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# Depredation of Diamondback Terrapin (Malaclemys terrapin) Nests in North Inlet, SC: Nest Predator Community and the Cues Used by Raccoons to Locate Nests

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# DEPREDATION OF DIAMONDBACK TERRAPIN (*MALACLEMYS TERRAPIN*) NESTS IN NORTH INLET, SC: NEST PREDATOR COMMUNITY AND THE CUES USED BY RACCOONS TO LOCATE NESTS

By

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Submitted in partial fulfillment of the
requirements for the degree of Master of Science
in Coastal Marine and Wetland Studies in the
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I dedicate this thesis to my family: my wife Marcy Buzuleciu, my parents Sam and Carol Buzuleciu, my sisters Lyn and Amanda Buzuleciu, and my grandparents Charlie and Larona Warren. This endeavor would not have been possible without the love, encouragement and support of my family.

# PREFACE

This thesis comprises four chapters: the first provides an introduction and framework for the importance of this study; the second chapter describes the process of creating and testing a predator exclusion cage for protection of simulated diamondback terrapin nests; the third chapter explains efforts identifying the diamondback terrapin nest predator community in North Inlet, SC, and details experiments designed to discover the cue(s) used by raccoons to locate terrapin nests; and the last chapter discusses implications of this study and suggestions for future research.

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# ABSTRACT

Predation on diamondback terrapin eggs has been studied in several terrapin populations across their broad geographic range; however, nest predators have not been studied in South Carolina. Objectives of this project were two-fold: first, identify predators of diamondback terrapin eggs in North Inlet, SC; and second, determine the source of olfactory cue(s) used by raccoons to locate terrapin nests. Terrapin nest predators were identified using a combination of camera traps, visual surveys and trackboards. Raccoons were dominant nest predators and depredated 347 of 349 (combined natural and simulated) terrapin nests during the 2013 nesting season. We identified the source of the olfactory cue used by raccoons to locate nests through a series of experiments using simulated terrapin nests. Our results support the conclusion that foraging raccoons primarily utilize the scent of soil disinterred by nesting females, and not scent from the turtles themselves. Lastly, in our efforts to design scent cue experiments, we realized the need for an effective nest predator exclusion device. We conceived and tested a new design for predator exclusion cages that protected 70-100% of nests through three trials (n = 4, 8, 84).

# CHAPTER ONE. Introduction

For many predators, eggs may indeed be nature's perfect food. Oophagy (egg-eating) constitutes a distinctive predatory strategy in that targeted prey are non-motile, though often camouflaged or guarded. Additionally, egg availability is often seasonally dependent, so facultative egg predators develop prey-specific foraging strategies (Denoël and Demars 2008). Predators wait for nesting or spawning season before actively foraging for eggs; as a consequence, some egg-layers have evolved defensive strategies such as mass nesting to overwhelm predators and reduce egg depredation (Bustard 1976). For oviparous species of conservation concern, such as the diamondback terrapin (*Malaclemys terrapin*), a better understanding of predator-prey interactions (especially egg predation) is required to improve management and conservation efforts.

## *Ecology and sources of mortality in diamondback terrapin populations*

Diamondback terrapins are a relatively small (~200-700 g) turtle species endemic to brackish, estuarine environments of North America (Fitzsimmons and Greene 2001). Anthropogenic pressures give rise to the majority of threats facing diamondback terrapins: habitat loss (due to human development, sea-level rise, and climate change); road mortality; nesting habitat alteration; boat propellers; invasive non-native plants; pollution; commercial harvest; oil spills; and crab pot by-catch (Daniels et al. 1993;

Wood and Herlands 1997; Hoyle and Gibbons 2000; Butler et al. 2006). Diamondback terrapins are especially vulnerable to habitat loss because of their typically high site fidelity, low dispersal between sites, and site philopatry exhibited by nesting females (Roosenburg 1991; Fitzsimmons and Greene 2001). In the future, heavily developed coastlines will exacerbate habitat loss due to sea level rise by preventing any up-elevation movement of estuaries (Daniels et al. 1993). Also, reduction in habitat may push gravid females into developed areas where they are more likely to encounter roads and be killed by vehicles in their search for nesting sites (Wood and Herlands 1997). Crab pots are another substantial source of terrapin mortality, especially because crabs, as well as most crab baits, are natural prey items for diamondback terrapins (Hoyle and Gibbons 2000).

While the majority of threats to terrapins are driven by anthropogenic activities, terrapins also experience mortality due to predation on adults, juveniles, and eggs (Butler et al. 2006). Little is known about aquatic predators of adult terrapins (Cecala et al. 2009), however, alligators are uncommon in North Inlet/Winyah Bay (W. Beckett Hills pers. obs.) and the shark community is comprised largely of piscivores and benthic feeders (Abel et al. 2006). Moreover, terrapin mortality is inversely related to age; so while predation is a major threat to terrapins, the rate of predation on eggs and hatchlings is far higher than predation on adults (Seigel 1980; Feinburg and Burke 2003; Draud et al. 2004). While freshwater turtles generally have higher egg mortality than either terrestrial or marine turtles, several studies have shown that diamondback terrapins face nest losses due to predation at rates ranging from 87% and higher (Iverson 1991; Feinberg and Burke 2003; Butler et al. 2004; Munscher et al. 2012). By comparison, a study of 19 species of terrestrial and marine turtles showed mean mortality of eggs (from oviposition to hatching) from 44 to 57% (Iverson 1991). Consequently, the combined effects of multiple anthropogenic impacts as well as those from natural sources collectively can exacerbate population declines and increase the probability of local extirpation (Browne and Hecnar 2007). Because South Carolina terrapins have a diet comprised mostly of marsh periwinkles, *Littoraria irrorata* (nearly 80% by volume; Tucker et al. 1995), local extirpation of diamondback terrapin populations could have trophic cascade implications (Silliman and Bertness 2002). Removal of periwinkle consumers can decimate stands of *Spartina alterniflora* in less than one year, showing that top-down control can drive saltmarsh primary productivity (Tucker et al. 1995; Silliman and Bertness 2002).

### *Conservation status and current conservation concerns*

The current conservation status and recent population estimates show that diamondback terrapins are near-threatened and numbers are thought to be in decline throughout much of their range (Seigel and Gibbons 1994; Fitzsimmons and Greene 2001; Butler et al. 2006; IUCN 2014). State protection (threatened, endangered or “species of special concern”) is afforded to diamondback terrapins in 11 of the 16 states in their range (Hart and Lee 2007). Due to a lack of surveys, current state-wide terrapin populations are largely unknown or thought to be declining (Butler et al. 2006). While a few states report stable terrapin populations, historical evidence suggests terrapin populations never recovered from intense harvests of the late 19th and early 20th centuries

(Coker 1906; Cook 1989; Butler et al. 2006). Catch records of terrapins in Maryland document annual harvests in excess of 40000 kg in 1891 (Cook 1989), which would equal approximately 50000 female terrapins. Contrast that century-old, single-state, annual harvest with a recent nationwide estimate of the diamondback population numbering 100000 individuals (van Dijk 2011) and it seems likely that shifting baselines have altered perception of a population that is now a fraction of its historical numbers. Maryland's antebellum terrapin harvest was not sustainable and fell to 373 kg within 30 years despite high market prices (~$2.70/kg in 1920; Cook 1989).

The most serious threats to terrapin populations are crab pot by-catch, habitat loss, and predation (Mitro 2003; Butler et al. 2006). While analyses of minimum viable population size indicate terrapins may be able sustain populations with fewer than 200 breeding females, these analyses do not account for either detrimental effects of reduced genetic diversity or catastrophic stochastic events (Mitro 2003; Shoemaker et al. 2013). Turtles have a long life span and exhibit a type III survivorship curve (Pearl 1928; Iverson 1991), so high early life mortality can be sustainable. While preserving adults is critical for overall conservation of the species, pockets of healthy turtle populations (with demographics containing juveniles as well as breeding-age members of both sexes) should be maintained as reservoirs for repopulation (Shoemaker et al. 2013). Moreover, proactive protection of nesting sites may help mitigate negative impacts by egg predators on turtle population demographics (Standing et al. 2000). Because terrapin, like most turtles, are long lived, cumulative negative effects of high egg and juvenile mortality may require many years to become apparent in populations (Browne and Hecnar 2007; Shoemaker et al. 2013).

An emerging threat to terrapin populations has been their growing popularity in China as an exotic food item. In recent years, as many as 6000 diamondback terrapins are reported as legal exports each year with over 27% of those coming from the wild; illegal trade numbers are unknown (CITES 2013). With a US population of diamondback terrapins estimated at 100,000, a yearly export of thousands of terrapins is a considerable threat (van Dijk 2011; CITES 2013). In May 2013, the diamondback terrapin was placed under review for protection under the Convention on International Trade of Endangered Species (CITES) for the aforementioned reasons (CITES 2013).

Another emerging threat for all reptile species with temperature dependent sex determination is the potential for long term reduction of either male or female individuals due to temperature induced skew of offspring sex ratios. For example, assuming no compensatory changes occur in gravid females with regard to nest site selection, an egg incubation temperature increase of 4° C could result in production of 100% female turtles (Jeyasuria et al. 1994; Roosenburg 1996).

Lastly, diamondback terrapins face a rising threat from a common terrapin nest predator: raccoons (Burger 1977; Roosenburg and Place 1994; Feinberg and Burke 2003; Butler et al. 2004). Raccoons are synanthropic, and like lice, pigeons, or rats, their populations flourish in proximity to human development. Ongoing urbanization is likely to result in a continued loss of nesting habitats for diamondback terrapins, while concurrently, raccoon populations are likely to increase (Roosenburg 1994; Prange and Gehrt 2004). Both estuarine and beach nesting turtles face a variety of risks from natural sources which are in turn amplified by anthropogenic impacts since both fewer nesting habitats and greater predation pressure are exacerbated by urbanization of coastal habitats (Roosenburg 1990; Klemens 2000).

### *Objectives and hypotheses*

First, we sought to characterize the as yet unidentified diamondback terrapin nest predator community in North Inlet, SC. Terrapin nest predators are known to vary considerably throughout the eastern and Gulf coasts, and organisms that depredate nests include a large host of animals as well as a few plant species (Burger 1977; Stegmann et al. 1988; Zimmerman 1992; Munscher et al. 2012). Among the potential predators on diamondback terrapin nests in North Inlet, we predicted that raccoons are the dominant nest predators. A second objective was to determine the olfactory cue(s) used by raccoons foraging for terrapin nests. To do so, we used simulated diamondback terrapin nests and a series of scent treatments to determine which scent(s) induce raccoons to engage in nest excavation. Because a major component of our experimental design necessitated temporary predator exclusion from simulated terrapin nests, we also sought to develop an effective, transportable, and low cost nest predator exclusion device which we then tested in several experimental trials.

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# CHAPTER TWO

## PREDATOR EXCLUSION CAGE FOR TURTLE NESTS: A NOVEL DESIGN

### Contribution of Authors and Co-Authors

Author: Samuel A. Buzuleciu II

Contributions: Developed and implemented experimental design. Conceived construction design for exclusion cages. Collected and analyzed data. Wrote first draft of the manuscript.

Co-Author: Megan E. Spencer

Contributions: Helped develop and implement experimental design. Helped modify construction design for exclusion cages. Helped collect data and provided feedback on early drafts of the manuscript.

Co-Author: Dr. Scott L. Parker

Contributions: Helped develop and implement experimental design. Provided advice on statistics as well as feedback on all drafts of the manuscript.

# Predator Exclusion Cage for Turtle Nests: A Novel Design

*Abstract*.—We describe and evaluate a novel nest predator exclusion device that has proven highly successful at preventing raccoons access to turtle eggs. Three exclusion devices (i.e. cages) were designed and deployed with the goal of denying raccoons access to turtle nests for 48 h. Over three trials, cage testing was conducted on 116 simulated diamondback terrapin nests (both baited and unbaited). The most successful design was a roughly conical cage constructed using wooden dowels for bars, a design later dubbed the "birdcage". The birdcage design is inexpensive, lightweight, and through three trials protected nests at rates of 100% (n = 4), 100% (n = 8), and 70% (n = 84). After further testing, this design may prove useful in aquatic turtle conservation, and also potentially in sea turtle conservation.

## INTRODUCTION

Predator exclusion is a straightforward and effective means of protecting vulnerable turtle nests from mammalian egg predators (Standing et al. 2000; Riley and Litzgus 2013). In contrast, predator removal by trapping, is time and labor intensive and can have unintended consequences that actually increase predation on turtle eggs. For instance, Barton and Roth (2008) observed elevated depredation rates of turtle nests because raccoon removal efforts caused release of a crab population (another nest predator) otherwise limited by predation pressure. Exclusion devices are useful for both experimentation (e.g. studies to elucidate cues used by predators foraging for turtle eggs; Buzuleciu and Parker in review) as well as conservation (e.g. mitigating effects of activities like camping, which may attract mesopredators and elevate predation pressure; Standing et al. 2000).

A wide range of freshwater and marine turtle species nest along ecological edge habitats which are often subject to elevated predation, especially from raccoons (Temple 1987; Ernst et al. 1994; Kolbe and Janzen 2002; Marchand et al. 2002; Strickland et al. 2010). Turtle nests may need as little as 48 hrs of predator exclusion to significantly increase survival probability (Burger 1977; Roosenburg 1992; Feinberg and Burke 2003; Butler et al. 2004). Therefore, temporary caging may be a viable method to protect turtle nests and also provides an alternative to predator removal, useful when predator removal is unethical (e.g. threatened or endangered predators), unpopular (e.g. charismatic or domestic predators) or costly.

Common exclusion devices used in protection of turtle nests include metal wire boxes and plastic mesh screens (NMSF and USFWS 2008; Kurz et al. 2011). These devices, however, may not be practical in some instances because of cost, difficulty deployment, or choice of materials (e.g. potential for metal to interfere with sea turtle navigation; Irwin et al. 2004). In the course of studying nest predators of diamondback terrapin (*Malaclemys terrapin*) eggs, we developed a new design for predator exclusion cages, with promising results for protection of turtle nests. Because raccoons are the dominant terrapin nest predators at our study site in North Inlet, SC, our predator exclusion devices were designed primarily to prevent raccoons from accessing terrapin nests. Effectiveness of alternative predator exclusion cages was tested for the purposes of a larger experiment in which simulated nests required 48 hrs of protection. Here we describe the results of an experiment testing efficacy of two novel predator exclusion cages compared to that of a predator exclusion design similar to that commonly used for excluding mammalian predators from turtle nests (NMSF and USFWS 2008; Kurz et al. 2011).

## MATERIALS AND METHODS

This study was conducted in Winyah Bay National Estuarine Research Reserve, part of the Belle Baruch Research Institute, Georgetown County, South Carolina (North Inlet estuary, 33.21° N, 79.11° W). Exclusion devices were tested in July 2013, in three documented diamondback terrapin nesting sites within the estuary.

Initially, three prototype exclusion devices were tested on simulated terrapin nests to evaluate their efficacy in excluding raccoons. Three exclusion devices were constructed: the first from metal ducting; the second design used plastic mesh; and the last design used wooden dowels. Diamondback terrapin nests in North Inlet average 11 cm in depth and are 3-8 cm in diameter with a narrow surface opening and a wider nest chamber (Buzuleciu and Parker in review). Cages were therefore designed to protect an area approximately three times the diameter of the widest part of nests to discourage predators from digging under the perimeter of the cage while attempting to access the nest.

The metal cage was created by making six, 7 cm vertical cuts on one end of galvanized steel ducting (1 mm thick sheet metal cylinder, 16 cm D x 25 cm L). The top of the cage was closed by folding down tabs of metal between cuts, forming a pinwheel design. This thin-walled, sharp-edged, inverted pail was then inserted 10 cm deep, into the sandy substrate surrounding nests.

The second cage design consisted of square panels of plastic mesh (25 cm x 25 cm, with <0.5 $cm^2$ grid) laid over the top of simulated nests, and held tightly to the surface of the ground with four, 8 cm long landscape staples (U-shaped round metal, 1 mm D). Small mesh was used since diamondback terrapin nests are much closer to the surface than sea turtle nests, for which larger mesh (e.g. construction fencing) forms an appropriate barrier (NMSF and USFWS 2008; Kurz et al. 2011).

Our third design used 12 wooden dowels (2 mm W x 600 mm L) pushed vertically into the ground to a depth of 15 cm and arranged in a circular pattern (~25 cm diameter) around a nest. A 25 × 25 cm square of galvanized steel hardware cloth (with 1 $cm^2$ grid) was laid directly over the nest and held to the ground by dowels as they were pushed through openings in the mesh. We found that starting with a slight upward concavity to the hardware cloth held it tighter to the ground once dowel tops were brought together; without this, the mesh was more easily lifted. Dowels were soaked in water overnight to allow enough flexibility to gather, cross and wrap the tops with fence wire. The finished cage design resembled the top of a birdcage or a tipi (Fig. 1).

To compare cage design efficacy we first created 16 simulated nests at a terrapin nesting site, all within an area of approximately 20 $m^2$. All nests were placed in microenvironments typically used by terrapin to construct nests in North Inlet, SC (i.e. sandy areas with low, salt tolerant vegetation). Nests were dug with a manual soil coring auger that extracted uniform cylinders 6 cm W and 10-12 cm in depth. Once nests were excavated they were immediately backfilled and tamped down using gloved hands (Strickland et al. 2010). In each test, researchers wore latex gloves and rubber boots to minimize transmission of human scent. Food rewards were deemed unnecessary (see Burke et al. 2005; Strickland et al. 2010) and indeed, our unprotected nests showed high rates of depredation throughout three experiments (see results section). In our first experiment, each cage design was used to cover four simulated terrapin nests. Four control nests were interspersed, simply excavated and refilled; they received no protection. All simulated nests were left for 48 hrs, then surveyed for predator-caused damage. Nests were considered depredated if predators dug more than 2 cm deep within 6 cm of the nest. Following success with the "birdcage" design, we conducted two additional trials using only the birdcage design.

In the second round of tests, canned mackerel was used to bait eight birdcages and eight control cages (dowels only, standing vertical, with an open top and no screen). Canned mackerel, placed at the surface, was used as a reward since mammalian predators have been shown to more vigorously (and more effectively) pursue highly desirable food items in simulated turtle nesting conditions, even when faced with exclusion cages (Kurz et al. 2011). Control cages were used to ensure that neither human scent nor dowels alone would be sufficient to deter predators. As before, the experiment site was approximately 20 $m^2$ and treatments were left for 48 hrs, then surveyed for damage by predators.

Following the above trials we deployed 84 smaller birdcages to protect simulated nests at three different nesting sites within the estuary. Smaller cages were used since this third trial was part of a larger experiment with a limited budget. These smaller cages were built with 10-12, 2 mm W × 300 mm L dowels, pushed 8-10 cm into the soil, creating an

~18 cm diameter cage. Two days after placement of our 84 caged nests, an additional 84 uncaged simulated nests were interspersed among caged nests. The two day intermission was a necessary element of our separate study testing whether age of nests affected depredation probability.

All three experimental trials took place between 11 July – 20 July 2013 during clear, dry weather and during active diamondback terrapin nesting in the estuary. Sites were monitored using trackboards and motion activated camera traps (Moultrie® Game Spy® M-880 Mini 8.0 Megapixel Digital Game Camera, Moultrie Feeders, AL, USA) to identify predators attempting to access simulated nests or bait. Trackboards were constructed using plywood sheets (approximately 6 mm thick and 60 cm W x 121 m L) coated with wet intertidal mud and smoothed with a trowel. Trackboards were placed in active animal movement corridors and recorded footprints over one night (10 h) following initial deployment. The day after deployment, tracks were photographed for identification. Details of imprinted tracks were sufficient to identify animals as small as rodents.

For each experiment, effect of cage type on frequency of nest predation was analyzed using a non-parametric Fisher exact test (with a Freeman-Halton extension for the 2×4 contingency table in the first experiment). Probability values less than 0.05 were considered significant. Statistical analyses were conducted using R, version 3.0.3.

## RESULTS

Overall, the birdcage design was more effective at protecting simulated nests than either metal or mesh cages (Table 1). Larger birdcages experienced no failures during both deployments (combining experiments one and two, n = 12). In our third experiment, smaller birdcage failure exposed nearly 30% of total nests (n = 84) to depredation while 84.5% of 84 unprotected nests were depredated two days later.

Experiment one: Two metal cages (50%) and four plastic mesh cages (100%) were defeated, and all control nests were disinterred (100%). However, all four birdcages successfully prevented predator access (0% failure). There was significant variation among treatments (Fisher's exact test, $P = 0.010$).

Experiment two: There was no apparent effect of materials used in construction of birdcage exclusion devices (i.e. dowels) or human scent on depredation rate. Depredation by treatment varied significantly with all eight open-top, baited, control cages depredated, whereas 100% of baited birdcage exclusion devices remained intact (Fisher's exact test, $P < 0.001$).

Experiment three: With smaller birdcages employed to protect simulated terrapin nests, nearly 30% of caged nests were depredated. These depredations resulted primarily from raccoons digging under the smaller diameter cages to access simulated nests. We also documented 23 cages (27%) with evidence of failed access attempts (e.g. aborted digs or broken dowels). Forty-eight hours after caged nest evaluation, uncaged nests experienced a depredation rate of 88% within 48 hrs following deployment. Depredation by treatment varied significantly for caged v. uncaged nests (Fisher's exact test, $P = 0.005$).

Throughout all three trials, all attempted cage breaches and defeated cages were the result of raccoons, as indicated by tracks, scat and digital images. While other documented nest predators were observed in the area during the terrapin nesting season, none were documented at our testing sites during cage evaluation experiments.

## DISCUSSION

Studies have shown that a high percentage of depredated diamondback terrapin nests (70-95%) are raided within 48 hrs of oviposition (Burger 1977; Roosenburg 1992; Feinberg and Burke 2003; Butler et al. 2004). Though nest depredation continues at lower rates until after hatching, we judged cage designs over the interval of the highest rate of nest depredation: the first 48 hrs. While the smaller birdcage experienced 30% failure rates over this interval, our larger birdcage design (made with both more and longer dowels) protected all enclosed nests (n = 12) for 48 hrs. Wooden dowels largely prevented raccoons from accessing the simulated nest chamber laterally and the hardware cloth prevented entry from directly above the nest. Pulling on dowels in an attempt to break into the cage simply causes stressed dowels to flex, while friction from the sandy substrate makes it difficult for predators to vertically extract the device. Budget constraints of the larger experiment necessitated use of a less expensive, and therefore, smaller cage. The reduction in both number and size of dowels, along with the associated loss of cage diameter and depth seemed to be the cause of observed elevated failure rates.

Plastic mesh was completely ineffective at excluding raccoons for 48 hrs. In contrast, plastic mesh is widely used as an exclusion device for sea turtle nests (NMSF and USFWS 2008; Kurz et al. 2012). There are several differences between the conditions in this study and past effort to protect sea turtle nests that may explain the higher than expected failure rates of our plastic mesh protected nests: (1) terrapin nests are relatively shallow nests and therefore easier to access; (2) a smaller area was covered by mesh, again related to the size of terrapin nests; and (3) we used smaller and more rigid mesh for our plastic screening, which may prove easier for raccoons to manipulate. Predator exclusion cages constructed using construction fencing, though frequently employed to protect sea turtle nests, can be defeated by mammalian predators at rates nearly equal to our small birdcage design (NMSF and USFWS 2008; Kurz et al. 2012).

The metal can cage was moderately (50%) effective at excluding raccoons for at least 48 hrs. Because it was designed exclusively for simulated nests, we were not concerned about potential negative effects that the metal construction material might have on shading of the nest, substrate moisture, or reflectivity and magnetic interference (Irwin et al. 2004; Riley and Litzgus 2013). A drawback of the can-cage was that friction from sand made both insertion and extraction difficult for researchers; this was apparently not so for raccoons, as defeated can cages were pulled up as opposed to pried open.

While results from recent research suggest no detriment to development of hatchlings protected by metal wire cages, long term effects of metal cages on sea turtle navigation are not yet resolved. (Riley and Litzgus 2013). Because the metal screen component of our birdcage design is secondary to the protection provided by the wooden dowels (i.e. screen is held taut and tight to the ground by dowels), the metal screen could be replaced with rigid plastic mesh before trials on sea turtle nests.

Although some traditional cage designs have a strong record of protection (e.g. 1:101 failure rate; Standing et al. 2000), these cages are prohibitively large (up to 1 m × 1 m wooden frame covered in metal hardware cloth) for use in remote settings. Moreover, the sheer size of the cages could deter gravid females approaching high density nesting beaches (Kurz et al. 2012). In contrast, components for as many as 28 birdcages (complete with dowels, tie wire and wire mesh) were carried unassembled in one large backpack or one 19 L bucket during our testing.

Our larger birdcage design is lightweight (~ 500 g), highly portable in pieces, reusable, of moderate cost (< $10/cage) and highly effective at deterring raccoons. For diamondback terrapins and other sand-nesting turtles, we would recommend trial use of our larger birdcage design as an alternative to more traditional plastic or metal mesh cages. Further tests should be undertaken using the birdcage design to determine its effectiveness at excluding other vertebrate predators on turtle eggs.

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TABLE 1: Comparison of predator exclusion cage design efficacy among alternative cage designs tested using simulated (baited and unbaited) diamondback terrapin nests.

| | Treatment | n (nests per treatment) | Number depredated | % depredated |
|---|---|---|---|---|
| Experiment 1 | Control (no protection) | 4 | 4 | 100 |
| | Metal | 4 | 2 | 50 |
| | Plastic | 4 | 4 | 100 |
| | Birdcage | 4 | 0 | 0 |
| Experiment 2 *baited | Control (open cage) | 8 | 8 | 100 |
| | Birdcage | 8 | 0 | 0 |
| Experiment 3 | Control (no cage) | 84 | 71 | 84.5 |
| | Birdcage | 84 | 25 | 29.8 |

FIGURE 1.—Predator exclusion cage designs: defeated plastic mesh with landscape staples pulled out and plastic folded back (top); nearly completed pinwheel top on metal can cage (middle); complete and baited birdcage design (bottom).

# CHAPTER THREE:

## SCENT OF DISINTERRED SOIL AS AN OLFACTORY CUE USED BY RACCOONS TO LOCATE NESTS OF DIAMONDBACK TERRAPIN (*MALACLEMYS TERRAPIN*)

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Contributions: Developed and implemented experimental design. Collected and analyzed data. Wrote first draft of the manuscript.

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# Scent of Disinterred Soil as an Olfactory Cue used by Raccoons to Locate Nests of Diamondback Terrapin (*Malaclemys terrapin*)

*Abstract*.—We studied depredation of diamondback terrapin (*Malaclemys terrapin*) nests in North Inlet, SC, by documenting nest predators as well as by determining the sensory cues used by raccoons (*Procyon lotor*) to locate terrapin nests. We used visual surveys and camera traps to monitor nesting sites and identify members of the local nest predator community. We conducted a series of experiments to determine whether raccoons use visual or olfactory cues to identify terrapin nests. We also determined which olfactory cues are important to raccoons foraging for terrapin eggs. Several potential nest predators were identified at terrapin nesting sites; however, raccoons were the dominant nest predators throughout the study area. We constructed simulated nests to determine which scent cues raccoons use to locate terrapin nests. Scent from disinterred soil resulted in four times higher predation rates compared to terrapin-scented simulated nests. Visual markers did not affect predation rates. Results indicate that scent associated with disinterred soil is the primary olfactory cue used by raccoons to identify locations of terrapin nests.

## INTRODUCTION

Depredation of eggs by terrestrial predators is a major source of mortality for aquatic turtles (Iverson 1991). High rates of depredation on turtle nests can result in poor juvenile recruitment and therefore negatively affect demographic structure of local populations (Congdon et al. 1993, 1994; Feinberg and Burke 2003; Browne and Hecnar

2007). Diamondback terrapins (*Malaclemys terrapin*) are near-threatened estuarine specialists endemic to coastal salt marshes of the eastern and southeastern United States (Ernst et al. 1994). Causes of terrapin population decline include habitat loss, crab pot mortality, commercial collection, as well as egg mortality from terrestrial vertebrate predators (Butler et al. 2006). In some diamondback terrapin populations for example, depredation rates of nests exceeds 90% (Feinberg and Burke 2003; Butler et al. 2004).

Raccoons are common predators on terrapin eggs over much of the terrapin's geographic range (Burger 1977; Roosenburg and Place 1994; Feinberg and Burke 2003; Butler et al. 2004). Raccoons exploit human-altered habitats and consequently, increases in raccoon populations are often associated with human development (Prange and Gehrt 2004). Because of widespread development in coastal areas, terrapin nesting habitats, even in conservation easements, are often located in close proximity to human habitation where increased raccoon population density may result in elevated predation pressure (Feinberg and Burke 2003; Munscher et al. 2012). Nesting ecology of diamondback terrapin may make them particularly susceptible to nest predation because suitable nesting sites are often restricted in estuarine environments due to limited availability of open, sandy areas that are free from tidal inundation (Roosenburg 1994). Accordingly, nest density can be relatively high in suitable habitats (e.g. up to 0.269 nests/$m^2$, Feinberg and Burke 2003; 0.123 depredated nests/$m^2$, this study). Limited nesting areas and high nest density, combined with relatively large numbers of resident raccoons likely results in concentrated predation pressure on terrapin eggs (Munscher et al. 2012).

Raccoons are highly effective predators possessing good vision, exceptional tactile perception, and an excellent sense of smell (Zeveloff 2002). Accordingly, raccoons may use a variety of sensory modalities, alone, or in combination to identify turtle nests, including those of diamondback terrapin. For example, raccoons apparently use vision to locate nests of some turtle species such as snapping turtle (Holcomb and Carr 2013). Unlike terrapins, however, snapping turtles construct visually conspicuous nests characterized by rounded piles of soil (Woosley 2005; Holcomb and Carr 2013). In contrast, nesting female terrapin attempt to hide the location of nests by obliterating evidence of digging and disguising nest openings by spreading sand and surface debris over the nest entrance (Burger 1977). Moreover, experiments where visual markers were added to simulated terrapin nests did not affect depredation rates indicating that visual cues were apparently not used by raccoons searching for terrapin nests (Tuberville and Burke 1994; Burke et al. 2005; Strickland et al. 2010). Tactile perception is a critical component of raccoon foraging behavior with nearly two-thirds of their somatosensory cortex dedicated to processing tactile information received from their forepaws (Welker and Seidenstein 1959; Welker et al. 1964). Tactile searching, however, would likely not be an efficient primary method for locating small (roughly 6 cm diameter), nests dispersed throughout nesting habitats comprised of potentially hundreds of square meters in area (Burger 1977; Feinberg and Burke 2003; Munscher et al. 2012). Finally, several studies on both ground nesting birds and turtles indicate that raccoons rely heavily on olfaction to locate nests with eggs (Wilhoft et al. 1979; Congdon et al. 1983; Whelan et al. 1994; Butler et al. 2004; Burke et al. 2005). Unlike tactile and visual sensory modalities, olfaction would appear to be an effective way for raccoons to search broad areas for terrapin nests. Collectively, these observations suggest that scent is the primary cue used by raccoons to locate terrapin nests.

Olfactory-searching predators foraging for turtle eggs must be able to follow discontinuous scent plumes to specific point sources (i.e. nests) scattered throughout the environment (Ache and Young 2005). While numerous studies have suggested possible scent cues used by raccoons to locate turtle nests, few have experimentally tested which specific olfactory cue or cues are used to identify and locate terrapin nests. For example, raccoons could potentially identify nest locations by scent of the nesting female, eggs themselves, or both (Congdon et al. 1983; Spencer 2002; Burke et al. 2005). Burke et al. (2005) suggested that in addition to scent of nesting females, soil surface disturbance and/or salt water may provide cues for predators to indicate presence of nests. While studying Painted Turtle nest predation, Strickland et al. (2010) also noted increased predation associated with surface soil disturbances. The experimental designs used by Burke et al. (2005), and Strickland et al. (2010), however, did not allow them to determine whether increased nest predation rates were due to visual or olfactory stimuli.

In addition to raccoons, several other animal species (e.g. ants, birds, armadillos and foxes) are also documented predators on diamondback terrapin eggs (Burger 1977, Zimmerman 1992; Butler et al. 2004). The impact of these predators on nests likely varies across the terrapin's broad geographic range (Burger 1977). For example, armadillos are predators on diamondback terrapin nests in Florida (Butler et al. 2004); whereas ants cause terrapin egg mortality in New Jersey (Burger 1977). To our knowledge no prior studies have documented the suite of predators on diamondback terrapin eggs in South Carolina.

The purpose of this study was twofold. Our first objective was to document types of terrapin nest predators in North Inlet, South Carolina, USA. Our second objective was to determine sensory cues used by raccoons to locate terrapin nests. To accomplish these goals, we monitored terrapin nesting activity throughout the spring and summer nesting season and identified terrapin nest predators using camera traps, visual site surveys and trackboard surveys. To determine how raccoons locate terrapin nests, we conducted a series of experiments using simulated nests to determine which sensory cues are used by raccoons to identify locations of terrapin nests. The first experiment tested the hypothesis that raccoons identify nest locations using scent left by the female during the process of nest construction. To our surprise, raccoons showed no preference for terrapin-scented simulated nests. We therefore conducted two additional experiments to identify sensory cues used by raccoons to locate terrapin nests.

## MATERIALS AND METHODS

*Study Area.*—The study was conducted at Winyah Bay National Estuarine Research Reserve, managed by the Belle Baruch Research Institute, Georgetown County, South Carolina (33.21° N, 79.11° W; Fig. 1). The site consists of approximately 7082 hectares of lowland forests and salt marsh habitat including extensive *Spartina* flats, tidal creeks and barrier islands.

*Site Selection and Descriptions.*—We conducted extensive site surveys within the study area and identified shared landscape characteristics associated with typical diamondback terrapin nesting sites. A geographic information system (GIS) was used to predict terrapin nesting sites based on a common set of habitat features. National

Wetlands Inventory (NWI) land use and orthorectified aerial photographs were compiled in ArcGIS (Esri 2010) following available digital data predicted to be associated with terrapin nesting (Fig. 2.; Cowardin et al. 1979). Based on this analysis, terrapin nesting sites in North Inlet are characterized by: (1) supra-tidal sand; (2) NWI class E2EM1 (consisting of emergent persistent wetlands); (3) saltmarsh flora (e.g. *Spartina patens* and *Juncus roemerianus*); and (4) proximate surface water (i.e., located within 100 m of nest sites). Using these criteria, we identified 13 potential nesting sites. From these, we chose three sites to include in our study based on the following constraints: (1) direct evidence of nesting; (2) site independence (i.e., > 200 m apart); and (3) accessibility for efficiency of equipment transport and monitoring.

The first site was located on a near-shore island (hereafter referred to as island site) approximately 40 m x 45 m surrounded by high salt marsh (dominated by Pickleweed (*Salicornia virginica*) and Needlerush (*Juncus roemerianus*)). Elevations of high salt marsh lie above mean high water levels (i.e. flooded only during higher than average high tides or storms) whereas low salt marsh elevations lie between mean sea level and mean high tide and are typically dominated by *Spartina alternaflora* (Adam 1993). The second site (hereafter referred to as dike site) is a raised linear embankment (approximately 5 m W x 1.5 m H x 400 m L) with access to nearby low salt marsh via a 2–3 m W man-made canal. The third site is a linear berm (hereafter referred to as berm site); approximately 2 m W x 0.5 m H x 200 m L, surrounded by high salt marsh. The island and berm are both heavily vegetated by salt tolerant vegetation while the dike site is covered by patchy grasses and salt tolerant vegetation. All three sites have a sandy substrate. Residential developments are located within 100 m of the dike site.

*Nesting Activity and Documentation of Nest Predators.*—We searched the three study sites for evidence of terrapin nesting by walking transects approximately every 2–3 days (0600–2000) from 09 May to 30 July 2013. We conducted surveys 33 days out of the approximately 65-day nesting season observed in the North Inlet in 2013. All three sites were surveyed during nearly all survey days (31 of 33; island surveys were not conducted on two survey days), and surveys were conducted in the following sequence: island, berm, dike. The island site is a roughly circular area physically divided by a downed tree. The perimeter and a smaller circular path within the perimeter were walked on both halves of the island each survey day. Two linear transects along each edge of both dike and berm sites were walked each survey. During surveys, we searched the ground for terrapin tracks, evidence of nesting activity, scat and tracks from predators, eggshells and depredated nests. For each depredated nest, we recorded the number of eggshells, condition of shells (e.g. dry, wet, presence of fresh egg contents), evidence of predators (e.g. scat/tracks) and latitude and longitude of the nest site (< 3 m horizontal accuracy; Rino 650®, Garmin, Schaffhausen, Switzerland). Nesting sites were also passively monitored for nesting females and for presence of nest predators using motion activated cameras (Moultrie® Game Spy® M-880 Mini 8.0 Megapixel Digital Game Camera, Moultrie Feeders, AL, USA). Cameras were mounted approximately 0.5 m above the ground on trees or existing fence posts. Two to three cameras were used to monitor each site. We placed trackboards in active animal movement corridors located in areas adjacent to nesting sites and used tracks to identify potential predators at study sites. Trackboards were constructed using plywood sheets (approximately 60 cm W x 6 mm H x 121 m L) coated with wet intertidal mud and smoothed with a trowel. Trackboards recorded footprints over one night (10 h) following initial deployment. The day after deployment, tracks were photographed for identification. Details of imprinted tracks were sufficient to identify animals as small as rodents.

*Simulated Nest Experiments*.—We conducted three separate experiments during terrapin nesting season (approximately 24 May to 28 July 2013) using simulated terrapin nests and a series of treatments to determine the sensory cues used by predators to locate terrapin nests. Because rainfall may mask evidence of nesting turtles (Bowen and Janzen 2005; Strickland et al. 2010), all experiments were conducted under dry weather conditions.

The first experiment ran from 29 May–1 June 2013 and tested the hypotheses that: raccoons use the scent of female diamondback terrapin to locate nests; and rain dilutes chemical cues associated with nests, thus reducing ability of predators to locate nests. Forty simulated nests were constructed at each of the three study sites. Simulated nests were constructed using a soil coring auger that extracted uniform cylinders 6 cm w x 10–12 cm in depth (natural nests in North Inlet are typically 3–4 cm diameter at the surface and 5–8 cm in the nest chamber with a mean depth of 11 cm; Scott Parker pers. obs.). Simulated nests were allocated to three scent treatments: terrapin scent, neutral scent, and no-scent control. Native fill sand was obtained from each site and scent treatments applied within 30 min of excavating simulated nests. Terrapin scent was created by placing an adult female terrapin in a 38 L plastic container (half filled with damp native sand moistened with dechlorinated tap water) for 1 hour (Marchand et al. 2002). The neutral scent treatment consisted of 2 mL CVS Pharmacy-brand aftershave per 1 L of dechlorinated tap water (Whelan et al. 1994). Artificially scented water was chosen as the neutral scent because it presumably has no food associated odor and would therefore reveal preferential predation on terrapin scented nests. The no-scent treatment consisted of native sand dampened with dechlorinated water and no added scent. Each simulated nest was dug with the auger and filled within 30 min with damp sand from the appropriate treatment using gloved hands. Filled nests were gently tamped down by hand. No food rewards were placed in simulated nests. Although predators could potentially become habituated to simulated nests without eggs and therefore ignore them, we found no evidence of this in our experiments (see also Burke et al. 2005; Strickland 2010). Depending on treatments, high (~90%) depredation rates persisted in all three of our experimental trials across sites (see Results section). Finally, half of all simulated nests across treatments were irrigated with dechlorinated tap water to test whether rainfall masks olfactory cues. For the rain treatment, water was dispensed evenly over nests by inverting a 19 L bucket with a perforated lid until a rain gauge suspended above the simulated nest registered 2 cm of water. Two centimeters of water was deemed adequate since two previous turtle nesting studies had observed reduced nest depredation with rainfall >1.27 cm (Bowen and Janzen 2005; Strickland et al. 2010).

To vary the spatial distribution of treatments, nests were constructed at 3–4 elevations at, and above the high tide line (e.g. 0 m, 0.5 m, 1 m). The high tide line was established as a reference point for nest construction because terrapin typically do not construct nests below the mean high tide line (Scott Parker pers. obs.). Nest treatments were rotated through elevations using an “n + 1” system wherein treatments advanced one elevation after each placement (e.g. terrapin scent 0 m, neutral scent 0.5 m, control 1 m; terrapin 0.5 m, neutral 1 m, control 0 m; etc.). Because distribution of upland vegetation is associated with tidal height, our design controlled for the possibility that predators might simply follow a line of vegetation and preferentially exhume simulated nests at a given elevation. Additionally, adjacent nests were never placed closer than 1.5 m to one another. Because natural nest depredation typically occurs within 48 hours of oviposition (Burger 1977; Roosenburg 1992; Feinberg and Burke 2003; Butler et al. 2004), all experiments were monitored on the day following setup and again 48–72 hours after initial setup. Nests were considered depredated if predators dug more than 2 cm deep within a 6 cm radius of the nest. To minimize scent cross-contamination, each scent treatment and all associated gear was assigned to an individual research assistant for each experiment. To mitigate human scent contamination, latex gloves and rubber boots were worn throughout construction of simulated nest arrays.

The second experiment (15–17 June) tested the hypothesis that disinterred soil is the primary cue used by predators to identify terrapin nests. In this experiment, we used the same three scent cues but applied them to simulated nests without overturning soil, while in a fourth treatment, soil was removed from the simulated nest and replaced as before (i.e. experiment one) but with no added scent. Terrapin scent was created as before except that the female terrapin was placed in dechlorinated water only (no sand) for 1 hour. Neutral and no-scent treatments were also in dechlorinated water only, with neutral scent added in the same ratio as described previously. To inoculate soil with scent treatments, a 3 cm diameter, thin-walled steel pipe was inserted 11 cm into the substrate at each simulated nest site. The bottom 9 cm of pipe was perforated to allow scent-treated water (250 ml per nest) to seep into the substrate of the simulated nest. Scent treatments thus irrigated a column of sand similar in volume to that of a natural terrapin nest. Tightly fitting dowels were inserted into each pipe to hold soil cores in place while the pipe was extracted from the ground. Using this procedure, we were able to localize scent treatments into soil cores without excavation. Fourteen simulated nests per treatment were constructed at each of our sites (n = 56 nests per site).

The third experiment (16–20 July) tested the hypothesis that scent from freshly excavated soil is the olfactory cue used by raccoons to locate terrapin nests. We excavated 28 simulated nests at each site with the auger and refilled those nests within 10 min using the recently removed soil as described previously. Immediately following construction of simulated nests, raccoon exclusion cages (ca. 18 cm diameter) were placed over simulated nests. Cages were constructed by laying a square of wire mesh (20 cm by 20 cm with 1 cm sq. grid) over the opening of the simulated nest. Ten to twelve wooden dowels (2 mm W x 30 cm L; soaked in water overnight to make them pliable) were then pushed vertically through the wire mesh and approximately 8–10 cm into the soil, encircling the nest and pinning the mesh to the ground. Dowel tops, approximately 4 cm from the end, were gathered, twisted together, and held in place with a wrap of metal tie wire. The resulting exclusion cage thus resembled the top of a birdcage. Caged nests were left undisturbed in the field for 48 h. Caging freshly excavated nests for 48 h presumably allowed the majority of volatile soil compounds to evaporate prior to the start of the experiment. Fifty-nine cages (70%) were successful at excluding raccoons for 48 h, while 25 nests were excluded from the experiment following cage failure. After the 48 h interval, 28 additional, non-caged simulated nests per site were constructed using the auger, as previously described, and the soil core was replaced into the simulated nest within 10 min with no added scent treatment. Additionally, half of all simulated nests (caged and newly constructed) were flagged with marking tape tied to the top of a dowel (20 cm length) which was inserted into the center of the nest. Flagging was used to test whether raccoons use visual cues to identify nests. On the afternoon of the third day, immediately following completion of the excavated/refilled simulated nests, all cages were removed. Previously caged (now considered "aged") and freshly excavated/refilled nests were left overnight. Frequency of depredated simulated nests was recorded beginning the following morning.

*Statistical analyses*.—For each set of experiments, effect of scent treatment on frequency of nest predation was analyzed using chi-square tests of independence. Probability values less than 0.05 were considered significant. Statistical analyses were conducted using SPSS statistical software, version 20. Because there was no significant difference in frequency of predation as a function of treatment among the three field sites (Exp 1: $X^2 = 0.1$, df = 4, $P = 0.99$; Exp. 2: $X^2 = 0.3$, df = 6, $P = 0.99$; Exp. 3: $X^2 = 0.9$, df = 6, $P = 0.99$), data from the three replicate sites were pooled for all subsequent analysis.

## RESULTS

*Nesting Activity*.—We identified 89 natural terrapin nests, all depredated as evidenced by excavated nest chambers and eggshells scattered near the opening of the nest. All nest depredations were complete, with no intact eggs remaining. Four depredated nests were found on the island site, while the dike and berm had 36 and 49 depredated nests, respectively. The first depredated nests were observed on 24 May and the number of depredated nests increased during June, peaking around 9 June (Fig. 3) with a maximum of 5 depredated nests recorded over a one day interval. Frequency of nests declined during July and no new depredated nests were observed after 28 July. The eight day interval ending on 28 July produced the fewest depredated nests per day (0.25 nests/day) with only 2 depredated nests.

During 165 hours of searching we did not observe any gravid female terrapins engaged in nest construction. One lethargic female terrapin was observed under vegetation at approximately midday, at the berm site. After 30 minutes of observation, she was captured by hand and determined not to be gravid (assessed by palpation); a thorough search of the area failed to produce evidence of any new nest construction.

*Nest Predators*.—Using scat, tracks, photographs and direct observation we recorded six potential predators within our study sites: raccoon (*Procyon lotor*), bobcat (*Lynx rufus*), feral hog (*Sus scrofa*), red fox (*Vulpes vulpes*), black bear (*Ursus americanus*) and one unidentified rodent. Camera traps captured 461 images of animals visiting our three sites (Table 1). Female terrapin were identified in four images but only depredated nests were found near the image locations in subsequent surveys. Of all positively identified animals recorded with camera traps, four were potential predators (bobcat, red fox, feral hog and raccoon). Of these, raccoons were the most frequently observed predators, accounting for 96.8% of all predator images. In 87 of 89 depredated natural nests, we documented evidence of predation by raccoons, with the remaining two nests depredated by a likely different, but unknown predator. Soil from these two nests was strewn over a large area with excavated soil pushed aside in several low mounds. A badly degraded paw print (either a feline or large canine track) was observed near the two anomalous depredated nests. Moreover, two bobcats and one red fox were also photographed at this site (dike site) during nesting season. The anomalous excavations were likely not conducted by raccoons which typically dig neatly into the neck of the nest chamber and pile soil at the mouth of the nest.

*Simulated Nest Experiments*.—Overall, 260 simulated nests (of 452 total simulated nests) were disinterred during the three experiments. Based on tracks, scat, and photographs, all 260 excavations were likely conducted by raccoons. No evidence of depredation by any other type of predator was observed during the experimental monitoring periods.

Experiment I, scent treatments: Simulated rainfall had no effect on frequency of nest predation ($X^2 = 0.1$, df = 2, $P = 0.95$), therefore rain and no-rain treatment data were pooled across scent treatments for all analyses of depredation frequency. Average nest depredation frequency across treatments for rainfall-treated simulated nests was 76% ± 9.3 compared to 73% ± 7.3 in no-rainfall scent treatments (Table 2). There was no significant difference in predation among terrapin scent, neutral scent, and no-scent control treatments ($X^2 = 0.8$, df = 2, $P = 0.67$; Fig. 4A). Percentage of depredated nests ranged from 70% in the terrapin scented treatment to nearly 80% in both the neutral and no-scent control treatments.

Experiment II, scent versus freshly excavated soil treatments: Frequency of depredation differed significantly among terrapin, neutral, no-scent, and freshly excavated soil treatments ($X^2 = 56.4$, df = 3, $P < 0.001$; Fig. 4B). Overall depredation frequency of terrapin, neutral and no-scent control treatments ranged from approximately 19–26% compared to approximately 88% in the freshly excavated treatment (Table 2, Fig. 4B).

Experiment III, flagged versus unflagged simulated nests and freshly excavated versus aged excavation treatments: Marking nests with flagging had no effect on frequency of predation for either freshly excavated or aged simulated nests ($X^2 = 0.1$, df = 2, $P = 0.97$; $X^2 = 0.4$, df = 2, $P = 0.8$; respectively), therefore flagged and unflagged simulated nests were pooled across excavation treatments for all analyses of depredation frequency. In contrast, freshly excavated simulated nests had depredation rates approximately six times (85%) those of simulated nests protected for 48 h with predator exclusion cages (14%; $X^2 = 70.6$, df = 1, $P < 0.001$; Fig. 4C).

## DISCUSSION

*Nesting Activity*.—Nesting activity in North Inlet had a distinct beginning (22 May), an ending near 13 July, with peak nesting activity around the first half of June. There was no evidence of bimodal nesting as has been described in other populations (e.g. Hildebrand 1932; Seigel 1980; Roosenburg 1991; Feinberg and Burke 2003).

Although we searched carefully for nesting females, only a single female was observed engaged in nest construction (captured using camera trap) over the course of nesting season. The physical and vegetation characteristics of nesting areas in North Inlet may contribute to the difficulty locating nesting females. For example, nesting habitats in North Inlet are discontinuous (often separated by hundreds of meters), and tend to be covered by relatively dense growth of low vegetation, as opposed to open sandy dunes described in previous studies (e.g. Burger 1977; Auger and Giovannone 1979; Roosenburg 1992; Munscher et al. 2012). In absence of large, open, sandy nesting areas in North Inlet, tracking nesting females via crawls was not possible (Butler et al. 2004). Because we were unable to locate intact, natural terrapin nests, we do not know how many natural nests with eggs survive to hatching, or what characteristics (e.g. location, timing of oviposition) might contribute to successful egg survival.

*Nest Predators*.—Because diamondback terrapin have a large latitudinal range, nest predators vary with population locality (Burger 1977; Ernst et al. 1994). Throughout their range, however, raccoons are implicated as the principal nest predator in the majority of studies (Burger 1977; Feinberg and Burke 2003; Butler et al. 2004; Munscher et al. 2012). Our results support this general conclusion: out of 324 depredated nests (both natural and simulated), raccoons were likely responsible for predation events in all but two instances. In addition to raccoons, red foxes and bobcats were identified at terrapin nesting areas and therefore could also be responsible for predation on terrapin nests. Feral pigs were common in the study area but we do not have conclusive evidence that they specifically sought out terrapin eggs for consumption. Nonetheless, feral pigs can have substantial negative impact on terrapin nesting areas by destroying critical nesting habitat through rooting/foraging behavior (Samuel Buzuleciu pers. obs.).

*Simulated Nest Experiments*.—Our initial hypothesis that raccoons locate terrapin nests using olfactory cues associated with female terrapin was not supported. Simulated nests in the first experiment were depredated with nearly equal frequency independent of scent treatment (terrapin scent: 70%, neutral scent: 78%, no-scent control: 78%). Our methodology used in this first experiment was similar to Burke et al. (2005, see figure 1, treatments 1 v. 5) however, results of Burke et al. (2005) showed no significant difference in depredation of no-scent vs. terrapin scented simulated nests in 2003 but significant difference between the two treatments the following year (2004). Similarly, treatment of simulated nests with artificial rainfall had no effect on depredation frequency. Thus, 2 cm of rainfall does not appear sufficient to mask scent of terrapin nests from raccoons. Our results differed from two previous studies that documented decreased predation rates on turtle nests when rainfall exceeded 1.27 cm/day (Bowen and Janzen 2005; Strickland et al. 2010). Because our rain treatment was limited in spatial and temporal scale it does not mimic large scale effects that would occur during storms where precipitation covers a wide geographic area. Under natural conditions, rainfall may depress predator activity thus reducing foraging activity during rainy weather, if so; this may explain why the simulated rainfall treatment did not result in lower depredation rates in this study. Nonetheless, our results indicate that while raccoons likely use olfaction to locate terrapin nests, scent of the female terrapin is apparently not a primary olfactory cue.

Informed by results of our first experiment, where all scent treatments experienced high rates of predation, our second experiment tested the hypothesis that excavated soil is the primary cue used by raccoons to locate terrapin nests. The results of our second experiment supported this hypothesis. There were nearly four times the number of disinterred simulated nests in the excavated nest treatment (88%) compared to non-excavated nests treated with terrapin, neutral and no-scent (approximately 23% ± 2.1 for non-excavated treatments). While Burke et al. (2005) and Strickland et al. (2010) suspected surface soil disturbance as an important cue for predators foraging for turtle eggs, our experimental design allowed us to isolate sub-surface soil disturbance (i.e. excavation and not simply surface disturbance) as the cue used by raccoons foraging for terrapin nests in North Inlet. The proximate sensory cue however, could be olfactory, visual or tactile.

Our third hypothesis, that raccoons use scent of freshly excavated soil to locate terrapin nests, was also supported. Freshly constructed simulated nests were excavated at rates six times those observed in simulated nests covered by exclusion cages for 48 h. Caged nests presumably allowed the majority of volatile chemical compounds to diffuse out of the soil and therefore these simulated nests were less easily detected by foraging raccoons after the exclusion devices were removed. Additionally, placement of flags into simulated nests across treatments allowed us to determine whether raccoons also use visual cues to locate nests. Raccoons showed no preference for excavating simulated nests identified by visual markers. These observations are similar to previous studies conducted on mammalian predators of turtle nests in which flagging nests did not have a significant effect on predation frequency (Tuberville and Burke 1994; Burke et al. 2005;

Strickland et al. 2010). The fact that freshly constructed simulated nests experienced six times the predation rates when compared to previously caged nests, coupled with the lack of significant effect of visual markers on frequency of nest predation, suggests that scent associated with recently excavated soil is the primary olfactory cue used by raccoons to locate terrapin nests.

What compounds are released as a result of soil excavation during nest construction? Saltmarsh soils are rich in microorganisms including bacteria, protists, and fungi (Adam 1993; Perillo et al. 2009). These microorganisms produce a variety of volatile organic and inorganic compounds via metabolism that are readily released into the air when soil is disturbed through processes such as nest construction (Adam 1993; Perillo et al. 2009; Gribsholt et al. 2003). Common soil-borne compounds produced via metabolism of salt marsh soil microbes include a variety of sulfurous molecules (e.g. hydrogen sulfide and dimethyl sulfide) as well as geosmin ($C_{12}H_{22}O$, an aromatic bicyclic alcohol; Trowitzsch et al. 1981; Steudler and Peterson 1984; Perillo et al. 2009). Geosmin, in particular, is a ubiquitous soil compound which is largely responsible for the smell of freshly turned earth. Humans can detect the scent of geosmin in concentrations of as little as 5 parts per billion (Smith et al. 2002), and given the highly developed olfaction of raccoons, it is likely that they can detect geosmin at much smaller concentrations. The release of volatile soil compounds during terrapin nest construction may therefore serve as an olfactory beacon which alerts predators to nest locations. Raccoons inhabiting coastal salt marshes may be habituated to associate presence of soil-borne volatile chemicals as indicators of food because digging activities of crabs and other invertebrate prey would also likely cause release of these compounds (Johnson 1970; Gribsholt et al. 2003; Parsons et al. 2013).

The results of this study provide strong evidence that raccoons rely primarily on olfactory cues caused by freshly excavated soil to identify locations of terrapin nests. Once nests are located, however, raccoons may use tactile sensory information to identify the entrance of the nest then excavate the filled-in portion of the nest chamber to extract the eggs. In this study for example, the majority of nests were precisely excavated such that the original diameter of the entrance hole and depth of the simulated nests were maintained. Similarly, appearances of natural depredated nests suggest that they are excavated in similar fashion. These observations suggest that raccoons may detect differences in sand density (i.e. packed versus loose) and use this information to help direct their digging efforts towards the nest chamber. Indeed, detection of differences in sand density using a thin probe is one method used by researchers to pinpoint the location of turtle nests in the field (after Blake 1974). Likewise, raccoons use olfaction to detect the general location of eggs of ground nesting birds, then use forepaws to identify specific position of eggs within dense vegetation (Bowman and Harris, 1980). Because tactile perception is only effective inside a relatively limited area within reach of the animal, olfactory cues are likely the primary stimuli that direct raccoons to specific nest locations.

Assuming release of volatile chemicals from freshly constructed nests occurs over a relatively short time frame (which our data seem to suggest), nests which remain undetected for the first 24–48 h may have a substantially higher probability of survival to hatching (Congdon et at. 1983, 1987; Feinberg and Burke 2003; Butler et al. 2004). The results of this study are consistent with that of previous work demonstrating that the majority of nest predation occurs within 24–48 h of nest construction (Congdon et at. 1983, 1987; Feinberg and Burke 2003; Butler et al. 2004). Additionally, the probability of nests remaining undetected after oviposition may depend on stochastic events such as weather conditions which suppress predator activity or predator foraging success (Bowen and Janzen 2005; Strickland et al. 2010) as well as factors such as nest site selection by the gravid female (Burger 1977; Roosenburg 1994). Identification of predator-specific olfactory cues released from soil during nest construction and investigations to elucidate biotic and abiotic factors influencing probability of survival of eggs in nests are both productive and much needed directions for future studies.

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TABLE 1: Total number of predator and non-predator species observed using motion activated camera traps from 22 May to 28 July, 2013 at North Inlet, SC. Data are sums of individuals observed from all three nesting sites during this 68 day period.

| | Bobcat | Fox | Hog | Raccoon | Unknown | Non-predator species (Deer, turkey, rabbit, etc.) | Total |
|---|---|---|---|---|---|---|---|
| Number of Images | 4 | 1 | 1 | 182 | 11 | 262 | 461 |

TABLE 2: Frequency of depredation on simulated diamondback terrapin nests for the three experimental trials conducted: 29 May to 1 June, 2013, Experiment 1; 15 June to 17 June, 2013, Experiment 2; 16 July to 20 July, 2013, Experiment 3. Overall results of effect of scent treatment on nest depredation are shown in Figure 3.

| Treatment | | | Number of Simulated Nests | Depredated Nests | % Depredated |
|---|---|---|---|---|---|
| Exp. 1 | Terrapin | Simulated rainfall | 20 | 13 | 65 |
| | | No rain | 20 | 15 | 75 |
| | Neutral | Simulated rainfall | 20 | 14 | 70 |
| | | No rain | 20 | 17 | 85 |
| | No scent control | Simulated rainfall | 20 | 19 | 95 |
| | | No rain | 20 | 12 | 60 |
| Exp. 2 | Terrapin | | 42 | 10 | 24 |
| | Neutral | | 42 | 8 | 19 |
| | No scent control | | 42 | 11 | 26 |
| | Excavation | | 42 | 37 | 88 |
| Exp. 3 | Fresh | Flagged | 42 | 32 | 76 |
| | | Unflagged | 42 | 39 | 93 |
| | Aged | Flagged | 30 | 2 | 7 |
| | | Unflagged | 29 | 6 | 21 |

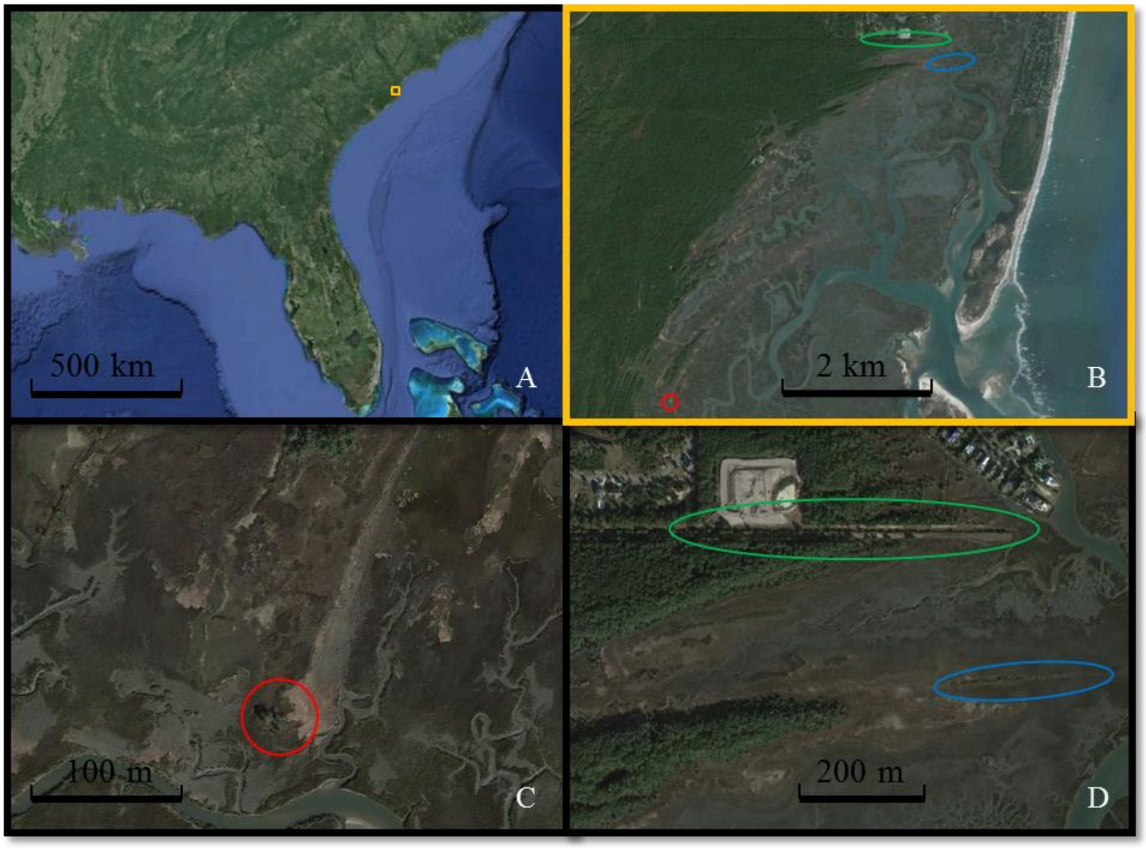

FIGURE 1.—Location of study sites in North Inlet, Georgetown County, South Carolina (A-D). Study sites, island (red circle), dike (green oblong), and berm (blue oblong) are located in sandy, dry, upland habitat (B).

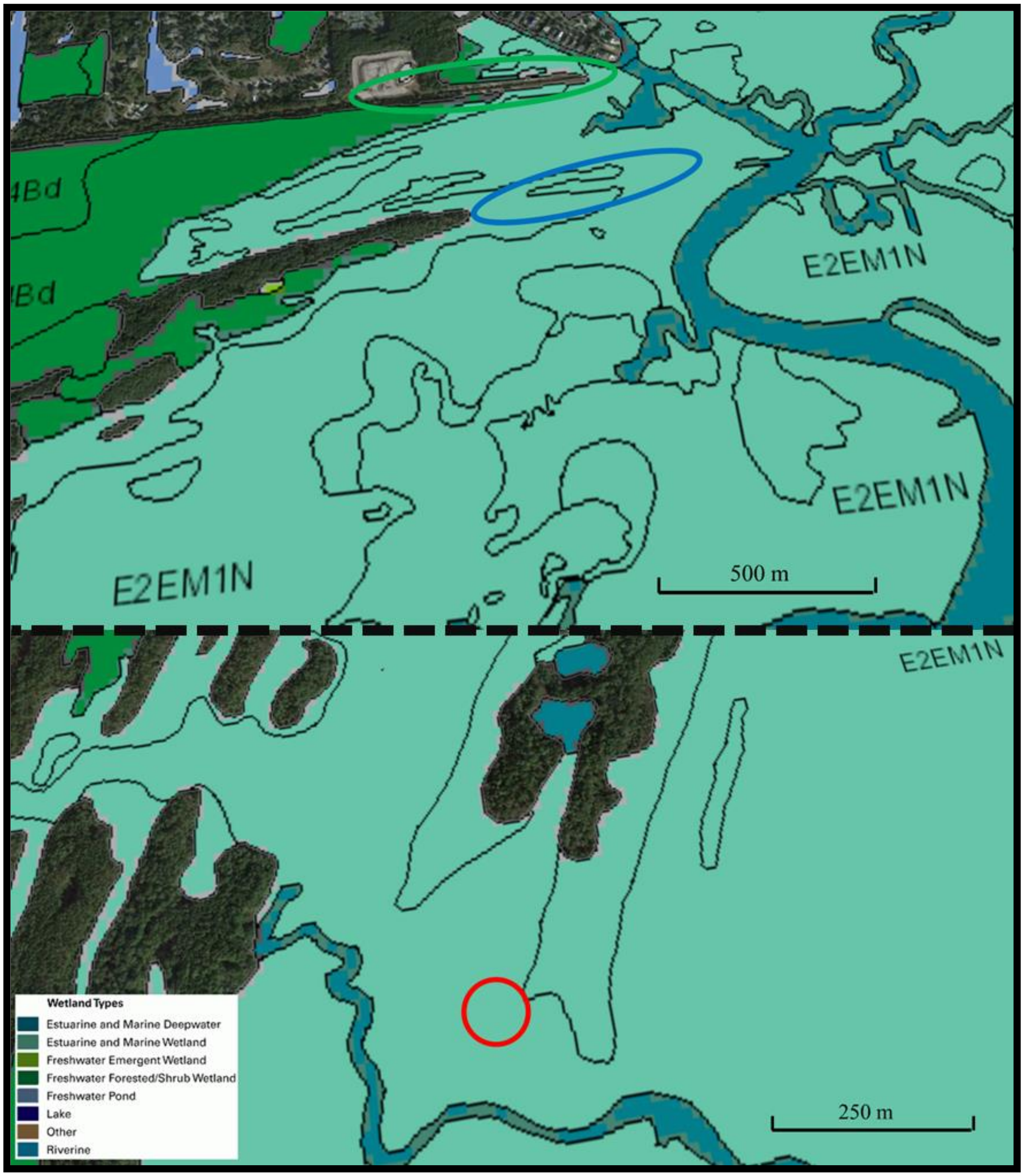

FIGURE 2.—National wetland inventory (NWI) classification of study sites in North Inlet, South Carolina: island (red circle), dike (green oblong), and berm (blue oblong).

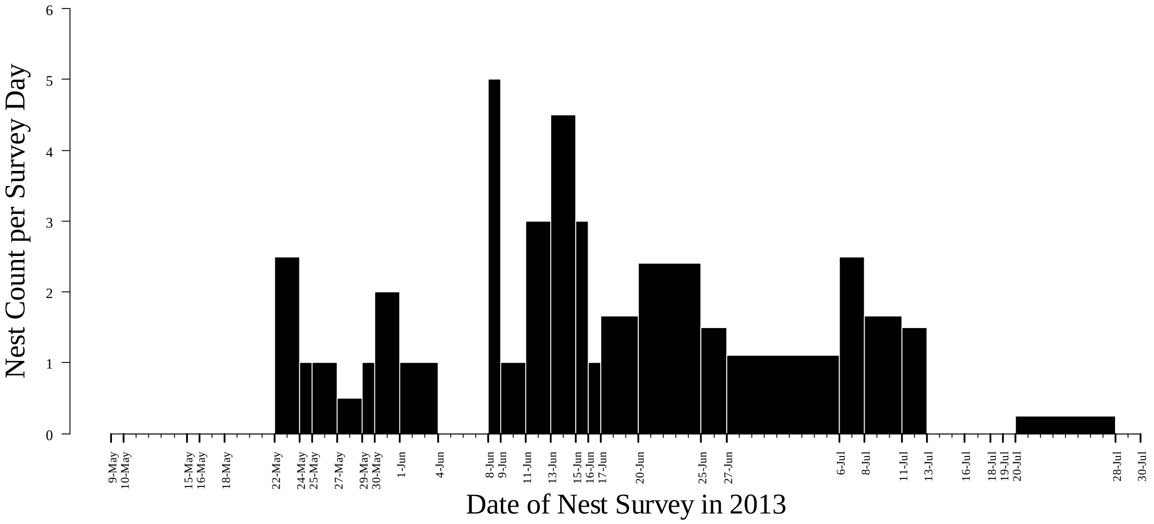

FIGURE 3.—Mean daily rate of nest depredation from 09 May to 30 June, 2013 (n = 89). X-axis represents survey days. Twelve survey days with no new depredated nests are included as indicated by bin values of zero. Bin width represents days between surveys while date to the right of each bar denotes date of completion for that survey period.

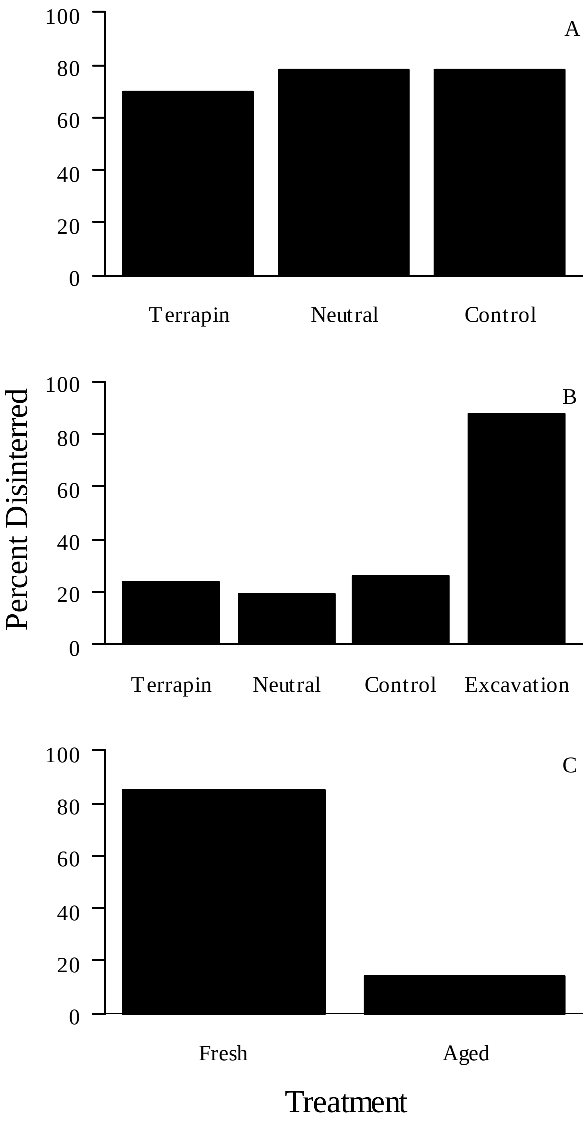

FIGURE 4.—Frequency of depredation of simulated diamondback terrapin nests treated with experimental scent, excavation, or aging treatments: A) Frequency of depredation on simulated nests treated with terrapin scent, neutral scent and no-scent control; B) Frequency of depredation on non-excavated simulated terrapin nests treated with either terrapin scent, neutral scent and no-scent control versus freshly excavated simulated nests; C) Frequency of depredation on freshly excavated/refilled simulated nests

compared to aged simulated nests (protected for 48 h with predator exclusion cages before start of experiment).

# CHAPTER FOUR: General Conclusions

*Summary*

Our research on diamondback terrapin nest predation had three major objectives: (1) develop an efficient nest predator exclusion device effective for diamondback terrapin as well as potentially other freshwater and marine turtle species; (2) characterize the diamondback terrapin nest predator community of North Inlet, SC; and (3) determine the olfactory cue used by raccoons to locate terrapin nests.

Summation of results for each objective (see also Fig. 1):

(1) Our design and implementation of a novel nest predator exclusion device was successful and met the needs of our greater experiment. Moreover, the new exclusion device could yet prove to have value beyond the scope of our experiment as a tool for conservation.

(2) Of 349 (combined natural and simulated) depredated nests, 347 had evidence indicating predation by raccoons. The remaining two nests were depredated by either a bobcat or a red fox.

(3) Lastly, raccoons rely primarily on olfaction to locate terrapin nests and the olfactory cue associated with terrapin eggs emanates from disinterred soil rather than the scent of female terrapin or eggs. After

locating a nest, raccoons seem to use tactile feedback to precisely excavate nest chambers.

While we identified the source of the olfactory cue, further studies will be required to identify the specific chemical compound(s) that raccoons follow when foraging for terrapin nests.

### *Future areas of research*

During the course of this study and others (Butler and Heinrich 2013), feral hogs have been observed foraging in terrapin nesting habitats. While we found no direct evidence of terrapin nest depredation by hogs, consumption of terrapin eggs seems likely, even if it is not targeted predation. Hogs have depredated sea turtle nests (Lewis et al. 1994) and they are a serious threat to fossorial herpetofauna (Jolley et al. 2010). Considering their foraging strategy of opportunistic rooting, hogs have almost surely consumed terrapin eggs and hatchlings in habitats dense with shallow terrapin nests. Still, future studies of nest predators will be required before we can define the impact, if any, of feral hogs and other potential predators observed in North Inlet, SC.

With diamondback terrapin nest depredation rates often observed around 90%, what are the factors enabling nest success? Studies have shown that higher nest density results in higher predation rates (Roosenburg 1992; Feinberg and Burke 2003). Therefore, it is possible that successful nests may be spatially isolated, which could indicate that maternal nest site selection is responsible for successful nests (Roosenburg 1992, 1994). For example, from 1987 to 1991, Roosenburg and Place (1994) monitored two neighboring nesting sites and reported very different results from the two sites. One site hosted lower density nesting and had depredation rates around 40%, while the other site (with dense nesting) had depredation rates around 80%.

As an alternative explanation for successful nests, Bowen and Janzen (2005) and Strickland et al. (2010) observed lower depredation rates correlated with heavy rain days; so, perhaps stochastic events explain successful nesting. While our simulated rainfall did not replicate these observations, we could not simulate large-scale natural rain which may keep predators under shelter instead of actively foraging. We did, however, experience a period of heavy rain from 4 June through 8 June, with nearly 11 cm of rainfall over 4 days and one 15 min interval recording 1.75 cm of rain (NOAA NERR CDMO 2014). This span correlated with zero observed depredated nests. A second span of heavy rain occurred from 27 June through 2 July as storms caused flooding and downed trees that limited site access for our team. North Inlet received over 10 cm of rain through 5 days, with one 15 min interval recording 1.47 cm of rainfall (NOAA NERR CDMO 2014). This span correlated with a low rate of depredated nests/day (as seen in chapter three, Fig. 3). This parallel of lower predation and heavy rain may support the earlier studies of Bowen and Janzen and Strickland et al., however, we could not quantify the number of intact nests deposited over these intervals as any cues would have been washed away. Also, terrapins prefer warm, clear days for nest construction (Burger and Montevecchi 1975; Seigel 1980). Therefore, these storms may have depressed predator foraging, or terrapin nesting, or both. In light of these observations, studies exploring the factors contributing to successful diamondback terrapin egg incubation may become part of an effective conservation management plan.

A third possibility exists which may explain terrapin population persistence under heavy nest depredation rates: These high depredation rates may be a relatively new phenomenon. The highest observed depredation rates (90% and up) have been from the most recent studies (Feinberg and Burke 2003; Butler et al. 2004; Munscher et al. 2012; this study 2013), and all of these studies have taken place within the past 17 years. Burger recorded depredation rates of 51% and 73% in 1973 and 1974 respectively (Burger 1977). Feinberg and Burke (2003) observed depredation rates exceeding 92% during their 1999 field season, 25-26 years later and less than 150 km from Burger's site. It is possible that coastal development pushed terrapin into more marginal nesting habitats, which could cause an increase in nest density as well as the positively correlated nest depredations rates (Roosenburg and Place 1994; Feinberg and Burke 2003). Additionally, other human actions have favored raccoon populations, such as removal of top predators (facilitating mesopredator release), and presentation of new food sources found in urban areas (Crooks and Soulé 1999; Prange and Gehrt 2004; Prugh 2009). With long-lived species like terrapins, coupled with a rapid increase in raccoon numbers, terrapin populations could be facing a new normal with higher than historic predation rates. Modern predation rates could be causing a shift toward an older terrapin demographic (Browne and Hecnar 2007). Turtles are long-lived and slow to mature, hatchlings are difficult to observe, and adults are most often encountered in surveys; combined, these factors could present the appearance of a healthy population demographic despite a reduction in recruitment going unnoticed, potentially for many years (Browne and Hecnar 2007). While current nest depredation rates may be sustainable, human activities have caused an increased number and intensity of threats to the nests of aquatic turtles through activities that support raccoon populations (Standing et al. 2000; Feinberg and Burke 2003; Browne and Hecnar 2007). Many coupled predator and prey populations have evolved a cyclic relationship of peaks and declines. However, human subsidized raccoon populations could be altering that balance with regard to predation of both turtle eggs and adults (Standing 2000; Browne and Hecnar 2007). Raccoons are neophilic, opportunistic predators that adapt well to human altered habitats and can easily learn to exploit new food sources (Prange and Gehrt 2004). Therefore, their populations may be independent of healthy prey populations from any one food source. Without knowledge of future impacts to the demographics of the diamondback terrapin, precaution and further study remain the best options to combat effects of human subsidized predators.

Another much needed area for future studies is whether or not soil-born compounds are commonly used by mammalian predators foraging for turtle eggs, and if so, which chemical compound, or compounds, function as the specific cue. After comparing their results to other, intra-guild turtle nest studies, Holcomb and Carr (2013) hypothesized that the amount of visibly disturbed soil seemed to indicate the likeliness that a nest would be depredated, with more disturbed soil associated with higher predation rates. Our results are consistent with their prediction. However, our results indicate that soil disturbance is an important, if not critical, olfactory (as opposed to visual) cue for raccoons attempting to locate terrapin nests. If soil is the source of the olfactory cue used by raccoons in multiple sites (yet to be determined), then the chemical responsible may be abundant. Geosmin, a ubiquitous soil molecule, appears to be a logical candidate for the specific chemical cue utilized by foraging raccoons. However, saltmarshes produce more dimethyl sulfide (DMS) than any ecosystem, and hydrogen sulfide ($H_2S$) is responsible for the pervasive rotten-egg smell of the salt marsh; any of these chemicals (along with a host of others) could be the specific cue signaling presence of a recently constructed terrapin nest (Steudler and Peterson 1984; Perillo et al. 2009). A suite of behavioral studies paired with gas chromatography–mass spectrometry (GC-MS) analysis would be required to identify the specific chemical(s) responsible; this investigation represents another avenue of much needed study.

While our study set a foundation for identifying the nest predator community on eggs of diamondback terrapins in North Inlet, SC, research on terrapin predators in the region is still minimal. Extensive nest predator studies have been conducted in Florida, New Jersey and New York, but many Gulf coast and mid-Atlantic terrapin nest predator communities have not yet been studied (Burger 1977; Feinberg and Burke 2003; Butler et al. 2004; Munscher et al. 2012).

Our nest predator exclusion device will require further testing but preliminary results are promising. Roosenburg (1992), Feinberg and Burke (2003), as well as Butler et al. (2004) found nest predation rates showed steep declines two days after nest construction. Therefore, temporary caging of nests using our exclusion design could prove an effective means of raising juvenile recruitment, particularly in populations of terrapins nesting in habitats where nests can be located by researchers shortly after nest construction (i.e. via crawls in sand, and absent thick vegetation; see Butler et al. 2004). Head-start programs have already been implemented keeping hatchlings temporarily maintained in captivity, allowing them to achieve a larger body size before releasing into the wild (Herlands et al. 2004). In addition to nest protection and head-start programs, future conservation efforts should emphasize mitigating human impacts on terrapin habitats, habitat rehabilitation, predator management, and restrictions on crab pots without turtle exclusion devices (TEDs). Effective conservation management will also require a serious consideration toward affording federal protection to diamondback terrapins. It is disconcerting that diamondback terrapins are protected in a majority of the states they inhabit and are now in review for international protection, yet they remain unprotected under federal regulations. A national population meta-analysis should be attempted to quantify diamondback terrapin populations to assess need for protection under the Endangered Species Act. Once completed, nest protection measures and knowledge of local nest predators will be essential tools in conservation and management of diamondback terrapins.

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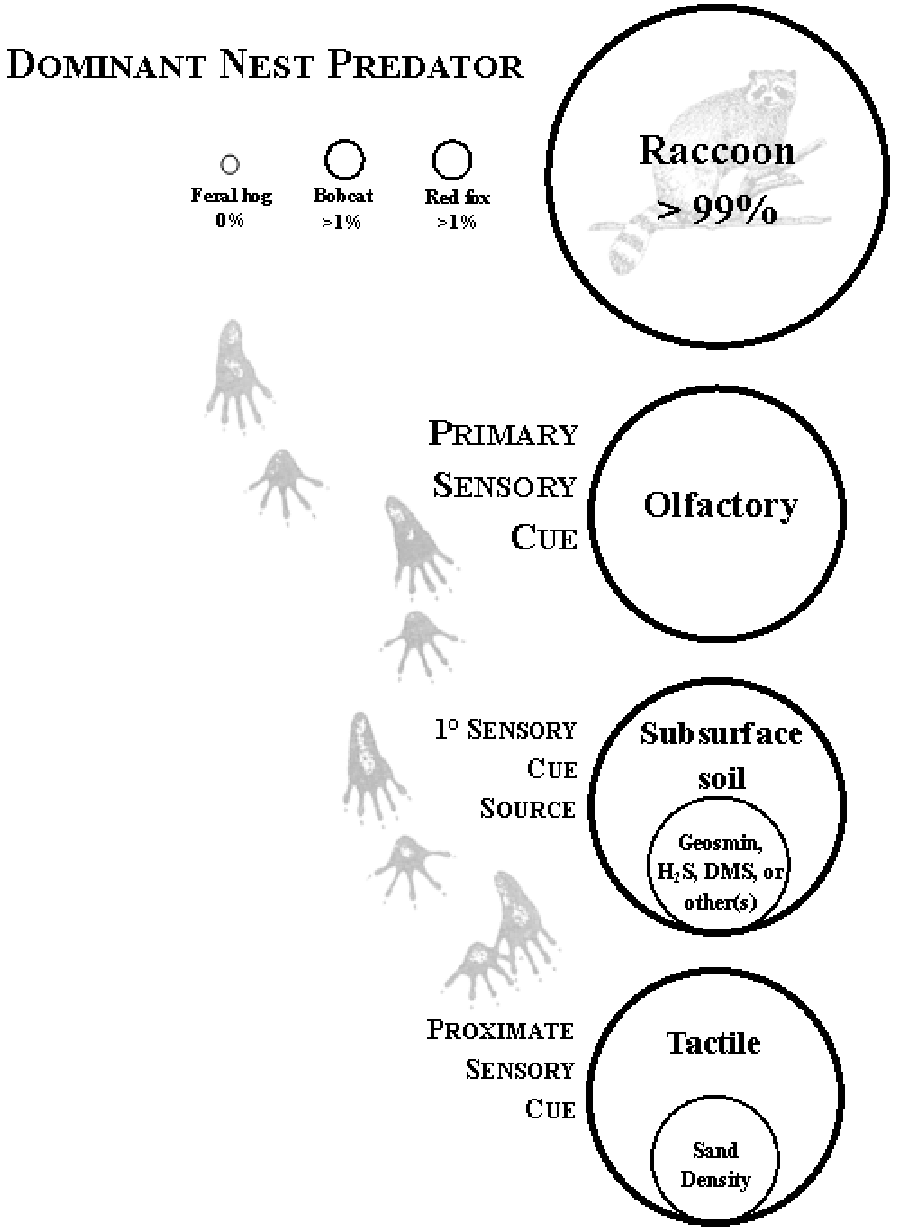

FIGURE 1.—Dominant nest predators (raccoons) and the cues they use to locate diamondback terrapin nests: (1) raccoons are the primary terrapin nest predator in North Inlet followed by likely predators: feral hogs, bobcats and red foxes; (2) raccoons utilize olfactory cues when foraging for terrapin nests; (3) the olfactory cue emanates from soil disinterred during nest construction, and the specific cue is a chemical compound found

in marsh soils, potentially geosmin, hydrogen sulfide or dimethyl sulfide; and (4) once a nest is located, raccoons likely use tactile perception of sand density to precisely excavate egg chambers.