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THERMAL CONDUCTIVITY OF SAND AND ITS EFFECT ON THE TEMPERATURE OF LOGGERHEAD SEA TURTLE (CARETTA CARETTA) NESTS

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The conductivity of sand at a depth of 30–50 cm was measured at 15 sites on the beach at Captiva Island in south-west Florida which is used by nesting loggerhead turtles (Caretta caretta). The mean daily temperature of the sand was correlated with conductivity at the same depth measured the same day (r=0.611). When day to day variation was removed the correlation between nest temperature and conductivity increased to 0.694. The sand was highly variable in its grain structure. The dominant variability (80.6%) was described by the first two principal components of a Principal Components Analysis (PCA). These two components were influenced mostly by percentages of large (>1 mm) and small (<500 μm) grains respectively. Conductivity was strongly correlated with the grain structure of the sand. The first three principal components describing sand grain structure, explained 84.1% of the variation in conductivity. Moisture content of the sand (always <5%) was not an important factor. Sites dominated by larger grains generally had poorer conductivity and were cooler. Comparisons of eight nests to seven adjacent random sites revealed no strong evidence for directional selection in nest placement relative to sand conductivity. The variance in conductivities recorded at nests was also not significantly different from the variance at random sites.

INTRODUCTION

The sex of a sea turtle is not genetically determined by heterogametic sex chromosomes, polygenic factors or arrhentoky, but rather by the environmental conditions (particularly temperature) experienced by the egg during a critical phase (Miller, 1985) of incubation (environmental sex determination (ESD): Bull, 1980, 1983; Yntema & Mrosovsky, 1982; Janzen & Paukstis, 1991). Therefore in common with several other animal groups which exhibit ESD, female turtles potentially have an unusual degree of manipulative control over the sex of their offspring (Schwartzkopf & Brooks, 1987).

Sea turtles lay their eggs in nests that are excavated on beaches. Once the female turtle has covered up the nest she returns to the sea and does not provide any care for the offspring. The only point at which turtles can exert control over the sex of their offspring is in the choice of position for the nest (Janzen, 1994a). Many nesting animals are known to choose their nest locations in response to microclimatic factors such as the thermal environment (e.g. birds, Walsberg, 1981; With & Webb, 1993; Wachob,
Freshwater turtles are also known to select their nesting locations (Bodie et al., 1996) in a manner that has been suggested to include manipulation of the sex of the offspring (Roosenberg, 1996). Whether sea turtles can also actively choose their nest sites in a way which results in a mixed sex ratio across the population has been the focus of some recent debate. This problem is of considerable ecological interest in the context of global warming which may potentially lead to single sex generations (Mrosovsky et al., 1984; Davenport, 1989; Janzen, 1994b; Dunham & Overall, 1994) if sea turtles do not actively select their nests with respect to temperature. At least some beaches appear to already produce single sex or heavily skewed sex ratios (Mrosovsky & Provancha, 1992; Chan & Liew, 1995).

It has been suggested frequently that sea turtles do actively select their nest sites using cues such as sand texture (Hendrickson & Balsingham, 1966; Carr & Hirth, 1962; Mortimer, 1982; Miller, 1985) and temperature (Stoneburner & Richardson, 1981). Stoneburner & Richardson (1981) used an infrared imaging device to follow emerged loggerhead turtles (Caretta caretta) up beaches in North Carolina, Georgia and Florida, USA. They found that the sites where turtles stopped to deposit eggs were generally associated with a marked increase (2.05–3.55°C) in sand temperature, and when turtles did not encounter such elevated temperatures they did not dig. It was consequently suggested that emerged loggerhead turtles may be sensitive to surface temperature cues in their nest site selection, and perform a specific behaviour ‘sand nuzzling’ which has the function of determining the sand temperature thus allowing them to locate suitable sites. This behaviour is also performed by other emerged sea turtles (Carr & Ogren, 1959) thus implying thermal selection of nesting sites may also be a more widespread phenomenon.

Some studies, however, have noted that the distribution of nests deposited on nesting beaches covers a wide area between the high water mark and the vegetation backing the beach (Hays & Speakman, 1993; Bjorndal & Bolten, 1992; Horrocks & Scott, 1991; Mrosovsky, 1983; Eckert, 1987). Bjorndal & Bolten (1992) for example divided the nesting beach at Tortuguero in Costa Rica into three zones: (i) the open beach, (ii) border area and (iii) inside the backing vegetation. They found large numbers of green turtles (Chelonia mydas) nesting across all three zones. Since the backing vegetation was considerably cooler than the border area and open beach (Spotila et al., 1987) it is unlikely that a single thermal cue triggered the nesting behaviour. Moreover there was little individual consistency in the nesting locations of individual turtles which were recorded laying repeat clutches. Hays & Speakman (1993) and Hays et al. (1995a) demonstrated that the deposition of nests by loggerhead turtles on beaches in Greece and Florida could be reasonably modelled by a combination of a random crawl distance from the sea combined with a constraint imposed by the beach head. This quasi-random patterning of nests with respect to distance up the beach might then also imply no specific selection process was occurring during nest deposition.

These studies have limitations for inferring the extent of nest site selection by sea turtles. Stoneburner & Richardson (1981) followed turtles along their crawls up nesting beaches. The sand is necessarily disturbed by the turtle as she crawls and the
surface temperatures are generally cooler than the subsurface because of cooling by convection to the cool night air and radiation to the cold night sky. A crawling turtle will scrape away the surface sand exposing warmer sand below. When she digs she will probably bring up even warmer sand from depth. This could therefore lead to the impression that the turtle had encountered a warm patch prior to digging.

Although some turtles recorded by Bjorndal & Bolton (1992) nested in cool backing vegetation, the majority (85%) nested in the border and open beach areas where they may have used temperature as a cue to site their nests. Our own previous studies (Hays & Speakman, 1993; Hays et al., 1995a) indicate only that nest site selection is random with respect to distance up the beach. This does not necessarily mean that the animals were nesting at random with respect to other cues like temperature. Turtles may have selected their nest sites using a cue which is itself randomly distributed with respect to distance up the beach, within a broad zone between the spring high water and vegetation lines. These latter studies therefore do not indicate the extent to which variation in sand temperature may be predictable from cues other than distance up the beach, and also whether this variation differs from that expected if the nests were deposited at random. In view of this conflicting evidence we sought to investigate the possible cues that sea turtles might employ to deposit their nests, thereby influencing the nest temperature.

Sea turtle nests are typically placed at depths between 25–150 cm. At these depths the dominant mechanism for heat transfer is conductance (de Vries, 1995), since opportunity for forced convection is reduced and there is no net radiation between the sand particles. Conductivity of the sand is therefore likely to be an important variable affecting the nest temperature at any particular site and thus potentially sex determination. The purposes of this study were: (a) to measure the conductivity of sand in situ adjacent to nests dug by sea turtles, and at randomly selected sites, and to relate these measures to the mean daily sand temperature at those sites; (b) to relate conductivities to sand moisture and grain structure; and (c) to compare the conductivities of measures made adjacent to actual nests with those made at a random distance up the beach along the same track perpendicular to the sea, to see if turtles were demonstrating any selectivity in their nest sites with respect to conductivity.

MATERIALS AND METHODS

Study site

Observations were made on the coast of the Gulf of Mexico in south-west Florida, on the island of Captiva (26°N 82°W) during June and July 1992. The beach is about 9 km long and varies between 10 and 50 m wide. The beach is backed by vegetation consisting predominantly of sea oats (Uniola paniculata), railroad vine (Ipomea pescaprae) and introduced Australian pine (Casuarina equesitifolia) (Le Buff, 1990). There was a readily discernible line delineating the vegetation from the open beach; the ‘vegetation line’. Observations were made
predominantly along the 3 km section of beach between the bridge joining Captiva to the adjacent island of Sanibel and ‘Tween Shores’ where the beach becomes backed by the highway.

**Detection of nests**

The beach was patrolled either at night and/or at dawn each day. When tracks were seen, but the turtles were not observed in the process of laying, it was established whether the nesting attempt had been successful by digging for the eggs. Nests were marked with wooden posts positioned a recorded direction and distance (always < 2 m) from the nest.

**Measurement of conductivity of sand in situ**

Measurements were made of conductivity at eight nests which varied from 1 m below the spring high water line (HWL) to 25 m above the spring HWL (the spring HWL was defined as the height of the spring high tide on the 1 July 1992). The same nests varied between 27 and 1 m below the vegetation line. All the nests were therefore on the open beach. Comparison sites for each nest site were selected using random numbers to define the distance of the comparison site from the vegetation line. Two nests were in a line perpendicular to the spring HWL and vegetation line. For these two nests only a single comparison site was selected. Observations were made at each nest and its own random comparison site on the same day, but different nests were not necessarily measured on the same day.

To avoid disturbing the eggs the conductivity was measured in the sand adjacent to the nests about 1 m away from the nest along a line parallel to the sea. Other studies of thermal relations of sea turtle nests have also adopted this policy of not measuring within the actual nest, as a conservation measure, see for example Mrosovsky & Provancha (1989). To measure conductivity in situ glass bottles were used which were filled with cold water. These bottles were buried in the sand and the rate at which they warmed up was measured relative to the temperature of a reference probe at the same depth in the sand about 60 cm away. The bottles measured approximately 15 cm high by 8 cm diameter and held 473 ml when full. The bottles had a plastic screw top which was pierced with a 3 mm diameter hole through which a thermistor probe (Grants Instruments) was inserted into the water inside. Since the bottles used had effectively identical shapes, sizes and construction materials the major variable factor influencing the rate at which the water in the bottles heated up to ambient was the conductivity of the surrounding sand at each site. The method provided a relative measure of conductivity allowing comparisons between sites.

The water bottles were cooled to between 10 and 15°C using a standard refrigerator and taken out into the field in an insulated bag. A 30–40 cm deep hole was quickly dug, initially by hand and at deeper levels using a narrow bladed trowel, 60 cm away from the place where the bottle would finally be located, along a line parallel to the sea. A temperature probe was pushed into the side wall of the hole at the base and the
sand was replaced, in the reverse order compared with its removal, and it was packed down to the original surface level. The installation of this probe which acted as a reference probe generally took 3–5 min. Between 15 and 30 min later a second hole was dug in the same way at the bottle location site. This hole was about 8 cm in diameter and 40–50 cm deep. A cold bottle was placed, with its temperature probe, into the hole so that it fitted snugly into the base and then repacked the appropriate sand on the top. The major heat exchange would be across the bottle sides and these were in contact with the undisturbed sand around the edges of the hole. This is because the top of the bottle was made of plastic which has a lower conductivity than glass and the sides had an area over seven times greater than the base. The temperatures of the water bottle and the reference probe were monitored at 1–3 min intervals using a data logger (Grants squirrel SQ1202 – precision 0.05°C) for a period of 15 h. Twenty-four hours later the site was revisited and the bottle and reference probe dug up. At 13 of the 15 sites where conductivity was measured a sample of between 0.3 and 0.5 kg of sand (sample size after Mortimer, 1990) was taken by scraping away the walls of the hole which had been adjacent to the bottle. These were very clearly defined when the bottle was removed. These samples were placed in sealed plastic bags, labelled and transported to Aberdeen for analysis. In addition we took sand samples from five other locations on the beach adjacent to known turtle nests.

**Sand sample analysis**

In Aberdeen the sand samples were removed from the sealed bags and placed in 500 ml beakers. Mass of the wet sample was taken and the samples were then dried at 60°C for 14 d to achieve constant mass. The dried samples were reweighed and the difference was equal to the moisture content of the sample (difference approach after Stancyk & Ross, 1978).

The dried samples were manually sieved through a tower of seven brass Endecott sieves (as in Horrocks & Scott, 1991) comprising sieves retaining fragments >3 mm, 2 mm, 1 mm, 500 μm, 212 μm, 106 μm and 63 μm. The fractions collected were weighed and then reconstituted. The reconstituted fractions were ashed in crucibles at 450°C for 24 h to burn off any organic fraction. The ashed samples were reweighed and the organic fraction assessed by difference from the original dry mass.

**Comparison of conductivities at nests and random sites**

If turtles select their nests using conductivity as a cue this might be apparent in several different ways, in a comparison of conductivity at nests and random sites on the beach. First, the turtles may show directional selection. That is they may preferentially choose a subset of the available conductivities which differs from the mean available conductivity. This would be apparent in a significantly different mean value at the nests (either higher or lower) and a reduced variance. Alternatively the turtles may not directionally select but choose sites which are consistently close to the beach mean. This effect would be apparent only as a
reduced variance but not significantly different mean. Finally turtles may seek out sites with exceptional conductivities to ensure production of either males or females. This effect would be apparent as a significantly increased variance in conductivity at nests compared with a sample of random sites. To explore these different possibilities the mean and variances of measured conductivities at nests and random sites on the beach were measured.

RESULTS

Conductivity

A typical pattern of increase in the bottle temperature at a single site with the parallel pattern for the adjacent reference probe is shown in Figure 1A. The reference probe did not alter in temperature throughout any measurement period and thus appeared to be unaffected by the presence of the bottle. The increase in temperature of the bottle was exponential. A log linear plot of difference between the bottle and reference probe temperatures against time revealed a linear relationship (Figure 1B). We fitted least squares fit regressions to these log/linear relationships. In all cases the $r^2$ for these relationships exceeded 0.98. The gradient of these lines (due to the logged axis the units are 'per min') was the measure of sand conductivity.

Across the 15 sites where conductivity measurements were made (eight nests and seven random sites) the conductivity varied three fold from a minimum value of $0.72 \times 10^{-3}$ to a maximum of $2.13 \times 10^{-3}$. There was no relationship between conductivity and distance of the site from the vegetation line ($F_{1,13}=1.84$, $P>0.05$) or distance from the spring HWL ($F_{1,13}=0.63$, $P>0.05$).
Relationship between conductivity and mean daily temperature

At nest sites on Captiva, and the adjacent island of Sanibel, single measures of temperature in the sand, at a given time and depth, can be used to reliably predict the average daily temperature over a 24h cycle at that site with an error of only 0.23°C (G.C. Hays, J.R. Speakman, A. MacKay & E. Lindblad, unpublished observations; see also Mrosovsky & Provancha, 1989). The measurements of temperature from the reference probes were therefore used to predict the average daily temperatures at each of the 15 measurement sites. There was a significant positive relationship between sand conductivity and the mean daily temperature at that site on the same day (Figure 2). The least squares fit regression equation: mean 24h temperature (°C) =28.6+1.74. Conductivity (min⁻¹x1000) (F₁,₁₃=7.77, P=0.015) explained 37.4% of the variability in the mean 24 h temperature. We removed the day to day variability in temperature by adjusting all measurements made on a given day relative to the mean across all days. Once the day to day variation had been eliminated the variation in mean nest temperature explained by conductivity increased to 48.1% (F=12.1, P=0.004).

Figure 2. The relationship between conductivity (gradient of the log converted difference between the bottle and reference probe temperatures x 1000) of a site and the mean daily temperature over 24 h at that site on the day of measurement. There was a positive relationship, i.e. sites with greater conductivity were warmer. The least squares fit regression line (shown) explained 37.4% of the variation in nest temperature.

Relationship between conductivity and sand parameters

The sand varied in moisture content from 0.2 to 4.1%, mean ±SD = 1.99 ±1.25%, N=15. There was no significant relationship between dampness of the sand and distance up the beach (F₁,₁₃=0.3, P>0.05). In addition conductivity was not related to moisture content (F₁,₁₃=1.23, P>0.05). The organic component (lost on ashing) was also relatively small and comprised between 0.6 and 1.3% of the sample (mean = 0.98 ±0.26%). Again this was not related to conductivity (F₁,₁₃=0.24, P>0.05) and also was not related to distance from the spring HWL (F₁,₁₃=0.88, P>0.05).

Histograms showing six representative size distributions of the dry samples are shown in Figure 3. Samples were highly variable in the size distribution of the particles they comprised. Some had large fractions of the largest component (>3 mm).
These fractions consisted almost exclusively of large shell fragments from bivalves. The most abundant size-class for almost all (N=17/18) samples was between 212 and 500 \( \mu m \) which consisted 12–69% of the total sample. Very small components (<106 \( \mu m \)) represented a small fraction of all samples (<1.3%).

Figure 3. Histograms showing the size distributions of sand samples collected at six typical sites on the beach at Captiva. Distance from the high water spring mark (on 1 July 1992) are also shown. Size categories from left to right in all plots are >3 mm, 2 mm, 1 mm, 500 \( \mu m \), 212 \( \mu m \), 106 \( \mu m \), 63 \( \mu m \). Samples were all dominated by the 212 \( \mu m \) fraction. Some samples also had high contributions of the large components which were mostly fragments of bivalve shells. The contribution of very small fragments (<106 \( \mu m \)) was universally low. There was no correlation between size distribution and distance up the beach.

A principal components analysis was performed to separate out the major axes of variability in the size distribution across all the samples. The raw data included were the percentage contribution of each fraction to the total dry mass. A correlation matrix was performed since the variances of the measures were different by up to a factor of ten (Jolliffe, 1986). The eigen values, per cent variation explained and coefficients to the original variables for the first four principal components are shown in Table 1. The first component explained 51.2% of the variability and was dominated by the effects of
the fractions $>1$ mm in size. The second component explained a further 29.4 % of the variation and was dominated mostly by the contributions of the smaller fractions ($<1$ mm). The first four principal components together explained 97.4% of the variation in the sand structure.

Table 1. Eigen values, explained variation and the coefficients with respect to the original variables for the first four principal components from the Principal Components Analysis of variation in sand structure across 18 sites on the beach at Captiva Island, south-west Florida. Dominant influential variables (coefficient $>0.4$) on each of the PCs are in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 mm</td>
<td>-0.421</td>
<td>0.106</td>
<td>0.090</td>
<td>0.793</td>
</tr>
<tr>
<td>2 mm</td>
<td>-0.484</td>
<td>0.217</td>
<td>0.164</td>
<td>0.191</td>
</tr>
<tr>
<td>1 mm</td>
<td>-0.458</td>
<td>0.163</td>
<td>0.148</td>
<td>0.561</td>
</tr>
<tr>
<td>500 μm</td>
<td>-0.025</td>
<td>-0.624</td>
<td>-0.515</td>
<td>0.014</td>
</tr>
<tr>
<td>212 μm</td>
<td>0.507</td>
<td>-0.062</td>
<td>0.250</td>
<td>-0.058</td>
</tr>
<tr>
<td>106 μm</td>
<td>0.309</td>
<td>0.830</td>
<td>0.103</td>
<td>-0.017</td>
</tr>
<tr>
<td>63 μm</td>
<td>0.157</td>
<td>0.491</td>
<td>-0.777</td>
<td>0.128</td>
</tr>
</tbody>
</table>

We entered scores for each sample along the first four principal components with the percentage water and percentage organic fraction as predictors in a stepwise multiple regression with conductivity as the dependent variable, for those sites where we had collected sand and also measured conductivity (N=13 sites). Scores on the first three principal components entered as significant predictors of conductivity. The best fit least squares regression: Conductivity=1.250+0.094 PC1+0.117 PC2-0.156 PC3 explained 84.1% of the variation in conductivity. Bivariate plots of conductivity as a function of scores on the first three principal components are shown in Figure 4A-C. Increases in scores for PC1 and PC2 had a positive effect on the conductivity (Figure 4A,B). Both PC1 and PC2 were negatively influenced by the presence of large grains ($>1$ mm for PC1 and $=500$ μm for PC2) and positively affected by small grains (212 μm for PC1 and $<212$, μm for PC2). In contrast PC3 had a slight negative effect and it was itself negatively influenced by the presence of the smallest grains ($<106$ μm).

Comparison of conductivity at sites selected for nesting and random sites

The mean conductivity across the eight nests was $1.303 \times 10^{-3}$ (SD=0.406, N=8), and across the seven random sites was $1.313 \times 10^{-3}$ (SD=0.33, N=7). We compared the conductivity of the nest sites with the random sites, along the same putative crawl path, perpendicular to the spring HWL and vegetation line, using a paired $t$-test. There was no significant difference in sand conductivity between the nest sites and the random sites ($t_{13}=-0.24, P=0.81$). The variance in conductivity at the nests was also not significantly different from the random sites (variance ratio $F_{6,7}=1.57, P=0.10$).
DISCUSSION

Relationship between conductivity and temperature

The mean beach temperature at depths of 30–50 cm was correlated with the conductivity of the sand at that particular site. Beach sites with high conductivity were also the warmest (Figure 2). This positive relationship probably reflected the fact that most of the heat budget of the deep sand was dominated by incoming solar radiation, as has been shown for nests of the freshwater pig-nosed turtle (*Carettochelys insculpta*) in Australia (Georges, 1992). Areas of high conductivity probably transferred this heat more effectively to deeper layers and therefore over a 24 h cycle these sites had greater mean temperatures. The domination of the heat budget of low layers in sand by incoming solar radiation at the sand surface also occurs in the Namib Desert (Seely et al., 1988) and is probably true for most unvegetated regions, like the open beaches used as nesting sites by sea turtles. The effects of solar radiation on deep sand temperatures have been experimentally demonstrated by shading areas...
of beaches from radiation which resulted in the deep sand temperature declining (Mrosovsky et al., 1995). The relatively low correlation of mean daily temperature at depth with conductivity (0.611) was in part because measurements were not all made on the same day. Hence some of the variation in the deep sand temperature reflected day to day variation in the incoming solar radiation. An alternative interpretation of these data is that the measurement of conductivity was sensitive to temperature differences between the sites because of the effect of sand temperature on water vaporization (de Vries, 1995). This latter interpretation seems unlikely however, first because water content of the samples was low, and second because the theoretical effect of vaporization on apparent conductivity in saturated soil over a 3°C temperature range at 30°C is only about 10% (de Vries, 1995), yet we recorded differences in apparent conductivity of over 120% between the coolest and warmest sites (Figure 1).

Sand conductivity therefore appears to be a major factor which is correlated with mean deep temperatures, once the effects of time have been removed. Little of the thermal variation on the open beach on Captiva was predictable from the position relative to the high water or vegetation lines. However, whilst position relative to the distance up the beach may be a poor cue for use by nesting turtles, the measurements made here suggest that by selecting sites with high (or low) conductivity the nesting turtle could potentially influence the temperature of her nest and hence the sex of her offspring.

**Conductivity and sand parameters**

Conductivity at Captiva was correlated with the sand structure (Table 1, Figure 4A–C). Despite the high conductivity of water (Schmidt Nielsen, 1973) and the effects of water on apparent soil conductivity (de Vries, 1995; Hillel, 1971), moisture content of the sand was not an important predictor of conductivity. This probably reflects the low moisture contents of all the samples (always <5%). It is possible that there was some moisture loss from the samples during transit. If this did happen the losses were probably small. We noted no gross changes in the feel of the material between collection and unpacking at Aberdeen and the measurements were consistent with those for other beaches. For example, Stancyk & Ross (1978) found nesting beaches used by green turtles on Ascension Island had water contents between 1.8 and 3.8%. However, in other locations water content may be of more importance. Horrocks & Scott (1991) reported slightly wetter sites used by hawksbill turtles averaging 5.5%. Mrosovsky et al. (1984) and Whitmore & Dutton (1985) found that leatherback turtles (*Dermochelys coriacea*) in Surinam nested close to the water edge where water contents of sand are likely to be much greater. Mortimer (1990) reported water contents of 2.57–12.87 g H₂O/g dry sand (i.e. 75–95% water) for sand collected on Ascension beaches but this must be erroneous as sand with greater than 65% would be thixotropic (Chapman, 1949).

Sand structure probably had an important effect on the conductivity because it influenced the amount of trapped air, which has a very low conductivity (Schmidt Nielsen, 1973), relative to the sand grains and shell fragments themselves (de Vries,
The regression equation relating conductivity to the principal components and coefficients of the different variable effects on the principal components large shell fragments are correlated with reduced conductivity whilst smaller sand grains are correlated increased conductivity. This may occur because the larger shell fragments have a more open structure which traps more air and thus acts as a better insulator, whilst smaller sand grains can be better packed and thus transfer heat more efficiently (de Vries, 1995). An alternative explanation is that the sand structure was significantly correlated with the moisture content of the sand but during transit most of the water in the samples was lost. Although we feel that this is unlikely, it represents another potential mechanism by which sand structure influenced conductivity.

The correlation between sand structure and conductivity means a potential mechanism exists by which a nesting turtle could select the temperature of her nest using the sand characteristics encountered when digging. Turtles could favour areas with a high shell content which would be correlated with low temperatures or favour fine sandy areas to obtain a high temperature. Previous Principal Components Analyses of sand taken from beaches (e.g. Jeffer, 1978) also point to a large diversity in the grain structure hence this is unlikely to be a result unique to the Captiva beach, although the extent of variation in beach structure will probably place constraints on the degree of choice that turtles may make at any particular site. The observed extent of within beach variability in sand structure may also explain the generally poor correlations of beach sand characteristics with total nesting populations of turtles and hatching success (e.g. Stancyk & Ross, 1978; Mortimer, 1990). As variation in sand characteristics within a beach can be enormous, the poor correlations may reflect the sampling protocols where each beach was defined from single samples (Stancyk & Ross, 1978) or pooled samples collected along a parallel line to the sea (e.g. Mortimer, 1990).

Nest site selection

Previous studies (Hendrickson & Balsingham, 1966; Mortimer, 1982; Stancyk & Ross, 1978; Mortimer, 1990; Horrocks & Scott, 1991) have characterized the sand from nesting beaches, or sites used by nesting turtles. These data are interesting, but cannot be used to infer selection because no parallel samples were collected from sites not used by turtles. Based on the rather limited comparison of eight nests to adjacent random positions, we have shown that although the clear potential exists for turtles to use the sand structure, which is correlated with the conductivity and temperature, and thus potentially the sex of their offspring, there was no significant difference in the mean conductivity of the sand adjacent to the nests relative to the random sites. The variance in the observed values in each group indicates that it is unlikely that an effect would become apparent if a much larger sample had been taken. This suggests that directional selection was probably not occurring. Since the beach temperatures reported here are close to the pivotal temperature for sex determination in loggerheads (Mrosovsky, 1988; Mrosovsky & Yntema, 1980; Yntema & Mrosovsky, 1982) directional selection is not necessarily anticipated. Rather we might expect individual turtles to pursue nest deposition strategies which would maximize the possibilities of producing offspring of a given sex. If this were the case we would
predict the variance of conductivities adjacent to nests would exceed that for a sample of random sites on the beach. The observed variance of the nest conductivities was 1.7 times greater than the variance at random sites, but this failed to reach significance \((P=0.10)\). At present therefore we have no compelling evidence supporting the suggestion that the sea turtles using this beach exploited the opportunity open to them of choosing their nest sites, by using sand structure. This supports our earlier conclusions, based on a random crawl distance model which successfully reproduced the observed pattern of nests (Hays et al., 1995b), that nest site selection by this population is a random process.

Although the opportunity exists for turtles to make these selective behaviours, they may not exploit this opportunity for several different reasons. First, there may be a poor correlation between the deep sand structure and the surface structure. Since digging is probably energetically costly (Sapsford & Hughes, 1978; Jackson & Prange, 1979) there may be a significant cost to locating suitable deep substrate. Second, mean temperature may be a poor indicator of the ultimate sex of the offspring and variance in temperature may be important (Georges et al., 1994). Finally, there may be abundant other opportunities for turtles to select the sex of their offspring which offset any need (or selective pressure) for further choice to be made on the open beach. For example, at some sites (e.g. Tortuguero in Costa Rica) approximately 10% of green turtles nest far into the vegetation at the back of the beach (Bjorndal & Bolten, 1992) where the shading effect of the vegetation leads to nest temperatures being up to 3°C cooler (Spotila et al., 1987). The same pattern occurs for Olive ridley turtles \((Lepidochelys olivacea)\) in Costa Rica (Standora & Spotila, 1985). Shading is also an important factor influencing the nest temperatures of the freshwater turtle \((Chrysemys picta)\) (Janzen, 1994a). At yet other locations turtles nest close to the sea where the nests are also cooler (Mrosovsky et al., 1984; Whitmore & Dutton, 1985). At many sites therefore the diversity of options available once the turtle has emerged may not necessitate further selection on the open beach between the spring HWL and the vegetation line using conductivity as a cue. Moreover, even over relatively small areas different beaches attract different numbers of nesting turtles (Anderson, 1981; Mortimer & Portier, 1989; Mortimer, 1990; Horrocks & Scott, 1991; Dodd, 1988), and interbeach thermal variation may be very large (Limpus et al., 1983; Hays et al., 1995a; Janzen, 1994a). The primary point at which natural selection is occurring for choice of sex of the offspring may therefore be before the turtle even leaves the sea to crawl onto the nesting beach. At present, however, we have only very rudimentary understanding of how turtles select the geographical zone of, and the specific beach on which they will nest (Mortimer, 1982).

Finally, this analysis has focused on the sex of the offspring, however nest selection may also affect hatchling survivorship and morphology (for example in the freshwater turtle \(Podocenemis unifilis\); de Souza & Vogt, 1994). Nest site selection is well known to affect survivorship and morphology in other groups of animals, e.g. Horseshoe crabs \(Limulus polyphemus\) (Penn & Brockmann, 1994) and lizards, \(Bassiana duperreyi\) (Shine & Harlow, 1996), with these effects being mediated in at least some species (e.g. the soft shelled turtle, \(Trionyx triunguis\)) by sand temperature (Leshem et al., 1991). In loggerheads there is some evidence that sands with larger grains and
more open structure are associated with poor hatchling success (Mortimer, 1990) (although the opposite appears to be the case for hawksbill turtles (Horrocks & Scott, 1991) and there is no apparent effect for green turtles (Mortimer, 1990)). There may then be a trade off between the advantages of selecting nests which have large grain structures and are thus likely to be cooler and possibly produce more males and the disadvantages of selecting such sites in terms of their potentially poorer hatching success.

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REFERENCES


