

## INTER-SEASONAL MAINTENANCE OF INDIVIDUAL NEST SITE PREFERENCES IN HAWKSBILL SEA TURTLES

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**Abstract.** Within a single population of hawksbill sea turtles (*Eretmochelys imbricata*), we found a behavioral polymorphism for maternal nest site choice with respect to beach microhabitat characteristics. Some females preferred to nest in littoral forest and in places with overstory vegetation cover, and others preferred to nest in more open, deforested areas. Nest site choice was consistent within and between nesting seasons two years apart. This was not a result of females simply returning to the same location along the shoreline; beach sections used by individual turtles varied between seasons. Nest site choice was not influenced by changes in beach environment (e.g., beach width and foliage cover) or by changes in females' reproductive output (e.g., clutch size), suggesting that fidelity to particular microhabitats is a major determinant of the observed nesting patterns. Because hawksbills exhibit temperature-dependent sex determination, if the behavioral polymorphism in nest site choice has a genetic basis, as is plausible, then this would have implications for sex ratio evolution and offspring survival. By taking an individual-based approach to the study of maternal behavior we reveal previously overlooked individual variation and hope to provide some impetus for more detailed studies of nest site choice.

**Key words:** *behavioral polymorphism; Eretmochelys imbricata; hawksbill sea turtle; nest-site choice; plasticity; preference; sea turtle; sex ratio; temperature-dependent sex determination.*

### INTRODUCTION

Incubation-induced variation in offspring phenotype is common in many egg-laying species. For example, nest environment can affect an offspring's body size (Brown and Shine 2004, Lloyd and Martin 2004), performance (Singer et al. 1988, Shine et al. 1997), survival (Roitberg 1998, Kolbe and Janzen 2001), and gender (Mrosovsky and Provancha 1992, Roosenburg 1996). Because of the direct effects of nest environment on offspring fitness, some researchers have hypothesized that females should actively choose nest sites to exploit offspring reaction norms (e.g., Shine and Harlow 1996, Brown and Shine 2004, Forstmeier and Weiss 2004). Although the implicit assumption underlying this hypothesis is that nest site choice is a plastic trait, repeated observations of the same female have seldom been carried out. If, in fact, individual females are consistent in their nest site choice, then this behavior might be genetically determined, with polymorphisms existing within a population.

Although a genetic basis for oviposition site selection has been documented in insects (Sezer and Butlin 1998, Barker and Starmer 1999, Bossart and Scriber 1999), studies on vertebrates have produced mixed results. Some studies have found equivocal evidence of within-individual consistency in nesting behavior (gecko, Bull et al. 1988; loggerhead turtle, Hays and Speakman 1993), while others have found evidence of individual female preferences (gecko, Bragg et al. 2000; painted turtle, Janzen and Morjan 2001; chelid turtle, Spencer and Thompson 2003; leatherback turtle, Kamel and Mrosovsky 2004). In a recent study, we found that individual hawksbill sea turtles (*Eretmochelys imbricata*), reptiles with temperature-dependent sex determination, differed in their preferences for nest microhabitat characteristics (e.g., amount of vegetation cover above the nest and distance traveled in littoral forest). Hawksbills lay several clutches in a season, and their nest site choices were consistent over the nesting season despite changes in the environment, including beach width, foliage cover, and weather conditions (Kamel and Mrosovsky 2005). One explanation for this observation is that the variation among females has a genetic basis and that nest site choice is a heritable trait. It is, however, also possible that between-season changes in female state (i.e., resource availability, mating success), rather than

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within-season changes in the terrestrial environment, are the important factors underlying changes in nesting preferences. To date, few researchers have explicitly assessed individual nesting preferences in a reptile across several nesting seasons (but see Janzen and Morjan 2001, Spencer and Thompson 2003).

With these considerations in mind, we returned to our Guadeloupe study site in 2004 to quantify the nest site choice of individuals whose preferences had already been characterized in 2002 (hawksbills nest on average every two years; see Richardson et al. 1999). Our aim was to assess the strength and persistence across breeding seasons of the previously observed intra-seasonal behavioral consistency.

## METHODS

### *Study site*

Trois Ilets beach (including Folle Anse, an adjacent beach) in Guadeloupe, French West Indies, is located on the western coast of Marie-Galante, a small island 40 km southeast of the island of Guadeloupe itself. The beach runs in a north–south direction and comprises 3.3 km of usable nesting habitat. Beach width varies between 1 and 15 m, both temporally and spatially (S. J. Kamel, *personal observation*). The open sand areas are generally wider at the start of the season and tend to become eroded as storms become more frequent later on. The beach is backed by a coastal littoral forest that thins out toward the southern end where sheds have been installed for public use. The foliage is more reduced during the drier months of May and June, but leaf cover increases when rain becomes more frequent in August. Tidal variations are negligible (<0.3 m), except when storms occur toward the end of the main nesting season, which takes place between May and October, with a peak in July (S. J. Kamel, *unpublished manuscript*). Turtles have unobstructed access to 3.3 km of shoreline and are presented with an unbroken forest line over the entire nesting beach.

### *Nest sampling and measurements*

Data were collected at Trois Ilets between 3 June and 10 September 2004 using the same protocols as those followed during the 2002 nesting season (for detailed description of the methodology, see Kamel and Mrosovsky [2005]). The beach was patrolled nightly from 2000 to 0400 hours; however, due to reduced personnel in 2004, the northern portion of the beach was patrolled less systematically than in 2002. Turtles were identified by Monel flipper tags located on the first, most proximal scale at the trailing edge of each flipper. We measured every turtle that we encountered, and all measurements were taken after laying had begun to minimize human impact on nest site choice.

For each nest, the following data were collected: (1) distance from the egg chamber to (a) the current water

line and (b) the forest line; (2) densiometer measures of percentage of overstory vegetation cover; (3) position along the beach; (4) beach zone location, categorized as: 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; (5) curved carapace length; and (6) time, date, and weather conditions. The location of each nest was recorded by triangulating the nest position relative to three colored strings placed around the nest site. Nests were triangulated at night and excavated ~70 d later. Clutch size was calculated by summing the number of eggshells (hatched eggs) and unhatched eggs. For turtles for which there were multiple clutch size measures, a mean clutch size value was used in all subsequent calculations.

A  $4 \times 2$  contingency test was used to determine whether females placed their nests nonrandomly with respect to the available beach habitat. Thirty-three transects spaced ~100 m apart were placed along the nesting beach. The width of each of the four defined beach zones was measured, except the width of the forest zone, which was truncated at 20 m. This was done because turtles were never seen nesting further than 20 m from the forest line. All values were summed for each zone and multiplied by 100 to obtain area estimates. We calculated the expected number of nests in each beach zone based on the area of each zone divided by the total area available for nesting.

To determine the within-individual consistency of nest site choice in 2004, we calculated repeatability ( $r$ ) estimates, using females for which two or more nests were documented during the season. We used the within and among female mean squares obtained from a one-factor model II ANOVA and the harmonic mean of the number of nests observed per female to calculate  $r$  (Lessells and Boag 1987, Boake 1989, Janzen and Morjan 2001). All analyses were done using GraphPad Prism version 3.00 (GraphPad Software, San Diego, California, USA).

Because the aim of this study was to compare nest site choices between years, we focused on females that we observed nesting both in 2002 and 2004. To determine whether nest site choice was consistent between seasons, we used a linear regression between nest variables for individuals seen in 2002 and 2004.

## RESULTS

Overall, turtles nested in all available beach microhabitats ( $n = 161$  nests): 3.1% of nests were in the open sand, 38.5% were in the low-lying vegetation, 37.3% were in the forest border, and 21.1% were in the forest (Table 1). The contingency analysis indicated that turtles nested nonrandomly with respect to the amounts of available beach microhabitat ( $\chi^2 = 73.74$ ,  $df = 3$ ,  $P < 0.0001$ ; Table 1).

TABLE 1. Estimated areas and percentage of total habitat for each of the four beach zones, together with the distribution of observed nests and expected nests based on the amount of available beach microhabitat.

Zone	Area (m <sup>2</sup> )	Percentage of total habitat	No. observed nests	No. expected nests
Open sand	6930	6.8	5	11
Low-lying vegetation	18 480	18.1	62	29
Forest border	10 560	10.4	60	17
Forest	66 000	64.7	34	104
Total	101 970	100.0	161	161

Note: The study site was located on Trois Ilets beach (including Folle Anse, an adjacent beach) in Guadeloupe, French West Indies.

Forty-eight turtles were observed nesting between two and six times in 2004. There was a significant repeatability of distance from the nest to the forest line ( $r = 0.36$ ,  $n = 48$  females and 133 nests,  $P < 0.0001$ ), position of nests along the beach ( $r = 0.49$ ,  $P < 0.0001$ ), percentage of overstorey vegetation cover ( $r = 0.69$ ,  $P < 0.0001$ ), and current water line ( $r = 0.35$ ,  $P < 0.0001$ ). These values were similar to those calculated for 2002 (Kamel and Mrosovsky 2005).

Thirteen turtles that were seen nesting in 2002 were also seen in 2004. For these turtles, there was a significantly positive between-year relationship for both mean distance of nests from the forest border (linear regression,  $r^2 = 0.61$ ,  $P = 0.002$ ; Fig. 1, Table 2) and the mean amount of vegetation cover above the nest (linear regression,  $r^2 = 0.796$ ,  $P < 0.0001$ ; Fig. 2, Table 2). The between-year relationship for mean position along the

beach was not significant (linear regression,  $r^2 = 0.01$ ,  $P = 0.75$ ; Fig. 3, Table 2).

Mean clutch size of the 13 turtles was significantly larger in 2004 ( $159 \pm 13$  eggs; mean  $\pm$  SD) than in 2002 ( $140 \pm 15$  eggs;  $t$  test,  $t_{1,24} = 3.38$ ,  $P = 0.003$ ). In addition, when all nests from both seasons were compared, mean clutch size was significantly larger in 2004 than in 2002 ( $159 \pm 29$  eggs,  $n = 86$  nests and  $137 \pm 26$  eggs,  $n = 64$  nests respectively;  $t$  test,  $t_{1,148} = 4.78$ ,  $P < 0.0001$ ).

#### DISCUSSION

Individual hawksbills were strikingly consistent in their nest microhabitat preferences both between and within seasons. These preferences were manifested as distance traveled into the littoral forest and, more particularly, the amount of vegetation cover above the nest. Importantly, they were maintained between years despite changes in the terrestrial environment and in females' reproductive output. For example, beach width, forest width, foliage cover, and weather conditions differed between years, as did clutch sizes. The 20-egg difference in mean clutch size between 2002 and 2004 points to a difference in condition of turtles, possibly related to their age or nutritional state (Bjorndal and Carr 1989, Clifford and Anderson 2001). Taken together, this information implies that fidelity to particular microhabitats is a major determinant of the observed variation in nesting patterns.

These persistent preferences are not simply a result of females returning to the same location along the shoreline, as evidenced by the lack of a between-season correlation for their position along the beach. Fidelity to a particular nesting beach and to a location along that beach has been the main focus of previous work on sea turtle nest site choice (Carr and Carr 1972, Bass et al. 1996, Richardson et al. 1999, Nordmoe et al. 2004). Our results confirm that at least some turtles return to the same nesting beach, but also reveal that in this population of hawksbills whether or not they return to the same beach section depends on the sampling time scale (i.e., months vs. years). Within a season there was

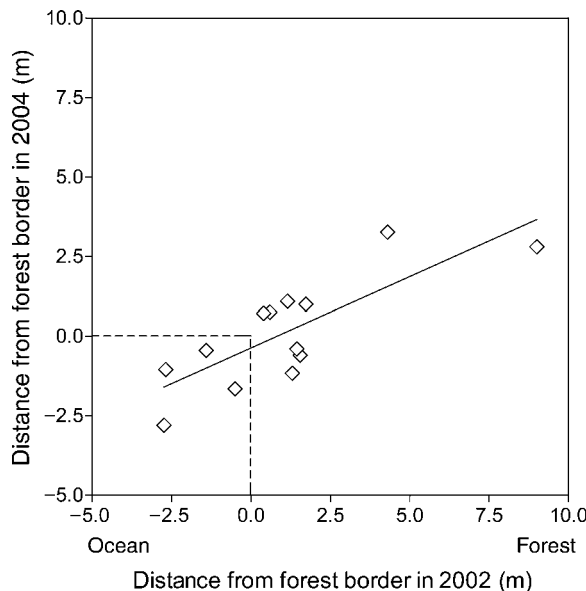


FIG. 1. Linear regression between mean distance of nests from the forest border for turtles seen nesting in 2002 and 2004 ( $n = 13$  turtles). The study site was located on Trois Ilets beach (including Folle Anse, an adjacent beach) in Guadeloupe, French West Indies.

TABLE 2. Percent overstory vegetation cover above the nest, distance of the nest from the forest border, position of nests along the beach, and the number of nests for turtles observed both in 2002 and 2004.

Turtle	Percent overstory vegetation cover		Distance from forest border (m)		Position along beach (m)	
	2002	2004	2002	2004	2002	2004
1	50.0 ± 28.3 (2)	68.3 ± 37.5 (3)	-4.2 ± 0.2 (2)	-3.3 ± 3.7 (3)	2207.0 ± 292.7 (2)	2354.0 ± 628.9 (3)
2	45.0 ± 7.1 (2)	50.0 ± 7.1 (2)	-0.4 ± 0.6 (2)	-0.8 ± 0.4 (2)	3314.0 ± 118.8 (2)	1141.0 ± 171.1 (2)
3	57.5 ± 10.6 (2)	35.0 ± 28.3 (2)	-1.6 ± 1.5 (2)	0.6 ± 2.3 (2)	1921.0 ± 153.4 (2)	2219.0 ± 114.6 (2)
4	37.5 ± 53.0 (2)	35.0 ± 7.1 (2)	-1.5 ± 4.9 (2)	0.7 ± 1.7 (2)	1140.0 ± 43.8 (2)	1652.0 ± 68.6 (2)
5	0.0 ± 0.0 (3)	0.0 ± 0.0 (2)	2.7 ± 0.3 (3)	2.8 ± 1.8 (2)	1970.0 ± 156.9 (3)	1973.0 ± 233.3 (2)
6	36.8 ± 23.1 (3)	51.7 ± 2.9 (3)	-1.7 ± 3.5 (3)	-1.0 ± 1.0 (3)	2791.0 ± 148.8 (3)	3267.0 ± 182.1 (3)
7	2.5 ± 5.0 (4)	3.3 ± 5.8 (3)	-1.3 ± 2.9 (4)	1.2 ± 0.8 (3)	2513.0 ± 571.1 (4)	895.0 ± 405.0 (3)
8	26.3 ± 7.5 (4)	17.5 ± 24.8 (2)	0.5 ± 1.0 (4)	1.7 ± 0.9 (2)	2370.0 ± 728.3 (4)	3190.0 ± 107.5 (2)
9	6.0 ± 8.2 (5)	5.0 ± 7.1 (2)	2.7 ± 1.9 (5)	1.1 ± 0.6 (2)	2189.0 ± 500.3 (5)	1856.0 ± 16.8 (2)
10	24.0 ± 13.42 (5)	25.0 ± 14.1 (2)	1.4 ± 1.5 (5)	0.5 ± 0.6 (2)	2293.0 ± 351.2 (5)	1898.0 ± 88.4 (2)
11	64.0 ± 35.8 (5)	85.0 ± 4.1 (4)	-9.0 ± 7.4 (5)	-2.8 ± 1.3 (4)	728.0 ± 539.2 (5)	2370.0 ± 288.7 (4)
12	16.7 ± 12.9 (6)	24.2 ± 30.7 (6)	-0.4 ± 1.9 (6)	-0.7 ± 3.7 (6)	2622.0 ± 160.1 (6)	1944.0 ± 403.9 (6)
13	43.3 ± 5.2 (6)	63.0 ± 9.7 (5)	-1.6 ± 1.5 (6)	-1.1 ± 1.5 (5)	1908.0 ± 394.1 (6)	2074.0 ± 369.8 (5)

Notes: All values are means ± SD with sample size (number of nests measured) in parentheses. Negative values for distance of the nest from the forest border indicate that nests are landward of the forest border, and positive values indicate that nests are seaward.

high consistency, but in different years different sections of the beach were selected.

The point we want to emphasize is that not only do microhabitat preferences exist and persist, but that these preferences differ greatly among females, that is, individuals within a single population have distinct microhabitat preferences. This phenomenon has not been salient before because most studies on nest site selection have been carried out at the population level (but see Janzen and Morjan 2001, Spencer and Thompson 2003). Even when the distributions of nest locations in a population take on a particular shape (Hays et al.

1995, Misenhelter and Rotenberry 2000, Fernandez and Reboreda 2002, Tiwari et al. 2005), nest site choice at the level of the individual may have a different pattern. For example, certain distributions may suggest random placement of nests but this distribution could arise because individuals differ in their preferences, which would result in no discernable population-level preference (e.g., Morris et al. 2003). Our data show that individual hawksbills do, in fact, exhibit consistent and repeatable behavioral polymorphisms in nest site choice.

High repeatability values might reflect an underlying genetic basis for polymorphic traits (Boake 1989,

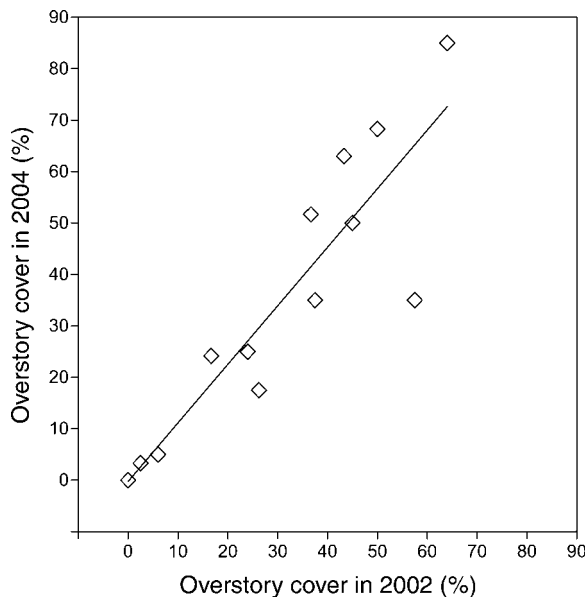


FIG. 2. Linear regression between mean percentage of overstory vegetation cover for turtles seen nesting in 2002 and 2004 ( $n = 13$  turtles).

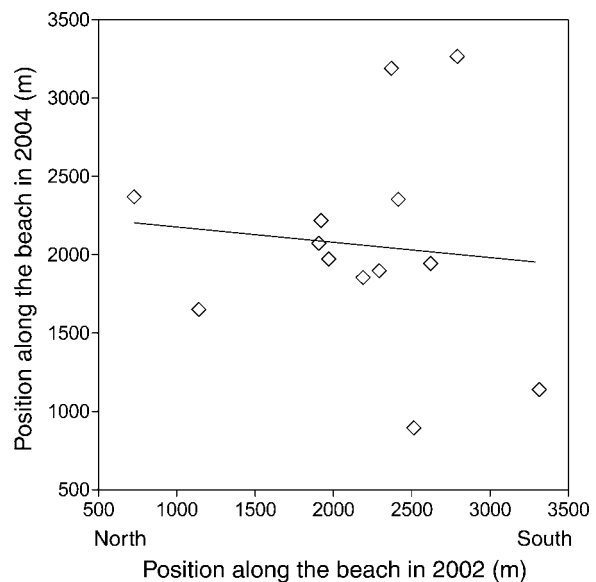


FIG. 3. Linear regression between mean position of nests along the beach for turtles seen nesting in 2002 and 2004 ( $n = 13$  turtles).

Brooks and Endler 2001), although non-heritable factors such as imprinting can also yield high values (e.g., see Boake [1989] and Kamel and Mrosovsky [2005] for more detailed discussions). If most of the variation among females is additive genetic, then repeatability also provides an accurate estimate of heritability (Falconer and Mackay 1996, Brooks 2002). Heritable variation among females in their choice of thermal characteristics of nest sites is an important component in theoretical models of sex ratio evolution in species with temperature-dependent sex determination (TSD; Bulmer and Bull 1982, Bull 1983). These models posit that sex ratio could evolve either through selection on maternal nesting behavior or through selection on the thermal sensitivity of embryonic sexual differentiation (that is, the range of temperatures at which embryos become male or female). Differences in nest site preferences result in differences in nest temperatures among beach microhabitats (Kamel and Mrosovsky 2006) and suggest that maternal nest-site choice may allow for the control of offspring sex ratio. With TSD, the phenotypic sex of the embryos is determined by the incubation temperature of the nest (reviewed in Wibbels 2003). In the case of sea turtles, warm temperatures produce female offspring and cooler temperatures produce males. Recently, Morjan (2003a) used simulations to investigate the influence of these two factors on the evolution of sex ratios in response to climate change in the painted turtle (*Chrysemys picta*). She concluded that embryonic response to temperature would evolve faster than maternal nest site choice. The simulation, however, used a heritability estimate for nest site choice of 0.2 (based on research with the painted turtle; Janzen and Morjan 2001), which is markedly lower than the 0.7 repeatability reported herein for hawksbills.

In conclusion, we have shown that individual preferences for nest microhabitat characteristics are maintained across nesting seasons and that this behavior is polymorphic in this hawksbill population. By taking individual preferences into account rather than regarding members of a population as a uniform group, we hope to provide the impetus for more detailed studies on nest site choice. For example, how widespread are individual nesting preferences and how are they maintained? How variable are individual preferences between populations of the same species nesting in different environments (Morjan 2003b, Ewert et al. 2005)? Is there a correlation between maternal preference and offspring performance and how does it relate to offspring development and survivorship (Wilson 1998, Valenzuela and Janzen 2001, Spencer and Thompson 2003, Lloyd and Martin 2004) and to offspring sex ratio (Schwarz-kopf and Brooks 1987, Shine 1999, Valenzuela and Janzen 2001, Warner and Shine 2005)? Other species, including freshwater turtles, have been studied in these contexts but sea turtles can lay as many as 11 clutches in

a season (e.g., Boulon et al. 1996) and they return to lay repeatedly over many years. These characteristics make them particularly suitable for research focusing on individual variation in maternal behaviors such as nest site choice.

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#### LITERATURE CITED

- Barker, J. S. F., and W. T. Starmer. 1999. Environmental effects and the genetics of oviposition site preference for natural yeast substrates in *Drosophila buzzatii*. *Hereditas* **130**: 145–175.
- Bass, A. L., D. A. Good, K. A. Bjorndal, J. I. Richardson, Z. M. Hillis, J. A. Horrocks, and B. W. Bowen. 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.
- Bjorndal, K. A., and A. Carr. 1989. Variation in clutch size and egg size in the green turtle nesting population at Tortuguero, Costa Rica. *Herpetologica* **45**:181–189.
- Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evolutionary Ecology* **3**:173–182.
- Bossart, J. I., and J. M. Scriber. 1999. Preference variation in the polyphagous tiger swallowtail butterfly (Lepidoptera: Papilionidae). *Environmental Entomology* **28**:628–637.
- Boulon, R. H., P. H. Dutton, and D. L. McDonald. 1996. Leatherback turtles (*Dermochelys coriacea*) on St. Croix, U.S. Virgin Islands: fifteen years of conservation. *Chelonian Conservation and Biology* **2**:141–147.
- Bragg, W. K., J. D. Fawcett, T. B. Bragg, and B. E. Viets. 2000. Nest-site selection in two eublepharid gecko species with temperature-dependent sex determination and one with genotypic sex determination. *Biological Journal of the Linnean Society* **69**:319–332.
- 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., and J. A. Endler. 2001. Female guppies agree to differ: phenotypic and genetic variation in mate-choice behavior and the consequences for sexual selection. *Evolution* **55**:1644–1655.
- Brown, G. P., and R. Shine. 2004. Maternal nest-site choice and offspring fitness in a tropical snake (*Tropidonophis mairii*, Colubridae). *Ecology* **65**:1627–1634.
- Bull, J. J. 1983. Evolution of sex determining mechanisms. Benjamin/Cummings, Menlo Park, California, USA.
- Bull, J. J., W. H. N. Gutzke, and M. G. Bulmer. 1988. Nest choice in a captive lizard with temperature-dependent sex determination. *Journal of Evolutionary Biology* **2**:177–184.
- Bulmer, M. G., and J. J. Bull. 1982. Models of polygenic sex determination and sex ratio control. *Evolution* **36**:13–26.
- Carr, A., and M. H. Carr. 1972. Site fixity in the Caribbean green turtle. *Ecology* **53**:425–429.
- Clifford, L. D., and D. J. Anderson. 2001. Food limitation explains most clutch size variation in the Nazca booby. *Journal of Animal Ecology* **70**:539–545.

- Ewert, M. A., J. W. Lang, and C. E. Nelson. 2005. Geographic variation in the pattern of temperature-dependent sex determination in the American snapping turtle (*Chelydra serpentina*). *Journal of Zoology London* **265**:81–95.
- Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. Fourth edition. Longman, New York, New York, USA.
- Fernandez, G. J., and J. C. Rebores. 2002. Nest-site selection by male Greater Rheas. *Journal of Field Ornithology* **73**:166–173.
- Forstmeier, W., and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* **104**:487–499.
- Hays, G. C., A. Mackay, C. R. Adams, J. A. Mortimer, J. R. Speakman, and M. Boerema. 1995. Nest-site selection by sea turtles. *Journal of the Marine Biological Association of the UK* **75**:667–674.
- Hays, G. C., and J. R. Speakman. 1993. Nest placement by loggerhead turtles, *Caretta caretta*. *Animal Behaviour* **45**:47–53.
- Janzen, F. J., and C. L. Morjan. 2001. Repeatability of microenvironment-specific nesting behaviour in a turtle with environmental sex determination. *Animal Behaviour* **62**:73–82.
- Kamel, S. J., and N. Mrosovsky. 2004. Nest site selection in leatherbacks, *Dermochelys coriacea*: individual patterns and their consequences. *Animal Behaviour* **68**:357–366.
- Kamel, S. J., and N. Mrosovsky. 2005. Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences. *Animal Behaviour* **70**:819–828.
- Kamel, S. J., and N. Mrosovsky. 2006. Deforestation: risk of sex ratio distortion in hawksbill sea turtles. *Ecological Applications* **16**:923–931.
- Kolbe, J. J., and F. J. Janzen. 2001. The influence of propagule size and maternal nest-site selection on survival and behaviour of neonate turtles. *Functional Ecology* **15**:772–781.
- Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**:116–121.
- Lloyd, J. D., and T. E. Martin. 2004. Nest-site preference and maternal effects on offspring growth. *Behavioral Ecology* **15**:816–823.
- Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology* **81**:2892–2901.
- Morjan, C. L. 2003a. How rapidly can maternal behavior affecting primary sex ratio evolve in a reptile with environmental sex determination? *American Naturalist* **162**:205–219.
- Morjan, C. L. 2003b. Variation in nesting patterns affecting nest temperatures in two populations of painted turtles (*Chrysemys picta*) with temperature-dependent sex determination. *Behavioral Ecology and Sociobiology* **53**:254–261.
- Morris, M. R., P. F. Nicoletto, and E. Hesselman. 2003. A polymorphism in female preference for a polymorphic male trait in the swordtail fish *Xiphophorus cortezi*. *Animal Behaviour* **65**:45–52.
- Mrosovsky, N., and J. Provancha. 1992. Sex ratio of hatchling loggerhead sea turtles—data and estimates from a 5-year study. *Canadian Journal of Zoology* **70**:530–538.
- Nordmoe, E. D., A. E. Sieg, P. R. Sotherland, J. R. Spotila, F. V. Paladino, and R. D. Reina. 2004. Nest site fidelity of leatherback turtles at Playa Grande, Costa Rica. *Animal Behaviour* **68**:387–394.
- Richardson, J. I., R. Bell, and T. H. Richardson. 1999. Population ecology and demographic implications drawn from an 11-year study of nesting hawksbill turtles, *Eretmochelys imbricata*, at Jumby Bay, Long Island, Antigua, West Indies. *Chelonian Conservation and Biology* **3**:244–250.
- Roitberg, B. D. 1998. Oviposition decisions as maternal effects. Pages 67–79 in T. A. Mousseau and C. W. Fox, editors. *Maternal effects as adaptations*. Oxford University Press, New York, New York, USA.
- Roosenburg, W. M. 1996. Maternal condition and nest site choice: An alternative for the maintenance of environmental sex determination? *American Zoologist* **36**:157–168.
- Schwarzkopf, L., and R. J. Brooks. 1987. Nest-site selection and offspring sex ratio in painted turtles, *Chrysemys picta*. *Copeia* **1**:53–61.
- Sezer, M., and R. K. Butlin. 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.
- Shine, R. 1999. Why is sex determined by nest temperature in many reptiles? *Trends in Ecology and Evolution* **14**:186–189.
- Shine, R., and P. S. Harlow. 1996. Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology* **77**:1808–1817.
- Shine, R., T. Madsen, M. Elphick, and P. S. Harlow. 1997. The influence of nest temperatures and maternal thermogenesis on hatchling phenotypes of water pythons. *Ecology* **78**:1713–1721.
- Singer, M. C., D. Ng, and C. D. Thomas. 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* **42**:977–985.
- Spencer, R. J., and M. B. Thompson. 2003. The significance of predation in nest site selection of turtles: an experimental consideration of macro- and microhabitat preferences. *Oikos* **102**:592–600.
- Tiwari, M., K. A. Bjørndal, A. B. Bolten, and B. M. Bolker. 2005. Intraspecific application of the mid-domain effect model: spatial and temporal nest distributions of green turtles, *Chelonia mydas*, at Tortuguero, Costa Rica. *Ecology Letters* **8**:918–924.
- Valenzuela, N., and F. J. Janzen. 2001. Nest-site philopatry and the evolution of temperature-dependent sex determination. *Evolutionary Ecology Research* **3**:779–794.
- Warner, D. A., and R. Shine. 2005. The adaptive significance of temperature-dependent sex determination: experimental tests with a short-lived lizard. *Evolution* **59**:2209–2221.
- Wibbels, T. 2003. Critical approaches to sex determination in sea turtles. Pages 103–134 in P. L. Lutz, J. A. Musick, and J. Wyneken, editors. *The biology of sea turtles*. Volume II. CRC Press, Boca Raton, Florida, USA.
- Wilson, D. S. 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* **79**:1884–1892.