MONGOOSE PREDATION ON SEA TURTLE NESTS: LINKING BEHAVIOURAL ECOLOGY AND CONSERVATION

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# Table of Contents

TABLE OF CONTENTS .................................................................................................................................................. III

LIST OF TABLES .......................................................................................................................................................... VI

- CHAPTER 1 ........................................................................................................................................................... VI
- CHAPTER 2 ........................................................................................................................................................... VI
- CHAPTER 3 ........................................................................................................................................................... VI
- CHAPTER 4 ........................................................................................................................................................... VII

LIST OF FIGURES ......................................................................................................................................................... IX

- GENERAL INTRODUCTION ........................................................................................................................................ IX
- CHAPTER 1 ........................................................................................................................................................ X
- CHAPTER 2 .......................................................................................................................................................... X
- CHAPTER 3 ......................................................................................................................................................... XI
- CHAPTER 4 ........................................................................................................................................................ XI

PREFACE ........................................................................................................................................................................ XII

THESIS FORMAT AND STYLE .................................................................................................................................... XII

CONTRIBUTION OF CO-AUTHORS .......................................................................................................................... XIII

ORIGINAL CONTRIBUTIONS TO KNOWLEDGE ....................................................................................................... XIV

- Overall Contributions ........................................................................................................................................... xiv
- Chapter 1 ........................................................................................................................................................ xiv
- Chapter 2 ........................................................................................................................................................ xiv
- Chapter 3 ........................................................................................................................................................ XV
- Chapter 4 ........................................................................................................................................................ XV

ACKNOWLEDGEMENTS .............................................................................................................................................. XVII

THESIS ABSTRACT ....................................................................................................................................................... 1

RÉSUMÉ ......................................................................................................................................................................... 3

GENERAL INTRODUCTION ...................................................................................................................................... 5

- BEHAVIOURAL ECOLOGY AND CONSERVATION: A HISTORICAL DIVIDE ...................................................... 5
- SEA TURTLE NEST PREDATORS: A CONSERVATION CONCERN ........................................................................ 6
- THE SMALL ASIAN MONGOOSE IN THE CARIBBEAN ....................................................................................... 8
- HAWKSBILL SEA TURTLE CONSERVATION IN BARBADOS ............................................................ 10
- THESIS STRUCTURE AND APPROACH ........................................................................................................... 12
- LITERATURE CITED ............................................................................................................................................ 14

CHAPTER 1 ................................................................................................................................................................. 22

- LINKING STATEMENT 1 ................................................................. 22
- ABSTRACT ......................................................................................... 23
- INTRODUCTION ................................................................................ 24
- MATERIALS AND METHODS ............................................................ 26
  - Study area and species ................................................................. 26
  - Spatial patterns of abundance and nest predation ....................... 27
  - Statistical analyses ..................................................................... 29
- RESULTS .......................................................................................... 30
  - Edge Responses ......................................................................... 30
  - Nest Predation ............................................................................ 31
  - Predation Risk .......................................................................... 31
  - Distribution of Mortality ............................................................. 31
- DISCUSSION .................................................................................... 32
LIST OF TABLES

CHAPTER 1

Table 1. Generalized Additive Mixed Models (GAMMs) used to model abundance and predation risk in relation to the open beach/vegetation edge on Bath Beach, Barbados. The table shows mongoose edge response (a), hawksbill sea turtle nest abundance (b), risk of mongoose predation on artificial nests (c), and risk of mongoose predation on hawksbill nests (d). Sample size, n, is the number of track pad checks in (a), the number of distance from edge intervals (15/yr over 2 yr) in (b), and the total number of monitored nests in (c) and (d). Adjusted $R^2$ is for the final model, where only significant predictors were retained. $s(\ldots)$ denotes predictors fitted as non-parametric smoothing terms; unbracketed predictors were fitted as typical parametric terms. $d.f.$ is the estimated degrees of freedom for each term. ... 42

Table S1 (Online supplementary material). Generalized Additive Mixed Models (GAMM) used to model edge response of mongoose abundance (a) and hawksbill sea turtle nest abundance (b) relative to the open beach/vegetation edge. Models presented here are parametric approximations of the non-parametric GAMMs presented in Table 1, with non-parametric smoothing terms replaced by parametric polynomial terms. Sample size, n, is the number of track pad checks in (a) and the number of distance from edge intervals (15/yr over 2 yr) in (b).................................................................... 43

CHAPTER 2

Table 1. The effect of nest depth and other variables on (a) predation risk and its components, (b) detection (probability of detection) and (c) capture (probability of predation following detection), for artificial sea turtle nests after 7 days of exposure. All predictors are standardized (mean = 0, SD = 1). % Dev. is the proportion of null model deviance explained......................... 74
Table 2. The effect of nest depth and other variables on (a) detection latency and (b) predation latency for artificial sea turtle nests exposed to mongooses predation for 7 days. All predictors are standardized (mean = 0, SD = 1). % Dev. is the proportion of null model deviance explained.

CHAPTER 3

Table 1. Generalized Linear Mixed Models of mongoose activity in hawksbill sea turtle nesting habitat at (a) broad (beach-level) and (b) fine (site-level) spatial scales. Parameter estimates and standard errors are the composite estimates from all models in the 95% confidence set of models selected by Akaike’s Information Criterion adjusted for small sample sizes (AICc). RI is a measure of the relative importance of each parameter, calculated as the sum of the Akaike weights of all models containing that parameter.

Table S1 (Supplementary Material). Generalized Linear Mixed Models of mongoose activity in (a) beach and (b) adjacent forest habitats at Bath Beach, Barbados. Parameter estimates and standard errors are the composite estimates from all models in the 95% confidence set of models selected by Akaike’s Information Criterion adjusted for small sample sizes (AICc). RI is a measure of the relative importance of each parameter, calculated as the sum of the Akaike weights of all models containing that parameter.

CHAPTER 4

Table 1. Models included in the 95% confidence set selected by Akaike’s Information Criterion adjusted for small sample sizes (AICc). The model Akaike weight, \( w_i \), is the probability of being the best model in the set of all 24 models considered. Classification accuracy (Acc.) is the proportion of nests whose fate was accurately predicted by the model. AUC is the area under the curve of receiver operating characteristic plots for each classification. The following abbreviations are used for model terms: Hab = habitat type (vegetation vs. open beach), Dist = distance from vegetation.
edge (m), Date = date of nest initiation, and Dens = nest density (total nests laid over the season per m²).

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 (AICc). RI is a measure of the relative importance of each parameter, calculated as the sum of the Akaike weights of all models containing that parameter.
LIST OF FIGURES

GENERAL INTRODUCTION

Figure 1. Location of Bath Beach, the primary east coast nesting site for hawksbill sea turtles in Barbados. ................................................................. 19

Figure 2. Typical nesting habitat for hawksbill sea turtles at Bath Beach, Barbados. Open nesting areas and sparse grass are interspersed with dense patches of shrubs. The main tourist developments are a public swimming area and bungalow-style cottages lining the beach 10-50 m inland of the high water mark. ........................................................................................................ 20

Figure 3. The frequency of hawksbill sea turtle nests recorded annually at Bath Beach from 1999-2005 that were or were not preyed on by mongooses (Figure based on data from Chapter 1). ......................................................... 21

CHAPTER 1

Figure 1. Abundance responses of mongooses and hawksbill sea turtles to edges between open sand and patches of vegetation at Bath Beach in Barbados. (a) Mongoose abundance measured as the probability of crossing a sand pad per 2-h interval and (b) hawksbill nest abundance measured as the proportion of total annual nests per m$^2$. For mongooses, data shown are presence/absence of mongooses tracks on sand pads for each 2-h check period (n = 978), with random jitter added to allow visualization of overlapping points. For hawksbill nests, open circles are proportional cumulative nest densities from 2004 and 2005 used in model calibration (n = 30). The solid lines are the GAMM edge response function and dashed lines are ±1 SE. The vertical dotted line marks the location of the edge, with positive values open sand and negative values within vegetation......................................................... 44

Figure 2. GAMM models of predation risk (a) for artificial nests over a 24-hour period (n = 204) and (b) for hawksbill sea turtle nests over a 60-day incubation period (n = 301) across the open sand-vegetation edge. Data
shown are the fates of individual nests (1 = predated, 0 = intact), with random jitter added to allow visualization of overlapping points. The solid lines show the final GAMM model for predation risk and dashed lines are ±1 SE. The vertical dotted line marks the location of the edge, with positive values open sand and negative values within vegetation.

Figure 3. Frequency of predated hawksbill sea turtle nests recorded from 1999-2005 across the open beach/vegetation edge (bars), and distribution of mortality predicted by the product of continuous edge response functions for mongooses and hawksbills (solid line).

CHAPTER 2

Figure 1. The effect of nest depth on (a) predation risk and its components, (b) detection (probability of detection) and (c) capture (probability of predation following detection), for hawksbill nests in vegetated beach habitat. Data shown are the status of individual nests (1, detected/preyed on; 0, not detected/preyed on) observed in 2004 and 2005 (n = 101 in a,b; n = 78 in c). The solid lines show the fitted GLM and dashed lines are ± 1 SE.

Figure 2. The effect of nest depth on (a) predation risk and its components, (b) detection (probability of detection) and (c) capture (probability of predation following detection), for artificial sea turtle nests after 6h (dotted line, filled squares), 24h (dashed line, open circles) and 7 days (solid line, filled circles). Error bars are ± 1 SE.

Figure 3. The effect of experimental treatment on (a) the probability of detection (squares), extensive digging (circles), and predation (triangles) and (b) the maximum excavation depth attained by mongooses digging for artificial sea turtle nests after 7 days of exposure. Error bars are ± 1 SE.

CHAPTER 3

Figure 1. Habitat map of Bath Beach, Barbados. Filled squares indicate location of monitoring plots relative to different habitats and the center of human activity (Beach Facility).
Figure 2. Spatial and temporal patterns of activity for mongooses and humans at Bath Beach, Barbados. (a) Habitat-scale variation in activity over the hawksbill nesting season. (b) Habitat-scale variation in activity among days of the week and throughout the day. (c) Variation in activity among monitoring sites and between edge and interior microhabitats. Error bars are +1 SE........................................................................................................... 101

Figure 3. Influence of tourist pressure and nest availability on (a) predator activity in beach habitat and (b) resulting sea turtle egg mortality from predation. Predictions in (b) are for hawksbill nests in vegetated nesting habitat over seven years of monitoring (1999-2005). ................................................................. 103

CHAPTER 4

Figure 1. The change in a) predation frequency (total predated nests) and b) daily predation risk (probability of predation over a 24h period) with age for nests in 2004-2005. Frequencies in a) are grouped in 5-day bins. Higher predation frequency in 2005 reflects the greater abundance of available nests ($n = 168$ in 2004, $n = 217$ in 2005). b) shows both empirical (dashed line) and kernel-smoothed (solid line) daily hazard functions for 2004-2005 combined. ..... 128

Figure 2. Reduction in model 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................................................................. 130

Figure 3. Survival of hawksbill 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) oviposition date (curves are for the 15$^{th}$ day of each month) and c) and the interaction between habitat and nest density (high = 0.05 nests/m$^2$, low = 0.005 nests/ m$^2$). ........................................................................................................ 131
PREFACE

THESIS FORMAT AND STYLE

This is a manuscript-based thesis, consisting of a collection of papers of which I am the primary author. All chapters have either been published or are intended for publication, and the style of each chapter is that of the scientific journal for which it has been prepared. The four manuscripts and associated journals are as follows:


CONTRIBUTION OF CO-AUTHORS

With advice from my co-supervisors, Donald Kramer and Julia Horrocks, I conceived the conceptual framework and sampling design of my research project. I collected all data, with the help of a large team of volunteer and paid assistants working under my supervision. The notable exception to this was the 5-year dataset (1999-2003) on sea turtle nesting and predation at Bath that was contributed by the Barbados Sea Turtle Project (BSTP). Barry Krueger and Jen Beggs were primarily responsible for the collection and compilation of the BSTP dataset and are co-authors of Chapter 1, which is has now been published. I selected and performed all statistical analyses and interpreted the results. I am the primary author on all manuscripts associated with this thesis and was responsible for writing all parts of them. Both Donald Kramer and Julia Horrocks are co-authors on all manuscripts, having each contributed substantially to the conceptual development of all chapters and provided extensive editorial feedback on each manuscript. Donald Kramer provided the funding for my field work and Julia Horrocks provided logistical support in the field and funded the collection and compilation of the BSTP data.
ORIGINAL CONTRIBUTIONS TO KNOWLEDGE

Overall Contributions

- The first detailed study of predatory interactions between the widely introduced small Asian mongoose and a threatened native species.
- The first investigation of the behavioural mechanisms underlying nest predation by mongooses, including fine-scale habitat selection, landscape use, temporal activity patterns, antipredator behaviour, and egg-finding behaviour with broad relevance to the conservation of turtles and other species with buried eggs such as iguanas.
- The innovative use of several statistical methods, including the first use of generalized additive mixed models (GAMMs) to model species-habitat relationships and the first application of Cox proportional hazards regression to model nest survival in turtles, demonstrating their utility in this context and providing a template for future work.

Chapter 1

- The first use of artificial nests in sea turtle research, confirming that short-term field experiments using artificial nests can be used to test hypotheses about long-term patterns of natural nest mortality.
- The use of a novel combination of passive predator tracking and artificial nests, providing the first demonstration that nest predation risk is directly related to fine-scale spatial variation in predator activity.
- A novel approach for modelling species interactions in fragmented landscapes using edge responses to predict contact rates, showing that the edge response functions for predators and prey can accurately predict the shape and spatial extent of edge effects on predation, and establishing a heuristic link between the existing models of species edge responses and observed patterns of species interactions.

Chapter 2
Establishment of a general theoretical framework for examining effects of burial depth on predation through two distinct mechanisms: detection and pursuit cost.

The first examination of how burial depth affects the detection and excavation of buried eggs, confirming the generality of the pattern of decreased risk with burial depth established in studies of seed-caching rodents and providing the first demonstration that excavation costs can play an important role in reducing predation risk.

The first investigation of the relative importance of disturbance and olfactory cues for a predator of sea turtle nests, revealing that disturbance provides a primary cue for nest detection by mongooses and providing an empirical basis for artificially increasing nest concealment as a conservation intervention.

Chapter 3

The novel use of passive tracking to reveal predator activity at multiple spatial scales, providing the first demonstration of fine-scale resource tracking by mongooses in time and space and empirical support for economic models of habitat selection where human disturbance is treated as a form of predation risk (risk-disturbance hypothesis).

One of the first investigations of indirect effects of human disturbance for threatened prey, showing that, in contrast to many forms of disturbance with direct negative impact for threatened populations, limited human activity on nesting beaches during the day may improve nest survival by deterring predators.

Chapter 4

The first quantification of the change in daily predation risk for turtle nests during egg development, revealing a non-linear relationship between risk and age and providing a framework for testing longstanding hypotheses about mechanisms of ontogenetic changes in egg vulnerability.
The first general model of sea turtle nest predation by mongooses, highlighting the strong effect of landscape structure on the risk of mongoose predation and demonstrating the utility of survival analysis for integrating spatial and temporal predictors of predation risk in general.
ACKNOWLEDGEMENTS

My doctoral project arose out of the friendship and collaboration of two exceptional people. Don Kramer and Julia Horrocks have been a supervisory dream-team, supporting my development as an independent scientist with creativity and scientific rigour, good judgement and good humour. Their mentorship over the course of my graduate studies has been invaluable and I am very grateful to both of them.

The supportive academic community of McGill University was important throughout my Ph.D. My supervisory committee members, Louis Lefebvre and Murray Humphries, contributed significantly to the early development of my project, and I am also grateful to Lauren Chapman, Colin Chapman, Linda Cooper, Frédéric Guichard, and Brian Leung for their helpful advice. Finally, Susan Bocti and Ancil Gittens at the Graduate Studies Office have provided much friendly help around critical deadlines.

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I had the good fortune to spend two terms as a visiting student at the Wildlife Conservation Research Unit (WildCRU) of Oxford University. I want to especially thank David Macdonald for hosting me at Tubney House, and the rest of the CRU for giving me such a warm welcome. In particular I’d like to thank Zeke Davidson, Harriet Davies, Lauren & Harry Harrington, Danielle Linton,
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My second stint as a visiting student was thanks to the generosity of Tony Sinclair at UBC who took me under his supervisory wing and with whom I had shared many stimulating discussions. I thank the members of the Sinclair lab for their friendship, in particular René Beyers, Caroline Jackson and Kris Metzger. I am grateful to Val LeMay for making sense of mixed models and Sarah Gergel for teaching me the ins and outs of landscape ecology.

Several individuals with no academic ties to my project have nonetheless made important contributions, and I would like to particularly thank Rob Ewers & Raphael Didham for encouraging me to develop the model of edge responses, Marc Cattet for a primer on chemical immobilization of wildlife, Claire Jardine for hands-on training in working with small mammals, David Nellis for friendly advice on working with mongooses in the field, and Karen Eckert for promoting my research through the WIDECAST network and encouraging me to attend regional meetings.

My field work in Barbados was really only possible because of the friendly collaboration of the Barbados Sea Turtle Project. In particular, Barry Krueger and Jen Beggs initiated me to sea turtle research and were instrumental in collecting and compiling the long term nesting data from Bath Beach, Darren Browne often stopped in to make sure all was well at Bath, and my first night patrol with Asanchia Harewood was the start of great friendship. I am especially grateful to Archie Bailey who mentored me in the art of finding turtle nests and to Michael Bailey who usually found them first.

Field work in Barbados may sound like a walk on the beach, but the following people know better. It is difficult to overstate the contributions made by the many people who assisted with data collection in the field: (2002) Adam Crosby; (2003) Diorys Pérez; (2004) Nancy Beaudoin, Ashley Craig, Jessica
Ford, Diorys Pérez and Corinne Sperling; (2005) Typhenn Brichieri-Colombi, Nancy Beaudoin, Erika Brown, Violet Compton, Jessica Ford, Diorys Pérez; and (2006) Jessica Ford. I am particularly indebted to Diorys Pérez whose knowledge of Caribbean natural history and network of contacts were essential throughout the project. In addition to the core field team, I am grateful for the field help provided by the following people: Sandra Binning, Margaret Leighton, Anna & Ted Leighton, Kyle Martin, Harris Mavromatis, Simon Pietrocatelli, Gabriel Perron, Allan Franklin, and Kamara Rhynd. I am equally grateful to Christina Saliba, Lese Turner, Michael Vilimek, and Sian Wilson who helped with video analysis in the lab.

Work in Barbados was facilitated by the Bellairs Research Institute, and in particular Richard Haynes who helped secure visas. I thank David & Maureen Marshall and Trevor & Sharon Carmichael who generously rented us their beach cottages at Bath for months at a time, as well as Archie & Pauline Bailey who hosted us in their home and kept us well-stocked with bananas. Anneliese and Gert Lampersdoerfer supplied us with our trusty field vehicle “Loretta” and afternoon coffee on every possible occasion. Gus Reader was very helpful in providing us veterinary supplies and methodological guidance for mongoose handling, and John from Bajon Chicken Ltd. supplied us with hundreds of chicken heads free of charge for baiting traps.

I am especially appreciative of the warm response of the Bath Beach community to our field team and their keen interest in turtle conservation. In particular, Gordon & Julie Bayne for feeding us and making us part of the family, Mark and the rest of clan DeFrettas for teaching us to cook fish and play dominoes, Michael & Sarah Carrington for adopting our pet mongoose, Colin & Dione Beadon for offering up their back yard for mongoose relocations, Bernard & Samantha from Ocean Echoes Stables for showing us the hills on horseback, Michael Webster for letting us raid his farm for produce, Gary Marshall for making sure we got out night fishing, and all the beach workers, Bird, Elridge, Anson, Carl, and the raking ladies for looking out for us in the field. A special thanks goes to Marley the mongoose for teaching us a great deal about mongoose.
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Most of all, I thank Jessica Ford for her love and patience, and for planning our wedding while I finished writing my thesis.
The introduced small Asian mongoose (*Herpestes javanicus*) is a widespread predator of sea turtle eggs and hatchlings in the Caribbean. I studied the behavioural ecology of mongoose predation on the nests of critically endangered hawksbill sea turtles (*Eretmochelys imbricata*) in Barbados. Combining short-term field experiments with seven years of hawksbill nesting data, I investigated how mongoose foraging behaviour, antipredator behaviour and landscape use explain the spatial and temporal patterns of sea turtle nest predation. An experiment combining artificial nests and predator tracking revealed a direct relationship between fine-scale variation in mongoose activity and nest predation risk. The combination of mongoose avoidance of open areas and the spatial distribution of hawksbill nests relative to patches of beach vegetation accurately predicted the observed peak in nest predation near the vegetation edge. Egg-burial depth by nesting hawksbills also affected predation risk, but this was primarily due to the increased digging effort required rather than any increase in nest concealment with depth. A second experiment with artificial nests confirmed the causal relationship between burial depth and predation risk and showed that substrate disturbance is a primary cue for nest detection by mongooses. At the landscape scale, mongooses tracked local nest abundance but showed a fine-scale negative response to human beach use, suggesting that human activity on nesting beaches may improve nest survival by deterring predators. Finally, an analysis of nest survival times showed that nests were most vulnerable to predation in first days following oviposition and that predation risk increased over the nesting season, providing a general framework for planning where and when predation reduction methods should be applied. I conclude that predation risk for sea turtle nests is likely to depend on: i) how predator nest-finding behaviour is modulated by nest characteristics such as cue availability and digging cost and ii) behavioural processes such as predator avoidance and resource tracking that drive patterns of landscape use and alter the contact rate between predators and nests. Despite the pessimistic views of some recent commentators, my thesis shows that
Behavioural Ecology can provide unique and relevant insight into the ecological processes underlying conservation problems.
RÉSUMÉ

La petite mangouste indienne (*Herpestes javanicus*) est une espèce introduite dans de nombreuses îles des Caraïbes et est un prédateur important des œufs de tortues marines. J’ai étudié l’écologie comportementale de la prédation par les mangoustes sur les nids de tortue imbriquée (*Eretmochelys imbricata*), une espèce en danger critique d'extinction, à la Barbade. En combinant des études expérimentales de courte durée avec des données de prédation des nids de tortues imbriquées s’échelonnant sur sept années, j’ai investigué comment le comportement d’approvisionnement, le comportement anti-prédateur, et l’utilisation du paysage par les mangoustes expliquent les patrons spatiaux et temporels de la prédation des nids. Une étude expérimentale combinant des nids artificiels et une mesure passive de l’activité des prédateurs a démontré une relation directe entre la variation spatiale de l’activité des mangoustes et le risque de prédation des nids. Conjointement, l’évitement des espaces dépourvus de végétation sur la plage par les mangoustes et la distribution spatiale des nids de tortues imbriquées en fonction de la végétation ont prédit de manière précise le patron de prédation élevé observé dans la zone bordée de végétation. La profondeur des nids affectait également le risque de prédation mais avait peu d’influence sur la détection des nids par les mangoustes. L’effet relié à la profondeur était surtout dû à l’effort d’excavation supplémentaire. Une deuxième étude expérimentale utilisant des nids artificiels a confirmé la relation directe entre la profondeur des nids et la prédation, démontrant que la mangouste utilise la perturbation du sable créée lors de la ponte comme principal indice de détection des nids. A l’échelle du paysage, l’activité des mangoustes suivait la disponibilité des nids de tortues sur la plage. Cependant, il y avait une relation négative entre l’activité des mangoustes et l’utilisation de la plage par les humains, suggérant que la présence humaine dans les aires de ponte pourrait améliorer la survie des nids de tortues en réduisant l’activité des prédateurs. Finalement, une analyse de la durée de survie des nids a démontré que le risque de prédation était le plus élevé dans les premiers jours suivant la ponte et le risque devenait de plus en plus
important au cours de la saison de ponte, créant un modèle pratique pour aider à planifier où et quand appliquer des méthodes pour réduire la prédation. En conclusion, le risque de prédation des nids de tortues marines varie en fonction des facteurs suivants : i) la modulation du comportement d’approvisionnement du prédateur en fonction des caractéristiques du nid tels que la disponibilité d’indices sensoriels et le coût d’excavation et ii) les processus comportementaux tels que les mouvements anti-prédateurs et le suivie de la disponibilité des ressources qui conjointement déterminent l’utilisation du paysage par les prédateurs et la probabilité de contact entre prédateurs et nids. Contrairement aux perspectives pessimistes proposées récemment par certains scientifiques, ma thèse démontre que l’écologie comportementale peut fournir des informations uniques et pertinentes sur les processus écologiques qui sont à la base des problèmes en conservation.
BEHAVIOURAL ECOLOGY AND CONSERVATION: A HISTORICAL DIVIDE

Behavioural ecology and conservation biology are both relatively young disciplines. Behavioural ecology emerged from the field of Ethology in the 1960s-1970, with a focus on exploring the adaptive significance of behavioural processes at the level of individual organisms (Owens 2006). Conservation Biology emerged in the mid-1980s in response to the growing biodiversity crisis (Soule 1985, Meine et al. 2006). Traditionally concerned mainly with population-level processes, it maintained a strong focus on applied outcomes and a unifying objective “to provide principles and tools for preserving biological diversity” (Soule 1985).

Despite common roots in the biology of wild animals, there was historically little overlap between Behavioural Ecology and Conservation Biology until the mid-1990s when a surge of interest in integrating the methods and theoretical framework of Behavioural Ecology with the rapidly expanding field of Conservation Biology (Ulfstrand 1996, Sutherland 1998, Caro 1999, Holway and Suarez 1999) resulted in a flurry of research and the emergence of the new integrative field of “Conservation Behaviour” (Blumstein and Fernandez-Juricic 2004). However, reviewing the progress of this field a decade later, several authors have concluded that the initial efforts to link the behaviour and conservation of animals have generally failed to produce the expected synergy and useful outcomes to date (Linklater 2004, Caro 2007, Angeloni et al. 2008).

Theory-driven questions of Behavioural Ecology often lack practical applicability to conservation problems and, conversely, application-driven research directed at a specific conservation issue may be ill-suited for advancing general theories about behaviour (Caro 2007). As a step toward bridging this gap, there has been a recent call for behavioural ecologists to design research programs to clearly address conservation questions, develop and test theory in fragile
ecosystems and focus research on high-profile threatened species, where contributions are likely to have the greatest impact (Blumstein and Fernandez-Juricic 2004, Caro 2007; see also http://www.animalbehavior.org/ABS/Conservation/thirteen.html).

Linking fundamental ecological questions with applied conservation objectives has served as a unifying goal throughout my Ph.D. By carrying out research on the behavioural ecology of an invasive predator interacting with a recovering population of critically endangered prey, I hoped to develop and test theory in a context where it could be directly applied. The central questions that I set out to answer in my doctoral thesis were: 1) what are the ecological and behavioural processes affecting mongoose predation on sea turtle nests, and 2) how can these be used to achieve conservation objectives for sea turtles? I focussed on the behavioural ecology (foraging ecology and space use) of mongooses with the objective of identifying the mechanisms (behavioural processes) giving rise to observed patterns of predation and applying this knowledge to develop new strategies and improve existing methods for reducing egg losses to mongooses and other introduced predators.

SEA TURTLE NEST PREDATORS: A CONSERVATION CONCERN

Sea turtles were once abundant throughout the world’s tropical oceans, filling an important ecological niche as consumers of sea grass, sponges and jellyfish. Over the last century, however, all seven of the world’s sea turtle species suffered massive population declines, and five are currently listed as endangered or critically endangered (IUCN 2009). Sea turtle population declines are primarily the direct consequence of human activities such as overexploitation, accidental by-catch, and degradation of foraging and nesting habitats. Since the pioneering work of Archie Carr in the 1950s (Carr 1967, Davis 2007), there has been an increasing global effort to preserve sea turtles as part of marine ecosystems; however, despite the dedicated activities of hundreds of conservation projects, sea turtle populations have continued to decline in most areas (IUCN 2009).
With the current conservation focus on reversing the decline of dwindling sea turtle populations, predation and other natural sources of mortality present an important practical challenge. While mortality of adult sea turtles as a result of attacks by non-human predators is thought to be relatively uncommon, eggs and hatchlings are extremely vulnerable to predation (Stancyk 1982). In the absence of human intervention, egg predators frequently destroy over 80% of available nests (Talbert et al. 1980, Nellis and Small 1983, Engeman et al. 2006b). Although life stage population models suggest that mortality of older juveniles and adults has the greatest effect on population dynamics, predation on eggs and hatchlings reduces recruitment and slows population recovery (Crouse et al. 1987, Heppell et al. 1996). Predation reduction is therefore an important component of most sea turtle conservation programmes (Leighton, unpublished survey data), with considerable time and resources devoted to reducing local predator activity or protecting individual nests (Engeman et al. 2002).

A wide array of species are known to exploit sea turtle eggs, ranging from crabs and insects, to reptiles, birds, rodents and even large carnivores (Stancyk 1982, Leighton unpublished survey data). However, small to mid-sized carnivores such as raccoons, domestic dogs and mongooses tend to be the most widespread and destructive predators (Stancyk 1982, Leighton unpublished survey data). The introduction of exotic mammals on oceanic islands, which provide critical nesting habitat for several sea turtle species, is particularly problematic. Introduced predators are often highly destructive, possibly due to the ability of many introduced species to coexist with people and achieve high densities in human-altered habitats. Many islands were historically free of mammalian predators, and lack of behavioural feedback combined with long generation times make sea turtle populations slow to adapt to presence of this new predatory threat. Human introduction of species such as rats, dogs, pigs, and mongooses therefore represents an important additional source of nest mortality in many areas (Stancyk 1982, Nellis and Small 1983, Leighton unpublished survey data). While sea turtle nest predation is commonplace and has been described in many studies of sea turtle nesting biology (e.g. Talbert et al. 1980, Stancyk 1982, Cornelius 1986,
Whiting et al. 2007), relatively few studies have focussed specifically on
predation (Fowler 1979, Nellis and Small 1983, Cornelius 1986, Macdonald et al. 
1994, Engeman et al. 2003) and the behavioural ecology of nest predation by most
nest predators, with the exception of raccoons that have been extensively studied
et al. 2002, Engeman et al. 2006b, Barton and Roth 2008), remains largely
unexplored.

THE SMALL ASIAN MONGOOSE IN THE CARIBBEAN

In the mid-1800s, the sugarcane-based economies of most of the Caribbean
islands were suffering severe losses due to crop damage by both black rats (Rattus
rattus) and Norway rats (R. norvegicus). Trapping, poisoning and professional rat
catchers were the solutions available at the time, but when these proved
insufficient to cope with the rat problem, estate owners turned to various forms of
bio-control. Early introductions included European ferrets (Mustela putorius),
cane toads (Bufo marinus), and Cuban army ants (Formica omnivora), none of
which was particularly successful in reducing cane damage (Nellis and Everard
1983).

The first successful introduction of small Asian mongooses was carried
out by W. B. Espeut, who had 5 females and 4 males shipped to his plantation in
Jamaica from Calcutta in 1872 (Horst et al. 2001). These flourished, and were
such prodigious rat-killers that by 1874 crop damage on the estate had all but
disappeared. This initial success precipitated a wave of introductions throughout
the Caribbean, with Barbados receiving its first shipment of mongooses from
Jamaica in 1882 (Nellis and Everard 1983). By 1900 mongooses had been
introduced to all of the major sugar-producing islands and, in addition to their
native range that spans southern Asia from Iraq to Malaysia, the current
worldwide distribution of the small Asian mongoose includes: all of the Greater
Antilles, 20 of the Lesser Antilles, Hawaii, Fiji, British Guiana, French Guiana,
Colombia, Suriname, Mauritius, and the islands of Korcula (Croatia), Mafia
(Tanzania), Ambon (Moluccas), and Okinawa (Japan) (Horst et al. 2001, Hays and Conant 2007).

On islands that had existed for millennia with few or no mammalian predators, the mongoose flourished in most available habitats and soon attained pest status due to frequent predation on domestic fowl and for its role as a vector of rabies (Everard et al. 1974, Nellis and Everard 1983). Mongoose introduction is widely believed to have had devastating effects on native fauna throughout the Caribbean. However, in most cases, solid evidence linking mongooses to species declines is lacking (Hays and Conant 2007) and the predatory behaviour and impact of mongooses on the majority of endemic species potentially threatened by them today is poorly documented (Nellis and Everard 1983, Leighton 2005, Engeman et al. 2006a, Hays and Conant 2007).

The biology of the small Asian mongoose has been studied almost exclusively in its introduced range (Hays and Conant 2007). Mongooses are intelligent and inquisitive, and bold predators, known to attempt to tackle prey over twice their size (Seaman and Randall 1962). They are best classified as dietary generalists capable of taking advantage of whatever food is locally available, from rodents, arthropods and toads, to garbage and fallen fruit (Baldwin et al. 1952, Seaman 1952, Pimentel 1955, Gorman 1975, Nellis and Everard 1983, Cavallini and Serafini 1995, Vilella 1998, Leighton 2005). They are strictly diurnal and forage primarily by sight (Hinton and Dunn 1967), but also have a good sense of smell and dig readily for prey hidden in sand or leaf litter using their clawed forepaws (Nellis and Everard 1983, Leighton 2005). Home ranges of males are considerably larger than those of females, although area estimates vary from 22 ha for females and 39 ha for males in Fiji (Gorman 1979) to 50 ha for females and 200 ha for males in Hawaii (Tomich 1969). Individuals generally forage alone or in small groups (Hays and Conant 2003), but home ranges overlap extensively and local densities can exceed 10 animals/ha where anthropogenic food is abundant (Nellis and Everard 1983, Leighton 2005).

The biology and range of introduction of the mongoose make it a likely candidate as a sea turtle nest predator. The earliest published report of nest
predation by mongooses was a description of mongooses attempting to excavate a green turtle (Chelonia mydas) nest in the US Virgin Islands (Seaman and Randall 1962). However, the first substantial evidence came from two studies of mongoose predation at several hawksbill sea turtle (Eretmochelys imbricata) nesting beaches in the US Virgin Islands (Small 1982, Nellis and Small 1983). Together, these revealed widespread predation throughout the US Virgin Islands but considerable variation in predation severity among beaches. However, the conservation implications of mongoose predation on sea turtle nests received no further investigation until the initiation of the current study in Barbados 20 years later.

HAWKSBILL SEA TURTLE CONSERVATION IN BARBADOS

Barbados, the easternmost island in the West Indian archipelago, is the second largest hawksbill rookery in the Wider Caribbean, and is therefore a regionally important nesting area for critically endangered hawksbill sea turtles. Overexploitation of hawksbills for meat, eggs, and shells led to a dramatic decline in Barbados hawksbill populations during the second half of the 20th century, and by the 1980s there was no longer any significant hawksbill nesting on the island (Beggs et al. 2007). The Barbados Sea Turtle Project, based at the University of the West Indies, was initiated in 1987 to restore and protect dwindling sea turtle populations. Activities include monitoring of over 20 nesting beaches around the island through beach patrols and reporting of nesting activities by the public, education programmes, in-water tagging of adults and juveniles, population genetics, and satellite telemetry of breeding adults. After over 20 years of continuous operation of the project and the establishment of a national moratorium on capturing hawksbills in 1998, hawksbill nesting has increased in recent years with an estimated population of 1,250 females nesting in Barbados, and more than 2,000 nests laid in 2004 (Beggs et al. 2007).

Concerns by the Barbados Sea Turtle Project over continued nest losses to mongooses led to the initiation of my Ph.D. project in fall 2003 at Bath Beach, the
primary nesting beach for hawksbills on east coast of the island (Figure 1). I first became involved with the project in 2002 through a NSERC Undergraduate Student Research Award, carrying out a pilot study aimed at documenting mongoose predation on hawksbill nests at Bath. A fellow student and I spent two months in the field at the start of the nesting season, waiting for nest predation to occur so we could study it and, in the mean time, spending our days observing mongooses in the back yard of our cottage. By the end of our stay, not a single nest had been predated but by that point I had learned quite a bit about sea turtle research and had become so interested in the behaviour and ecology of the mongooses that I decided to return the following year to start my Ph.D.

The main hawksbill nesting season in Barbados is from June to August, but low levels of nesting occur year round (Beggs et al. 2007). The beach landscape at Bath is a fragmented mixture of vegetated and non-vegetated habitats. Fragmentation is broadly defined as a process whereby continuous habitat is broken apart into discontinuous patches, resulting in both habitat loss and a change in habitat configuration (Fahrig 2003). Human development of the beach front has led to the fragmentation of beach vegetation that presumably once grew continuously along the high water mark (as can be seen at the extreme edges of the beach and at nearby beaches lacking cottages), resulting in numerous patches of dense shrubs separated by open sandy areas lacking ground vegetation (Figure 2). Female hawksbills emerge from the ocean at night and nest in both open and vegetated areas of the beach, although vegetation is preferred where it is available (Horrocks and Scott 1991, Kamel and Mrosovsky 2006). The nesting turtle uses her hind flippers to excavate a 40-60 cm-deep cavity into which she deposits 100-200 soft-shelled eggs, each roughly 5 cm in diameter. She then refills the cavity, packs down the sand, conceals the location by scattering loose sand over the site, and returns to the ocean. Incubation lasts about 60 days, and hatchlings emerge at the sand surface a few days after hatching.

The Barbados Sea Turtle Project has carried out regular monitoring of hawksbill nesting at Bath since 1999. Annual nesting has increased substantially over this period, but the proportion of nests lost to mongoose predation has also
increased proportionally (Figure 3). Mongooses are the primary vertebrate predator of turtle eggs and hatchlings in Barbados, although red crabs (*Gecarcinus lateralis*) and ghost crabs (*Ocypode quadrata*) commonly infiltrate nests and may damage or remove a portion of the clutch. Domestic dogs and rats are present at many nesting beaches but evidence of nest predation is rare. Egg poaching by humans was common historically, but public education campaigns and increased legal repercussions have largely controlled this practice in Barbados in recent years.

**THESIS STRUCTURE AND APPROACH**

Field work associated with my doctoral research spanned 5 years, beginning with the pilot project in the summer of 2002 and ending with a final field experiment in the spring of 2006. The main data collection took place during two 6-month field seasons in 2004 and 2005, involving a team of 4-6 research assistants each summer, many of whom carried out independent research projects. The energy and dedication of these assistants over the years made it possible to address a wide array of questions about the behavioural ecology of mongooses and its implications for sea turtle conservation. In addition to the studies described in the subsequent chapters of this thesis, we carried out a large-scale mark and recapture study to determine overall population densities and rates of immigration/emigration, capturing nearly 100 individuals at Bath beach over a three-year period (Leighton 2005). Radio telemetry of 15 mongooses over two seasons allowed us to study movement, habitat preferences, seasonal home range shifts, denning behaviour, and male-female differences in the use of nesting habitat. A study of nest-raiding behaviour using video monitoring of predation events allowed us to document rates of egg removal, the number of individuals involved, digging behaviour and the importance of social interactions. Establishment of a long term feeding site visited by over 30 marked individuals allowed us to conduct field experiments exploring the importance of social foraging in nest predation, the effects of novel objects, social context, distance
from cover and human disturbance on mongoose vigilance behaviour, the effect of familiarization to novelty on mongoose trappability, and the effectiveness of hot pepper as a deterrent. Finally, in 2007, I carried out a survey of sea turtle projects to determine the diversity, regional prevalence and impact of vertebrate nest predators in the wider Caribbean. Although data from these projects are not included in my thesis and will be published elsewhere, the simultaneous investigation of many facets of mongoose predation on sea turtle nests provided a rich context for developing and testing the ideas presented in the subsequent chapters.

In the first three chapters of my thesis, I explored the behavioural processes underlying patterns of sea turtle nest predation. In Chapter 1, I began by examining habitat selection of mongooses and sea turtles with the conservation objective of determining how the habitat structure of nesting beaches affects sea turtle nest mortality. This context allowed me to explore the more general question of how edge response behaviour affects species interactions in fragmented landscapes. In Chapter 2, I attempted to understand the mechanisms of nest-finding behaviour with the goal of determining how specific nest characteristics affect predation risk. Inspired by the extensive body of work on seed recovery by scatter hoarding rodents (Vander Wall 1990), I examined how the process of nest predation is affected by egg burial depth and the availability of sensory cues. In Chapter 3, I looked at how antipredator behaviour and resource tracking alter landscape use by mongooses, with the goal of understanding the effect varying human activity and nest abundance have on the risk of nest predation. This provided an ideal context to explore the controversial concept of positive indirect effects of human disturbance for threatened populations. Finally, in Chapter 4, I combined the findings of the previous three chapters to develop a general model of mongoose predation on sea turtle nests, with the goal of providing a practical tool for predicting nest survival and optimizing nest protection approaches.
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Figure 1. Location of Bath Beach, the primary east coast nesting site for hawksbill sea turtles in Barbados.
Figure 2. Typical nesting habitat for hawksbill sea turtles at Bath Beach, Barbados. Open nesting areas and sparse grass are interspersed with dense patches of shrubs. The main tourist developments are a public swimming area and bungalow-style cottages lining the beach 10-50 m inland of the high water mark.
Figure 3. The frequency of hawksbill sea turtle nests recorded annually at Bath Beach from 1999-2005 that were or were not preyed on by mongooses (Figure based on data from Chapter 1).
CHAPTER 1

PREDICTING SPECIES INTERACTIONS
FROM EDGE RESPONSES:
MONGOOSE PREDATION ON HAWKSBILL SEA
TURTLE NESTS IN FRAGMENTED BEACH HABITAT

LINKING STATEMENT 1

In fragmented landscapes, habitat structure can have a strong effect on the spatial pattern of species interactions. In Chapter 1, I use microhabitat selection and edge response behaviour of mongooses and nesting sea turtles to model fine-scale spatial variation in sea turtle nest predation.
ABSTRACT

Because species respond differently to habitat boundaries and spatial overlap affects encounter rates, edge responses should be strong determinants of spatial patterns of species interactions. In the Caribbean, mongooses (*Herpestes javanicus*) prey on hawksbill sea turtle (*Eretmochelys imbricata*) eggs. Turtles nest in both open sand and vegetation patches, with a peak in nest abundance near the boundary between the two microhabitats; mongooses rarely leave vegetation. Using both artificial nests and hawksbill nesting data, we examined how the edge responses of these species predict spatial patterns of nest mortality. Predation risk was strongly related to mongoose abundance but was not affected by nest density or habitat type. The product of predator and prey edge response functions accurately described the observed pattern of total prey mortality. Hawksbill preference for vegetation edge becomes an ecological trap in the presence of mongooses. This is the first study to predict patterns of predation directly from continuous edge response functions of interacting species, establishing a link between models of edge response and species interactions.
INTRODUCTION

Habitat fragmentation can affect communities by altering interactions among species (Didham et al. 2007; Fagan et al. 1999). In fragmented landscapes, animals often respond to habitat structure by avoiding or aggregating near edges, resulting in strong gradients of species abundance (Ewers & Didham 2006a; Lidicker 1999). Where two interacting species both occur on either side of an edge, such edge responses may simply amplify or reduce the frequency of normal interactions. However, where species occupy distinct habitats, the edge provides a unique context for their interactions and edge responses may have a strong effect on where and how often interactions take place.

Where predators and prey interact in fragmented landscapes, edge responses may influence the spatial distribution of both predation risk, the probability of predation for an individual prey in a given time interval, and total prey mortality, the total number of prey killed by predators in a given time interval. The spatial distribution of predation risk affects the relative availability of suitable ‘core’ habitat for prey (Robinson et al. 1995). Total prey mortality determines the energy flow from prey to predators, altering the dynamics of both populations (Cantrell et al. 2001; Fagan et al. 1999). The spatial distribution of prey mortality will not necessarily match that of predation risk in fragmented landscapes. In some cases, prey may actively avoid the locations of highest risk (e.g. Bowers & Dooley 1993). In others cases, attraction to edges may lead to convergence of predator and prey abundances, resulting in heavy mortality near the edge and creating an ‘ecological trap’ for prey (Gates & Gysel 1978; Ries & Fagan 2003).

If predation is proportional to contact rate between predators and prey, the principle of mass action provides a simple prediction of how edge responses will affect predation risk and total prey mortality. Mass action predicts that contact rate among species will be proportional to the product of their local densities (Cosner et al. 1999). It follows that 1) predation risk for individual prey across the edge will be directly proportional to the gradient of predator abundance and 2) the
spatial distribution of total prey mortality across the edge will be directly proportional to the product of predator and prey abundances. Factors other than simple contact rate could, however, affect edge-related patterns of predation. In particular, density dependent processes may be important. If predators actively search for prey primarily in areas of high prey density, per capita predation risk may be higher in these areas (Keyser *et al.* 1998; Lariviere & Messier 1998; Marchand & Litvaitis 2004). On the other hand, risk could be reduced through dilution effects if predators under-match prey abundance (Foster & Treherne 1981; Inman & Krebs 1987). Habitat characteristics that change across the edge, such as the structural complexity of vegetation, may also affect predation risk by altering the ability of predators to detect or pursue prey (Bergman *et al.* 2006; Hampton 2004).

Studies of species interactions in fragmented landscapes have found no consistent effect of edge (Batary & Baldi 2004; Donovan *et al.* 1997; Lahti 2001; Paton 1994), limiting our ability to make general predictions about how fragmentation affects communities. Despite the intuitive importance of edge responses in determining the location and frequency of species interactions in fragmented landscapes, the relationship between edge-related gradients in species abundance and observed patterns of species interactions has not been rigorously explored. Numerous studies have examined edge-related patterns of predation (reviewed by Batary & Baldi 2004), as well as the individual edge responses of predatory species (reviewed by Chalfoun *et al.* 2002) and of their prey (reviewed by Ries & Sisk 2004). Surprisingly, however, no studies appear to have examined quantitatively the relative importance of predator abundance, prey abundance, and edge structure in determining the pattern of predation near edges.

We investigated predation by introduced *Herpestes javanicus* [small Asian mongoose, (E. Geoffroy Saint-Hilaire)] on nests of *Eretmochelys imbricata* [hawksbill sea turtle, (Linnaeus)] in fragmented beach habitat in Barbados, West Indies. Hawksbill populations have suffered significant declines in recent decades, and the species is currently listed as Critically Endangered (IUCN 2007). Mongoose predation at hawksbill nesting beaches in the Caribbean can be intense,
with destruction of all available nests reported for some beaches (Nellis & Small 1983). We measured gradients of abundance of mongooses and sea turtle nests across the edge between patches of vegetation and open sand. We examined predation at two temporal scales: short-term predation of artificial nests and multi-annual predation of natural hawksbill nests.

Using the mongoose-hawksbill system, we explored the ability of continuous edge response functions to predict patterns of per capita predation risk and total prey mortality across the edge. We found that the edge response of mongooses was a strong predictor of the edge effect on predation risk for hawksbill nests and that the product of mongoose and hawksbill edge responses accurately modelled the spatial pattern of total nest mortality. We suggest that this simple and general approach for linking species interactions to underlying edge responses may help to predict the consequences of landscape fragmentation for species interactions in other systems.

MATERIALS AND METHODS

Study area and species

The study was carried out at Bath (13.187° N, 59.476° W), an important nesting beach for hawksbill sea turtles on the east coast of Barbados. Nesting at Bath occurs year-round with a peak from June-August (Beggs et al. 2007). The number of hawksbill nests recorded annually at Bath has varied considerably (Range: 15 to 217, Mean = 76.9), but showed a steady increase over the study period from 1999 to 2005.

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 et al. 2001). Mongooses are diurnal generalist carnivores that thrive in human-altered habitats (Quinn & Whisson 2005). Individual home ranges overlap extensively, and in areas such as Bath, where anthropogenic food is abundant, local densities can exceed 10 animals/ha (Leighton 2005; Nellis & Everard 1983). Other than crabs that sometimes burrow
into nests, mongooses are the sole predator of turtle eggs at our site. Mongooses avoid contact with humans but do not have important local predators.

Female hawksbills emerge from the ocean at night to nest, and may crawl more than 100 m in search of a suitable nest site. Nesting turtles use their hind flippers to excavate a 40-60 cm-deep cavity into which they deposit 100-200 soft-shelled eggs, each roughly 5 cm in diameter. They then refill the cavity, pack down the sand, conceal the location by scattering loose sand over the site, and return to the ocean. Incubation lasts about 60 days, and hatchlings emerge at the sand surface a few days after hatching.

Bath beach is a 1.12 km-long stretch of sand, with a cottage-lined access road parallel to the water and a local picnic area near the centre. Hawksbill nesting is confined to the area between the high water mark and barriers 10-50 m inland associated with the road and cottages. Nesting habitat is a fragmented mixture of two main microhabitat types. Approximately 60% of the potential nesting area is “open beach”: sandy areas planted with shade trees but devoid of other vegetation except sparse grass in some areas. The remaining 40% is “beach vegetation”: dense patches of low shrubs [especially *Coccoloba uvifera* L. and *Thespesia populnea* (L.)], generally 1-3 m high. Beach vegetation forms 11 fragments ranging in area from 45-1650 m² (mean = 600 m²). Vegetation occurs along the berm in some areas and along the inland margin of the open beach in other areas, resulting in a total of approximately 1 km of open beach-vegetation edge. The transition between vegetated and open beach microhabitats is sharp. We operationally defined “edge” as the outer border of continuous leafy vegetation, measured to the nearest 0.1 m.

*Spatial patterns of abundance and nest predation*

Data on hawksbill nesting at Bath were collected from 1999-2005 as part of the long-term monitoring program of the Barbados Sea Turtle Project, University of the West Indies. Nests were located during the day from the disturbance left by the laying turtle, and the nest location was confirmed by excavation. We
monitored nests on daily beach surveys to determine if they were predated by mongooses (signs of digging, mongoose tracks, at least one egg removed from nest), hatched (signs of hatchling emergence, hatched shells at bottom of nest), or destroyed through other processes such as beach erosion.

We measured edge response of nesting hawksbills by calculating the cumulative density of nests laid during each nesting season in 1-m intervals parallel to the edge (between 8 m into the vegetation and 6 m onto the open beach). To do this, we used MapInfo 6.5 to separate a digital map of the beach into 1-m contour intervals relative to the edge of all vegetation fragments and divided the number of nests in each interval by the total area of the interval. We standardized densities among years by dividing densities for a given year by the total number of nests laid that year, generating proportional cumulative nest densities used for modelling edge response. To reduce bias due to stochastic effects of small sample size for densities calculated from years where nest numbers were low, we calibrated the edge response model using data from 2004 and 2005 which had both the largest number of nests and comparable sample sizes (n = 168 in 2004, n = 217 in 2005), and used the pooled data from 1999-2003 for model evaluation (Guisan & Zimmermann 2000).

Data on mongoose edge response and predation of artificial nests were collected during a 3-week period in October 2003, late in the main hawksbill nesting season. We measured mongoose edge response using a total of 163 “track pads”, 0.5 x 0.5 m patches of natural sandy substratum smoothed to pick up the tracks of passing animals. We measured the pattern of predation using 204 artificial nests, which consisted of sixteen 15-g pieces of sausage buried 15 cm beneath the surface of the sand. This is somewhat shallower than the uppermost eggs in natural nests (approximately 30 cm), allowing artificial nests to be discovered and predated rapidly by mongooses. All track pads and artificial nests were placed along the 160 m edge of the largest vegetation fragment (1650 m²), located near the centre of the beach. We randomly assigned each pad and nest a location along the 160 m edge, and a position across the edge gradient. Positions included -8, -7, -6, -5, -4, -3, -2, -1, 0, 1.5, 3, and 5 m from the edge, with
negative values in vegetation and positive values on the open beach. We deployed pads and nests in 10 series, with approximately 16 pads and 20 nests per series and a minimum of 2 days between series. We monitored each track pad during the daylight (05:00-19:00) portion of a 24-hour period, recording presence/absence of mongoose tracks every 2 hours. At the end of 24 hours, we determined the fate of each artificial nest (intact or predated as indicated by digging, tracks and missing sausage) and removed all pads and nests in the series.

**Statistical analyses**

We used Generalized Additive Mixed Models (GAMMs) to describe edge-related patterns in species abundance and to explore factors affecting the pattern of predation risk across the edge. Generalized Additive Models (GAMs) provide a flexible framework for modelling species-habitat relationships (Guisan et al. 2002), allowing predictors to be fitted either as parametric terms or as non-parametric smoothing terms (Hastie & Tibshirani 1987). GAMMs extend this framework to allow variables to be modelled as random effects (Wood 2004). We used the mixed model framework of GAMMs to account for correlation structures in the data, including year as a random variable in hawksbill nest models, series in artificial nest models, and track pad identity to control for repeated measures when modelling mongoose activity. We calculated the spatial extent of edge responses as the distance between local extrema of the second derivative of each edge response function (Ewers & Didham 2006b), using parametric polynomial terms to approximate the non-parametric smoothing terms in the original function. Models were fitted using package MGCV 1.3-19 in R 2.4.0 (Wood & Augustin 2002).

We tested the prediction that predation risk is driven by patterns of predator abundance for both artificial nests and hawksbill nests using GAMMs to model the relationship between mongoose abundance and fate of individual nests (predated/intact). We included nest abundance (proportional cumulative density) and habitat type (vegetation/open beach) as additional predictors to test for the
possible influence of density dependent processes and habitat characteristics on predation risk. We calculated classification accuracy for each model using sensitivity-specificity plots to select the optimal probability cutoff (Hosmer & Lemeshow 2000). We used R package ROCR 1.0-1 (Sing et al. 2005) to calculate the area under the curve in receiver operating characteristic (ROC) plots for each classification, providing a measure of model discrimination. ROC values range from 0 to 1, with 0.5 indicating random discrimination, values above 0.7 considered acceptable discrimination, and values above 0.9 extremely rare (Hosmer & Lemeshow 2000).

To test the prediction that the product of continuous edge response functions for interacting species should predict the spatial pattern of total mortality, we multiplied mongoose and hawksbill edge response functions and used the Kolmogorov-Smirnov test to compare the resulting function with the observed distribution of predated hawksbill nests across the edge.

RESULTS

*Edge Responses*

Mongooses and hawksbills both showed a highly significant response to the edge of beach vegetation. The GAMMs show that distance from the edge alone explained 21% of the variance in mongoose activity (Table 1a) and 87% of the variance in hawksbill nest density (Table 1b) (see Table S1 in supplementary material for equivalent parametric fits). The mongoose edge response extended from 3.4 m within vegetation to 1.5 m onto the open beach. Mongoose abundance dropped 96.5% across the edge, with the probability of mongoose tracks during a 2 hour check period decreasing from 0.62 within vegetation to 0.02 on the open beach (Figure 1a). The hawksbill edge response extended from 2.9 m within vegetation to 2.5 m onto the open beach. Proportional cumulative density of hawksbill nests increased from 0.05 on the open beach to 0.23 near the edge of vegetation (peak at 0.2 m within vegetation) and decline to 0.01 within vegetation, resulting in a 97.5% change in density across the edge (Figure 1b). The hawksbill
edge response model, calibrated using data from 2004-2005, explained 68% of the variation in cumulative nest density across the edge for the pooled 1999-2003 data, suggesting that the shape of the edge response function was representative of the pattern of nesting in previous years.

Nest Predation

Of 204 artificial nests, 120 (59.3%) were predated within 24 h. Of 551 hawksbill nests recorded from 1999-2005, 149 (27.0%) were predated by mongooses during the 60-day incubation period, with annual predation rates ranging from 17.9% to 38.9%. Of the 301 nests located within the range over which edge responses were measured (between 8 m into the vegetation and 6 m onto the open beach), 144 (47.9%) were predated. Thus, only 5 predation events (3.4% of all mongoose predation) occurred outside this range.

Predation Risk

Predation risk for both real and artificial sea turtle nests showed a highly significant positive relationship with mongoose abundance (Table 1c,d). However, neither nest abundance nor habitat type explained additional variation in predation risk for either real or artificial nests. The final model with mongoose activity as the sole predictor explained 46% of the variance in predation risk for artificial nests and 16% of the variance for hawksbill nests. The spatial pattern of predation risk for both real and artificial nests closely reflected the edge response of mongooses, being low on the open beach and increasing sharply within vegetation (Figure 2). The final models with mongoose abundance as the only predictor correctly predicted nest fate in 82% of artificial nests and 69% of hawksbill nests. Both models showed reasonable discrimination, with area under the ROC curve being 0.88 for artificial nests and 0.74 for hawksbill nests.

Distribution of Mortality
The product of edge response functions for mongooses and hawksbills accurately predicted the distribution of total hawksbill nest mortality across the edge, with a strong peak in mortality 1.0 m into vegetation (Figure 3). There was no significant difference between predicted and observed patterns of mortality (Kolmogorov-Smirnov test: $D = 0.060, P = 0.97$).

DISCUSSION

*A simple link between edge responses and predation*

The spatial pattern of predation risk for sea turtle nests across the sand-vegetation edge in beach habitat was strongly related to the gradient of mongoose abundance. This was true both for artificial nests exposed to predators for 24 hours and for natural nests of hawksbills that remained vulnerable throughout their 60-day incubation. Furthermore, the distribution of hawksbill nest mortality across the edge was accurately described by the product of mongoose and hawksbill edge responses. This first use of edge responses of interacting species as basic predictors of the spatial pattern of interactions suggests that this approach may provide a simple framework for understanding patterns of predation near edges.

The main assumption of this approach is that predation rate is proportional to contact frequency. Where strong gradients of density exist, density dependent processes have the potential to alter the relationship between contact frequency and predation rate. Nest abundance did not affect predation risk, suggesting that mongooses are not specifically searching for nests near the edge where nest densities are highest. One possibility is that actual nest densities at any particular time were simply too low to promote increased nest-searching behaviour by mongooses (Lariviere & Messier 1998) and that predation in this system is primarily incidental. If this is the case, we might expect nest density to be a more important predictor of predation at higher-density nesting beaches or with continuing recovery of hawksbill populations in the future.
Differences in habitat characteristics also have the potential to alter the likelihood that contact results in predation. Bergman et al. (2006) examined the spatial distribution of wolf kills in relation to wolf movements and prey abundance and found that kills occurred primarily in habitats where prey were most vulnerable. In our study, whether a nest was located in the open or in vegetation per se was not a significant predictor of predation risk for either natural or artificial nests beyond the effect of mongoose abundance, suggesting that those mongooses present in open habitats were as likely to detect and prey upon encountered nests as those mongooses present in vegetation. This is not particularly surprising because disturbance of the sand created by nesting turtles and researchers creating artificial nests is substantial, and these cues are likely to be equally reliable in vegetated and open habitats. Furthermore, there was no indication that predation risk was either higher or lower than predicted by mongoose abundance right at the edge.

Peaks in prey mortality: the signature of an ecological trap

The close match between predicted and observed distributions of total nest mortality suggests that measuring continuous edge responses for predators and prey at the appropriate scale for each species allows fine-grained prediction of the location and shape of peaks in prey mortality. In our study, the peak in predation occurred 1 m inside the boundary of vegetated beach habitat, rather than being centred on the edge itself. This points to a potential source of confusion in previous studies where predation was measured only in “edge” and “non-edge” habitats and no edge effect was found (Lahti 2001). It is possible that in some of these cases, the edge effect occurred at some intermediate distance from the edge or at a different spatial scale than the one used in the study. Indeed, using our approach to model interactions among species with typical edge responses described in previous studies (Ewers & Didham 2006b; Lidicker 1999; Ries et al. 2004) suggests that peaks in species interactions should occur often and predictably at some distance from the edge itself.
In order to effectively manage populations in fragmented landscapes, it is important to know where key species interactions are taking place. Specifically, when overlap of predator and prey abundances predicts strong peaks in prey mortality associated with edges, this may signal the existence of an important ecological trap for prey species (Gates & Gysel 1978; Robertson & Hutto 2006; Schlaepfer et al. 2002). The high concentration of hawksbill nests in the border of beach vegetation fragments agrees with previous evidence that hawksbills prefer to nest in vegetated beach habitat (Ficetola 2007; Horrocks & Scott 1991; Kamel & Mrosovsky 2006). The introduction of cryptic predators such as mongooses creates an ecological trap for hawksbills which continue to prefer to nest in vegetation, despite much higher predation risk in vegetated habitat than in the adjacent non-vegetated portions of the beach (Robertson & Hutto 2006; Schlaepfer et al. 2005). In such cases, accurately predicting the location and width of peaks in predation would allow spatially explicit management approaches for protecting prey species such as localized predator control or the designation of appropriate buffer zones around reserves.

Artificial nests and predator tracking as new tools for sea turtle conservation

Data on predation can be difficult and labour-intensive to obtain, especially where the species of interest are rare (Engeman et al. 2006). We show that two relatively simple and inexpensive techniques, artificial nest experiments and passive tracking of predator abundance, applied over a three-week period, successfully predicted multi-annual spatial patterns of nest predation for hawksbills. Engeman et al. (2003; 2005) recently developed the first passive tracking methods for sea turtle nest predators to improve control of raccoons and armadillos on nesting beaches in Florida. Our study confirms the applicability of passive tracking for introduced mongooses in the Caribbean and establishes a practical method for using tracking data to predict spatial patterns of predation. Artificial nests have been widely used to document edge effects on avian nest predation (Batary & Baldi 2004) but their use for studies of reptile nests is a new development and has
thus far been limited to freshwater turtles (Marchand et al. 2002). There is a risk in using short term experiments to predict long-term patterns, and the use of artificial nests has been specifically criticized (Moore & Robinson 2004; Wilson et al. 1998). The availability of a long-term data set on hawksbill nest predation allowed us to directly compare patterns of predation from short term artificial nest experiments to those for hawksbill nests over several years. While absolute predation risk was much higher for artificial nests than for natural nests, the pattern of predation risk across the edge was strikingly similar. The strong relationship between measured mongoose abundance and predation risk, and similarity of GAMM models for both real and artificial nests, suggest that passive tracking and artificial nests provide reliable information on predation in this system. These methods may be particularly useful in cases where management decisions require a rapid assessment of relative predation risk in areas where long-term monitoring data are unavailable.

While introduced mongooses have been suggested as an important threat to sea turtle eggs in the Caribbean (Coblentz & Coblentz 1985; Nellis & Small 1983; Small 1982), this is the first study of factors affecting predation in this system. We confirm that mongoose predation can result in significant egg mortality and show that predation risk is directly related to patterns of mongoose abundance. Mongooses moving in the open respond to humans by seeking refuge in vegetation, and the spatial pattern of mongoose abundance relative to vegetative cover is consistent with avoidance of beach-goers. This suggests that in more isolated areas, mongooses may venture further onto the open beach, resulting in higher predation rates such as 100% predation reported by Nellis & Small (1983) for certain beaches in the U.S. Virgin Islands. These findings are broadly relevant to hawksbill sea turtle conservation in the Caribbean where introduced mongooses are abundant, and point to the general importance of habitat structure in modulating the impact of invasive species on native species decline (Didham et al. 2007).
In this study we show that edge response functions for predators and prey can be used to predict the shape and spatial extent of edge effects on predation. Our approach allows quantification of the influence of density dependent processes and habitat-specific effects, allowing these to be taken into account when modelling predation. However, even where such effects occur, their impact may be small relative to the effect of predator abundance, and we suggest that product of predator and prey edge response functions may provide a robust approximation of the pattern of prey mortality in many systems. By establishing a heuristic link between existing models of species edge responses (e.g. Ewers & Didham 2006b; Ries & Sisk 2004) and observed patterns of species interactions in fragmented habitat (e.g. Brand & George 2000; Gates & Gysel 1978), the approach developed here may help resolve the ongoing controversy over the general importance of fragmentation for predator-prey interactions.

ACKNOWLEDGEMENTS

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This research adhered to the Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research (published on the Animal Behaviour website), the legal requirements of the country in which the work was carried out and all institutional guidelines.
LITERATURE CITED


Table 1. Generalized Additive Mixed Models (GAMMs) used to model abundance and predation risk in relation to the open beach/vegetation edge on Bath Beach, Barbados. The table shows mongoose edge response (a), hawksbill sea turtle nest abundance (b), risk of mongoose predation on artificial nests (c), and risk of mongoose predation on hawksbill nests (d). Sample size, n, is the number of track pad checks in (a), the number of distance from edge intervals (15/yr over 2 yr) in (b), and the total number of monitored nests in (c) and (d). Adjusted R² is for the final model, where only significant predictors were retained. s(…) denotes predictors fitted as non-parametric smoothing terms; unbracketed predictors were fitted as typical parametric terms. d.f. is the estimated degrees of freedom for each term.

<table>
<thead>
<tr>
<th>Model</th>
<th>n</th>
<th>adj. R²</th>
<th>predictors</th>
<th>d.f.</th>
<th>F (T)*</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Mongoose Activity</td>
<td>978</td>
<td>0.21</td>
<td>s (distance from edge)</td>
<td>3.78</td>
<td>20.40</td>
<td>&lt;&lt; 0.001</td>
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<tr>
<td>b) Hawksbill Nest Density</td>
<td>30</td>
<td>0.87</td>
<td>s (distance from edge)</td>
<td>5.34</td>
<td>10.04</td>
<td>&lt;&lt; 0.001</td>
</tr>
<tr>
<td>c) Artificial Nest Predation Risk</td>
<td>204</td>
<td>0.46</td>
<td>s (mongoose activity)</td>
<td>1.00</td>
<td>50.81</td>
<td>&lt;&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>s (nest density)</td>
<td>1.00</td>
<td>0.517</td>
<td>0.473</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Habitat</td>
<td>1.00</td>
<td>(0.543)</td>
<td>0.547</td>
</tr>
<tr>
<td>d) Hawksbill Nest Predation Risk</td>
<td>301</td>
<td>0.16</td>
<td>s (mongoose activity)</td>
<td>1.00</td>
<td>44.48</td>
<td>&lt;&lt; 0.001</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>s (nest density)</td>
<td>1.00</td>
<td>1.17</td>
<td>0.281</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Habitat</td>
<td>1.00</td>
<td>(1.356)</td>
<td>0.176</td>
</tr>
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</table>

* GAMMs use F-values to test significance of nonparametric smoothing terms, while T-values (in parentheses) are used for parametric terms.
**Table S1 (Online supplementary material).** Generalized Additive Mixed Models (GAMM) used to model edge response of mongoose abundance (a) and hawksbill sea turtle nest abundance (b) relative to the open beach/vegetation edge. Models presented here are parametric approximations of the non-parametric GAMMs presented in Table 1, with non-parametric smoothing terms replaced by parametric polynomial terms. Sample size, n, is the number of track pad checks in (a) and the number of distance from edge intervals (15/yr over 2 yr) in (b).

<table>
<thead>
<tr>
<th>Model</th>
<th>n</th>
<th>adj. $R^2$</th>
<th>Model terms</th>
<th>Estimate</th>
<th>SE</th>
<th>T</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Mongoose Activity</td>
<td>978</td>
<td>0.21</td>
<td>Intercept</td>
<td>-1.179</td>
<td>0.146</td>
<td>-8.08</td>
<td>&lt; 0.001</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Distance from edge</td>
<td>-0.567</td>
<td>0.075</td>
<td>-7.51</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(Distance from edge)$^2$</td>
<td>-0.048</td>
<td>0.011</td>
<td>-4.30</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>b) Hawksbill Nest Density</td>
<td>30</td>
<td>0.80</td>
<td>Intercept</td>
<td>-1.603</td>
<td>0.165</td>
<td>-9.70</td>
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<td></td>
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<td>Distance from edge</td>
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<td>0.090</td>
<td>-0.67</td>
<td>0.510</td>
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<td></td>
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<td></td>
<td>(Distance from edge)$^2$</td>
<td>-0.182</td>
<td>0.037</td>
<td>-4.91</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(Distance from edge)$^3$</td>
<td>0.008</td>
<td>0.003</td>
<td>2.51</td>
<td>0.018</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>(Distance from edge)$^4$</td>
<td>0.003</td>
<td>0.001</td>
<td>3.62</td>
<td>0.001</td>
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Figure 1. Abundance responses of mongooses and hawksbill sea turtles to edges between open sand and patches of vegetation at Bath Beach in Barbados. (a) Mongoose abundance measured as the probability of crossing a sand pad per 2-h interval and (b) hawksbill nest abundance measured as the proportion of total annual nests per m². For mongooses, data shown are presence/absence of mongooses tracks on sand pads for each 2-h check period (n = 978), with random jitter added to allow visualization of overlapping points. For hawksbill nests, open circles are proportional cumulative nest densities from 2004 and 2005 used in model calibration (n = 30). The solid lines are the GAMM edge response function and dashed lines are ±1 SE. The vertical dotted line marks the location of the edge, with positive values open sand and negative values within vegetation.
Figure 2. GAMM models of predation risk (a) for artificial nests over a 24-hour period (n = 204) and (b) for hawksbill sea turtle nests over a 60-day incubation period (n = 301) across the open sand-vegetation edge. Data shown are the fates of individual nests (1 = predated, 0 = intact), with random jitter added to allow visualization of overlapping points. The solid lines show the final GAMM model for predation risk and dashed lines are ±1 SE. The vertical dotted line marks the location of the edge, with positive values open sand and negative values within vegetation.
(a) Artificial Nest Predation Risk

Distance from Vegetation Edge (m)

(b) Hawksbill Nest Predation Risk

Distance from Vegetation Edge (m)
Figure 3. Frequency of predated hawksbill sea turtle nests recorded from 1999-2005 across the open beach/vegetation edge (bars), and distribution of mortality predicted by the product of continuous edge response functions for mongooses and hawksbills (solid line).
CHAPTER 2

HOW DEPTH ALTERS DETECTION
AND CAPTURE OF BURIED PREY:
EXPLOITATION OF SEA TURTLE EGGS BY
MONGOSES

LINKING STATEMENT 2

In Chapter 1, I showed that nest location can have a strong effect on predation risk. Here I examine how nest-finding behaviour of mongooses is affected by other characteristics of sea turtle nests, namely egg-burial depth and the availability of sensory cues.
ABSTRACT

Predators are an important source of mortality for animals that lay their eggs in buried nests. We asked how depth alters the process of predation for buried prey. We outlined a general model of predation risk where depth may alter both prey detection and subsequent capture: deeper prey are detected less often since the strength of olfactory cues decreases with burial depth and, once detected, are further protected by the costs of digging. Using this framework, we examined how burial depth influenced egg predation for critically endangered hawksbill sea turtles (*Eretmochelys imbricata*) by introduced mongooses (*Herpestes javanicus*) in Barbados. We tested the effect of nest depth on detection and subsequent predation using observational data on hawksbill nests over a two year period and an experiment with artificial nests. For both real and artificial nests, depth had little effect on nest detection by mongooses but, once detected, shallower nests were much more likely to be preyed on. Mongooses appear to use depth-invariant surface cues to detect buried eggs, but increase digging persistence in response to olfactory cues. We argue that excavation cost is an important but overlooked mechanism protecting deeply buried resources. For reptiles with buried nests, the relationship between depth and predation risk leads to important predictions about how changes to nesting habitat or the predator community will affect egg survival and offspring sex ratio. More generally, identifying the mechanisms by which burial depth protects prey is essential for understanding how resource burial strategies evolved and are maintained in predator-prey systems.
Many animals bury valuable resources. Rodents and carnivores often bury food in shallow caches for future consumption (Vander Wall, 1990). Other species including many reptiles and invertebrates protect their reproductive investment by concealing eggs in underground nests (e.g. Cornelius, 1986; Iverson et al., 2004; Reale and Roff, 2002). Such buried resources become easy prey for any animal capable of locating and gaining access to them. One of the proposed benefits of burial is the reduction of predation risk without the necessity of active guarding (Vander Wall, 1993). Factors that influence access to buried resources are therefore expected to have a strong effect on predation risk.

One of the principal factors expected to affect predation of buried resources is the depth of burial. There is good evidence that burial depth reduces recovery and theft of buried seed caches by rodents (Geluso, 2005; Lockard and Lockard, 1971; Reichman and Oberstein, 1977; Vander Wall, 1993), and predation of buried molluscs and other marine prey by birds is also negatively related to depth (Richardson, 1985; Zwarts et al., 1996). The effect of depth on predation risk is assumed to rely on the lowered probability that predators will discover the buried resource; once detected, the resource is often very vulnerable. Effects of depth on prey detection are well-supported by the literature on seed predation, where detection depends primarily on olfactory cues (Geluso, 2005; Vander Wall, 1998, 2000) that decrease in strength with depth (Reichman, 1981). In some cases, however, the resource may be protected by the cost to the predator of excavating buried prey (Vander Wall, 1993). These costs are likely to be especially important for deeply buried prey or predators with limited digging capacity. However, the possible effects of depth on aspects of foraging other than detection, including excavation, removal and handling of buried prey have received relatively little attention (but see Lockard and Lockard, 1971; Richardson, 1985; Ward and Saltz, 1994). Distinguishing the underlying mechanisms relating burial depth to predation risk is important for understanding the nature of predator-prey interactions and has implications for the evolution of burial behavior. In particular, resource burial strategies and optimal burial depth
are likely to depend strongly on whether depth affects the ability of predators to
detect prey, to access detected prey, or both.

Viewing predation as a sequence of foraging behaviors, each with an
associated probability of occurrence, provides a useful framework for exploring
the roles of different possible mechanisms linking depth with predation. Lima and
Dill (1990) developed a general model of the predation process, identifying
several distinct components of predation risk. A simplified version of their model,
adapted for predation of buried prey, considers that when a foraging predator
encounters buried prey, the probability of prey mortality, d, is the product of the
probability that the buried prey is detected, q, and the probability that, once
detected, the prey is successfully excavated or captured, c:

\[
d = qc
\]

Using this framework, we identify four broad categories for the mechanistic
relationship between burial depth and predation. Where concealment increases
with depth but prey of all depths are easily accessible, detection mechanisms will
dominate. This is the likely scenario for theft of shallow seed caches by rodents of
the same or similar-sized species (Vander Wall, 1998, 2000). On the other hand,
where cues for prey detection are independent of depth but excavation is costly,
capture mechanisms will dominate. We might expect this scenario where surface
cues provide a reliable indication of prey location but deeply buried prey are more
costly to excavate or more likely to evade capture (Richardson, 1985; Ward and
Saltz, 1994). Thirdly, where depth has no effect on prey concealment and costs of
excavation are trivial, we expect no relationship between depth and predation.
This type of scenario is probably common where animals use spatial memory to
retrieve food from shallow caches (Devenport et al., 2000). Finally, there may be
many circumstances where depth affects both detection and capture, and predation
is influenced by a combination of these mechanisms.

Nest predators are an important source of egg mortality for many animals
with buried nests, and this is particularly well documented for reptiles (Spencer
and Thompson, 2003; Stancyk, 1982). Buried eggs may remain undefended for
months in some species and protective effects of deeper burial therefore have the
potential to increase nest survival substantially. However, we are aware of no studies of how depth affects the process of predation for buried eggs. Many nest predators are thought to rely primarily on smell to locate eggs (Cornelius, 1986; Stancyk, 1982), suggesting that burial depth may influence nest detection by obscuring olfactory cues. However, in contrast to scatter-hoarded food that is generally buried in shallow caches and requires minimal digging effort to recover, burial depth for nests is often substantial and digging may be costly. We therefore predicted that depth would affect both detection and capture of buried eggs by nest predators.

We asked how nest depth affects the process of predation for buried sea turtle eggs. We studied predation by the small Asian mongoose (*Herpestes javanicus* E. Geoffroy Saint-Hilaire), an introduced predator, on the nests of critically endangered hawksbill sea turtles (*Eretrmochelys imbricata* Linnaeus) in Barbados, West Indies. Sea turtles provide an excellent model system for studying predation of buried eggs because nests are easily located by researchers and can be monitored throughout development. We measured depths of hawksbill nests over two nesting seasons (2004–2005) and examined several ecological factors potentially affecting nest depth for this species. We used these data to assess the effects of nest depth on detection and subsequent predation of hawksbill nests by mongooses. Finally, we used artificial nests to confirm the effects of depth experimentally and to explore the role of visual and olfactory cues in nest detection and predation.

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. Hawksbill nesting is confined to the area between the high water mark and barriers associated with a beachside road and cottages 10-50 m inland. 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 nest year-round at Bath with a peak from June to August (Beggs et al., 2007). Female hawksbills emerge from the ocean at night and nest readily in both open and vegetated habitats, although they prefer to nest in beach vegetation where this is available (Horrocks and Scott, 1991; Kamel and Mrosovsky, 2006b). The nesting turtle uses her hind flippers to excavate a 40-60 cm-deep cavity into which she deposits 100-200 soft-shelled eggs, each roughly 5 cm in diameter. She then refills the cavity, packs down the sand, conceals the location by scattering loose sand over the site, and returns to the ocean. Incubation lasts about 60 days, and hatchlings emerge at the sand surface a few days after hatching.

The small Asian mongoose (Herpestes javanicus) was introduced to many Caribbean islands for rat control in the late 1800s and has become an important predator of sea turtle nests (Hays and Conant, 2007; Leighton et al., 2008; Nellis and Small, 1983). Individual home ranges overlap extensively, and, in areas such as Bath, where anthropogenic food is abundant, local densities can exceed 10 animals/ha (Leighton, 2005; Nellis and Everard, 1983). Mongooses are strictly diurnal but avoid contact with humans and generally restrict their foraging to vegetated areas of the beach (Chapter 1). They have a good sense of smell and dig readily for prey hidden in sand or leaf litter using their clawed forepaws. Other than crabs and insects that sometimes infiltrate the nest and may damage or remove a portion of the clutch, mongooses are the sole predator of turtle eggs at our site.

**Hawksbill nest monitoring**

We collected data on hawksbill nesting at Bath in 2004 and 2005, with morning beach surveys carried out daily from May to September. 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
international protocol (Schroeder and Murphy, 1999). Nest depth was measured using a tape measure (± 0.5 cm) as the distance from the sand surface to the top of the egg mass (Limpus et al., 1983). The excavated sand was replaced and the site concealed by scattering loose sand over the nesting area. During daily surveys, all incubating nests were checked visually for signs of mongoose activity. Shallow (<10 cm deep) excavation above the location of the buried eggs was taken as evidence that mongooses had detected the nest (Howard et al., 1968; Lockard and Lockard, 1971). A nest was considered preyed on when extensive excavation (>10 cm deep) occurred and there was evidence that the eggs had been reached (eggs/shells visible in the hole or the surrounding area).

**Artificial nest experiment**

Artificial nests were constructed by disturbing a 50-cm radius area to simulate disturbance created by a nesting turtle (crushed vegetation, displaced ground litter and scattered sand), digging a 15-cm diameter cylindrical hole in the centre of the disturbed area using a post hole digger, placing five 8-g pieces of sausage and an indicator flag in the bottom of the hole, refilling the hole using the excavated sand, packing down the sand, and applying approximately 5 ml of sausage scent evenly to the surface of the sand in a 30-cm radius around the hole using a plastic spray bottle. Indicator flags consisted of a 15-cm piece of orange flagging tape anchored to the bottom of the nest hole by a 60-cm piece of thin nylon string tied to a buried stick. Pilot trials showed that indicator flags sitting on top of buried bait were consistently pulled out of the nest when the bait was removed but not before. Sausage scent, intended to simulate olfactory cues left on the sand surface by the nesting turtle, was created by boiling sausages in water for 1 hour, removing the broth and storing it frozen in 200-ml samples that were thawed overnight at 4°C for use the following day.

Each trial involved 20 artificial nests placed in vegetated habitat at one of six sites along the beach. Each site consisted of a continuous patch of vegetation growing along the berm (mean patch area ± SD; 355 ± 63.8 m²). Each site was divided into four contiguous blocks, with five nests per block and each nest
assigned to different treatment: 15-cm-deep nests, 30-cm-deep nests, 45-cm-deep nests, “disturbance-only” (disturbance and a 30-cm hole with an indicator flag but no bait or sausage scent), and “smell-only” (sausage scent applied to undisturbed sand). Nests were assigned random co-ordinates within each block. All nests were created 2-10 m inland from the seaward edge of vegetation because turtles at Bath rarely nest more than 10 m into vegetation and predation risk decreases near the edge (Chapter 1).

Between 11 April and 5 May 2006, we ran two series of trials at each of six different sites along the beach for a total of 240 nests. All artificial nests at a given site were created the same day between 09:00 and 12:00. Nests were deployed at a new site each day. A second series of trials was conducted at each site 10 days after the first series.

Artificial nests were checked after 6 hours, 24 hours, and 7 days for evidence of detection (superficial excavation < 10 cm deep), digging (substantial excavation > 10 cm deep) and predation (indicator flag pulled out, bait removed) by mongooses. To measure variation in mongoose activity among sites we used track pads, 0.7 x 0.7 m patches of natural sandy substratum smoothed to record tracks of passing animals (Chapter 1). We created three track pads at each site, with pads set 1.5 m inland of the seaward edge of vegetation and 20 m apart. We cleared all track pads daily at 12:00 and checked for tracks at 17:00. We used the total number of mongoose trails crossing the tracking surface of all three pads per hour of exposure as an index of local mongoose activity. All artificial nests were removed at the end of the experimental period and the substrate was characterized using three binary variables: presence of rocks (> 1 cm diameter), presence of roots intersecting the nesting cavity, and high or low soil moisture as indicated by the cohesion of the sand lifted between the two blades of the hole post digger.

Statistical analyses

We used a series of regression models to explore the influence of nest depth on detection and predation of hawksbill nests by mongooses. We used logistic regression to test the effect of depth on predation risk (d = the probability
of nest predation over the 60-day incubation period) and the two components of predation risk described in equation [1]: detection ($q =$ the probability of detection over the 60-day incubation period) and capture ($c =$ the probability of predation following detection). Data were coded as 1 if the event occurred, and 0 if it did not. We tested the effect of depth on predation latency (days between laying and predation) and its components: detection latency (days between laying and detection) and capture latency (days between detection and predation) using ordinary least squares regression and log-transformed latency measures. In addition, we used ordinary least squares regression to test whether hawksbill nest depth was affected by microhabitat type (vegetation vs. open beach), nesting date and year.

For artificial nests, we used generalized linear mixed models (GLMMs) to assess the influence of nest depth on predation over the 1-week monitoring period using data from the 15-cm, 30-cm and 45-cm deep nests and including site as a random effect. As with hawksbill nests, we examined the effect of depth on predation risk and its components: detection and capture. We modeled predation risk after 6 h, 24 h, and 7 days to explore how the relationship between depth and risk changed over time. We tested the effect of depth on detection latency and predation latency using the time period in which detection or predation occurred as an ordinal response variable ($1 =$ 0-6 h, $2 =$ 6-24 h, $3 =$ 24 h-7 d). Distance to the vegetation edge, date of nest construction, site-specific mongoose activity during the 1-week monitoring period, and substrate characteristics (presence of rocks, roots and moist sand) were included as additional predictors in all models. Before being included in models, predictors were tested for strong collinearity (VIF was < 3 in all cases indicating little collinearity) and standardized (mean = 0, SD = 1) to allow meaningful comparison of regression coefficients (Quinn and Keough, 2002).

We assessed the relative importance of disturbance and olfactory cues during different stages of the predation process by comparing “disturbance-only”, “smell-only” and 30-cm treatments. We used GLMMs to test the effect of treatment on the probability of detection, extensive digging (> 10 cm deep), and
predation after 7 days of exposure, and the maximum excavation depth attained by mongooses during this period. All analyses were carried out using R v. 2.7.2 (R Development Core Team, 2008).

RESULTS

Hawksbill nest depth and predation

We obtained depth measurements for 258 hawksbill nests at Bath in 2004 (n = 79) and 2005 (n = 179). Depth to the top of the egg mass ranged from 0 cm (eggs exposed) to 55 cm (mean ± SD; 29.5 ± 9.0 cm). Nests in vegetation were shallower than nests on the open beach (mean ± SE; vegetation: 25.9 ± 0.85 cm; open: 31.8 ± 0.68 cm; t = 4.9, P < 0.001), and nest depth decreased slightly over the nesting season (slope = -0.032 cm/day, t = -1.2, P = 0.05). Microhabitat and date effects did not interact significantly (t = 1.0, P = 0.32), and nest depths did not differ between years (t = -0.54, P = 0.59).

Risk of mongoose predation is much higher for nests in beach vegetation than for those on the open beach (Chapter 1). To ensure that the relationship between depth and predation risk was not confounded by shallower nests in vegetated microhabitats, we restricted our analysis to hawksbill nests in vegetation (n = 101).

Predation risk for hawksbill nests was inversely related to egg burial depth (Figure 1). Predation risk for nests in vegetation was 62%, dropping from nearly 90% for exposed eggs to around 30% for 45-cm deep nests (Z = -2.56, P = 0.011, deviance explained = 5.4%, n = 101; Figure 1a). Although the probability of mongooses detecting a nest was not significantly related to depth (Z = -1.42, P = 0.15, deviance explained = 1.9%, n = 101; Figure 1b), deeper nests were less likely to be preyed on after detection (Z = -2.19, P = 0.029, deviance explained = 6.9%, n = 78; Figure 1c).

The majority of predation events occurred early in incubation. Of 62 predated nests, 33 (53.2%) were preyed on within one week of laying and 16 (25.8%) were preyed on within the first 24 hours. We found no significant
relationship between depth and predation latency ($t = 0.86, P = 0.39, n = 62$), detection latency ($t = 0.82, P = 0.42, n = 78$) or latency to predation following detection ($t = -0.93, P = 0.35, n = 62$) for hawksbill nests.

**Artificial nest experiment**

At one of six sites (site 6), both series of artificial nests remained untouched by mongooses throughout the entire experiment; therefore, only nests from the remaining five sites were used in analyses ($n = 200$). Track pads at site 6 received a mean ± SD of $0.19 ± 0.26$ mongoose visits per hour which was significantly lower than the mean of $0.47 ± 0.41$ for the other five sites (Poisson GLM: $Z = -2.80, P = 0.005, n = 266$).

Of the 120 artificial nests containing sausage, 114 (95.0%) were detected, 101 (84.2%) received extensive digging, and 51 (42.5%) were successfully preyed on by mongooses. Predation risk for artificial nests decreased sharply with nest depth (Table 1; Figure 2). Predation risk increased quickly over time for 15-cm nests, reaching 97.9% after one week, rose more gradually to 25.6% for 30-cm nests and remained close to 0% for 45-cm nests (Figure 2a). The probability of nest detection was high and apparently unrelated to depth (Figure 2b). As with hawksbill nests, the strongest effect of depth was in the final phase of nest predation where, once detected, shallower nests were much more likely to be reached and successfully preyed on (Figure 2c). Of the other predictors included in the model, only the position of nests relative to the seaward edge of vegetation had an important effect, with an increased risk of predation following detection for nests nearer to the edge.

Of the 51 artificial nests preyed on by mongooses, 20 (39.2%) were preyed on within the first 6 hours of exposure and 40 (78.4%) within the first 24 hours (Table 1). We found no significant effect of depth on detection latency, but shallow nests were preyed on significantly more quickly than deeper nests (Table 2). Nests created in later trials were detected and preyed on more quickly by mongooses, and detection latency was lower for nests located far from the seaside edge of vegetation. Although detection tended to occur more rapidly when
mongoose activity was higher, there was no relationship between mongoose activity and predation risk.

Overall, mongooses did not respond to sausage scent in the absence of disturbance (Figure 3a, “smell-only”) but did respond to disturbance in the absence of olfactory cues (Figure 3a, “disturbance-only”) by exploring the site and digging. The probability of detection was equivalent for 30-cm and disturbance-only treatments (30-cm vs. disturbance-only: $t = 0.00, P = 1$), but probability of detection for the smell-only treatment was significantly lower (disturbance-only vs. smell-only: $t = 6.35, P < 0.001$). The probability of extensive digging was significantly lower for the disturbance-only treatment than for 30-cm nests (30-cm vs. disturbance-only: $t = 2.31, P = 0.02$) and much lower for the smell-only treatment (disturbance-only vs. smell-only: $t = 3.92, P < 0.001$). For comparison with 30-cm nests, disturbance-only and smell-only nests were considered preyed on when mongooses dug to a depth of 30 cm. This rarely occurred, and the probability of predation for 30-cm nests was much higher than for disturbance-only and smell-only treatments (30-cm vs. disturbance-only: $t = 3.88, P < 0.001$ and disturbance-only vs. smell-only: $t = 0.00, P = 1$). The maximum depth reached by digging mongooses also differed considerably among treatments (Figure 3b). Mongooses dug to an average depth of 16 cm for 30-cm nests but only reached 11 cm for the disturbance-only treatment (30-cm vs. disturbance-only: $t = 4.35, P < 0.001$). Excavation for the smell-only treatment was rarely more than a 1-2 cm deep scuff mark (disturbance-only vs. smell-only: $t = 8.10, P < 0.001$).

DISCUSSION

Most studies of prey burial depth have concluded that deep burial reduces predation risk primarily by making prey harder to detect (Geluso, 2005; Vander Wall, 1990, 1993). We found that, although deep burial protects turtle eggs from predation, there was no significant effect of depth on the probability of detection in either natural or artificial nests. Thus, unlike the majority of previous research
on burial depth which has focused on seed-caching rodents, increased concealment does not appear to be a major advantage of deeper burial in this system. Deeper nests were, however, much less likely to be preyed on following detection suggesting that the costs of excavating deeply buried prey can have a significant impact on predation risk. Although generally overlooked in previous work, digging cost may in fact be a mechanism of widespread importance. Given the diversity of taxa that protect resources by burying them and the ecological importance of this process (Vander Wall, 1990), we argue the need for a more comprehensive mechanistic framework relating burial depth to resource vulnerability.

Treating predation as a series of stages, each of which may be influenced independently by depth, allows mechanisms acting on different components of predation risk to be isolated and characterized. Our model assumes that, for buried resources, detection and excavation are the main stages of predation that are likely to be influenced by depth, though in functionally different ways. This simple formulation may be too restrictive for some systems. Lima and Dill (1990) included prey behavior in their model and this elaboration may be appropriate where prey are capable of escaping predation (e.g. burrowing prey or hatchlings). In addition, prey consumption following capture and the proportion of available prey items consumed might also depend on depth, especially where prey are motile and nest depth affects escape success. Nevertheless, we suspect that dividing predation of buried prey into a detection phase, where cue availability is the primary constraint, followed by an excavation phase, where energetic costs of prey capture become important, will be applicable to most situations.

Although protective effects of deep burial might be expected from foraging theory and studies of seed predation (e.g. Vander Wall, 1993), our study is the first empirical investigation of how depth affects predation risk for buried eggs. We present both observational evidence from natural hawksbill nests and experimental evidence from artificial sea turtle nests demonstrating that depth is a causal factor affecting predation risk in this system. One implication of these findings is that factors influencing the depth that female turtles dig or altering the
depth of existing nests will also affect predation risk. Nests were shallower in vegetation, perhaps because of interference from the roots of shrubs or because females selected shallower nest depths to compensate for cooler nesting habitat (Iverson et al., 2004; Kamel and Mrosovsky, 2006a). The depth of freshly laid nests also decreased gradually over the nesting season, possibly due to sand compaction from increasing rainfall or changes in turtle characteristics such energy reserves that influence digging effort. Once laid, nest depth may also change over time due to wave action or wind erosion (Koch et al., 2007). Finally, anthropogenic changes can have important indirect effects on predation risk by altering nest depth. For example, if tourism increases beach compaction making nests more difficult to dig (Horrocks and Scott, 1991) or if beach development forces turtles to nest in suboptimal habitat for excavation, nest predation could increase. A second implication of our findings is that the impact of environmental perturbations on predation is likely to be quite different if detection or excavation cost is the primary mechanism linking depth to predation risk. For instance, changes in soil humidity that have been shown to affect availability of olfactory cues for detection (Vander Wall, 1998) are unlikely to affect predation of sea turtle nests unless they also affect the cost of excavation.

**Digging costs protect deeply buried prey**

Our study suggests that mechanisms linking depth to predation for relatively deeply buried prey may differ fundamentally from those proposed for shallow burial where depth-sensitive olfactory cues control detection (e.g. Geluso, 2005). Given the anecdotal evidence suggesting that olfactory cues may be used by mongooses (Nellis and Small, 1983) and many other nest predators (Cornelius, 1986; Stancyk, 1982) to locate sea turtle nests, we expected that nest depth would play a greater role in detection. For both natural and artificial nests, the majority of nest detection and predation events occurred in the first few days following laying while surface cues associated with nesting were fresh. The reliability of visual and olfactory surface cues signaling the presence of buried eggs is likely to decrease rapidly over time. It therefore seemed plausible that depth might play a
greater role for nests that escaped early detection. However, when we examined the relationship between depth and detection for hawksbill nests that had not been detected within the first week, we found no evidence of such an effect (unpublished analyses). In other studies where the timing of nest predation has been reported, predation frequently occurs during the first few days following laying (e.g. mongooses (Nellis and Small, 1983); raccoons: (Davis and Whiting, 1977; Stancyk et al., 1980); coatis, dogs: (Fowler, 1979)). This supports the idea that, for sea turtles at least, nest detection by predators may be largely independent of depth. However, the non-significant trend of decreased detection at the greatest depths could indicate the existence of some depth-related process influencing detection that might be more evident with larger sample sizes. In addition, where predation on late-incubation nests is common (e.g. predators that visit the beach irregularly) we might expect depth to play a greater role in detection. A number of studies have reported frequent predation of nests near the end of incubation or in the process of hatching (Fowler, 1979; Nellis and Small, 1983). In such cases, predation might well be triggered through a combination of mechanisms: olfactory cues from hatched eggs or decomposing failed eggs and auditory cues associated with hatchling movement may provide new information about nest location (Nellis and Small, 1983), while hatchling migration to the sand surface simultaneously increases the sensory signal and decreases digging cost by reducing nest depth.

In systems where the detection of buried prey is unrelated to depth, we would expect the presence of depth-invariant surface cues to elicit digging behavior by predators. In artificial nests where we manipulated the availability of visual and olfactory information on the surface we found that disturbance of the sand was sufficient to elicit extensive digging whereas olfactory surface cues alone were not. It is possible that sausage scent applied to the sand surface provided an olfactory signal that was too weak, did not persist long enough in the environment or was simply not associated with buried food. However, the simultaneous presence of olfactory surface cues and buried prey increased both the depth mongooses were willing to dig and the probability of successful
predation. This suggests that although disturbance of the sand is a primary cue for detection and extensive digging, the scent of prey acts as a reinforcing cue once digging has been initiated. It is likely that mongooses and other predators use excavation to acquire additional information about buried prey. The strength and quality of the olfactory signal emitted by buried prey can carry information on depth (Reichman, 1981), prey size (Geluso, 2005), and freshness (Hall and Parmenter, 2008), all of which may be used by predators to assess whether to continue investing in digging or give up and save energy for the pursuit of more profitable prey. Despite our efforts to create visual and olfactory cues similar to those left by a nesting turtle, the strength and availability of these cues will be different in natural nests. In particular, sea turtle nests contain multiple potential sources of olfactory information (e.g. the smell of the nesting turtle on the sand surface, the smell of cloacal secretions that coat the eggs as they are laid, as well as smells emanating from the buried eggs themselves), and further research is needed to establish their relative importance as cues for nest predators.

Many factors other than depth influence predation risk for buried prey, and it is reasonable to expect that these may also affect detection and excavation of prey differently. Substrate characteristics may influence detection by altering transmission of olfactory cues through the soil (Geluso, 2005; Vander Wall, 1998) but can also affect digging costs (Vander Wall, 1993; Ward and Saltz, 1994). At Bath, patches of beach vegetation generally occupy a transition zone between open sand and inland forest. Substrate properties vary greatly across this gradient with loose and sandy soil nearer the water and increasingly compact soil containing more organic matter further inland. The location of nests relative to the seaward edge of vegetation had no effect on whether a nest was detected, but nests further inland were much less likely to be preyed on following detection, suggesting that denser substrate increases excavation costs. Although we found no significant effect of variation in moisture, rocks, or roots, where trends approached significance rocky soils seemed to deter predators whereas roots might actually facilitate predation, perhaps by loosening the sand (see Horrocks and Scott, 1991). Leighton et al (2008) found that predation risk for hawksbill
nests was higher in areas where mongooses were most active due to increased probability of mongooses encountering a nest. We might therefore expect variation in local predator activity to influence detection but not necessarily excavation. Although we found no effect of mongoose activity on probability of detection or subsequent predation, when mongoose activity was higher there was a trend for artificial nests to be discovered more quickly. Nellis & Small (1983) suggested that predator learning is likely to be an important factor affecting sea turtle nest predation. Although predation risk did not increase for artificial nests over the three week experimental period, the fact that exploration latency decreased over time supports the idea that learning may be strengthening the association between surface cues and the presence of buried prey for this novel food source. The complete and consistent absence of predation in one of six locations used in the experiment, despite continual, if somewhat lower, predator activity in the area, also supports the idea that predator learning is an important factor affecting local nest predation rates.

The strong relationship between depth and the probability of predation following detection supports the idea that the process of digging for sea turtle nests is costly for mongooses. Energetic costs of digging are likely to be substantial (Vander Wall, 1993), particularly in drier sand, and an individual mongoose may spend over half an hour actively removing sand before the eggs are reached (PA Leighton, unpublished data). Increased costs of antipredator vigilance may also be important for mongooses. Typically, vigilance requires the mongoose to withdraw from the excavation hole and assume a sitting-up posture. Digging is frequently interrupted by vigilance bouts, and these presumably become more costly as the excavation deepens. Another potential cost that increases with nest depth is the risk tunnel collapse. While excavating a hatched nest, members of the Barbados Sea Turtle Project found a dead mongoose buried in the nest cavity into which it had presumably burrowed and been trapped (BH Krueger, personal communication). Mongooses may therefore be reluctant to enter fully into the hole, potentially imposing a depth limit on excavation in certain substrates.
Having established that depth increases the costs of prey capture, it would be of interest to measure these costs in relation to the energetic value of buried prey. This would allow a better understanding of the limit of excavation depth expected for an optimally foraging predator given the energetic benefits of successful predation (Vander Wall, 1993). Prey size is predicted to have an effect on detection since larger buried prey are often more conspicuous (Geluso, 2005; Richardson, 1985), but such an effect seems unlikely for sea turtle nests where clutch sizes are consistently large. However, predation risk may be higher for species or populations with larger average clutch volumes since higher prey value is predicted to increase the giving-up-depth for predators.

**Nest depth and conservation**

It is common practice for sea turtle conservationists to dig to the top of the egg mass to determine the location of the clutch (Schroeder and Murphy, 1999), and such procedures can yield valuable information about predation risk. Our study suggests that conservation measures taken to protect individual sea turtle nests from predation should target shallow nests, especially those located in vegetated parts of the beach. In the context of the model presented here, strategies for protecting individual nests _in situ_ can be usefully categorized as those that function by reducing detection (e.g. erasing tracks of the nesting turtle) and those that act by increasing prey capture costs (e.g. physical deterrents). Both approaches have many variants (reviewed in Stancyk, 1982), but the optimal method may depend on how predators detect prey and whether digging cost is a major deterrent. If, as in our study, disturbance is widely used by predators as a primary cue for nest detection, manipulating detection probability by reducing visible disturbance is likely to be effective. However, in cases where depth-mediated olfaction plays a major role in detection, masking scent cues or replacing surface sand could be important. These are relevant considerations for researchers who excavate nests for data collection as this may substantially increase the probability of detection by predators if researcher disturbance is not well concealed. Manipulating digging costs for predators, where feasible, is also
likely to be effective. A physical barrier (e.g. protective screen) buried beneath the sand may increase costs of excavation sufficiently to deter some predators (Stancyk, 1982), but care must be taken that any protective device does not become an additional cue for nest detection by predators or human poachers. Our study shows that mongooses dig in response to disturbance even in the absence of buried food. An interesting conservation strategy might be to create an abundance of artificial disturbances in nesting habitat prior to the main nesting season. If predator digging efforts rarely result in successful predation this may weaken the association between disturbances and the presence of buried food.

A wide array of species prey on sea turtle nests (reviewed in Stancyk, 1982). Identifying predator characteristics associated with different nest predation mechanisms could provide a general basis for predicting which of these species is likely to pose the greatest threat under different conditions. Our study suggests that destructiveness of different predator species is likely to be related to how depth affects risk. If depth primarily affects prey capture costs, then the impact of a given predator should depend on the relative cost of digging for that species. This in turn should depend on the average burial depth of prey, substrate characteristics and the predator’s digging capacity. All else being equal, digging capacity is likely to increase with predator size. Thus, we might expect larger predators such as feral dogs to pose a greater threat to sea turtle nests than smaller predators such as mongooses and rats, and deeper-nesting sea turtle species such as leatherbacks to be largely immune to nest predation by smaller predators. The experimental procedure we used to establish the relationship between depth and predation risk for mongooses provides a general template that could easily be adapted for other predator species. Studies examining nest-finding behavior for other nest predators under a variety of ecological conditions (different habitats, times of day, exposure to human disturbance) could provide an experimental basis for predicting when a given predator will pose a serious threat to nesting turtles and how introduced predators are likely to impact turtle species differently.

Most turtles and many other egg-burying reptiles show temperature-dependent sex determination (TSD) where the sex of developing embryos is
determined by temperature conditions of the nest. In sea turtles, where warmer nests produce females, most studies that have estimated the hatchling sex ratio for specific nesting beaches have found these to be female-biased, with projections of greater than 90% female hatchlings common (reviewed in Wibbels, 2003). Where nest predation is related to nest depth, this has the potential to influence the overall sex ratio of hatchlings in two main ways. First, where depth has a direct effect on nest temperature (e.g. Valenzuela, 2001), hatchlings of one sex will be more likely to be preyed on. If shallow sea turtle nests are warmer and predators remove the shallowest nests first, this should theoretically work against female bias by removing many of the all-female nests from the population. Secondly, where microhabitat affects both nest depth and nest temperature, predation risk will be unequal among microhabitats and difference in temperature among habitats may result in higher mortality for hatchlings of one sex (Oz et al., 2004). Kamel and Mrosovsky (2006a) found that hawksbill nests in forested beach microhabitats were the only ones likely to produce male hatchlings, while 100% female hatchlings were predicted in open beach and sparsely vegetated microhabitats. In areas such as Bath where the shallowest nests are located in densely vegetated microhabitats and predators favor these areas for foraging, the coolest nests may in fact be at the highest risk. In such cases, nest predators may help drive female biased hatchling sex ratios to an extreme by selectively consuming the small proportion of nests that are most likely to produce males.

Resource burial depth can be thought of as the outcome of an evolutionary game between prey and predators (Andersson and Krebs, 1978; Dally et al., 2006). As such, the relationship between depth and predation risk is likely to be quite general for predator-prey systems: foragers seeking burrowing prey, nest predators seeking eggs, scatter-hoarders seeking seeds, diving animals seeking prey, and parasitoids seeking buried eggs or larvae. Optimal burial depth for prey is a function of the community of predators or kleptoparasites in which the behavior evolved. The introduction of exotic predators such as mongooses has the potential to create a strong selection pressure for deeper burial, while loss of important natural predators may favor shallower burial. Such changes may have
important long-term consequences, especially where burial depth affects other processes such as seed germination rate, sex-determination of buried eggs or the emergence success of young. Further research into the economics of foraging decisions made by animals that prey on buried resources would greatly improve our ability to predict how ongoing anthropogenic changes are likely to impact such communities.

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LITERATURE CITED


Table 1. The effect of nest depth and other variables on (a) predation risk and its components, (b) detection (probability of detection) and (c) capture (probability of predation following detection), for artificial sea turtle nests after 7 days of exposure. All predictors are standardized (mean = 0, SD = 1). % Dev. is the proportion of null model deviance explained.

<table>
<thead>
<tr>
<th>Variable</th>
<th>a) Predation risk (n = 120, % Dev. = 66.1%)</th>
<th>b) Detection (n = 120, % Dev. = 27.6%)</th>
<th>c) Capture (n = 114, % Dev. = 70.3%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>nest depth (cm)</td>
<td>-4.035 (0.844, &lt; 0.001)</td>
<td>-0.599 (0.477, 0.209)</td>
<td>-4.542 (1.070, &lt; 0.001)</td>
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<tr>
<td>distance from vegetation edge (m)</td>
<td>-1.100 (0.399, 0.006)</td>
<td>-0.390 (0.566, 0.491)</td>
<td>-1.223 (0.435, 0.005)</td>
</tr>
<tr>
<td>presence of rocks</td>
<td>-0.485 (0.404, 0.230)</td>
<td>-0.533 (0.467, 0.254)</td>
<td>-0.410 (0.429, 0.339)</td>
</tr>
<tr>
<td>presence of roots</td>
<td>0.566 (0.422, 0.180)</td>
<td>0.482 (0.468, 0.303)</td>
<td>0.284 (0.461, 0.538)</td>
</tr>
<tr>
<td>presence of moist sand</td>
<td>0.186 (0.370, 0.615)</td>
<td>0.242 (0.537, 0.652)</td>
<td>0.108 (0.413, 0.795)</td>
</tr>
<tr>
<td>date of nest construction</td>
<td>0.405 (0.400, 0.312)</td>
<td>1.845 (1.253, 0.141)</td>
<td>0.336 (0.424, 0.428)</td>
</tr>
<tr>
<td>local mongoose activity</td>
<td>-0.028 (0.426, 0.948)</td>
<td>0.138 (0.441, 0.755)</td>
<td>-0.374 (0.449, 0.404)</td>
</tr>
</tbody>
</table>
Table 2. The effect of nest depth and other variables on (a) detection latency and (b) predation latency for artificial sea turtle nests exposed to mongooses predation for 7 days. All predictors are standardized (mean = 0, SD = 1). % Dev. is the proportion of null model deviance explained.

<table>
<thead>
<tr>
<th>Model</th>
<th>a) Detection Latency</th>
<th>b) Predation Latency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$(n = 114, % \text{Dev.} = 21.9%)$</td>
<td>$(n = 51, % \text{Dev.} = 30.9%)$</td>
</tr>
<tr>
<td>Variable</td>
<td>Estimate</td>
<td>SE</td>
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<tr>
<td>nest depth (cm)</td>
<td>0.189</td>
<td>0.209</td>
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<tr>
<td>distance from vegetation edge (m)</td>
<td>-0.560</td>
<td>0.268</td>
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<td>presence of rocks</td>
<td>0.200</td>
<td>0.216</td>
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<tr>
<td>presence of roots</td>
<td>-0.237</td>
<td>0.219</td>
</tr>
<tr>
<td>presence of moist sand</td>
<td>0.088</td>
<td>0.236</td>
</tr>
<tr>
<td>date of nest construction</td>
<td>-1.046</td>
<td>0.270</td>
</tr>
<tr>
<td>local mongoose activity</td>
<td>-0.401</td>
<td>0.229</td>
</tr>
</tbody>
</table>
**Figure 1.** The effect of nest depth on (a) predation risk and its components, (b) detection (probability of detection) and (c) capture (probability of predation following detection), for hawksbill nests in vegetated beach habitat. Data shown are the status of individual nests (1, detected/preyed on; 0, not detected/preyed on) observed in 2004 and 2005 ($n = 101$ in a,b; $n = 78$ in c). The solid lines show the fitted GLM and dashed lines are ± 1 SE.
Figure 2. The effect of nest depth on (a) predation risk and its components, (b) detection (probability of detection) and (c) capture (probability of predation following detection), for artificial sea turtle nests after 6h (dotted line, filled squares), 24h (dashed line, open circles) and 7 days (solid line, filled circles). Error bars are ± 1 SE.
Figure 3. The effect of experimental treatment on (a) the probability of detection (squares), extensive digging (filled circles), and predation (open circles) and (b) the maximum excavation depth attained by mongooses digging for artificial sea turtle nests after 7 days of exposure. Error bars are ± 1 SE.
Excavation depth (cm)

- 30 cm
- Disturbance-only
- Smell-only

Probability
- Detection
- Extensive digging
- Predation

a)

b)
CHAPTER 3

SUN, SEA AND THE SCARECROW EFFECT:
CAN HUMAN DISTURBANCE BENEFIT THREATENED
SPECIES BY SCARING OFF PREDATORS?

LINKING STATEMENT 3

In Chapter 1, I documented strong avoidance of the open beach by mongooses foraging in sea turtle nesting habitat, hypothesizing that this was driven by avoidance of humans that are viewed as a predatory threat. Here I test this hypothesis by exploring the relationship between human beach use and the temporal patterns of mongoose activity at multiple spatial scales within the coastal landscape.
ABSTRACT

Most wild animals show a direct negative response to human disturbance; however, disturbance may also have positive indirect effects by altering species interactions. In the Caribbean, introduced mongooses (Herpestes javanicus) are an important predator of the nests of critically endangered hawksbill sea turtles (Eretmochelys imbricata). We asked whether daytime visitor activity could benefit hawksbills by reducing mongoose activity in nesting habitat. We used track stations to measure how mongooses alter their space use in response to fluctuating human beach use and availability of hawksbill nests, and estimated the indirect impact of disturbance on egg predation for 7 years of hawksbill nesting. Human activity substantially decreased mongoose use of nesting habitat. Mongoose activity increased with abundance of nests and was lower at the edge than the interior of beach vegetation, but neither factor altered relative sensitivity to disturbance. We estimated that, in addition to deterring mongooses from accessing nests on the open beach, human activity has the potential to reduce predation of nests in vegetation by up to 20% at our site, with the greatest per capita impact at low volumes (< 50 visitors). Forms of human disturbance of sea turtle nesting habitat are manifold and negative, but our study indicates that there are positive aspects of allowing human use of nesting beaches. Where such positive indirect effects of disturbance exist, optimizing the trade-off with direct negative impacts of disturbance provides a potential tool supporting the regulation of tourist volumes in fragile ecosystems.
INTRODUCTION

Human disturbance is increasingly common and tends to have direct negative effects on species (Frid and Dill 2002, Blumstein et al. 2005). However, disturbance can also have profound indirect effects by altering the interactions among species in a community: negative effects of disturbance on one species are likely to have positive consequences for its competitors or prey (Gill et al. 1996, Crooks and Soule 1999). These positive indirect effects may in some cases be sufficient to offset direct negative effects of disturbance, creating a net benefit of disturbance for certain species. The idea that human activities may have positive indirect effects and that human disturbance could be manipulated to improve survival and recruitment of threatened or commercially valuable species is an appealing concept for conservation and management. However, its applicability has rarely been tested (but see Gill 1996, Nevin and Gilbert 2005) and the general conditions under which indirect benefits of human disturbance might occur have not been thoroughly explored.

The degree to which manipulating human activity could effectively shield threatened prey from predation depends critically on how predators respond to disturbance. Foraging theory provides clear predictions about how disturbance should impact predators: disturbance increases foraging costs, causing predators to decrease foraging rate and use of disturbed habitat (Frid and Dill 2002). However, habitat attractiveness should also be affected by the relative availability of prey and habitat structures that provide refuge from disturbance, and both of these may alter sensitivity of predators to disturbance (Yasue 2006, Jayakody et al. 2008).

Sea turtle nesting beaches around the world are increasingly developed for human recreation. Nest predators are an important source of egg mortality, particularly species such as dogs, raccoons and mongooses that thrive in human-modified landscapes (Stancyk 1982). There is anecdotal evidence that human activity in sea turtle nesting habitat may deter predators and reduce local predation rates (Talbert et al. 1980). This suggests that the “scarecrow effect” of
tourist activity on nesting beaches may be a silver lining to otherwise overwhelmingly negative effects of human encroachment on critical nesting habitat.

In order assess this possibility empirically and establish a framework for exploring indirect effects of human disturbance in other systems, we examined how daytime tourist activity at an important nesting beach for hawksbill sea turtles (*Eretmochelys imbricata*) in Barbados affected beach use by a destructive introduced nest predator, the small Asian mongoose (*Herpestes javanicus*). We then used this information to quantify the indirect effects of different levels of tourist activity for hawksbill nest survival.

METHODS

**Species and Study Area**

The study was carried out at Bath (13.187° N, 59.476° W), the primary east coast hawksbill nesting beach in Barbados. The beach is relatively undeveloped, accessible by a single road that runs the length of the beach and is lined with bungalow-style cottages. Beach habitat at Bath is a fragmented mixture of open sandy areas planted with shade trees but otherwise devoid of vegetation, and dense patches of shrubs [especially *Coccoloba uvifera* L. and *Thespesia populnea* (L.)]. Directly adjacent to the beach is a 150 m wide strip of managed grassland, creating a buffer between the beach and the surrounding coastal forest habitat that dominates the east coast of the island. Bath is a popular destination for local beach-goers and large weekend picnics are commonplace. The beach facility and parking lot, located near the north end of the beach, form the hub of human activity.

The small Asian mongoose (*Herpestes javanicus*) was introduced to many Caribbean islands for rat control in the late 1800s and has become an important predator of sea turtle nests (Nellis and Small 1983, Hays and Conant 2007, Chapter 1). Mongooses are strictly diurnal, becoming active at dawn (approx. 05:00) and becoming inactive shortly before sun-down (Nellis and Everard 1983).
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 and Everard 1983, Leighton 2005). When foraging in beach habitat, mongoose activity is generally confined to beach vegetation (Chapter 1). Opportunistic generalists, mongoose diet ranges from vertebrates to fallen fruit and varies considerably among islands (Nellis and Everard 1983). In addition to raiding sea turtle nests, mongooses at Bath actively hunt for crabs and insects and forage opportunistically on garbage and dead fish.

Data Collection

Activity of humans and mongooses was monitored from April to September 2005, spanning the peak of the hawksbill nesting season at Bath.

Predator activity.—Mongoose activity at Bath was measured using 13 track monitoring sites: 7 in vegetated beach habitat along the boundary between open sand and dense beachside vegetation and 6 in forest habitat along the forest-grassland edge. Each site contained 6 “track pads”: 0.5 m X 0.5 m patches of beach sand, smoothed to pick up the tracks of passing animals (Chapter 1). Track pads were arranged in a rectangular grid with 3 pads placed at 10 m intervals along the habitat edge (“edge” microhabitat) and a parallel set of 3 pads placed 5 m from the edge (“interior” microhabitat; Figure 1.). Track pads were created at the beginning of April and monitored until the end of August. Monitoring took place two days per week, Wednesday and Sunday, to capture weekly fluctuation in human activity. Plots were checked at 8:00, 12:00 and 16:00 to measure mongoose activity during the early morning (5:00-8:00), late morning (8:00-12:00), and afternoon (12:00-16:00). During each check, the number of distinct mongoose trails crossing the surface of each track pad was recorded and the pad was cleared for the following check using a dustpan brush. Clearing for the morning check was carried out at dusk on the day prior to monitoring. Tracks of mongooses were easily distinguishable from those of other mammals present in the area, primarily feral cats and dogs.
**Human activity.**—Beach-scale human activity was assessed during each check period by counting the number of vehicles in the car park near the beach facility. Vehicles were recorded in three separate classes: “cars” were any vehicle seating 4-5 passengers, “vans” were vehicles seating up to 20 passengers, and “buses” were vehicles typically seating over 50 passengers. Vehicle tallies were converted to an approximate number of visitors by assuming that all vehicles were filled to capacity. Site-scale human activity was assessed at each check by counting the number of visitors visible within a 50 m radius of each monitoring site. Visitor counts from the start and end of each check period were averaged as a measure of human activity during that period.

**Turtle nest availability.**—Nest availability was assessed through daily beach surveys during which new nests were located and the status (incubating, predated, or hatched) of existing nests was checked. A nest was considered available to mongooses if it had not been predated or hatched and was within 6 m of vegetated habitat (Chapter 1). Total available nests on the beach was used a measure of daily beach-level nest availability, while site-level availability was the number of nests within a 25 m radius of each monitoring site.

**Statistical Analyses**

We took an information theoretic approach to model selection and inference. Models containing all subsets of the parameters of interest were ranked by Akaike’s Information Criterion adjusted for small sample sizes (AICc) and a 95% confidence set of candidate models was selected for use in inference (Burnham and Anderson 2002). Composite parameter estimates and standard errors incorporating model selection variance were calculated for all parameters in the confidence set using conventional model averaging. In addition, the sum of Akaike weights of all candidate models containing a given parameter was calculated as a measure of that parameter’s relative importance (Burnham and Anderson 2002).

We used a first set of models to describe variation in human and mongoose activity at different spatial scales (between habitats, microhabitats, and
monitoring sites) and temporal scales (between months, days of the week and times of day). A second set of models examined how variation in human activity and sea turtle nest availability affected space use by mongooses. At the habitat scale, we looked at how total beach visitors and available nests influenced mean mongoose activity at beach monitoring sites. At the site scale, we looked at how visitor head counts and local nest availability affected mongoose activity.

We used a mixed model framework (GLMMs) to account for spatial and temporal correlations in the data. We used sampling week as a temporal blocking factor, including it as a random effect in all models. The empirical temporal autocorrelation function showed no strong association between observations at any time lag and including a temporal autocorrelation term had no effect on model likelihood (Likelihood ratio test: $\chi^2 = 2.04$, df = 1, $P = 0.15$.) so this was omitted. Site-scale models were fitted with Gaussian spatial correlation structure to account for autocorrelation among sites. We log-transformed mongoose activity (trails per m$^2$ per hour of track pad exposure) to meet distributional assumptions. Exploratory analyses using smoothing functions fitted by generalized additive models (GAMs) revealed a non-linear relationship between human activity and log mongoose activity that was best approximated by log-transforming measures of human activity. Before being included in models, predictors were tested for strong collinearity (VIF was < 3 in all cases indicating little collinearity) and standardized (mean = 0, SD = 1) to allow meaningful comparison of regression coefficients (Quinn and Keough 2002).

Finally, we estimated the indirect impact of visitors on sea turtle nest predation by predicting mongoose activity across a range of disturbance levels using the fitted beach-scale model and translating this into total egg mortality from predation for nests in vegetated habitat utilising the known relationship between local mongoose activity and hawksbill predation risk at Bath (Chapter 1). Predictions were made using nest locations from 7 years of Bath nesting data (1999-2005) collected by the Barbados Sea Turtle Project. All analyses were carried out using R v.2.8.1 (R Foundation for Statistical Computing, Vienna, Austria).
RESULTS

*Predator activity*

Patterns of mongoose activity were markedly different in beach and forest habitats so these data were analyzed separately. In beach habitat, mongoose activity increased over the summer, was higher on Wednesdays than on Sundays, decreased throughout the day, and was higher in interior than edge microhabitats (Figure 2; GLMM: Adj. $R^2 = 0.45$, $n = 172$ checks; additional model details in Supp. Material). In addition, the drop in activity throughout the day tended to be more pronounced on Sundays. By contrast, mongoose activity in the adjacent forest habitat remained constant throughout the summer (Figure 2), did not differ between Wednesdays and Sundays, and peaked in the middle of the day rather than in the early morning (GLMM: Adj. $R^2 = 0.07$, $n = 165$ checks). Activity was higher in interior than edge microhabitats, but this effect was less pronounced than in beach habitat.

*Human activity*

Total beach visitors varied considerably among months without a clear seasonal trend (Figure 2) and increased throughout the day, especially on Sundays (GLM: Adj. $R^2 = 0.54$, $n = 85$ checks). Local head counts showed similar temporal trends and revealed non-uniform human activity along the beach (GLMM: Adj. $R^2 = 0.37$, $n = 597$ checks; Figure 2c), with greater activity near popular swimming areas (e.g. Site 1) and nearer to the beach facility (e.g. Sites 6 and 7).

*Turtle nest availability*

The number of available hawksbill nests at Bath increased steadily from 2 nests in early April to 67 nests at the end of July, declining to 36 by the end of August as nests began to hatch. Available nests within 25 m varied considerably among sites, ranging from 0 nests throughout the season (Site 6) to a maximum of 15 nests (Site 5).
Predator response to disturbance and nest availability

Mongooses reduced their use of beach habitat in response to increasing human activity, both at the scale of the whole beach and at the scale of individual monitoring sites (Table 1). The response was nonlinear, with a sharp drop in habitat use in response to moderate increases in human activity and relatively little change thereafter (Figure 3a). Mongoose beach use increased linearly with turtle nest availability, both locally and at the beach scale. The response of mongooses to human activity was qualitatively similar in edge and interior microhabitats and changed little with increasing nest abundance (Table 1).

Indirect effects of human activity on nest predation

Estimated egg mortality from predation varied considerably among years but was consistently greater than 50% for nests in vegetated habitat. Variation in visitor counts over the range observed at Bath has the potential to alter egg predation by up to 20%, with the strongest per capita impact occurring at relatively low visitor volumes (< 50 visitors; Figure 3b).

DISCUSSION

We found that low to moderate levels of daytime human activity substantially decreased the use of sea turtle nesting habitat by mongooses and that mongooses responded to disturbance at relatively fine spatial and temporal scales. Together, these results suggest that fine-scale variation in human activity can have important indirect consequences for sea turtle nest survival. Effects of human activities on interactions among species are rarely considered in studies of disturbance (Sutherland 2007), and this is the first study to attempt to quantify the importance of such effects in an applied context. Our approach to quantifying and predicting positive consequences of human disturbance has potential broad applicability for management of endangered species where critical habitats for foraging or
reproduction are under increasing pressure from human activities (Taylor and Knight 2003).

The net impact of human disturbance in a given ecological context is likely to depend on other measures of habitat quality (Frid and Dill 2002). Mongoose activity was substantially higher in areas of the beach where nests were most abundant and at the end of the nesting season when sea turtle nest densities were highest. However, there was little evidence that nest availability affected sensitivity to disturbance: mongooses showed a consistent negative response to disturbance even when nests were abundant. In practical terms, this means that greater levels of human activity or other predation reduction methods would be required to maintain predation risk at a constant low rate as nest densities increase. However, disturbance is still likely to be most beneficial in areas where nest density is high, since the same reduction in local predator activity will protect more nests. Mongoose are generalist foragers, and it is likely that availability of other food sources may also have contributed to observed patterns of space use. In particular, mongooses are known to feed on human garbage (Nellis and Everard 1983, Quinn and Whisson 2005), and availability of anthropogenic food likely offsets the costs of disturbance in nesting habitat. An important management implication of this is that reducing anthropogenic food through public education and proper containment of garbage is likely to reduce habitat quality for nest predators and produce similar indirect benefits for nest survival.

Habitat structure has the potential to dramatically alter species interactions (Didham et al. 2007, Chapter 1). In particular, microhabitats that serve as refuges are predicted to reduce the costs of disturbance by allowing species to avoid direct confrontation or reduce vigilance without leaving the habitat altogether (Frid and Dill 2002, Jayakody et al. 2008). Mongoose activity was higher within patches of beach vegetation than at the edge, consistent with fine-scale avoidance of disturbance-prone microhabitats (Chapter 1). However, the proportional reduction in mongoose activity in response to increased human activity was similar in edge and interior microhabitats, suggesting that mongooses respond to direct disturbance by leaving the disturbed habitat rather than simply shifting their
activity away from the edge. Given that few hawksbill sea turtles nest more than 5 m into vegetation (Chapter 1), this means that the majority of nests in vegetation should benefit from positive indirect effects of human activities. At a broader scale, mongooses show near-complete avoidance of vegetation-free portions of the beach where over 50% of hawksbill nesting habitat at Bath occurs (Chapter 1). The consistent presence of humans on the open beach is likely driving this pattern of space use, and there is evidence that mongooses venture further from vegetation when human activity is very low (P. Leighton, unpublished data). Thus, although nests deep in vegetation may only benefit from a modest reduction in predation risk due to direct disturbance of predators, moderate levels of human activity are sufficient to effectively protect nests in more exposed microhabitats by making them inaccessible.

Where disturbance poses little direct threat, we might expect predators to habituate rapidly to “human scarecrows” resulting in a reduced effect of disturbance over time (Baudains and Lloyd 2007). Mongooses at Bath consistently avoided open areas and more exposed microhabitats, and preliminary analyses showed no evidence of a change in sensitivity to disturbance over the time scale of our study. Given that mongooses are not actively persecuted by humans and have no important predators in their introduced habitat, this consistent avoidance response is somewhat surprising. Mongooses are extremely successful invaders (Hays and Conant 2007), and it is possible that the combination of high opportunism with fine-scale anti-predator behaviour and neophobia is a recipe for success for species introduced to novel environments where resources and threats are equally unknown (Mettke-Hofmann et al. 2002, Schlaepfer et al. 2005). Thus, the same selective forces that favour invasion success may therefore select for “hard-wired” negative responses to disturbance stimuli (Frid and Dill 2002), imposing an adaptive limit to habituation for invasive generalists. Rapid habituation could limit the application of human disturbance as a tool to manage predation, and further research into the process and limits of habituation in natural systems is needed (Sutherland 2007). Specifically, research is needed into the time scale of habituation, which
components of disturbance have the greatest impact (e.g. noise vs visual disturbance), and what type of disturbance regimes minimizes habituation. Recent work has shown that habituation to humans can be reversed through aversive conditioning (Kloppers et al. 2005), and this type of approach could potentially be used to enhance the responsiveness of predators to inoffensive tourists.

**Conclusions**

Our study demonstrates that human activity can substantially alter the predation risk landscape in critical habitat for an endangered species. On sea turtle nesting beaches, even low levels of daytime human beach use have the potential to improve nest survival by displacing predators. An obvious application of this is to encourage increased beach use at times or in locations where nests are most vulnerable. Such targeted disturbance might be achieved, for instance, by organizing early morning nature hikes or improving pedestrian beach access near high-density nesting areas. Night patrols of the beach are commonly used by conservation groups to collect data on nesting turtles, but are also effective in reducing human poaching of eggs and nesting turtles (J. Horrocks, unpublished data) and increasing patrol frequency in predation hotspots could help deter nocturnal predators. Beach vegetation plays an important role in modulating predator response to disturbance; however, vegetation is also important nesting habitat (Horrocks and Scott 1991). Reducing vegetation density or height is likely to decrease its value as a refuge for predators. For instance, owners of beach cottages at Bath routinely trim beachside vegetation and this appears to reduce local mongoose activity (P. Leighton, unpublished analyses). At a broader scale, our study suggests that the least disturbed beaches are likely to be the most impacted by mongoose predation. While further development of pristine habitats for heavy tourist use cannot be encouraged, preserving such habitats as public-access nature reserves and promoting low-impact activities such as research or ecotourism may, in some circumstances, have significant conservation benefits.

An inevitable trade-off exists between positive indirect effects of disturbance and direct negative effects, both of which are likely to increase with
human activity. For instance, heavy pedestrian traffic is thought to decrease sea
turtle nest success through increasing sand compaction (Horrocks and Scott
1991). Such effects are likely to be mild relative to egg mortality from predation
over the range of visitor numbers in this study, but may be substantial at more
heavily-developed tourist beaches. Having established that disturbance could be
beneficial, a practical extension would be to identify the optimal level of
disturbance for management under different conditions. Costs and benefits of
disturbance can be summed to identify the range of disturbance levels that will
result in a net benefit for a target species or group of species and pinpoint when
this benefit will be the greatest. Evaluating direct and indirect effects of human
disturbance in an optimality framework has the potential to provide an important
tool supporting the regulation of tourist volumes in fragile ecosystems.

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Fellowship to J.H. and the Earthwatch Institute and its volunteers.
LITERATURE CITED


Table 1. Generalized Linear Mixed Models of mongoose activity in hawksbill sea turtle nesting habitat at (a) broad (beach-level) and (b) fine (site-level) spatial scales. Parameter estimates and standard errors are the composite estimates from all models in the 95% confidence set of models selected by Akaike’s Information Criterion adjusted for small sample sizes (AICc). RI is a measure of the relative importance of each parameter, calculated as the sum of the Akaike weights of all models containing that parameter.

<table>
<thead>
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<th>Parameter</th>
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<td></td>
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Table S1 (Supplementary Material). Generalized Linear Mixed Models of mongoose activity in (a) beach and (b) adjacent forest habitats at Bath Beach, Barbados. Parameter estimates and standard errors are the composite estimates from all models in the 95% confidence set of models selected by Akaike’s Information Criterion adjusted for small sample sizes (AICc). RI is a measure of the relative importance of each parameter, calculated as the sum of the Akaike weights of all models containing that parameter.

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</tr>
</tbody>
</table>
Figure 1. Habitat map of Bath Beach, Barbados. Filled squares indicate location of monitoring plots relative to different habitats and the center of human activity (Beach Facility).
**Figure 2.** Spatial and temporal patterns of activity for mongooses and humans at Bath Beach, Barbados. (a) Habitat-scale variation in activity over the hawksbill nesting season. (b) Habitat-scale variation in activity among days of the week and throughout the day. (c) Variation in activity among monitoring sites and between edge and interior microhabitats. Error bars are +1 SE.
**Figure 3.** Influence of tourist pressure and nest availability on (a) predator activity in beach habitat and (b) resulting sea turtle egg mortality from predation. Predictions in (b) are for hawksbill nests in vegetated nesting habitat over seven years of monitoring (1999-2005).
CHAPTER 4

MODELLING RISK OF SEA TURTLE NEST PREDATION BY INTRODUCED MONGOSES: A NEW TOOL FOR CONSERVATION AND MANAGEMENT

LINKING STATEMENT 4

In the first three chapters, I demonstrated the importance of a variety of behavioural processes in determining patterns of nest predation. Here I combine these to develop a general predictive model of the spatial and temporal patterns of sea turtle nest predation by mongooses.
ABSTRACT

Nest predation is an important practical challenge for sea turtle conservation, reducing hatchling recruitment and slowing recovery of threatened populations. Accurately forecasting where and when predation will occur has the potential to optimize predation management. The small Asian mongoose (*Herpestes javanicus*) is an important introduced predator of sea turtle eggs and hatchlings throughout the Caribbean. We used survival analysis to model the spatial and temporal patterns of sea turtle nest predation by mongooses, using 7 years of predation data from an important nesting beach for critically endangered hawksbill sea turtles (*Eretmochelys imbracata*) in Barbados. Daily predation risk was high initially, decreasing rapidly following oviposition but increasing again near the end of development. Predation risk increased over the nesting season, was highest in and near patches of beach vegetation, and increased with nest density on the open beach but not in vegetation. We demonstrate the utility of survival analysis for predicting predation of sea turtle nests by an introduced predator with widespread impact, providing a practical tool for conservation where mongooses have been introduced.
INTRODUCTION

Predators present an important practical challenge for the conservation of many threatened birds and reptiles worldwide (Stancyk 1982, Chalfoun et al. 2002, Kolbe and Janzen 2002). Predation of eggs and hatchlings contributes to the global decline of endangered sea turtle populations by reducing hatchling recruitment and slowing population recovery (Stancyk 1982). The widespread introduction of destructive nest predators on oceanic islands, which provide critical nesting habitat for many sea turtle species, is particularly problematic. In the absence of human intervention, predators frequently destroy over 80% of available nests (Talbert et al. 1980, Nellis and Small 1983, Engeman et al. 2006). Predation reduction 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. 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 and Litvaitis 2004, Chapter 1). Spatial aggregation of nests can also affect predation either by increasing per capita risk through attracting predators to high-density areas (e.g. Marchand and Litvaitis 2004), or decreasing it through dilution effects (e.g. Eckrich and Owens 1995).

Predation risk is also likely to vary temporally, both seasonally and throughout egg development. Several authors have suggested that predation risk should change over the nesting season due to shifts in predator activity related to nest availability (Chapter 3) or predator learning (Chapter 2, Stancyk 1982, Nellis and Small 1983), but seasonal changes in predation risk have only been
documented in a few studies (Fowler 1979, Talbert et al. 1980, Engeman et al. 2003). Predators use visual and olfactory cues to locate nests (Chapter 2, Stancyk 1982, Rollinson and Brooks 2007). Cue availability is thought to decreased rapidly following oviposition and increase at the end of incubation as eggs hatch and hatchlings move toward the surface (Chapter 2, Stancyk 1982, Nellis and Small 1983). Several studies have reported more frequent nest predation near the start (Chapter 2, Stancyk et al. 1980, Nellis and Small 1983, Goncalves et al. 2007) or end (Fowler 1979, Nellis and Small 1983) of incubation, but the relationship between daily predation risk and nest age has not been rigorously explored.

While spatial effects on predation risk have received considerable attention, temporal effects have remained elusive. This may be in part due to the fact that popular analytical 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. Survival analysis methods enjoy great popularity in human biomedical research but have only recently been adopted in studies of nest predation (Nur et al. 2004, Heisey et al. 2007). The Mayfield method of estimating nest survivorship (Mayfield 1961) has a long history of use in avian biology but formal parametric (i.e. weibull regression) and semi-parametric (i.e. Cox proportional hazards regression) survival analysis approaches have a number of important advantages including the ability to model the effect of covariates (Heisey et al. 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 spatial and temporal patterns of 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).

Here, we use a survival analysis framework to construct a predictive model of spatial and temporal patterns of sea turtle nest predation by an exotic
predator, the small Asian mongoose (*Herpestes javanicus*). Mongooses were widely introduced in the Caribbean in the late 1800s and have been blamed for the subsequent decline of native fauna on many Caribbean islands (Nellis and Everard 1983, Hays and Conant 2007). Attempts to eliminate mongooses have been largely ineffective, and mongooses still pose a significant threat to sea turtle eggs and hatchlings (Nellis and Small 1983, Chapter 1). Despite their widespread introduction and suggested impact, the predatory behaviour of exotic mongooses on threatened endemic species is poorly documented (Hays and Conant 2007). We used data from a long-term study of hawksbill sea turtle (*Eretmochelys imbricata*) nesting in Barbados to examine the effects of nest age, oviposition date, nest location, and local nest density on risk of mongoose predation. We calibrated the model with nesting data from 2004-2005 and evaluated it by predicting sea turtle nest mortality for 1999-2003. To date, studies of sea turtle nest predation have been primarily descriptive (Fowler 1979, Nellis and Small 1983, Macdonald et al. 1994), and show a strong geographic and taxonomic bias toward predation by native raccoons on loggerhead sea turtles along the south-east coast of the United States (e.g. Ratnaswamy et al. 1997, Engeman et al. 2006, Barton and Roth 2008). The goal of this research is to use the behavioural processes underlying sea turtle nest predation by mongooses to develop a predictive model of nest survival with practical relevance for conservation management.

**METHODS**

*Species and study area*

The study was carried out at Bath (13.187º N, 59.476º 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 et al. 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 (Chapter 1). Incubation lasts approximately 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 et al. 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 (Chapters 1 & 3). 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 and 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 1999-2005 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, and the position of the eggs was determined by careful excavation (Schroeder and Murphy 1999). Incubating nests were checked to determine if they had been preyed on by mongooses (signs of digging, mongoose tracks, at least one egg removed from nest), hatched (signs of hatchling emergence, hatched shells at bottom of 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 is a flexible approach, involving a non-parametric estimation of how
daily nest survival varies with nest age (the baseline hazard function) and modelling the effects of covariates on nest survival by increasing or decreasing this baseline hazard function. 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 uncensored (not preyed on) on the date of hatch/failure.

In order to create a model that was both ecologically meaningful and practical to apply, we used previous work on the ecology of sea turtle nest predation by mongooses to select predictors that reflected the main behavioural processes known to affect predation risk (Chapters 1-3) while also being straightforward to measure in the field. Mongooses forage primarily in beach vegetation, with activity decreasing sharply across the habitat boundary between patches of vegetation and the open beach (Chapters 1 & 3). In addition, shallower nests are at greater risk of predation, and nests in vegetation are significantly shallower than nests on the open beach (Chapter 2). 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 date of nest initiation to model the combined effects of increasing mongoose activity in beach habitat over the nesting season (Chapter 3) and learning by predators (Chapter 2) on predation risk. We used cumulative nest density (total nests laid over the season per m²) to model 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 (Chapter 3, 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. Since 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 (lowest model AIC). We considered possible interactions between distance and habitat, density and habitat, and density and date. We included study year as a random effect to control for unexplained variation in survival among years. All continuous variables were standardized (mean = 0, SD = 1) to allow meaningful comparison of coefficients (Quinn and Keough 2002).

We took an information theoretic approach to model selection and inference. We ranked models containing all subsets of parameters by Akaike’s Information Criterion adjusted for small sample sizes (AICc) and selected a 95% confidence set of candidate models for use in inference (Burnham and 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. In addition, we calculated the sum of Akaike weights of all candidate models containing a given parameter as a measure of that parameter’s relative importance (Burnham and Anderson 2002). We assessed performance of each model by using it to predict whether each nest survived long enough to hatch successfully (65 days), and comparing this to the observed fate of nests. We calibrated models using nesting data from 2004-2005, and evaluated each model by predicting the fate of nests from the 5 previous years (1999-2003). 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 and 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 indicate excellent discrimination (Hosmer and Lemeshow 2000).

We carried out all analyses in R v.2.8.1 (R Foundation for Statistical Computing, Vienna, Austria) using the following packages: “survival” (main
survival models), “muhaz” (hazard function estimation), “ads” (density calculations), and “ROCR” (classification statistics).

RESULTS

A total of 551 hawksbill nests was recorded from 1999-2005, 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 few days of laying, and this pattern was consistent between years (Figure 1a). Estimated daily predation risk was highest for freshly laid nests but dropped quickly with nest age, increasing slightly near the end of development (Figure 1b).

There was evidence of a scale-dependent effect of local nest density on predation risk, with density of nests within a 4-6 m radius of the focal nest explaining the most variation in predation risk (Figure 2). 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 24 candidate nest survival models considered, eight were retained in the 95% confidence set of models selected by AICc (Table 1). All eight models 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).

Survival of nests in vegetated habitat was substantially lower than nests on the open beach, being lowest deep in vegetation and increasing across the vegetation edge (Table 2; Figure 3a). Nests laid later in the nesting season were more likely to be preyed on (Figure 3b). Nests in high-density areas had lower survival overall but this effect differed among habitats, with a strong effect for nests on the open beach but relatively little effect in vegetation (Figure 3c). There was little support for the importance of other interactive effects (Table 2).
DISCUSSION

Accurately forecasting where and when predation will occur has the potential to dramatically increase the effectiveness and reduce the costs of predation management (Engeman et al. 2002, Engeman et al. 2003). Here, we illustrate the utility of survival analysis for predicting predation of hawksbill sea turtle nests by an introduced predator with widespread impact. We demonstrate that nest survival changes with both habitat context and over time, and provide an important quantification of the underlying relationship between nest age and predation risk. Focussing on variables that are routinely measured in sea turtle conservation programs, the current model can be readily validated and applied in other locations where mongooses are present and provides a template for modelling nest predation for other turtle and predator species.

Changes in predation risk over time

In sea turtles, predation risk for eggs is directly linked to nest detectability (Chapter 2). Previous studies have reported frequent predation early in development (Stancyk et al. 1980) or close to hatching (Fowler 1979). Analysis of 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 end of incubation (Nellis and Small 1983). However, overall predation risk at our site appears to be primarily driven by high nest vulnerability during first 4-5 days following oviposition. Although 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 behaviour. For instance, mongooses at our site use disturbance of sand by the nesting turtle as a primary cue for nest detection (Chapter 2), but other predators such as coatis (Nasua nasua and N. 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 marked increase at the end of incubation observed in studies of coati predation (Fowler 1979, Tiwari et al. 2006).

Foraging theory predicts that predators can increase foraging efficiency by tracking prey availability at fine spatial and temporal scales (Stephens 1987, Hall and Kramer 2008). Previous work at Bath documented an important increase in mongoose activity in nesting habitat as nest availability increased over the nesting season in 2005, predicting a corresponding increase in predation risk (Chapter 3), and the current study supports this prediction. Other studies have documented seasonal shifts in predator activity at nesting beaches (Engeman et al. 2003, Maros et al. 2003), and tracking of nest abundance by predators is probably a widespread phenomenon. 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 (Chapter 2, Stancyk 1982, Nellis and Small 1983). Although learning effects could not be distinguished from changes in predator activity in this study, future work examining the relative importance of predator learning is warranted. In particular, if increasing predation risk over time is results from individual predators becoming specialized, predator control might be used strategically to remove problem animals from the population (Nellis and Small 1983, Engeman et al. 2003). However, a recent study on effects of raccoon removal showed that even intensive trapping did not produce the expected long-term reduction in predation risk once predator control was terminated (Engeman et al. 2006), and effective application of this approach has yet to be demonstrated.

Beach vegetation drives spatial patterns of predation risk

Landscape structure can have important effects on species interactions (Fagan et al. 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 and Janzen 2002, Chapter 1). Consistent with previous work showing fine-scale variation in predation across the vegetation-
open beach edge (Chapter 1), we found that nests in vegetated habitat had < 50% chance of surviving to hatch (Figure 2a) and that predation occurred nearly exclusively in or very near patches of beach vegetation. The overall proportion of nests preyed on annually by mongooses at our site (27%), roughly matched the availability of vegetated nesting habitat at the beach scale (~40%). Where introduced mongooses are present at sea turtle nesting beaches, the proportion of nesting habitat that is vegetated may provide therefore a useful general index of overall predation risk. However, avoidance of the open beach by mongooses in our study appears to be driven by the presence of humans that are viewed as a predatory threat (Chapter 3) and nests in open areas may therefore to be at 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 and 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. Mongoose activity is generally high in vegetated habitat (Chapter 3),
and it is likely that rapid predation of most available nests in vegetation over-rides
effects of local density. Mongooses rarely venture onto the open beach, however,
and foraging individuals may be more willing to risk exposure in open areas
where nests density is consistently high and nests have been discovered
previously. Although the best model selected by AICc included density effects, the
second best model without density effects explained roughly the same proportion
of the variation and performed slightly better in classification (Table 1). Given the
complexities involved with measuring and interpreting density effects, we suggest
that the more parsimonious model lacking density effects is sufficient to provide
robust estimation of predation risk for practical application.

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 and 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 prior to the peak of nesting and again later in the season when
total nest abundance is highest may be effective. If, as in our study, risk is 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 and Warren
1998, Barton and Roth 2008), reducing predator access to certain section of the
beach (i.e. through strategic fencing or removal of vegetated corridors), reducing vegetation height to make it poor refuge habitat (Chapter 3, Leighton, unpublished data), or increasing human activity in high-risk nesting areas (Chapter 3, Talbert et al. 1980) 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 et al. 2004). Risk models are particularly useful in identifying which nests should be moved or protected, and specifically targeting nests at high risk of predation could significantly increase the cost-effectiveness of such procedures. Our study suggests that the first days following oviposition are critical for nest survival and that nest protection efforts should ideally target freshly laid nests. Methods that afford 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 by allowing nests to survive the short initial 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 relocating at-risk or partially preyed on nests to non-vegetated areas of the beach is an effective strategy at our site.

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 intense speculation by sea turtle biologists for decades (Stancyk 1982, Nellis and 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 provides a new approach by investigating how age-specific risk factors affect daily predation risk throughout development, and what the impact of these factors is on the overall probability of nest success (Nur et al. 2004)? An experimental approach is ideal for isolating and exploring 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 (Chapters 1 & 2) and freshwater turtles (Hamilton et al. 2002, Marchand and Litvaitis 2004, Rollinson and Brooks 2007), and combined with survival analysis techniques, provide a promising approach for testing longstanding hypotheses about the mechanisms of sea turtle nest predation.

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LITERATURE CITED


Table 1. Models included in the 95% confidence set selected by Akaike’s Information Criterion adjusted for small sample sizes (AICc). The model Akaike weight, $w_i$, is the probability of being the best model in the set of all 24 models considered. Classification accuracy (Acc.) is the proportion of nests whose fate was accurately predicted by the model. AUC is the area under the curve of receiver operating characteristic plots for each classification. The following abbreviations are used for model terms: Hab = habitat type (vegetation vs. open beach), Dist = distance from vegetation edge (m), Date = date of nest initiation, and Dens = nest density (total nests laid over the season per m$^2$).

<table>
<thead>
<tr>
<th>Model Terms</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>$r^2$</th>
<th>AUC</th>
<th>Acc.</th>
<th>AUC</th>
<th>Acc.</th>
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<td>Hab + Dist + Date + Dens + Hab*Dens</td>
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<td>0.889</td>
<td>82.3%</td>
<td>0.918</td>
<td>84.9%</td>
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<td>84.9%</td>
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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). RI is a measure of the relative importance of each parameter, calculated as the sum of the Akaike weights of all models containing that parameter.

<table>
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<th>Parameter</th>
<th>Estimate</th>
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<th>RI</th>
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<td>0.27</td>
</tr>
<tr>
<td>Date X Density</td>
<td>-0.006</td>
<td>0.140</td>
<td>0.268 -0.280</td>
<td>0.17</td>
</tr>
</tbody>
</table>
**Figure 1.** The change in a) predation frequency (total predated nests) and b) daily predation risk (probability of predation over a 24h period) with age for nests in 2004-2005. Frequencies in a) are grouped in 5-day bins. Higher predation frequency in 2005 reflects the greater abundance of available nests ($n = 168$ in 2004, $n = 217$ in 2005). b) shows both empirical (dashed line) and kernel-smoothed (solid line) daily hazard functions for 2004-2005 combined.
Figure 2. Reduction in model 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.
Figure 3. Survival of hawksbill 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) oviposition date (curves are for the 15th day of each month) and c) and the interaction between habitat and nest density (high = 0.05 nests/m², low = 0.005 nests/m²).
A.

B.

C.
FINAL CONCLUSIONS

SYNTHESIS AND FUTURE DIRECTIONS

In my doctoral research, I set out to explore the interface between Behavioural Ecology and Conservation Biology by identifying behavioural processes underlying sea turtle nest predation by mongooses and using this insight to develop and improve methods for reducing predation risk for sea turtles.

I chose to focus my research on three main aspects of mongoose behavioural ecology: space use, foraging, and antipredator behaviour. I found that patterns of nest predation for sea turtles could be explained by several distinct mechanisms: edge response behaviour of both hawksbills and mongooses (Chapter 1); nest characteristics that affected cue availability and the cost of pursuit of buried prey (Chapter 2); mongoose antipredator behaviour in the form of avoidance of open microhabitats (Chapter 1) and of direct encounters with people (Chapter 3); and fine-scale tracking of nest abundance in time and space by predators (Chapters 3 and 4). Behaviour may also influence sea turtle nest predation in ways that I did not explicitly explore. I chose to use passive tracking to examine patterns of space use, since it provided a fine-grained view of population patterns of mongoose activity at multiple spatial scales. However, one disadvantage of this approach is that it does not distinguish the relative contribution of individual animals to overall predation risk. Individuals are likely to vary in space use, with important differences between males and females (Tomich 1969, Gorman 1979, Leighton unpublished data), and information on individual behaviour is essential for assessing the role of other potentially important behavioural processes such as learning (Nellis and Small 1983) or the frequency-dependent use of different foraging strategies to locate nests (Giraldeau and Caraco 2000). Such individual differences have the potential to create a non-linear relationship between mongoose density and predation risk and to alter the relative effectiveness of different predation reduction strategies.
Based on the behavioural processes investigated, I proposed a number of novel methods for reducing predation on sea turtle nests. Since mongoose rely on patches of beach vegetation for access to nests, altering vegetation height and spatial arrangement could decrease predation by reducing the suitability of vegetation as refuge habitat (Chapter 1). Creation of artificial disturbances similar to those left by nesting turtles could weaken the association between disturbance and buried food (Chapter 2). Increasing human activity in high-risk nesting areas and reducing the availability of other attractive food sources such as garbage could also help reduce local predator activity (Chapter 3). Short-term deterrents (i.e. hot pepper) or temporary protective devices could be used to protect nests for the first few days following oviposition where predation risk is highest (Chapter 4).

In addition, there are many ways that existing methods for predation reduction could be refined. In particular, the risk models presented throughout this thesis provide a promising set of tools for optimizing the timing and location of conservation interventions. The location of nests relative to vegetation and nest depth provide useful risk criteria that can be used to inform nest relocation and protection. Mongoose removals are likely to be most effective if removal efforts focus on areas of high mongoose activity and are timed with the period of highest overall nest vulnerability. Predator tracking has already been shown to be extremely useful in guiding predation reduction efforts (Engeman et al. 2003, Engeman et al. 2005), and could be combined with strategic deployment of artificial nests to refine spatial predictions of risk. Finally, artificially increasing nest concealment of fresh nests and avoiding nest manipulations that increase the availability of surface cues for detection of nests by mongooses are precautions that could be emphasized in protocols for routine sea turtle nest monitoring programs (Schroeder and Murphy 1999). Although many of these ideas have intuitive appeal, an important step before widespread application will be the careful validation of these methods in the field to assess their effectiveness and to identify potential adverse consequences (Ratnaswamy et al. 1997, Irwin et al. 2004).
More generally, my doctoral research has pointed to a number of promising avenues for future work. Chapter 1 outlined a general framework for using edge responses to predict species interactions. Such edge effects on species abundance are often treated as a static property of a population in a given landscape context (Ewers and Didham 2006a), but in reality the magnitude and extent of edge responses are likely to vary greatly over time with predictable effects on species interactions. A good theoretical framework exists for parametric modelling of edge response shape (Ewers and Didham 2006b), and a dynamic view of edge responses could be especially important for modelling species interactions where both predators and prey are motile. Chapter 2 raised the possibility that if habitat and depth affect incubation temperature, habitat selection by predators and higher vulnerability of shallow nests are likely to influence hatchling sex ratio in predictable ways. Since nest predation is widespread and frequently severe, such impacts may be substantial and could be usefully explored through a combination of field studies and modeling. Finally, it would be useful to explore the extent to which the processes that I identified while working on a single beach can be extrapolated to predict variation in predation among beaches. Chapter 3 suggests that the spatial pattern of predation could be markedly different at beaches with very high or very low human activity and that cultural transmission of learned nest-raiding behaviour could also lead to very different levels of predation among sites (Chapter 2, Nellis and Small 1983). Logistical and budgetary constraints generally limit the number of beaches that can be visited regularly by conservation teams, so predicting where to look for nest predation could help focus predation reduction efforts on areas where they will have the most impact.

LINKING BEHAVIOURAL ECOLOGY AND CONSERVATION

addresses both the interests of academic behavioural ecologists and the needs of the community of conservation practitioners has many challenges. Scientific rigour often requires sophisticated statistical methods and the resulting models may be complex and intractable to many conservation practitioners. This can be eased to a great extent by careful study design and selection of appropriate variables with clear applied relevance. Effective communication of conservation-relevant research outcomes to conservation managers is another practical challenge. Scientific publications are not an ideal channel for such communication since discipline-specific jargon can limit their accessibility and they may never be read by managers (Caro 2007).

In addition, even once such communication barriers are overcome there are many practical challenges to the implementation of behaviour-based conservation strategies in the field. Perhaps the greatest challenge is the direct and increasing pressure placed by human society on fragile ecosystems. Even if the behavioural mechanisms linking introduced predators and mortality of endangered endemic species are understood, in many cases this knowledge will have little applied relevance in the face of overwhelming anthropogenic effects such as the degradation of critical habitats or direct exploitation of threatened populations. Indeed, in many sea turtle nesting areas in the Caribbean human exploitation of sea turtle populations is commonplace, with adults actively harvested for meat and nearly all available eggs collected for human consumption (Leighton, unpublished survey data). In such areas, non-human predators may be present but understanding their behavioural ecology contributes little to alleviating the most immediate threats to sea turtle survival.

The potential contributions of Behavioural Ecology to addressing the global biodiversity crisis must therefore be considered within a wider context, where developing an optimal management strategy for a given species or ecosystem requires the integration of biological knowledge with insights from sociology, political science and economics. Behavioural ecology can be integral to developing management strategies for ensuring the long-term persistence of a species within a community or ecosystem, but the implementation of such
strategies may not be possible until changes in human attitudes and associated destructive behaviours remove the most immediate threats to population persistence. Education is a powerful tool for catalyzing changes in human behaviour, and has been recognized as a key component in many conservation programs (Brewer, 2002). In Barbados, aggressive education campaigns by the Barbados Sea Turtle Project, aimed at raising awareness about the threats to hawksbill sea turtles and the role of this species in the coral reef ecosystem, have helped shift public perception of this species from a commercially valuable commodity to its current status as a protected species and a source of national pride. Similarly, beyond direct application of research findings to alter adult mortality or juvenile recruitment, field research can have strong indirect benefits for conservation by raising public awareness about important ecological processes that may be poorly understood. My personal experience has been that carrying out research on a sea turtle nesting beach has a catalytic effect on social engagement: research activities inspire curiosity and public interest, and involving the public in research activities such as beach monitoring or the release of hatchling turtles provides a combination of education and direct contact with nature that can go a long way toward transforming an attitude of exploitation to one of stewardship.

In conclusion, despite the challenges of aligning research objectives among fields and implementing conservation solutions drawn from behavioural research within the broader socio-political landscape, I remain convinced that the integration of Behavioural Ecology and Conservation Biology is both possible and desirable, and others share this view (Blumstein and Fernandez-Juricic, 2004; Buchholz, 2007; Caro, 2007; Linklater, 2004). In particular, Behavioural Ecology has an important role to play in conservation planning, providing a unique mechanistic understanding of the biology underlying conservation issues and the necessary framework for developing novel and cost-effective management approaches.
LITERATURE CITED


