Depredation of Painted Turtle (Chrysemys picta) nests: influence of biotic, abiotic

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Depredation of Painted Turtle (*Chrysemys picta*) nests: influence of biotic, abiotic and anthropogenic factors at local and habitat scales

by

Jeramie Troy Strickland

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Program of Study Committee:
Fredric Janzen, Major Professor
William Clark
Diane Debinski

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This thesis is dedicated to my parents Virdell B. Berry, James Booker, in loving memory of my grandparents Elizabeth and Silas Strickland, and my best friend Deantwan R. Williams, for all of their unconditional love, encouragement, and support from day one.
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CHAPTER 1. INTRODUCTION

The following introductory chapter briefly explains why predator-prey interactions are important, and then outlines some of the history and development of key predator-prey interaction models and theories. Next, I will provide a brief summary of how predator and prey populations affect each other and community interactions, and what influences the dynamics of these interactions. This is followed by a closer look at how biotic and abiotic factors can influence predator-prey systems, and the role that humans potentially play in contemporary systems. Next, I will highlight the value of turtle nest depredation as a model system for exploring complex predator-prey interactions, including a review of key literature on rates of nest depredation in populations of freshwater turtles. This chapter concludes with a closer look at the pressing needs in this research area, setting the stage for my upcoming data chapters.

Why are predator-prey interactions important?

Ecologically, predation involves more than just transferring nutrients and energy from one organism to the next (Smith et al., 2001). In sequence, predators must encounter, detect, identify, approach, and consume prey for predation to be successful. Predator-prey interactions and dynamics are important factors in the ecology of populations, particularly in terms of community structure and organization. For example, Gibbons (1990) found a decline in a population of Slider Turtles (*Trachemys scripta*) due to constant predation on younger turtles by alligators (*Alligator mississippiensis*). As a result, this particular turtle population had little juvenile recruitment. Furthermore, predation is an important force evolutionarily, because natural selection favors more evasive prey (e.g. characters of prey will be selected that increase its ability to avoid
being eaten) and more effective predators (e.g. predators evolve more efficient mechanisms for catching and eating its prey), leading to predator-prey arms races (Brodie and Brodie, 1999a; Brodie and Brodie, 1999b). Thus, predation can be a strong agent of natural selection (Boughey 1973; Purves et al., 2008).

Predation plays a huge role in mortality of almost all animal populations. Under certain circumstances, predators can significantly impact prey populations (Errington, 1946; Korpimaki and Krebs, 1996). For example, Gregoire (2008) found that the presence of fish predators negatively affected the survival and behavior of tadpoles. However, Errington (1943, 1946, 1963), in some of his seminal work examining the effects of predators on vertebrate populations, suggested that predators feed on the ‘surplus’ and have little impact on prey populations. The degree to which predators impact prey population dynamics may depend on circumstances such as precipitation (Bowen and Janzen, 2005), spatial and temporal dynamics via edge effects (Kolbe and Janzen, 2002; Temple, 1987), local habitat characteristics (Baber and Babbit, 2004; Kuehl and Clark, 2002), predator or prey abundance (Miller et al., 1996), or anthropogenic factors (Gibbs, 2002). The numbers of some predators may depend on the abundance of prey, and predation may be involved in the regulation of some prey populations (Begon et al., 1996). Predation is typically assumed to depend on predator-prey encounter rates, creating a frequency-dependence in predator-prey interactions. Thus, the responses of prey and predator populations are assumed to be proportional to the products of their respective population densities (Smith et al., 2001). Others argue that prey cycles are driven by predation (Korpimaki and Krebs, 1996). A classic example of a predator-prey cycle involves the snowshoe hare (Lepus americanus) and lynx (Lynx
lynx), in which cycles of growth and decline in each population were correlated, such that the snowshoe hare population declined as the predatory lynx population peaked (MacLuiich, 1937). Clearly, predation can potentially stabilize prey populations, or can result in unstable population fluctuations.

In response to the selective pressure of predation, animal prey species have evolved a wide range of anti-predation strategies including crypsis, intimidation, camouflage, warning coloration, mimicry, polymorphism, chemical defenses (Stiling, 1992; Smith et al., 2001; Stiling, 2002; Russell, 2005), and masking or synchronous behaviors (Tucker et al., 2008). Thus, prey defenses can potentially be a stabilizing factor in predator-prey interactions (Purves et al., 2008).

Real-life interactions between predators and their prey can comprise an even more complex system than has been modeled historically. It often involves direct and/or complex interactions between multiple species. Predator-prey interactions at one trophic level can influence predator-prey interactions at the next trophic level (Smith et al., 2001). For example, though blue jays typically prey on insects, they may in turn be prey for snakes, which may themselves be the prey of hawks. Another example in which predation has beneficial impacts on complex community structure and interactions is at Isle Royal National Park in Michigan. Previously, populations of large herbivores (moose) were overgrazing, which lead to widespread changes in species vegetation composition. Such habitat alteration resulted in nutrient-poor plants species competitively replacing preferred plants, which eventually lead to a significant reduction in the moose population due to starvation. The moose population exceeded the carrying capacity of its environment. Shortly afterwards, timber wolves (predators) migrated to
the area, helping to keep the moose population in check. More importantly, the habitat began to recover and regain its original character (Giesel, 1974).

**When did predator-prey interactions start gaining attention and why (development of predation theory and models)?**

Mathematical models of populations and predation are among the oldest and most commonly used in the field of ecology. The first predator-prey interaction model was proposed by A. J. Lotka, a physical scientist and mathematician. Shortly afterwards, A. Volterra, an Italian mathematician, independently developed a similar model in 1925 (Smith et al., 2001; Purves, 2008). These models, jointly referred to as the ‘Lotka-Volterra model,’ provide much of the basis for our understanding of predator-prey dynamics today. The Lotka-Volterra predation model assumes that as prey density increases, each predator will consume more prey (functional response) or the size of a predator population will change (numerical response) (Smith et al., 2001). One of the most common and widely accepted logic and mathematical theories suggest that when prey are abundant, their predators will increase in numbers, which in turn will cause the prey population to decline. After a while, the prey population will start to recover, and the cycle will start all over again.

In 1935, mathematician W. Bailey, and ecologist A. J. Nicholson, identified several limitations of the Lotka-Volterra model. They developed a model describing host-parasitoid relationships (Nicholson and Bailey, 1935). Predators differ from parasitoids in that their attacks remove the prey from the population, while parasitoids do not remove the host from the prey population (Smith et al., 2001). Certain features of the Nicholson and Bailey model allow an approximate estimate of prey in the next
generation, unlike the Lotka-Volterra models. Similarly, both the Lotka-Volterra and the Nicholson-Bailey models highlight the influence of predators on prey populations.

Nearly three decades later, Rosenzweig and MacArthur (1963) developed a series of graphic models that takes into account a broader range of predator-prey interactions. These models are commonly referred to as the ‘Rosenzweig-MacArthur model of a stable cycle of interaction’. This model is somewhat similar to the Lotka-Volterra model in that the prey have no refuge from the predator, and the growth rates of both prey and predator populations are a function of predator-prey encounter rates. However, the later version by Rosenzweig and MacArthur is an elaboration that integrates logistic self-limitation, and non-linearity in the density/consumption relationship.

**Impact of biotic and abiotic factors in predation events: environmental cues used by predators**

Biotic and abiotic factors can significantly influence predator-prey dynamics. Therefore interactions between biotic and abiotic factors may be of considerable interest in understanding predator-prey dynamics. Over time, predators have evolved a wide range of tactics for hunting prey and may alter predatory behavior plastically in response to immediate conditions. Predators could change their hunting tactics based on sensory, visual, or olfactory cues that are associated with the targeted prey species. These cues may be direct, such as habitat changes (e.g. vegetation shading or shade cover), which may make some mesopredators more vulnerable to being eaten by top predators. Visual cues are usually instantaneous and provide information about the presence of a prey item at a given point of time. In contrast, olfactory cues, which are particularly sensitive to meteorological factors (e.g. precipitation) and atmospheric conditions (e.g., turbulence, airflow, see Conover, 2007) indicate the current or recent presence of a prey item in a
given area. It is commonly assumed that mammalian predators search for prey using
olfaction, however, few experimental studies have been carried out to test this assumption
(Russell, 2005). Olfaction can play a prominent role in predator-prey interactions
involving mammals as the predator and their prey. In addition, predator sensory cues
involved in prey detection may be context-dependent. For example, some researchers
have documented that vision is perhaps the most important predatory sense for coyotes in
windless enclosures, while olfaction is more important than vision in enclosures that are
open to air movement (Wells, 1978; Wells and Lehner, 1978). Thus, both local and
habitat characteristics may influence predation, and examining predation under multiple
influences is rarely done.

**Anthropogenic effects on predation**

In addition to natural local and habitat effects on predation, anthropogenic factors
may influence predation and, hence, predator-prey dynamics. Humans can impact animal
populations in various ways, both directly (e.g. animals injured or killed by vehicles;
Steen and Gibbs 2004, Gibbs and Shriver, 2002; Aresco, 2005) and indirectly (e.g.
elevated predation risk near habitat edges; Temple, 1987; Kolbe and Janzen, 2002). The
ways in which humans and their activities affect biological communities can vary both
spatially and temporally. Habitats that are altered by anthropogenic activity and
structures could potentially form habitat edges, with enhanced depredation along habitat
edges (Temple, 1987; Kolbe and Janzen, 2002). For example, supplementing predators
with human-derived food can enhance population numbers of predators and,
subsequently, increase or decrease prey numbers (Vander Lee et al., 1999; Hamilton et
al., 2002; Cooper and Ginnett, 2000). Alternatively, elevated human activity can repel
predators and, thereby, provide a basis for increasing prey population size (e.g. white-tailed deer) (Cooper and Ginnett, 2000). Some have found that supplemental food can attract non-target species and predators including raccoons (Rollins, 1996; Cooper and Ginnett, 2000). Thus, prey near supplemental food sources could be at greatest risk of depredation. Despite the potential for anthropogenic structures to impact wildlife populations and communities, through such interactions, these indirect impacts have not been thoroughly investigated.

**Depredation of turtle nests**

Because turtles are components of communities, they serve as prey for other species. Nesting turtles and their nest predators are a great system to investigate some of the major predator-prey interaction issues mentioned above. Predation is the main cause of nest failure for most turtle populations (Congdon et al., 1983; Marchand et al., 2004). Understanding the factors that lead to variation in the numerical and functional response of important nest predators will advance our understanding of the effects of predation on nesting populations, and communities. In addition, understanding the components of predator-prey interactions is especially important for nesting turtle populations given the imperiled status of many turtle populations worldwide. Experimental studies can explore the roles of various biotic and abiotic factors in influencing probability of nest depredation. Because anthropogenic structures are often situated within turtle nesting habitats, we can compare rates of predation between nests that are laid closer vs. farther from anthropogenic structures. Modeling the point patterns of predated turtle nest locations will allow us to see if predation rates change with distance to anthropogenic
structures. Turtle nests and their predators provide a model system to further understand the direct and indirect effects of humans on turtle nest depredation.

The variation in recorded data and fluctuations about nest survival and predation rates of freshwater turtle nests, even among subspecies, suggests the need for further research to help better understand the causes of these differences. For example, some turtle populations (Trachemys scripta), can suffer nearly 100% nest depredation (Cagle, 1950), while other populations generally suffer only 15% nest depredation (Moll and Legler, 1971). Researchers, managers, and conservationists need to identify what is attracting predators to turtle nests (both directly and/or indirectly), which will help them design strategies to help reduce nest predation of imperiled turtle species. Reducing turtle nest predation can be very important, particularly in areas where turtle populations are declining due to little or no recruitment (e.g. Davis and Whiting, 1977; Hopkins et al., 1981; McMurtray, 1986; Ratnaswamy and Warren, 1997). Perhaps a better understanding of turtle predator-prey interactions will be valuable to researchers, conservationists, and managers whose goals are to help establish self-sustaining turtle populations. However, for such information to be useful, investigators must get a better grasp about what is attracting or deterring predators to turtle nests.

Factors affecting turtle nest survival are of special interest to researchers, managers, and conservationists, because turtle populations are declining world-wide (Behler, 1997; Gibbons et al., 2000). Rhodin (1999) investigated the severity of the turtle crisis on a global scale. He infers that of the then approximate 293 taxa of freshwater turtles, sea turtles, and tortoises, 3% are currently extinct in the wild. In addition, 4% are critically endangered, 11% are endangered, and 21% are vulnerable to becoming
endangered. As a result, researchers and conservation biologists are becoming more and more concerned about world-wide turtle population declines.

Predator search efficiency may be influenced by local or habitat factors. For example, local factors such as soil disturbance or turtle urine may attract raccoons, or coyote scent may deter raccoons for fear of predation by coyotes. Habitat features may alter predatory response to local cues by enhancing attractant cues or exaggerating aversion deterrents in habitats where predators are more vulnerable to higher-order predators (Kuehl and Clark, 2002; Gehrt and Clark, 2003).

Research examining the role of odor and olfactory cues in predator-prey interactions has become more popular over the last three decades (Russell, 2005). The co-evolutionary history of North America’s mammalian and reptilian fauna allows for an excellent opportunity to investigate the role of odor in helping predators detect prey. Olfactory cues can play an important role in many predator-prey processes. It is commonly assumed that mammalian predators use olfactory cues to help locate their prey (Russell, 2005). The underlying mechanisms that mammalian predators use to locate turtle nests are still unclear. To my knowledge, no study has simultaneously examined the impacts of habitat characteristics (shade cover; e.g., unshaded, moderately shaded, and unshaded habitats), attractants such as turtle urine, turtle egg mucus, soil disturbance, and deterrents such as coyote urine on the nest success of freshwater turtles. Very few studies have investigated how habitat profile influences nest predation and nesting success for turtles (Marchand, 2002; Marchand et al., 2004). A better understanding of the role of olfactory cues in raccoon (predator) and turtle (prey) interactions may lead to a great ability to protect some turtle populations that are declining from predators.
Anthropogenic factors may also play a role in raccoon detection and depredation of turtle nests. Turtle nests that are closer to anthropogenic structures that form habitat edges could attract more predators than nests that are farther away. In addition, some anthropogenic structures such as campsites, recreational vehicles, trash cans, and toilets can attract raccoons. As a result, nests that are closer to these anthropogenic structures could have a higher probability of being encountered by predators. Despite the potential for anthropogenic structures to impact wildlife populations and communities, through such interactions, these indirect impacts have not been thoroughly investigated.

Moreover, observational studies on natural nest depredation can complement experimental studies of nest depredation cues to increase our understanding of the specific cues predators use to locate turtles nests. Consequently, any change in predator foraging behavior (i.e. local cues used) and its relationship to distance from anthropogenic structures may result in decreased or increased nest survival (Vander Lee et al., 1999; Bowen and Janzen, 2005). Further studies are necessary to quantify the long-term effects of anthropogenic structures on the population dynamics of ground-nesting species and their nest predators. Enhanced survival and attraction of predators to supplemental food sources may affect sympatric species that are ecologically and evolutionarily valuable through competition and predation.

For the painted turtles (Chrysemys picta) that our lab has studied for over 20 years at the Thomson Causeway on the Mississippi River in northwest Illinois (Thomson, Illinois), nest predation percentage has fluctuated significantly, ranging from as low as ~20% in 1997 to as high as ~96% in 2005 (Figure 1). These fluctuations in nest success could result from changes in predator density or predator search efficiency (e.g., the
number of nests destroyed per predator). Raccoons (*Procyon lotor*) have been identified as the primary predator of painted turtle nests and hatchlings (Kolbe and Janzen, 2002). The locations of turtle nests on the local landscape could influence probability of depredation by raccoons due to differential habitat use by coyotes and humans. The Thomson Causeway contains a small road, camping areas, trash bins, a fish cleaning table, and toilet facilities that may contain supplemental resources that are easy for raccoons to detect. Thus, raccoons may be subject to both attraction to, and repulsion from, turtle nesting areas for different reasons. This field site, with its diversity of habitats, anthropogenic use, and frequency of turtle nesting, make it an excellent site to conduct experimental and observational studies of raccoon-turtle nest predator-prey dynamics. Such data are useful for integrating information about the ecological mechanisms responsible for patterns of nest depredation.

**Purpose and Structure of Thesis**

The primary purpose of this thesis is to:

- examine which local cues predators use to locate turtle nests
- determine if predation rates vary across different types of shading habitats
- examine the anthropogenic impacts of predation on turtle nests

This thesis contains a general introduction, followed by two stand-alone data chapters, each with their own abstract, introduction, methods, results, discussion, management implications, acknowledgements, and references, which will be submitted to scientific journals for publication. For this reason, there is some repetition of themes and background literature in each of the two data chapters. Chapter 2 of this thesis explores the role of local sensory cues, along with habitat characteristics (i.e. vegetation shading),
on turtle nest depredation with an experiment using simulated turtle nests. The goal is to
determine which cues predators use to locate turtle nests, and whether those cues vary
between different habitat types. Chapter 3 of this thesis presents an observational test of
the hypothesis that anthropogenic structures attract predators by examining whether
natural turtle nests located near anthropogenic structures have historically suffered higher
mortality. The final chapter of this thesis contains concluding remarks about each of the
studies and a general discussion of all results. In addition, this chapter examines the
broader implications of the results, along with where further research should be directed.
These chapters are then followed by an appendix, which include additional results
pertinent to the research presented in Chapters 2 and 3.

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Team for Southeast Region U.S. Fish and Wildlife Service, Atlanta, Georgia and National Marine Fisheries Service, Washington, DC.


Figure 1. Annual natural nest predation intensity as a function of number of nests laid across years (1995-2008) for the painted turtles (*Chrysemys picta*) at the Thomson Causeway on the Mississippi River in northwest Illinois (Thomson, Illinois)
CHAPTER 2. DEPREDATION OF PAINTED TURTLE NESTS EXAMINING POTENTIAL ATTRACTANTS AND DETERRENTS ON A HABITAT SCALE

By Jeramie T. Strickland¹, and Fredric J. Janzen²

A paper submitted to Journal of Wildlife Management

ABSTRACT

Understanding how predator attractants and deterrents, as well as habitat features, affect depredation of turtle nests is important because nest predators can influence the demographic structure of turtle populations. We investigated cues used by predators to locate turtle nests in three habitats (heavily shaded, moderately shaded, and unshaded). We constructed artificial turtle nests in areas used by nesting painted turtles (Chrysemys picta) and foraging predators, primarily raccoons (Procyon lotor). We also assessed the influence of olfactory cues on nest depredation using coyote and turtle urine, and turtle egg mucus. Overall, 22% of the simulated nests displayed evidence of depredation. Habitat type did not influence probability of nest depredation. Similarly, the presence of coyote and turtle urine, and turtle egg mucus, combined or individually, did not significantly alter depredation rates. Instead, predators seemed to locate simulated nests based solely on surface soil disturbance, because such disturbance significantly increased the probability of a nest being depredated. These findings provide valuable insights into the effects of surface soil disturbance on the population dynamics of nesting turtles and their predators.
INTRODUCTION

Predation is a fundamental process that shapes communities and population structure (Gotelli 2001). In some cases, the relationships between predators and their prey are so intricate that population crashes in one species can directly impact the abundance of other species (Madsen and Shine 1996, O’Donoghue 1998, Berger 1999, Reed 2006). In other cases, however, predators may depend upon a variety of prey species, and thus declines in one prey species may have minimal impacts on predator populations. The types of predator-prey relationships can thus vary dramatically depending on predator/prey densities (e.g., Andren 1992). Of particular importance in mediating predator-prey relationships is the ability of prey to escape (or conceal themselves) and that of predators to detect prey. Thus, selection should be strong on traits in both predators and prey that mediate these interactions.

Abiotic factors can also play a significant role in affecting predator-prey dynamics, especially in nest depredation. Habitat and landscape features and soil type (Martin and Roper 1988, Kuehl and Clark 2002, Spencer 2002), along with climatic factors like precipitation (Kolbe and Janzen 2002a, Bowen and Janzen 2005), can influence the probability of nest depredation as well as nest success (the proportion of nests laid that produce live hatchlings). Nest features may also affect the ability of predators to locate nests. For example, aspects of the surrounding nesting area may influence the ability of predators to find nests by impeding or facilitating predators’ search and sensory cues. Such factors may exert selection on nesting behaviors by organisms that determine nest features and thereby influence the probability of predation.
The dynamics of turtle nesting and nest predators comprise an excellent system to explore these issues. Nest predators can be important in structuring turtle populations, even causing populations to decline (Spencer and Thomson 2005), and nesting behavior by turtles may influence the probability of predation (Spencer 2002). Survivorship during the egg or neonate stage is extremely low in turtles, largely due to nest depredation (Congdon 1983, Marchand 2002, Spencer 2002). Consequently, life histories of many long-lived reptiles reflect the challenge of coping with high early mortality (Law 1979, Michod 1979). A growing number of studies of turtle nest depredation is shedding light on predator-prey dynamics, and the evolution of search strategies of predators and evasion strategies of prey. Still, community relationships between predators and prey (e.g., coyotes, raccoons, and turtles) are not adequately understood, and could shed basic insight into predator-prey interactions. Furthermore, the sub-lethal effects of predation are complex and can affect prey on different levels, but their impacts on reptilian life-history stages are poorly unknown (Downes and Shine 1998, Downes and Shine 1999, Spencer et al. 2001, Spencer 2002). In turn, variation in patterns of nest depredation highlights the need to better understand the roles of abiotic factors, predator population dynamics, and habitat use on turtle nest depredation.

In this study, we leverage 20 years of information on natural patterns of turtle nest depredation to perform field experiments to assess the impacts of habitat (shade cover) and predator sensory features on nest detection. Since turtle nests can be difficult to locate in large numbers, we employed artificial nests to facilitate addressing these questions. Ransom et al. (1987) demonstrated that artificial nests are an acceptable substitute for real nests when studying nest depredation of ground-nesting birds. Such
data are extremely useful for integrating information about which ecological mechanisms are responsible for predation and which cues are used by predators to locate prey nests. The purpose of these experiments was to examine predatory behavior of raccoons in response to coyote urine (coyotes can be a predator of both turtle eggs and raccoons), turtle urine emitted prior to oviposition, turtle egg secretions emitted during oviposition, and soil disturbance created by oviposition. Specifically, we investigated (1) the relative importance of different habitats (shade cover; e.g., unshaded, moderately shaded, and unshaded) and nest predators on turtle nest success, (2) which cues the nest predators use to find nests, and (3) how consistent depredation patterns are across different habitats.

We predicted that raccoons would show aversion to nests with coyote urine, and that the presence of turtle urine, turtle egg mucus, and soil disturbance would increase nest depredation over controls. In addition, we predicted that nest depredation patterns would greatly differ between habitats (shade cover) due to habitat preferences by raccoons and, potentially, to increased risk sensitivity of raccoons to depredation by coyotes in open habitats, and that they should exert different selective pressures on reproductive strategies of turtles that nest in these study areas. These experiments provide a better understanding of the role of habitats and top predators (coyotes) on depredation of turtle nests by mesopredators (raccoons).

STUDY AREA

Approximately 150-300 painted turtle nests are laid each year at South Potter’s Marsh on the Thomson Causeway near Thomson, Illinois, USA (41°57’N, 90°7’W), likely making it the largest known population of nesting painted turtles. The Thomson Causeway is a 450 x 900 m island near the eastern bank of the Mississippi River. The
South Potter’s Marsh nesting area (1.5 ha) occurs on the east side of the island along the backwaters. Approximately half of the nests belong to females that oviposit multiple times in a single nesting season, while the other half of the nests belong to females that nest once each nesting season (Schwanz and Janzen 2008).

METHODS

Study Organism

Painted turtles (Chrysemys picta) are small-to medium-sized aquatic freshwater turtles whose geographic range extends from the Atlantic to the Pacific Ocean and from southern Canada to the Gulf of Mexico (Ernst et al. 1994). Females may lay up to three clutches of eggs in a nesting season, depending on their age and size. The nesting season occurs from late May to early July, depending on weather conditions. Neonates hatch in August and September and typically remain in the nest throughout the winter, migrating from the nest to water the following spring. Mortality is high in these early life stages due to nest depredation (e.g., Bowen and Janzen 2005), over winter mortality (e.g., Weisrock and Janzen 1999), and mortality during migration due to predation (e.g., Paitz et al. 2007).

Urine collection

Urine was collected on the Thomson Causeway from turtles searching for nest sites during the first three weeks of the field season. When a turtle is disturbed while looking for an appropriate place to nest, she releases urine that she has sequestered for nesting as a potential defense mechanism (e.g., Patterson 1971). The urine was collected by simply lifting the female off the ground and holding her above a clean container. In 2007, urine was collected from a small number of females. In 2008, we collected urine
from a large number of females before the onset of the experiment. Coyote urine was purchased from McGregor Small Animal Control Products (McGregor Small Animal Control, Sandwich, MA). This research was conducted under scientific collecting permits (NH07.0073 and NH08.0073) from the Illinois Department of Natural Resources, and an Institutional Animal Care and Use Protocol permit (12-03-5570-J) from Iowa State University.

**Turtle egg mucus collection or secretions emitted during oviposition**

As turtle eggs are laid, they are coated with a clear, sticky, mucus-like substance (Ewert 1985). This substance can serve as an attractant for fire ants for sea turtle nests (Allen et al. 2001). For the 2008 experiment, we added this treatment to see if predators were attracted to the smell of this mucus-like substance independent of turtle urine.

Turtle eggs were collected on the Thomson Causeway from painted turtle nests in 2008. The turtles were observed nesting, and after construction, we excavated the nests immediately. Using a syringe, each egg was rinsed with 3 ml of distilled water to collect the egg mucus. The egg mucus was stored in a plastic container and placed in a refrigerator until used. Sterile gloves were worn at all times during this procedure.

**Artificial nesting design and success measures**

Artificial nests were constructed using a small hand shovel during daylight hours. Nest depth mimicked that of natural painted turtle nests (~10 cm) (Morjan 2003). To reduce the chances of introducing confounding variables, sterile gloves were worn at all times to mask human scent. Eight nest treatments were established in all possible combinations of soil disturbance, coyote urine, turtle urine, and turtle egg mucus (See Tables 1 and 2). Surface soil disturbance was accomplished by digging a 10x10 cm
cavity, inverting the soil, and backfilling. Locations receiving an olfactory cue had 3 ml of turtle egg mucus, turtle urine, and/or coyote urine emptied with a syringe directly on the top of the “nests”. “Control” nests did not receive any soil disturbance or liquid treatments. Researchers stood directly over control nests and did not apply anything (see Tables 1 and 2).

Nest treatments were established across three types of habitat: unshaded, moderately shaded, and shaded areas in 2007. There were a total of 20 blocks in 2007, and 18 blocks in 2008, with each experimental treatment repeated twice within each block (Table 1, 64 artificial nests per treatment; Table 2, 12 artificial nests per treatment). To reduce spatial dependence within each block, nests were constructed 2 m apart from each other, similar to distances between natural painted turtle nests at the Thomson Causeway (Valenzuela and Janzen 2001), forming a matrix of artificial nests. A flag was placed ~1 m from each artificial nest to mark its location and minimize the probability of attracting potential predators. There was no rain within the first two days of all nest construction, reducing chances of diluting treatments and affecting the surface of the soil.

**Habitat types**

To examine the effect of habitat shading on predation, we selected three types of habitats in 2007. All experimental areas and habitats were used by both nesting painted turtles and nest predators (J. Strickland, personal observations). The unshaded (Figure 1a) areas contained a heterogeneous ground cover with a mixture of grassy and sandy patches and many isolated trees. The moderately shaded areas (Figure 1b) contained some trees. The shaded (Figure 1c) study area contained many trees. These areas
provided an ideal setting and opportunity to investigate predator-prey relationships in this system.

**Predation monitoring**

Artificial nests were monitored for signs of digging by predators each day for 4 days (trial 1: 12-16 June 2007), 8 days (trial 2: 19-27 June 2007), and 4 days (trial 3: 17-21 June 2008), respectively. A nest was considered depredated if there were any signs of digging at the nest site. Nests were considered successful if no digging was apparent. Habitat effects were not evaluated in trial 3 due to catastrophic flooding of the Mississippi River. All trials took place within the normal nesting season of painted turtles at our site, which is mid-May until early July (Morjan 2003).

**Predation recordings**

To identify predators, wildlife cameras (Stealth Cam v. 1.1 STC-WD2-1R) were installed in the study areas by affixing them to trees. Each camera had a motion-sensitive mechanism to trigger X number of photographs in Y number of seconds. Every 2-3 days the cameras were rotated to reduce the effects of habituation of predators to the nest location and to sample predator activity over a larger area.

**Data Analysis**

Likelihood ratio G-tests (i.e. 2 x 2 or 2 x 3 contingency/categorical test) were used to determine whether the presence or absence of disturbance, coyote urine, turtle egg mucus, and turtle urine influenced predation rates. These G-tests helped identify variables that are related to nesting success across habitats and different treatments. Assuming that nest predation events are independent (Valenzuela and Janzen 2001) (Figure 5), the probability of nesting success was calculated for each habitat and
treatment across each habitat on the basis of predation rates (Sauer and Williams 1989). In addition, predation rates were compared across experimental blocks. Statistical tests were conducted using Pop Tools version 2.7.5 (Hood 2006).

RESULTS

Depredation of artificial nests in this study always occurred within three days after construction, consistent with previous studies of natural painted turtle nests at this site (Kolbe and Janzen 2002a). The assumption of independence of artificial nest predation within each experimental block is supported because not all nests in any given treatment were excavated within each block. Additionally, Figure 5 illustrates a scatter of depredated artificial painted turtle nests within a block, providing additional support for the argument that nest depredation events are independent. Furthermore, nest predator photography was unsuccessful at documenting predators of artificial nests because cameras were not at the nests that were predated on some nights or were not triggered properly to take a high quality photograph. Thus, we were not able to photograph predators of artificial nests, although foraging raccoons were recorded (Figure 2) disturbing C. picta nests at our study site on 5 June 2007 (22:27:09), 25 June 2008 (02:57:52), and 26 June 2008 (02:11:53).

Overall predation rates on natural painted turtle nests in 2007 and 2008 were ~50% and ~47% respectively. Predation rates on artificial nests varied between experimental blocks significantly in both 2007 (G = 38.58, df = 19, P = 0.005) and 2008 (G = 54.32, df = 17, P < 0.001). Additionally, predation rates on artificial nests varied between the three treatment trials in this study, with 14% in the first trial, 4% in the second trial, and 38% in the third trial. Overall, ~8% (22/280) of the artificial nests were
depredated in 2007 and ~38% (95/252) were depredated in 2008. Of these, 82% were depredated on the first night, 15% on the second night, and 3% on the third night. Moreover, artificial nests had a higher probability of depredation earlier in the nesting season, similar to previous studies on natural nests of Painted Turtles at this field site (Kolbe and Janzen 2002a), as the second trial experienced the lowest depredation.

Depredation was homogeneous among unshaded (9%), moderately shaded (5%), and shaded (9%) habitats ($G = 3.077$, df = 2, $P = 0.21$) (Figure 6). Similarly, the presence of coyote urine in 2007 (6%; $G = 0.657$, df = 1, $P = 0.41$), turtle urine in 2007 (5%; $G = 1.738$, df = 1, $P = 0.19$) and in 2008 (25%; $G = 0.027$, df = 1, $P = 0.86$) (Figure 7), and turtle egg mucus in 2008 (35%; $G = 0.184$, df = 1, $P = 0.52$) (Figure 8) did not significantly influence depredation of artificial nests. In contrast, artificial nests with soil disturbance experienced a significant increase in depredation compared to undisturbed artificial nests in both 2007 ($G = 6.316$, df = 1, $P = 0.01$) and 2008 ($G = 55.39$, df = 1, $P < 0.001$) (Figures 6, 7, and 8). This result suggests that soil disturbance attracts predators to the artificial nests, because 41% (108/266) of the disturbed nests showed evidence of depredation compared to 3% (9/266) of the undisturbed nests.

**DISCUSSION**

Artificial nest experiments are generally conducted to gain an understanding of the processes affecting natural nests. We used artificial turtle nests to measure and assess the impacts of predator sensory cues on turtle nest detection. Our results indicated that turtle nests receiving soil disturbance are at a greater risk of discovery by predators than nests where soil disturbance is minimal or not present. These findings provide valuable
insights into the effects of soil disturbance on the population dynamics of nesting turtles and their predators.

In some previous artificial turtle nest depredation experiments, avian eggs were placed in the artificial turtle nests to monitor nest success (Hamilton et al. 2002, Marchand et al. 2002, Marchand et al. 2004). Lindell (1999) concluded that results from artificial nest depredation experiments could depend on the type of eggs used in the experiment. Therefore, we did not use avian eggs in this experiment to help reduce any potential confounding effects.

For those nests receiving olfactory cues, we applied 3 ml treatments for several reasons. First, we possessed limited amounts of stored turtle urine. In addition, we wanted to keep the treatments constant. Andelt and Woolley (1996) placed about 3 ml of several attractants in a capsule to determine whether several urban mammals were attracted to the bait stations. Using 3 ml of each attractant, they found significant treatment effects of some attractants on visits to the scent stations by squirrels, domestic dogs, and domestic cats. Raccoons and skunks were also attracted to the scent stations, but the effects were non-significant. Thus, this quantity of urine treatment also seemed sufficient to attract such potential nest predators in our study.

Predators destroyed 22% (117/532) of our artificial nests in a similar manner to real painted turtle nests (Figure 4). Annual predation rates on natural nests at this site vary from 20-96%, and most of this predation occurs within the first few nights after oviposition (Kolbe and Janzen 2002a). Even though predation rates on our artificial turtle nests may not completely reflect average predation rates on natural nests at our field site (~50%, Kolbe and Janzen 2002a), our intent was to determine the relative
effects of surface soil disturbance, turtle egg mucus, turtle urine, and coyote urine on
depredation while controlling other conditions as much as possible in our field situation.
Therefore, any potential biases due to the artificial nests were constant over all treatments
and habitats. Overall, artificial nest depredation in 2008 was 38%, which falls well
within the range of depredation percentage of painted turtle nests over the last two
decades at the Thomson Causeway. Nonetheless, other researchers have found both
elevated (King et al. 1999) and reduced (Davison and Bollinger 2000) predation rates at
artificial terrestrial avian nests compared to those detected at natural nests (Hamilton et
al. 2002). Nest predation rates reported for natural turtle nests (e.g., Congdon et al. 1983,
63%; Burke et al. 1998, 84.2%) often are greater than the average predation rate for our
artificial nests. However, rates of predation in our experiment (22% overall) were similar
to those reported for a group of painted turtle nests in Michigan (Tinkle et al. 1981, 21%),
and northern bobwhites in New Hampshire (Marchand et al. 2002, 22%). In many
instances, predators dug holes approximately 10 cm deep when visiting artificial nests
(Figure 4). This observation further suggests that artificial nests were recognized as
painted turtle nests by at least some members of the mammalian predator community at
our field site because natural painted turtle nest cavities are ~ 10 cm deep (Morjan 2003).

The original question was whether surface soil disturbance, along with the
presence or absence of urine and/or turtle egg mucus, affected the likelihood of nest
depredation. Only the surface soil disturbance treatment affected predation rates,
increasing the likelihood of a nest being depredated. This finding suggests that predators
use visual cues to locate the nests, as opposed to being attracted by the scents of turtles or
repelled by the scents of coyotes. Our results are consistent with those of Burke et al.
(2005) who found that “digging” (surface soil disturbance) by the egg-layer is what predators use to locate nests. Still, Hamilton et al. (2002) and Burke et al. (2005) found no significant differences in nest depredation with respect to visual cues. On the other hand, consistent with Hamilton et al. (2002) and Burke et al. (2005), we found no significant differences in nest depredation with respect to olfactory cues.

We further considered the possible impact of other cues that might indicate the location of painted turtle nests, such as human scent, flags, slough water, and rocks (Colbert & Janzen, unpublished data). Small rocks (< 5 cm$^2$) and flags are used to identify turtle nests at the Thomson Causeway. A majority of the nesting turtles enter the nesting area from the slough. P. Colbert and F. J. Janzen (Iowa State University, unpublished data) found that neither slough water, nor rocks or flags used to mark nests, had any apparent influence on predation rates, which is also consistent (flags) with the findings of Burke et al. (2005) and Tuberville and Burke (1994), although Rollinson and Brooks (2007) found that marking nests with Popsicle sticks increased predation rates (probably birds in their case). While applying treatments, we wore gloves and closed-toed shoes at all times to avoid leaving human scent, even though other investigators have concluded that human scent or nest excavation (Kolbe and Janzen 2002a) without gloves had no effect on predation rates at this site.

The first two experimental trials were performed when painted turtle nests at South Potter’s Marsh experienced low predation rates. Trial three took place following a major flood at the field site. Prior to the flood, there were extremely low predation rates on painted turtle nests. Following the flood, nest predation rates reached as high as 60%, perhaps indicating the hunger level of raccoons that had been treed for about 10 days.
Future experiments should be geared towards evaluating the impacts of environmental extremes like floods, which are expected to increase in frequency with ongoing climate change (Jha et al. 2004), on nest survival and predation. Also, golf hole diggers could be used to construct artificial ‘control’ nests in future experiments, which will help to create even better ‘control’ nests.

Although we found no substantial evidence that different habitats, turtle urine, turtle egg mucus, or coyote urine influenced turtle nest depredation, we did find that predators at this site appear to associate visual cues with the presence of turtle nests. Nocturnal predators have eyes that are adapted to see well at night. Thus, the anatomy of the raccoon’s eye could be related to their nocturnal foraging behavior and success. Raccoons have a hypersensitive retinal region, which could extend their visual capacity during nocturnal periods (Ninomiya et al. 2005). In summary, we conclude that soil disturbance is an important (presumably visual) cue used by foraging predators to locate painted turtle nests. Investigators of turtle nests who refrain from disturbing the soil surface around nests may avoid influencing predation rates. It would be useful to determine whether the results of this study are applicable to other ground-nesting animals, such as certain birds, sea turtles, etc. Further studies could provide valuable insights into the long-term effects of surface soil disturbance on the population dynamics of nesting species and their predators.

** MANAGEMENT IMPLICATIONS **

Our results have important management and conservation implications for managing predator populations and mitigating potential effects on turtle nest depredation. Factors affecting turtle nest survival are of special interest to researchers, managers, and
conservationists of turtles, because turtle populations are declining world-wide (Rhodin 1999, Gibbons et al. 2000). Rhodin (1999) investigated the severity of the turtle crisis on a global scale, inferring that of the then 293 turtle taxa, 3% are currently extinct in the wild. In addition, 4% are critically endangered, 11% are endangered, and 21% are vulnerable to becoming endangered. As a result, researchers, managers, and conservation biologists are becoming more and more concerned about the world-wide turtle population declines. Although *C. picta* is among the most abundant and widespread turtles in the U.S. (Marchand and Litvaitis 2004), we suspect that some of the factors limiting this species also would affect populations of threatened species in the area such as Blanding’s turtles, as well as other imperiled populations throughout the world. Our results provide valuable insights into the effects of surface soil disturbance on the predator-prey dynamics of nesting turtles and their predators. A concrete example how the results of this study can be applied to turtle population management is where researchers and managers could work to help camouflage (e.g. with a hand broom or rake) nests of imperiled species of turtles, since raccoons seem to be attracted visually to disturbed soil surfaces. This approach should be more time and cost-effective than prior methods to reduce depredation of turtle nests (e.g., Ratnaswamy et al. 1997). Future studies could implement raking as an experimental treatment to see if such raking decreases nest predation rates. Additionally, for future research, a better understanding of the role of sensory and visual cues in raccoon (predator) and turtle (prey) interactions may lead to a greater ability to protect some turtle populations that are declining due to nest depredation.
ACKNOWLEDGMENTS

We thank the U.S. Army Corps of Engineers, the U. S. Fish & Wildlife Service and the Illinois Department of Natural Resources for allowing us to conduct this research on their field site, the 2007 and 2008 Turtle Camp crews for extensive field assistance, M. Hoy for assisting with the experimental set up and data collection, the entire Janzen lab for reviewing proposals and manuscripts, J. Church for assisting with the statistical analyses, and W. Clark and D. Debinski for guidance. The Graduate Minority Assistantship Program and the Agricultural Experiment Station at ISU supported J. T. Strickland. An ESA SEEDS Special Project grant and an NSF LTREB grant DEB-0604932 to F. J. Janzen provided funding for this research.


LITERATURE CITED


TABLE 1

Experimental design showing treatments \((n=64)\) that were randomly applied to each nest. 3 ml of turtle and/or coyote urine were poured over the nest sites where applicable. Only in 2007 were habitats pre-selected shaded \((n=8)\), moderately shaded \((n=8)\), and unshaded \((n=4)\).

<table>
<thead>
<tr>
<th>Treatment #</th>
<th>Surface soil disturbance applied</th>
<th>Turtle urine applied</th>
<th>Coyote urine</th>
</tr>
</thead>
<tbody>
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<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>2</td>
<td>Yes</td>
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</tr>
<tr>
<td>3</td>
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<td>4</td>
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<td>5</td>
<td>No</td>
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</tr>
<tr>
<td>6</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>7</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>8 (control)</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
</tbody>
</table>
**TABLE 2**

Experimental design showing treatments \((n=12)\) that were randomly applied to each nest in 2008. 3 ml of turtle and/or turtle egg mucus were poured over the nest sites where applicable.

<table>
<thead>
<tr>
<th>Treatment #</th>
<th>Surface soil disturbance applied</th>
<th>Turtle urine applied</th>
<th>Turtle egg mucus</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Yes</td>
<td>Yes</td>
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<td>2</td>
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<td>5</td>
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</tr>
<tr>
<td>7</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>8 (control)</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
</tbody>
</table>
Description of the study sites and 3 different types of habitats in 2007. There are eight different treatment combinations that were repeated twice within each experimental block. (Figure 1a) unshaded – no trees; 56 nests with 2 replicates of 8 different treatments within each block. (Figure 1b) moderately shaded – some trees; 112 nests with 2 replicates of 8 different experimental treatments within each block. (Figure 1c) shaded – many trees; 112 nests with 2 replicates of 8 different experimental treatments within each block.
Figure 2. Raccoon (*Procyon lotor*) excavating painted turtle (*Chrysemys picta*) nest in Thomson, Illinois U.S.A.

Figure 3. Coyote den found near study area in Thomson, Illinois, U.S.A.

Figure 4. (Left) Depredated artificial painted turtle (*Chrysemys picta*) nest on 18 June, 2008. (Right) Depredated natural painted turtle (*C. picta*) nest on 9 June, 2008.

Figure 5. Scatter of depredated artificial painted turtle nests within a block, supporting the argument that nest depredation events are independent.
Disturbed vs Undisturbed Nest Depredation
Summer 2007

Figure 6. Artificial nest depredation percentages across shading habitats, and comparisons between disturbed and undisturbed soil surfaces.

Nest Depredation 2008 (Experiment 1)

Figure 7. Artificial nest depredation percentages across different treatments including the presence/absence surface soil disturbance, turtle urine, and coyote urine.

Nest Depredation 2008 (Experiment 2)

Figure 8. Artificial nest depredation percentages across different treatments including the presence/absence surface soil disturbance, turtle urine, and turtle egg mucus.
CHAPTER 3. IMPACTS OF ANTHROPOGENIC STRUCTURES ON PREDATION OF PAINTED TURTLE (CHRYSEMYs PICTA) NESTS

By Jeramie Strickland¹, and Fredric J. Janzen²

A paper to be submitted to Biological Conservation

ABSTRACT

Despite the potential for anthropogenic factors to indirectly impact wildlife populations, these indirect impacts have been poorly studied. The relationship between spatial distribution of 1375 painted turtle (Chrysemys picta) nests, in regards to distance from anthropogenic structures and nest depredation, was investigated over 6 years for a population on the Mississippi River. Nests in closer proximity to all anthropogenic structures were more likely to encounter depredation in two years but lower depredation in another. In the remaining three years, all of which were characterized by more extreme levels of depredation, there did not seem to be any nest survival patterns in relation to distance from anthropogenic structures. Over all years combined, the survival probability of nests decreased with increasing distance from all anthropogenic structures. We further tested the possible impact of supplemental food attractant structures (e.g. camp pad, trashcan, fish table) vs. non-supplemental food attractant structures (e.g. road, horseshoe pits, latrines, benches) on probability of nest depredation. However, our results did not reveal a significant difference between the food attractant structures and the non-supplemental food attractant structures in probability of depredation of proximal turtle nests. This study has broad implications for conservation of ground-nesting species because any anthropogenic activities that alter predator behavior could differentially impact prey species.
INTRODUCTION

Habitat alteration or human activity can influence wildlife populations in multiple ways. Altered habitats may represent suboptimal environments, and occupation of those habitats may have costs for organisms. Contact with humans can negatively impact survival or behavior of individuals (Tyning, 1990). These influences can be spectacularly, or subtly, detrimental. For example, roads that bisect habitats can serve as a direct (e.g. animals struck by vehicles) (Steen and Gibbs 2004, Gibbs and Shriver 2002, Aresco 2005) or indirect (e.g. enhanced depredation of nests along the habitat edges) (Temple 1987, Kolbe and Janzen 2002) source of mortality.

Human impacts can also alter community interactions that have ramifications for wildlife populations in more complex ways. Biological communities are largely structured through numerous abiotic and biotic interactions. Thus, where one strand of this web is extirpated by human activities, the effects can reverberate. For example, supplementing predators with human-derived food can enhance population numbers of predators and, subsequently, increase or decrease prey numbers (Vander Lee et al. 1999, Copper and Ginnet, 2000, Hamilton et al., 2002). Alternatively, elevated human activity can repel predators and, thereby, provide a basis for increasing prey population size (e.g. white-tailed deer) (Cooper and Ginnett, 2000). Supplemental food can attract non-target species and predators (Rollins, 1996); Greenwood (1981) concluded that raccoons primarily forage in sites where seeds from agricultural crop fields are available. More recent studies have shown that some nest predators incidentally find prey nests while foraging for alternate food (Vickery et al., 1993). Thus, nests near supplemental food sources could be at greatest risk of depredation.
The ways in which human activities and habitat alterations affect biological communities appear to vary substantially both temporally and spatially. For example, lightly traveled roads should have a low direct effect on wildlife mortality, but the impact increases when traffic is heavy. Similarly, nests located closer to anthropogenic structures that form habitat edges such as roads (e.g., Temple, 1987; Kolbe and Janzen, 2002) should be more likely to succumb to predators than nests located farther away. The potential for anthropogenic structures to attract predators by unintentional provisioning of food may increase local predation on nests. This suggests that human impacts on wildlife populations not only may be direct, but also may be indirect by altering community interactions, such as predation events. Anthropogenic structures in proximity to supplemental food for predators therefore may attract predators and increase depredation of nearby non-target nests. Despite the potential for anthropogenic factors to impact wildlife populations, these indirect impacts have been poorly studied. Even more surprisingly, temporal and spatial variation in such systems is largely unexplored.

Turtle nests and their predators are a good system for addressing this important ecological question. For turtles, mortality rates are highest during the egg stage (Congdon et al., 1983; Pough et al., 2004), and predation is responsible for the majority of nest mortality (Congdon et al., 1983; Ernst et al., 1994; Marchand et al., 2002, 2004). Thus, nest success is a key determinant of recruitment rates in many turtle populations. In fact, high nest mortality has caused some turtle populations to decline (Gibbons, 1968). In addition, the location of a nest may increase the offspring’s vulnerability to predation during incubation or pre-emergence (Spencer, 2002; Spencer and Thompson, 2003), as well as post-emergence (Downes and Shine, 1999; Kolbe and Janzen, 2002).
Furthermore, supplementing predators with food may reduce predation in turtles, yet other studies suggest that supplemental foods can increase predation (Cooper and Ginnet, 2000). These conflicting results warrant further investigation.

In this study, we targeted 6 years of data to investigate the effects of anthropogenic structures on depredation of painted turtle (Chrysemys picta) nests. Modeling the point patterns of such nest locations allows us to determine whether depredation changes with distance to anthropogenic structures. The purpose of this study was to test the hypothesis that anthropogenic structures attract turtle nest predators, leading to increased depredation of nearby nests, and assess whether such patterns vary with annual intensity of nest depredation.

**MATERIALS AND METHODS**

The relationship between spatial distribution of turtle nests, in regards to distance from anthropogenic structures and nest predation, was investigated on a 450 x 900m island at the South Potter’s Marsh on the Mississippi River in Thomson, Illinois at the Thomson Causeway Recreation Area (TCRA). The painted turtle population at this site has been well studied (Weisrock and Janzen, 1999; Janzen and Morjan, 2001). The area contains a recreational vehicle campground that contains a circular road, campsites, trash bins, a fish cleaning table, and toilet facilities. These anthropogenic structures may contain attractants for nest predators (J. Strickland, pers. obs). Because anthropogenic structures are situated within the nesting habitat, we compared depredation between nests that are laid closer vs. farther from anthropogenic structures.

During the nesting season (mid-May-late June), the predation status of each nest was monitored at least every three days from oviposition until the end of the nesting
season. Depredated nests were detected by observing broken eggshells outside the nest, clear excavation of the nest cavity, and absence of intact eggs in the nest. In mid-September of each year, all presumably intact nests were excavated and any eggs or hatchlings noted, and final predation status was determined. Nests were considered either depredated or intact. Intact nests at the end of the nesting season were determined in September to be depredated if a conspicuous, empty hole was observed in the ground where the nest was previously recorded. Raccoons (*Procyon lotor*) are the primary predator of painted turtle nests at this site (Kolbe and Janzen, 2002).

**Data and Spatial Analyses**

The objective of this study was to determine whether nest depredation varied across the nesting habitat as a function of distance from anthropogenic structures. In addition, we evaluated which particular anthropogenic structures influenced nest predation. If nest depredation does vary as a function of proximity to, or type of, anthropogenic structure, the data can be partitioned appropriately to further address questions related to spatial-dependent depredation. Nest depredation and nest location data over 6 years (1997, 1998, 2001, 2002, 2003, 2005, total number of turtle nests = 1375) were used to test the hypothesis that probability of nest depredation is greater near anthropogenic structures. Our lab has been investigating reproductive and nesting biology of painted turtles at the study site for over 20 years. Nest predation intensity has fluctuated significantly, ranging from as low as ~20% in 1997 to as high as ~96% in 2005. For this reason, we wanted to compare patterns of nest depredation between low (~30%), medium (~60%), and high (~90%) years. Therefore, we chose to analyze data
for years when overall nest depredation was similar to the low, medium, and high rankings.

Logistic regression (SAS Institute, V.9.1, 2008) was used to test whether nest depredation increases or decreases with distance from an anthropogenic structure. The probability that a nest was depredated was modeled where the response variable was categorical (1=depredated, 0=intact), and the predictor variable (distance from closest anthropogenic structure) was continuous. Distance to the closest anthropogenic structure for each nest was scaled to the nearest meter to accommodate imprecision (e.g., a nest located 7.39 m from a trash can would be scaled to 7 m). Such scaled measurements were used to compare whether or not nests laid closer to such structures were more likely to be depredated. To visualize and evaluate the relationship between nest depredation probability across continuous distances to closest anthropogenic structure, we used a cubic spline technique originally developed for visualizing fitness functions and natural selection (Schluter 1988; see also Kolbe and Janzen 2002a). Standard errors for the spline were calculated by bootstrapping the data 50 times.

Measures derived from the Akaike Information Criterion (AIC) were also used. This statistical procedure allowed us to select the model that best describes the data. Furthermore, this model-selection procedure helped identify which particular variable(s) was (were) important in influencing nest depredation. All interactions and combinations of variables (anthropogenic structures and distance to closest anthropogenic structure) were run using logistic regression, and then each model was assessed using AIC, specifically QAIC (Burnham and Anderson, 1998; Davros and Debinski, 2006). The
lowest QAIC value indicated the best model among the alternate models examining the data.

RESULTS

Nests in closer proximity to all anthropogenic structures were more likely to experience depredation in two of the six years used in the analysis (Table 1). The probability of nest depredation decreased with increasing distance from anthropogenic structures in 1998 and 2000. However, in 2003, nests laid farther from anthropogenic structures were more likely to experience depredation. In other years (1997, 2001, 2005), all of which had especially high or low predation intensity (Table 1), there does not seem to be any nest depredation patterns in relation to distance from anthropogenic structures.

Over all six years, we observed a strong relationship supporting the argument that the depredation probability of nests changes with increasing distance from anthropogenic structures (Figure 1 and Table 2). The chosen model did not include type of structures separately or individually (e.g. benches, latrines, camp pads, horseshoe pits, or road). Instead, this “reduced” model, which has the lowest QAIC value, only includes distance to all anthropogenic sites. In general, probability of nest depredation is predicted to increase modestly, but significantly, with distance from an anthropogenic structure (e.g., 0.63 at 10 m distance and 0.51 at 1 m distance) (Figure 1). This outcome contradicts the hypothesis that nests in closer proximity to anthropogenic structures should experience higher depredation.

Cubic spline analyses were used to visualize and evaluate the relationship between nest depredation probability and continuous distances to closest anthropogenic structure. Cubic spline and logistic regression results were usually consistent with higher
probabilities of nest depredation farther from anthropogenic structures in 1997, 2001, 2003, 2005, and overall, but not in 1998 and 2000. Thus, overall patterns illustrate a significant increase in the probability of nest depredation for nests farther from anthropogenic structures (Figure 1).

We explored this matter more fully by testing whether there was a significant difference between structure type and spatial probability of nest depredation (Table 3). There was no significant evidence that nest depredation depended on distance to any particular type of structure. Nonetheless, the closer a nest is located to an anthropogenic structure, the better the chances of avoiding predators, further supporting the findings of the “reduced” model (Table 2).

We further tested the possible impact of supplemental food attractant structures (e.g. camp pad, trashcan, fish table) vs. non-supplemental food attractant structures (e.g. road, horseshoe pits, latrines, benches) on probability of nest depredation (Table 4). In a model accounting for the type of anthropogenic site (food or non-food) and nest distance from site, we find that site is not significantly related to the probability of predation. In a model accounting for food/non-food site and a nest located 9 meters away from a given site, the odds of predation are 3 to 2 if the nest were located adjacent to the site. The farther the distance away, the greater the odds of predation (Figure 1). Thus, at this field site, anthropogenic structures most likely to possess supplemental food did not enhance the odds of depredation on proximal turtle nests.

DISCUSSION

Nest construction and nest-site selection is a pre-requisite for successful breeding in a wide range of both vertebrate and invertebrate taxa (Hansell, 1984). In the process of
nest building, individuals must make several decisions to choose a suitable environment, habitat, and nest site. Previous literature further suggests that nest-site choice could influence predation risk and nest success, which in turn could influence the life-history evolution of nesting species (e.g., Martin, 1995). Nest-site selection has important consequences for survival of freshwater turtles, because nest predation is extremely high in most turtle populations. While predation is a natural source of mortality for turtles, anthropogenic activities can alter predator behavior, influencing nest success; and both can be key factors affecting the persistence and survival of turtle populations that are declining. Anthropogenic activities can both directly and indirectly impact nesting animals (e.g., elevated nest predators attracted to anthropogenic subsidies and resources, see Boarman, 1997), populations, and wildlife communities. For example, recreational trails have been shown to alter bird breeding communities in different ecosystems. Additionally, anthropogenic disturbance by recreation can result in behavioral changes by nesting species (e.g. species displacement or nest abandonment, see Miller and Knight, 1998).

In this multi-year field study, we examined the effects of distance from anthropogenic structures on nest depredation in a population of painted turtles. We show that, in some years, turtle nests are subject to predation pressure that is inversely related to the proximity of nests to anthropogenic structures. In contrast, logistic regression and cubic spline analyses over all years combined revealed that probability of depredation of turtle nests was correlated with distance from any anthropogenic structure, indicating that nests located closer to anthropogenic structures were less likely to encounter depredation. Additionally, the differences observed between the logistic regression and the cubic
spline statistical results suggest more years of data are necessary to get a better understanding about these differences. Furthermore, we find no significant evidence of a difference in spatial-dependent depredation between structures with supplemental food attractant capacity and structures without such food attractants.

Research employing experimental nests to examine patterns of nest depredation provides another perspective on these observational findings. Experimental studies strongly implicate visual cues as a primary means by which raccoons locate turtle nests (Strickland and Janzen, 2008, unpublished data; Strickland et al., unpublished data), although such nest predators possess excellent olfactory capabilities (Conover, 2007). Thus, raccoons often might be deterred by anthropogenic structures, assuming they have a fear of humans or pets (e.g. dogs), even when supplemental food is associated with such structures. Several campers who visit the TCRA own dogs, which may deter raccoons and other mammalian turtle nest predators. In these cases, turtle nests located farther from anthropogenic structures would be expected to suffer a higher probability of depredation.

Certain anthropogenic structures are more likely to contain supplemental food resources than other structures. Nonetheless, our results did not reveal a significant difference between the food attractant structures and the non-supplemental food attractant structures in probability of depredation of proximal turtle nests. This finding suggests that supplemental food attractant structures do not influence the foraging success of turtle nest predators at this particular study site. Others have suggested that supplementing predators with food resources may be a way to reduce nest predation (Crabtree and Wolf, 1988; Vanderlee et al., 1999). Furthermore, Boag et al. (1984) and Miller et al. (2000)
suggested that predation risk tended to decrease with decreasing distance from anthropogenic trails in their study. Contrarily, Miller et al. (1998) reported an increase in predation on nests located near anthropogenic trails.

Nest-site choice in relation to distance from anthropogenic structures may have important ramifications for nest success and offspring survival not only during the incubation period, but also because *C. picta* hatchlings hibernate terrestrially (Weisrock and Janzen, 1999). Because raccoons are edge-inhabiting animals, their densities and activities typically increase in fragmented habitats (Harris, 1984). If this is the case, selective pressures from nest predators such as raccoons could favor turtles that nest farther from anthropogenic structures or edges, or in intact patches of habitat, because predation was greater on nests that were constructed closer to anthropogenic structures than nests constructed further from anthropogenic structures in some years (e.g., 1998 and 2000).

Consequently, any change in predator foraging behavior and its relationship to distance from anthropogenic structures may result in decreased or increased nest survival (Vander Lee et al., 1999; Bowen and Janzen, 2005). Our models reject the original hypothesis only in some years. Thus, the results of this study suggest that anthropogenic structures could reduce recruitment in freshwater turtle populations in some years, but generalizations regarding the negative impacts of anthropogenic structures should be made with caution, just as others have suggested (Hamilton et al., 2002).

Anthropogenic activities could influence predator foraging behavior patterns by potentially providing supplemental food. Thus, raccoons and other predators could be increasingly attracted to nesting areas (Cooper and Ginnett, 2000). This study has broad
implications for conservation of ground-nesting species because any anthropogenic activities that attract or deter additional predators could negatively or positively impact such species. For example, campers and visitors should avoid leaving trash or any other supplemental food items in such habitats, especially during the turtle nesting season, given that our results show that distance to anthropogenic structures could directly, or indirectly, influence nest depredation rates. The nesting season is extremely important, particularly in this population of painted turtles because most nest depredation takes place within 72 hours following oviposition (Kolbe and Janzen, 2002a) and the persistence of this turtle population depends on substantial survival of nestlings (Spencer and Janzen, in preparation). Thus, results from this study on a common, easily studied turtle may inform conservationists about strategies for protecting other species with similar nesting behaviors and life histories.

Further research could focus on modeling nest survival times. Future emphasis should be geared towards modeling nest survival times to see if nests that are laid closer to the anthropogenic structures are destroyed quicker than the nests that are laid farther away. This can be done using survival times (e.g. proportional hazard analysis). Additional studies are necessary to quantify the long-term effects of anthropogenic structures on the population dynamics of ground-nesting species and their nest predators.

ACKNOWLEDGEMENTS

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manuscripts, A Trapp II, J. Church, L. Kasuga, R. McNeeley E. Otárola-Castillo, the Iowa State University Statistics Consulting Department for assisting with the data and statistical analyses, and W. Clark and D. Debinski for guidance. The Graduate Minority Assistantship Program and the Agricultural Experiment Station at ISU supported J. T. Strickland. An ESA SEEDS Special Project grant and an NSF LTREB grant DEB-0604932 to F. J. Janzen provided funding for this research.

LITERATURE CITED


Table 1. Effects of distance from the closest anthropogenic structure on predation of painted turtle nests. Logistic regression results for the relationship between distance from all anthropogenic structures combined and nest predation. Results from logistic regression analyses with the distance from closest anthropogenic structure as the independent variable and nest fate as the dependent variable. The predation rates and number of nests laid for each year are also provided.

<table>
<thead>
<tr>
<th>Year</th>
<th>1997</th>
<th>1998</th>
<th>2000</th>
<th>2001</th>
<th>2003</th>
<th>2005</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Depredated</td>
<td>19.7</td>
<td>35.9</td>
<td>59.1</td>
<td>89.5</td>
<td>57.1</td>
<td>95.8</td>
</tr>
<tr>
<td>% Not Depredated</td>
<td>81.3</td>
<td>64.1</td>
<td>41.9</td>
<td>10.5</td>
<td>42.9</td>
<td>4.2</td>
</tr>
<tr>
<td>Number of Nests</td>
<td>198</td>
<td>178</td>
<td>168</td>
<td>215</td>
<td>326</td>
<td>285</td>
</tr>
<tr>
<td>Parameter Estimate (slope)</td>
<td>-0.0351062</td>
<td>-0.1678296</td>
<td>-0.1223292</td>
<td>0.01387886</td>
<td>0.0873857</td>
<td>0.0072824</td>
</tr>
<tr>
<td>P</td>
<td>P = 0.3830</td>
<td>P &lt; 0.001*</td>
<td>P &lt; 0.0023*</td>
<td>P = 0.1243</td>
<td>P &lt; 0.0006*</td>
<td>P = 0.9209</td>
</tr>
<tr>
<td>Standard Error</td>
<td>0.04</td>
<td>0.042</td>
<td>0.04</td>
<td>0.09</td>
<td>0.02557</td>
<td>0.07</td>
</tr>
</tbody>
</table>

Table 2. Shows the model that was chosen by the QAIC method with the lowest QAIC value. This model only shows ‘distance’ to any anthropogenic structure to be the variable influencing predation rates, regardless the type of structure.

Table 3. Model testing for an effect for distance and type of anthropogenic site, and probability of nest predation. Please also note that all parameters were compared to the road to get these values and no significant differences were detected between parameters other than distance to all structures.

Table 4. Supplemental food attractant structures (e.g. camp pad, trashcan, fish table, vs. non-supplemental food attractant structures (e.g. road, horseshoe pits, latrines, benches).
Figure 1. Cubic spline for the probability of nest depredation as distance from anthropogenic structures increases. Analyses for all six years combined are shown. Dashed lines bracketing the spline represent standard errors calculated by bootstrapping the original data 50 times.
CHAPTER 4. CONCLUSIONS

Predator-prey interactions and dynamics are important factors in the ecology of populations, particularly in terms of community structure and organization. Under certain circumstances, predators can significantly impact prey populations (Errington, 1946; Korpimaki and Krebs, 1996). The degree to which predators impact prey population dynamics may depend on circumstances such as precipitation (Bowen and Janzen, 2005), spatial and temporal dynamics via edge effects (Temple, 1987; Kolbe and Janzen, 2002), local habitat characteristics (Kuehl and Clark, 2002; Baber and Babbit, 2004), predator or prey abundance (Miller et al., 1996), or anthropogenic factors (Gibbs, 2002). Nest predators can be important in structuring turtle populations, even causing populations to decline (Spencer and Thomson, 2005), and nesting behavior by turtles may influence the probability of predation (Spencer, 2002). Understanding the components of predator-prey interactions is especially important for nesting turtle populations given the imperiled status of many turtle populations worldwide.

Predation is the main cause of nest failure for most turtle populations (Congdon et al., 1983; Marchand et al., 2004). Survivorship during the egg or neonate stage is extremely low in turtles, largely due to nest depredation (Congdon, 1983; Marchand, 2002; Spencer, 2002). Excessively high levels of nest predation have been suggested as a potential direct cause of population decline for some turtle populations (Gibbons, 1968). Poor nest success can result from both biotic and abiotic factors, in addition to anthropogenic influences. Because turtles are components of communities, they serve as prey for other species. Nesting turtles and their nest predators are a great system to investigate some of the major predator-prey interaction issues mentioned above.
Moreover, observational studies on natural nest depredation can complement experimental studies of nest depredation cues to increase our understanding of the specific cues predators use to locate turtles nests.

Painted turtles (Chrysemys picta) are freshwater turtles whose geographic range extends from the Atlantic to the Pacific Ocean and from southern Canada to the Gulf of Mexico (Ernst et al., 1994). Field studies of turtle reproduction are increasingly important, as the life-history strategies of long-lived species are incompletely understood and turtles are recognized as essential components of many ecological communities. Mortality is high in these early life stages due to nest depredation (e.g., Bowen and Janzen, 2005), over winter mortality (e.g., Weisrock and Janzen, 1999), and mortality during migration due to predation (e.g., Paitz et al., 2007). Furthermore, predation is an important force evolutionarily, because natural selection favors more evasive prey and more effective predators, leading to predator-prey arms races (Brodie and Brodie, 1999a; Brodie and Brodie, 1999b). Still, the cues used by predators to detect turtle nests are inadequately known. The dynamics of turtle nesting and nest predators comprise an excellent system to further explore these issues.

Experimental studies can explore the roles of various biotic and abiotic factors in influencing probability of nest depredation. The first project examined the role of local sensory cues, along with habitat characteristics (i.e. vegetation shading), on turtle nest depredation with an experiment using simulated turtle nests. We used artificial turtle nests to measure and assess the impacts of predator sensory cues on turtle nest detection. The goal was to determine which cues predators use to locate turtle nests, and whether those cues vary between different habitat types.
Specifically, we examined which local cues predators use to locate turtle nests, and evaluated if predation rates varied across different types of shading habitats. Habitat type did not influence probability of nest depredation. Similarly, the presence of coyote and turtle urine, and turtle egg mucus, combined or individually, did not significantly alter depredation rates. Instead, predators seemed to locate simulated nests based solely on surface soil disturbance, because such disturbance significantly increased the probability of a nest being depredated. These findings provide valuable insights into the effects of surface soil disturbance on the population dynamics of nesting turtles and their predators. A concrete example how the results of this study can be applied to turtle population management is where researchers and managers could work to help camouflage (e.g. with a hand broom or rake) nests of imperiled species of turtles, since raccoons seem to be attracted visually to disturbed soil surfaces. Our results provide valuable insights into the effects of surface soil disturbance on the predator-prey dynamics of nesting turtles and their predators.

Additionally, despite the potential for anthropogenic structures to impact wildlife populations and communities, through such interactions, these indirect impacts have not been thoroughly investigated. Because anthropogenic structures are often situated within turtle nesting habitats, we compared rates of predation between nests that are laid closer vs. farther from anthropogenic structures. The second project presents an observational test of the hypothesis that anthropogenic structures attract predators by examining whether natural turtle nests located near anthropogenic structures have historically suffered higher mortality. Anthropogenic factors may also play a role in raccoon detection and depredation of turtle nests. Turtle nests and their predators provide a model
system to further understand the direct and indirect effects of humans on turtle nest depredation. I show that in some years, turtle nests are subject to predation pressure that is inversely related to the proximity of nests to anthropogenic structures. In other years, 3/6, there does not seem to be any nest survival patterns in relation to distance from anthropogenic structures. Over all years combined in the study, I observed a strong relationship supporting the argument that the survival probability of nests decreased with increasing distance to anthropogenic structures, which is contrary to my previous findings when looking at responses between individual years. Additionally, I tested whether or not there was a significant difference between structure type and spatial probability of nest predation. There is no significant evidence that nest predation was dependent of distance to any particular type of structure. I further tested the possible impact of supplemental food attractant structures (e.g. camp pad, trash can, fish table) vs. non-supplemental food attractant structures (e.g. road, horse shoe pits, latrines, benches). No significant differences were detected when comparing the supplemental food attractant structures vs. non-supplemental food attractant structures. This study has broad implications for conservation of ground-nesting species because any anthropogenic activities that attract or deter additional predators could negatively or positively impact such species.

Factors affecting turtle nest survival are of special interest to researchers, managers, and conservationists of turtles, because turtle populations are declining worldwide (Rhodin, 1999; Gibbons et al., 2000). Our overall results shown in this thesis have important management and conservation implications for managing predator populations and mitigating potential effects on turtle nest depredation. Researchers, managers, and
conservationists need to identify what is attracting predators to turtle nests (both directly and/or indirectly), which will help them design strategies to help reduce nest predation of imperiled turtle species. A better understanding of the role of olfactory cues in raccoon (predator) and turtle (prey) interactions may lead to a great ability to protect some turtle populations that are declining from predators.

Reducing turtle nest predation can be very helpful, particularly in areas where turtle populations are declining due to little or no recruitment (e.g. Davis and Whiting, 1977; Hopkins et al., 1981; McMurtray, 1986; Ratnaswamy and Warren, 1997). Perhaps a better understanding of turtle predator-prey interactions will be valuable to researchers, conservationists, and managers whose goals are to help establish self-sustaining turtle populations. However, for such information to be useful, investigators must have a better understanding of what is attracting or deterring predators to turtle nests. Although painted turtles are among the most abundant and widespread turtles in the U.S. (Marchand and Litvaitis, 2004), we suspect that some of the factors limiting this species also would affect populations of threatened species in the area such as Blanding’s turtles, as well as other imperiled populations throughout the world.

**Recommendations for future research**

There are several potential avenues for continued work on this species. Still, more research is needed to obtain better understanding of the role of sensory and visual cues in raccoon (predator) and turtle (prey) interactions. Additional studies could implement raking as an experimental treatment to see if such raking decreases nest predation rates. Future studies are necessary to quantify the long-term effects of anthropogenic structures on the population dynamics of ground-nesting species and their nest predators. For
instance, future studies could explore whether turtles are nesting closer or farther from
edges or anthropogenic structures, and responses relative to other variables such as turtle
and raccoon population size. If this is so, are the years when predation rates are the
highest, can one see a possible “correlation” or trend that more nests are laid closer to
edges or anthropogenic structures? Doing so may help protect some turtle populations
that are declining due to nest depredation. On a separate note, researchers could explore
the survival and behavior patterns of turtle hatchlings once they make it to the water, and
further look at the population structure of this well-established turtle nesting population.

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APPENDIX A. AN EXPERIMENTAL ANALYSIS OF MARKERS AND EDGE EFFECTS ON DEPREDATION OF TURTLE NESTS

By Jeramie Strickland¹, Paul Colbert², and Fredric J. Janzen¹

A paper to be submitted to Journal of Herpetology

ABSTRACT

Understanding how potential predator cues and habitat features affect predation of turtle nests is important because nest predators can influence the demographic structure of turtle populations. We constructed artificial turtle nests in an area used by nesting painted turtles (Chrysemys picta) to investigate the relative importance of visual and olfactory signals (both natural and anthropogenic) and edge effects on nest predation. Overall, 34% of the simulated nests displayed evidence of predation. Neither rocks or flags used to mark nests (visual and olfactory cues left by researchers) nor slough water (a presumably olfactory cue left by nesting turtles) significantly influenced predation rates. Instead, predators located artificial nests based solely on surface soil disturbance and proximity to habitat edges. These results suggest that predators use select natural cues (as opposed to anthropogenic markers) and habitat edges to locate painted turtle nests, confirming outcomes from prior observational studies at this site. These findings provide valuable insights into the impact of anthropogenic markers, surface soil disturbance, and edge effects on the population dynamics of nesting turtles and their predators.
Predator-prey dynamics are important factors in the ecology of populations, especially in terms of community structure and organization. For oviparous tetrapods, nest predation is of particular interest because it is a primary cause of reproductive failure (amphibians, Gregoire and Gunzburger, 2008; birds, Ricklefs, 1969; Zanette, 2002; reptiles, Congdon et al., 1983) and is thus a key determinant of recruitment rates. Indeed, high nest mortality has been implicated in the decline of some avian (Ricklefs, 1969; Martin and Guepel, 1993) and turtle (Gibbons, 1968) populations. As such, an understanding of the factors that influence predator foraging success is critical to population studies and management.

Predators could adopt hunting tactics based on sensory cues associated with targeted prey species. Olfaction is thought to play a prominent role in predator-prey interactions involving mammalian predators and their prey, although few experimental studies have been carried out to test this assumption (Russell, 2005). Raccoons are particularly important predators of turtle nests (Mitchell and Klemens, 2000), using sight and/or olfaction to locate nests (Zeveloff, 2002; Ninomiya et al., 2005). Hence, identifying how raccoons locate turtle nests has significant management implications.

Studies of turtle reproductive biology generally involve a system that allows identification of individual nests. Surveying flags or other markers are often used for this purpose (e.g. Tuberville and Burke, 1994). Rollinson and Brooks (2007) found that marking artificial nests with Popsicle sticks increased predation rates. Thus, in addition to cues left behind by nesting turtles (soil disturbance, scent trails left by turtles traveling to and from nest sites, etc.), researchers could potentially add informative attractants and thereby elevate predation rates.
Predator search efficiency and the utility of sensory cues may be influenced by local or habitat factors. Nest predators frequently direct their prey-searching activities along ecological edges, such as any transition between forests, roads, lawns, water, and other open habitats (Marchand and Litvaitis, 2004). This nonrandom behavior increases the chances of predation along such edges, as documented in previous observational studies involving turtle nests (Temple, 1987; Kolbe and Janzen, 2002a, b). Still, such observations have not been subjected to experimental study.

As a supplement to over 20 years of observational study, we used artificial nests to examine predator behavior in response to the presence or absence of soil disturbance, rocks, flags, slough water, and forest and slough edges. Artificial nests can enhance understanding about factors that influence natural nest detection and lead to increased nest predation. Use of artificial nests ensures adequate sample sizes and allows for placement of treatments according to the experimental design (Whelan et al., 1994). Specifically, we experimentally investigated (1) the relative importance of various visual and olfactory cues from both natural and anthropogenic sources on turtle nest predation and (2) the effect of nest spatial distribution (i.e., near vs. far from slough or forest edges) on survival.

MATERIALS AND METHODS

Study site

This research was conducted at the Thomson Causeway Recreation Area near Thomson, Illinois, USA (41°57’N, 90°7’W), where typically 150-300 painted turtle (Chrysemys picta) nests are deposited each year between mid May and early July, and studied as part of a long-term project (Weisrock and Janzen, 1999; Janzen and Morjan,
2001). The Thomson Causeway is a 450 x 900 m island near the eastern bank of the Mississippi River. The South Potter’s Marsh nesting area (1.5 ha) is a campground on the east side of the island, bordered to the east by a backwater slough and to the south and west by wooded areas (Kolbe and Janzen, 2002a), creating ecological edges. Predation of Chrysemys nests varies spatially, typically occurring more frequently along these edges, and ranges from <20% to >95% among years (Kolbe and Janzen, 2002a; Bowen and Janzen, 2005).

**Data collection**

*Effect of soil disturbance, rocks, and flags (experiment 1)*

Artificial nests were constructed between 1800-1830 h on 13 June 2005 in areas used by nesting painted turtles and nest predators. Eight nest treatments were established in all possible combinations of presence/absence of soil disturbance, rocks, and flags. Surface soil disturbance was accomplished by digging a 10x10 cm cavity, inverting the soil, and backfilling. Nest depth mimicked that of natural painted turtle nests (~10 cm) (Morjan, 2003). A ~2-cm$^3$ piece of gravel (i.e., rock) and/or a wire stake surveyor flag was placed at the location of nests where these treatments were applied. Each treatment and treatment combination was replicated twice within each of two blocks located a few meters from the slough (see Figure 1). Nests in each block were constructed 2-m apart from each other, similar to distances between natural painted turtle nests at the Thomson Causeway (Valenzuela and Janzen, 2001), forming a 4x4 matrix of artificial nests with treatment positions randomized within each block.

No rain occurred during or after nest construction, reducing chances of affecting the surface of the soil. Artificial nests were monitored overnight for signs of digging by
predators. A nest was considered depredated if there were any signs of digging at the nest site. Nests were considered successful if no digging was apparent.

Effects of soil disturbance, slough water, and habitat edges (experiment 2)

Artificial nests in this experiment were constructed between 1800-1830 h on 15 June 2005, again in areas used by nesting painted turtles and nest predators. Four nest treatments were established in all possible combinations of presence/absence of soil disturbance and slough water. Locations receiving an olfactory cue had ~20 ml of slough water emptied directly on the top of the “nests”. Each treatment and treatment combination was replicated twice within each of six blocks; two located a few meters from the west forest edge, two located a few meters from the slough, and two located in the center of the nesting area (~50 m between the forest and the slough) (see Figure 1). Again, nests in each block were constructed 2-m apart from each other, forming a 2x4 matrix of artificial nests with treatment positions randomized within each block. No rain occurred during this experiment, which ran for 36 h. The same criteria as in the first experiment were used to assess predation.

Data Analysis

Likelihood ratio G-tests were used to determine whether the presence or absence of soil disturbance, rocks, flags, slough water, and habitat location influenced nest predation. Assuming that nest predation events are independent (Valenzuela and Janzen, 2001), the probability of nest success was calculated for each treatment on the basis of predation percentage (Sauer and Williams, 1989). Statistical tests were conducted using Pop Tools version 2.7.5 (Hood, 2006).
RESULTS

The overall predation rates on natural painted turtle nests and artificial nests in 2005 were 95% (272/285) and 34% (27/80), respectively. All predation on nests occurred at night.

Small rocks and wire stake flags did not significantly attract or repel nest predators, indicating that predators did not use researcher-generated cues to locate artificial turtle nests. Predation rates on artificial nests with rocks were identical to those on artificial nests without rocks (8/16 in each case). Similar results for nest predation were obtained with respect to the presence or absence of flags (again, 8/16 in each case). In contrast, artificial nests that received soil disturbance were significantly more likely to be destroyed compared to nests that did not receive any soil disturbance (15/16 vs. 0/16; G = 229.4, df = 1, P < 0.001). Seven of the eight natural *Chrysemys* nests constructed on the same day as this experiment were depredated.

The results of the second experiment mirrored those of the first experiment, where relevant. Most predation on artificial nests occurred on the first night. Only four of 12 predation events in this experiment took place during the second night. All four of the natural *Chrysemys* nests constructed on the same day as this experiment were depredated within 24 h. Once again, artificial nests with soil disturbance were significantly more likely to be depredated than were artificial nests without soil disturbance (12/24 vs. 0/24; G = 85.4, df = 1, P < 0.001). Similar to the results for rocks and flags, artificial nests that received slough water were no more likely to be depredated than were nests that did not receive any slough water (5/24 vs. 7/24; G = 1.7, df = 1, P = 0.193). Most strikingly, rates of predation for artificial nests located near habitat edges were significantly elevated.
compared to those of artificial nests located in the middle of the study site ($G = 73.3$, df = 2, $P < 0.001$). For both edge areas, 6/16 artificial nests were depredated, whereas no artificial nests were depredated in the central area. These overall findings indicate that predators at this field site used local soil disturbance to detect artificial turtle nests.

**DISCUSSION**

Field studies of turtle reproduction are increasingly important because the life-history strategies of long-lived species are incompletely understood and turtles are recognized as essential components of many ecological communities (Moll and Moll, 2004). Predation is the main cause of nest failure for most turtle populations (e.g. Congdon et al., 1983; Ernst et al., 1994), yet the cues used by predators to detect turtle nests are inadequately known. In addition, field studies of turtle reproduction depend on the assumption that researchers do not influence predation rates. We employed artificial nests to examine cues used by predators to locate turtle nests. While use of artificial nests is controversial, they allow experimental control over treatments and confounding factors (Whelan et al., 1994). We document that such nests provide valuable insights into predator behavior, as others have also found (e.g. Marchand et al., 2002).

Most of the nesting turtles enter the area from the slough. Scent trails left by turtles while traveling from water to nest sites might aid predators in locating nests. Moreover, in earlier years we often used surveying flags to mark nests, switching to small rocks in more recent years. We found that neither slough water, nor rocks or flags used to mark nests, had any apparent influence on predation on artificial nests. Although Rollinson and Brooks (2007) found that marking nests with Popsicle sticks increased predation rates, our results are consistent with the findings of Burke et al. (2005) and
Tuberville and Burke (1994) concerning nest flags. Also, presence or absence of turtle eggs in nests does not seem to be an important factor influencing predator behavior at the Thomson Causeway with respect to anthropogenic markers. Natural *Chrysemys* nests (containing eggs) marked with flags exhibit similar rates of predation as natural nests without such flags (e.g. 117/151 vs. 36/49 in 1998), reflecting the lack of differential predation on artificial nests with and without flags in our experiment.

Disturbance of the soil surface was the sole local determinant of nest predation in this study. Not one artificial nest without the soil disturbance treatment was depredated in either experiment. These results imply strong selection for more fastidious nesting behavior in painted turtles at our site or for nesting just prior to (or during) a substantive precipitation event, either of which would better camouflage a nest. Indeed, Bowen and Janzen (2005) found that *Chrysemys* nests constructed at our site on days with substantial rainfall (>1.27 cm) were significantly less likely to be depredated than nests constructed on days with little or no rainfall.

As with many natural avian (Angelstam, 1986; Paton, 1994) and turtle (Temple, 1987; Kolbe and Janzen, 2002a, b; Marchand et al., 2002; Marchand and Litvaitis, 2004) nests, we document that artificial nests are subject to predation pressure that is inversely related to the proximity of the nests to an ecological edge. Because raccoons are edge-inhabiting animals, their densities and activities typically increase in fragmented habitats (Harris, 1984). Although other predators inhabit the nesting area of our long-term study site, raccoons are the dominant predators (Bowen and Janzen, 2005). Consequently, raccoon-induced selection substantially disadvantages turtles that nest closer to habitat edges where predation risk is elevated. Such a pattern of selection at our site favors the
typical behavior exhibited by older painted turtles, which tend to nest farther from water than younger females (Harms et al., 2005). The ecological and evolutionary ramifications of this scenario need to be more fully explored, because older females already produce larger offspring (Bowden et al., 2004) with enhanced post-hatching survivorship compared to younger females in this population (Paitz et al., 2007). That is, why don’t younger females in this population delay reproduction given that the odds of successfully recruiting offspring at this life stage seem to be stacked against them?

Factors affecting survival of turtle nests are of special interest because turtle populations are declining globally (Gibbons et al., 2000; Klemens, 2000). Predation is a major factor limiting populations of freshwater turtles (Marchand et al., 2002). Still, management attempts to create new nesting areas to enhance recruitment (e.g. Kiviat et al., 2000) might be unsuccessful if the cues that predators use to locate nests are not carefully considered. In our case, anthropogenic markers appear not to influence the probability of nest destruction by predators. Moreover, our experimental findings provide valuable insights into the impact of surface soil disturbance and habitat edge effects on the population dynamics of nesting turtles and their predators.

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Figure 1. Each treatment and treatment combination was replicated twice within each of six blocks; two located a few meters from the west forest edge, two located a few meters from the slough, and two located in the center of the nesting area (~50 m between the forest and the slough). Nests in each block were constructed 2-m apart from each other, forming a 2x4 matrix of artificial nests with treatment positions randomized within each block.