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## Characteristics of a Leatherback Nesting Beach and Implications for Coastal Development

JOHN H. ROE<sup>1,2</sup>, PATRICIA R. CLUNE<sup>1</sup>, AND FRANK V. PALADINO<sup>1</sup>

<sup>1</sup>Indiana-Purdue University, Fort Wayne, Indiana 46805 USA [paladino@ipfw.edu];

<sup>2</sup>Present Address: University of North Carolina at Pembroke, Pembroke, North Carolina 28372 USA [john.roe@uncp.edu]

**ABSTRACT.** – Coastal development can alter the natural dynamics of beach environments, with strong implications for associated biota. Sea turtles nest on oceanic beaches and often depend upon a specific range of conditions for successful nesting. In the case of the critically endangered leatherback turtle (*Dermochelys coriacea*), we know little regarding what features they select for nest sites, including how they respond to anthropogenic development. We examined relationships between leatherback nest frequency, beach environments, and tourism development at Playa Grande, Costa Rica, the location of the largest current nesting population in the eastern Pacific Ocean. Developed beach sections had shallower slopes, lower pH, and less air-filled pore space, but higher water content and salinity than undeveloped areas. Developed areas were also comprised of more sand in the smaller grain size classes relative to undeveloped sections. Leatherback nesting was positively correlated with deepness of the offshore approach, beach slope and elevation, pH, and sand in intermediate size classes (0.025-mm diameter), but negatively correlated with sand in the smallest silt size class (< 0.0625-mm diameter). Leatherback nesting frequency was 3.4 times higher in undeveloped sections of the beach relative to developed areas, while nonnesting emergences were 2.6 times more likely in developed relative to undeveloped areas. It is apparent that coastal development has impacted beach environments with consequences for leatherback nest site distribution. It is likely that additional development of the beach under mixed-management plans to support a growing tourist industry will further degrade the attractiveness and quality of the beach for leatherback nesting.

**KEY WORDS.** – Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; marine turtle; nest site selection; nesting behavior; beach erosion; tourism; Costa Rica

The selection of a nest site is a hierarchical process for a sea turtle. First, a female must choose a beach and offshore approach that she can safely access from the sea. Next, the turtle must select an emergence site, then move to a location that is not only suitable for digging a nest, but that also offers conditions favorable for embryo survival, development, hatchling emergence, and travel back to the sea. From an evolutionary perspective, nest site selection should reflect costs and benefits to both the female and her clutch—though sometimes behaviors favorable for the nesting female are costly to the clutch and vice versa, and a tradeoff may occur (Mortimer 1990; Bjorndal and Bolten 1992). Beaches and adjacent offshore areas vary naturally in several important environmental features that turtles can use as proximal cues of nest site quality. Such factors include offshore bathymetry and obstructions (Mortimer 1982), slope and elevation of the beach (Wood and Bjorndal 2000; Kikukawa et al. 1999), beach vegetation (Hays et al. 1995; Karavas et al. 2005), and chemical and physical attributes of the sand (Stancyk and Ross 1978; Stoneburner and Richardson 1981; Mortimer 1990; Garmestani et al. 2000). Responses to such environmental cues can affect adult survival, clutch viability, and hatchling success (Wood and Bjorndal 2000; Kamel and Mrosovsky 2004).

Anthropogenic development can introduce variation to the beach environment, with potential consequences for

turtle nesting. The removal of natural vegetation and construction of jetties, seawalls, buildings, and other structures disrupts natural beach accretion and erosion cycles, ultimately leading to a reduction in beach width, slope, and elevation resulting from the loss of sand (Garcia and Servera 2003). Many turtles prefer to nest on wide or steeply sloping beaches, presumably because areas with reduced beach width and elevation are at a higher risk of flooding (Horrocks and Scott 1991; Garmestani et al. 2000; Wood and Bjorndal 2000). Sea turtles also tend to avoid nesting in areas with artificial lighting because hatchlings may become disorientated while travelling from the nest to the sea, or because adults themselves are disturbed by the light (Mortimer 1982; Witherington 1992; Salmon et al. 1995). Exposed pilings may also deter females from nesting (Bouchard et al. 1998). For these reasons and others, it is not surprising that many turtles either tend to avoid nesting on beaches near development or have experienced population declines as a consequence of development (Stancyk and Ross 1978; Mortimer 1982; Kikukawa et al. 1999).

Leatherback turtles (*Dermochelys coriacea*) in the Pacific Ocean have declined precipitously in recent decades, in part as a consequence of fisheries bycatch, direct harvest, environmental pollution, and destruction and degradation of nesting beaches (Chan and Liew 1996;

Spotila et al. 2000; Sarti Martínez et al. 2007; Santidrián Tomillo et al. 2008). The leatherback is listed as Critically Endangered by the International Union for the Conservation of Nature (2009). Detailed information on leatherback nesting behavior could improve the protection and management of their few remaining nesting beaches, as well as identify restoration initiatives to improve the quality of degraded beaches.

Leatherbacks tend to nest on high-energy, dynamic beaches that are free of offshore obstructions, with steeply sloping shorelines and offshore depth profiles (Pritchard 1971; Mrosovsky 1983; Eckert 1987). However, the microsite characteristics that leatherbacks use to select nest sites are not well understood. Some have suggested that leatherbacks employ a “scatter nesting” approach in response to dynamic and unpredictable beach environments (Mrosovsky 1983; Eckert 1987), but leatherbacks exhibit some degree of nesting fidelity and avoidance of specific structures, suggesting that individuals are not nesting randomly but instead are able to assess environments and respond to environmental variation during the nesting process (Kamel and Mrosovsky 2004; Nordmoe et al. 2004; Hernández et al. 2007). We lack a detailed understanding of which specific environmental cues leatherbacks respond to on a consistent basis when selecting a nest site. Here, we examine how attributes of the offshore approach, beach slope profiles, and physical and chemical attributes of the sand vary along a beach, and assess whether any of these factors correlate with beachfront development and nesting in leatherbacks.

## METHODS

**Study Site.** — Nesting behavior of leatherback turtles (*Dermochelys coriacea*) was studied from 2003 to 2005 at Playa Grande (10°20'N, 85°51'W), a beach within the Parque Nacional Marino Las Baulas (PNMB), located on the Pacific coast of Costa Rica (Fig. 1). The beach is bordered by a rocky headland at the north and an estuary at the south. Additionally, the northernmost 900 m and southernmost 700 m of the beach are bordered by several houses and hotels, while the central 2.1 km is undeveloped. Developed areas of the beach had buildings within 100 m of the open sand or vegetation ecotone, although in most cases development was much closer (< 50 m, Fig. 2).

**Nest Census.** — The beach was patrolled from 1 October to 15 February each year to locate nesting females, following the methods of Steyermark et al. (1996) and Reina et al. (2002). Teams of observers walked the beach nightly, concentrating efforts around the hours of high tide and surveying for turtles or turtle tracks, at which point the turtle was observed to confirm whether egg laying occurred. All turtle encounters were classified as either 1) resulting in egg laying, hereafter referred to as “nesting emergences”, or 2) emergences when eggs were not laid, including observations of false crawls, digging of

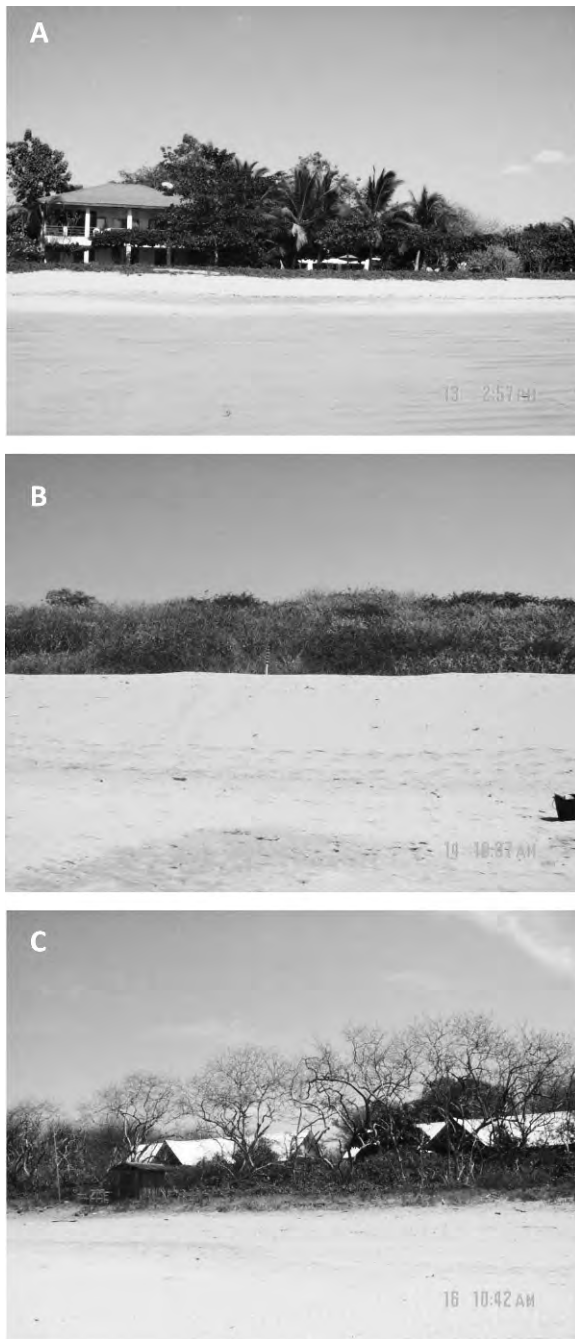


**Figure 1.** Map of Costa Rica and location of Parque Nacional Marino Las Baulas (lighter gray). Note that three nesting beaches are within the park, including Playa Ventanas, Playa Grande, and Playa Langosta. Playa Tamarindo is also shown, but is not part of the park.

the body pit only, or aborted nesting attempts, hereafter referred to as “nonnesting emergences.” To facilitate the recording of encounter locations, the 3.6-km-long beach was marked at 100-m intervals along the north-to-south coastal axis to demarcate 37 sections. Our observations of leatherbacks were undertaken in accordance with all applicable laws and under the approval of the Purdue University Animal Care and Use Committee.

**Beach Characteristics.** — Several physical and chemical characteristics of the beach were measured within each zone. At the beginning of each zone (i.e., every 100 m), the beach profile from the low tide line to the vegetation was determined using the method of Emery (1961). Additionally, sand cores were taken from five random locations in each zone between the high tide line and the vegetation, the area of the beach where the majority of nests are laid (Nordmoe et al. 2004). Sand cores were collected from 45 cm below the surface down to 1 m, which is within the range of typical nest depths for leatherbacks (Billes and Fretey 2001). Sand samples were immediately weighed, placed in plastic bottles, and sealed for later processing.

Water content of each sample was measured as the weight lost following 24 hrs in a drying oven at 105°C. We then mixed each dried sample with an equal volume of double deionized water, and measured pH and salinity after 24 hrs using a Horiba U-10 water quality checker. Organic content was determined gravimetrically by H<sub>2</sub>O<sub>2</sub> oxidation (Carver 1971). For this procedure, 10% H<sub>2</sub>O<sub>2</sub>



**Figure 2.** Images of the beach at (A) the north (0.2–0.3 km), (B) middle (2.0 km), and south (3.5 km) sections of Playa Grande, Costa Rica. Note the proximity of buildings to the beach and disruption of vegetation at the north and south ends of the beach, and the high elevation dune and uninterrupted backing vegetation in the middle section. Photos: Patricia Clune.

was added to 2 g of oven-dried and ground sand, and the mixture was heated until the reaction ceased. After any remaining  $H_2O_2$  evaporated and the sand had cooled, the sand was reweighed and organic content determined. To determine carbonate content, 10 ml of 3 M HCl was added to a 1-g sample of sand with known water content, and the solution was swirled until a constant weight was

reached (Allison and Moodie 1965). Proportion carbonate content was calculated using the following equation:

$$\text{carbonate} = 0.2727 \left[ \frac{\text{mass}_i - \text{mass}_f}{\text{mass}_i} \right] \quad [1]$$

Porosity and air-filled pore space were determined for 50-g samples of dry sand in accordance with methods of Vomocil (1965). Porosity (St) ( $\% \text{ cm}^3$ ) is defined as the percentage of the bulk volume not occupied by solids and was calculated as

$$\text{St} = 100 \left[ 1 - \left( \frac{D_b}{\rho_p} \right) \right] \quad [2]$$

where  $D_b$  is the bulk density (mass of the oven-dried soil in bulk volume [ $\text{g}/\text{cm}^3$ ]) and  $\rho_p$  is the particle density (density of solid particles collectively [ $\text{g}/\text{cm}^3$ ]). For a detailed description of bulk and particle density calculations, refer to Blake (1965). Air-filled pore space (S) ( $\% \text{ cm}^3$ ) for each sample was then calculated as

$$S = \text{St} - \text{Pv} \quad [3]$$

where Pv is the water content on a volume basis ( $\text{g H}_2\text{O}/\text{cm}^3$ ), and assuming the density of water is 1 g/ml.

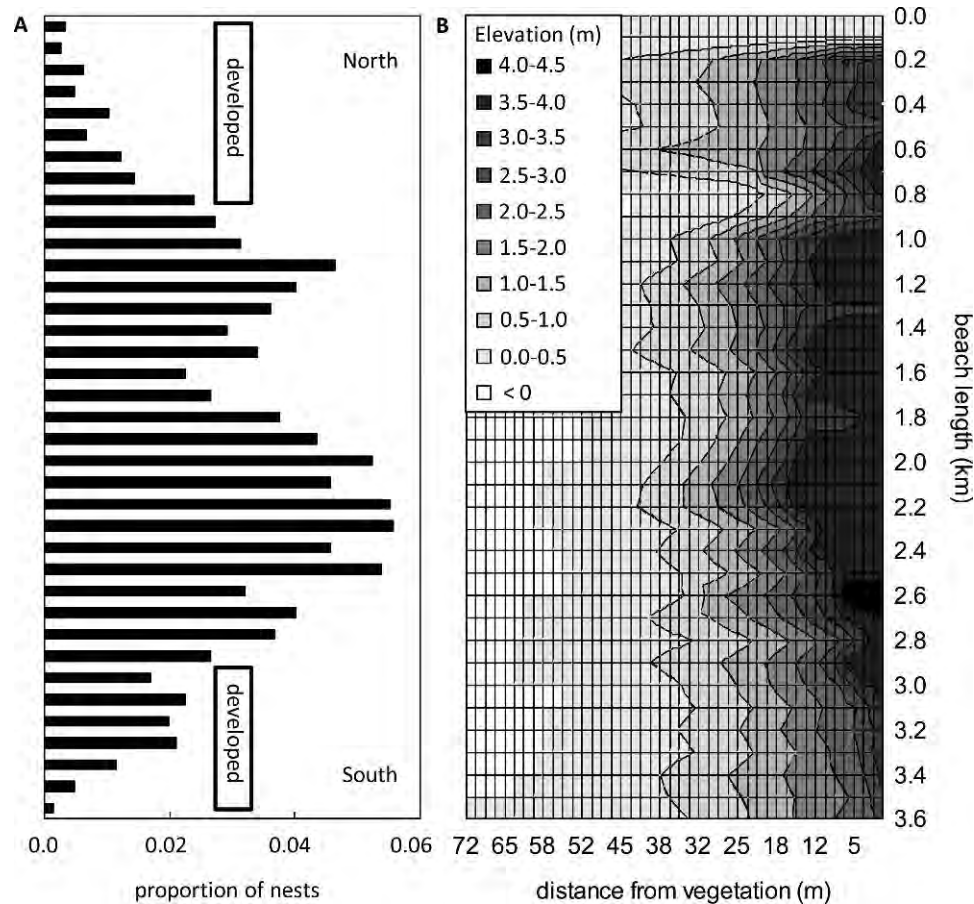
Sand particle size distribution was determined by pouring each sample through a series of sieves with mesh sizes of 2, 1, 0.5, 0.25, 0.125, and 0.0625 mm, corresponding to values of -1 (very coarse), 0 (coarse), 1 (medium), 2 (fine), 3 (very fine), and 4 (silt), respectively, on the Phi scale of particle size classification. Samples were shaken on a mechanical shaker for 5 min, and the remaining contents were weighed and expressed as a proportion of the total sample.

**Bathymetry.** — Water depth was determined along transects running from the shore to 2 km offshore using a boat and depth finder. Along each transect, we recorded depth (0.1 m) and associated coordinate positions. Location and depth data were then plotted using ArcGIS 9.3 (ESRI, Inc. Redlands, CA). A depth map was then created by applying kriging procedures that estimate values in areas for which we had no data.

**Statistical Analyses.** — Statistical analyses were performed with SPSS 17.0 (Chicago, IL). Statistical significance was accepted at the  $\alpha \leq 0.05$  level except for multiple related comparisons, where the Dunn-Sidak method was applied to constrain the experiment-wide Type I error to 0.05.

To assess whether turtles nested randomly along the coastal axis of the beach, we used chi-square tests, with the null hypothesis that frequency of nesting emergence or nonnesting emergence is equal among sections. The sections were then classified as occurring in the developed or undeveloped regions of the beach. We then examined whether frequency of nesting emergences differed between developed and undeveloped beach sections using analysis of variance (ANOVA). Additionally, we assessed whether the proportion of nonnesting emergences from the total number of emergences differed between developed and undeveloped beach sections using





**Figure 3.** Frequency distribution of leatherback nests (A) relative to the beach elevation profile (B). Development occurs between 0.0 and 0.8 km and between 3.0 and 3.6 km.

ANOVA, using arc-sin transformed percentage of non-nesting emergences as the dependent variable.

To determine whether beach physical and chemical characteristics differed between developed and undeveloped sections, we used a multivariate analysis of variance (MANOVA) with slope, pH, porosity, water content, organic content, carbonate, air-filled pore space, and salinity as the dependent variables, and zone type (developed or undeveloped) as the independent variable. In the above analysis, all dependent variables were either  $\log_{10}$ - or arcsin-transformed to meet assumptions of normality and equality of variances.

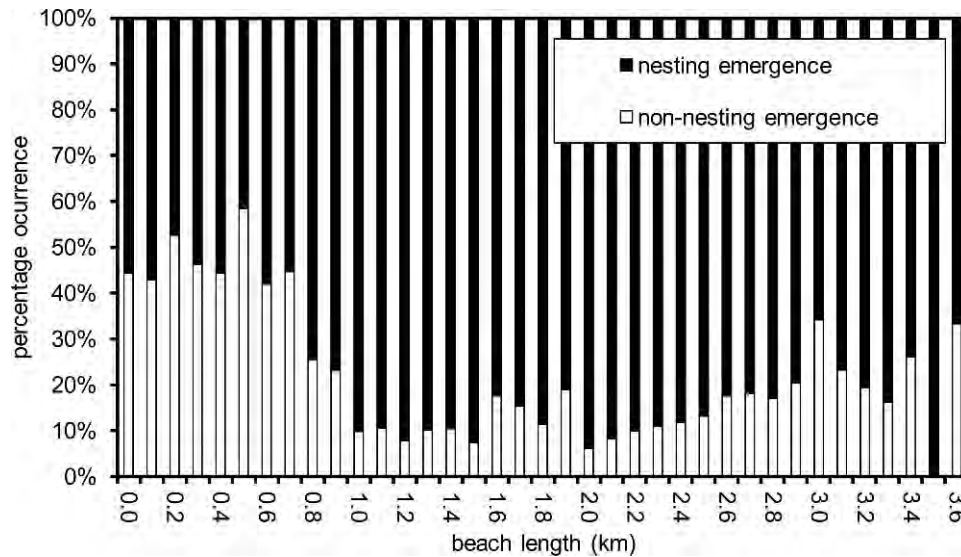
We examined relationships between frequency of nesting emergences and beach and bathymetric characteristics using regression analyses. We used multiple stepwise linear regression to assess whether pH, porosity, water content, organic content, carbonate, air-filled pore space, or salinity were associated with the number of nests or the proportion of nonnesting emergences in a zone. We assessed relationships between beach profiles and frequency of nesting and proportion of nonnesting emergences using nonlinear regression. We used a series of linear regressions to assess relationships between nesting frequency or proportion of nonnesting emergences and amount of sand in the different particle size classes. Finally, correlations between

nesting frequency and water depths extending at 50-m intervals from each zone's midpoint perpendicular to the coastal axis were assessed using a series of linear regressions.

## RESULTS

*Spatial Distributions of Nesting and Nonnesting Emergences.* — We identified 1470 leatherback nests over the 2 nesting seasons. Nest placements were not evenly distributed among sections along the north-to-south coastal axis ( $\chi^2 = 533.9$ ,  $p < 0.001$ ; Fig. 3). Nesting frequency was lowest at either end of the beach, generally corresponding to the areas of anthropogenic development (ANOVA:  $F_{1,35} = 82.4$ ,  $p < 0.001$ ). Nest frequency in developed areas was  $17 \pm 3$  (mean  $\pm$  SE) compared with  $57 \pm 3$  in the undeveloped sections.

We observed 310 nonnesting emergences, and these observations were not evenly distributed among beach sections ( $\chi^2 = 66.9$ ,  $p < 0.01$ ). A higher percentage of total emergences did not result in egg laying (i.e., a nonnesting emergence) in the developed sections of the beach (ANOVA:  $F_{1,35} = 24.9$ ,  $p < 0.001$ ; Fig. 4). Nonnesting emergences comprised  $34.6\% \pm 3.8\%$  of total emergences in the developed beach sections, but only  $13.1\% \pm 1.0\%$  in undeveloped sections.



**Figure 4.** Percentage of leatherback nesting and nonnesting emergences along Playa Grande. Development occurs between 0.0 and 0.8 km and between 3.0 and 3.6 km.

*Environmental Characteristics.* — Sand characteristics differed between developed and undeveloped sections with respect to both chemical and physical attributes. Undeveloped areas had steeper slopes, higher pH, and more air-filled pore space, but lower water content and salinity than developed areas (MANOVA: Wilks'  $\lambda = 0.37$ ,  $F_{8,25} = 5.22$ ,  $p = 0.001$ ; Table 1). Undeveloped areas had significantly higher proportions of sand particles in the medium and fine size classes than developed areas, while developed areas were comprised of more particles in the very fine and silt size classes relative to undeveloped areas (MANOVA: Wilks'  $\lambda = 0.22$ ,  $F_{6,27} = 15.90$ ,  $p < 0.001$ ; Fig. 5).

*Environmental Correlates of Nest Spatial Distribution.* — Nest frequency was negatively correlated with sand salinity and positively correlated with pH, together explaining nearly 60% of the variation in our stepwise regression model ( $F_{2,31} = 23.37$ ,  $r^2 = 0.597$ ,  $p < 0.001$ ). Nesting frequency was also positively correlated with beach slope ( $F_{1,35} = 35.58$ ,  $p < 0.001$ ; Figs. 3 and 6). Additionally, nest frequency was positively correlated with the amount of sand in the fine particle size class, but negatively correlated with the amount of particles in the silt size class (Table 2; Fig. 7). Percentage of nonnesting emergence was negatively correlated with beach slope ( $F_{1,35} = 5.22$ ,  $r^2 = 0.13$ ,  $p < 0.029$ ) and pH ( $F_{1,33} = 10.76$ ,  $r^2 = 0.29$ ,  $p < 0.007$ ), and

positively correlated with silt ( $F_{1,34} = 25.88$ ,  $r^2 = 0.44$ ,  $p < 0.001$ ).

Nesting frequency was not significantly correlated with adjacent nearshore depth profiles within 0.4 km of the beach, but from 0.5 to 1 km nest frequency was positively correlated with water depth (Table 3; Fig. 8).

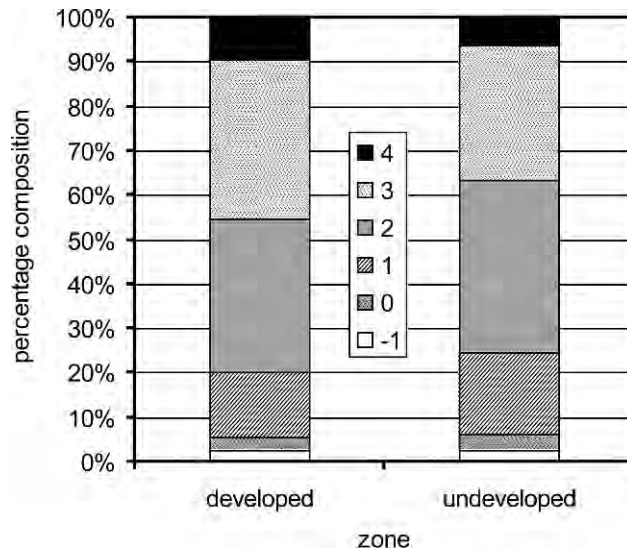
## DISCUSSION

*Nest Site Choice.* — Leatherbacks at Playa Grande nested nonrandomly with respect to several environmental variables. Nest frequency was related to aspects of the offshore approach, beach slope along the water-to-vegetation axis, physical and chemical characteristics of the sand, and anthropogenic development. Because we were limited to examining correlations of nest frequency with environmental factors, we cannot conclusively demonstrate that turtles were exhibiting avoidance of or preference for any environmental feature. Nevertheless, we identified a suite of environmental variables that may serve as proximal cues for females when selecting nest sites. These findings, along with those of Kamel and Mrosovsky (2004) and Hernández et al. (2007) suggest that leatherbacks are able to assess and respond to some forms of spatial environmental variation during the nesting process.

Several of the environmental correlates of nest frequency likely serve as indicators of nest site quality.

**Table 1.** Comparison of sand physical and chemical characteristics between developed and undeveloped sections of the beach at Playa Grande, Costa Rica. Values are means  $\pm$  SE.

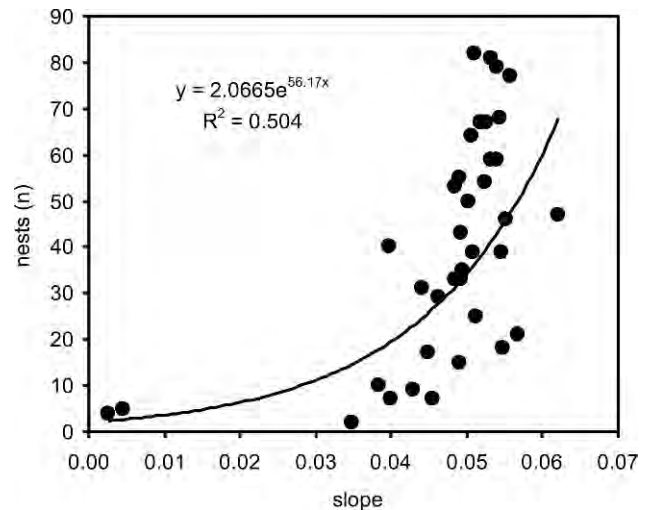
Zone	Slope (m)	pH	Water (%)	Salinity (ppt)	Air-filled pore space (% cm <sup>3</sup> )	Carbonate (% CO-C)	Organic content (%)	Porosity (% cm <sup>3</sup> )
Developed	0.041 $\pm$ 0.004	8.4 $\pm$ 0.1	0.11 $\pm$ 0.02	0.13 $\pm$ 0.02	0.58 $\pm$ 0.01	0.13 $\pm$ 0.01	0.034 $\pm$ 0.003	0.68 $\pm$ 0.01
Undeveloped	0.052 $\pm$ 0.001	8.7 $\pm$ 0.1	0.07 $\pm$ 0.01	0.05 $\pm$ 0.01	0.63 $\pm$ 0.01	0.15 $\pm$ 0.01	0.038 $\pm$ 0.003	0.69 $\pm$ 0.01



**Figure 5.** Percentage composition of sand particles in 6 size classes on developed and undeveloped beach sections of Playa Grande, Costa Rica. Particle classes correspond to the Phi scale, ranging from very coarse (Phi = -1, 2-mm diameter) to silt (Phi = 4, 0.0625-mm diameter).

For instance, emergence adjacent to areas with deeper water and limited shallow offshore obstructions (e.g., coral reefs, rocks, sandbars) presumably reduces the probability of injury and energy expenditure for such a large, soft-skinned, and pelagic animal during their approach to the beach (Pritchard 1971; Eckert 1987). By choosing a steeper littoral approach, a turtle may also position itself to emerge on a more steeply sloping section of beach. Such an emergence would minimize overland travel distance and time to access high elevation areas that are less prone to flooding from tides, storm surges, or groundwater (Hendrickson and Balasingham 1966; Pritchard 1971). Consistent with these explanations, leatherbacks at Playa Grande nested more frequently in beach sections with steeper slopes, higher elevation dunes, and deeper offshore areas, while nonnesting emergences were negatively correlated with beach slope. Hernández et al. (2007) also noted leatherbacks nesting in areas with steeper littoral slopes.

It is less clear to what extent correlations between sand attributes and nest frequency could reflect the quality of the nest environment. Physical characteristics of the substrate



**Figure 6.** Relationship between leatherback nesting frequency and beach slope at Playa Grande, Costa Rica.

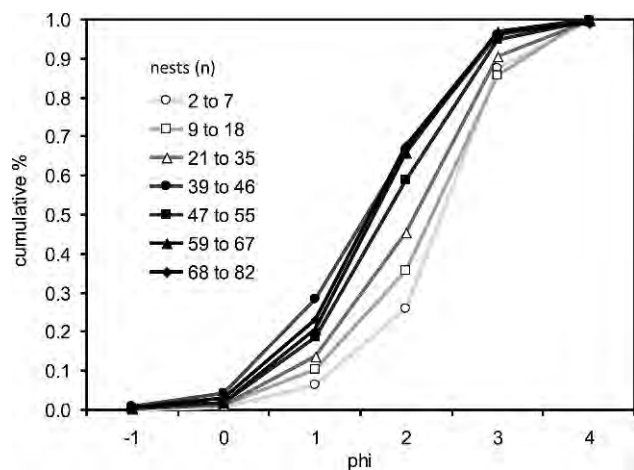
can influence respiratory gas diffusion, hydration, stability of the nest cavity, and in turn egg survival and performance of hatchlings (Kraemer and Bell 1980; McGhee 1990; Mortimer 1990; Ackerman 1997). Leatherbacks at Playa Grande nested in association with beach sections having proportionally more particles in the fine size classes and less silt. False crawls and aborted nesting attempts were also more common in areas with higher silt content. Nests in sand with large particle sizes can experience lower survivorship, though female green turtles (*Chelonia mydas*) do not select nest sites based on this attribute (Mortimer 1982, 1990). Loggerhead turtles (*Caretta caretta*) nest in areas with well-sorted sands in the medium to fine size classes, while avoiding smaller grain sizes prone to compaction (Karavas et al. 2005). Leatherbacks and other sea turtles often nest successfully on beaches with widely variable particle diameters (Carr and Ogren 1959; Hendrickson and Balasingam 1966, Pritchard 1971; Stancyk and Ross 1978; Mortimer 1982), suggesting sand particle size alone is not likely a cue to which nesting turtles are particularly responsive.

With respect to sand chemical properties, nest frequency was negatively correlated with salinity and positively correlated with pH, while nonnesting emer-

**Table 2.** Relationships between the number of leatherback nests and sand grain sizes along Playa Grande, Costa Rica.

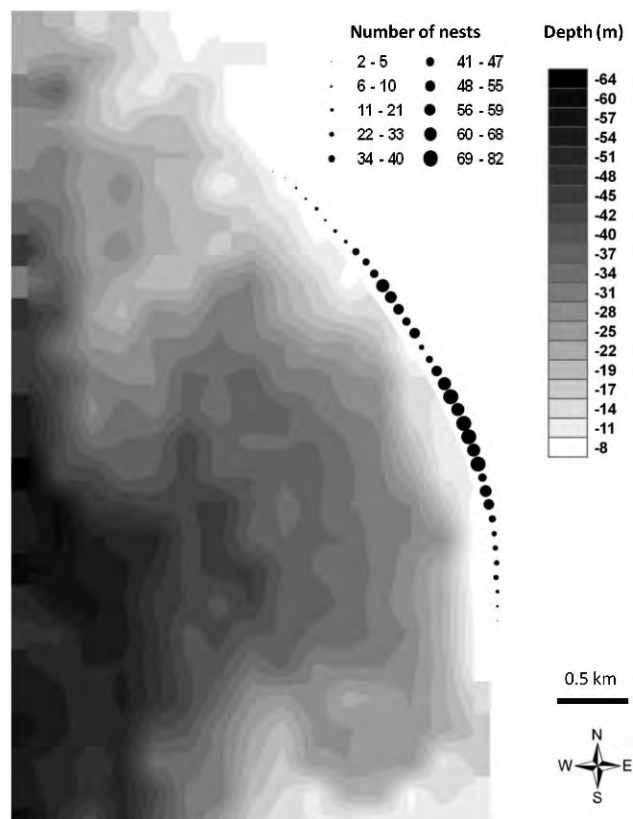
Phi	Description	$\beta$	df	F	R <sup>2</sup>	p <sup>a</sup>
-1	Very coarse	0.244	1, 5	0.32	0.06	0.598
0	Coarse	-0.024	1, 5	0.00	0.00	0.959
1	Medium	0.681	1, 5	4.33	0.46	0.092
2	Fine	0.955	1, 5	51.28	0.91	0.001**
3	Very fine	-0.545	1, 5	2.11	0.30	0.206
4	Silt	-0.869	1, 5	15.40	0.76	0.011*

<sup>a</sup> \* Significant at  $\alpha = 0.05$ . \*\* Significant at  $\alpha = 0.008$  after Dunn-Sidak adjustment.



**Figure 7.** Comparison of cumulative sand particle size distributions among sections that differ in leatherback nesting frequency at Playa Grande, Costa Rica. Particle classes correspond to the Phi scale, ranging from very coarse (Phi = -1, 2-mm diameter) to silt (Phi = 4, 0.0625-mm diameter).

genes were negatively correlated with pH. Females of other sea turtles nest on beaches with low salinity or conductivity (Johannes and Rimmer 1984; Wood and Bjorndal 2000), and clutch survival can be negatively associated with sand salinity (Mortimer 1990). However, eggs of the freshwater alligator snapping turtle (*Macrochelys temminckii*) were not sensitive to variation in salinity of the incubation substrate (Rauschenberger et al. 2004), and embryos from slider turtles (*Trachemys scripta*) did not incorporate ions from highly conductive nest substrates during incubation (Nagle et al. 2001). Embryos would certainly be sensitive to extremes in the chemical and mineral constituents of the nest environment, but given 1) the relatively narrow ranges of pH (7.6–8.9) and salinity (0.01–0.25 ppt) detected along the beach, 2) our uncertainties of biological effects such limited variation would have on the clutch, and 3) questions as to the reliability of these cues or a female's ability to sense such variation (Wood and Bjorndal 2000),



**Figure 8.** Spatial distribution of leatherback nesting frequency on Playa Grande, Costa Rica, relative to offshore bathymetry.

we are skeptical whether these correlations reflect female responses to these cues per se. Alternatively, these physical and chemical characteristics could be associated with other more critical cues to which turtles are responding during the nesting process.

*Implications for Coastal Development.* — Anthropogenic development is one such factor to which leatherbacks are potentially responding at Playa Grande. Nesting activity was consistently highest along sections of undeveloped beach, the only exception occurring around the 1.6–1.7-km segment, where storm activity and

**Table 3.** Relationships between number of leatherback nests per beach section and water depth at increasing intervals from shore at Playa Grande, Costa Rica.

Distance from low tide line (km)	df	$\beta$	F	R <sup>2</sup>	p <sup>a</sup>
0.1	1, 35	0.246	2.25	0.06	0.143
0.2	1, 35	-0.053	0.10	0.00	0.756
0.3	1, 35	0.075	0.20	0.01	0.660
0.4	1, 35	0.324	4.10	0.11	0.050*
0.5	1, 35	0.472	10.01	0.22	0.003**
0.6	1, 35	0.524	13.22	0.27	0.001**
0.7	1, 35	0.482	10.56	0.23	0.003**
0.8	1, 35	0.475	10.17	0.23	0.003**
0.9	1, 35	0.538	14.29	0.29	0.001**
1.0	1, 35	0.579	17.62	0.34	< 0.001**

<sup>a</sup> \* Significant at  $\alpha = 0.05$ . \*\* Significant at  $\alpha = 0.005$  after Dunn-Sidak adjustment.



floodwater discharge from the forest periodically wash out the beach dune, with additional anthropogenic disturbance by bulldozer to improve drainage in the recent past (Fig. 3; Nordmoe et al. 2004; F. Paladino, *pers. obs.*). It is also noteworthy that nonnesting emergences (as a proportion of total emergences) were nearly three times more likely in developed sections of the beach relative to undeveloped areas, suggesting some mismatch between cues used in the initial approach and those used to assess nest site quality on the beach following emergence. Apparent avoidance of developed areas has been observed previously at Playa Grande, Costa Rica (Steyermark et al. 1996; Nordmoe et al. 2004) and at Playa Paraguito, Venezuela (Hernández et al. 2007), but these studies did not specifically assess how beach environments varied according to proximity to development. Developed segments of the beach had shallower slopes, lower elevations, lower pH, higher salinity, and more silt than did undeveloped areas—all of which are chemical and physical factors to which leatherbacks respond when selecting a nest location. Nearly all of these environmental factors can also be linked to the impacts of erosion, which is a process typically accelerated by many forms of coastal development (García and Servera 2003), especially that which displaces stabilizing vegetation (Levin et al. 2006). As beaches adjacent to developed areas erode, dune elevation decreases, subjecting a larger area to a higher frequency of seawater flooding, compaction, and further erosion from tides and storm surges (Meyer-Arendt 1991). We suggest that erosion may also bring about several associated chemical and physical alterations to the beach environment, such as higher water content and salinity (from increased frequency and duration of seawater flooding) and silt deposition.

While dune erosion is one plausible mechanism explaining leatherback nest distributions, we cannot discount other effects of anthropogenic development that can impact turtle nesting such as artificial light, silhouette of background, or other disturbances associated with human activity. In particular, given its importance to turtle nesting, future studies should explore variation in artificial light intensity along the beach and assess whether photopollution factors into adult nest site selection and hatchling success at PNMB (e.g., Witherington 1992; Salmon et al. 1995). It should also be noted that we cannot demonstrate that beach development alone has altered beach physical and chemical characteristics, nor has it necessarily caused the observed turtle nesting distribution—only that these factors were correlated with development. Such a link could be strengthened by demonstrating a change in spatial nest distribution under different stages of beach development, but unfortunately we lack data on nest distribution at Playa Grande prior to the establishment of the Tamarindo Wildlife Refuge in the late 1980s, and then as a national park in 1991 (Spotila and Paladino 2004). There has been little change to either

tourism development or leatherback nest distributions along the beach throughout our long-term monitoring (Steyermark et al. 1996; Nordmoe et al. 2004). Thus, it is plausible that natural processes could also account for the relationships observed in this study, but to examine such factors here without additional data would be speculative.

Despite the limitations, we argue that our findings have important implications for conservation and management of high quality nesting beaches. The recent collapse of the leatherback population at Playa Grande is most likely a consequence of increased fisheries bycatch and the residual effects from an earlier egg harvest industry (Santidrián Tomillo et al. 2008). However, beaches outside of the PNMB, such as nearby Playa Tamarindo and Playa Flamingo, once hosted nesting leatherbacks that soon disappeared following coastal development (Steyermark et al. 1996), implicating beachfront development as a contributor to leatherback declines and local extinctions in this region and perhaps others. Leatherbacks are known to shift to different nesting beaches in response to changing beach quality or for undetermined reasons (Girindot and Fretey 1997; Hilterman and Goverse 2007; Santidrián Tomillo et al. 2007), raising the possibility that a nesting beach may be vacated following disruption resulting from anthropogenic development as well.

With the inclusion of Playa Grande as part of a national park, rates of beachfront development have been slowed relative to other areas of Costa Rica (Spotila and Paladino 2004), yet protection of Playa Grande and its nesting leatherbacks remains tenuous. The Costa Rica Ministry of Environment and Energy must continually entertain proposals from developers to convert PNMB into a mixed-management park for sustainable development in support of coastal ecotourism (Spotila and Paladino 2004). Such opportunities could provide much needed resources for the park, but perhaps at the expense of the availability and quality of leatherback nesting sites. It remains to be seen whether or to what degree beaches can be developed “sustainably”—that is, in a manner that supports a growing tourist industry and associated infrastructure while maintaining high-quality and attractive nesting environments for leatherbacks.

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