Intra-annual Loggerhead and Green Turtle Spatial Nesting Patterns

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Abstract - We analyzed a 15-year (1989–2003) dataset of spatial nesting locations for Loggerhead and Green Turtles along a 40.5-km stretch of beach encompassing the Archie Carr National Wildlife Refuge along the Atlantic coast of Florida. To assess whether there are differences in spatial distribution influenced by temporal site-selection cues, we divided each season into quartiles and analyzed the autocorrelative patterns of the nest distributions within each time frame. Fundamentally, intraspecific differences in nest spatial patterns from the beginning to the end of the nesting season were minor. Though the temporal grain of the analyses may not be able to discern affects of fine-scale fluctuations (e.g., high- and low-tide events), these results suggest that environmental variables that change over the nesting season (e.g., ocean temperatures, daylength, and existing human activities) are not significantly influencing where these sea turtles place their nests.

Introduction

After oviposition, female sea turtles abandon their nests. Hence, in the absence of parental care, the location of the nest is a critical determinant of egg survivorship. Not surprisingly, nest-site selection is non-random and somewhat predictable (Tiwari et al. 2005, Weishampel et al. 2003). The drivers of this behavior, the extent to which they are genetically hardwired or influenced by the environment, are unknown. Sea turtles are renowned for natal homing that enables them with a high degree of accuracy to return to the general region of their birth (Bowen 1995, Carr and Carr 1972, Miller 1997). Displacement studies have shown that juvenile *Caretta caretta* Linnaeus (Loggerheads) (Avens et al. 2003) and *Chelonia mydas* Linnaeus (Green Turtles) (Lohmann et al. 2004) reorient themselves towards their capture site. This compassing ability has been attributed, in part, to geomagnetic and visual cues (Avens and Lohmann 2003). Additional environmental factors that may affect fine-scale migratory behaviors, such as those which relate to nest-site selection, include marine (such as coastal landmarks, currents, chemical gradients, and low-frequency sound; e.g., Carr 1972; Hughes 1974; Lohmann and Lohmann 1993, 1996; Marcovaldi and Laurent 1996; Mortimer 1995) and terrestrial (such as beach slope, presence of vegetation, sand texture, and artificial lighting; e.g., Kamel and Mrosovsky 2004, 2005; Kikukawa et al. 1996; Provancha and Ehrhart 1987; Salmon et al. 1995; Whitmore and Dutton 1985; Witherington 1992) properties.

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The coastline of east-central Florida is home to the highest concentration of nesting, threatened Loggerhead Turtles in the western hemisphere (Ehrhart and Raymond 1983), representing ≈ 25% of all Loggerhead Turtle nests worldwide (US Fish and Wildlife Service 2006). These beaches also have the highest concentration of nesting, endangered Green Turtles in the continental United States (Ehrhart and Raymond 1987), representing ≈ 35% of US Green Turtle nests (US Fish and Wildlife Service 2006). Our previous study on this beach (Weishampel et al. 2003) documented the high level of spatial consistency in inter-annual nesting behaviors of Loggerhead and Green Turtles. However, the fact that Loggerhead nesting has been occurring earlier in the nesting season by about 10 days over the last 15 years (Pike et al.2006, Weishampel et al. 2004) suggests that some behaviors may be more plastic. Here, we assess their intra-annual spatial patterns. These analyses relate to the question of whether or not environmental parameters that change within nesting seasons—such as lunar cycles, day length, storm events, human activities, etc.—alter the spatial patterns of nest-site selection (Fig. 1); however, they do not explicitly test for such environmental influences.
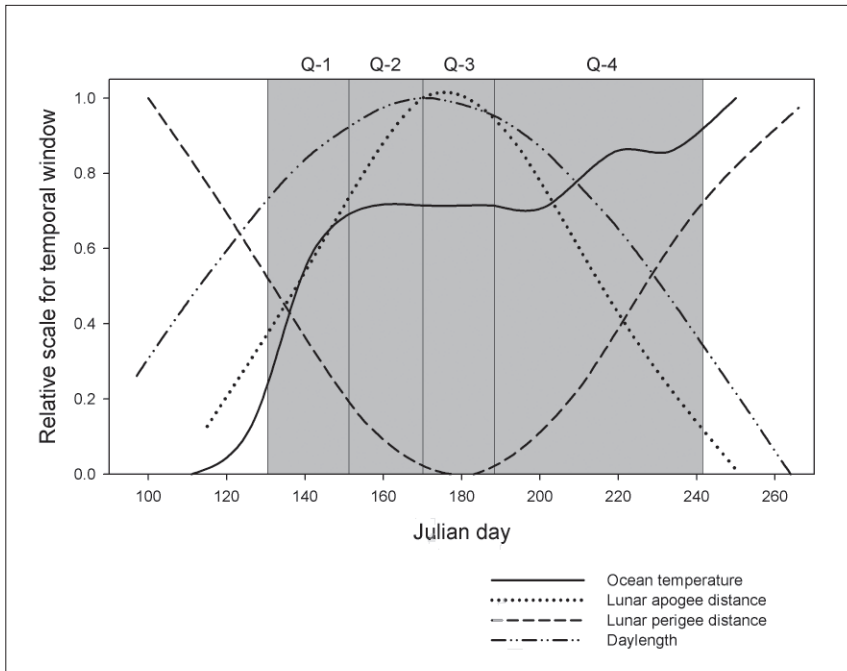

Figure 1. Examples of environmental parameters which vary over a nesting season that could potentially influence spatial nesting patterns. These were scaled to represent the maximum and minimum values for the measurement period. Ocean temperatures were long-term averages off the Melbourne, FL coast. The lunar and solar properties were calculated for 2002. The grey panels reflect the extent of the Loggerhead nesting quartiles for 2002.

Methods

Nesting data collection

The study area is a stretch of beach along a barrier island on the east coast of Florida south of Cape Canaveral. This 40.5-km of coastline was divided into eighty-one 0.5-km sections. The southern 21 km includes the Archie Carr National Wildlife Refuge extending from Sebastian Inlet to Melbourne Beach. Human density and commercial development increases towards the northern boundary, which extends to the Patrick Air Force Base. Following the Index Nesting Beach Survey (INBS) protocols from the Florida Fish and Wildlife Conservation Commission (Witherington and Koeppel 2000), all sea turtle nesting events within each 0.5-km section were counted daily in dawn surveys from 1989–2003. Species were identified from track characteristics. These surveys typically extend from the beginning of May until the end of August. Because of discrepancies in the initiation and duration of the surveys, we examined a window (10 May–30 August) that represented a consistent sampling effort and the majority (98.1% for Loggerheads, 95.8% for Green Turtles) of recorded annual nesting events (Weishampel et al. 2004).

Spatio-temporal data analyses

Within the 113-day window, the nesting season for each species was arbitrarily divided into quartiles based on nest numbers. This breaks the nesting season into smaller time frames, where presumably there are different environmental factors, and eliminates the influence of nest number. Though other quantile divisions could have been used, it was thought that quartiles would provide a sufficient number of nests distributed across the 81 beach sections for comparison. This is especially important for the analysis of Green Turtle nests, which tend to have very low densities in the northern end of the study area. To determine whether or not spatial nesting patterns differed among quartiles, Pearson correlation coefficients were calculated for the average number of nests in a given 0.5-section. To further assess spatial patterns over the nesting season and to test for statistical differences, we calculated autocorrelation values across a range of lag distances using semivariance (Dale et al. 2002) for each quartile for each year. Semivariograms, which are plots of semivariance (γ) against lag distances (d), where x is the number of nests at location i and n is the total number of sample pairs for a given lag, were produced to visualize spatial patterns using the equation:

$$\gamma(d) = \frac{1}{2n} \sum_i (x_i - x_{i+d})^2$$

The resulting semivariogram plots are characterized by three values termed sill, range, and nugget. The sill is the value where the semivariance levels off, depicting the amount of variance. The range is the distance at which the levelling occurs, depicting the scale of autocorrelation. The nugget is the

semivariance at a lag distance of 0, depicting the variance below the sampling resolution, i.e., 0.5 km. For each quartile, the resulting semivariograms were fitted to standard models to estimate the three descriptors using GS+ software (Gamma Design 2005). The values for each quartile for the two species over the 15-year period were compared using an ANOVA approach. Though the coastline from end to end of the study area is not perfectly straight, we treated the 40.5-km area and the 0.5-km sections as though they comprised a linear transect.

Results

The nest tallies from the annual surveys within the 10 May–August 30 window are shown in Figure 2. Green Turtle nesting is characterized by annual high-low fluctuations in nest number (Hughes 1995, Weishampel et al. 2003). The difference in the timing of nesting is depicted in Figure 3.
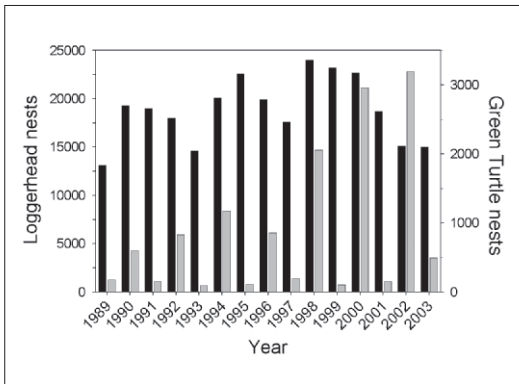

Figure 2. Loggerhead (black) and Green Turtle (grey) nest counts from the study area within the 10-May to 30-August window.
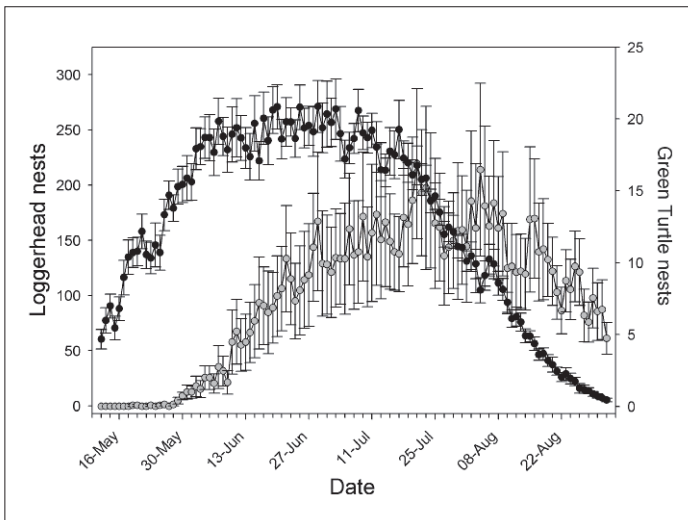

Figure 3. Average daily numbers of Loggerhead (black) and Green Turtle (grey) nests between 10-May and 30-August from 1989 to 2003. Extension bars are measures of standard error.

Loggerhead nesting along this beach peaks in mid- to late June whereas Green Turtle nesting peaks in mid- to late July. There is substantially more variation around the daily nest numbers in Green Turtles, which reflects the biennial pattern of nest numbers. The shape of the nesting distributions within this window is further quantified by the average number of days representing each quartile over this 15-year period (Fig. 4). The daily nesting patterns of Loggerheads has a rapid rise and slow decline towards the end of the season where the Green Turtle has a slow rise and a rapid decline. However, Loggerhead and Green Turtles have been found to nest sporadically before May 10 and after August 30, respectively, which may yield more of a beginning and ending tail for each species. Though the timing of nesting is different, the two species generally show similar spatial patterns of annual nest distribution (Weishampel et al. 2003); there are significantly more nests in the southern half of the study area than the more human-impacted northern half (Fig. 5). Furthermore, these intraspecific patterns are

Figure 4. Average number of days included in each quartile (Q) from 1989 to 2003 for Loggerhead (black) and Green Turtle (grey) nests. Extension bars are measures of standard deviation.
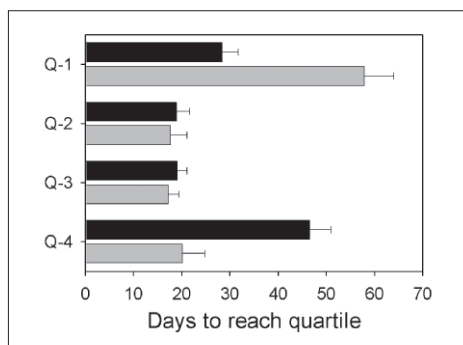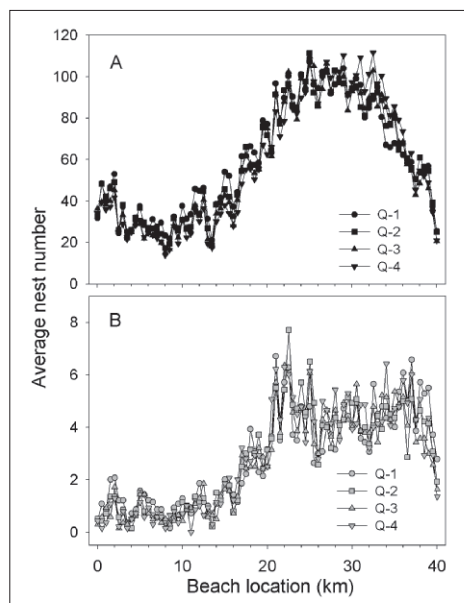

Figure 5. Spatial distribution of average nest number for (A) Loggerhead and (B) Green Turtles along the 40.5-km coastline from north to south for seasonal quartiles from 1989 to 2003.

significantly correlated ($P < 0.01$) from quartile to quartile (Table 1). This is mirrored by the similar intraspecific semivariograms for each quartile (Fig. 6). The general autocorrelation patterns for both species are representative of those found with a gradient response. However, Loggerhead semivariograms were best modeled using a spherical model (average $R^2 = 0.98$), whereas Green Turtle semivariograms were best modeled using an exponential model (average $R^2 = 0.63$). Given the discrepancy in number of nests for the two species, it is not surprising that the sill and nugget values differ (Table 2). The ranges, which represent the scale of autocorrelation, also differ with Loggerheads having smaller ranges by about 20 m. When comparing within species, only the nugget values differed significantly for Loggerheads for first and fourth quartiles; otherwise, the spatial patterns were not significantly different. The higher nugget value suggests that there is more spatial structure below the sampling scale in the first quartile than the fourth quartile.

Table 1. Pearson correlation coefficients for nest number from 1989 to 2003 averaged for each 0.5-km beach segment for a given nesting-season quartile (Q). The lower left and upper right correlations correspond to Loggerhead and Green Turtle nest numbers along the 40.5-km beach, respectively. All correlations are significant at the $P < 0.01$ level.

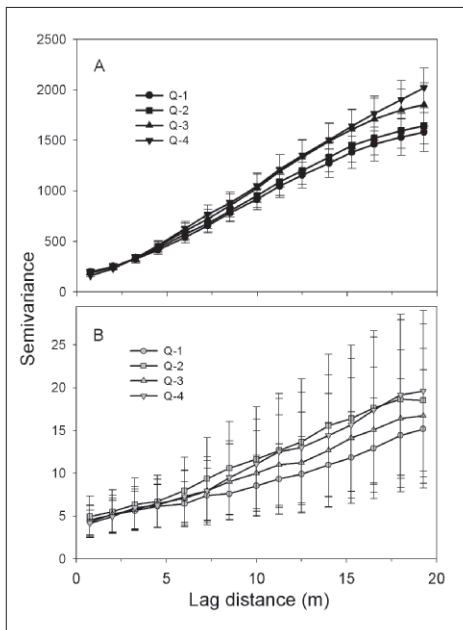|	Q-1	Q-2	Q-3	Q-4
Q-1	1.00	0.91	0.91	0.90
Q-2	0.99	1.00	0.95	0.94
Q-3	0.98	0.99	1.00	0.95
Q-4	0.96	0.98	0.98	1.00

Figure 6. Average semivariograms for (A) Loggerhead and (B) Green Turtle nests for each intra-seasonal quartile across the 1989–2003 period. Extensions are measures of standard error.

Discussion

Though there were significant annual fluctuations in the numbers of Loggerhead and Green Turtle nests, there were little discernible intraspecific spatial differences in the within-season nesting patterns on this important stretch of beach, as was also found by Tiwari et al. (2005) with Green Turtles in Tortuguero, Costa Rica. Thus, it is probable that early season nesters follow similar cues as mid- and late season nesters. This suggests there is no temporal trend to reduce competition for nests sites. However, this lack of difference could reflect the relatively coarse temporal scale of analysis, i.e., quartiles ranged from ≈ 20 to ≈ 60 days. Perhaps a finer division of the nesting season may yield spatial differences associated with finer scale environmental fluctuations. Additionally, the degree of spatial similarity may reflect multiple nesting events by the same female within a season, but over two or three quartiles. Multiple nesting events of Loggerheads have been observed to be confined within 4.8 km on North Carolina beaches (Webster and Cook 2001), well below the ≈ 30 km range found in the semivariogram. Also, multiple nesting events of Green Turtles on these central Florida beaches occur within 1.7 km on average (Johnson and Ehrhart 1996). The fact that there is autocorrelation for both species may be important when making comparative, statistical observations of nest differences (e.g., survivorship, predation) along this beach.

Knowledge about the intra-annual spatial patterns of nesting could have implications regarding egg-survival estimates associated with inundation due to sea-level rise (Fish et al. 2005) or erosion due to storms (Smith and Trembanis 2001). Because the spatial nesting patterns are consistent throughout the season, mortality estimates after localized flooding would be fairly straightforward. If the goal of beach management is maintaining nest numbers, these findings suggest that strategies (Garcia et al. 2003) that restrict beach use or reduce nest predation may be able to focus on high nesting areas throughout the egg-laying season.

Table 2. Average semivariance descriptors for Loggerhead and Green Turtle species for each quartile over the 15-year period. Standard errors are in parentheses. Intraspecific values with different superscripts are significantly different ($P < 0.05$) based on a Tukey-Kramer post hoc analysis.

	Loggerhead				Green Turtle			
	R^2	Sill	Range	Nugget	R^2	Sill	Range	Nugget
Q-1	0.98	1983.3	30.8	47.3[A]	0.55	19.9	46.2	2.8
	(0.0)	(259.8)	(2.0)	(14.8)	(0.1)	(8.9)	(14.8)	(1.1)
Q-2	0.98	2010.3	30.4	36.4[A,B]	0.70	26.1	54.4	2.6
	(0.0)	(218.5)	(1.8)	(2.5)	(0.1)	(13.4)	(13.9)	(1.3)
Q-3	0.98	2355.3	33.9	17.4[A,B]	0.67	28.3	52.4	2.7
	(0.0)	(222.7)	(2.3)	(8.4)	(0.1)	(16.3)	(12.5)	(1.1)
Q-4	0.98	2392.8	31.8	4.8[B]	0.58	30.4	56.6	1.9
	(0.0)	(223.0)	(1.6)	(1.8)	(0.1)	(15.8)	(14.7)	(0.6)

However, if the management goal is more appropriately designed to pro-
mote overall biodiversity, it is recommended that strategies cover a wider
region of the beach which potentially may maintain genetic variation
(Encalada et al. 1999) and demographic diversity (i.e., sex ratios) as a
result of different thermal regimes (Baptistotte et al. 1999).

Acknowledgments

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