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Predicting nest survival in sea turtles: when and where are eggs most vulnerable to predation?

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Abstract

Nest predation is an important practical challenge for the conservation of egg-laying reptiles, with the potential to reduce hatchling recruitment and slow the recovery of threatened populations. Accurately forecasting where and when predation will occur has the potential to optimize predation management. Survival analysis, a set of statistical techniques recently popularized in studies of avian nest success, provides a unique approach for modelling variation in egg mortality risk throughout development. We used Cox proportional hazards regression to model the survival of sea turtle eggs from predation by the small Asian mongoose *Herpestes javanicus*, a widely introduced and destructive sea turtle nest predator in the Caribbean. We evaluated the ability of models to predict egg survival using 7 years of nest predation data for critically endangered hawksbill sea turtles *Eretmochelys imbracata* in Barbados. Daily predation risk was the highest for freshly laid nests, decreasing rapidly with nest age but increasing again near the end of development. Predation risk was the highest in and near patches of beach vegetation, increased over the nesting season and increased with nest density on the open beach but not in vegetation. Survival models calibrated using data from 2004 to 2005 showed excellent discrimination and $\geq$84% accuracy when predicting the fate of nests from previous years. Our study provides the first quantification of the daily variation in predation risk for incubating turtle eggs, revealing a narrow time window early in development during which the application of predation reduction measures is likely to have the greatest impact on nest survival. More generally, we demonstrate the utility of survival analysis for generating fine-scale predictions of spatiotemporal variation in turtle egg mortality, providing a flexible tool for the conservation of sea turtles and other egg-laying reptiles.

Introduction

Nest predators present a practical challenge for the conservation of many threatened birds and reptiles worldwide (Stancyk, 1982; Chalfoun, Thompson & Ratnaswamy, 2002; Kolbe & Janzen, 2002). Predation is an important source of mortality for the eggs and hatchlings of endangered sea turtles (Stancyk, 1982). Although sea turtle populations appear to be most sensitive to mortality of juvenile and adult stages (Crouse, Crowder & Caswell, 1987; Heppell, 1998), heavy nest predation can have long-term demographic impacts (Heppell *et al*., 1996), and recent empirical (Dutton *et al*., 2005) and theoretical (Mazaris, Broder & Matsinos, 2006) evidence suggests that the survival of eggs and hatchlings is important for population recovery. The widespread introduction of exotic mammalian predators on oceanic islands, which provide critical nesting habitat for many sea turtle species, is particularly problematic. In the absence of human intervention, mammalian predators frequently destroy over 80% of the available nests (Talbert *et al*., 1980; Nellis & Small, 1983; Engeman *et al*., 2006; Ficetola, 2008). Predation mitigation is therefore a fundamental component of many sea turtle conservation programs, with considerable time and resources devoted to reducing local predator activity or protecting individual nests (Engeman *et al*., 2002). However, such activities are often carried out without a good understanding of predator foraging ecology, and could be optimized by a clear set of predictions about which nests are at the greatest risk of predation and how risk changes over time.

Nest location has long been recognized as an important determinant of predation risk for turtle nests (e.g. Fowler, 1979; Kolbe & Janzen, 2002; Caut *et al*., 2006). Turtle nesting areas typically contain a mixture of vegetated and non-vegetated habitats, and habitat selection by both nesting turtles and nest predators can lead to uneven patterns of predation risk across the landscape (Fowler, 1979; Marchand & Litvaitis, 2004; Leighton *et al*., 2008). Spatial aggregation of nests can also affect predation, either by increasing per capita risk through attracting predators to

high-density areas (e.g. Marchand & Litvaitis, 2004) or by decreasing it through dilution effects (e.g. Eckrich & Owens, 1995).

Predation risk is also likely to vary temporally, both seasonally and throughout egg development, but such effects are less well documented. Several authors have suggested that predation risk should change over the nesting season due to shifts in predator activity related to nest availability or to predator learning (Stancyk, 1982; Nellis & Small, 1983; Leighton, Horrocks & Kramer, 2009), but seasonal changes in predation risk have only been documented in a few studies (Fowler, 1979; Talbert *et al*., 1980; Engeman *et al*., 2003). In addition, various studies have reported more frequent nest predation near the start (Stancyk, Talbert & Dean, 1980; Nellis & Small, 1983; Goncalves, Cechin & Bager, 2007; Leighton *et al*., 2009) or the end (Fowler, 1979; Nellis & Small, 1983) of incubation, but the relationship between daily predation risk and nest age has not been rigorously explored.

One possible reason why temporal determinants of sea turtle nest predation have remained elusive is that many popular statistical methods for modelling the binary probability of a nest surviving to hatch, such as logistic regression, cannot account for fine-scale temporal changes in predation risk experienced by individual nests throughout development (Nur, Holmes & Geupel, 2004). Survival analysis methods enjoy a longstanding popularity in human biomedical research (Andersen, 1991), but have only recently been adopted in studies of nest predation (Nur *et al*., 2004; Heisey, Shaffer & White, 2007). By explicitly modelling the daily mortality rate of nests throughout development and the effects of covariates on this baseline, survival analysis offers a powerful predictive framework for integrating the spatial and temporal patterns of predation risk. Although ideally suited to studies of turtle nests where fine-scale survival data are often available from routine nest monitoring (Nur *et al*., 2004), to our knowledge, the application of survival analysis in the context of turtle nest predation is limited to a single study (Engeman *et al*., 2006).

We used survival analysis to model sea turtle nest predation by a destructive exotic predator, the small Asian mongoose *Herpestes javanicus*. Since its introduction to the Caribbean in the late 1800s, the mongoose has been blamed for the extinction or the extirpation of numerous native species throughout the region (Nellis & Everard, 1983; Hays & Conant, 2007), and continues to pose a significant threat to sea turtle eggs and hatchlings (Nellis & Small, 1983; Leighton *et al*., 2008). Using data from a long-term study of hawksbill sea turtle *Eretmochelys imbricata* nesting in Barbados, we examined the effects of nest age, oviposition date, nest location and local nest density on hawksbill nest survival.

Most previous work on sea turtle nest predation has been primarily descriptive (e.g. Fowler, 1979; Nellis & Small, 1983; Macdonald *et al*., 1994), with a strong geographic and taxonomic bias toward predation by native raccoons on loggerhead sea turtles along the south-east coast of the USA (e.g. Ratnaswamy *et al*., 1997; Engeman *et al*., 2006; Barton & Roth, 2008). The goals of this research were to develop a predictive model of predation risk for sea turtle nests threatened by an introduced predator of widespread importance in the Caribbean and, more generally, to explore the potential of survival analysis to provide unique and practical insights for predation management in sea turtle nesting areas.

Materials and methods

Species and study area

The study was carried out at Bath (13.187°N, 59.476°W), the primary nesting beach for hawksbill sea turtles on the east coast of Barbados. Hawksbills nest year-round at Bath, with a peak from June to August (Beggs, Horrocks & Krueger, 2007). Approximately 60% of the nesting area is open beach: sandy areas lacking ground vegetation except sparse grass in some areas. The remaining 40% is vegetated with dense patches of shrubs [especially *Coccoloba uvifera* L. and *Thespesia populnea* (L.)]. Hawksbills emerge from the ocean at night and nest readily in both open and vegetated habitats (Leighton *et al*., 2008). Incubation lasts *c*. 60 days, and hatchlings emerge at the sand surface a few days after hatching.

Mongooses were introduced to the Caribbean from India in 1872 to control rodents in sugar cane plantations and are currently found on all major cane-producing islands (Horst, Hoagland & Kilpatrick, 2001). In Barbados, mongooses forage on the beach throughout the day but avoid contact with humans and generally restrict their activity to vegetated areas of the beach (Leighton *et al*., 2008). Individual home ranges overlap extensively, and, in areas such as Bath, where anthropogenic food is abundant, local densities can exceed 10 animals ha^{-1} (Nellis & Everard, 1983; Leighton, 2005). Other than crabs and insects that may damage or remove a portion of the clutch, mongooses are the sole predator of hawksbill eggs at our site.

Hawksbill nest monitoring

Data on hawksbill nesting at Bath were collected through daily beach surveys from 1999 to 2005 as part of the long-term monitoring program of the Barbados Sea Turtle Project, University of the West Indies. During surveys, nests laid the previous night were located using fresh disturbances of sand and vegetation left by the nesting turtle. The presence of eggs was confirmed through careful excavation by hand of sand directly above the eggs following a standard protocol (Schroeder & Murphy, 1999). In most cases, researchers located nests before the onset of mongoose predation. In order to reduce the impact of researcher disturbance on subsequent nest detection by mongooses, the nest location was re-concealed by replacing the excavated sand and scattering loose sand over the nesting area. Incubating nests were checked to determine whether they had been preyed on by mongooses (signs of digging, mongoose tracks, at least one egg removed from the nest),

hatched (signs of hatchling emergence, hatched shells at the bottom of the nest) or been destroyed through other processes such as beach erosion.

Statistical analyses

We used Cox proportional hazards regression, a widely used method of survival analysis (Nur *et al*., 2004; Heisey *et al*., 2007), to model the effect of nest age and other covariates on the risk of mongoose predation. Proportional hazards regression performs a non-parametric estimation of how daily nest survival varies with nest age (the baseline hazard function) and models the effects of covariates on nest survival by increasing or decreasing this baseline hazard function. In our analysis, the survival time for each nest was the number of days elapsed between nest initiation and predation. Nests that hatched successfully or that failed due to other causes were considered censored (not preyed on) on the date of hatch/failure.

Mongooses forage primarily in beach vegetation, with activity decreasing sharply across the habitat boundary between patches of vegetation and the open beach (Leighton *et al*., 2008). In addition, shallower nests are at a greater risk of predation, and nests in vegetation are significantly shallower than nests on the open beach (Leighton *et al*., 2009). We therefore included habitat type (vegetation vs. open beach) and distance to the edge of the nearest patch of beach vegetation (positive distances for nests in the open and negative distances for nests within vegetation) as predictors in the model to capture the effects of habitat context on predation risk. We included the date of nest initiation to model the combined effects of increasing mongoose activity in beach habitat over the nesting season and learning by predators (Leighton *et al*., 2009) on predation risk. We used the cumulative annual nest density (total nests laid over the season per m^2) at each nest location to model the effects of varying local nest density and inter-annual variation in nest abundance. Cumulative density is higher than instantaneous nest density but is expected to be correlated with it and has the advantages of being straightforward to measure and avoiding assumptions about which stages of nest development to include when estimating density (Tiwari *et al*., 2006). Density was calculated as the number of nests within a given radius of the focal nest divided by the area of a disc of that radius. As we had no *a priori* prediction about the spatial scale at which the nest density might affect predation risk, we fitted a series of preliminary models of nest survival as a function of density for radii of 1–20 m around the focal nest and selected the radius that explained the most variation in nest survival [minimized Akaike's information criterion adjusted for small sample sizes (AIC_c)]. For each continuous predictor, we explored the importance of potential non-linear effects by comparing models that included quadratic polynomials, cubic polynomials or the natural log of that predictor and selecting the formulation that minimized AIC_c for use in subsequent model selection. We considered interactions between habitat type and distance, density and date in order to test the hypothesis that the determinants of mongoose predation may be different in preferred vegetated beach habitat versus avoided open habitats. We also considered the interaction between density and date to test the hypothesis that the seasonal effects are stronger in locations or years with higher nest density. We included study year as a random effect to control for the unexplained variation in survival among years. All continuous variables were standardized (mean = 0, SD = 1) to allow a meaningful comparison of coefficients (Quinn & Keough, 2002).

We took an information theoretic approach to model selection and inference. We ranked models containing all subsets of parameters by AIC_c and selected a 95% confidence set of candidate models for use in inference (Burnham & Anderson, 2002). We calculated composite parameter estimates and standard errors incorporating model selection variance for all parameters in the confidence set using conventional model averaging.

Although the same nest-searching protocol was used from 1999 to 2005, increased research effort in 2004–2005 resulted in an assessment of the timing of nest predation that was more accurate than in the previous years. In addition, an increase in hawksbill nesting in Barbados throughout our study period (Beggs *et al*., 2007) led to an uneven distribution of nests among years, with only 30% total nesting in our study occurring between 1999 and 2003 ($n = 166$ nests) versus 70% between 2004 ($n = 168$ nests) and 2005 ($n = 217$ nests). We therefore used the larger sample of high temporal resolution nesting data from 2004 to 2005 as a training dataset to develop our survival models, and retained the 1999–2003 nesting data as a separate dataset for evaluating the ability of fitted models to predict nest fate under varying conditions (Guisan & Zimmermann, 2000). We assessed the performance of each model by using it to predict whether each nest survived long enough to hatch successfully (65 days), and comparing predictions to the observed fate of nests. We calculated classification accuracy using sensitivity-specificity plots to select the optimal risk cutoff for the 2004–2005 data and applying this cutoff when predicting the fate of the 1999–2003 nests (Hosmer & Lemeshow, 2000). We used the area under the curve (AUC) of receiver–operating characteristic plots for each classification as a measure of model discrimination. AUC values range from 0 to 1, with 0.5 indicating random discrimination, values above 0.7 considered acceptable discrimination, and values above 0.9 rare and indicating excellent discrimination (Hosmer & Lemeshow, 2000). We carried out all analyses in R v.2.8.1 (R Development Core Team, 2008).

Results

A total of 551 hawksbill nests was recorded from 1999 to 2005, with 225 (41.8%) located in vegetation and 313 (58.2%) on the open beach. Mongooses preyed on 149 (27.0%) nests, with annual predation rates ranging from 17.9 to 38.9%.

The majority of nest predation occurred within the first days following laying, and this pattern was consistent

between years (Fig. 1a). Estimated daily predation risk was the highest for freshly laid nests but declined quickly with nest age, increasing slightly near the end of development (Fig. 1b).

There was evidence of a scale-dependent effect of local nest density on predation risk, with the density of nests within a 4–6 m radius of the focal nest explaining the most variation in predation risk (Fig. 2). The density of nests within a 5 m radius around each nest was therefore used as the measure of nest density in subsequent analyses.

Of the 127 candidate nest survival models considered, 16 were retained in the 95% confidence set of models selected by AIC_c (Table 1). The predictive power of models appeared to be driven by the main effects of habitat, proximity to vegetation and nest initiation date, as evidenced by the retention of these variables in all models in the confidence set (Table 1). The survival of nests in vegetated habitat was substantially lower than nests on the open beach, being the lowest deep in vegetation and increasing across the vegetation edge (Table 2; Fig. 3a). Nests laid later in the nesting season were more likely to be preyed on and this effect was non-linear, with a greater increase in mortality toward the end of the nesting season (Fig. 3b). The effect of nest density differed substantially among habitats (Table 2), with a strong negative relationship between density and survival for nests on the open beach but not in vegetation (Fig. 3c). There was little support for the importance of other interactive effects (Table 2). All 16 models in the confidence set showed excellent discrimination and high classification accuracy when predicting the fate of nests used in model calibration (2004–2005) and performed equally well when predicting the fate of nests from previous years (1999–2003).

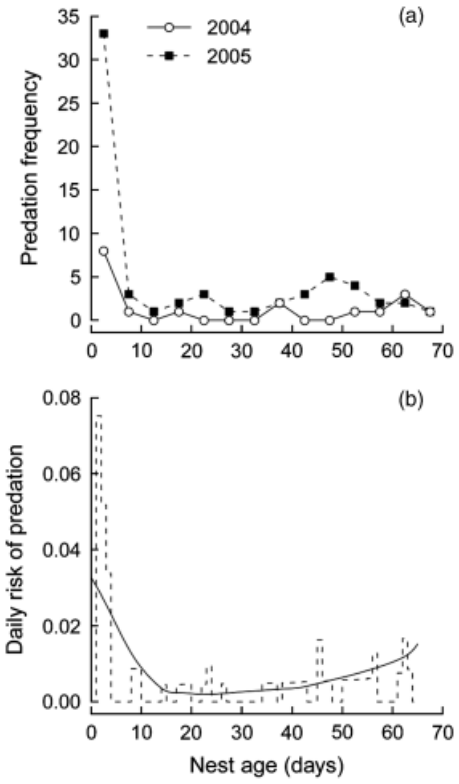

Figure 1 The change in (a) predation frequency (total predated nests) and (b) daily risk of predation (probability of predation over a 24-h period) with age for nests in 2004–2005. Frequencies in (a) are grouped in 5-day bins. The higher predation frequency in 2005 reflects the greater abundance of available nests ($n = 168$ in 2004, $n = 217$ in 2005). Lines in (b) are empirical (dashed line) and kernel-smoothed (solid line) daily hazard functions for 2004–2005 combined.

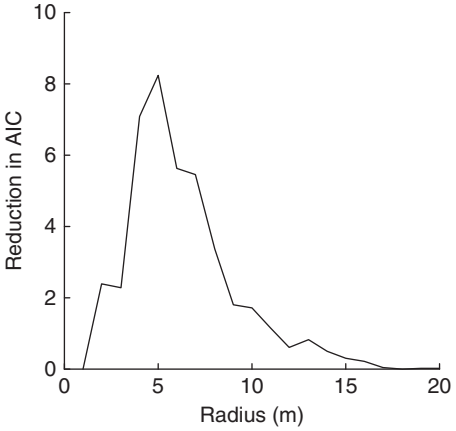

Figure 2 Reduction in model Akaike's information criterion (AIC) for the univariate relationship between nest density (total nests laid over the season per m^2) and predation risk, with density estimated from nests within an increasing radius of the focal nest. AIC reduction is relative to the null (intercept-only) model, with zero indicating no improvement and higher values corresponding to greater explained variation.

Discussion

Accurately forecasting where and when predation will occur has the potential to drastically increase the effectiveness and reduce the costs of predation management (Engeman *et al.*, 2002, 2003). Our study demonstrates the utility of survival analysis for predicting predation of hawksbill sea turtle nests by an introduced predator with widespread impact, providing a unique quantification of the underlying relationship between nest age and predation risk.

Changes in predation risk over time

In sea turtles, the predation risk for eggs is directly linked to nest detectability (Leighton *et al.*, 2009). Previous studies have reported frequent predation early in development (Stancyk *et al.*, 1980) or close to hatching (Fowler, 1979). Analysis of nest survival times provided evidence for both patterns at our site, consistent with previous work in the US Virgin Islands that found frequent mongoose predation at the start and the end of incubation (Nellis & Small, 1983). However, the overall predation risk at our site appears to be driven primarily by high nest vulnerability during the first 4–5 days following oviposition. Excavation and

Table 1 Models included in the 95% confidence set selected by Akaike's information criterion adjusted for small sample sizes (AIC_c)

						Calibration		Evaluation	
Model terms	LogLik	AIC_c	ΔAIC_c	w_i	r^2	AUC	Acc. (%)	AUC	Acc. (%)
Hab + Dist + Date + Date^2 + Dens + Hab × Dens	−355.48	723.26	0.00	0.19	0.41	0.891	82.19	0.905	84.21
Hab + Dist + Date + Date^2	−357.89	723.92	0.66	0.14	0.40	0.888	82.19	0.908	84.87
Hab + Dist + Date + Date^2 + Dens + Hab × Dens + Hab × Dist	−355.15	724.69	1.43	0.09	0.41	0.893	82.19	0.903	84.87
Hab + Dist + Date + Date^2 + Dens + Hab × Dens + Hab × Date	−355.36	725.12	1.87	0.07	0.41	0.892	82.19	0.907	84.21
Hab + Dist + Date + Date^2 + Dens	−357.46	725.14	1.88	0.07	0.40	0.887	82.19	0.907	84.21
Hab + Dist + Date + Date^2 + Dens + Hab × Dens + Date × Dens	−355.48	725.36	2.10	0.07	0.41	0.891	82.19	0.905	84.21
Hab + Dist + Date + Date^2 + Hab × Dist	−357.66	725.52	2.27	0.06	0.40	0.888	81.85	0.906	85.53
Hab + Dist + Date + Date^2 + Hab × Date	−357.89	725.98	2.73	0.05	0.40	0.888	82.19	0.907	84.87
Hab + Dist + Date + Date^2 + Dens + Hab × Dens + Hab × Dist + Hab × Date	−355.08	726.67	3.41	0.03	0.41	0.893	82.19	0.905	84.21
Hab + Dist + Date + Date^2 + Dens + Hab × Dist	−357.22	726.73	3.47	0.03	0.40	0.887	80.82	0.904	84.87
Hab + Dist + Date + Date^2 + Dens + Hab × Dens + Hab × Dist + Date × Dens	−355.14	726.80	3.54	0.03	0.41	0.893	82.19	0.904	84.87
Hab + Dist + Date + Date^2 + Dens + Date × Dens	−357.45	727.19	3.93	0.03	0.40	0.887	82.19	0.908	84.87
Hab + Dist + Date + Date^2 + Dens + Hab × Dens + Hab × Date + Date × Dens	−355.35	727.21	3.95	0.03	0.41	0.892	82.19	0.907	84.21
Hab + Dist + Date + Date^2 + Dens + Hab × Date	−357.46	727.22	3.97	0.03	0.40	0.887	82.19	0.908	84.87
Hab + Dist + Date + Date^2 + Hab × Dist + Hab × Date	−357.65	727.59	4.34	0.02	0.40	0.888	81.85	0.905	86.18
Hab + Dist + Date + Date^2 + Dens + Hab × Dens + Hab × Dist + Hab × Date + Date × Dens	−355.06	728.76	5.51	0.01	0.41	0.892	82.19	0.904	84.21

The model Akaike weight, w_i, is the probability of being the best model in the set of all 127 models considered. Classification accuracy (Acc.) is the proportion of nests whose fate was accurately predicted by the model.
In addition following abbreviations are used: Hab, habitat type (vegetation vs. open beach); Dist, distance from vegetation edge (m); Date, date of nest initiation; Dens, nest density (total nests laid over the season per m^2); LogLik, log likelihood of the model; AUC, area under the curve of receiver–operating characteristic plots for each classification.

Table 2 Composite parameter estimates and standard errors from models in the 95% confidence set selected by Akaike's information criterion adjusted for small sample sizes (AIC_c)

			95% CI	
Parameter	Estimate	SE	Upper	Lower
Distance from vegetation edge	**−1.614**	**0.589**	**−0.465**	**−2.762**
$Habitat_{vegetation}$	**1.427**	**0.699**	**2.790**	**0.063**
Date of nest initiation	**0.490**	**0.192**	**0.865**	**0.116**
Date^2	**0.243**	**0.094**	**0.427**	**0.059**
Density of nests	0.640	0.438	1.494	−0.215
$Habitat_{vegetation}$ × density	**−0.772**	**0.381**	**−0.028**	**−1.515**
$Habitat_{vegetation}$ × distance	−0.774	0.998	1.171	−2.719
$Habitat_{vegetation}$ × date	0.093	0.396	0.865	−0.678
Date × density	0.011	0.117	0.240	−0.218

Predictors whose 95% confidence interval does not include zero are in bold.

re-concealment of nests by researchers before mongoose predation may have resulted in an overall nest vulnerability in this study that was higher or lower than in unmanipulated nests. Although we lacked a control group of unmanipulated nests to assess the effects of nest manipulation on predation in this system, such an investigation would be interesting and worthwhile. In particular, careful concealment of conspicuous freshly laid nests by researchers could potentially reduce predation risk during a critical period of high nest vulnerability, providing an additional conservation technique that could be easily applied during routine monitoring.

Although a rapid decline in cue availability following oviposition and increase near the end of incubation as hatchlings emerge from eggs are likely to occur in most turtle species, the relative importance of these cues for nest detection may vary among predators with different sensory capacities or nest searching behavior. For instance, mongooses at our site use disturbance of sand by the nesting turtle as a primary cue for nest detection (Leighton *et al.*,

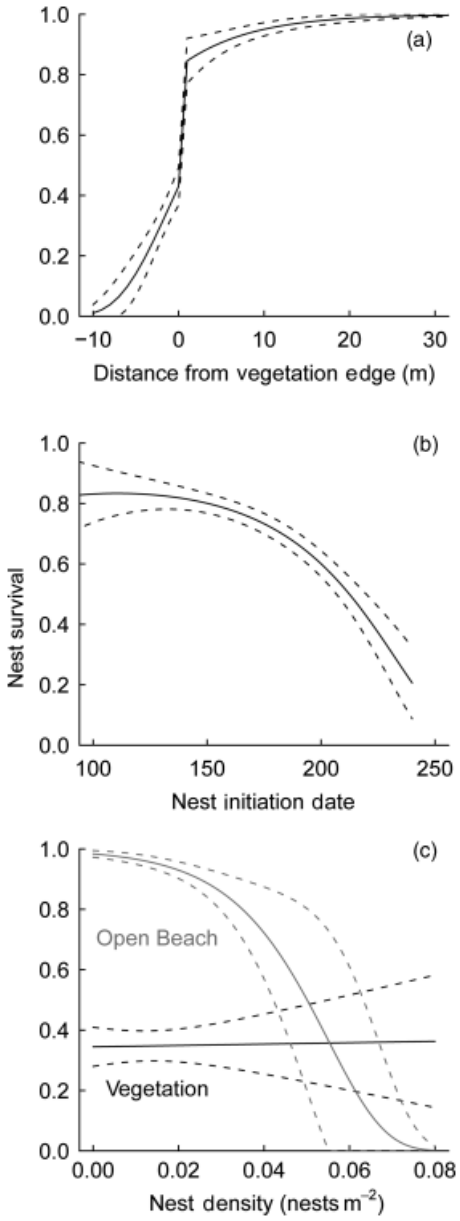

Figure 3 Predicted probability of survival to hatching (65 days of incubation) for hawksbill *Eretmochelys imbracata* nests as a function of (a) distance from the edge of beach vegetation (negative values are within vegetation; positive values are on the open beach), (b) nest initiation date (days since 1 January) and (c) the interaction between nesting habitat (open beach vs. beach vegetation) and nest density. Dashed lines are ± 1 SE.

2009), but other predators such as coatis (*Nasua nasua* and *Nasua narica*) are thought to rely more heavily on olfactory cues from buried eggs (Cornelius, 1986). Olfactory cues released by the buried eggs may remain available after surface cues have disappeared and increase near hatching, which may explain the more gradual decline in predation frequency following oviposition and the marked increase at the end of incubation observed in studies of coati predation (Fowler, 1979; Tiwari *et al*., 2006). Barton & Roth (2008) found that loggerhead nests in areas with high ghost crab density were at a greater risk of predation by raccoons, presumably because ghost crab tunnels entering incubating nests and the odors resulting from egg predation by crabs facilitated nest detection by foraging raccoons. Such interspecific facilitation may alter the timing of predation, increasing the likelihood of predation occurring during the mid-incubation period, once crabs or other invertebrate predators have infiltrated the nest.

Foraging theory predicts that predators can increase foraging efficiency by tracking prey availability at fine spatial and temporal scales (Stephens, 1987; Hall & Kramer, 2008). Previous work at Bath documented an important increase in mongoose activity with increasing nest availability, and it is likely that the increase in predation risk over the nesting season observed in the current study resulted from mongooses tracking seasonal changes in nest abundance. Other studies have documented seasonal shifts in predator activity at nesting beaches (Engeman *et al*., 2003; Maros *et al*., 2003), and the tracking of nest abundance by predators may be a widespread phenomenon. However, another possibility is that accumulated experience with nests over the course of the nesting season results in a predator population that is more effective at locating nests (Stancyk, 1982; Nellis & Small, 1983; Leighton *et al*., 2009). Learning effects could not be distinguished from changes in predator activity in this study, but future work on the relative importance of predator learning could provide useful insights for management. In particular, where increasing predation risk over time results from individual predators becoming specialized, predator control might be used strategically to remove problem animals from the population (Nellis & Small, 1983; Engeman *et al*., 2003).

Beach vegetation drives spatial patterns of predation risk

Landscape structure can have important effects on species interactions (Fagan, Cantrell & Cosner, 1999; Didham *et al*., 2007), and edge effects on predation risk in fragmented landscapes are widely reported in the nest predation literature (Chalfoun *et al*., 2002; Kolbe & Janzen, 2002; Leighton *et al*., 2008). Consistent with previous work showing a fine-scale variation in predation across the vegetation-open beach edge (Leighton *et al*., 2008), we found that nests in vegetated habitat had $<50\%$ chance of surviving to hatch (Fig. 2a) and that predation occurred nearly exclusively in or very near patches of beach vegetation. However, the avoidance of the open beach by mongooses in our study area appears to be driven by the presence of humans that are viewed as a predatory threat (Leighton, Horrocks & Kramer, 2010), and nests in open areas may therefore be at a greater risk on beaches with lower human use. Beach vegetation is likely to be an important predictor of nest predation risk for other predators that use vegetation as a refuge while foraging such as coatis that also prey almost exclusively on nests in or near vegetation (Fowler, 1979;

Cornelius, 1986), and for invertebrate predators such as ants (Wetterer *et al*., 2007) or mole crickets (Caut *et al*., 2006) that are associated with beach vegetation. However, other predators such as raccoons (*Procyon lotor*) and wild and domestic canids readily prey on nests in all habitat types (Fowler, 1979; Cornelius, 1986; Whiting *et al*., 2007). These differences underline the importance of understanding predator foraging ecology for making accurate predictions about nest predation risk.

Numerous studies have shown that nest density can influence predation risk in birds (Andren, 1991), but evidence for density-dependent predation in turtle nests is mixed. Increased risk for individual nests in high-density areas has been shown in a few studies (Burger, 1977; Marchand & Litvaitis, 2004), but other studies report no effect (Fowler, 1979; Burke *et al*., 1998). One possible factor contributing to this discrepancy is that the scale at which nest density is measured varies widely among studies, from whole beach sections (Fowler, 1979; Tiwari *et al*., 2006) to within 1 m radius of a given nest (Burger, 1977). We found that the scale of measurement had a strong effect on the relationship between nest density and risk and that this relationship also varied substantially with habitat context, suggesting that negative results from studies where density has been measured at a single spatial scale or averaged across different habitats should be interpreted with caution. The fact that a higher density of hawksbill nests increased the predation risk exclusively for nests laid on the open beach is consistent with high mongoose activity in vegetated habitats but avoidance of open habitats (Leighton *et al*., 2008) as foraging individuals are more likely to risk exposure to investigate sand disturbances in areas where turtles nest frequently or where nests have been found previously. A practical consequence is that relocating many high-risk nests to the same low-risk area of the open beach could inadvertently increase predation by creating an area of high nest density that attracts predators, similar to the elevated hatchling mortality from marine predators that occurs in the water adjacent to high-density nesting areas (Wyneken *et al*., 2000).

From risk models to conservation

An important application of risk models is to provide objective guidelines for optimizing conservation action. Conservation approaches for reducing sea turtle nest predation generally fall into two categories: manipulating predator activity, usually by predator removal (e.g. Coblentz & Coblentz, 1985; Engeman *et al*., 2002), or protecting individual nests, either by applying protective devices to nests *in situ* (e.g. Ratnaswamy *et al*., 1997; Yerli *et al*., 1997) or by relocating the entire clutch to low-risk areas (Stancyk *et al*., 1980). Predator removal often has only a short-term effect (Engeman *et al*., 2006) and its impact could be optimized by synchronizing removal efforts with periods of highest predation risk. If nests are most vulnerable early in development and later in the nesting season, reducing predator abundance before the peak of nesting and again later in the season when the total nest abundance is highest may be effective. If, as in our study, risk is the highest for nests near vegetation, techniques for reducing local predator activity should target beaches or beach sections with a high proportion of vegetated nesting habitat. In addition to direct removal of predators, which is costly and can have undesirable indirect effects on ecological communities (Ratnaswamy & Warren, 1998; Barton & Roth, 2008), reducing predator access to a certain section of the beach (i.e. through strategic fencing or removal of vegetated corridors), reducing vegetation height to make it poor refuge habitat or increasing human activity in high-risk nesting areas (Talbert *et al*., 1980; Leighton *et al*., 2010) may provide alternative management strategies.

Nest protection and relocation can be time consuming and may have adverse consequence for egg survival (Boulon, 1999) and possibly for embryonic development (Irwin, Amy & Lohmann, 2004). In particular, movement of sea turtle eggs more than 4–8 h post-laying can result in high egg mortality unless it is carried out extremely carefully (Miller, 1997). Risk models are particularly useful in identifying which nests should be moved or protected, and specifically targeting nests at a high risk of predation could significantly increase the cost-effectiveness of such procedures. Our study suggests that the first 2 days following oviposition are critical for nest survival and that nest protection and relocation efforts should ideally target freshly laid nests. Thus, methods that provide short-term protection (i.e. increasing nest concealment, application of predator-aversive substances or temporary screening) may nonetheless have a strong overall effect on survival if they allow nests to survive the initial 24–48-h period of highest vulnerability. Our results suggest that only nests near vegetation need specific protection from mongoose predation on beaches with high human use, and that relocation of freshly laid (within 4–8 h of laying) or partially preyed on nests to non-vegetated areas of the beach could be an effective strategy.

Our study provides general guidelines for managing mongoose predation that are likely to be applicable throughout the Caribbean and in other regions where mongooses have been introduced. Although sea turtle species differ considerably in nest site selection behavior, proximity to beach vegetation or other types of cover is likely to provide a consistent index of the relative risk of predation by mongooses and possibly other cryptic nest predators. Evaluating model predictions using predation data from other locations and other sea turtle species will help refine these guidelines and yield further insight into the predation process.

Testing hypotheses about nest predation mechanisms: the role of survival analysis

Why and how nest vulnerability to predation changes over time has been the source of speculation by sea turtle biologists for decades (Stancyk, 1982; Nellis & Small, 1983; Cornelius, 1986). Changes in cue availability over time and predator learning mechanisms are hypotheses with intuitive

appeal but have yet to be rigorously tested. Survival analysis techniques allow the effects of time-varying risk factors on daily mortality risk to be modelled, providing an intuitive framework for testing such hypotheses (Nur *et al*., 2004). An experimental approach is ideal for isolating the effects of different potential mechanisms, but predation experiments are often not acceptable or feasible when working with sea turtles and other endangered species. Field experiments with artificial nests have recently been used successfully to study nest predation in both sea turtles (Leighton *et al*., 2008, 2009) and freshwater turtles (Hamilton, Freedman & Franz, 2002; Marchand & Litvaitis, 2004; Rollinson & Brooks, 2007), and combined with survival analysis techniques, provide a promising method of testing longstanding hypotheses about the mechanisms of sea turtle nest predation.

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