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Individual Nest Site Selection in Hawksbill Turtles Within and Between Nesting Seasons

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ABSTRACT. – We analyzed 410 nest locations from 150 individual nesting hawksbill turtles (*Eretmochelys imbricata*) on the northeastern Brazilian coast during 8 nesting seasons from 2006 to 2014 to evaluate individual nesting preferences. We determined the consistency of nest site choice within and between nesting seasons for open sand and vegetation nest microhabitats and also for nest site distances from the current waterline, highest spring tide, vegetation line, and position along the beach. We found that behavioral consistency within seasons was more robust than between seasons. This suggests that a decrease in the consistency of nest site choice may be related to progressive landscape changes in the nesting environment, driving behavioral flexibility in nesting preferences.

KEY WORDS. – Reptilia; Testudines; *Eretmochelys imbricata*; hawksbill sea turtle; individual nesting preferences; nest site choice; behavioral flexibility; preference; sea turtle

Although hawksbill turtles (*Eretmochelys imbricata*) spend most of their lifetimes in the sea, they need sandy beaches to successfully incubate their eggs. The absence of parental care in this species further makes nest site selection an important mechanism to maximize fitness (Resetarits 1996), but choosing an appropriate site is not without challenges. For example, nests located close to the sea can provide easy access for hatchlings to reach the water; however, this location increases the probability of loss by flood or erosion (Marigatoulis 2005). On the other hand, nests located farther inland are safer from inundation but are subject to desiccation, hatchling disorientation, penetration of roots, and predation (Wood and Bjørndal 2000). Moreover, different microhabitats within the nesting beach influence the incubation temperature (Kamel and Mrosovsky 2006a) and therefore hatchling sex ratios in the nest (Robins 2003).

The study of individual preferences for particular nest sites (Kamel and Mrosovsky 2004, 2005, 2006b) may explain the variation in nesting behaviors seen within sea turtle populations. Sea turtles are interesting taxa to investigate nest site preferences because they lay several clutches each nesting season, usually returning to the same beach area within and between nesting seasons. The study of such behavior contributes to a better understanding of the biology of this species and, in addition, can improve conservation strategies (Kamel and Mrosovsky 2006a).

The aim of this research was to study the individual nesting preferences of hawksbill turtles along the southern

coastline of Rio Grande do Norte, northeastern Brazil, during the 2006–2014 nesting seasons. A decrease in the consistency of nest site choice, caused by changes in nest-site preferences over time, may reflect behavioral plasticity as a result of a dynamic nesting environment. As such, our main goal was to investigate individual nesting profiles and possible declines in nest site consistency in *E. imbricata* using several nest parameters recorded over 8 nesting seasons.

METHODS

Study Site. — The study area is located in northeastern Brazil in the southern section of the state of Rio Grande do Norte (Fig. 1). The monitored beach area is approximately 4.2 km in length, within the municipality of Tibau do Sul (lat 06.190121°S, long 35.084720°W); this area consists of Chapadão, Minas, and Sibau beaches (Fig. 1). The beach landscape is surrounded by cliffs, interspersed with dunes, exposing a generally narrow band of beach, from 0 m (in areas where the cliffs touch the sea) up to 40 m. The sand is fine grained and of a pale yellow color. The vegetation is composed primarily of pioneer herbaceous species, such as *Paspalum vaginatum* (Poaceae), *Blutaparon portulacoides* (Amarantaceae), *Ipomoea pes-caprae* (Convolvulaceae), and *Remirea maritima* (Cyperaceae). A few meters above the pioneer herbaceous vegetation, the diversity of plants increases, with *Chrysobalanus icaco* (Chrysobalanaceae) and *Melocactus* (Cactaceae) found in dense clusters, as well as a few coconut

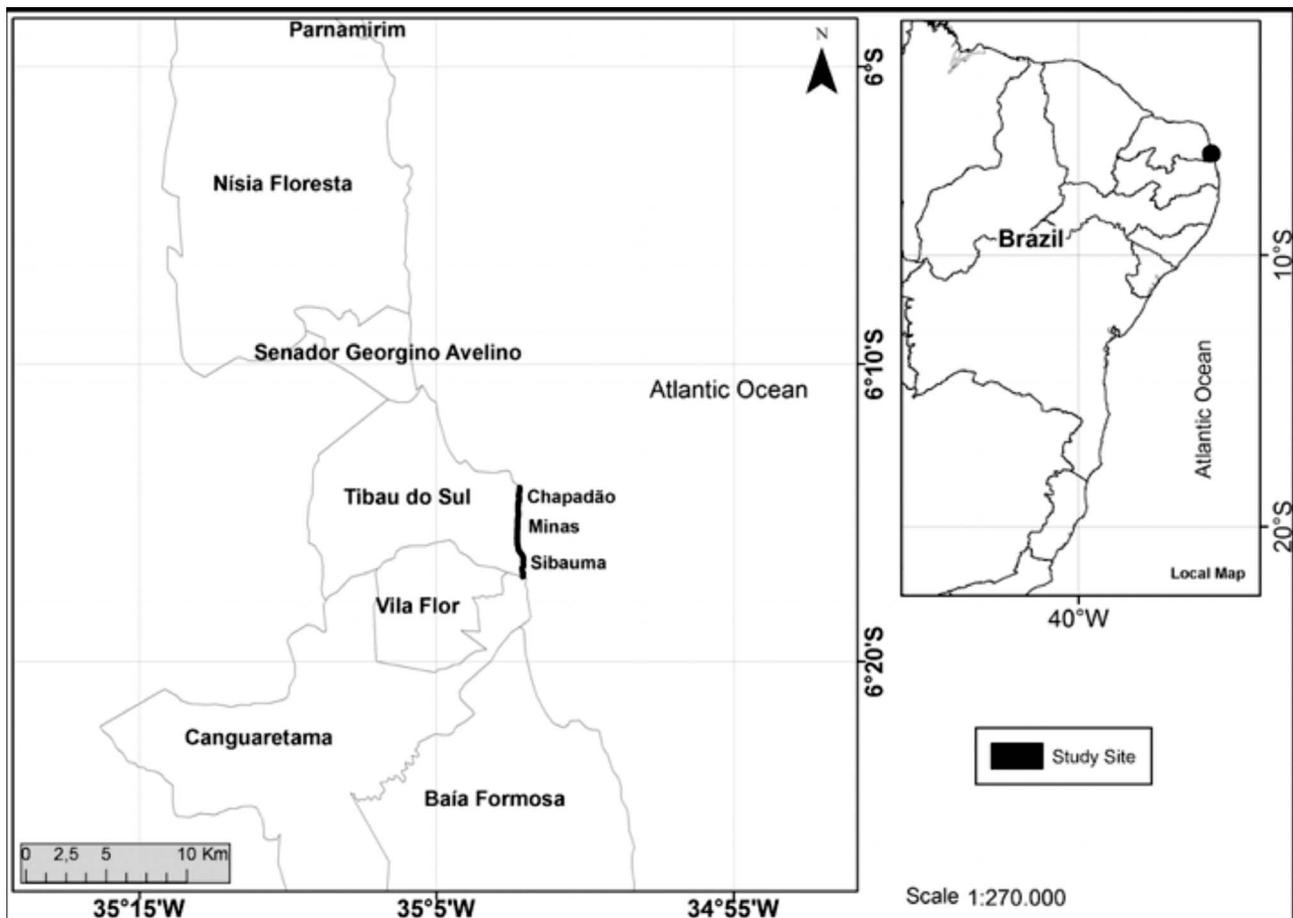


Figure 1. Location of the study site at Tibau do Sul municipality, northeastern Brazil (lat 6°13'40"S, long 35°03'05"W).

trees, *Cocos nucifera* (Arecaceae). However, only the herbaceous vegetation is accessible to the turtles. The dense cluster of vegetation, as well as the cliffs and the road, mark the maximum upper limit that is accessible to the turtles (Fig. 2). This region experiences a mesotidal, semidiurnal regime where normal tides attain a maximum of 2.0 m and spring tides have a range of 3.2 m (Hayes 1979).

Data Collection. — During the nesting seasons from 2006 to 2014, intensive nightlong patrols occurred from 10 December to 15 April, from 1900 to 0430 hrs, to intercept and mark nesting females with inconel metal tags (#681 National Band and Tag Company) applied to both front flippers. Each nest was marked with a numbered stake, and we performed morning patrols to record the nest distance measurements from the previous night.

Measurements. — For each encounter of a female that nested successfully, we collected the following data (Fig. 2):

1. Distance from current waterline (DW), which is the distance from the nest to the current waterline at the moment of egg laying. This measurement represents how far the turtle has crawled and was the only measurement recorded at night.
2. Distance from the highest spring tide line (DS), defined as the distance from the nest to the marked spring tide,

which is visualized as a line of marine detritus on the beach. Nests located below the spring tide line are given a negative value.

3. Distance from vegetation (DV), defined as the distance from the nest to the line of vegetation. Values within the vegetation are negative.
4. Position along the beach (PB), which is estimated based on GPS coordinates of the nest location.
5. Microhabitat categorization, either open sand (OS), which is characterized by the presence of fine granular sand soil without any vegetation; vegetation (VG), which comprises areas with herbaceous species; and sand slope (SL), which is characterized by formations of sandbanks. These formations are generally ephemeral, and their occurrence varies within and between nesting seasons as a line that coincides with the spring tide line. As a result, every nest located in this microhabitat is below the maximum high spring tide (negative value for DS) and therefore is washed over during incubation.

The number of measurements differed among DW, DS, and DV; DS and DW had the largest sample size because the highest spring tide and current waterlines are permanently present on the beach, and as a result, those distances were always recorded. DV is the most sensitive

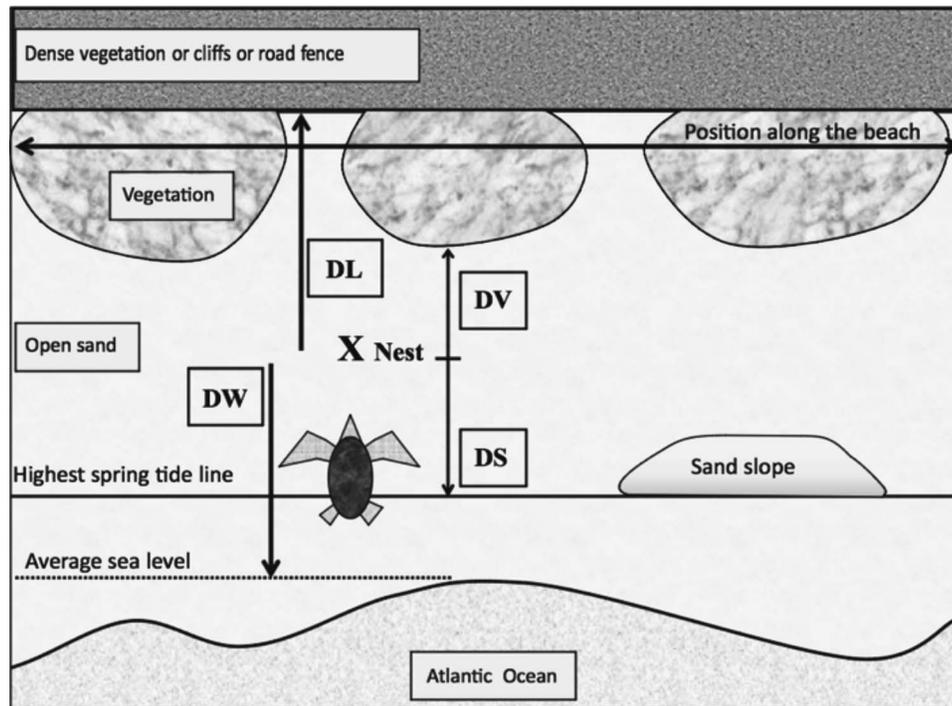


Figure 2. Schematic of the nest site distances. Distance from current waterline (DW), distance from highest spring tide line (DS), distance from vegetation line (DV), distance from the maximum upper limit (DL), and position along the beach (PB). The microhabitats vegetation, sand slope, and open sand are also indicated.

measurement since there are several locations where vegetation is absent (Fig. 2). In these cases, no measurements were taken.

Analyses. — We first tested behavioral consistency for specific microhabitats using a χ^2 test. The analysis was performed using all 3 microhabitats (OS, VG, and SL) and was subsequently repeated without SL, as it constitutes a natural obstacle forcing turtles to choose OS.

We calculated within-season repeatability, a measure of the consistency of a behavior based on analysis of variance (Bell et al. 2009), using turtles that nested at least twice in a given season and combining all seasons in a single data set; here we consider a remigrant turtle to be a new turtle. We calculated between-season repeatability using only remigrants, and we combined all nests in a single data set independent of nesting season. We computed a p -value using a Monte Carlo technique; we ran the repeatability for 2000 randomized samples and compared the distribution of resampled data with the observed data.

We also used a linear correlation test to compare distance-based nesting preferences. We first compared the distance measurements of a nest site (d) versus the measurement of a subsequent nest ($d+1$). In order to analyze the decline in consistency within seasons, we performed 3 different correlations: 1) between d and $d+1$, 2) between d and $d+2$, and 3) between d and $d+3$. For the between-season data, we correlated 4) the average distance measurement among all nests within the same season versus the average distance measurement of a subsequent season and 5) between a random distance within 1 season versus another random distance of a subsequent season. In

this last case, we sampled 2000 random sets and used a Fisher test to average over the set of obtained p -values. When we found a marginally significant p -value ($0.05 < p < 0.1$) and the next p -values were greater, we considered this evidence of a decline in repeatability. Additionally, as the p -value is, in essence, a probability, we also interpreted a large increase in p -value (10 times or more) over time as a tendency for consistency decay (Rohatgi 1984). All analyses were performed on the full data set and then repeated on a more restricted data set, limited to individuals seen nesting at least twice in at least 2 seasons. Analyses were performed using the software R (R Development Core Team 2012).

RESULTS

Data. — We recorded 410 nest locations from 150 individual hawksbill turtles in the study area for 8 nesting seasons. A total of 78 individuals were recorded nesting only once, and 72 nested from 2 to 6 times within a season. Twenty-three individuals were seen nesting in 2 seasons, 20 in 3 nesting seasons, and 6 in 4 nesting seasons; 27 individuals were recorded in at least 2 nesting seasons and nested at least twice in each season and made up the restricted group. The average beach stretch that females nested within the entire 4.2 km was 1830 ± 1030 m.

Analyses. — Within seasons, females nested non-randomly with respect to the OS and VG microhabitats ($\chi^2 = 6.12$, $p = 0.013$). However, when all seasons were combined, the pattern was no longer significant ($\chi^2 = 2.82$, $p = 0.093$). If we included SL, we found no

Table 1. Results of analysis of variance–based repeatability corresponding to the distances: vegetation line (DV), highest spring tide line (DS), current waterline (DW), and position along the beach (PB).

	Vegetation line	Spring tide line	Current waterline	Position along beach
Repeatability (within)	$p = 0.095$ $r = 0.583$ $n = 370$	$p = 0.41$ $r = 0.52$ $n = 410$	$p = 0.125$ $r = 0.54$ $n = 392$	$p < 0.00001$ $r = 0.65$ $n = 409$
Repeatability (within + between)	$p = 0.214$ $r = 0.55$ $n = 370$	$p = 0.34$ $r = 0.52$ $n = 410$	$p = 0.11$ $r = 0.54$ $n = 392$	$p < 0.00001$ $r = 0.68$ $n = 409$
Repeatability (selected set within)	$p = 0.021$ $r = 0.65$ $n = 165$	$p = 0.093$ $r = 0.58$ $n = 172$	$p = 0.21$ $r = 0.55$ $n = 149$	$p < 0.00001$ $r = 0.69$ $n = 171$
Repeatability (selected set within + between)	$p = 0.059$ $r = 0.61$ $n = 165$	$p = 0.17$ $r = 0.57$ $n = 172$	$p = 0.18$ $r = 0.56$ $n = 149$	$p < 0.00001$ $r = 0.81$ $n = 171$

individual microhabitat preferences either within individual seasons ($df = 1$, $\chi^2 = 2.73$, $p = 0.098$) or across all seasons combined ($df = 1$, $\chi^2 = 1.01$, $p = 0.31$).

Within seasons, we found no significant repeatability for DW or DS, weak repeatability for DV ($r = 0.58$, $p = 0.09$), but significant repeatability for PB ($r = 0.68$, $p < 0.00001$). When all seasons were combined, we found significant repeatability only for PB ($r = 0.65$, $p < 0.00001$; Table 1).

With respect to DW, DS, and DV, correlation analyses were not significant for most comparisons (Table 2). Only the d vs. $d+1$ correlation was significant for DV, and the d vs. $d+2$ was significant for DW. This suggests a lack of within-season consistency of nesting preferences for these measures. No between-season correlations were significant, suggesting that turtles were not consistent between seasons as well. However, with respect to PB, correlations were significant between all nest combinations (Table 2), suggesting high repeatability for this measure. Interestingly, in the d vs. $d+3$ correlation, the p -value was more than 10 times higher than in the d vs. $d+1$ correlation, potentially indicating a repeatability decay. The results were largely similar when considering only the restricted set of turtles (Tables 1 and 2).

DISCUSSION

The main finding of this article is that the consistency of nest site choice decreased as a function of time.

Specifically, we found a decrease in repeatability when using distance from the vegetation line, spring tide line, and current waterline as well as microhabitat preferences (Tables 1 and 2). Repeatability p -values increased once we considered larger nesting intervals within 1 season or when we included several seasons.

For position along the beach, however, all analyses revealed a significant repeatability both within and between seasons. On a stretch of beach in Tortuguero, Costa Rica, twice as long as our study site (8 km), nesting hawksbill turtles showed a similar site fixity (1670 ± 1480 m; Bjorndal et al. 1985). Strong site fidelity has been observed for island populations (Richardson et al. 1999; Diez and van Dam 2007); however, when turtles nest on the mainland, it is possible that nesting occurs more widely. We found that around 50% of individual turtles were observed nesting only once, though some individuals were observed nesting in adjacent areas within the state of Rio Grande do Norte, Brazil (Santos et al. 2013). It is possible that some turtles select a restricted range of nesting sites and that others tend to distribute their nests more widely. To date, individuals tagged within our study site have never been recorded nesting in other states; an ongoing satellite tracking study promises to clarify this issue.

With respect to distance from the current waterline, the significant correlation seen only for d vs. $d+2$ was intriguing. Interestingly, the period of time that corre-

Table 2. Results for the correlation analysis for nest distances: vegetation line (DV), highest springtide line (DS), current waterline (DW), and position along the beach (PB).

	Vegetation line	Spring tide line	Current waterline	Position along beach
Within (d vs. $d+1$)	$p = 0.020$ $n = 141$	$p = 0.063$ $n = 161$	$p = 0.14$ $n = 148$	$p < 0.0001$ $n = 160$
Within (d vs. $d+2$)	$p = 0.15$ $n = 59$	$p = 0.53$ $n = 70$	$p = 0.008$ $n = 63$	$p = 0.0004$ $n = 69$
Within (d vs. $d+3$)	$p = 0.79$ $n = 17$	$p = 0.55$ $n = 23$	$p = 0.35$ $n = 20$	$p = 0.0041$ $n = 22$
Between (using the average)	$p = 0.88$ $n = 38$	$p = 0.78$ $n = 52$	$p = 0.68$ $n = 42$	$p = 0.0065$ $n = 52$
Between (random sampling)	$p = 0.99$ $n = 44$	$p = 0.99$ $n = 52$	$p = 0.99$ $n = 49$	$p < 0.0001$ $n = 52$

sponds to 2 subsequent nesting events, where the average interesting interval is 15 d for this population (Santos et al. 2013), is close to 1 whole lunar cycle (28 d), when the same tidal conditions are likely to repeat. This significant correlation could thus be related to a preference for coming ashore at a specific tidal height. This condition is not observed in the dyad comparisons (d, d+1) or in (d, d+3), when there are different lunar influences on the tide. Repeatability of distance to the current waterline may be a consistent phenomenon within a given season for those nests that occur at the same point in the lunar cycle point (i.e., interleaved nests). Indeed, Dobbs et al. (1999) found a significant correlation between nesting activity of hawksbill turtles and tidal height in the northern Great Barrier Reef, Australia.

Our work corroborates some previous results in the literature that have found repeatability of nesting preferences in the hawksbill turtles within a season (Kamel and Mrosovsky 2005). We also detected repeatability for microhabitat selection: turtles that nested in sand preferred sand, while turtles that selected vegetation preferred vegetation. However, when evaluating between-season consistency, our results contrasted from data from the French West Indies, where hawksbill turtles maintained their interseasonal nesting preferences (Kamel and Mrosovsky 2006b). The authors suggested that behavioral flexibility in those turtles was limited, and repeatability between seasons was as strong as within seasons (Kamel and Mrosovsky 2006b). Our findings suggest a different mechanism where a female's behavior is much more labile. We suggest that changes in repeatability may indicate behavioral plasticity, meaning that sea turtles may be sensitive to current environmental conditions and may be able to select the best location to lay their eggs by taking into account the physical aspects of a nesting area.

The nesting beach in the French West Indies is under a negligible tidal regime and appears to be more stable, in contrast to our study area, where the beach is relatively narrow, tides reach up to 3.2 m, and strong erosion occurs frequently. The region we studied is also very windy, and there are moving dunes in the surroundings, contributing to progressive changes in vegetation and sand slope formations along the beach. In addition, they analyzed data across 2 seasons, whereas in this work we recorded nesting data for 8 seasons. In conclusion, the beach dynamic is likely to be influencing nesting preferences of *E. imbricata* with respect to the presence or absence of critical environmental variation.

The high numbers of nests located in sand slope microhabitat (48%) highlight the importance of this natural microhabitat for this population. Indeed, the distance measures also show that nests were concentrated close to the highest spring tide line. Although we did not explore hatchling production here, the sand slope microhabitat, even with nests being washed over during incubation, still produces hatchlings, and nests usually have longer periods of incubation, possibly playing an important role in the sex

ratio of the population (Marcovaldi et al. 2014). This region has been subject to erosion at least since the Pleistocene (Dominguez and Bittencourt 1996; Bezerra et al. 2003), and turtles that nest there have likely been dealing with this instable environment for generations.

Although we have taken an individual-based approach, it is still interesting to evaluate how individual nest site preferences influence population-level patterns. We found that the majority of nests were located in open sand (OS+SL), which differs from other hawksbill rookeries in Brazil (Serafini 2009) as well as in the Caribbean (Horrocks and Scott 1991; Kamel and Mrosovsky 2005, 2006a, 2006b). However, when we exclude SL, which represents situations where the turtle had no other available microhabitat than open sand, 64% of the remaining nests were located in vegetated areas. In this way, the preference becomes consistent with that broadly described for hawksbill turtles: to nest in areas with at least some vegetation (Horrocks and Scott 1991; Kamel and Mrosovsky 2005, 2006a, 2006b; Serafini et al. 2009).

Nest site preferences may vary because of natural landscape changes or even due to the animal's accuracy in approaching the beach. We found that hawksbills consistently returned to the same position along the beach. However, if a turtle changes its position even by several meters, it may encounter a landscape with a different availability of microhabitats. In our analyses, we did not consider nesting attempts that were aborted, as those attempts are typically very quick and virtually impossible to attribute to a particular nesting turtle during beach patrols. Across the 8 nesting seasons, the mean of successful nesting attempts was 61% (range 51%–72%), which is lower than the percentage found in other rookeries (76% on Milman Island [Dobbs et al. 1999], 65% at Buck Island National Monument [Hillis 1994], and 63% in Antigua [Hoyle and Richardson 1993]) but similar to Cousin Island, Seychelles (56%–60%; Allen et al. 2010).

Finally, we want to highlight that these results are also important for conservation efforts and policies. Although the beaches in the study site are narrow, these hawksbill turtles, listed as critically endangered by the International Union for Conservation of Nature (2014), were observed nesting more inland of the highest spring tide line (up to 31 m) than in Barbados (22.5 m; Horrocks and Scott 1991). How far inland turtles travel to nest is key information for policies that aim to protect nesting beaches, as effective beach management plans should limit the use of artificial lights, buildings, or heavy human traffic in areas that overlap with those used by nesting turtles while being cognizant of current threats due to sea-level fluctuations. Nesting beaches are currently being compressed between coastal development and coastal erosion, and we encourage local governmental agencies to establish coastal development strategies compatible with the conservation of sea turtles.

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