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Sea Turtle Nesting Habitat on the US Naval Station, Guantanamo Bay, Cuba: A Comparison of Habitat Suitability Index Models

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Abstract. – **Sea turtle species observed nesting at the US Naval Station at Guantanamo Bay, Cuba (GTMO) include greens (*Chelonia mydas*) and hawksbills (*Eretmochelys imbricata*), both of which are classified as endangered by the World Conservation Union (IUCN). As Cuba and its neighbors continue to develop their coasts, all efforts should be made to preserve this important nesting refuge. Habitat suitability index models are one tool with which managers can generate hypotheses and experiment with management options. This study used an observational dataset of nests and measured habitat variables to develop habitat suitability index models in a geographic information system. The first objective was to compare the performance of 3 different habitat model-building approaches in order to determine which technique, if any, provides reliable information on sea turtle nesting habitat preferences. A habitat suitability index score for each beach zone was computed using 1) suitability indices with expert weights, 2) unscaled environmental variables with regression-based weights, and 3) a combination of suitability indices with regression-based weights. The second objective was to use the models to lend insight into important environmental descriptors of suitable sea turtle habitat for GTMO. All models predicted moderately well with 40% prediction rates, even though they assigned different weights to the variables. Moderate model performance may be attributed to low samples sizes and/or nest site fidelity that is unrelated to environmental factors. Overall, differences between empirical and expert model results reflect a shift from a regional (Caribbean) to a local scale of analysis (GTMO). However, in all models, compaction of the substrate was almost twice as influential as the other variables, indicating that the looser the sand, the more suitable the habitat. Conservation implications and suggestions for future research are discussed.**

Key Words. – **Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; *Chelonia mydas*; sea turtle; habitat suitability; models; nesting; environmental; fidelity; multiple regression; validity; conservation; Guantanamo Bay; Cuba**

Studies and conservation efforts that focus on nesting habitats are needed to ensure the survival of endangered sea turtle populations (Lutz and Musick 1997; Klemens 2000; Witherington 2000). Species observed nesting at the US Naval Station at Guantanamo Bay, Cuba (GTMO) (Fig. 1) include greens (*Chelonia mydas*) and hawksbills (*Eretmochelys imbricata*). Hawksbills are classified as critically endangered (IUCN 2006) and greens as endangered (Seminoff 2004) by the World Conservation Union. The Convention on International Trade in Endangered Species of Wild Fauna and Flora prohibits commerce of sea turtle products for participating nations. The US Endangered Species Act of 1973 lists sea turtles as endangered, and the National Environmental Protection Act of 1969 requires the conservation of sea turtles and their habitat by federal agencies such as the US Navy.

Sea turtle populations are often monitored on nesting beaches because they can exhibit relatively strong nest site fidelity by returning to their natal beaches or previous nesting sites (Bjorndal 1995). We considered the greens and hawksbills observed nesting on GTMO as populations unique to the military base.

Nesting seasons vary widely among sea turtle species in terms of frequency and timing; most Caribbean species nest every 2 to 3 years from March through September (Márquez 1990). Several nests of eggs may be laid each season. Hawksbills average 2.3 nests per season (Márquez 1990), and greens tend to nest 2 to 3 times per season (Carr et al. 1978). Females reach sexual maturity at around 15 to 20 years (Bjorndal 1995), and have average lifespans of 50 to 100 years; sea turtles are relatively long-lived compared with other vertebrates (Klemens 2000).

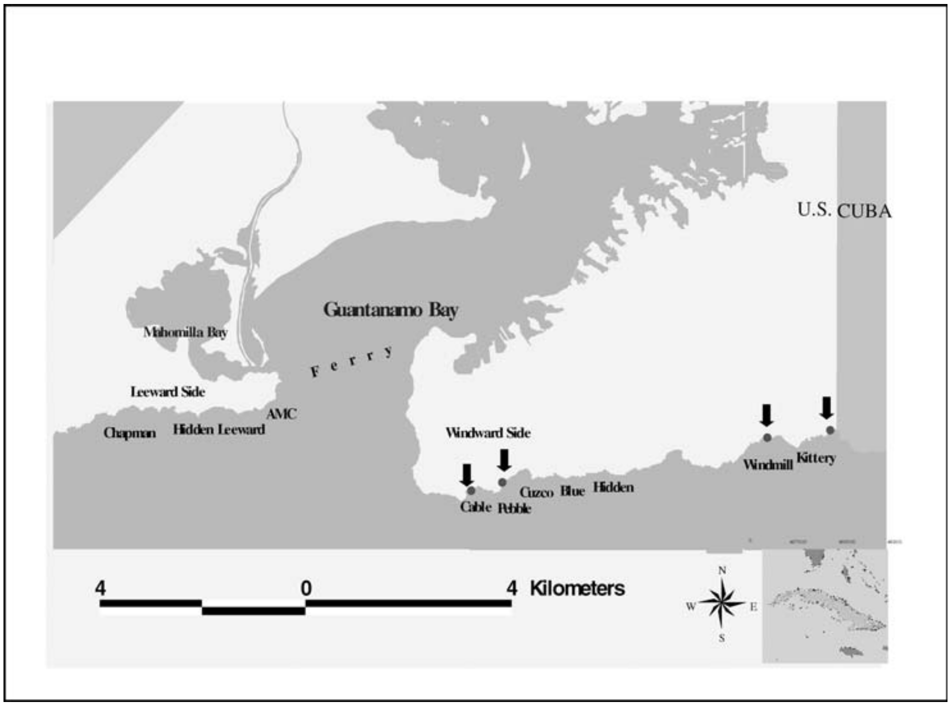

Figure 1. Map of study beaches on the US Naval Station at Guantanamo Bay. Inset map shows Cuba.

Therefore, population declines may not be obvious to managers or adequately addressed with short-term management plans (Magnuson 1990). Better understanding of sea turtles' habitat needs is critical for the survival of these species.

General threats to sea turtles include illegal fishing and by-catch, poaching of eggs from nests, and the development of nesting beaches for tourism, any combination of which may cause irreversible extirpations (Carr 1967). Natural resource managers at GTMO monitor threats to sea turtle nesting habitat including artificial lighting, concrete surfaces, and beach driving, and implement conservation plans for sea turtle habitat.

Geographic information systems (GIS) and associated models of sea turtle nesting preference are potentially important tools that can aid managers in the development of conservation plans. This study uses habitat suitability index (HSI) models to explore the spatial preferences of nesting turtles at GTMO. One goal of the study was the development of tools for wildlife managers who are limited to working with small datasets and rapid environmental assessments. If effective, such tools could be economical alternatives to costly, time-consuming monitoring. Predictions of suitable habitat sometimes serve as justification for delaying development projects until more in-depth studies can be undertaken. Another benefit to HSI models is that environmental variables can be artificially inflated or deflated in order to estimate management decisions' impacts on a species' habitat.

HSI Models

HSI models are deductive wildlife-habitat relationship models developed by the US Fish and Wildlife Service (USFWS) to simplify and represent the major environmental factors influencing a target species (USFWS 1981; Morrison et al. 1992). An HSI model should represent the best balance and interaction of variables for suitable habitat. Incorporation of HSI models within a GIS framework provides an approach for assessing spatial differences in potential habitat quality. HSI models in a GIS framework have previously been developed for sea turtle marine habitat (Schmid 1994; Coyne et al. 1998), but to our knowledge HSI models for sea turtle nesting habitat have not been created.

One objective of this study was to test the best approach to HSI building for sea turtle nesting habitat on GTMO. In the USFWS manual "Development of Habitat Suitability Models" (1981), several model-building techniques are described.

A weighted component index model, using expert opinion, transforms each input environmental variable to a suitability index (SI) ranging from 0.0 (unsuitable) to 1.0 (optimal). The SI transformation can be based on expert opinion and/or a literature review. When empirical data are available, SI scores are often determined from a graph of habitat classes against species abundance. An SI score of 1.0 is given to the habitat class with the highest observed abundance; a score of 0.0 is assigned to habitat classes with no abundance. This method allows managers to easily understand the importance of a single variable to habitat suitability (HS). In models with multiple variables, the weighted composite index (CI) is a weighted arithmetic mean (or the geometric mean in cases with limiting variables such as food sources) of all the SIs, again with a range from 0.0 to 1.0 (USFWS 1981; Stoms and Estes 1993).

In a regression HSI model approach, linear least squares regression is used to relate environmental variables to variation in the abundance or density of the target species. The results are normalized by the maximum observed density to produce an HSI score between 0.0 (unsuitable) and 1.0 (optimal).

In addition to the CI and regression methods, our study employed a third approach, which is a combination of the two. In this "combined" model, coefficients from the regression HSI model are used to weight the relative importance of the variables, which are represented by SI scores (0.0–1.0). This approach is essentially the same as the expert-weighted component index model, except that the weights are the standardized regression coefficients from the regression approach. This empirical approach eliminates the need for expert opinion to determine the relative weights of variables and can lead to more site-specific models with higher predictive accuracy (Morrison et al. 1992). The final scores are, again, CIs ranging from 0.0 (unsuitable) to 1.0 (optimal).

METHODS

In this study, we compared the performance of 3 HSI model-building approaches for the GTMO site. An HSI score for each area was computed using 1) suitability indices with expert weights, 2) unscaled environmental variables with regression-based weights, and 3) suitability indices with regression-based weights. We tested the ability of each model to predict observed HS classes (low, medium low, medium high, and high) and the ability to rank areas relative to others in terms of observed nest density (ND) (1–15). Based on the most accurate HSI model-building approach, we then explored the relative importance of individual environmental variables as indicators of nesting HS.

Observed Nest Density

For many HS studies, ND is assumed to represent HS (USFWS 1981). An observed nest attempt, or a body pit in the sand, was the unit of measurement for this study. From the dataset we were not able to distinguish "false" nests, or abandoned nesting attempts, from successful nests, nor could we have attributed false nesting to poor environmental conditions vs. other disturbances such as predators. Our study's criterion for suitable habitat was essentially female nest site preference, so regardless of whether eggs were laid or not, if a female attempted to dig a nest, this site was interpreted as "suitable."

Resident volunteers on GTMO recorded nest attempts from 1999 to 2001 for Windmill, Kittery, Cable, and Pebble beaches (Fig. 1). The beaches were partitioned into 15 50-m-wide zones following methods from other sea turtle habitat studies (Loop et al. 1995) (for example, see Fig. 2). Over the 2.5 years, a reasonable temporal window for a typical 2- to 3-year nesting cycle, observations of fresh sea turtle nests were collected at a time-step ranging from 2 to 30 days. Volunteers recorded a total of 318 fresh turtle nests by walking an entire beach in the mornings,

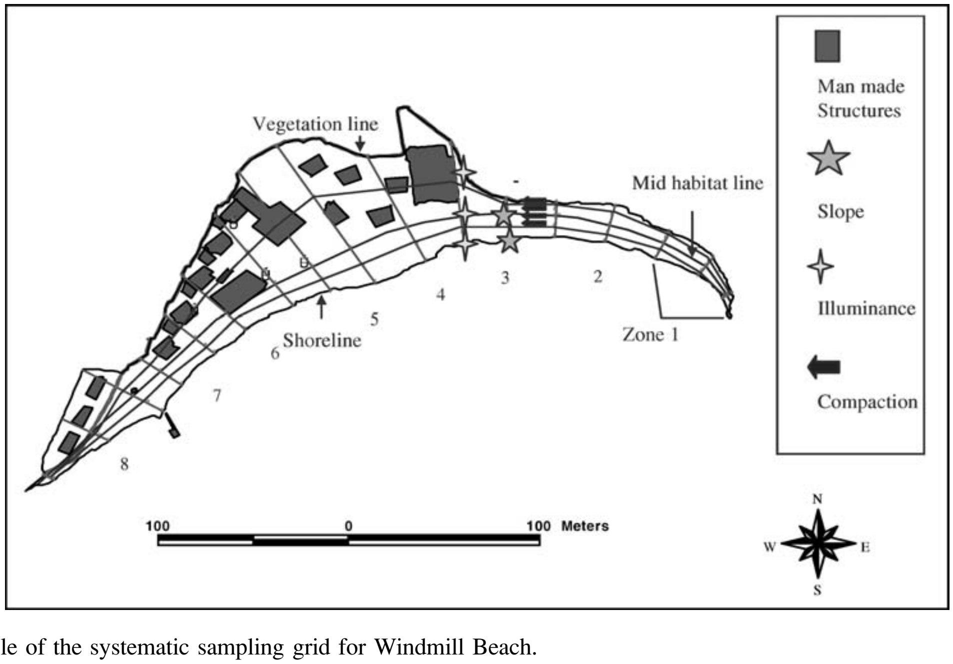

Figure 2. Example of the systematic sampling grid for Windmill Beach.

and recording the location of nests and tracks on datasheets. Eighty-nine percent of the nests were determined to be those of hawksbills based on the tracks' alternating crawl patterns and small size. Nests were observed throughout the year with a peak in the spring and summer. ND was calculated by dividing the number of nests by the area of the zone and by the number of days sampled, thereby accounting for variation in volunteer effort and beach widths.

Derivation of the Environmental Variables

Justification for our environmental variables (Table 1) and data collection methods were derived from an extensive review of the literature and consultations with sea turtle experts Karen and Scott Eckert (Nicholas School of the Environment and Earth Sciences, Duke University), and Blair Witherington (Florida Fish and Wildlife Conservation Commission).

Table 1. Environmental variables and expert weights for greens and hawksbills, and the average of the weights between the 2 species. This review represents a useful synopsis of research and interviews of experts about turtle nesting habitat.

Environmental variable	Literature and expert opinion	Mean weight	Hawksbills weight	Greens weight
Historical nesting records	Nest site fidelity is highest for greens, lower for hawksbills (Márquez 1990).	No Data	No Data	No Data
Compaction of sand	Recreational use, vehicle traffic, and sand replacement from erosion (beach renourishment) can increase compaction of the sand (Nelson 1988). A low compaction level can increase the amount of energy required to dig the nest, whereas a high compaction level may prevent digging and may cause abandonment of nesting attempts (Steinitz et al. 1998; Lutz and Musick 1997). Other studies (Williams et al. 1983; Horrocks and Scott 1991; Trindel et al. 1998).	3	3	3
Slope	Steep slopes can increase the amount of energy required to reach a preferred nesting site. Low slopes may allow tides to inundate nests. Low slopes may also increase the distance a female has to crawl to reach a high and dry area above the tide line (Moncada et al. 1999). Greens prefer low slopes (Márquez 1990; Williams et al. 1983). Smaller hawksbills can crawl up steeper slopes (Schoeder and Murphy 1999). Other studies (Horrocks and Scott 1991; Loop et al. 1995; Wood and Bjorndal 2000; Garmestani et al. 2000).	1.5	2	1
Artificial lighting	Sea turtles use visual cues such as shapes, shadows, and silhouettes for the timing and location of nest placement (Ernest and Brun 1998). Artificial lighting has been shown to disrupt nest-site selection, increase nest abandonment, and disorient nesting females emerging or returning to the sea (Magnuson 1990; Lutz and Musick 1997; Witherington 2000). Other studies (Williams et al. 1983; Horrocks and Scott 1991; Woody et al. 1998).	3	3	3
Percentage of vegetation	Hawksbills prefer perimeter areas of a beach next to vegetation. The roots may loosen compact substrate, or make substrate more compact with moisture, making digging easier (Mortimer 1995). However, roots may become an obstacle in some cases (Bustard and Greenham 1968). Other studies (Loop et al. 1995; Garmestani et al. 2000).	1.5	3	0
Zone width	Greens nest on wide beaches (Márquez 1990). Hawksbills can traverse wider beaches with little energy expenditure (Schoeder and Murphy 1999). Other studies (Loop et al. 1995; Chávez 1998; Moncada et al. 1999; Garmestani et al. 2000).	1.5	1	2
Percentage of man-made obstacles	Seawalls, sandbags, rock piles, and other barriers can prevent females from reaching nesting sites. Anthropogenic obstacles such as seawalls, kiddy pools, artificial reefs, parking lots, cabanas or sports courts may become barriers (Steinitz et al. 1998).	2	3	1
Percentage of sand	Greens prefer loose, sandy areas. Hawksbills are known to dig in compact soils near vegetation (Márquez 1990; Williams et al. 1983).	2	2	2
Percentage of debris	Debris in the sand can impede nest digging (K. Eckert, *pers. comm.*, 2001).	2	2	2

Environmental data were collected in the field by the senior author and Tandora Grant (Zoological Society of San Diego) in April of 2001. All 4 beaches were mapped with a global positioning system (GPS) unit (Trimble, Inc.) with submeter accuracy, and then sampled using a systematic grid (see Fig. 2) for the following variables.

Vegetation Percentage. — Canopy perimeters of trees and bushes were mapped from the ground using the GPS. Two square meters for each palm tree were added to approximate the extent of a root ball. Vegetation that bordered but was outside the zone could have contributed to habitat with its roots (loosening or compacting the sand) or foliage (providing cover), or could have attracted turtles visually. Therefore, the bordering vegetation area was included and estimated to be 1 m wide times its length. Percentage of vegetation cover per zone was the final variable.

Man-Made Obstacles Percentage. — Structures such as cabanas, tables, roads, and sport courts, but not point structures such as signs, were considered obstacles to nesting habitat. We mapped the perimeters of obstacles with the GPS and calculated the percentage of area for each zone.

Illuminance. — Illuminance, or ambient light, was measured in lux with a Minolta T-10/T-10M illuminance meter with a silicon photocell. Illuminance readings were taken at night before moonrise at 3 points along zone transects: shoreline, midhabitat line, and vegetation line (see Fig. 2). The light meter was held about 10 cm over the sand (the approximate height of a turtle's eye) in each of 4 directions—towards shore, away from shore, and in either direction parallel to shore. Because of the high variability of the light meter readings in response to changes in angle to the sand, an average of 3 readings was reported for each direction. Then, readings were summed for each transect, and averaged between 2 edge transects in order to approximate the amount of illuminance a female turtle might experience while searching for suitable habitat in the center of the zone. One limitation of the light meter is that urban glow above treetops and cliffs, which may disturb turtles (USFWS 1999), did not register above 0.0 lux and, therefore, was not included in this study.

Compaction. — A Dickey John soil compaction tool (Forestry Suppliers, Inc.) measured the average depth (in inches) of sand at which the substrate withstood 250 pounds per square inch (PSI) of pressure. Higher readings represented looser substrate. One designated researcher (for consistency) took 3 measurements at 4 points along a transect (see Fig. 2). The mean of the 3 measurements was calculated, and the mean of the 4 sample points was the compaction variable for each zone.

Sand Percentage. — While taking the compaction measurements, we also recorded a visual estimate of the predominant substrate class: sand, pebbles, or soil with a high percentage of clay. The number of sample points containing sand was divided by the total number of sample points in order to approximate the percentage of sand for each zone.

Debris Percentage. — While taking compaction measurements, we also recorded the presence or absence of debris such as wood, trash, or other potential obstacles to digging. The number of sample points containing debris was divided by the total number of sample points to calculate percentage of debris for each zone.

Width. — The distance from the shoreline to the back of the beach (the "vegetation line" in Fig. 2) was used to determine zone width. Distance was sampled 3 times and then averaged for each zone.

Slope. — A clinometer was used to measure slope along transects from the shoreline to the midhabitat line, and again from the midhabitat line to the back of the beach (see Fig. 2). Two readings along each transect were taken in order to account for the intertidal berms along the shore, and any irregular topology closer to the back of the beach where vegetation could affect erosion patterns. For consistency, one researcher measured the angle between her eye and the eye of a researcher of approximately the same height.

Because the widths of the zones vary, slope was normalized by the distance between researchers. First, the distance was divided by the total transect distance in order to calculate the percentage of the transect being assessed. Then, the percentage of transect was multiplied by the slope value. The normalized slope value represented the average steepness of the crawl from the shoreline to the back of the beach, where most nests were found.

Variable Selection

To reduce the number of variables in the HSI models and to minimize potential intercorrelation between independent variables, a Pearson's correlation matrix was calculated (Table 2). In order to minimize spatial dependence, we used only odd-numbered zones that did not share a boundary. Where high colinearity was present, the variable with the stronger relationship with ND was chosen to remain in the model. After this step, only man-made obstacles, debris percentage, illuminance, compaction, and width remained. It is important to note that the other 3 variables could still be important descriptors of habitat preference. The same variables were used in all models in order to compare the performance of the 3 model-building methods.

Suitability Index Graphs

In order to standardize the environmental variables, they were transformed to an SI scale in a histogram and assigned an SI score from unsuitable (0.0) to optimal (1.0). To create appropriate axes for the histograms, ND measurements were pooled from the 15 zones. Then, the optimal number of class breaks (low, medium low, etc.) was determined based on the CLASSITNT program (B. Buttenfield, Colorado State University) that calculates variance in a dataset using different numbers of classes.

Table 2. A Pearson's correlation matrix was used to test the correlation (*R*) of nest density (ND) and the individual variable in order to reduce the number of variables in the models.

	ND	Percentage of vegetation	Percentage man-made	Illuminance	Compaction	Percentage of sand	Percentage of debris	Width	Slope
ND	1.000								
Percentage of vegetation	−0.367	1.000							
Percentage man-made	−0.547	−0.098	1.000						
Illuminance	−0.310	−0.587	0.186	1.000					
Compaction	0.909	−0.047	−0.481	−0.267	1.000				
Percentage of sand	0.565	−0.473	−0.329	0.494	0.583	1.000			
Percentage of debris	0.466	0.860	−0.038	−0.569	0.681	0.300	1.000		
Width	−0.401	−0.658	0.825	0.141	−0.557	−0.236	−0.368	1.000	
Slope	0.390	−0.658	−0.597	−0.642	0.498	0.271	0.671	−0.795	1.000

Four classes minimized variance for all variables except sand percentage, which required 5 classes. Using the optimal number of classes, numerical class thresholds were derived based on "natural breaks," calculated in ArcView 3.2 (ESRI, Redlands, CA) using Jenks optimization statistic (Jenks and Coulson 1963; Dent 1999). Mean ND per class was calculated for each environmental class, and graphed in an SI histogram. For that calculation, we again used odd-numbered zones that did not share boundaries to minimize spatial dependence and to reserve some zones for model testing. Finally, using the histograms, we assigned SI scores for each environmental variable to both even- and odd-numbered zones (Fig. 3).

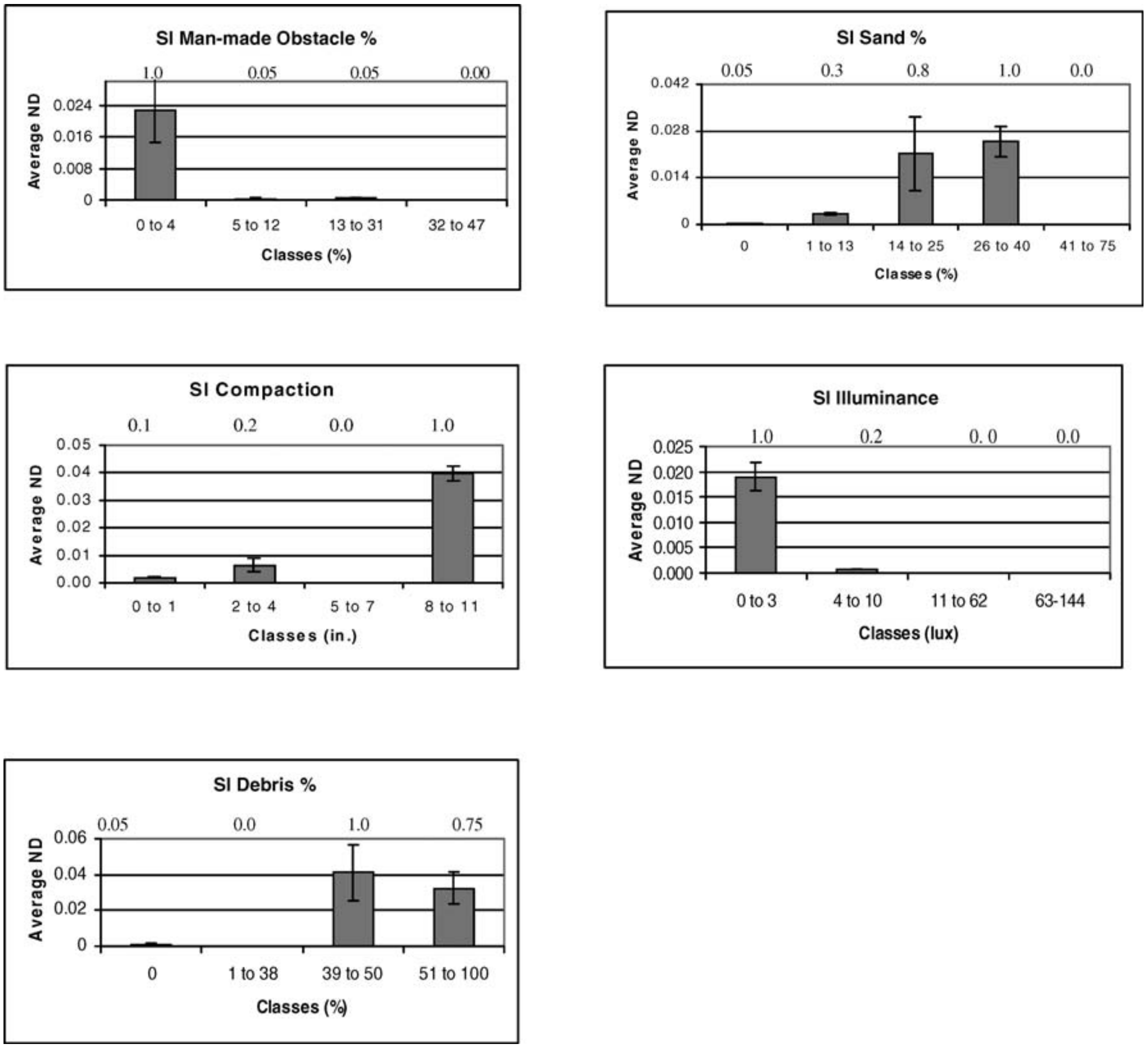

Figure 3. SI graphs for 5 environmental variables. Error bars show variation in the average ND per environmental class. The SI score is shown above the bars.

Model 1 – Expert Model

Sea turtle researchers Karen and Scott Eckert gave their expert opinions on the relative weights of the variables in terms of their importance to greens and hawksbills (Table 1). Their opinions were based on the literature and their research experience in the wider Caribbean, without having visited the study area. We multiplied the expert-based weights for each variable by the SI scores (Fig. 3), and calculated the mean score for the zone, the CI score. The arithmetic mean was chosen over the geometric mean because we assumed that no variable could be limiting while nest site fidelity (which may or may not be related to the environment) was a possible factor influencing nest site selection. CI scores were used to rank the zones from 1 through 15, or from least suitable to most suitable. Predicted ranks were then compared to observed ND rankings, from 1 to 15.

Model 2 – Regression HSI Model

The regression HSI model was based on a linear least squares multiple regression model of observed nest densities and environmental data. In this exercise we also used odd zones that did not share boundaries, and regression residuals were checked for normal distributions. An alpha = 0.05 confidence level was used in significance testing.

Predicted ND was then converted to an HSI score by normalizing to maximum observed ND:

$$\text{HSI} = \text{predicted density}/\text{maximum observed density}$$

Model output was an HSI score for each zone. HSI scores were ranked from 1 through 15, and compared to the ranks of observed ND from 1 through 15.

Model 3 – Combination Model

The combination model combined the SI graphs used in the expert model (Fig. 3) with standardized beta coefficients from the regression model output. Standardized beta coefficients were used because they account for different measurement units. The absolute value of the coefficients was used because the SI score already reflected the negative or positive influence of the variable on ND. The weighted mean SI scores were calculated, ranked from 1 through 15, and compared to observed ranks.

Assessment of Model Error

The simplest and most widely used measure of HS model accuracy is the number of correctly classified habitat areas (Fielding and Bell 1997). The final HSI score for each zone was ranked relative to the others, from 1 through 15. The ranks also corresponded to more general HS classes (low, medium low, medium high, high). The numerical HS class thresholds were determined using the same "natural breaks" methodology described earlier. Predicted ranks and HS classes were then compared to observed ranks and classes in scatterplots.

To quantify and compare model accuracies, 3 criteria were used: 1) the percentage of zones correctly assigned to their observed HS class, 2) the percentage of zones assigned to HS classes below their observed HS class (underpredicted zones), and 3) the strength of the relationship between observed and predicted ranks based on the Spearman's rank correlation coefficient. A confidence level of alpha = 0.05 was used for the last criterion.

RESULTS

Model 1 – Expert Model

Based on weights assigned by sea turtle experts (Table 1), component index scores for the expert model were computed as follows:

$$\begin{aligned} CI = [&2 \times SI \text{ man-made\%} + 3 \times SI \text{ illuminance} \\ &+ 3 \times SI \text{ compaction} + 2 \times SI \text{ sand\%} \\ &+ 2 \times SI \text{ debris\%}]/12 \end{aligned}$$

The expert model correctly assigned HS classes to 40% of the zones (Fig. 4). This model, however, underpredicted 30% of the zones, including some odd-numbered calibration zones that were used to create the SI graphs and contained high nest densities (i.e., Windmill 1

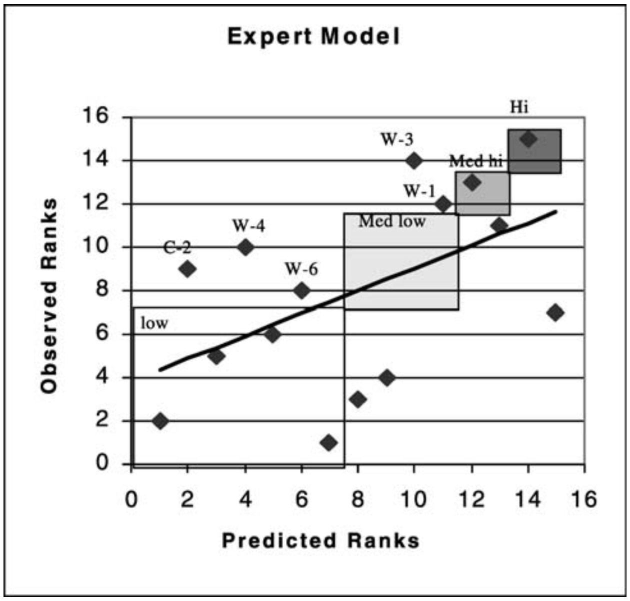

Figure 4. Expert model classing performance. HS classes are represented by boxes. Zones that fall inside the box are correctly classified. Lighter boxes represent low and medium-low HS classes. Darker boxes represent medium-high and high HS classes. Labeled points were underpredicted, meaning that good habitat was not predicted (W-1 = Windmill 1, W-2 = Windmill 2, W-4 = Windmill 4, W-6 = Windmill 6, and C-2 = Cable 2).

Variable	ß	P-value
Man-made %	.22	.37
Illuminance	-.597	.13
Compaction	1.686	.04
Sand %	-.37	.23
Debris %	-.902	.11

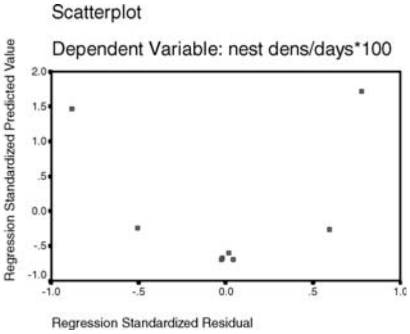

Figure 5. Regression output for the regression HSI model and a plot of the residuals.

and 3). This model correctly predicted the zone with the highest ND, Pebble 2. The overall fit between observed ranks and predicted ranks was moderately strong ($r_s = 0.521$, $p = 0.05$).

Model 2 – Regression HSI Model

Multiple regression analysis showed that this model accounted for about 89% of the variability in ND (Fig. 5), but the results were not significant ($p = 0.08$). In addition, the residuals showed a U-shaped distribution, indicating some problems with the assumptions of regression analysis (independence, linearity, normal distributions).

Strong, but not statistically significant intercorrelation between variables (see Table 2) caused the signs on the beta coefficients (β) of 3 variables to be in the opposite direction from their individual correlations with ND. For purposes other than testing the model-building technique, fewer variables could have been used to eliminate this problem. Indeed, removing compaction from the model returned the signs to their proper direction. However, the same number of variables (5) was needed in each model to compare the 3 approaches. Despite problems with the regression model, the unstandardized beta coefficients from the regression output were used to build the regression HSI model:

$$\begin{aligned}\text{Predicted } ND = {} & -0.006 + (0.001 \times \text{man-made\%}) \\ & + (-0.001 \times \text{illuminance}) \\ & + 0.013 \times \text{compaction}) \\ & + (-0.001 \times \text{sand\%}) \\ & + -0.0005 \times \text{debris\%})\end{aligned}$$

$$HSI \text{ score} = \text{predicted } ND/0.0726$$

The model assigned correct HS classes to 40% of the zones (Fig. 6). However, none of the correctly predicted zones was in the higher HS classes and 33% of the zones were underpredicted by the model. The Spearman's correlation coefficient between observed ranks and predicted ranks was weak and not significant at $r_s = 0.089$ ($p = 0.74$).

Model 3 – Combination Model

The combination model used the absolute value of the standardized beta weights from the regression output (Fig. 5) as coefficients on SI values. The CI scores were derived using the following model:

$$\begin{aligned}CI = {} & [1.69 \times SI \text{ compaction} + 0.902 \times SI \text{ debris\%} \\ & + 0.22 \times SI \text{ man-made\%} + 0.597 \\ & \times SI \text{ illuminance} + 0.037 \times SI \text{ sand\%}]/4.46\end{aligned}$$

The model correctly assigned 40% of the zones to their observed HS class (Figs. 7 and 8). Pebble 2 contained the highest ND in the dataset and was correctly predicted. The model underpredicted 5 zones (30%). The Spearman's correlation coefficient between observed ranks and predicted ranks was the highest of the 3 models ($r_s = 0.55$, $p = 0.03$).

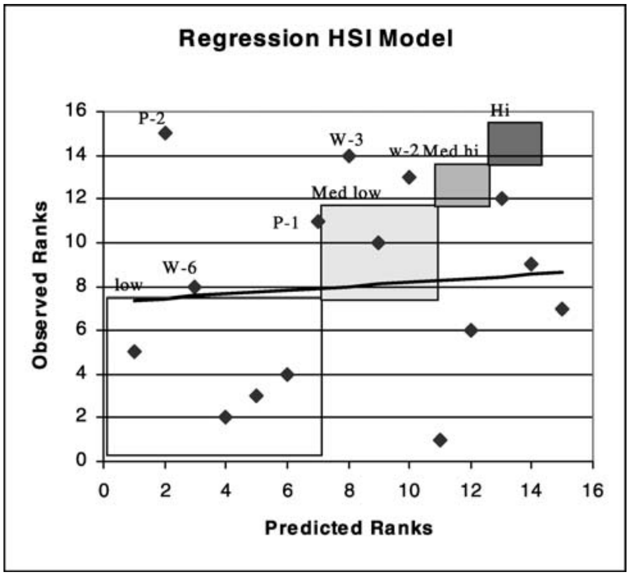

Figure 6. Regression HSI model classing performance. HS classes are represented by boxes. Zones that fall inside the box are correctly classified. Lighter boxes represent low and medium-low HS classes. Darker boxes represent medium-high and high HS classes. Labeled points were underpredicted, meaning that good habitat was not predicted (W-2 = Windmill 2, W-3 = Windmill 3, W-6 = Windmill 6, P-1 = Pebble 1, and P-2 = Pebble 2).

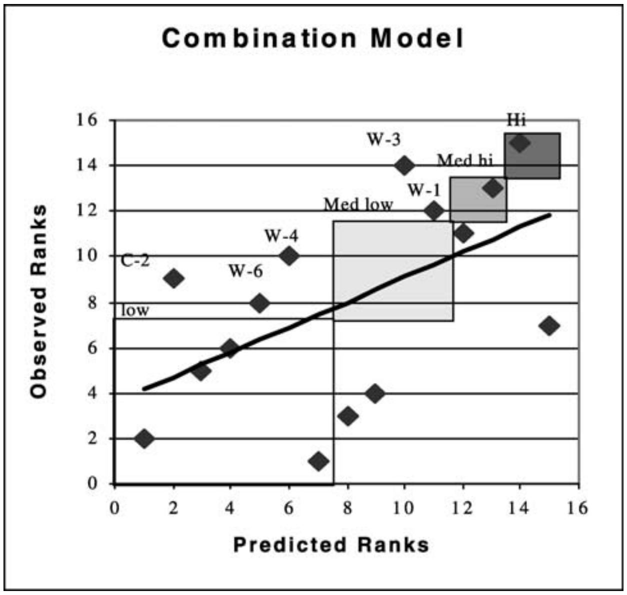

Figure 7. Combination model classing performance. HS classes are represented by boxes. Zones that fall inside the box are correctly classified. Lighter boxes represent low and medium-low HS classes. Darker boxes represent medium-high and high HS classes. Labeled points were underpredicted, meaning that good habitat was not predicted (W-1 = Windmill 1, W-3 = Windmill 3, W-4 = Windmill 4, W-6 = Windmill 6, and C-2 = Cable 2).

A concise comparison of the expert model, regression HSI model, and combination model using the 3 accuracy criteria can be found in Table 3.

Influential Environmental Variables

The combination model outperformed the other models, so we used it to answer the question of which environmental variables were most correlated to ND on GTMO. To rank the importance of the variables, the absolute value of the standardized beta coefficients were used (Fig. 5). To supplement this information, the SI graphs (Fig. 3) and Pearson's correlation coefficients (Table 2) determined the positive or negative influence of a variable, and the most and least suitable ranges. SI graphs also provided an idea of the thresholds (ranges) for HS. A synopsis of this information is provided in Table 4.

Compaction was almost twice as influential as the other variables in the combination model, as noted by its standardized beta of 1.6 compared to 0.9 for percentage of debris. By itself, compaction was positively correlated with ND ($R = 0.628$) (Table 2). This implies that the less compact, or looser the sand, the more suitable the habitat. The SI graphs show that most nesting occurred in zones where the cone penetrometer reached 8 to 11 inches below the surface of the substrate at 250 PSI.

Percentage of debris was ranked second in the model and was positively correlated with ND ($R = 0.466$). The SI graphs show that out of the 8 zones used in the analysis, almost no nesting occurred in zones with less than 38% debris.

Illuminance was ranked third in the model and was negatively correlated with ND ($R = -0.310$). The SI graph indicates a threshold response; any zone with more than 3 lux of light received very little nesting.

Percentage of sand was ranked fourth in the model, and was positively correlated with ND ($R = 0.565$). This implies that the more sand, the more suitable the habitat. Indeed, the SI graphs show sand percentage and ND increased almost linearly.

Percentage of man-made obstacles had the least influence in the model, and was negatively correlated

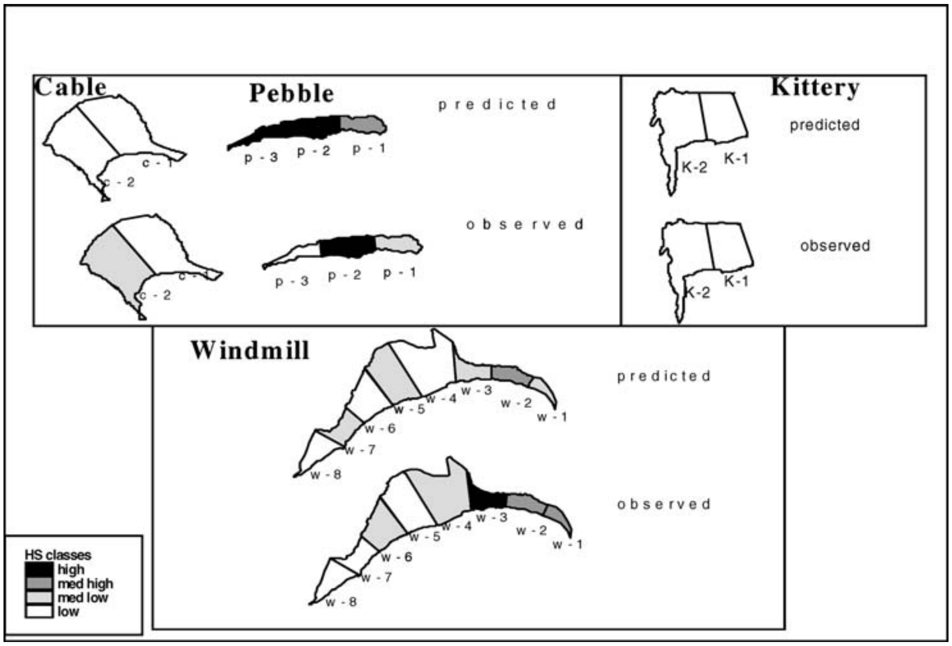

Figure 8. Maps of predicted and observed HS classes for each zone in the study area based on combination model results.

Table 3. Comparison of the expert model, regression habitat suitability index (HSI) model, and combination model using 3 accuracy criteria.

Model	Percentage of zones with correct HS class	Percentage of zones in underpredicted HS class	Spearman's correlation[a]	Overall performance
Expert	40	30	0.521*	Moderate
Regression	40	30	0.089	Moderate
Combination	40	30	0.550*	Moderate

[a] Asterisks indicate statistical significance ($p = 0.05$).

with ND ($R = -0.547$). The results imply that the more man-made obstacles, the less suitable the habitat. The SI graph shows a threshold response: most nesting occurred where obstacles covered less than 4% of the zone.

Slope, width, and vegetation percent were not used in the models, because of significant colinearity with other variables. However, they may be important or even causal variables for HS. Individually, slope was correlated with ND at ($R = 0.390$), width at ($R = -0.401$) and percentage of vegetation at ($R = -0.386$) (Table 2).

DISCUSSION

We compared the environmental variable weights from the combination model to those suggested by experts, and most of the weights were similar in both weight and direction of the sign with a few exceptions (Table 5). Overall, differences in empirical (regression-based) and expert weights reflect a shift from regional (Caribbean) to a local, site-specific scale of analysis (GTMO). The role of each variable in the models may depend both on the range of variation at the site, the day of sampling, and/or relationships with other variables.

Compaction ranked high in both models, but experts suggested that the preference for loose or compact sand may depend on the species. The SI graph indicates that loose sand was preferred at GTMO, where hawksbills are abundant. Studies on beach renourishment in Florida support these results (Nelson and Dickerson 1998). A multiple regression study similar to this one in Japan also suggests loose sand was preferred by loggerheads (Kikukawa et al. 1999).

Percentage of debris received an intermediate ranking by both the empirical model and by the experts. It is interesting that percentage of debris was predicted to be a negative influence by experts, whereas the individual correlation with ND at GTMO was positive (Table 2). This relationship deserves further investigation. In our study area, debris percentage may be correlated to lack of beach recreation, because people generally do not recreate on beaches with trash. A lack of recreation could increase HS by decreasing disturbances such as altered slope, sand compaction, noise, and light pollution. Also, debris and turtles could be riding in the same ocean currents and accumulating on the same beaches.

Experts predicted illuminance would be the most influential variable affecting HS, but illuminance received an intermediate weight in the empirical model. Two zones of interest were Windmill 5 and 6 (Fig. 8), where 13 total nests were observed, despite an average of 10 lux of light recorded in April of 2001. There may have been variation in the lighting of these zones over the study period, or perhaps other variables, such as the soft sand near the volleyball courts (closest to the shoreline in Fig. 2), compensated for high illuminance. Illuminance was also correlated with compaction (Table 2), which may have affected the validity of the regression model.

Percentage of vegetation was predicted by experts to be important for HS, especially for hawksbills. However, the correlation matrix did not detect this relationship, perhaps because of low sample size and/or low environmental variation at the site—GTMO is dry and the beaches contain very little vegetation compared to other beaches in the Caribbean. At Barbados, for example, vegetation was positively correlated with hawksbill ND (Horrocks and Scott 1991). It is important to note, however, that in some vegetated areas, for example a solitary tree on Pebble 2, hawksbills crowd each other and excavate eggs from other females' chambers in order to nest in this preferred spot. Meanwhile, zones with a higher vegetation percent such as Windmill 4, 5, and 6, or Cable 1 (Fig. 8) contained fewer nest observations, possibly because of counteracting

Table 4. Relative importance of environmental variables in the combination model.

Importance	Variable	Individual R with ND	Most suitable range	Least suitable range
Highest	Low compaction	Positive	8–11 inches	0–7 inches
	Percentage of debris	Positive	39%–100%	0%–39%
	Illuminance	Negative	0–3 lux	3–144 lux
	Percentage of sand	Positive	14%–40%	0%–14%
Lowest	Percentage man-made	Negative	0%–13%	26%–40%

Table 5. Comparison of the empirically-based combination model weights and expert model weights.[a]

Variable	Regression weight and direction	Expert weight and direction
Low compaction	Very high (+ or −)	High (+)
Percentage of debris	Medium (+)	Medium (−)
Illuminance	Low (−)	Very high (−)
Percentage of sand	Low (+)	Medium (+)

[a] The plus sign (+) indicates a positive influence on habitat, and the minus sign (−) indicates a negative influence on habitat.

disturbances such as concrete and artificial lighting. Removing these disturbances may entice hawksbills to nest near that vegetation. Despite model differences, we agree with the experts that vegetation deserves a high weight on GTMO.

Other studies at GTMO tested the idea that sampling a larger number of nesting beaches less frequently might improve the validity of the results. In a technical report to GTMO, we examined observations of 33 zones over 10 beaches (Fig. 1) collected at an annual time-step, and we also collected environmental data for the 33 zones in April of 2001 (Alberts et al. 2001). However, we did not find that variance in this observational dataset was explained by the environmental data to a reasonable degree. The infrequent temporal sampling of the observations in the annual dataset likely produced errors of omission, because turtle nesting evidence can be erased with weather or human traffic throughout the year. Together, results of Alberts et al. (2001) and this study reinforce the need for weekly sampling over a larger study area on GTMO.

Conservation Recommendations

Because nesting preferences within the GTMO site cannot be predicted based solely on the environmental variables collected during this study, we suggest that nest site fidelity plays a role. To test this hypothesis, a larger study area and longer study period is required. GTMO authorities should allow volunteer access for sea turtle observations at all beaches at least once a week for at least 8 consecutive years. Experts suggest 8 years of nest observations can be used to estimate population totals and long-term data are critical for studying population trends. Those data may allow the construction of an HSI model that would more accurately predict nest densities at GTMO, and perhaps be robust enough to use at other sites in the Caribbean.

Based on our results, compaction levels of the substrate on GTMO's beaches should not be altered, for example, with additional construction, beach nourishment, or heavy equipment (USFWS 1999). Vehicular traffic should be prohibited on beaches because it compacts sand alters the beach slope, and could crush nests that are not roped off. Artificial illuminance is a negative influence on nesting habitat. At the time of this study, on most GTMO beaches nighttime lighting (e.g., volley ball courts, cabana lights, and parking lot lights) was minimized when beaches were not in use. This regulation should be expanded to all beaches throughout the year, and enforced. Eliminating or controlling light pollution (see Witherington 2000) on all beaches throughout the year may encourage females to return to otherwise suitable nesting sites. Man-made obstacles are a threat to habitat, and additional beach development should be prohibited. Because percentage of sand was important in the model, the substrate should not be amended with soils or sand, nor should sand be removed. Although the vegetation variable was not included in the models, planting more trees on beaches such as Pebble has been recommended to increase HS for hawksbills (Alberts et al. 2001). The role of the percentage of debris in the model contradicted expert opinion, suggesting that more studies on how debris affects nesting habitat at GTMO would be useful.

Since 2001, new development on GTMO has reportedly not affected sea turtle habitat or nesting. Steps to protect turtle habitat since 2001 include activities such as education and outreach and an improved bollard-and-cable system to keep vehicles off the beaches around known nesting areas.

Conclusions

Morrison et al. (1992) stated, "In general, most HSI or habitat models can be expected to account for roughly half the variation in species density or abundance. On-site environmental conditions generally account for even less variation in population density when migratory species are considered." Indeed, our models successfully classified 40% of the zones. Therefore, these models may be used for the theoretical purpose of exploring relationships between environmental variables and HS. The modeling process can help shape future habitat studies, and places GTMO in the context of the literature on sea turtle nesting patterns in the wider Caribbean. However, none of the HSI models did extremely well in predicting observed HS classes, implying that influences beyond these environmental variables, such as nest site fidelity, may contribute to HS. In addition, small sample size, a common issue for endangered species datasets, may have contributed to poor model performance. Continued weekly monitoring will be needed at GTMO in order to make sound management decisions.

Many studies on endangered species, such as this one, are forced to use small opportunistic datasets and low-cost rapid environmental assessment methods. Short studies complicate management decisions, especially for species like sea turtles with long maturation periods (ca. 20 years), long lives (ca. 100 years), migratory habits, and demonstrated nest site fidelity. For example, on a beach where poaching began in the 1920s, the females may continue to nest on their natal beach until the last one dies in the year 2000 (Magnuson 1990). Similarly, today's nesting patterns may be caused by habitat conditions that existed decades ago, and managers may falsely conclude that their current practices, such as "controlled egg poaching" or "sustainable development" are not affecting sea turtle populations. For researchers without historical data, it is difficult to tease apart the influences of environmental conditions, nest site fidelity, and historical poaching. To deal with the lack of historical data, future researchers might consider using qualitative methods such as surveys or questionnaires of local community members (Roca and Sedaghatkish 1998; Tambiah 1999). Recollections of past nesting or poaching activities could be incorporated as a presence/absence historical nesting variable in future HSI models.

The comparison between the 3 HSI model-building techniques showed that there was little difference between the predictive ability of the empirically based combination model and the expert model. We conclude that GTMO managers could have relied on expert opinion for weighting their HSI models, yet had they done so, interpretation of the influential variables would have been different, as noted in earlier sections. The multiple regression approach did not yield statistically valid results with either the weekly or the annual dataset. Our study raises the question of whether the statistical validity of a model is more important than its predictive accuracy. We suggest that the degree of validity required in modeling should be determined by the goal of the exercise and perhaps the scale of the study area. For example, in this study, ranking 5 variables against each other was a useful exercise for GTMO managers, but using so many variables created statistical problems in the regression models. Perhaps managers of small areas, such as a city park, can use models with high predictive rates but low validity, because the models are not intended for extrapolation or academic purposes. In contrast, managers of larger areas, such as extensive federal lands, might require statistically valid models, even though the models cannot predict species' densities at small scales.

Besides observations of nest site fidelity, little is known about why sea turtles prefer some beaches over others (Carr 1967; Owens et al. 1982; Meylan et al. 1990; Plotkin et al. 1992; Allard et al. 1994). Several questions remain: Why did turtles choose their nesting beaches over others generations ago? How can we improve nesting habitat for sea turtles? How can we mimic suitable sea turtle nesting habitat for the purpose of nest relocations? How much and what kinds of beach disturbances can sea turtles tolerate? HSI models are one tool with which managers can generate hypotheses and experiment with management options, without directly experimenting with the natural environment. Because the sea turtle populations at GTMO are protected by US law and coastal development is relatively restricted, GTMO managers are in a position to perform more geographically extensive, long-term studies on sea turtle habitat. As Cuba and its neighbors continue to develop their coasts, all efforts should be made to preserve this important nesting refuge.

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LITERATURE CITED

ALBERTS, A.C., GRANT, T.D., GERBER, G.P., COMER, K.E., TOLSON, P.J., LEMM, J.M., AND BOYER, D. 2001. Critical reptile species management on the US Naval Base, Guantanamo Bay, Cuba. Report to the US Navy for Project 62470-00-M-5219. Zoological Society of San Diego, Center for Reproduction of Endangered Species.

ALLARD, M.W., MIYAMOTO, M.M., BJORNDAL, K.A., BOLTEN, A. B., AND BOWEN, B.W. 1994. Support for natal homing in green turtles from mitochondrial DNA sequences. Copeia 1:34–41.

BJORNDAL, K. A. 1995. Biology and conservation of sea turtles. Washington: Smithsonian Institution Press, 615 pp.

BUSTARD, H.R. AND GREENHAM, P. 1968. Physical and chemical factors affecting hatching in the green sea turtle *Chelonia mydas*. Ecology 49:269–276.

CARR, A. F. 1967. So excellent a fishe. Garden City, NY: Natural History Press, 248 pp.

CARR, A.F., CARR, M.H., AND MEYLAN, A.B. 1978. The ecology and migrations of sea turtles. VII. The West Caribbean green turtle colony. Bulletin of the American Museum of Natural History 162:1–46.

CHÁVEZ, M.T.E. AND REU, G.C. 1998. Caracterización del sitio de anidación en la playa de "Lagunas de Chacahu", Oax. para la especie *Lepidochelys olivacea* (tortuga golfina). Proceedings of the 18th International Symposium on Sea Turtle Biology and Conservation, Mazatlán, Mexico, pp. 186–188.

COYNE, M. S., MONACO, M. E., AND LANDRY, A. M., JR. 1998. Kemp's ridley habitat suitability index model. In: Abreu-Grobois, F.A., Briseno-Duenas, R., Márquez-Millan, R., and Sarti-Martínez, L. (Compilers) Proceedings of the 18th International Symposium on Sea Turtle Biology and Conservation, NOAA Tech. Mem. NMFS-SEFSC-436:60.

DENT, B. D. 1999. Cartography: Thematic Map Design. Fifth Edition. Dubuque, IA: W.C. Brown, 417 pp.

ERNEST, R. G. AND BRUN, F. 1998. Coastal roadway lighting manual. Ecological Associates, Inc. for Florida Power & Light Co., Jensen Beach, FL.

FIELDING, A.H. AND BELL, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

GARMESTANI, A.S., PERCIVAL, H. F., PORTIER, K.M., AND RICE, K.G. 2000. Nest-site selection by the loggerhead sea turtle in Florida's Ten Thousand Islands. Journal of Herpetology 34: 504–510.

HORROCKS, J.A. AND SCOTT, N.M. 1991. Nest site location and nest success in the hawksbill turtle *Eretmochelys imbricata* in Barbados, West Indies. Marine Ecology Progress Series 69:1–8.

[IUCN] INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES. 2006. 2006 IUCN Red list of threatened species. www.iucnredlist.org (7 September 2006).

JENKS, G.F. AND COULSON, M.R. 1963. Class intervals for statistical maps. International Yearbook of Cartography 3:119–134.

KIKUKAWA, A., KAMEZAKI, N., AND OTA, H. 1999. Factors affecting nesting beach selection by loggerhead turtles (*Caretta caretta*): a multiple regression approach. Journal of Zoology, London 249:447–454.

KLEMENS, M.W. 2000. Turtle conservation. Washington, DC: Smithsonian Institution Press, 334 pp.

LOOP, K., MILLER, J., AND LIMPUS, C. 1995. Nesting by the hawksbill turtle (*Eretmochelys imbricata*) on Milman Island, Great Barrier Reef, Australia. Wildlife Research 22:241–252.

LUTZ, P. L. AND MUSICK, J. A. 1997. The Biology of Sea Turtles. Boca Raton, FL: CRC Press, 146 pp.

MAGNUSON, J. J. 1990. Decline of the Sea Turtles. Washington, DC: National Academy Press, 260 pp.

MÁRQUEZ, R.M. 1990. Sea Turtles of the World. FAO Species Catalogue. Volume 11. Rome, Italy: Food and Agriculture Organization of the UN, 81 pp.

MEYLAN, A., CASTANEDA, P., AND COOGAN, C. 1990. First recorded nesting by Kemp's ridley in Florida, USA. Marine Turtle Newsletter 48:8–9.

MONCADA, F, CARRILLO, E., SAENZ, A., AND NODARSE, G. 1999. Reproduction and nesting of the hawksbill turtle, *Eretmochelys imbricata*, in the Cuban archipelago. Chelonian Conservation and Biology 3:257–263.

MORRISON, M. L., MARCOT, B. G., AND MANNAN, R. W. 1992. Wildlife-habitat relationships concepts and applications. Madison, WI: The University of Wisconsin Press, 341 pp.

MORTIMER, J.A. 1995. Teaching critical concepts for the conservation of sea turtles. Marine Turtle Newsletter 71:4.

NELSON, D. A. 1988. Life history and environmental requirements of loggerhead turtles. US Fish and Wildlife Service Biological Rep. 88(23), US Army Corps of Engineers TR EL-86-2 (Revised), 34 pp.

NELSON, D.A. AND DICKERSON, D.D. 1988. Effects of beach nourishment on sea turtles. Proceedings of the Beach Preservation Technology Conference 88. Florida Shore and Beach Preservation Association, Inc. pp.285–293.

OWENS, D. W., GRASSMAN, M. A., AND HENDRICKSON, J. R. 1982. The imprinting hypothesis and sea turtle reproduction. Herpetologica 38:124–135.

PLOTKIN, P.T., BYLES, R.A., ROSTAL, D.C., AND OWENS, D.W. 1992. Arribadas: social events or simply aggregations? Preliminary results from satellite telemetry. In: Salmon, M. and Wyneken, J. (Compilers) Proceedings of the 11th Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Mem. NMFS-SEFSC-302, pp. 85–96.

ROCA, E. AND SEDAGHATKISH, G. 1998. Rapid Ecological Assessment—U.S. Naval Station, Guantanamo Bay Cuba. Washington, DC: The Nature Conservancy.

SEMINOFF, J.A. 2004. *Chelonia mydas* In: IUCN 2006. 2006 IUCN Red List of Threatened Species. www.iucnredlist.org (7 September 2006).

SCHOEDER, B. AND MURPHY, S. 1999. Population surveys (ground and aerial) on nesting beaches. In: Eckert, K. L., Bjornadal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.) Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp. 45–55.

SCHMID, J.R. 1994. A GIS model for the analysis of marine turtle habitat associations. In: Bjorndal, K.A., Bolten, A.B., Johnson, D.A., and Eliazar, P.J. (Compilers). Proceedings of the 14th Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Mem. NMFS-SEFSC-351, pp. 279–282.

STEINITZ, M J., SALMON, M., AND WYNEKEN, J. 1998. Beach renourishment and loggerhead turtle reproduction: a seven year study at Jupiter Island, Florida. Journal of Coastal Research 14: 1000–1013.

STOMS, D.M. AND ESTES, J.E. 1993. A remote sensing research agenda for mapping and monitoring biodiversity. International Journal of Remote Sensing 14:1839–1860.

TAMBIAH, C. 1999. Interview and market surveys. In: Eckert, K. L., Bjornadal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.) Research and Management Techniques for the Conservation of Sea Turtles. Washington, DC: IUCN/SSC Marine Turtle Specialist Group Publication No. 4.235, pp. 156–165.

TRINDEL, R. N., ARNOLD, D., MOODY, K., AND MORFORD, B. 1998. Nourished beaches and marine turtle nesting in Florida: an evaluation of recent projects. In: Abreu-Grobois, F.A., Briseno-Duenas, R., Márquez-Millan, R., and Sarti-Martínez, L. (Compilers). Proceedings of the 18th International Symposim on Sea Turtle Biology and Conservation. NOAA Tech. Mem. NMFS-SEFSC-436, pp. 217–218.

[USFWS] US FISH AND WILDLIFE SERVICE. 1981. Standards for the Development of Habitat Suitability Index Models. Volume 103. ESM, Release 1-81. Washington, DC: Division of Ecological Services, 171 pp.

[USFWS] US FISH AND WILDLIFE SERVICE. 1999. Hawksbill sea turtle. In: Multi-Species Recovery Plan for South Florida. Vero Beach, FL: US Fish and Wildlife Service, pp. 4-615–4-627.

WILLIAMS, W. N., O'HARA, J., GALLAGHER, R. M., WORTH, D. F., PERRY, B. D., AND WILCOX, J. R. 1983. Spatial and temporal trends of sea turtle nesting on Hutchinson Island Florida 1971–1979. Bulletin of Marine Science 23:55–66.

WITHERINGTON, B.E. 2000. Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches. St. Petersburg, FL: Florida Marine Research Institute Technical Report TR-2, 73 pp.

WOOD, D.W. AND BJORNDAL, K. A. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. Copeia 2000:119–128.

WOODY, K., HORROCKS, J., AND VERMEER, L. 1998. Factors influencing within-beach nest distribution in hawksbill turtles. In: Abreu-Grobois, F.A., Briseno-Duenas, R., Márquez-Millan, R., and Sarti-Martinez, L. (Compilers) Proceedings of the 18th International Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Mem. NMFS-SEFSC-436.

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