



Nest site selection in leatherbacks, *Dermochelys coriacea*: individual patterns and their consequences

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We determined individual nest placement patterns for female leatherbacks nesting at Awa:la-Ya:lima:po, French Guiana, by measuring distance from the nest to several landscape features, such as the highest spring tide line (HSTL) and the vegetation line. Distance from the nest to the HSTL differed significantly between females, indicating the existence of individual nesting patterns. There was a significant repeatability of nest site choice relative to the HSTL, indicating that females showed within-individual consistency in their nest placement. Despite individual preferences, there was much within-individual variation and a lack of predictability in the nesting patterns; that is, the locations of subsequent nests could not be predicted based on knowledge of previous nest choices, indicating a certain degree of scatter. The significant repeatability suggests that nest choice behaviour in female leatherbacks is heritable and may show the potential for further evolution. We tested sea-finding ability of hatchlings, a potential consequence of nest site choice, in Matapica, Suriname, by using orientation arenas to quantify the strength and direction of travel after emergence. The orientation tests showed that hatchlings were unable to move seaward in vegetated arenas, providing evidence that vegetation acts as a strong selective pressure driving nest placement seaward. It appears that leatherbacks have adopted a regional rather than a local optimum for nest placement patterns, possibly resulting from their weak beach fidelity and the frequent erosion and destruction of their nesting beaches. We discuss the evolutionary and conservation implications for this species in the context of current environmental changes.

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In many species without protracted parental care, a mother's nesting behaviour and preferences can affect the development and survival of her offspring. In sea turtles, nest success is believed to be influenced by a number of interacting ecological factors such as temperature (Yntema & Mrosovsky 1980), moisture (McGehee 1990) and chloride toxicity (Bustard & Greenham 1968). Nests laid too near the water are at a higher risk of being inundated by waves or washed away by beach erosion (Eckert 1987; Hilterman 2001; Hilterman & Groverse 2002). Problems may also arise when nests are laid too near the supralittoral vegetation, as roots may penetrate into the nest chambers and destroy the eggs (Wood & Bjørndal 2000). Increased distance to the water may also adversely affect hatchlings by impairing their sea-finding ability and causing them to become disoriented.

Leatherback turtles can lay up to 11 clutches in a season (Boulon et al. 1996) and often place their nests in the open sand near the water, but rarely in the vegetation

(Whitmore & Dutton 1985; Godfrey et al. 1996). They tend to nest on dynamic beaches, where the environment may not be predictable from one nesting event to the next (Hendrickson & Balasingam 1966; Schulz 1975). Although they do show a preference for the open sand, leatherbacks may nevertheless have evolved a nest placement strategy within this zone in response to their environment, where individual nesting patterns may be random, resulting in an increased probability of there being some reproductive success.

Alternatively, turtles may not show random nest placement. In this case, there may be individual differences in nesting patterns with variation between individuals. Measuring the repeatability of the behaviour is useful in this context: it quantifies the proportion of the total variation in the trait that is due to differences between individuals (Falconer 1981; Lessells & Boag 1987; Boake 1989). Thus, it is a measure of the within-individual consistency of the trait. Repeatability is useful because (1) consistent individual differences are required for selection to act on the trait in a meaningful way, and (2) it places an upper bound on heritability and thus on evolutionary responses to selection (Boake 1989). Characterizing the phenotypic

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distribution of a trait, particularly in terms of variability both within and between females, is essential to understanding its evolution (Boake 1989).

A comprehensive understanding of the evolution of nest site choice requires not only documenting phenotypic and genotypic variation of nest site preferences among females within populations, but also quantification of the fitness consequences of particular nest site preferences and identification of the selective forces acting on such variation. Therefore, we investigated hatchling sea-finding ability as one potential consequence of nest placement.

In summary, this study's aim was to resolve which of the two competing hypotheses of nest site choice was occurring: that of random nest placement by individuals or that of different consistent choices made by individuals. In addition, we investigated hatchling sea-finding to gain insight into the adaptive value of nest site selection in this species.

MATERIALS AND METHODS

Nest Placement

Study site

Awa:la-Ya:lima:po beach is situated within the large estuary complex of the Mana and Maroni rivers on the western side of French Guiana. This is a dynamic area with mud bank displacements originating from the Amazon River and moving westwards, affecting beaches and mangrove (*Avicennia* spp.) swamps on a yearly basis. The rainy season in French Guiana extends from January to June but climatic variations are tempered within the estuary. The sand is relatively fine-grained and the supralittoral vegetation is composed mainly of beach creepers and, further inland, coastal forest. The beach is also subject to fluvial and tidal currents as well as the Guiana current (see Figures in Fretey & Girondot 1989). During the 2001 nesting season, tidal height varied between 3 and 4 m (Service Hydrographique et Océanographique de la Marine: <http://www.shom.fr>), with winds playing a more important role in June. Nesting occurs mainly between April and August (Chevalier & Girondot 1998).

Sampling of nests

Data were collected at Awa:la-Ya:lima:po between 31 March and 26 June 2001. The beach extends for approximately 4 km and was patrolled nightly, from 2 h before to 2 h after high tide, because previous work has demonstrated that peak nesting occurs at and around the nighttime high tide (Girondot & Fretey 1996; Chevalier & Girondot 1998). Individual turtles were identified by their passive integrated transponder numbers (PIT; Trovan, Paris, France), located in the right shoulder muscle. PIT tags were either already present from implantation during previous tagging seasons or were implanted after laying had begun (Chevalier & Girondot 1998). Because of the high density of turtles on the beach, not all turtles could be measured. Turtles that were encountered while they were digging their nest cavities were measured, so that the sample was spatially representative. We took all measurements after laying had begun, because leatherbacks

are less likely to abort nesting at this stage (personal observations).

Patrollers on other beach sections who came across a turtle that was part of our study had been instructed to put a stick 1 m away from the nest cavity and record time, weather, location and nesting status of the turtle. Subsequently, the distance measurements were taken at this location. Most of these distance measures were recorded the same night but when this was not possible, we recorded distance measures the following day.

To exclude the impact of human presence on nest site choice, we did not measure turtles that were surrounded by large groups of people. The presence of tourists on this beach was a minimal factor except for a 2-week period in mid-April. During this period, four nesting events by different turtles were excluded due to disturbances that may have influenced the choice of nest site. Other nests laid by these four turtles were included in the analyses.

Measurements

For each female, we collected the following data.

(1) Distance from the egg chamber to the current water line (CWL), defined as the height of the water at the time of laying.

(2) Distance from the egg chamber to the highest spring tide line (HSTL), which is the point at which the water reaches its maximum tidal height. The highest spring tide occurred early in the field season, on 7 April 2001, and tides with similar height occurred every 2 weeks after. The highest spring tide left a distinct line of debris along the beach making this a recognizable landmark.

(3) Distance from the egg chamber to the vegetation (VEG), defined as the point at which a dense layer of beach creeper covered the sand.

(4) Latitude and longitude coordinates of the nest sites, accurate to within 5 m, were recorded by a global positioning system (GPS; model Garmin eTrex Summit 2000). Accuracy of the GPS was checked prior to departure and on arrival at the nesting beach.

(5) Position along the beach; the patrolled area was divided into four sections of approximately 1 km in length (see Figure 2 in Chevalier & Girondot 1998).

(6) Zone of the beach; three zones were defined: vegetation (dense covering of vegetation), border (slight vegetation, sand still visible) and open (sand, with negligible vegetation). Nests were placed in one of these categories.

(7) Size of the turtle: over-the-curve carapace length, measured alongside the medial dorsal ridge of the carapace.

Statistical analyses

We analysed data for longitudinal coordinates of the nests parallel to the shoreline and measures of distance from the nests to the water lines and to the vegetation line using a one-factor model II analysis of variance, ANOVA (Sokal & Rohlf 1981).

To calculate the repeatability (r) of nest choice, we focused on the 41 females for which three or more nestings were documented during the season. Within- and between-female mean variances obtained from the one-factor ANOVA were used along with the harmonic mean

of the number of nesting events per females to calculate r (see equations 2–5 of Arnold 1994; Lessells & Boag 1987; Boake 1989).

To determine the consistency of nest placement relative to distance from the highest spring tide line, we tested for correlations between different combinations of two observed nest choices. Statistical analyses were done using GraphPad Prism version 3.00 (GraphPad Software 1999). Results were considered significant at an alpha of 0.05.

Hatchling Sea-finding

Study site

Due to logistic constraints, we conducted the experiments on hatchling sea-finding at Matapica beach, Suriname, between 29 July and 5 August 2002. The beach is located on a sand spit approximately 60 m wide and 7.5 km long, separated from the coastal mangrove forest by a lagoon. The foreslope is dynamic, often changing within the same day (Schulz 1975; Hilterman 2001). Beyond the HSTL, there is an area of sand roughly 50 m wide, and in some sections, it is covered by dense vegetation composed mainly of beach creepers.

Experimental design

We used five orientation arenas, four of which consisted of a circular trench 5 m in radius, dug 30 cm deep and 15 cm wide and divided into 16 equal segments by thin wood barriers. Arena 1 was below the high tide line, on compact and often wet sand. No trench was dug there, but a circle divided into 16 segments was drawn in the sand. The arenas were within 50 m of each other and their relative placement along the beach is summarized in Fig. 1. Within all arenas, except arena 1, the ocean was not visible at hatchling eye level.

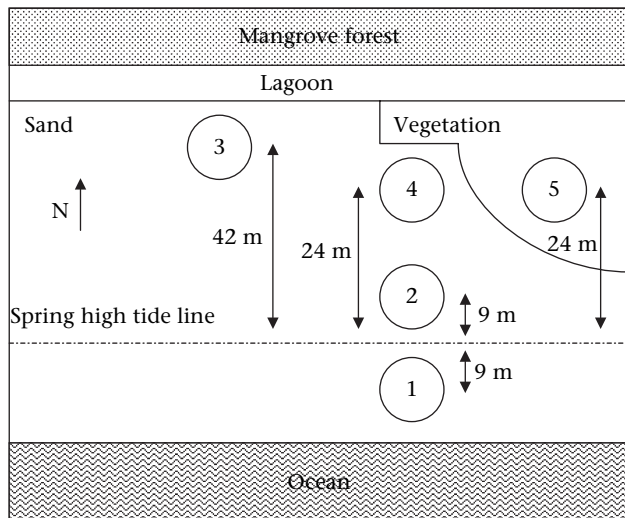


Figure 1. Diagram of the orientation arenas used in the study at Matapica beach, Suriname. The radii of the arenas were 5 m and each arena was divided into 16 equal segments. Distances from the centre to the spring high tide line are indicated.

We gathered naïve hatchlings after emergence from five nests that had been marked after laying and had been surrounded by a wire trap 4–5 days before expected emergence. We patrolled the beach nightly at 1600, 1900, 2100, 2300, 0200 and 0500 hours to determine whether any of the hatchlings had emerged. Once an emergence was seen, 100 hatchlings from each clutch were put in a bucket and the orientation tests were run. Clutches were divided into five groups, one for each arena; all hatchlings were used only once and then released. Each experiment consisted of placing hatchlings in the centre of the arenas. Arenas were near enough that releasing hatchlings in all five arenas was completed within minutes, effectively controlling for variations in weather and lighting patterns. To avoid interfering with hatchling orientation, the experimenter remained seated at a distance until the end of the trial. At the end of the 30-min test, the number of hatchlings in each segment as well as those still within the centre of the arena was recorded. Trials were run on 5 nights, using a different clutch each night.

Statistical analyses

We performed circular statistics (Batschelet 1965) to determine the direction of orientation and the strength of direction. The length of the line vector (\mathbf{r}) within the arena is an indication of the consistency of orientation in a given direction. A line equal to the radius of the circle indicates perfect orientation. Rayleigh's test was used to determine whether orientation was significantly different from random within each arena. When groups showed significant orientation, we used Watson's F test to check for differences in direction between arenas. Analyses were done using Oriana, version 1.06 (Kovach Computing Services 1994).

RESULTS

We recorded the location of 342 nests from 170 female leatherback turtles. Of these, 85 turtles were seen nesting once and 85 were seen nesting multiple times, for a total of 252 nests. We focused our analyses on 41 females for which we documented three or more nesting events within the season.

Population-level Preferences

Turtles preferred the third kilometre of the beach (chi-square test: $\chi^2_3 = 87.13$, $P < 0.0001$), placing 53% of their nests in that location (Fig. 2). They had a distinct preference for the open sand, placing 85% of their nests in that zone (chi-square test: $\chi^2_2 = 201.1$, $P < 0.0001$; Fig. 3). Overall, the distribution of the distance from the nests to the highest spring tide line was leptokurtic ($g_2 = 6.37$) and significantly skewed landward ($g_1 = 1.08$, $P = 0.004$; Fig. 4a). Distances measured from the vegetation were similarly distributed ($g_2 = 12.99$, $g_1 = 2.73$, $P < 0.0001$; Fig. 4b). In contrast, the distribution of the distance travelled inland from the current water line was normal (Fig. 4c).

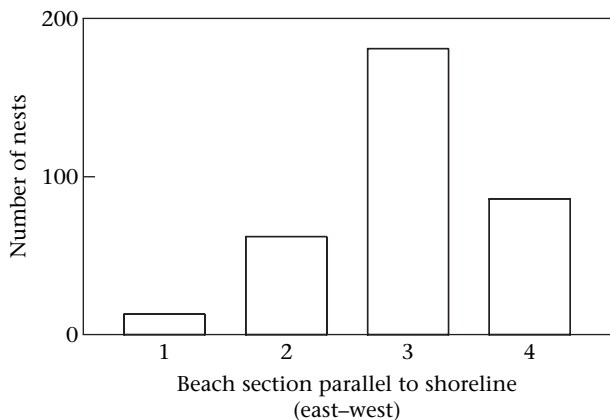


Figure 2. Distribution of nests parallel to the shoreline among the four 1-km divisions on Awa:la-Ya:lima:po beach ($N = 342$).

Individual-level Preferences

The 41 turtles (3–7 clutches/turtle) did not differ in their parallel placement of nests relative to the shoreline (ANOVA: $F_{40,124} = 1.14$, $P = 0.27$) or their placement of nests with respect to distance from the vegetation (ANOVA: $F_{40,124} = 1.3$, $P = 0.16$), but did differ in their placement of nests with respect to distance from the highest spring tide line and from the current water line (ANOVA: $F_{40,124} = 1.78$ and 1.63 , $P = 0.009$ and 0.02 , respectively). There were three outlier values that resulted from leatherbacks nesting on a soccer field landward of the third beach section. Nonparametric Kruskal–Wallis tests were done to prevent these values from skewing the outcomes and, overall, the results were similar to those obtained from the parametric tests. Upon removal of the outliers, the results for nest site choice with respect to the highest spring tide line remained significant, although less so (ANOVA: $F_{40,121} = 1.76$, $P = 0.01$).

There was no significant correlation between carapace length and any of the distance measures ($N = 170$ for each), indicating that the size of the turtle was not a factor in nest choice (vegetation: $r^2 = 0.009$, $P = 0.1$; current water line: $r^2 = 0.006$, $P = 0.2$; highest spring tide line: $r^2 = 0.015$, $P = 0.08$).

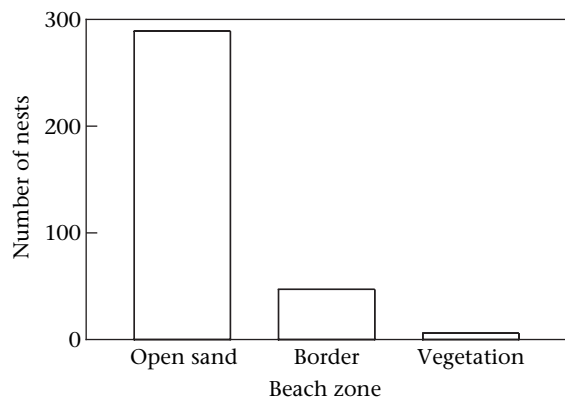


Figure 3. Distribution of nests among beach zones on Awa:la-Ya:lima:po beach ($N = 342$).

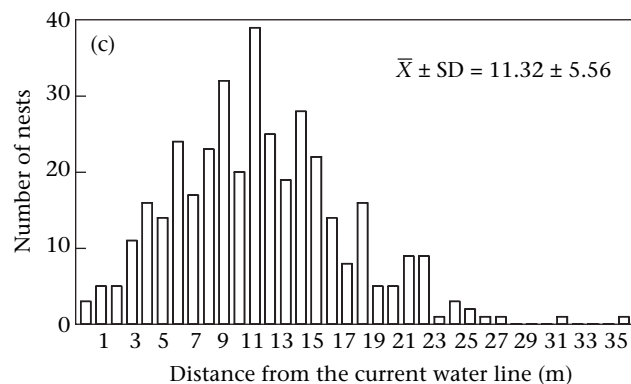
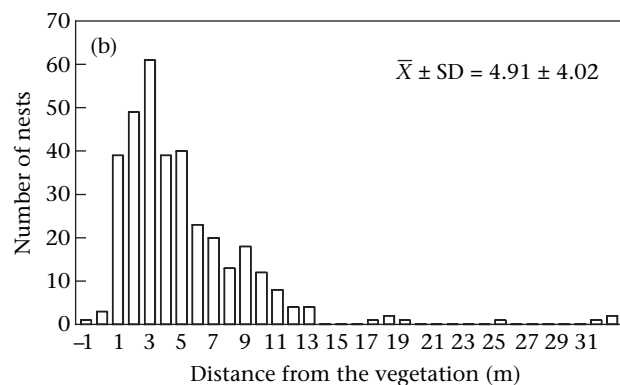
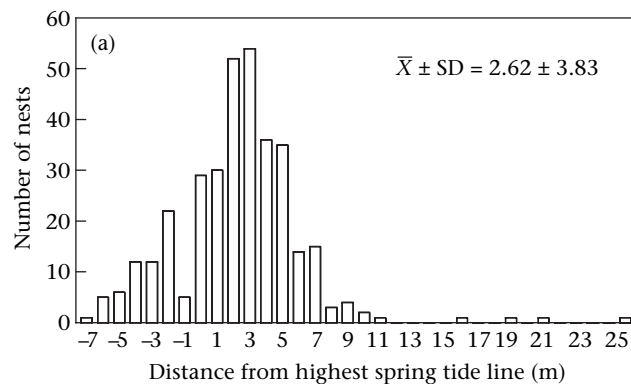


Figure 4. Frequency distributions of the distance between nest sites and (a) the highest spring tide line (HSTL), (b) the vegetation and (c) the tide line at the time of laying (the current water line) for all nests measured ($N = 342$). Negative values in (a) and (b) indicate nests that were laid below the HSTL and in the vegetation, respectively.

Repeatability

The 41 multiple nesters averaged 4.29 observed nests (harmonic mean) during the 3 months of the study and nested on the full range of the available beach with respect to section and zone, and therefore, in nearly the full range of nest microenvironments (Fig. 5). Despite this considerable variation, there was a significant repeatability of distance from the nest to the highest spring tide line (repeatability: $r = 0.18$, $N = 41$ females and 164 nests, $P = 0.009$). That is, individual females showed a preference for nesting at particular distances from the highest spring tide line. We obtained similar results when we included all 85 multiple nesters (2–7 clutches/turtle) in the analysis

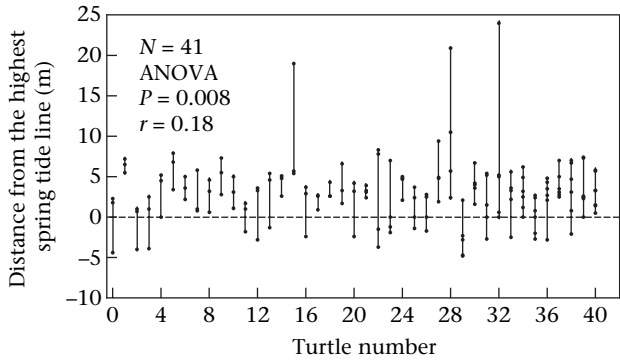


Figure 5. Distance from the highest spring tide line for turtles seen nesting three to seven times.

(repeatability: $r = 0.21$, $N = 85$ females and 252 nests, $P = 0.01$).

Consistency of Nest Placement Patterns

Correlations between distance from the HSTL of the first and second observed nests and between the first and last observed nests in turtles seen nesting at least three times were not significant ($r^2 = 0.04$, $P = 0.26$ and $r^2 = 0.08$, $P = 0.08$, respectively; Fig. 6a, d). Similar results were obtained by correlating previous and subsequent nest choices in four-clutch nesters. However, nest placements were significantly and positively correlated between the second and third observed nests and between two

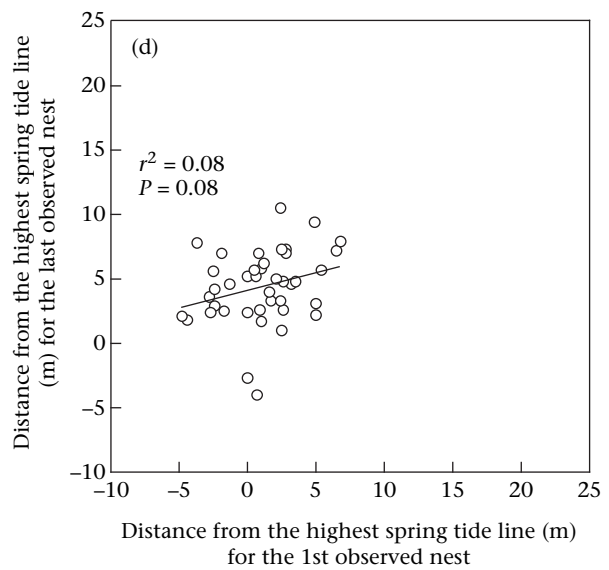
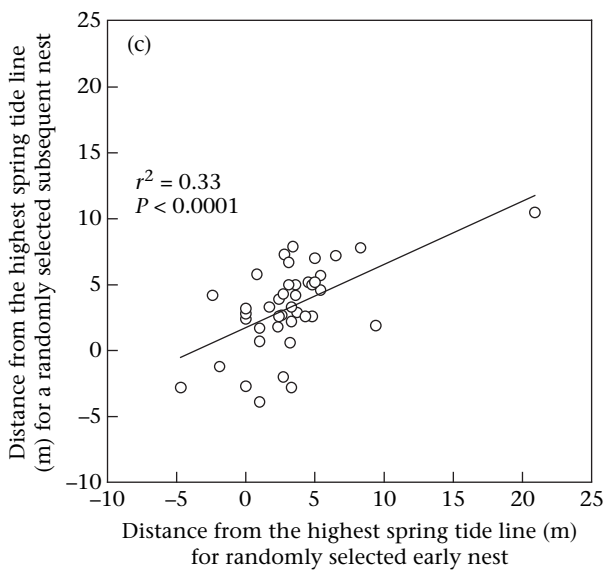
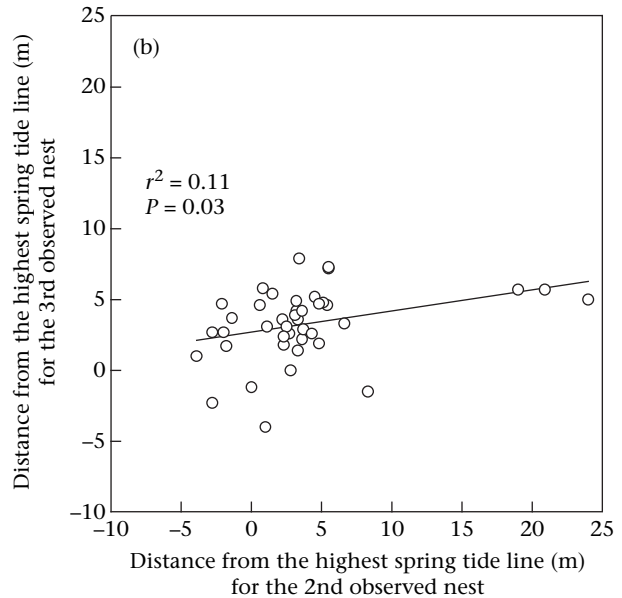
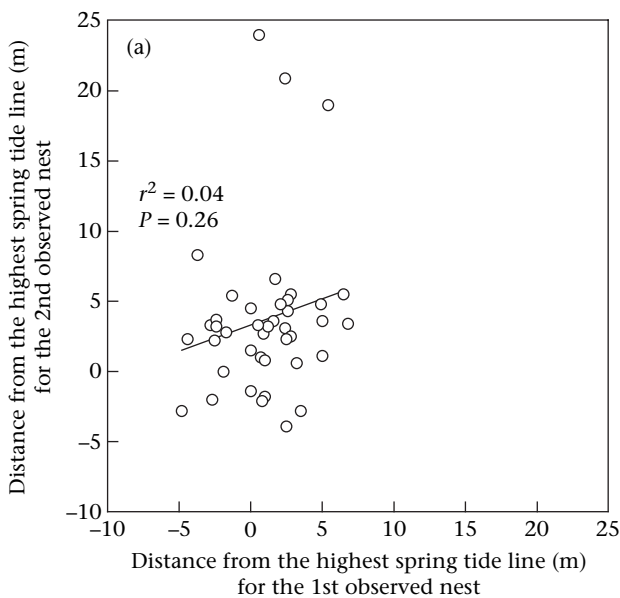


Figure 6. Relationship between the distance to the HSTL for (a) the first and second observed nests, (b) the second and third observed nests, (c) two randomly selected nests and (d) the first and last observed nests, for turtles seen nesting at least three times. When significant outliers were removed, the r^2 and P values changed to (a) $r^2 = 0.01$, $P = 0.47$; $N = 38$, (b) $r^2 = 0.07$, and $P = 0.11$; $N = 38$ and (c) $r^2 = 0.24$ and $P = 0.001$; $N = 40$.

randomly sampled nest placements ($r^2 = 0.33, P < 0.0001$ and $r^2 = 0.11, P = 0.03$, respectively; Fig. 6b, c), but this may be partly due to outliers.

Orientation Tests

We combined data from each trial, resulting in five replicates for the five arenas. Overall, orientation differed significantly from random in all arenas (Rayleigh's test: $P < 0.001$ in all cases; Fig. 7), with hatchlings showing strong seaward orientation except those in arena 5, which oriented landward. Arena 5 was also the only one in

which some hatchlings remained in the centre at the end of the test; 36% of hatchlings failed to reach the trenches after 30 min. Hatchlings in arena 1 showed near-perfect orientation; this was the only arena where the ocean was visible at turtle eye level. Turtles in the other arenas were still able to orient in a seaward direction, despite a lack of this visual cue.

There were no significant differences between hatchlings in arenas 1, 2 and 3 in their direction of orientation. Orientation in arena 4, although generally seaward, differed significantly from that in arenas 1 and 3 (Watson's F test: $F_{198} = 10.48$ and 6, $P < 0.001$ and $P = 0.02$, respectively) and orientation in arena 5 differed significantly

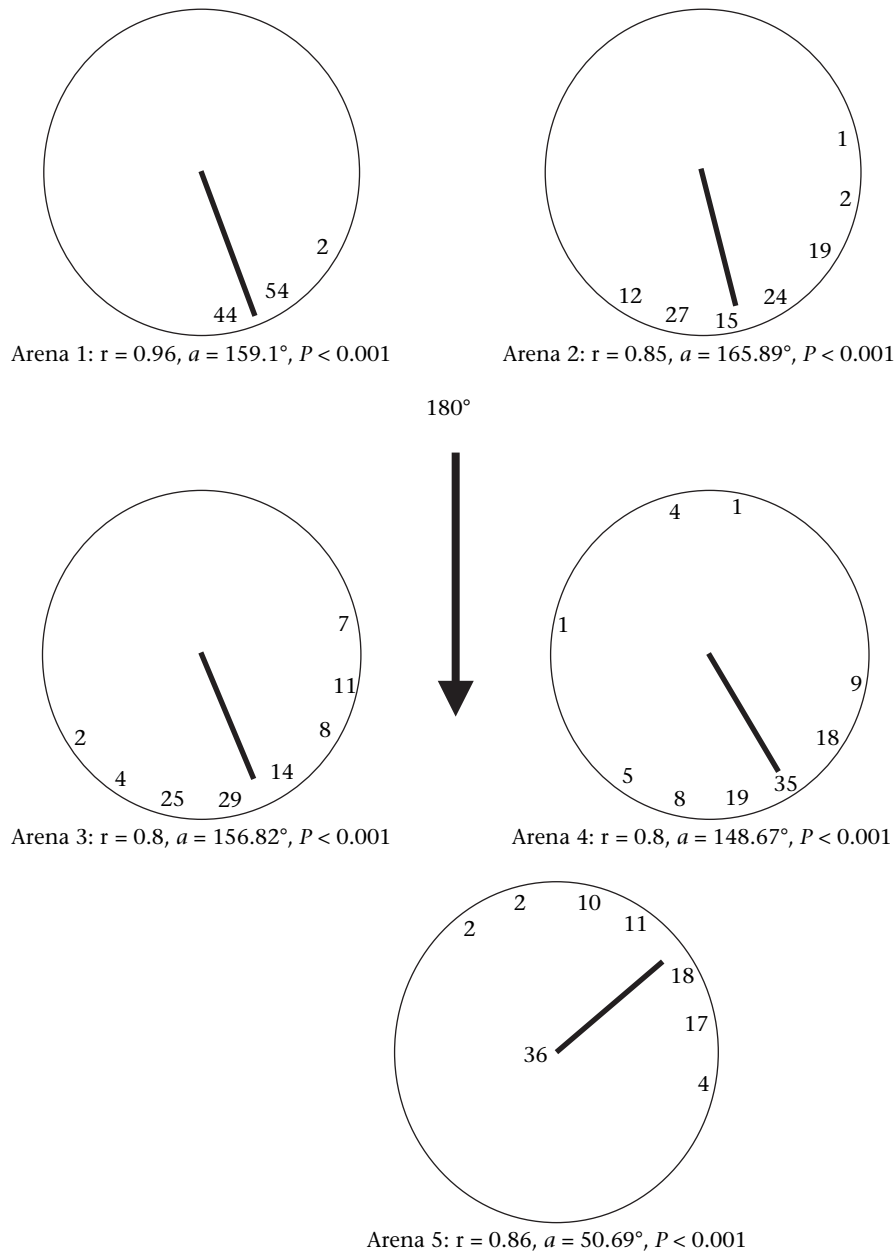


Figure 7. Results of the orientation experiments on leatherback hatchlings. The numbers represent the hatchlings and their location at the end of the trial; the number in the centre of arena 5 indicates the remaining hatchlings in that arena after the trial. Mean angle of dispersion, a , is indicated by the line. The arrow defines the most seaward direction (180°). Line length indicates the strength of orientation and is represented by the vector r and by its corresponding P value.

from that in all other arenas (Watson's F test: $F_{162} = 411.38, 286.5, 7245.48$ and $242.97, P < 0.001$ in all cases).

DISCUSSION

Nesting Patterns

Two hypotheses were considered to explain leatherback nest site choice, that of random individual nest placement or that of particular preferences that vary between individuals. Based on our results, the nesting patterns of leatherbacks cannot be characterized in a simple manner. There appear to be two main aspects of this behaviour: one aspect emphasizes nonrandom repeatable choices and the other reflects scatter in the actual nesting patterns.

The consistency of nest placement with respect to distance from the HSTL was not due to females repeatedly returning to the very same nest site, because they come ashore at various locations along the beach. It also appears that the majority of females prefer nesting at or around the HSTL. The significant repeatability indicates that nest site choice with respect to the HSTL is not random. This runs counter to previous studies of individual leatherback nest placement, which concluded that nest site choice with respect to the water line is random (Eckert 1987; Tucker 1989). However, a reanalysis of the data in Eckert (1987, Figure 4) and Tucker (1989, Figure 21) showed patterns similar to those reported here (ANOVA: $F_{19,75} = 2.01, P = 0.02$; ANOVA: $F_{21,110} = 2.28, P = 0.004$, respectively). Repeatability of the distance from the nest to the water line was significant (repeatability: $r = 0.2, N = 20$ females and 95 nests, $P = 0.02$; $r = 0.18, N = 22$ females and 132 nests, $P = 0.004$, respectively). These results reflect a tendency for individuals to nest at different distances from the water line.

In addition to spatial variability, as seen by the females' lack of preferences for locations parallel to the shoreline, turtles vary their nest placement in time, laying an average of five clutches per season at 10-day intervals (Boulon et al. 1996). A similar pattern of spatial and temporal variability was found in the studies of Eckert (1987) and Tucker (1989). That different populations of turtles show similar nesting patterns in different environments is not surprising because the high levels of gene flow may be preventing local adaptation. Analysis of mitochondrial DNA revealed that gene flow exists within the Atlantic basin between mainland nesting populations such as French Guiana and South Africa and island nesting beaches such as Trinidad and St-Croix (Dutton et al. 1999).

Adaptive Value

Patterns of nest site selection by leatherbacks arise from two opposing pressures: the disadvantages of nesting too low on the beach and the disadvantages of nesting too high. We examined one of the potential disadvantages of nesting too high, the hatchlings' ability to orient towards the sea. The orientation experiments showed that hatchlings were unable to move in a seaward direction when released in the vegetation. These results are consistent

with previous studies (Godfrey & Barreto 1995), and provide convincing evidence that vegetation, which tends to occur on the upper stretches of beaches, is a pressure for not nesting too high. Of our sample of 342 nests, 85% were placed in the open sand. Hatchlings in all the open sand arenas were able to travel seaward, irrespective of distance, but other selective agents could include increased travel times and exposure to predators for hatchlings emerging further from the water. Moreover, because some beaches may be littered with debris, or vegetation may be further inland, sometimes beyond lagoons behind the beach, hatchlings that emerge far from the ocean or that are faced with these disruptive cues could have impaired sea-finding ability. Tracks of different individuals from these sites may run in opposite directions, in contrast to the straighter and seaward-directed tracks seen for nest sites on the lower beach (Fig. 8).

Nesting too near the water also has its costs. Nests dug at the surf line or in areas of massive beach erosion are almost always completely destroyed (Duque et al. 2000). However, nests laid below the high tide line that are washed over without being washed away can still produce large numbers of hatchlings (Leslie et al. 1996; Hilterman 2001; Torres 2003). Although the hatch rates of inundated nests are often reduced (Whitmore & Dutton 1985), hatchlings that do emerge are closer to the water and less vulnerable to predation and disorientation.

Females appear to have responded to these opposing pressures by nesting at intermediate distances from the HSTL. By avoiding the vegetation- and debris-covered areas, they reduce the risk of disorientation for the hatchlings, and consequent increased exposure to predators, but increase the chances of lower hatch rates following wash-over by tides. The strongly peaked distribution of the mean of each individual's distance from the HSTL provides an example of stabilizing selection (Crumpp 1981), with most females placing their nests at or around the HSTL. Although individual preferences were identified, there was also much within-individual variation, probably reflective of the unpredictability of how high the water will actually rise on the more dynamic beaches (Mrosovsky 1983). Nest choice in this species may reflect a regional rather than a local adaptation, because leatherbacks frequently move between beaches in the Guianas (Hilterman 2001; Hilterman & Groverse 2002) and there are also cases of movement between Puerto Rico and the U.S. Virgin Islands (Eckert et al. 1989). Throughout their lifetimes, leatherbacks may encounter a variety of beach profiles, where nesting higher up may be preferred on some beaches and nesting low may be preferred on others; however, most turtles appear to opt for an intermediate nest site choice (this study), which probably reflects conditions in a general region, rather than on one specific beach type.

Evolutionary Potential

Because nest placement has important consequences for offspring survival, it is likely that this behaviour is or has been under strong selection. If nest site selection has

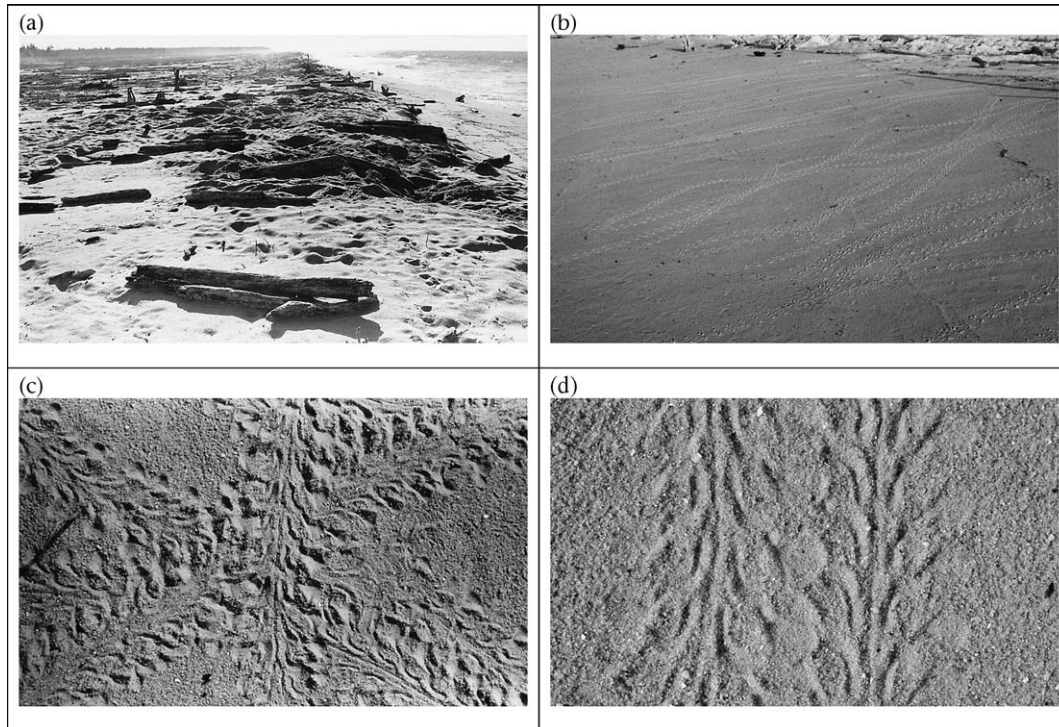


Figure 8. (a) Upper zone of a leatherback nesting beach typical of the dynamic coastline in the Mana region, east of Pointe-Isère, French Guiana. (b) Lower beach zone lacking in disruptive cues, as shown by the straight and seaward-directed hatchling tracks. (c, d) Tracks of different hatchlings from the same nest site may run in different directions when hatchlings are faced with disruptive cues on the upper beach.

a genetic basis, then individual females should be consistent in their particular choice of nesting sites; that is, their choices should be repeatable (Boake 1989). The significant repeatability of nest site choice with respect to distance from the HSTL suggests that this behaviour may show evolutionary potential. The repeatability was similar to Janzen & Morjan's (2001) estimate of nest site choice in painted turtles, *Chrysemys picta* ($r = 0.18$). In this case, it appears that leatherbacks may have the opportunity for further evolution of nest site choice in response to selection. This is particularly important in the context of current environmental changes and habitat destruction and alteration.

A capacity for further evolution of nest site selection within a beach, coupled with weak fidelity to particular beaches, may allow leatherbacks to colonize new nesting beaches and to adapt to novel environments. If environmental change is rapid, the shorter maturation period of leatherbacks, estimated between 5 and 14 years (Zug & Parham 1996), may place them at an advantage over other longer-maturing sea turtle species (e.g. green turtles, *Chelonia mydas*: 12–36 years, Frazer & Ehrhart 1985; Frazer & Ladner 1986; loggerheads, *Caretta caretta*: 20–63 years, Parham & Zug 1997).

Implications for Conservation

The present results also bear on management policies. A common conservation practice is to relocate doomed nests, those in danger of being washed over or destroyed,

to safer places higher up on the beach (Eckert & Eckert 1990; Boulon et al. 1996). Although different opinions exist on the utility of this practice (Eckert & Eckert 1990; Hilterman 2001), it appears that the lack of strong predictability in nest placement does not permit one to determine whether a particular nest is laid by a turtle with a low nesting tendency trait or if it is simply the lowest nest from a turtle with a high nesting tendency trait. Although selection may have acted to remove the most extreme nesting patterns from the population, there is no evidence to suggest that doomed nests are laid by particularly bad nesters. In fact, if nest site selection is heritable, then low nesters must have some degree of reproductive success, since they continue to be represented in the population. It therefore appears that nest relocation need not have any detrimental effects and that relocating nests can be used to increase recruitment to the population.

Another environmental phenomenon that may become a threat to this species is global warming. The phenotypic sex of sea turtles is determined by the ambient temperature of the embryo within a thermosensitive period during incubation. High nest temperatures produce all female offspring; therefore, global warming could potentially lead to a massive feminization of turtle populations (Mrosovsky et al. 1984; Janzen 1994). Of the sea turtle species, leatherbacks may best be able to cope with climate change. They have the widest geographical distribution of any reptile and show relatively weak beach fidelity (Dutton et al. 1999; Hilterman & Groverse 2002); the latter almost certainly reflects the frequent disappearance and reappearance of their nesting beaches. Their

migratory nature, tendency to place some nests in the cooler wash-over zone of beaches and individual nesting preferences may allow this species to mitigate the effects of long-term climate change.

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References

- Arnold, S. J. 1994. Multivariate inheritance and evolution: a review of concepts. In: *Quantitative Genetic Studies of Behavioral Evolution* (Ed. by C. R. B. Boake), pp. 17–48. Chicago: University of Chicago Press.
- Batschelet, E. 1965. *Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms*. Washington, D.C.: American Institute of Biological Sciences.
- Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behaviour. *Evolutionary Ecology*, **3**, 173–182.
- Boulon, R. H., Dutton, P. H. & McDonald, D. L. 1996. Leatherback turtles (*Dermochelys coriacea*) on St Croix, U.S. Virgin Islands: fifteen years of conservation. *Chelonian Conservation and Biology*, **2**, 141–147.
- Bustard, H. R. & Greenham, P. 1968. Physical and chemical factors affecting hatching in the green sea turtle, *Chelonia mydas*. *Ecology*, **49**, 269–276.
- Chevalier, J. & Girondot, M. 1998. Dynamique de ponte des tortues marines en Guyane française pendant la saison 1997. *Bulletin de la Société Herpétologique de France*, **85–86**, 5–19.
- Crump, M. L. 1981. Variation in propagule size as a function of environmental uncertainty for tree frogs. *American Naturalist*, **117**, 724–737.
- Duque, V. M., Paez, V. P. & Patino, J. A. 2000. Nesting ecology and conservation of the leatherback turtle, *Dermochelys coriacea*, at La Playona, Chocoan Gulf of Uraba, Columbia, in 1998. *Actual Biology*, **22**, 37–53.
- Dutton, P. H., Bowen, B. W., Owens, D. W., Barragan, A. & Davis, S. K. 1999. Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). *Journal of the Zoological Society of London*, **248**, 397–409.
- Eckert, K. L. 1987. Environmental unpredictability and leatherback sea turtle (*Dermochelys coriacea*) nest loss. *Herpetologica*, **43**, 315–323.
- Eckert, K. L. & Eckert, S. A. 1990. Embryo mortality and hatch success in in situ and translocated leatherback sea turtle, *Dermochelys coriacea*, eggs. *Biological Conservation*, **53**, 37–46.
- Eckert, K. L., Eckert, S. A., Adams, T. W. & Tucker, A. D. 1989. Inter-nesting migrations by leatherback sea turtles (*Dermochelys coriacea*) in the West Indies. *Herpetologica*, **45**, 190–194.
- Falconer, D. S. 1981. *Introduction to Quantitative Genetics*. 2nd edn. New York: Longman.
- Frazer, N. B. & Ehrhart, L. M. 1985. Preliminary growth models for green, *Chelonia mydas*, and loggerhead, *Caretta caretta*, sea turtles in the wild. *Copeia*, **1985**, 73–79.
- Frazer, N. B. & Ladner, R. C. 1986. A growth curve for green sea turtles, *Chelonia mydas*, in the U.S. Virgin Islands, 1913–1914. *Copeia*, **1986**, 798–802.
- Fretey, J. & Girondot, M. 1989. Hydrodynamic factors involved in choice of nesting site and time of arrivals of leatherbacks in French Guiana. In: *Ninth Annual Workshop on Sea Turtle Conservation and Biology*, NOAA Technical Memorandum NMFS-SEFC-232 (Ed. by S. A. Eckert, K. L. Eckert & T. H. Richardson), pp. 227–229. Jekyll Island, Georgia: Georgia Sea Turtle Cooperative.
- Girondot, M. & Fretey, J. 1996. Leatherback turtles, *Dermochelys coriacea*, nesting in French Guiana, 1978–1995. *Chelonian Conservation and Biology*, **2**, 204–208.
- Godfrey, M. H. & Barreto, R. 1995. Beach vegetation and seafinding orientation of turtle hatchlings. *Biological Conservation*, **74**, 29–32.
- Godfrey, M. H., Barreto, R. & Mrosovsky, N. 1996. Estimating past and present sex ratios of sea turtles in Suriname. *Canadian Journal of Zoology*, **74**, 267–277.
- GraphPad Software, 1999. *GraphPad Prism*. Version 3.00. San Diego: GraphPad Software.
- Hendrickson, J. R. & Balasingam, E. 1966. Nesting beach preference of Malayan sea turtles. *Bulletin of the National Museum of Singapore*, **33**, 69–76.
- Hilterman, M. L. 2001. *The Sea Turtles of Suriname, 2001*. Amsterdam: Biotopic Foundation.
- Hilterman, M. L. & Goverse, E. 2002. *Aspects of Nesting and Nesting Success of the Leatherback Turtle (Dermochelys coriacea) in Suriname, 2001*. Amsterdam: Biotopic Foundation.
- Janzen, F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 7487–7490.
- Janzen, F. J. & Morjan, C. L. 2001. Repeatability of microenvironment-specific nesting behaviour in a turtle with environmental sex determination. *Animal Behaviour*, **62**, 73–82.
- Kovach Computing Services, 1994. *Oriana for Windows*. Version 1.06. Pentraeth: Kovach Computing Services.
- Leslie, A. J., Penick, D. N., Spotila, J. R. & Paladino, F. V. 1996. Leatherback turtle, *Dermochelys coriacea*, nesting and nest success at Tortuguero, Costa Rica, in 1990–1991. *Chelonian Conservation and Biology*, **2**, 159–168.
- Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.
- McGehee, M. A. 1990. Effects of moisture on eggs and hatchlings of loggerhead sea turtles (*Caretta caretta*). *Herpetologica*, **46**, 251–258.
- Mrosovsky, N. 1983. Ecology and nest-site selection of leatherback turtles, *Dermochelys coriacea*. *Biological Conservation*, **26**, 47–56.
- Mrosovsky, N., Dutton, P. H. & Whitmore, C. P. 1984. Sex ratios of two species of sea turtle nesting in Suriname. *Canadian Journal of Zoology*, **62**, 2227–2239.
- Parham, J. F. & Zug, G. R. 1997. Age and growth of loggerhead sea turtles (*Caretta caretta*) of coastal Georgia: an assessment of skeletochronological age-estimates. *Bulletin of Marine Science*, **61**, 287–304.
- Schulz, J. P. 1975. Sea turtles nesting in Suriname. *Zoologische Verhandlungen*, **143**, 1–143.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. New York: W. H. Freeman.
- Torres, C. 2003. Hatching success estimates for leatherback turtles (*Dermochelys coriacea*) on Ya:lima:po beach, French Guiana using

two sampling methods. In: *Proceedings of the 22nd Annual Symposium on Sea Turtle Biology and Conservation*, NOAA Technical Memorandum NMFS-SEFC-503 (Ed. by J. A. Seminoff), pp. 168–169. Miami: National Marine Fisheries Service.

- Tucker, A. D.** 1989. The influence of reproductive variation and spatial distribution on nesting success for leatherback sea turtles (*Dermochelys coriacea*). M.Sc. thesis, University of Georgia.
- Whitmore, C. P. & Dutton, P. H.** 1985. Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname. *Biological Conservation*, **34**, 251–272.
- Wood, D. W. & Bjorndal, K. A.** 2000. Relation of temperature, moisture, salinity and slope to nest site selection in loggerhead sea turtles. *Copeia*, **1985**, 119–128.
- Yntema, C. L. & Mrosovsky, N.** 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica*, **36**, 33–36.
- Zug, G. R. & Parham, J. F.** 1996. Age and growth in leatherback turtles, *Dermochelys coriacea* (Testudines: Dermochelyidae): a skeletochronological analysis. *Chelonian Conservation and Biology*, **2**, 244–249.