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NEST SITE SELECTION BY SEA TURTLES

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The distribution of 38 nests of loggerhead turtles (*Caretta caretta*) on beaches on Sanibel and Captiva islands, south-western Florida (26°26'N 82°16'W), and of 70 first digging attempts by green turtles (*Chelonia mydas*) on Ascension Island (7°57'S 14°22'W), was quantified. For loggerhead turtles on Sanibel and Captiva, nests were clumped close to the border between the open sand and the supra-littoral vegetation that backed the beaches. This spatial pattern of nests was closely reproduced by assuming simply that turtles crawled a random distance above the most recent high water line prior to digging. In contrast, green turtles on Ascension Island clumped their first digging attempts on the uneven beach above the springs high water line, crawling up to 80 m to reach this beach zone.

INTRODUCTION

Sea turtles spend most of their adult lives in the sea but emerge onto beaches to lay their eggs in nests which they excavate in the sand. As with many other oviparous animals, the position of the nest may strongly influence the probability of offspring survival (cf. Hays & Speakman, 1993). In addition, the sex of sea turtles is determined principally by the incubation temperature of the eggs (Yntema & Mrosovsky, 1982), and therefore the nest position, by influencing the nest temperature, may also influence the sex of the hatchlings (Morreale et al., 1982). Yet despite this importance of nest placement in influencing the reproductive fitness of sea turtles, little is known regarding the factors that initiate nest excavation. This has led to the suggestion that nest site selection may be a 'complicated' process (Dodd, 1988) and has provoked speculation concerning possible micro-habitat cues that may initiate the digging process (Stoneburner & Richardson, 1981). Alternatively, other authors have implied that the selection of a nest site is essentially a random process leading to nests being widely scattered (Mrosovsky, 1983; Eckert, 1987).

One method of investigating possible cues used in nest-site selection would be to conduct controlled manipulations of beach characteristics and then to observe the subsequent behaviour of turtles emerging from the sea to nest. Such manipulations, have not, however, been performed and furthermore may be undesirable in conservation terms. An alternative approach is to document the spatial pattern of excavations in

relation to a naturally occurring range of beach conditions. In this paper we pursue the latter approach, making observations at two contrasting rookeries and for two species: for green turtles (*Chelonia mydas*) nesting on Ascension Island in the South Atlantic (7°57'S 14°22'W) and for loggerhead turtles (*Caretta caretta*) nesting on Sanibel and Captiva Islands, south-western Florida (26°26'N 82°16'W). By quantifying the spatial pattern of nesting attempts at these two sites in relation to readily observed beach features, we develop hypotheses for the factors initiating nest excavation.

METHODS

Loggerhead turtles on Sanibel and Captiva

Loggerhead turtles typically nest on the islands of Sanibel and Captiva from early May until late August (Le Buff, 1990). In relation to other nesting beaches in Florida, these islands support only a small nesting population with <100 nests laid each season. These nesting beaches are characterized by being backed by dense supra-littoral vegetation. We termed the border between this vegetation and the beach, the 'vegetation line'; the region inland from the vegetation line the 'vegetation zone'; and the region seaward of the vegetation line the 'open beach'.

Throughout the nesting season, nest sites were marked by volunteers of the Sanibel and Captiva Conservation Corporation. Nests were identified by direct observation of laying turtles or by carefully digging for the eggs. During our visit to the study site (28 June to 15 July 1992) we measured the distance of nests from the vegetation line as this was the clearest feature on the beaches. During this period we also recorded the proportion of turtles that, on approaching to within 2.5 m of the vegetation line, had (a) penetrated the vegetation zone and attempted to dig, or had (b) attempted to dig on the open beach immediately in front (<2.5 m) of the vegetation line.

To measure the beach gradient we used a telescopic rifle sight mounted on a spirit level with the unit fixed to a photographic tripod. Using the spirit level to ensure that the telescopic sight was horizontal, we aligned the sight on a graduated 1.5-m long measuring pole which was held vertically with the base resting on the sand surface 5 m away. The vertical height of the beach between the measuring pole and the sight was then calculated simply as the height of the sight minus the aligned height read off the measuring pole through the sight. By testing this apparatus with targets of known height, the accuracy was shown to be within 2 cm over a horizontal distance of 5 m. Tidal height data were taken from local tide tables.

Green turtles on Ascension Island

Several thousand nests are laid annually by green turtles on Ascension Island, with the height of the nesting season occurring between February and May (Mortimer & Carr, 1987). Between 8 February and 8 April 1992, Long Beach, one of the major green turtle nesting beaches on the island, was patrolled on foot at night to locate turtles attempting to nest. This beach was characterized firstly by a general absence of supra-littoral vegetation. Secondly, large breakers had created a very distinct area of com-

pacted sand below the springs high water line (HWL), while above this springs HWL the beach had a very undulating topography as a result of previous turtle excavations. Craters in the sand above the springs HWL were typically 30–60 cm deep and 1–2 m in diameter. We measured the straight line distance of the turtles' first digging attempts from both the springs HWL and the current HWL.

RESULTS

Loggerhead turtles on Sanibel and Captiva

We recorded the position of 38 nests. Nests were constructed from 30 m to the seaward side of the vegetation line, to 2 m into the vegetation zone. Nests were not uniformly distributed within this range, tending to be clumped close to the vegetation line (Figure 1A).

Between 28 June and 15 July 1992, 26 crawls were observed that included a digging attempt. Of these, 11 crawls penetrated the vegetation zone only one of which resulted in a nest being laid; 10 crawls resulted in nests immediately (<2.5 m) in front of the vegetation line; and five crawls resulted in nests on the open beach >2.5 m from the vegetation line. Thus for a turtle crawling close (<2.5 m) to the vegetation line, the probability of successful nest excavation was $(1+10)/21=0.52$. No turtles that had crawled into the vegetation line subsequently came out and nested on the open beach.

In an attempt to explain the distribution of loggerhead turtle nests we hypothesized that turtles might simply crawl a 'random' distance prior to nest excavation. To test this hypothesis we defined the following parameters: (a) the width of the beach between the most recent HWL and the vegetation line, (b) the probability of successful nest excavation in the vegetation zone and on the open beach, and (c) the random-crawl distance.

(a) *Beach width.* A distinct springs HWL was not evident on the beaches. Instead there was a series of wrack lines on the beach reflecting various high tides. On 1 July the tidal height in relation to chart datum was 1.1 m. For 40 sections of beach where this HWL

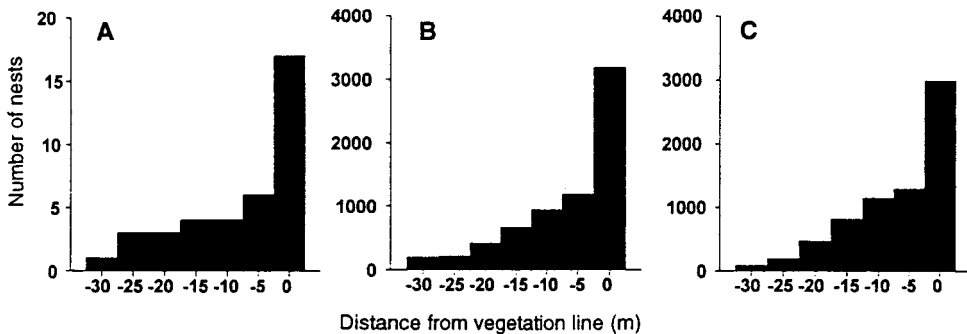


Figure 1. (A) The observed distribution of loggerhead turtle nests on Sanibel and Captiva in relation to the vegetation line (minus signs denote distances to the seaward side). (B) The modelled distribution of nests resulting from 10,000 crawls assuming that turtles crawled a normally distributed (mean=22 m, SD=11 m) random distance above the most recent HWL. (C) The modelled distribution of nests resulting from 10,000 crawls assuming that turtles crawled a uniformly distributed (limits 5 m to 40 m) random distance above the most recent HWL.

was clearly evident, the distance from this HWL to the vegetation line averaged 18.7 m (SD=8 m). The gradient of the beach below this HWL averaged 8.2% (N=6, SD=0.8%). The mean height of the high tides during May, June and July was 0.89 m (SD=0.12). Thus, using the measured distribution of distances from the HWL on 1 July to the vegetation line, the measured beach gradient, and the known tidal heights, we calculated that during May, June and July the distance between the most recent HWL and the vegetation line averaged 21.3 m (SD=8.1 m).

(b) *Probability of successful nest excavation.* From the observed results we assumed that if a crawling turtle approached to within 2.5 m of the vegetation line, then there was a 0.52 probability of a nest being successfully excavated and that all such nests would be within 2.5 m of the vegetation line, i.e. that no turtles would penetrate further than 2.5 m into the vegetation zone.

(c) *Random-crawl distance.* We assumed that turtles crawled a random distance above the most recent HWL. There are a number of random distributions that we may have examined, but for simplicity we used (i) a normal distribution of random-crawl distances with a standard deviation equal to the mean distance divided by two, and (ii) a uniform distribution of random-crawl distances with a lower limit of 5 m above the HWL.

For the normal distribution we varied the mean random-crawl distance from 10 m to 60 m above the HWL and for the uniform distribution we varied the upper limit between 10 and 60 m above the HWL. For each simulation we generated the nest distribution in relation to the vegetation line resulting from 10,000 crawls, and then compared the modelled results with the observed distribution. Statistical significance was calculated using a G-test (Sokal & Rohlf, 1981). To ensure that the number of observations in each class was >5, we compared the observed and modelled results at

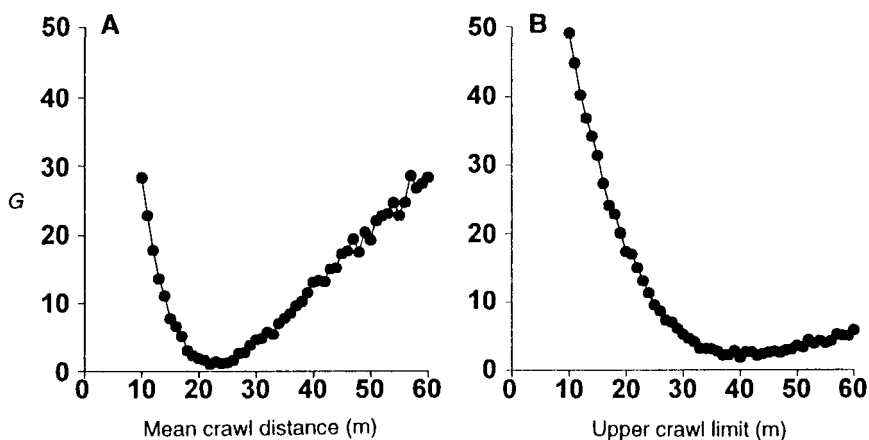


Figure 2. For loggerhead turtle nests on Sanibel and Captiva, the variation in the G value between the observed (Figure 1A) and modelled (Figure 1B,C) nest distributions assuming (A) different mean distances above the most recent HWL for a normally distributed random-crawl length and (B) different upper limits above the most recent HWL for a uniformly distributed random-crawl length. A G value of <5.99 signifies that the observed and modelled nest distributions did not differ significantly ($P>0.05$).

three distance intervals from the vegetation line: 2.5 to -2.5 m, -2.5 to -17.5 m and -17.5 to -32.5 m (positive values represent distances measured to the landward side and vice versa). For three classes (2 df), a G value of <5.99 signifies that the observed and modelled distributions did not differ significantly ($P>0.05$). For the normally distributed mean random-crawl distance, when the mean crawl distance was between 17 and 33 m there was no significant difference between the observed and modelled results (Figure 2A). Similarly for the uniformly distributed mean random-crawl distance, when the upper limit for the crawl length was between 30 and 59 m there was no significant difference between the observed and modelled results (Figure 2B).

Thus, by assuming a variety of distributions for the random-crawl distance, modelled nest distributions were readily generated which closely matched the observed pattern.

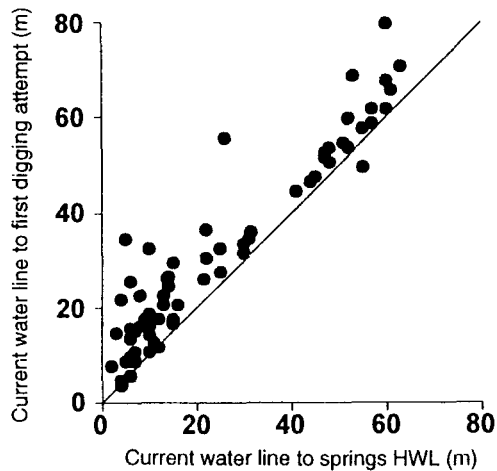


Figure 3. For green turtles on Ascension Island, the distance crawled by turtles before their first digging attempt in relation to the distance to the springs HWL. The line of equivalence is shown, i.e. digging attempts on the springs HWL lie on this line, digging attempts short of the springs HWL lie below this line and digging attempts beyond the springs HWL lie above this line.

Green turtles on Ascension Island

The position of 70 first digging attempts was recorded. The distance crawled from the current water line prior to the first digging attempt ranged from 4 to 80 m (mean 31.2 m, $N=70$, $SD=19.9$). Turtles crawled further before attempting to dig when the springs HWL was further from the current water line (Figure 3), with 99% (69 out of 70) of first digging attempts being made above the springs HWL. The mean position of first digging attempts was 7.3 m above the springs HWL ($N=70$, $SD=6.6$ m).

DISCUSSION

Loggerhead turtle nests on the beaches in south-western Florida tended to be concentrated close to supra-littoral vegetation. A similar spatial pattern has been reported previously for loggerhead turtles nesting in the Mediterranean (Hays & Speakman,

1993). In both these studies, penetration into the vegetation zone was limited and the probability of nest excavations being aborted in the vegetation zone was high. This was presumably due to roots that impeded digging. Thus the constraint imposed on the inland distribution of nests by vegetation appears to be common to these two widely separated rookeries.

The spatial pattern of nests has also been documented previously for other species of sea turtle. These studies have tended to concentrate on examining the implications of nest placement for either the survival and/or sex of the hatchlings. For example, for hawksbill turtles (*Eretmochelys imbricata*) nesting in Barbados, Horrocks & Scott (1991) found that nests tended to be clumped in the beach zone which maximized hatchling survival, while for leatherback turtles nesting in the Guineas and the Virgin Islands, nests have been reported to be widely dispersed, possibly due to the unpredictable pattern of hatchling survival on these beaches (Mrosovsky, 1983; Eckert, 1987). However, such studies have not directly addressed the question of how sea turtles select where to start nest excavation. Furthermore, an analysis of only the distribution of nests, ignores those nesting attempts that were aborted, and consequently may not reveal the true spatial pattern of digging attempts and hence the underlying mechanism of nest site selection. For example, of the 21 digging attempts that were observed on Sanibel and Captiva between 28 June and 15 July 1992, 48% were aborted. We therefore included the probability of successful nest excavation in different beach zones into the random-crawl-distance model.

The random-crawl-distance model developed in our study allowed the quantitative testing of the qualitative arguments that have been proposed before regarding random nest placement by sea turtles (Mrosovsky, 1983; Eckert, 1987). By assuming a random-crawl distance, the observed distribution of nests could be closely reproduced (Figure 1). This reproduction of the observed spatial pattern of nests occurred regardless of whether it was assumed that the random-crawl distance was normally or uniformly distributed, and furthermore occurred using a wide range of mean random-crawl distances (Figure 2). This sensitivity analysis illustrates the robustness of the evidence in support of the hypothesis that turtles on Sanibel and Captiva simply crawl a random distance prior to beginning nest excavation. Clearly, micro-habitat cues do not need to be invoked to explain the observed nesting pattern for this population. Furthermore, the model clearly demonstrates how a random-crawl distance can generate a clumped nest distribution, due to variations in the success of nest excavation in different beach zones. The wider applicability of this type of random-crawl-distance model will need to be ascertained by application to other larger loggerhead rookeries.

In contrast to our evidence for the random-crawl-distance hypothesis to explain nest site selection for loggerhead turtles, it has been suggested elsewhere (Stoneburner & Richardson, 1981) that micro-habitat cues, in particular surface sand temperature, may initiate nest excavation for this species. For loggerhead turtles nesting on the Atlantic coast of the USA, Stoneburner & Richardson (1981) used a thermal imager to examine the sand temperature along crawls and immediately behind turtles at the nest site. They reported that the surface temperature of the disturbed sand at the nest site was 2–4°C

greater than along the crawl and therefore suggested that an abrupt increase in sand temperature was the cue that initiated excavation. These results, while clearly very striking, may however, have been an artefact of their methodology. Since the sand is disturbed by a turtle both as it crawls and as it digs, the temperature of the disturbed sand at the surface will be strongly dependent on the original depth of that sand. Thus the abrupt temperature increase reported at nest sites by Stoneburner & Richardson (1981) may simply have been due to deeper warmer sand being brought to the surface when the turtles started to dig. Furthermore, Stoneburner & Richardson (1981) failed to explain what caused this anomalous thermal feature (e.g. no correlation was reported with beach topography, the HWL, sand grain size etc.), and why this feature was found only immediately behind nesting turtles and not on the beaches when turtles did not nest.

In contrast to our observations with loggerhead turtles, for green turtles on Ascension Island, there was a strong suggestion that nest site selection was not a random process but that beach topography was involved in initiating nest excavation, since turtles usually attempted to nest only after they had crawled into the uneven beach zone above the springs HWL. Similarly there is evidence from other green turtle rookeries implicating the importance of beach topography. For example, there have been anecdotal observations in Malaya and Sarawak (Hendrickson, 1958), Australia (Bustard et al., 1975), Ascension Island (Mortimer, 1981) and Aldabra Atoll (Mortimer, 1988) that green turtles often begin to dig a nest upon crawling into a crater left by a previous nesting excavation. Conversely, when irregularities in the beach surface topography on Long Beach, Ascension Island, were completely removed by storm waves during the 1978 nesting season, the turtles that emerged on subsequent nights crawled extensively across the beach without attempting to nest (Mortimer, 1981), suggesting that the unusually smooth beach surface lacked the necessary cues needed to initiate nest excavation.

In summary, we would suggest that on the two contrasting sea turtle rookeries examined here, there are different processes involved in nest site selection. For green turtles on Ascension Island, the importance of uneven beach topography in initiating nest excavation was strongly implicated. By contrast, for loggerhead turtles on Sanibel and Captiva islands, the distribution of nests could be explained without implicating exogenous cues in nest site selection, but instead simply by assuming an endogenous random-crawl distance with a constraint to successful nest excavation being imposed by supra-littoral vegetation.

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