018), the difference in the effect of sand particle size may reflect the local adaptation of Green Turtles for improving reproductive outputs. This is not surprising because variability in the effect of environmental factors is evident among sea turtle populations (Kelly et al. 2017). Alternatively, suitable sand particle size for nesting success in the Green Turtle may change in relation to other microhabitat characteristics such as precipitation and moisture, and possibly for maintaining adequate sand temperature.

Understanding the complexity in the effects of sand particle size in further studies will be important for conservation of endangered Green Turtles.

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Literature Cited

Ackerman, R.A. 1980. Physiological and ecological aspects of gas exchange by sea turtle eggs. American Zoologist 20:575–583.

Aini Hasanah, A.B., F. Nik, A. Amiruddin, and N. Nurolhuda. 2014. Understanding nesting ecology and behaviour of Green Marine Turtles at Setiu, Terengganu, Malaysia. Marine Ecology 36:1003–1012.

Booth, D.T. 2017. Influence of incubation temperature on sea turtle hatchling quality. Integrative Zoology 12:352–360.

Booth, D.T., A. Dunstan, I. Bell, R. Reina, and J. Tedeschi. 2020. Low male production at the world's largest Green Turtle rookery. Marine Ecology Progress Series 653:181–190.

Chan, E.H. 2010. A 16 year record of Green Turtle and Hawksbill Turtle nesting activity at Chagar Hutang Turtle Santuary, Redang Island, Malaysia. Indian Ocean Turtle Newsletter 12:1–5.

Chan, E.H. 2013. A report on the first 16 years of a long-term marine turtle conservation project in Malaysia. Asian Journal of Conservation Biology 2:129–135.

Chatting, M., S. Hamza, J. Al-Khayat, D. Smyth, S. Husrevoglu, and C.D. Marshall. 2021. Feminization of Hawksbill Turtle hatchlings in the twenty-first century at an important regional nesting aggregation. Endangered Species Research 44:149–158.

Cuevas, E., M.Á. Liceaga-Correa, and I. Mariño-Tapia. 2010. Influence of beach slope and width on Hawksbill (*Eretmochelys imbricata*) and Green Turtle (*Chelonia mydas*) nesting activity in El Cuyo, Yucatán, Mexico. Chelonian Conservation and Biology 9:262–267.

Delaney, D.M., and F.J. Janzen. 2018. Offspring dispersal ability covaries with nest-site choice. Behavioral Ecology 30:125–133.

Doody, J.S., E. Guarino, A. Georges, B. Corey, G. Murray, and M. Ewert. 2006. Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. Evolutionary Ecology 20:307–330.

Flitz, B.A., and S.J. Mulin. 2006. Nest-site selection in the Eastern Box Turtle, *Terrapene carolina carolina*, in Illinois. Chelonian Conservation and Biology 5:309–312.

Foley, A.M., S.A. Peck, and G.R. Harman. 2006. Effects of sand characteristics and inundation on the hatching success of Loggerhead Sea Turtle (*Caretta caretta*) clutches on low-relief mangrove islands in southwest Florida. Chelonian Conservation and Biology 5:32–41.

Gatto, C.R., and R.D. Reina. 2020. Sea turtle hatchling locomotor performance: incubation moisture effects, ontogeny and species-specific patterns. Journal of Comparative Physiology B 190:779–793.

Hays, G.C., C.R. Adams, J.A. Mortimer, and J.R. Speakman. 1995. Inter- and intra-beach thermal variation for Green Turtle nests on Ascension Island, South Atlantic. Journal of the Marine Biological Association of United Kingdom 75:405–411.

Herve, M. 2020. RVAideMemoire: Testing and Plotting Procedures for Biostatistics. R package version 0.9-78. https://CRAN.R-project.org/package=RVAideMemoire.

Hornbaker, D.J., R. Albert, I. Albert, A.-L. Barabási, and P. Schiffer. 1997. What keeps sandcastles standing? Nature 387:765.

Horrocks, J.A., and N.M. Scott. 1991. Nest site location and nest success in the Hawksbill Turtle *Eretmochelys imbricata* in Barbados, West Indies. Marine Ecology Progress Series 69:1–8.

Hothorn, T., and A. Zeileis. 2015. partykit: a modular toolkit for recursive partytioning in R. Journal of Machine Learning Research 16:3905–3909.

International Union for the Conservation of Nature (IUCN). 2020. IUCN Red List of Threatened Species, 2020. http://www.iucnredlist.org.

Kassambara, A. 2020. rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R package version 0.6.0. https://CRAN.R-project.org/package=rstatix.

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

Kolbe, J.J., and F.J. Janzen. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. Ecology 83:269–281.

Kubota, T., and S. Ahmad. 2006. Wind environment evaluation of neighborhood areas in major towns of Malaysia. Journal of Asian Architecture and Building Engineering 5:199–206.

Lolavar, A., and J. Wyneken. 2021. Effects of supplemental watering on Loggerhead (*Caretta caretta*) nests and hatchlings. Journal of Experimental Marine Biology and Ecology 534:151476. https://doi.org/10.1016/j.jembe.2020.151476.

López-Castro, M.C., R. Carmona, and W.J. Nichols. 2004. Nesting characteristics of the Olive Ridley Turtle (*Lepidochelys olivacea*) in Cabo Pulmo, southern Baja California. Marine Biology 145:811–820.

Miller, J.D., C.J. Limpus, and M.H. Godfrey. 2003. Nest site selection, oviposition, eggs, development, hatching, and emergence of Loggerhead Turtles. Pp. 125–143 *In* Loggerhead Sea Turtles. Bolten, A.B., and B.E. Witherington (Eds.). Smithsonian Institution Press, Washington, D.C., USA.

Mitchell, T.S., and F.J. Janzen. 2019. Substrate influences turtle nest temperature, incubation period, and offspring sex ratio in the field. Herpetologica 75:57–62.

Mitchell, T.S., J.A. Maciel, and F.J. Janzen. 2013. Does sex-ratio selection influence nest-site choice in a reptile with temperature-dependent sex determination? Proceedings of the Royal Society B 280:20132460. https://doi.org/10.1098/rspb.2013.2460.

Mohd Fauzi, M., L.H. Lee, and K.H.S. Mohd. 2014. Coastal vulnerability assessment towards sustainable management of Peninsular Malaysia coastline. International Journal of Environmental Science and Development 5:533–538.

Mohd Salleh, S., H. Nishizawa, T. Ishihara, S.A. Mohd Sah, and J.C.A. Jalal. 2018. Importance of sand particle size and temperature for nesting success of Green Turtles in Penang Island, Malaysia. Chelonian Conservation and Biology 17:116–122.

Mohd Salleh, S., H. Nishizawa, S.A. Mohd Sah, and K.C.A. Jalal. 2020. Reproductive seasonality and environmental effects in Green Turtle (*Chelonia mydas*) nesting at Penang Island, Malaysia. Journal of the Marine Biological Association of the United Kingdom 100:645–650.

Mortimer, J.A. 1990. The influence of beach sand characteristics on the nesting behavior and clutch survival of Green Turtles (*Chelonia mydas*). Copeia 1990:802–817.

Mortimer, J.A. 1995. Factors influencing beach selection by nesting sea turtles. Pp. 45–51 *In* Biology and Conservation of Sea Turtles. Bjorndal, K.A. (Ed.). Smithsonian Institution Press, Washington, D.C., USA.

Nishizawa, H., J. Joseph, Y.K. Chong, S.A. Syed-Kadir, I. Isnain, T.A. Ganyai, S. Jaaman, and X. Zhang. 2018. Comparison of the rookery connectivity and migratory connectivity: insight into movement and colonization of the Green Turtle (*Chelonia mydas*) in Pacific-Southeast Asia. Marine Biology 165:77.

Prange, H.D., and R.A. Ackerman. 1974. Oxygen consumption and mechanisms of gas exchange of Green Turtle (*Chelonia mydas*) eggs and hatchlings. Copeia 1974:758–763.

Price, J.T., B. Drye, R.J. Domangue, and F.V. Paladino. 2018. Exploring the role of artificial lighting in Loggerhead Turtle (*Caretta caretta*) nest-site selection and hatchling disorientation. Herpetological Conservation and Biology 13:415–422.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Seminoff, J.A., C.D. Allen, G.H. Balazs, P.H. Dutton, T. Eguchi, H.L. Haas, S.A. Hargrove, M. Jsensen, D.L. Klemm, A.M. Lauritsen, et al. 2015. Status review of the Green Turtle (*Chelonia mydas*) under the Endangered Species Act. Technical Memorandum NOAA-NMFS-SWFSC-539. National Oceanic and Atmospheric Administration, La Jolla, California, USA. 571 p.

Speakman, J.R., G.C. Hays, and E. Lindblad. 1998. Thermal conductivity of sand and its effect on the temperature of Loggerhead Sea Turtle (*Caretta caretta*) nests. Journal of the Marine Biological Association of the United Kingdom 78:1337–1352.

Stewart, T.A., D.T. Booth, and M.U. Rusli. 2019. Influence of sand grain size and nest microenvironment on incubation success, hatchling morphology and locomotion performance of Green Turtles (*Chelonia mydas*) at the Chagar Hutang Turtle Sanctuary, Redang Island, Malaysia. Australian Journal of Zoology 66:356–368.

Therneau, T., and B. Atkinson. 2019. rpart: Recursive Partitioning and Regression Trees. R package version 4.1-15. https://CRAN.R-project.org/package=rpart.

Van De Merwe, J., K. Ibrahim, and J. Whittier. 2006. Effects of nest depth, shading, and metabolic heating on nest temperature in sea turtle hatcheries. Chelonian Conservation and Biology 5:210–215.

Vangla, P., and G.M. Latha. 2015. Influence of particle size on the friction and interfacial shear strength of sands of similar morphology. International Journal of Geosynthetics and Ground Engineering 1:6. https://doi.org/10.1007/s40891-014-0008-9.

Wallace, B.P, A. D. DiMatteo, B. J. Hurley, E. M. Finkbeiner, A. B. Bolten, M. Y. Chaloupka, B. J. Hutchinson, F. A. Abreu-Grobois, D. Amorocho, K. A. Bjorndal, et al. 2010. Regional management units for marine turtles: a novel framework for prioritizing

conservation and research across multiple scales. PLoS ONE 5:e15465. https://doi.org/10.1371/journal.pone.0015465
Wang, H.-C., and I.-J. Cheng. 1999. Breeding biology of the Green Turtle, *Chelonia mydas* (Reptilia: Cheloniidae), on Wan-An Island, PengHu archipelago. II. Nest site selection. Marine Biology 133:603–609.
Wood, D.W., and K.A. Bjorndal. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in Loggerhead Sea Turtles. Copeia 2000:119–128.
Wong, C.L., T. Venneker, S. Uhlenbrook, A.B.M. Jamil, and Y. Zhou. 2009. Variability of rainfall in Peninsular Malaysia. Hydrology and Earth System Sciences Discussions 6:5471–5503.
Yalçin-Özdilek, Ş., H.G. Özdilek, and F.S. Ozaner. 2007. Possible influence of beach sand characteristics on Green Turtle nesting activity on Samandağ Beach, Turkey. Journal of Coastal Research 23:1379–1390.

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