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Spatiotemporal patterns of annual sea turtle nesting behaviors along an East Central Florida beach

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Abstract

The Florida coastline from Melbourne Beach to Wabasso Beach is one the most important nesting areas for loggerhead turtles (*Caretta caretta*) in the Western Hemisphere and for green turtles (*Chelonia mydas*) in the United States. In this study, we quantified the spatial patterns of numerous loggerhead ($N \approx 400{,}000$) and green turtle ($N \approx 14{,}000$) and less numerous ($N \approx 100$) leatherback (*Dermochelys coriacea*) beach ascents from 1989–1999 in terms of their autocorrelative properties along 40.5 km within this critical reproductive zone. Nesting and non-nesting emergence patterns of loggerhead and green turtles were non-random, favoring the southern half of the study area. Perhaps due to low numbers or differences in nesting behavior, leatherback nest distributions were not significantly different from random. Loggerhead and green turtle nest locations exhibited similar clinal patterns. They were positively autocorrelated at distances less than 10 km and negatively at distances greater than 30 km. These patterns were significantly correlated interannually.

Keywords: Archie Carr National Wildlife Refuge; Autocorrelation; Green turtle; Leatherback; Loggerhead; Moran's I; Nesting behavior

1. Introduction

Reproducing in predictable sites, which previously have proven successful, is an evolutionary stable strategy (Switzer, 1993; Schjørring et al., 2000). Though evidence from tag returns (Meylan, 1995) is somewhat scanty and the application of satellite telemetry (e.g. Hughes et al., 1998; Cheng, 2000; Nichols et al., 2000) is in its infancy, it is generally accepted that sea turtles possess a high degree of accuracy in returning to previous nesting grounds (Carr and Carr, 1972;Carr, 1975) as well as the general region of their birth (Miller, 1997). This natal homing has been supported by molecular genetic studies (Bowen, 1995). Whether navigation cues are learned as hatchlings or as adults is unknown. Thus, present nesting patterns may reflect conditions from past decades such as river flood events that inundated nesting areas or periods of harvesting (Bjorndal et al., 1999). Moreover, if site fidelity persists from generation to generation, present nesting patterns may reflect conditions from past centuries.

Why turtles choose to nest on some beaches and not others is speculative (Van Meter, 1992). Hypotheses for ecological spatial patterns are usually linked to the distribution of resources or other critical features (Koenig, 1999). For sea turtles, potential marine factors include: olfactory cues (Carr, 1972), low-frequency sound such as surf noise, magnetic fields (Lohmann and Lohmann, 1993, 1996), characteristics of offshore currents, the presence of offshore reefs and rocks (Hughes, 1974; Mortimer, 1995; Marcovaldi and Laurent, 1996), and mortality from shrimp trawling (Talbert et al., 1980; McDaniel et al., 2000). Potential terrestrial factors include: beach slope and width (Provancha and Ehrhart 1987; Kikukawa et al., 1996), sand texture, dune vegetation (Whitmore and Dutton, 1985), interspecific competition (Mortimer, 1995), predation (Shoop et al., 1985), artificial lighting (Witherington, 1992; Salmon et al., 1995), and human activities (Kikukawa et al., 1999) such as beach nourishment (Crain et al., 1995; Steinitz et al., 1998; Davis et al., 1999) or other protection methods (Bouchard et al., 1998). Furthermore, it has been suggested that there is a positive feedback between

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sea turtles and the nesting beach dunes (Bouchard and Bjorndal, 2000), i.e. nesting introduces nutrients to these depauperate beach systems that helps maintain stability of the highly dynamic dune habitat that in return promotes nesting.

During the nesting season, most gravid sea turtles nest at least twice, although individuals of some species may nest only once and others more than ten times. Rarely some turtles nest hundreds of kilometers away from their initial nest site in a season (Stoneburner and Ehrhart, 1981); most renest within a 0–5 km vicinity (Carr and Carr, 1972; Miller, 1997). Often females laden with eggs emerge from the surf, but for unknown reasons decide not to nest. This aborted nesting termed somewhat inaccurately (Miller, 1997) a ''false crawl'' (Stoneburner and Richardson, 1981) can happen without explanation or be caused by artificial lighting or activity of people on the beach, e.g. the presence of turtle watch groups has been shown to alter crawling trajectories associated with nesting (Johnson et al., 1996). Other possibilities for these aborted nesting attempts (as reported for loggerhead turtles by Dodd, 1988) include differences in beach substrate caused by restoration (Raymond, 1984) or inclement weather (Hughes et al., 1967). However, in Queensland, Australia, loggerhead turtles have shown not to exhibit the aborted nesting behavior (Limpus, 1985). After an aborted attempt, most turtles typically return to the same beach or area where they first emerged the same or the subsequent night (Miller, 1997).

In selecting a nesting site, sea turtles seem to exhibit coarse and fine grain behaviors as defined by Carr (1975). There is a coarse-scale, regional homing ability termed ''philopatry'' and a fine-scale ability termed site ''fixity'' or ''tenacity'' to locate a particular beach near where they emerged previously. Perhaps there is even a finer-scale behavior related to microsite conditions, e.g. sand temperature or presence of vegetation on dunes, which determines the final nest-site choice (Stoneburner and Richardson, 1981; Wood and Bjorndal, 2000). Expanding on the general findings of the Carr and Carr (1972) Tortuguero study of green turtle nesting, we quantified the annual fine-scale spatial patterns of nesting and non-nesting emergences for three threatened or endangered species from 1989–1999 in terms of their autocorrelative properties. The spatial grain and temporal consistency of their behaviors were compared. Such spatial analyses are of basic importance to conservation efforts (Koenig, 1999). They allow for an interpretation of scales of behavioral patterns in relation to environmental parameters and processes (Levin, 1992; Ranta et al., 2000) that can be critical for developing monitoring or management principles that may help regulate human activities (Arianoutsou, 1988) or guide land acquisition for reserves.

2. Methods

2.1. Study site

The study area is a 40.5-km stretch of beach along a barrier island complex on the east coast of Florida, USA (Fig. 1). This coastline was mapped into 81, 0.5-km sections. The study area in Archie Carr National Wildlife Refuge, which was designated in 1989, constitutes the southern 21.0-km region from Sebastian Inlet to Melbourne Beach. The Central Brevard study area consists of the remaining 19.5-km stretch that extends northward from Melbourne Beach to the southern boundary of Patrick Air Force Base. Human density and commercial development are higher towards the northern end of the study area. Together these beaches attract more nesting, threatened loggerhead turtles (*Caretta caretta*) than anyplace else in the western hemisphere (Ehrhart and Raymond, 1983); an estimated 25% of all loggerhead turtles in the USA nest here (US Fish and Wildlife Service, 2001). Also, these beaches attract more nesting, endangered green turtles (*Chelonia mydas*) than anyplace in the continental United States (Ehrhart and Raymond, 1987); an estimated 35% of US green turtles nest here (US Fish and Wildlife Service, 2001). Furthermore, these beaches occasionally provide nesting areas for endangered leatherback turtles (*Dermochelys coriacea*).

2.2. Emergence behavior monitoring

All nesting and non-nesting (i.e. false crawl) marine turtle emergences from the ocean to the shore were tallied daily and identified to species based on track characteristics from May through August in dawn surveys from 1989 to 1997. In 1998 and 1999, surveys began in April and ran through August. Methods conform to the Florida Fish and Wildlife Conservation Commission Index Nesting Beach Survey (INBS) Program established in 1989 (see description by Witherington and Koeppel, 2000). Although numerous studies have focused on the spatial distribution of nests perpendicular to the ocean (e.g. Mrosovsky, 1983; Whitmore and Dutton, 1985; Bjorndal and Bolten, 1992; Hays and Speakman, 1993; Hays et al., 1995; Wang and Cheng, 1999; Wood and Bjorndal, 2000), here we considered the annual distribution patterns along the beach in regions parallel to the ocean in a similar fashion as Eckert (1987) and Steyermark et al. (1996) did for leatherbacks.

2.3. Spatiotemporal data analyses

Autocorrelation analysis was run to determine whether the observed nesting and non-nesting emergences at one location were significantly correlated to similar emergences at other sampling locations within the 40.5

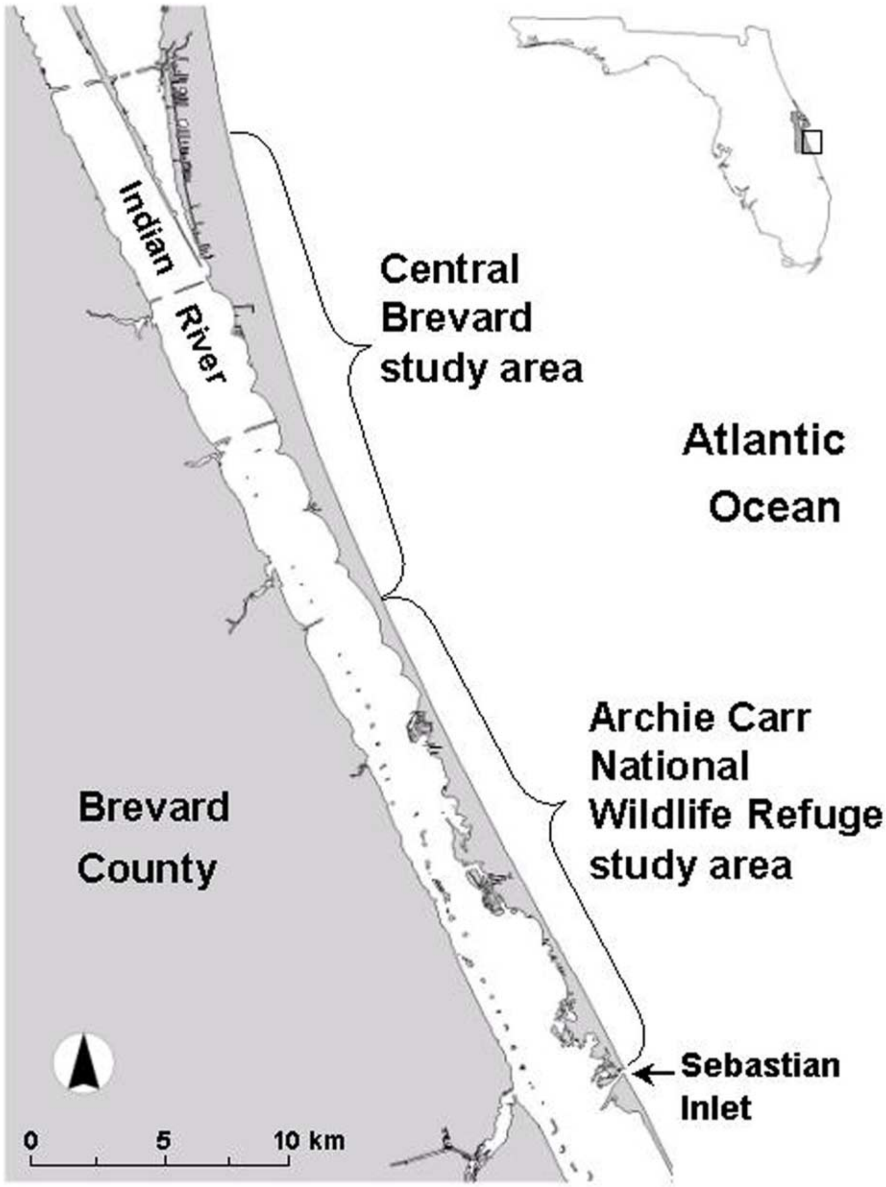

Fig. 1. Location of 40.5-km stretch of beach surveyed in this study. Brevard County, Florida is represented by the gray area.

km study area. To accomplish this, we used Moran's I (Griffith, 1988), a weighted product–moment correlation coefficient. Moran's I behaves like Pearson's correlation coefficient typically ranging between −1 and +1 (Legendre and Fortin, 1989). This measure (I) for a given distance interval (d) corresponds to:

$$I(d) = \frac{\sum_i \sum_j w_{ij}(x_i - \bar{x})(x_j - \bar{x})}{W \sum_i (x_i - \bar{x})^2}$$

where x represents the value of interest (e.g. number of emergences), $w_{ij} = 1$ when the distance between the pair of points corresponds to d, otherwise $w_{ij} = 0$, and W is the number of pairs being compared. Though the beach from one end of the study area to the other is curved as seen in Fig. 1, we treated the 40.5-km area and the 0.5-km sections as though they comprised a linear transect.

Correlograms that depict the coefficients as a function of a range of lag distance between pairs of localities were used to summarize the patterns of geographic variability (Sokal and Oden, 1978a). To determine how spatial autocorrelation patterns differ from those with random distributions, the emergence values for each 0.5-km section were randomly permuted and reanalyzed 100 times. The maximum and minimum autocorrelation values provided 99% confidence envelopes for these values for a given lag distance. Additionally, to compare inter-annual variation in nest distribution within a species, intra-annual variation in nest distribution between species, and the inter-annual relationship between nesting and non-nesting emergences, we used the non-parametric Spearman's correlation coefficient.

3. Results

3.1. Annual emergences

The annual surveys of the relative abundances of the three sea turtle species nesting emergences are shown in Fig. 2. Over this 11-year period, the average number of nests per kilometer per year along the surveyed area was ≈480 for loggerheads, ≈15 for green turtles, and ≈0.2 for leatherbacks. The latter half of the survey showed higher nest numbers of the three species. Also noticeable was the biennial (i.e. high one year and low the next year) pattern of nesting found in green turtles noted elsewhere (Hughes, 1995). These patterns hold true for the non-nesting emergences of the loggerhead and green turtles. During this survey period, there were only two leatherback non-nesting emergences documented; both occurred in 1992. Hence, because of the low numbers, they were not considered in the analyses. Annually, for both loggerhead (0.86:1) and green turtle (1.08:1), the frequency of non-nesting and nesting emergences was nearly equivalent, i.e. 1:1 (Fig. 3). Only for green turtles during the record high year (1998) was there substantially more non-nesting than nesting events (1.35:1).

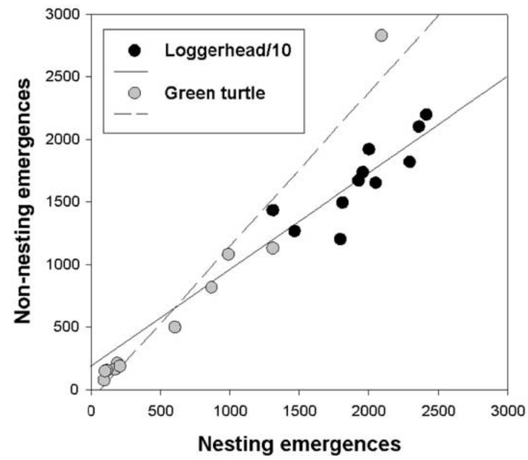

Fig. 3. Correlation of nesting to non-nesting emergence behavior. Note that the emergence numbers for loggerhead turtles are divided by 10.

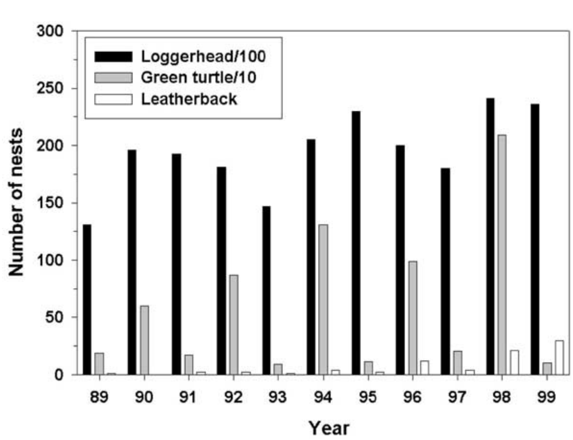

Fig. 2. Sea turtle nest counts from May–August beach surveys from 1989–1999. April surveys were included in 1998 and 1999. Note that the numbers of loggerhead and green turtle nests were divided by 100 and 10, respectively.

3.2. Spatial patterns of emergences

The average annual spatial locations of loggerhead and green turtle and to a certain extent leatherback turtle nests were concentrated in the southern portion of the 40.5-km stretch, the Carr Refuge Study Area (Fig. 4). There was a decline towards the Sebastian Inlet at the extreme southern end. These spatial patterns were consistent for the non-nesting emergence data. The change in survey commencement in 1998 was designed to improve leatherback monitoring, as they tend to emerge earlier in the spring than the other two species. Though increasing the number of recorded leatherback emergences, this change did not have an effect on the spatial patterns observed for the other species. Autocorrelation patterns up to a lag distance of 20 km followed a non-random gradient behavior (Turner et al., 1991) for loggerhead and green turtle nests (Fig. 5). Loggerhead nest numbers were significantly positively and negatively autocorrelated at distances of <8 and >13 km, respectively. The gradient for green turtle nests was not as steep. Green turtle nests were significantly positively and negatively autocorrelated at distances of <5 and >18 km, respectively. Though displaying an increase in negative autocorrelation with increasing distance, leatherback nests fell within the random envelopes. The spatial distributions of nests and non-nesting emergences were significantly correlated each year for loggerhead and green turtles (Fig. 6) although the correlations of green behavior mirrored the up and down every other year pattern. Thus, it is not surprising that the autocorrelation patterns for the non-nesting emergences for loggerhead and green turtles were nearly identical to nesting emergences (Fig. 5).

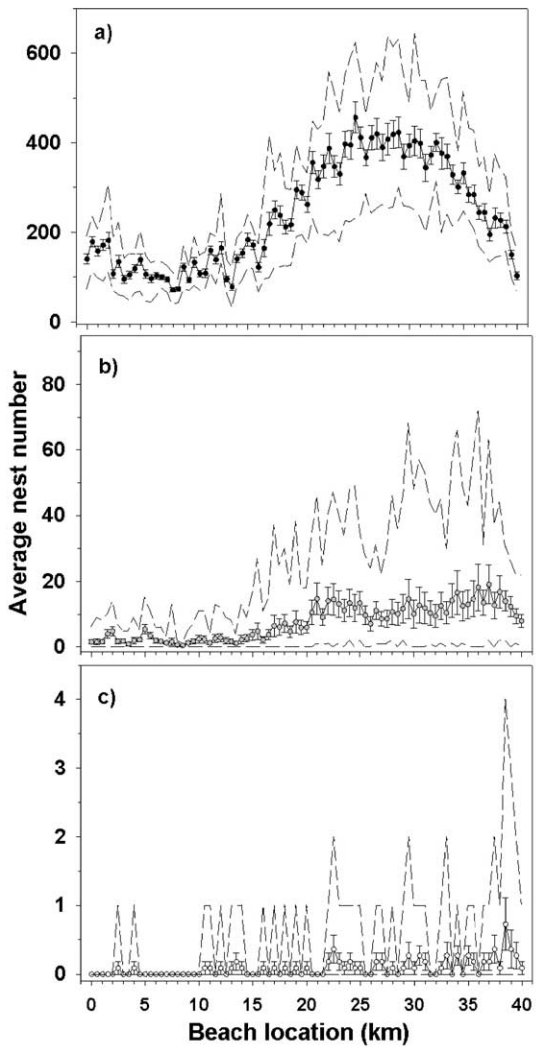

Fig. 4. Spatial distribution of average number of (a) loggerhead, (b) green, and (c) leatherback turtle nests along the 40.5-km beach (0 is the north end). Extensions above and below circles are ±1 standard error. Dashed lines are maximum and minimum values.

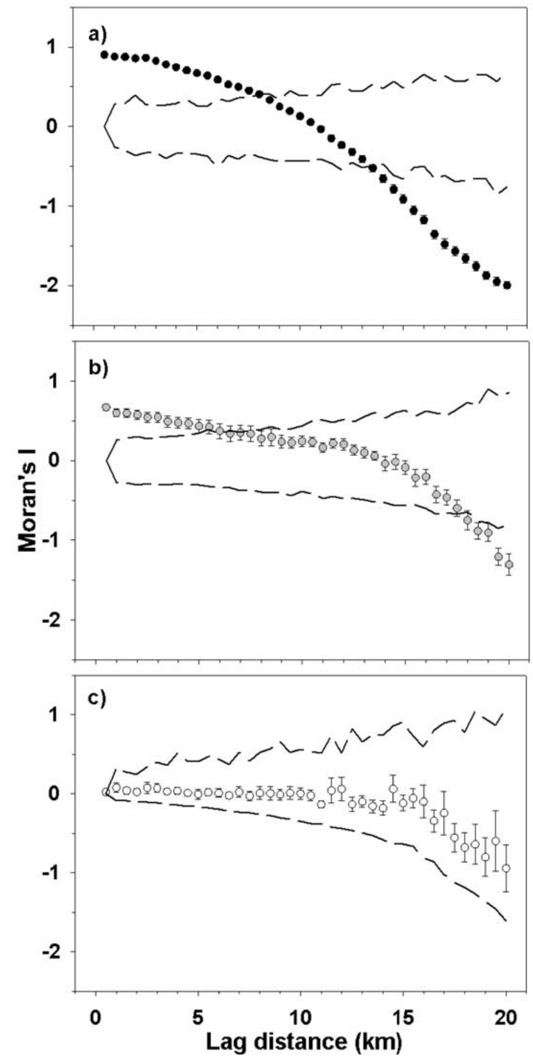

Fig. 5. Average Moran's I values of (a) loggerhead, (b) green, and (c) leatherback turtle nests from 1989–1999. Extensions above and below circles are ±1 standard error. Dashed lines are random confidence envelopes ($P<0.01$).

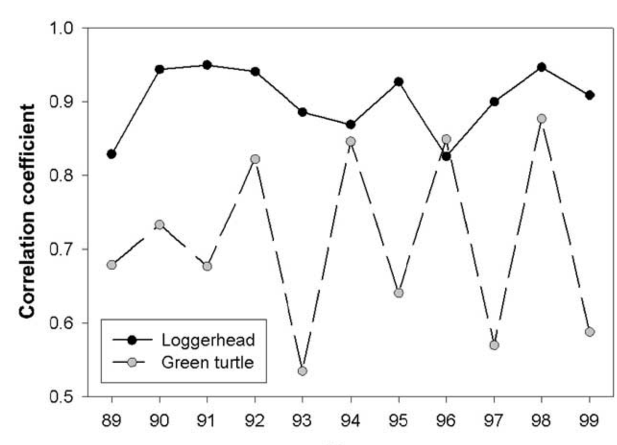

Fig. 6. Annual Spearman's Rho correlation coefficients between nest and non-nesting emergence numbers for a given 0.5-km section along the study area. All correlations are significant ($P<0.01$).

3.3. Interspecific and interannual correlations

In terms of interannual, intraspecific relationships, both distributions of loggerhead and green turtle nests were significantly correlated for all years (Table 1). Correlation values for the loggerheads (average Spearman's coefficient = 0.90) were higher ($P<.001$) than green turtles (0.61). This may be explained in part by the two-year nesting cycle observed in the green turtles (Fig. 2) which also relates to the higher standard errors (Fig. 5) than found with loggerhead nest patterns. Though there were several significant interannual correlations among leatherback nesting patterns prior to lengthening the survey period in 1998, most patterns were spatially unrelated. Significant correlations were found between interspecific nest locations (Fig. 7). Each year the spatial patterns of loggerhead and green turtle nests were significantly, positively correlated. The spatial

Table 1
Interannual Spearman's correlation coefficients for spatial distributions of (a) loggerhead, (b) green turtle and (c) leatherback nests (none recorded in 1990)

	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
(a)										
1990	*0.91*									
1991	*0.89*	*0.91*								
1992	*0.89*	*0.90*	*0.95*							
1993	*0.88*	*0.91*	*0.89*	*0.88*						
1994	*0.88*	*0.91*	*0.89*	*0.90*	*0.94*					
1995	*0.88*	*0.91*	*0.89*	*0.91*	*0.94*	*0.94*				
1996	*0.86*	*0.89*	*0.85*	*0.90*	*0.94*	*0.94*	*0.94*			
1997	*0.83*	*0.89*	*0.81*	*0.91*	*0.90*	*0.91*	*0.91*	*0.91*		
1998	*0.89*	*0.90*	*0.87*	*0.94*	*0.94*			*0.92*	*0.94*	
1999	*0.83*	*0.86*	*0.90*	*0.89*	*0.92*	*0.92*	*0.90*	*0.90*	*0.86*	*0.89*
(b)										
1990	*0.61*									
1991	*0.66*	*0.59*								
1992	*0.67*	*0.70*	*0.66*							
1993	*0.54*	*0.68*	*0.59*	*0.58*						
1994	*0.68*	*0.72*	*0.69*	*0.86*	*0.*					
1995	*0.46*	*0.48*	*0.72*	*0.53*	*0.56*	*0.55*				
1996	*0.76*	*0.66*	*0.72*	*0.80*	*0.53*	*0.81*	*0.54*			
1997	*0.55*	*0.59*	*0.66*	*0.67*	*0.52*	*0.66*	*0.52*	*0.61*		
1998	*0.64*	*0.59*	*0.65*	*0.80*	*0.46*	*0.86*	*0.53*	*0.77*	*0.63*	
1999	*0.32*	*0.46*	*0.52*	*0.51*	*0.43*	*0.57*	*0.51*	*0.48*	*0.62*	*0.51*
(c)										
1990	0.									
1991	−0.02	0.								
1992	−0.02	0.	*0.49*							
1993	−0.01	0.	−0.02	−0.02						
1994	−0.02	0.	−0.04	−0.04	−0.03					
1995	−0.03	0.	−0.03	−0.03	−0.02	−0.04				
1996	−0.05	0.	0.16	−0.07	−0.05	0.06	0.16			
1997	−0.03	0.	*0.33*	−0.04	−0.03	−0.05	−0.04	*0.23*		
1998	−0.06	0.	−0.08	−0.08	−0.06	0.05	−0.08	0.15	0.02	
1999	−0.07	0.	0.07	0.07	−0.07	*0.26*	0.07	*0.22*	0.01	*0.33*

Italics represent $P < 0.05$.

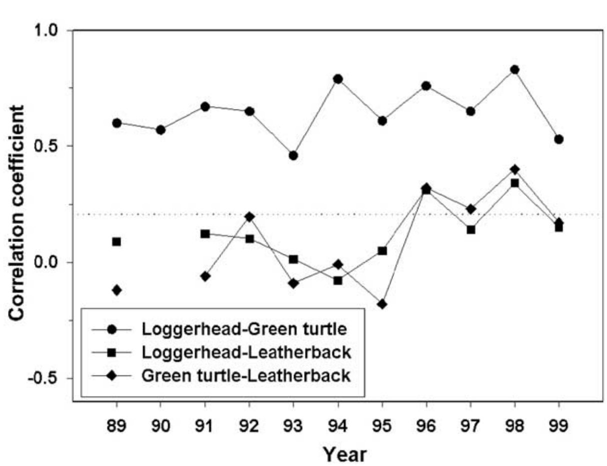

Fig. 7. Annual bivariate correlations of sea turtle nest locations between species. Markers above the dotted line indicate significant ($P < 0.05$) relationships.

patterns of leatherback nests were significantly, positively correlated to loggerheads and green turtle nests in a few years when the number of leatherback nests was higher. However, it was somewhat surprising that they were not correlated during the record leatherback nesting season, 1999.

4. Discussion

4.1. Emergence numbers

The increasing trends in nest numbers for all three species have been documented for the entire state of Florida (Witherington and Koeppel, 2000). This is not unexpected since the Archie Carr Wildlife Refuge and the central Brevard study areas, though only representing 13% of the monitored Florida beaches, represent the bulk of the nests in the state. However, recent increases in green turtle nests since the mid-1970s have also been noted in the Atlantic Basin, in Tortuguero, Costa Rica (Bjorndal et al., 1999) and Ascension Island (Godley et al., 2001). Both increases and declines in nest numbers for leatherback nests have been recorded during this sampling period in French Guiana (Girondot and Fretey, 1996) and Costa Rica (Campbell et al., 1996; Steyermark et al., 1996), respectively.

For these nesting beaches roughly 50% of all emergences were non-nesting. This percentage of non-nesting behaviors for loggerheads was comparable to those observed in the early 1980s for beaches within and just to the north of the study area (Ehrhart and Raymond, 1987; Provancha and Ehrhart, 1987) and generally fall in line with other reports from the southeastern USA (Dodd, 1988).

4.2. Emergence distributions

On islands such as Ascension Island (Carr and Carr, 1972; Godley et al., 2001) or Okinawajima (Kikukawa et al., 1996) with distinct sandy and rocky shores, the distribution of sea turtles nests is patchy in part due to the coastal geology. However, on long stretches of seemingly homogenous sandy beach, nest distributions are generally not random (Carr and Carr, 1972). For random environments there is no spatial autocorrelation where in fine-grained systems positive autocorrelations flip to negative and back again over longer distances (Ranta et al., 2000). Along this 40.5 km beach, loggerhead and green turtle nesting behaviors exhibited spatial autocorrelation. The pattern resembled a simple gradient type of response, i.e., there was not any flip-flopping back and forth between positive and negative autocorrelation values. If behavior reflects present conditions, this signifies that changes in the environmental grain are coarse relative to the sea turtles response behaviors.

In addition to the beaches shown here or elsewhere in Florida (Provancha and Ehrhart, 1987), non-random patterns can be seen in nesting site maps for numerous species from Tortuguero (Carr and Carr, 1972; Bjorndal et al., 1985; Campbell et al., 1996) and Las Baulas (Steyermark et al., 1996) Costa Rica, Praia do Forte, Brazil (Marcovaldi and Laurent, 1996), and Fethiye Beach, Turkey (Baran and Türkozan, 1996). However, some nest distributions such as those for Tortuguero would produce finer-scale autocorrelation patterns than observed in this study. Comparable to the distributions of leatherbacks in Las Baulas (Steyermark et al., 1996), the nests for green turtles and loggerheads increased as the density of human development was lower. This follows the regression results of Kikukawa et al. (1999) which found a positive correlation between nesting and distance from human settlement. Though contrary to the findings of Campbell et al. (1996) and Steyermark et al. (1996), our meager data found leatherback turtles to be nesting in a spatially unpredictable manner as found by Eckert (1987).

The similarity of spatial patterns of non-nesting emergences to nesting emergences for loggerhead and green turtles implies that the turtles are either not nesting significantly beyond the 0.5-km section where they originally emerged or individuals are swimming approximately the same distance and direction after an aborted nesting attempt. However, without recapture or radio telemetry data the particular scenario cannot be discerned. Furthermore, the fact that the ratio of nesting to non-nesting emergences is consistent along the 40.5-km stretch, indicates that although there are fewer nests in the northern half of the study area, no particular environmental factor is more prevalent in one region generating increased non-nesting emergent behavior. This suggests that nesting areas are selected for prior to beach ascent (Provancha and Ehrhart, 1987). Hence, non-nesting emergences may not simply be a response to a stimulus (e.g. human activity) but some sort of innate behavior.

Though correlation does not imply causation, Sokal and Oden (1978b) suggest that correlogram similarity for different measures imply similarity in the underlying processes responsible for the pattern (Turner et al., 1991). Thus, although loggerhead and green turtles may be responding to similar present or historical mechanisms of a similar grain, the leatherback turtles in this study area may be responding to others. Generally, interspecific differences in the major aspects of sea turtle nesting behaviors tend to be minor (Hendrickson, 1995). Hence, it is understandable that spatial patterns in emergence behaviors between loggerhead and green turtles were significantly correlated. Interspecific differences (e.g. between leatherback and green turtles; Whitmore and Dutton, 1985) and similarities (e.g. between hawksbill (*Eretmochelys imbricata*) and green turtles; Bjorndal and Bolten, 1992) in vertical spacing on the same beach have been found. Parallel to the surf, hawksbill and green turtles along a 35-km beach in Costa Rica (Bjorndal et al., 1985) and hawksbill and loggerhead turtles along a 14-km beach in Brazil (Marcovaldi and Laurent, 1996) were visibly correlated. These overlaps in nesting sites indicate the possibility of interspecific spatial competition; however, on these beaches nesting is separated temporally with leatherbacks beginning to nest in late February–early March, followed by loggerheads in mid-April, lastly green turtles in mid-May. Furthermore, the nest density is not sufficiently high to suggest that density-dependent nest destruction by other nesting turtles (Girondot et al., 2002) occurs.

4.3. Interannual patterns of emergence distributions

Over this 11-year period, loggerhead and green turtles consistently emerged in a fairly predictable fashion along these East Central Florida shores. Because this study did not follow specific turtles through tracking or telemetry, we cannot definitively state the degree of site tenacity for individual turtles. However, the significant interannual correlations suggest that there is undoubtedly something that is causing the repeated spatial patterning for loggerhead and green turtles. Whether it is environmentally produced each season or neurologically ingrained is not apparent. Such striking similarity in spatial distribution of nests was observed by Carr and Carr (1972) for green turtles during over a 6-year period in Tortuguero, Costa Rica and Godley et al. (2001) for green turtles on Ascension Island >20 years after previous studies.

4.4. Conservation implications

Examining how spatial patterns of a population distribution change provides a more sensitive assessment of a population's stability than enumeration alone. The increase in numbers and remarkable consistency in spatial patterns during this sampling period bodes well for sea turtle nesting in this important coastal region. This success may be in part due in part to the ongoing efforts of the Brevard County Environmentally Endangered Lands (EEL) Program and the United States Fish and Wildlife Service to purchase and protect these beaches. Though human population and influences have grown towards the northern end of the study area since 1989, the prevalence of aborted nesting attempts, which are often attributed to human activities, remained spatially consistent and were not elevated towards the more developed areas. The predictability found in this study indicates that sampling strategies to monitor these beaches may not need to be as labor intensive as outlined by the Florida Fish and Wildlife Conservation Commission

Index Nesting Beach Survey (INBS) Program to be accurate. The similarity in patterns between loggerhead and green turtle nesting behaviors suggests that management policies focusing on preserving beach areas for one species may be effective for both.

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