



Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences

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We investigated individual nest site choice behaviour and its fitness consequences in female hawksbills nesting at Trois Îlets, Guadeloupe. We found a significant repeatability of nest site choice, suggesting that this behaviour is heritable and may show the potential for further evolution. By looking at possible consequences of nest site choice, we found that hatching success was similar among different beach zones, but the ability of hatchlings to emerge from the nest was impaired in areas subject to tidal inundation. Sea-finding tests showed that hatchlings were more susceptible to disorientation in areas deeper in the forest. Maintaining phenotypic diversity in nest site choice could derive from variation in the environment, where a constantly shifting balance between phenotypes would be promoted by environmental change over time. Alternatively, the different nesting behaviours could be maintained through frequency-dependent selection. Phenotypic sex of sea turtle embryos is determined by the incubation temperature of the nests, and different beach zones have different thermal properties. Females that nest in areas that produce the rarer sex may therefore gain a fitness advantage.

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Nest site selection, that is, nonrandom placement of eggs within a particular area, has been documented in many species of amphibians, reptiles and birds (e.g. Madsen & Shine 1999; Halloy & Fiano 2000; Misenhelter & Rotenberry 2000). The nest environment is especially important in species lacking parental care, because the consequences of poor nest site choice cannot be compensated for by behaviour of the parents.

Nest site choice is not typically considered a life history trait even though a genetic basis for oviposition behaviour has been documented in several species (Singer et al. 1988; Sezer & Butlin 1998; Réale & Roff 2002). However, if one considers other life history traits such as egg or clutch size, these have evolved to maximize parental fitness in specific habitats and, therefore, organisms need a consistent environmental context to optimize these traits (Resetarits 1996). It has been argued that if females can discriminate among sites, then nest site choice could be a viable mechanism for providing this environmental context to allow for the optimization of traits such as egg and clutch size (Resetarits 1996).

Studies of nest site choice are most often done at the population level and there is a large body of literature

describing population-level nesting preferences (e.g. Seddon & Davis 1989; Penn & Brockmann 1994; Misenhelter & Rotenberry 2000). However, a limitation of these studies is that one must be cautious when making inferences about individual nesting preferences from the distribution of nest locations in a population. The lack of a population preference could be due to (1) no actual preference or (2) having individuals that differ in their preferences, so that these average out to no preference at the level of the population, thereby masking individual variation (e.g. Morris et al. 2003). As well, there is no way to determine how inflexible or how susceptible a particular trait is to environmental factors with these types of data.

Sea turtles are ideal organisms for studying nest site choice because they lay multiple clutches within a nesting season at 10–20-day intervals, so the behaviour can be measured repeatedly within a reasonable time frame. They lack parental care, making nest site choice particularly important for the survival of their offspring. This behaviour is also of interest in turtles, because they show temperature-dependent sex determination (TSD) (Wibbels 2003). High consistency of maternal nest site choice may allow for control over offspring sex ratios and this maternal trait is a parameter included in theoretical treatments of the evolution of TSD (Bulmer & Bull 1982; Roosenburg & Niewiarowski 1998; Morjan 2003). Data on individual variation in nest site choice are limited in

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turtles, although there are some data on the consistency of individual nest site choice (Eckert 1987; Tucker 1989; Janzen & Morjan 2001; Kamel & Mrosovsky 2004).

As our study organism, we chose the hawksbill sea turtle, a circumtropically distributed species, often seen around reefs and shallow coastal habitats in the Caribbean and tropical western Atlantic (Witzell 1983). Tidal variations on these beaches are often negligible but hurricanes and tropical storms later in the nesting season can destroy significant portions of the beach (Fortuna & Hillis 1998). Hawksbills show relatively strong beach fidelity, often returning to the same areas within and among breeding seasons (Hoyle & Richardson 1993; Bass et al. 1996). We predicted that because of the strong beach fidelity in hawksbills and their tendency to nest in a relatively stable, predictable environment, they should show high within-individual consistency of nest site choice.

Repeatability is one measure used to determine this, as 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). Repeatability is useful because (1) only traits that are manifested consistently within and differently among individuals can respond to selection and (2) it places an upper limit on heritability and, therefore, on the evolutionary response to selection (Boake 1989; Arnold 1994; Janzen & Morjan 2001). Additionally, quantifying the consequences of particular females' preferences and identifying the selective forces acting on such variation will provide a link between offspring fitness and maternal nesting behaviour (Kolbe & Janzen 2001). Accordingly, we also investigated two consequences of nest site choice: hatching success and hatchling sea-finding ability.

In this study, we sought to determine whether and how nest site choice varies among individuals and to quantify the impacts of this maternal behaviour on reproductive success, by evaluating offspring survival and behaviour.

METHODS

Study Site

This work was conducted at Trois Ilets and Folle Anse beaches, Guadeloupe, French West Indies. Both beaches are located on the western coast of Marie-Galante, a small island 40 km southeast of the island of Guadeloupe itself. Folle Anse is 1.3 km long and is located 200 m north of Trois Ilets, which is 2.0 km long; they run in a north-south direction. Both beaches are backed by forest, except for some open areas towards the southern end of Trois Ilets, where sheds have been installed for public use. Trois Ilets is a narrower beach, ranging from 1 to 9 m in width compared to Folle Anse beach, which varies between 1 and 15 m in width. The area between the beaches contains a warehouse and a pier and is lit by a floodlight, but turtles rarely nested on the adjacent sand. Due to the proximity of the two beaches and to the fact that turtles move between them, we refer to both beaches as Trois Ilets. Beach width does not vary greatly and tidal variations are negligible, although storms sometimes occur

towards the end of the main nesting season, which appears to occur between May and October, with a peak in July.

Sampling of Nests

We collected data at Trois Ilets between 28 May and 10 October 2002. The beach was patrolled nightly from 2000 to 0400 hours. Turtles were identified by Monel flipper tags located on the first, most proximal scale at the trailing edge of each flipper. All turtles that were encountered were measured; all measurements were taken after laying had begun, as disturbances during any other nesting phase will often cause the female to abort nesting.

Measurements

For each female, we collected the following data.

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

(2) Distance from the egg chamber to the forest line, defined as the point at which the dense forest formed an unbroken line.

(3) Percentage of overstorey vegetation cover, defined as the amount of cover directly above the nest and measured with a densiometer (dimensions $18.2 \times 18.0 \times 8.4$ cm, $L \times W \times H$) similar to a convex spherical densiometer, which is commonly used to assess canopy density (e.g. Lemmon 1956). Our apparatus consisted of a gridded mirror divided into 210 7-mm² squares. Vegetation cover was calculated by summing the amount of shading (out of five possible values: 0, 0.25, 0.50, 0.75, 1) in each square and dividing by 210. The horizontal field of view was approximately 26° and the vertical field of view was approximately 12°. Measurements were done during the day.

(4) Position along the beach: numbered tags were placed parallel to the shoreline at 20-m intervals along the patrolled area.

(5) Zone of the beach: four zones were defined: forest (completely surrounded by trees), forest border (near the forest but not completely surrounded), low-lying vegetation (presence of grass or beach creepers), and open sand. Nests were placed in one of these categories.

(6) Size of the turtle: over-the-curve midline carapace length was measured from the anterior-most point of the nuchal scute to the start of the separation between the two posterior-most marginal scutes.

(7) Time, date and weather conditions.

Hatching Success

We recorded the location of each nest by triangulating the nest position relative to three coloured strings placed around the nest site. The experimenter (S.K.) returned approximately 70 days later to excavate the nests. Upon excavation, eggs were categorized as hatched (only the eggshell remained), pipped (at least the head protruding

out of the shell) or unhatched. Unhatched eggs were opened and were broadly categorized as undeveloped, early, mid or late embryonic death. The numbers of live and dead hatchlings remaining in the nest were also counted. Hatching success was defined as the number of hatched eggs divided by the total number of eggs. Pipped eggs were considered to be hatched but not emerged. Emergence success was defined as the number of hatched eggs minus the number of pipped eggs and hatchlings remaining in the nest divided by the total number of eggs. To validate this method, eggs from a sample of nests ($N = 5$) were counted initially when the turtle was laying and subsequently upon excavation. Clutch sizes determined at laying and after emergence were within five eggs for these nests.

Hatchling Sea-finding Ability

We conducted orientation tests between 7 August 2003 and 22 August 2003. Four orientation arenas were used, which consisted of a circular trench 2 m in radius, dug 50 cm deep and 15 cm wide and divided into 16 equal segments by thin wood barriers. The arenas were located within 50 m of each other and their placement along the beach is illustrated in Fig. 1. The percentage of vegetation cover at four directions in the arenas was measured with the densiometer. To do this, the densiometer was rotated 90° from its usual position for measuring canopy cover to measure the vegetation cover at turtle eye level and then angled upward at 45° from the ground. The arenas were all level and the ocean was not visible at hatchling eye level. Hatchlings were gathered after emergence from

nests ($N = 6$) that had been marked after laying and had been surrounded by a wire trap 4–5 days before expected emergence. The beach was patrolled nightly at 1800, 2000, 2300, 0200 and 0500 hours to check whether any of the hatchlings had emerged. Once an emergence was seen, hatchlings were put in a covered bucket and the orientation tests were run. Lights were not used during the tests. Clutches were divided into four groups, one for each arena. Hatchlings from three clutches were used more than once; however, studies have shown that repeated testing has little effect on sea-finding ability (Mrosovsky & Shettleworth 1968) so this point is not discussed further. Each experiment consisted of placing hatchlings in the centre of the arenas. Arenas were near enough to each other that hatchlings were released in all four arenas 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 20-min test, the number of hatchlings in each segment as well as those still within the centre of each arena was recorded; the hatchlings were subsequently released. Results from two trials are not shown because one group of hatchlings from clutch 3 escaped and one group of hatchlings from clutch 4 was unusually lethargic and few moved from the centre of the arena.

Statistical Analyses

To assess individual differences in nest site choice, we analysed the data using a one-factor model II ANOVA (Sokal & Rohlf 1981). To calculate the repeatability (r) of nest choice, we used the 51 females for which two or more nests were documented during the season. We used the mean variances from the ANOVA and the harmonic mean of the number of nests observed per female to calculate r (Lessells & Boag 1987; Boake 1989). For nonparametric analyses of variance, beach zones were given ranks from 1 to 4, with the zone nearest the water having rank 1. For the sea-finding tests, circular statistics (Batschelet 1965, 1981) were used to determine the direction of orientation and the strength of direction. The length of the line vector (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 (a value of $r = 1$) indicates perfect orientation. Rayleigh's test was used to check whether orientation was significantly different from random within each arena. Analyses were done using Oriana, version 1.06 (Kovach Computing Services, Anglesey, Wales). Means are expressed as $\bar{X} \pm SD$ and results are considered significant at an alpha level of 0.05.

RESULTS

Nesting Patterns

We recorded the location of 183 nests from 76 hawksbill turtles. Of these, 51 turtles were observed nesting two or more times for a total of 153 nests.

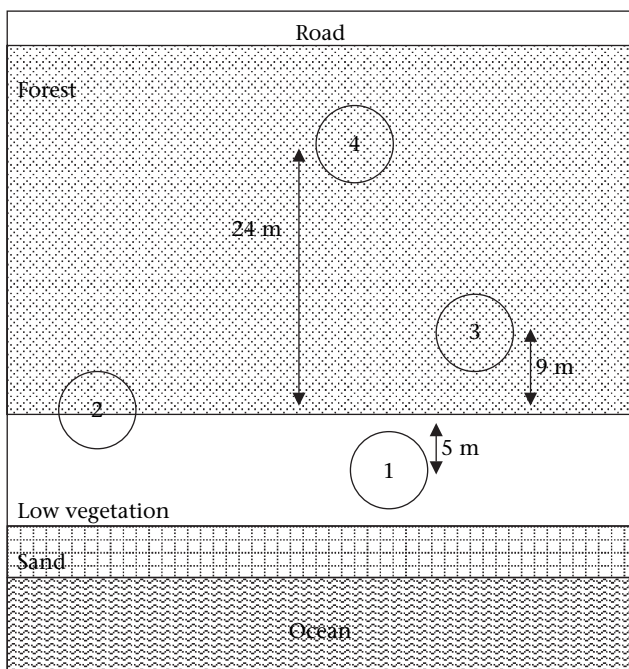


Figure 1. Diagram of the orientation arenas. The radii of the arenas were 2 m and each arena was divided into 16 equal segments. Distances from the centre to the forest line are indicated.

Population Preferences

Nests were mainly placed in areas with at least some vegetation (forest: $N = 35$, 19.2%; forest border: $N = 72$, 39.3%; low-lying vegetation: $N = 61$, 33.3%; open sand: $N = 15$, 8.2%). Overall, the mean distance from the current water line to the nest was 9.1 ± 4.5 m ($N = 183$) and the mean distance from the nest to the forest line was 0.8 ± 3.7 m ($N = 183$). Negative values are seaward of the forest line and positive values are seaward (Fig. 2). The mean percentage of overstorey vegetation cover was $32.8 \pm 28.9\%$ ($N = 183$).

Individual Preferences

The 51 females that were seen nesting more than once (2–6 clutches/turtle) showed a preference for one of the four defined beach zones (Kruskal–Wallis test: $H_{51} = 98.19$, $P < 0.0001$). Individuals also nested consistently with respect to position along the beach (ANOVA: $F_{50,102} = 5.29$, $P < 0.0001$). There were also significant differences among the turtles in their nest site choice with respect to distance from the forest line (ANOVA: $F_{50,102} = 2.74$, $P < 0.0001$), distance from the current water line (ANOVA: $F_{50,102} = 2.02$, $P = 0.001$) and percentage of overstorey vegetation cover (ANOVA: $F_{50,102} = 7.49$, $P < 0.0001$).

For turtles that nested two to six times, the mean number of observed nests was 3.1 (harmonic mean = 2.64) during the study. These turtles nested along the entire beach with respect to section and to zone. There was a significant repeatability of distance from the nest to the forest line (repeatability: $r = 0.40$, $N = 51$ females and 153 nests, $P < 0.0001$; Fig. 2), distance from the nest to the current water line ($r = 0.23$, $P = 0.001$), position of nests along the beach ($r = 0.62$, $P < 0.0001$; Fig. 3), and percentage of overstorey vegetation cover ($r = 0.71$, $P < 0.0001$;

Fig. 4). We also measured the distance between each pair of nests laid by an individual female as an index of interest distance. The overall mean interest distance for an individual turtle with respect to position along the beach was 594 ± 499 m ($N = 51$). The overall mean for an individual turtle with respect to distance from the forest line was 2.1 ± 1.1 m. There were also significant correlations between successive nest site choices for all four measures (Table 1). The weakest correlations were seen with respect to distance from the nest to the current water line and in the combinations with the lowest sample size.

There was no correlation between size of the nesting turtles, as measured by curved carapace length and any of the nest measurements (Pearson's product-moment correlation: location along the shoreline: $r = 0.10$, $P = 0.39$; percentage of vegetation cover: $r = 0.10$, $P = 0.36$; forest line: $r = 0.07$, $P = 0.55$; current water line: $r = 0.02$, $P = 0.84$; for all these measures $N = 76$).

Hatching Success

The mean hatching success for the 86 excavated nests was $86.5 \pm 12.4\%$ (Fig. 5). Emergence success was similar to hatching success except in nests that were inundated by high tides (Fig. 5). The mean emergence success for five nests that were inundated was $14.3 \pm 12.3\%$ and the mean emergence success for the other 81 nests was $84.6 \pm 13.5\%$. Overall, there was no significant variation in hatching success among the four beach zones (ANOVA: $F_{3,82} = 0.84$, $P = 0.48$). However, the two nests with the lowest emergence success were located in the open sand, and the nest with the highest emergence success was located in the forest border. We also found a significant correlation between mean clutch size and mean distance from the nest to the forest border line; turtles nesting further inland tended to have larger clutches (Pearson's product-moment correlation: $r = 0.42$, $N = 23$ turtles, $P = 0.04$). The mean clutch size was 137 ± 26 eggs.

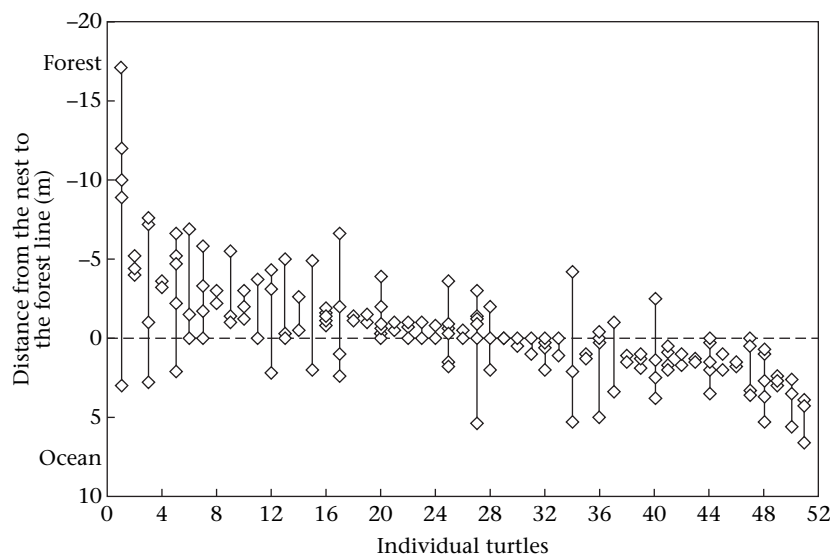


Figure 2. Distance from the nest to the forest line for turtles seen nesting between two and six times ($N = 51$). The horizontal dashed line represents the start of the forest; nests above the line were in the forest and nests below were not.

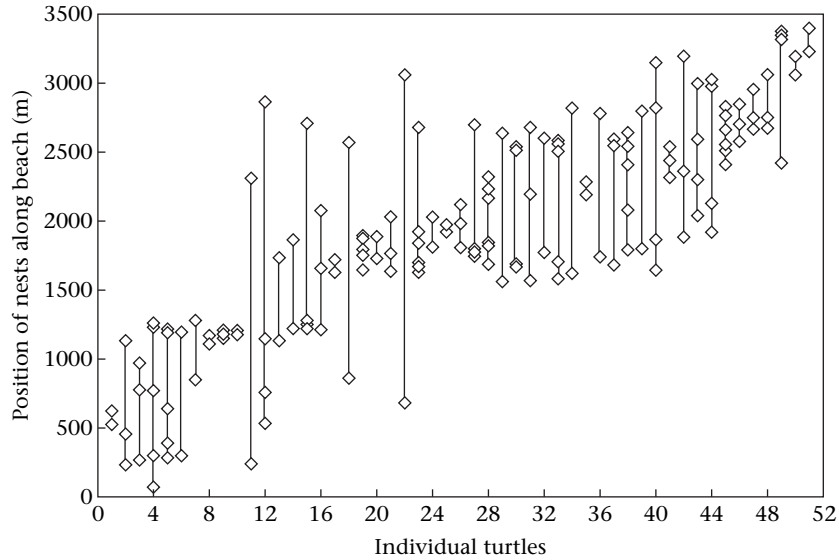


Figure 3. Position of nests along the beach for turtles seen nesting between two and six times ($N = 51$).

Sea-finding Tests

Orientation was generally seaward (Fig. 6) and significantly different from random in all but two trials (Rayleigh's test: $P < 0.05$ in 40 of 42 cases). Orientation was not significantly different from random for two trials in the most landward forest arena (Arena 4) (clutch 3: $r = 0.27$, $N = 43$, $P = 0.35$; clutch 4: $r = 0.3$, $N = 35$, $P = 0.17$). In these trials, hatchlings showed a weak (albeit nonsignificant) landward orientation.

DISCUSSION

Individual nest site choice behaviour is often overlooked in life history studies and is less frequently emphasized

than other traits such as egg size, egg number and the trade-off between the two (Resetarits 1996). In species lacking parental care, nest placement is of great importance because where a mother chooses to lay her eggs will influence her fitness, mainly through the survival of her offspring. In the present study, there was a significant repeatability of female choice, with some females preferring to nest in the low-lying vegetation, others in the forest border and others still in the forest itself. Additionally, females not only showed high fidelity to these beach zones, but also high fidelity with respect to location along the shoreline.

Repeatability values in this study for vertical distance up the beach and percentage of overstorey vegetation cover above the nest are the highest observed to date for nest

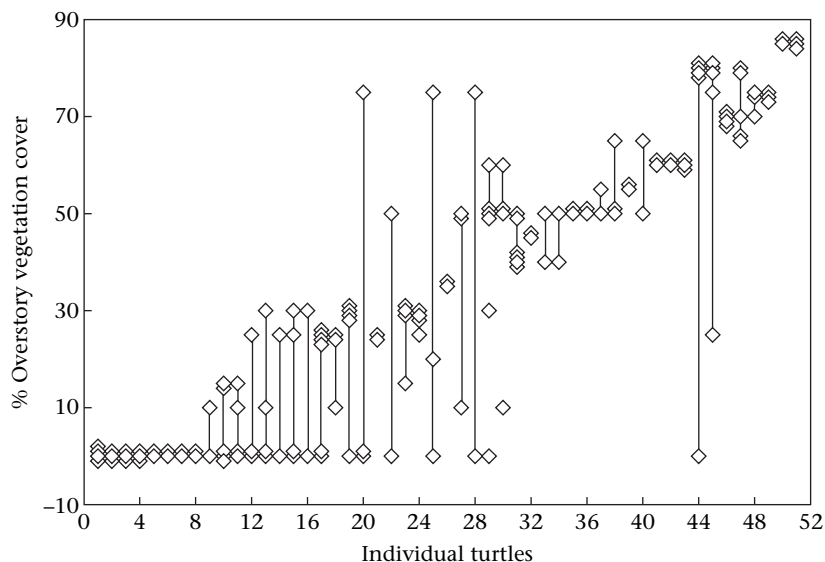


Figure 4. Percentage of overstorey vegetation cover above the nest for turtles seen nesting between two and six times ($N = 51$).

Table 1. Correlation coefficients (r) and P values for comparisons between measures of successive nest sites for all observed nests

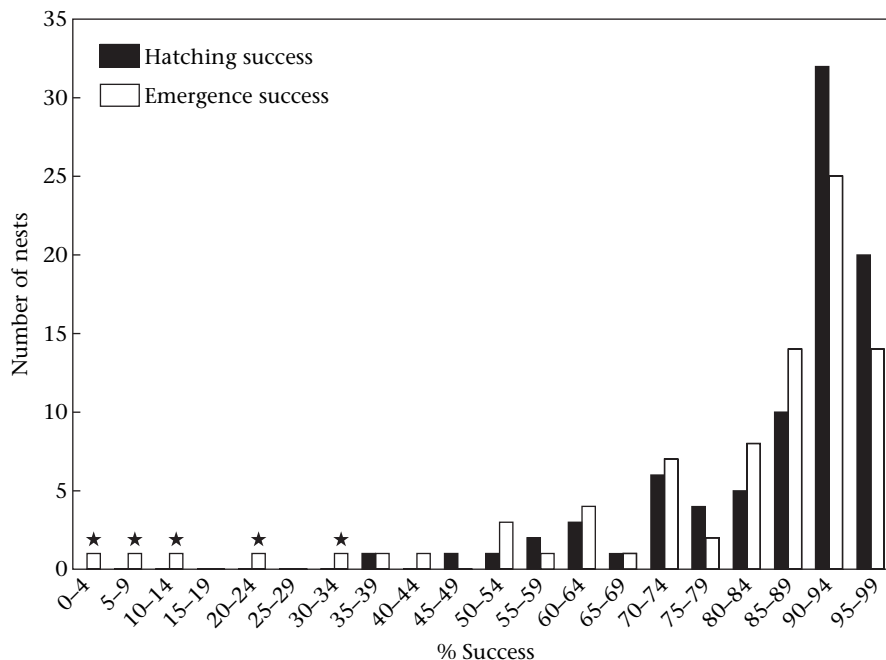
Measure	Nest comparison	N	r	P
Distance of nest from forest line	1 vs 2	51	0.71	<0.0001
	2 vs 3	29	0.66	0.0001
	3 vs 4	16	0.62	0.01
	4 vs 5	8	0.20	0.65
Distance of nest from water line	1 vs 2	51	0.53	<0.0001
	2 vs 3	29	0.37	0.04
	3 vs 4	16	0.10	0.76
	4 vs 5	8	0.24	0.57
% Vegetation cover above nest	1 vs 2	51	0.80	<0.0001
	2 vs 3	29	0.79	<0.0001
	3 vs 4	16	0.89	<0.0001
	4 vs 5	8	0.30	0.46
Location of nest along shoreline	1 vs 2	51	0.57	<0.0001
	2 vs 3	29	0.77	<0.0001
	3 vs 4	16	0.83	<0.0001
	4 vs 5	8	0.78	0.02

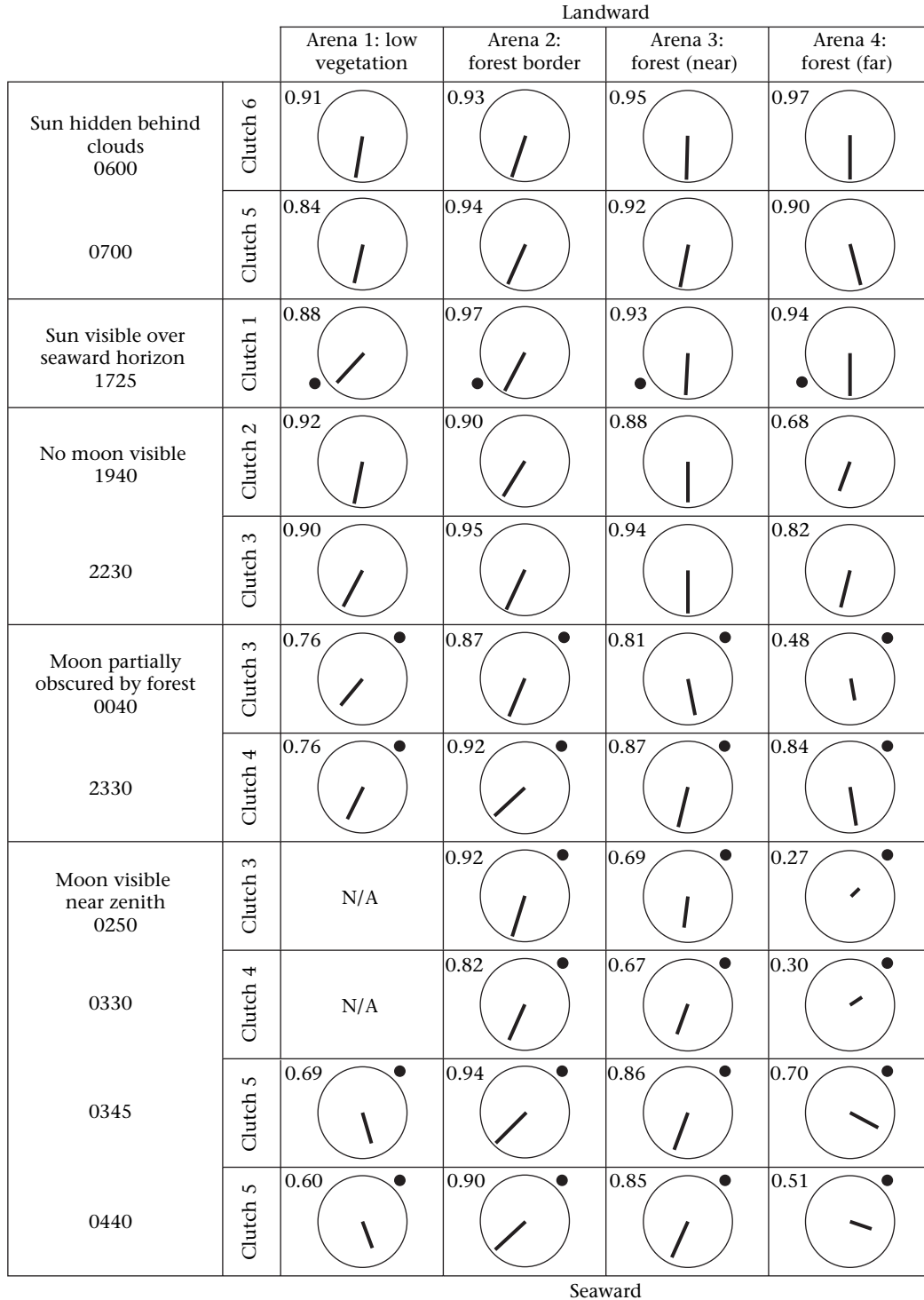
site choice in turtles (Janzen & Morjan 2001: $r = 0.18$; Kamel & Mrosovsky 2004: $r = 0.18$) and higher than some of those obtained in studies that have focused on other repeatable traits. For example, the repeatabilities of female preferences for male secondary sexual traits have been studied and are variable (e.g. guppy colour patterns, $r = 0.58$: Godin & Dugatkin 1995; grasshopper calling songs, $r = 0.25$: Butlin & Hewitt 1986; swordfish pigment patterns, $r = 0.50$; Morris et al. 2003). It has been argued that variability in female mating preference is biologically significant because it can potentially alter the rate and direction of evolution by sexual selection and because

heritable variation is necessary for evolutionary change (Jennions & Petrie 1997; Brooks 2002). Similarly, heritable differences among females in their nest site preferences may allow for the evolution of this behaviour in response to environmental or anthropogenic changes.

The existence of variation among females in their nest site choice behaviour permits quantitative evaluation of the fitness consequences of different female preferences, in this case for nesting in particular habitats. Hatching success per se was remarkably similar in all beach zones, indicating that variation in microhabitat characteristics (i.e. vegetation cover, soil texture, etc.) did not greatly affect the embryos' ability to develop. This differs from Wilson's (1998) findings that differences in microhabitat affected the embryonic survival of freshwater turtles. Nevertheless, even though microhabitat did not affect hatching success, five nests that were exposed to 2 days of high waves during a tropical storm had greatly reduced emergence successes, with nests nearer to the water being more severely affected. There is therefore an increased risk of nest failure resulting from placing nests too near the water.

There are also costs of nesting too far inland. When hatchlings emerge at the surface, they must reach the sea before being preyed upon or desiccated. Sea-finding in marine turtles depends on visual cues and hatchlings orient towards the brightest direction, which is generally seaward (Mrosovsky & Kingsmill 1985; Salmon et al. 1992). Although sea-finding in hawksbills has been studied less than in some other turtle species, there is much evidence pointing to the importance of visual cues. First, hatchlings are attracted to bright lights (Philibosian 1976; S. J. Kamel, unpublished data). Second, when surrounded by a wall producing a visually homogenous situation in all

**Figure 5.** Frequency distribution of the hatching and emergence successes for 86 nests at Trois Ilets beach. The stars indicate the emergence success of inundated nests.



Seaward

Figure 6. Results of the orientation experiments on hawksbill hatchlings. Line length indicates the strength of orientation and is indicated by the *r* vector in the top left-hand corner. All vectors were significantly different from random except for two trials in Arena 4; there were at least 30 hatchlings run in each trial. The dark circles indicate the position of the moon during the nighttime trials and the sun during the daytime trials. The time of the trial is indicated on the left as are the weather conditions during the tests.

directions, but not cutting off other cues such as surf sounds or odours, orientation was poor and vectors were close to zero. However, orientation was restored by re-introduction of a visual cue: hatchlings moved away from a dark obstruction erected above one side of the wall

(Mrosovsky 1970). Third, when far into the forest, as in some of the present tests, orientation was much impaired only when the moon was visible on the landward side of the test arena (Fig. 6, right column: tests with moon visible). Even in the near forest, orientation vectors in this

condition were somewhat smaller than those for the forest border zone. In contrast, when the moon was not visible, but auditory and other cues were presumably similar, orientation was good. It may seem surprising that orientation based on visual cues is possible within a littoral forest. However, the densiometer measurements of cover in different directions (Table 2) show that the situation within the forest was not equivalent to the tests with a visually homogeneous surrounding wall. In all the arenas, both in the horizontal plane at ground level, and with the densiometer angled up at 45°, there was more vegetation cover in the landward direction (Table 2). Even a small chink of light can affect sea-finding orientation, as shown by experiments in which a pinhole for light was made in covers otherwise blindfolding hatchlings (Mrosovsky & Kingsmill 1985). If there are only small openings in the vegetation, the associated brightness differentials between seaward and landward directions can be easily overwhelmed by the presence of moonlight. But if the obstructions in the seaward direction are few, as is the case in the border and low vegetation zones, once the gaze is directed above the horizontal, then moonlight has only minor influence. These points suggest that even within a forest, visual cues are used by hawksbills for sea-finding. However, it is emphasized that the main aim of these tests with arenas was not to learn about proximate cues but to discover whether orientation of hatchlings was impaired when they were within the forest. The results demonstrated that in certain conditions of moonlight severe disorientation can occur, thus constituting a cost of nesting too far away from the water.

Another cost of nesting in the forest is increased exposure to terrestrial predators. We observed land crabs (*Gecarcinus lateralis*) attacking and dragging hatchlings into their burrows. Other land crabs (*Cardisoma* sp.) were also seen preying on the hatchlings. It was our impression that these crabs were present in higher densities in the forest than on the beach. Evidently, there are trade-offs associated with nesting in the various beach microhabitats and the question then arises as to why strong differences among individuals exist and why they are maintained.

High repeatability estimates have been used as indirect evidence that a trait in question is heritable. Because of the difficulties inherent in estimating quantitative genetic parameters, especially in species with long generation times, researchers often use repeatability as an estimate of heritability. However, this is only a reliable guide if additive genetic variation accounts for most of the differences among individuals (Boake 1989; Brooks 2002). If it

only accounts for a small proportion of the variation, then repeatability will substantially exceed heritability. Several studies have attempted to measure repeatabilities and heritabilities of female mate choice (e.g. Bakker 1993; Jang & Greenfield 2000) and most recently, Brooks & Endler (2001) found that the only component of female guppy (*Poecilia reticulata*) mate choice that displayed significant heritable variation was the mean time a female spends associating with a particular male. Therefore, it is important to interpret repeatabilities of female choice with caution. However, it is possible that there is a strong heritable component to nest site choice in the hawksbill, because despite environmental variation, field estimates are much higher than in many controlled laboratory experiments on the repeatability of behaviours. Furthermore, several studies have found heritable variation in insect oviposition preference or oviposition behaviour (Singer et al. 1988; Sezer & Butlin 1998; Réale & Roff 2002).

Alternatively, consistency of behaviour may arise through several possible nonheritable factors (Widemo & Sæther 1999). For example, hatchlings might imprint on their environment once they emerge from the nest, and return to nest in this same environment many years later. This possibility seems less likely, however, because nests laid in the forested areas are generally cooler and produce more males than females (2002 nesting season: 28 May–23 November; mean beach zone temperatures: forest: $27.78 \pm 0.45^\circ\text{C}$; forest border: $28.55 \pm 0.59^\circ\text{C}$; low-lying vegetation: $28.94 \pm 0.69^\circ\text{C}$; open sand: $29.43 \pm 0.63^\circ\text{C}$; temperatures were taken at a depth of 30 cm; unpublished data). This means that very few females would imprint on the forested areas, a trend not currently observed, as an important proportion of females prefer nesting in vegetated areas. If, however, males carried the genes for nest site preference, they could pass them on to their daughters, thus allowing for a larger proportion of forest nesters. Imprinting also appears to be an unlikely scenario, due to its inherent riskiness. If a female placed her first nest in a poor-quality habitat, then subsequent nests would also be doomed (Lotem 1993; Janzen & Morjan 2001).

Another possibility is that motivation or state could affect decision making (Bilde et al. 2002) and lead to differences among individuals, but hawksbills appeared to be unaffected by human or natural disturbances. Several observations were made of females aborting their nesting attempts, because of obstructions (e.g. roots, tree branches), lights or noise from people on the beach, only to return on a subsequent occasion to nest in the same

Table 2. Percentage of vegetation cover at four points in each arena at (1) hatchling eye level (HEL) and (2) at a 45° angle from the ground

Direction	% Low-lying vegetation		% Forest border		% Forest (near)		% Forest (far)	
	HEL	45°	HEL	45°	HEL	45°	HEL	45°
Landward	100	95	100	95	99	90	99	90
Seaward	95	0	50	45	85	85	95	89
Left	85	50	98	95	100	95	100	80
Right	95	0	100	93	98	95	100	85

zone. It appears unlikely that turtles will repeatedly nest only in areas where their prior experience has been a positive one.

Environmental variation may also cause differences in nesting patterns, but we found no correlation between nest placement and weather conditions, time of night or date ($P > 0.05$, data not shown). In fact, the strongest correlation between any of these measures had an r value of 0.1 and a P value of 0.16 (date versus current water line). Condition of the animal may also affect nest site choice, however, we found no correlation between size of animal and any of our measures of nest location. We did find a positive correlation between mean distance from the forest border and mean clutch size, indicating that females that nested in the forest laid larger clutches. This could have implications for sea turtle demography, because nests incubated at temperatures in the forest zone mainly produce male offspring (unpublished data), and this might be a case of females in good reproductive condition biasing their offspring sex ratios to produce high-quality males (Trivers & Willard 1973). It would be interesting to look at repeatability of nest site choice over several seasons, to see whether differences among females are due to short-term effects or whether individual preferences are stable over the longer term, as found by Janzen & Morjan (2001) in painted turtles, *Chrysemys picta*.

These results also pose an interesting challenge to find an explanation for the differences between hawksbill nesting patterns and those of another sea turtle species, the leatherback, *Dermochelys coriacea*. Individual hawksbills have consistent nesting patterns; leatherbacks have higher within-individual variation. These differences in behaviour may mirror differences in nesting habitats. Leatherback beaches can be expected to change within a season, whereas hawksbill beaches are often relatively stable. On dynamic beaches where unpredictability of tidal height and beach topography is common and in fact a predictable feature of the environment, a greater scattering of nests within individuals, and correspondingly a lower repeatability, may be selected for; it should increase the likelihood that at least some nests produce hatchlings. On beaches that are often stable with little tidal variation, in most years a variety of types of nest locations will produce hatchlings. Therefore, there will be less pressure to scatter nests, and repeatability will be higher.

The maintenance of phenotypic diversity in nest site choice behaviours could derive from variability in the environmental hazards encountered from year to year. When beach-destroying storms are rare, turtles laying nests near the water may produce more hatchlings that reach the water than turtles laying further in the forest. But when storm years occur, turtles that lay further inland will be fitter. A constantly shifting balance between phenotypes will be promoted by variation in the environment over time.

The high repeatability found in the present study could represent a polymorphism for female nest site choice, with certain females preferring particular zones. Assuming a genetic basis, the polymorphism may be maintained through frequency-dependent selection. Sea turtles have

temperature-dependent sex determination, with females being produced at high temperatures and males being produced at low temperatures (Wibbels 2003). Different beach zones have different thermal properties; some areas are likely to produce primarily males and others primarily females. The different nest site choices may be maintained by the increased fitness advantages when females produce the rarer sex.

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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.
- Bakker, T. C. M. 1993. Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature*, **363**, 255–257.
- Bass, A. L., Good, D. A., Bjørndal, K. A., Richardson, J. I., Hillis, Z. M., Horrocks, J. A. & Bowen, B. W. 1996. Testing models of female reproductive migratory behaviour and population structure in the Caribbean hawksbill turtle, *Eretmochelys imbricata*, with mitochondrial DNA sequences. *Molecular Ecology*, **5**, 321–328.
- 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.
- Batschelet, E. 1981. *Circular Statistics in Biology*. London: Academic Press.
- Bilde, T., Maklakov, A. A., Taylor, P. W. & Lubin, Y. 2002. State-dependent decisions in nest site selection by a web-building spider. *Animal Behaviour*, **64**, 447–452.
- Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behaviour. *Evolutionary Ecology*, **3**, 173–182.
- Brooks, R. 2002. Variation in female mate choice within guppy populations: population divergence, multiple ornaments and the maintenance of polymorphism. *Genetica*, **116**, 343–358.
- Brooks, R. & Endler, J. A. 2001. Female guppies agree to differ: phenotypic and genetic variation in mate-choice behaviour and the consequences for sexual selection. *Evolution*, **55**, 1644–1655.
- Bulmer, M. G. & Bull, J. J. 1982. Models of polygenic sex determination and sex ratio control. *Evolution*, **36**, 13–26.
- Butlin, R. K. & Hewitt, G. M. 1986. Heritability estimates for characters under sexual selection in the grasshopper, *Chorthippus brunneus*. *Animal Behaviour*, **34**, 1256–1261.
- Eckert, K. L. 1987. Environmental unpredictability and leatherback sea turtle (*Dermochelys coriacea*) nest loss. *Herpetologica*, **43**, 315–323.
- Falconer, D. S. 1981. *Introduction to Quantitative Genetics*. 2nd edn. New York: Longman.

- Fortuna, J. L. & Hillis, Z. M.** 1998. Hurricanes, habitat loss and high temperatures: implications for hawksbill hatch success at Buck Island Reef National Monument. In: *Proceedings of the Seventeenth Annual Sea Turtle Symposium N.O.A.A. Technical Memorandum NMFS-SEFSC-415* (Ed. by S. P. Epperly & J. Braun), pp. 183–185. Miami, Florida: U.S. Department of Commerce.
- Godin, J. G. J. & Dugatkin, L. A.** 1995. Variability and repeatability of female mating preference in the guppy. *Animal Behaviour*, **49**, 1427–1433.
- Halloy, M. & Fiano, J. M.** 2000. Oviposition site selection in *Pleurodema borellii* (Anura: Leptodactylidae) may be influenced by tadpole presence. *Copeia*, **2000**, 606–609.
- Hoyle, M. & Richardson, J. I.** 1993. *The Jumbo Bay Hawksbill Project, 1987–1992*. Athens: University of Georgia Sea Turtle Cooperative.
- Jang, Y. W. & Greenfield, M. D.** 2000. Quantitative genetics of female choice in an ultrasonic pyralid moth, *Achroia grisella*: variation and evolvability of preference along multiple dimensions of the male advertisement signal. *Heredity*, **84**, 73–80.
- 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.
- Jennions, M. D. & Petrie, M.** 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society*, **72**, 283–327.
- Kamel, S. J. & Mrosovsky, N.** 2004. Nest-site selection in leatherbacks (*Dermochelys coriacea*): individual patterns and their consequences. *Animal Behaviour*, **68**, 357–366.
- Kolbe, J. J. & Janzen, F. J.** 2001. The influence of propagule size and maternal nest-site selection on survival and behaviour of neonate turtles. *Functional Ecology*, **15**, 772–781.
- Lotem, A.** 1993. Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature*, **362**, 743–745.
- Lemmon, P. E.** 1956. A spherical densitometer for estimating forest overstorey density. *Forest Science*, **2**, 314–320.
- Lessells, C. M. & Boag, P. T.** 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.
- Madsen, T. & Shine, R.** 1999. Life history consequences of nest site variation in tropical pythons (*Liasis fuscus*). *Ecology*, **80**, 989–997.
- Misenhelter, M. D. & Rotenberry, J. T.** 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology*, **81**, 2892–2901.
- Morjan, C. L.** 2003. How rapidly can maternal behavior affecting primary sex ratio evolve in a reptile with environmental sex determination. *American Naturalist*, **162**, 205–219.
- Morris, M. R., Nicoletto, P. F. & Hesselman, E.** 2003. A polymorphism in female preference for a polymorphic male trait in the swordtail fish *Xiphophorus cortezi*. *Animal Behaviour*, **65**, 45–52.
- Mrosovsky, N.** 1970. The influence of the sun's position and elevated cues on the orientation of hatchling sea turtles. *Animal Behaviour*, **18**, 648–651.
- Mrosovsky, N. & Kingsmill, S. F.** 1985. How turtles find the sea. *Zeitschrift für Tierpsychologie*, **67**, 237–256.
- Mrosovsky, N. & Shettleworth, S. J.** 1968. Wavelength preferences and brightness cues in water finding behaviour of sea turtles. *Behaviour*, **32**, 211–217.
- Penn, D. & Brockmann, H. J.** 1994. Nest-site selection in the horseshoe crab, *Limulus polyphemus*. *Biological Bulletin*, **187**, 373–384.
- Philibosian, R.** 1976. Disorientation of hawksbill turtle hatchlings, *Eretmochelys imbricata*, by stadium lights. *Copeia*, **1976**, 824.
- Réale, D. & Roff, D. A.** 2002. Quantitative genetics of oviposition behaviour and interactions among oviposition traits in the sand cricket. *Animal Behaviour*, **64**, 397–406.
- Resetarits, W. J., Jr.** 1996. Oviposition site choice and life history evolution. *American Zoologist*, **36**, 205–215.
- Roosenburg, W. M. & Niewiarowski, P. E.** 1998. Maternal effects and the maintenance of environmental sex determination. In: *Maternal Effects as Adaptations* (Ed. by T. A. Mousseau & C. W. Fox), pp. 307–322. Oxford: Oxford University Press.
- Salmon, M., Wyneken, J., Fritz, E. & Lucas, M.** 1992. Sea-finding by hatchling sea-turtles – role of brightness, silhouette and beach slope as orientation cues. *Behaviour*, **122**, 56–77.
- Seddon, P. J. & Davis, L. S.** 1989. Nest site selection by yellow-eyed penguins. *Condor*, **91**, 653–659.
- Sezer, M. & Butlin, R. K.** 1998. The genetic basis of oviposition preference differences between sympatric host races of the brown planthopper (*Nilaparvata lugens*). *Proceedings of the Royal Society of London, Series B*, **265**, 2399–2405.
- Singer, M. C., Ng, D. & Thomas, C. D.** 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution*, **42**, 977–985.
- Sokal, R. R. & Rohlf, F. J.** 1981. *Biometry*. 2nd edn. New York: W. H. Freeman.
- 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.
- Trivers, R. L. & Willard, D. E.** 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**, 90–91.
- Wibbels, T.** 2003. Critical approaches to sex determination in sea turtles. In: *The Biology of Sea Turtles. Vol. II* (Ed. by P. L. Lutz, J. A. Musick & J. Wyneken), pp. 103–134. Boca Raton, Florida: CRC Press.
- Widemo, F. & Sæther, S. A.** 1999. Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends in Ecology and Evolution*, **14**, 26–31.
- Wilson, D. S.** 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology*, **79**, 1884–1892.
- Witzell, W. N.** 1983. *Synopsis of Biological Data on the Hawksbill Turtle Eretmochelys Imbricata*. FAO Fisheries Synopsis No. 137. Rome, Italy: Food and Agriculture Organization of the United Nations.