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FACTORS AFFECTING PREDATION ON WOOD TURTLE (*GLYPTEMYS
INSCULPTA*) NESTS IN THE UPPER PENINSULA OF MICHIGAN

By

Jenny Lynn Rutherford

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2010

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ABSTRACT

FACTORS AFFECTING PREDATION ON WOOD TURTLE (*GLYPTEMYS INSCULPTA*) NESTS IN THE UPPER PENINSULA OF MICHIGAN

By

Jenny Lynn Rutherford

Understanding predator foraging habits and nesting ecology of turtles is essential for the long term management of predator and prey. The objectives of this study were to (1) collect descriptive data on nesting ecology, including nest predation rate of a Wood Turtle population in the Upper Peninsula of Michigan, (2) investigate potential cues used by predators for location of Wood Turtle nests, and (3) determine effects of the distance of nests from a river on predation. Natural nests (identified by oviposition behavior of females) were marked and monitored for predation. Additionally, simulated nests were created with 1 of 4 treatments applied: soil disturbance, turtle-scented water, soil disturbance and turtle-scented water, and distilled water (control). In a second experiment, artificial nests with buried chicken eggs were created at varying distances from the river and monitored for predation. Natural nest in this study experienced a low predation rate (4/7) compared to other studies. This result may be an artifact of small sample size or the remoteness of the study area, absence of human disturbance and resulting low density of raccoons. My results also suggest that nest predators used soil disturbance cues primarily for locating nests. Thus, applying a chemical cue to artificial nests in future empirical nest predation studies may be irrelevant. Nest predation decreased as nest distance from the river increased, which may have important conservation implications for future management plans.

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INTRODUCTION

Wood Turtles (*Glyptemys insculpta*) are one of the most terrestrial pond turtles (Family: Emydidae) in North America (Kaufman, 1992). They inhabit meadows and riparian or floodplain habitat for most of the summer (Arvisais et al., 2004). During early-spring and late-fall they inhabit sandy to partially rocky streams where mating occurs (Arvisais et al., 2004). Wood Turtles overwinter in rivers under the ice by lodging themselves under logs or resting on the river bottom (Greaves and Litzgus, 2007). Individuals generally occupy small home ranges (1.05 ha) (Harding and Bloomer, 1979) and demonstrate home range fidelity (Carroll and Ehrenfeld, 1978). Wood Turtles travel short distances (except during the nesting season), but have been found up to 300 m from a stream (Kaufman, 1992; Arvisais et al., 2002). Wood Turtles are opportunistic omnivores, eating in or out of water (Harding and Bloomer, 1979). Their diet includes leaves (*Salix*, *Alnus* and *Fragaria* sp.), berries (*Rubus*, *Vaccinium* and *Fragaria* sp.), algae, fungi, mollusks, dead fish, tadpoles, mice and earthworms (Harding and Bloomer, 1979).

Wood Turtle populations are sparsely distributed throughout the northeastern United States and southern Canada (Ernst et al., 1994). Numerous studies have documented that Wood Turtle populations are declining throughout their range (Harding and Bloomer, 1979; Ernst and McBreen, 1991; Harding, 1991; Ernst et al., 1994; Burger and Garber, 1995; Daigle and Jutras, 2005; Suamure et al., 2007). Harding and Bloomer (1979) observed noticeable declines of Wood Turtle populations in Michigan and New

Jersey due to collecting turtles for the pet trade, urban development and human recreation. Burger and Garber (1995) found that Wood Turtles were declining due to human recreation, pollution, and increased predator abundance because of human-altered habitat. Agricultural practices are responsible for high adult mortality and injuries in southern Quebec, Canada (Daigle and Jutras, 2005; Suamure et al., 2007). A mark-recapture study showed that habitat destruction caused a Wood Turtle population to decline by 50% in seven years (Daigle and Jutras, 2005).

Terrestrial nesting habitat is vital to a healthy Wood Turtle population and thus, nesting ecology studies are a research priority (Bowen and Gillingham, 2004). Favored nesting sites are open sandy soil or gravel, well-elevated and devoid of disruptive vegetation (Farrell and Graham, 1991). They are usually in south facing areas that receive ample sunshine (Arvisais et al., 2004). Natural nesting habitat includes sand or gravel point bars and eroding stream banks (Harding, 1997). Additionally, Wood Turtles utilize human-created nesting areas, such as gravel pits, gravel roadsides and railroad grades (Brooks et al., 1992). Female Wood Turtles exhibit nest site fidelity between years and in the northern part of their range have relatively short nesting periods (Walde et al., 2007). The onset of nesting depends on annual weather patterns, but typically begins in late-May to early-June and ceases in mid- to late-June in Michigan (Harding and Bloomer, 1979; Walde et al., 2007). Nesting can occur anytime during daylight hours, but is most common in early morning and evening, and is often triggered by rain (Walde et al., 2007). Females nest once per year, lay 5-13 (average 10) eggs per clutch (Harding and Bloomer, 1979) and exhibit genetically dependent sex determination (GSD) (Harding, 1997).

Information on nesting ecology (including suitable nesting area parameters such as slope, aspect, substrate and size) is lacking for Wood Turtle populations in Upper Michigan.

Wood Turtles are characterized by low reproductive success, a long juvenile period (12-15 years) (Kaufman, 1992) and long life spans (> 40- 50 years; Harding, 2008). As a result of these life history traits, increased adult mortality rates can greatly impact Wood Turtle populations. Human activities, such as the building of roads, agricultural activities and deforestation, can rapidly increase adult mortality rates (Brooks et al., 1991, Daigle and Jutras, 2005). If mortality rates exceed recruitment rates, then such populations will be extirpated (Compton et al., 2002). In the last thirty years, nest predation and adult mortality rates have increased dramatically in parts of Michigan (Harding, 2008).

Predation rates on turtle nests are generally high and vary between turtle populations and species of turtles. Nest predation rates of Blanding's Turtle (*Emydoidea blandingii*) in Michigan were 67% (Congdon et al., 1983). Predation rates of Snapping Turtle (*Chelydra serpentina*) nests in Michigan were 70% (Congdon et al., 1987) and in New York 94% (Petokas and Alexander, 1980). A study in Florida found that 89% of Yellow-bellied Slider (*Trachemys scripta*) nests were depredated (Hamilton et al., 2002). Several studies have demonstrated that turtle nest predation is increased in areas with high human disturbance and subsequently increased predator numbers (Harding and Bloomer, 1979; Congdon et al., 1987; Harding, 1991, Burger and Garber, 1995). Most nest predation occurs 24-48 hours after nest creation (Harding, 1997).

Nest predation does not always mean nest failure though, because predators may not destroy all eggs. However, nest predation does reduce the number of eggs and

exposes eggs to changed temperature and moisture conditions (Marchland, 2004). Areas that have low predator densities generally have higher nest survival than areas with high predator densities (Walde et al., 2007). Few studies provide information on nest predation rates and nest success rates of Wood Turtle populations that are not influenced by human disturbance. Additionally, information on the status and size of Wood Turtle populations is lacking (Bowen and Gillingham, 2004).

Predators, mainly raccoons (*Procyon lotor*), are the primary cause of nest failure and hatchling mortality (Harding and Bloomer, 1979; Congdon et al., 1983). Raccoons are described as “human-subsidized predators” because they are capable of thriving in altered habitat and exhibit increased population densities where there is human disturbance. Raccoons are opportunistic omnivores with a diet that includes turtle eggs, bird eggs, crayfish, invertebrates and berries (Schoonover and Marshall, 1951). Raccoons are nocturnal and typically forage along river banks where food is likely to be found in water and on land (Cagle, 1949). It is unclear what cues are used by raccoons to locate nests, but turtle-associated chemical cues have been proposed (Spencer, 2002). Many species of turtles expel liquid from their bladders onto eggs during oviposition. The reason for this is unclear, but studies suggest that this liquid may facilitate digging, repel predators (Patterson, 1971), or moisten eggs to prevent desiccation (Jackson and Walker, 1997).

Contradictory statements are present in the literature concerning whether raccoons use chemical, visual or tactile cues while searching for turtle nests (Burke et al., 2005). Spencer (2002) suggests that raccoons locate turtle nests using chemical cues derived from the urine, bodies or eggs of turtles. However, several studies found that soil

disturbance cues and thus, tactile or visual senses are used by raccoons to locate nests (Wilhoft et al., 1979; Hamilton et al., 2002; Strickland and Janzen, 2008). Wilhoft et al., (1979) found that raccoons located artificial nests with turtle eggs, dove eggs, chicken eggs and ping pong balls in the absence of turtle urine, suggesting that vision or tactile senses are used rather than chemical senses. Hamilton et al. (2002) found that nest survival was not affected by the presence of chemical cues. Strickland and Janzen (2008) found that the presence of coyote or turtle urine did not affect nest predation rates and proposed that predators locate nests based on soil disturbance. Further investigation is necessary to better understand predator foraging behavior and turtle nest cues responsible for nest location.

There is also evidence that nest site selection by female turtles affects predation rates (Iverson, 1991; Kolbe and Janzen, 2002; Marchland et al., 2002; Spencer and Thompson, 2003). Strickland et al., (2010) found that predation rates of artificial nests increased near habitat edges (e.g., slough and forest), while Marchland et al. (2002) found that predation on artificial nests decreased as distance from water increased. Spencer and Thompson (2003) studied the turtle *Emydura macquarii* in Australia and found that predation rate decreased as the distance between nest sites and water increased. Congdon et al. (1987) reported that nests situated less than 30 m from water are more susceptible to raccoon predation. High predation rates of turtle nests near water are likely the result of predators using efficient foraging strategies to gather resources. The optimal foraging model states that animals act to maximize energy intake while minimizing energy costs (Charnov, 1976). In contrast, some studies suggest that nest placement does not affect nest success (Congdon et al., 1983; Rowe et al., 2005). Rowe et al., (2005) found no

relationship between Painted Turtles (*Chrysemys picta*) nest success and the distance between nests and water. No studies to my knowledge have examined the effects of nest distance from water on nest predation in Wood Turtles.

Objectives and Project Significance

The objectives of this study were to: (1) collect descriptive data concerning nesting ecology and estimate the nest predation rate of a Wood Turtle population in the western Upper Peninsula of Michigan, (2) examine potential nest cues used by mammalian predators for location of Wood Turtle nests and (3) determine the relationship between predation and distance from river shoreline for artificial turtle nests.

In Michigan, Wood Turtles are a Regional Forester Sensitive Species, which means that population viability is a concern (Bowen and Gillingham, 2004). Therefore, conservation of nesting habitat and documentation of nest predation rates have been identified as priority needs (Bowen and Gillingham, 2004; Casper and Buech, 2005).

The sensory ecology of turtle nest predators is poorly understood (Wilhoft et al., 1979). Understanding predator foraging habitats may lead to effective conservation programs for both predator and prey. Nesting ecology studies are necessary for turtles that are declining at significant rates, because management of nesting habitat or creation of artificial nest sites may increase recruitment rates and population sizes. The results of this study will provide insight into what cues predators use to locate turtle nests, and thus will aid in creating artificial nests that mimic natural nests for future nest predation studies. For example, if it is found that soil disturbance is used primarily by raccoons to locate nests, then applying turtle derived cue to artificial nests may not be necessary.

Creating artificial turtle nests similar to natural nests will provide better estimates of predation rates in future empirical studies. Results will also provide information on predator behavior in response to artificial turtle nests, which may have potential for decreasing predation on natural nests (i.e., artificial nests may confuse predators or distract them away from natural nests).

How the distance of nests from rivers affects predation has not been investigated for Wood Turtle populations. Development of artificial nesting beaches could be used to manage Wood Turtle population sizes, and nests created at greater distances from a river may have increased survival rates compared to nests closer to the river. This study will also provide information on the foraging ecology of Wood Turtle nest predators.

Hypotheses

Previous studies provide evidence of increased predation rates for Wood Turtle nests in areas with high human activity (Harding, 1991; Brooks et al., 1992; Tuttle and Carroll, 1997). If human influence has an effect on turtle nest predation, then areas with no human influence should experience lower predation rates than those exposed to human influence. I predict that predation rates on Wood Turtle nests will be lower in remote areas with little human influence than areas with high human influence, because predator density should be lower in these areas.

A number of studies have found that raccoons were able to locate nests without turtle scent associated with them (Wilhoft et al., 1979; Hamilton et al., 2002; Strickland and Janzen, 2008; Strickland et al., 2010). Raccoons were able to find simulated nests with ping pong balls (which obviously lack turtle chemical cues) and even chewed on

these artificial eggs (Wilhoft et al., 1979). These studies suggest that raccoons may use soil disturbance cues but do not address the possibility of predators using both soil-derived and turtle derived cues. Therefore, my second hypothesis is that raccoons use both turtle-derived and soil-derived cues to locate turtle nests because sensitivity to multiple cues (visual and chemical) should increase the probability of nest detection. If raccoons use chemical cues from both turtles and soil disturbance, then nests with turtle scent and soil disturbance should have significantly higher predation rates than nests with only turtle scent or soil disturbance associated with them. If raccoons use only turtle scent to locate nests, then nests with turtle scent should be depredated more than nests with soil disturbance, and nests with soil disturbance should experience predation rates similar to those of control nests.

Nest predators, such as raccoons, concentrate their foraging activities along habitat edges and water edges where food is abundant (Temple, 1986). Thus, I hypothesize that nest proximity to the river influences its probability of being encountered and depredated by a predator. I predict that will have increased encounter rates than nests further from the river. I predict that predation rates of artificial nests near the river will be higher than nests further from the river.

METHODS

Study Area

The study site was in the western upper peninsula of Michigan along a 1.5 km section of river in the Ottawa National Forest. The exact location is not disclosed for protection of the resident Wood Turtle population. The location of the study site is isolated, being several kilometers from a paved road, with little to no recent human disturbances (e.g., no fishing, hiking or logging). There was no evidence of human activity (except for me and two research assistants) at my study site in 2009 and 2010. The meandering river had sandy/gravel bars (i.e., nesting beaches) that stuck out on point bars which were ideal for nesting. The opposite side had cut banks (clay banks measuring 10-20 m high), which were not ideal for nesting because of the steep slope and hard clay substrate. The river contained numerous rocky riffles, deep pools and a sandy bottom. The river was about 5 to 10 m across and a few cm to several meters deep. There were also two log jams about 0.7 km apart, which provided basking sites and refuges for turtles. The surrounding floodplain habitat was a mature mixed hardwood-conifer forest with small beaver-caused clearings. Woody plants were diverse along the river, but consisted mainly of silver maple (*Acer saccharinum*), white spruce (*Picea glauca*), white cedar (*Thuja occidentalis*) and tag alder (*Alnus rugosa*). The dominant ground cover consisted of ostrich fern (*Matteuccia struthiopteris*), reed canary grass (*Phalaris arundinacea*) and canada reed grass (*Calamagrostis canadensis*).

Natural History Observations

Daily surveys for Wood Turtle nests were conducted late-May through late-June 2009, which is when nesting activity was most common. Binoculars (8x) were used to locate nesting Wood Turtles on suitable nesting beaches (i.e., sand and gravel bars). Turtles were usually observed from a canoe or an adjacent river bank to minimize disturbance to turtles and nesting beaches. When a turtle was located, it was observed until nesting activity ceased. After a natural nest was located, it was marked with a stick marker poked into the ground 1 m inland from the nest. Distance to the river's edge and nearest vegetation were measured for each nest using a 100 m measuring tape. A clinometer was used to measure the slope of each nest, a compass was used to measure aspect (compass direction in degrees facing away from nest), and date and weather were noted. Natural nests were checked daily for predation and recorded as depredated (all eggs consumed), partially depredated (not all eggs consumed) or non-depredated (no eggs consumed). The number of depredated nests that were not monitored was also counted daily. Egg shells from depredated nests were counted to estimate clutch size and discarded into the river to prevent re-counting of depredated nests.

Nest predation rates for natural nests were calculated by dividing the number of depredated nests by the total number of monitored nests. The total number of predator tracks (trails) observed on beaches 1, 3, and 5 were counted 5 times prior to nesting and 5 times during nesting ($N = 5$ per time period). These beaches were evenly spaced along the 1.5-km section of river and were chosen to reduce the likelihood of re-counting tracks from the same individual. A paired t-test in PASW (18.0) was used to compare track counts before and after nesting.

For descriptive purposes and for use in the following experiments, various parameters were measured for each beach used by nesting Wood Turtles. A 100 m measuring tape was used to measure beach length and width (water edge to vegetation edge). Substrate was classified as sand, gravel or mixed sand and gravel. A clinometer was used to measure the slope of each beach, and a compass was used to measure aspect (general direction in degrees that the beach was facing).

Additionally, Wood Turtles were captured by hand (unless they were nesting) and data were recorded for a long term monitoring study by the Ottawa National Forest service. Turtles were notched on their carapace with a file (Cagle, 1939) if not already marked, and identification numbers were noted. Data on sex, length and width of carapace, age, weight, reproduction, behavior, activity, date, time, and weather were noted. Turtles were released immediately after processing.

Experiment 1: Effects of Artificial Nest Treatment on Predation

Two hundred twenty-four artificial nests were constructed between late-May and mid-June, which is when nesting usually occurs in Wood Turtle populations in the northern part of their range (Walde et al., 2007). One hundred sixteen artificial nests were constructed between May 27 and June 2, 2009 (Period 1) and 108 nests between June 11 and June 23, 2009 (Period 2). For each period, 32-40 nests were created at 3-5 day intervals along the river (Table 1).

One of four treatments was applied to artificial nests: (1) turtle-scented water (turtle-derived chemical cue) (2) soil disturbance (soil-derived cue), (3) turtle-scented water plus soil disturbance and (4) distilled water (i.e., no turtle-scented water or soil

disturbance, which served as a control). Nests were always made in groups of four (one nest per treatment), placed 2 m apart in a symmetrical arrangement with nest treatment randomized within the group. Nest treatment was assigned by randomly selecting a wire-stemmed flag labeled with nest treatment. Nest groups were separated by at least 10 m to prevent non-independence between nest groups. All artificial nests were constructed in areas that had evidence of Wood Turtle activity (e.g., nest digs and tracks) in previous (Ottawa National Forest, unpublished data) and current years (i.e., 2009).

Table 1. The number of artificial nests created at each nesting area (beach) and date of creation (N = 224, 56 per condition). The number of artificial nests created at each nesting area depended upon the size of the area.

Date of Creation	Beach									Total
	1	2	3	4	5	6	7	8	9	
27-May-09	8		8	8	8	8				40
30-May-09	8	8	4	12				4	8	44
2-Jun-09			8	8	4	8		4		32
11-Jun-09	8		8	8	4	8				36
17-Jun-09	4	8	8	8	8					40
23-Jun-09	8	8	8		4		4		4	32
Total	36	24	44	44	28	24	4	8	12	224

Water from an aquarium, containing a wild-caught Wood Turtle, was used to obtain turtle-derived chemical cues for application to artificial nests. A female Wood Turtle collected from my study area on May 19, 2009 was transported to Marquette. The turtle was then placed in a 20 gallon aquarium in a lab at Northern Michigan University. The turtle remained in the tank for five days, after which it was returned and released at

the site of capture. The turtle was fed greens and 1-2 earthworms per day. The aquarium contained distilled water 20 cm deep and a rock with a wooden platform for basking. A heating lamp was used to heat one side of the aquarium. The room, water and basking site temperatures were 24°C, 12°C and 30°C, respectively. Control water was obtained from another 20 gallon (75.7 L) aquarium that contained no turtle, distilled water 20 cm deep, a rock and a wooden platform. Therefore, water from this aquarium had all conditions the same as the turtle aquarium, except it did not contain a turtle. Turtle water and control water were placed in 473 mL sterile plastic freezer containers, labeled and frozen until use. Turtle-scented water was discolored and the smell of turtle excrement was detectable by a human. Additional cues, such as eggs and turtle tracks, may be associated with ovipositing; however, turtle-scented water was used a turtle-derived cue because it could be applied without disturbing the soil.

Nests with soil disturbance were created by digging a 10-cm-deep hole with a trowel. Average nest depth, derived from depredated nests of Wood Turtles, is approximately 10 cm (Brooks et al., 1992). The nest cavity was re-filled with sand and/or gravel and the top of the surface was smoothed to mimic natural nest surfaces. Nests with turtle-scented water were created by applying 60 mL of turtle-scented water from a sterile measuring cup to the top of undisturbed soil. Turtle water was poured so as to prevent soil disturbance. Nests with both treatments were created by digging a 10 cm hole with a trowel, filling in the hole and applying 60 mL of turtle scented water on top. Control treatments (no turtle water or soil disturbance) received 60 mL of control water from another sterile measuring cup applied directly on the artificial nest.

Rubber gloves and rubber boots were worn to decrease the likelihood that human scent would attract or deter predators. Nests were marked with a wire-stemmed flag to allow relocation of the nests. Flags were positioned 1 m inland from the river and were planted at arms' length to minimize scent and disturbance around the nest site. Markers were labeled with nest treatment (e.g., B, D, T or C) and positions were sketched on a site map. Recent studies report that nest markers do not attract or repel nest predators (i.e., raccoons) and thus have no effect on nest predation (Burke et al., 2005; Strickland et al., 2010). No nests were disturbed by humans, probably because of the remoteness of the site. Nests were checked for predation on three consecutive mornings following nest creation and recorded as depredated or non-depredated. In previous studies, nests were most commonly depredated 24-48 hours following egg laying (Tinkle et al., 1981; Congdon et al., 1983). Nests were counted as depredated if digging was visible or the nest cavity was exposed, and non-depredated if no apparent disturbance occurred. If a nest cavity was exposed, it was left untouched. Nest predators were identified based on tracks surrounding the nest.

A Loglinear Logit saturated model was used to identify significant differences between treatment effects (PASW 18.0). The dependent variable was nest fate (categorical, depredated or non-depredated) and the independent variable was nest treatment. The logit approach was appropriate because one of the categorical variables was clearly dependent, and this method is more effective than traditional chi-square analysis when many cells have frequencies of zero. One limitation of the logit model is that it does not control for beach effects on the dependent variable. Thus, data was additionally analyzed using a randomized block experimental design to block for beach.

Only one randomly selected data point per beach was used in the analysis, lowering sample size to $N = 9$. A Cochran's Q test (Cochran, 1950) was applied to determine nest treatment effects on nest predation, with beach as the blocking effect. To test for significant differences between treatments, a multiple comparisons test was applied (Marascuilo and McSweeney, 1967). Similar results were found for both approaches mentioned above. Hence, beach did not have an effect on the variable being tested, so only the logit model is presented in the results.

Additionally, a paired t-test was computed by PASW Statistics (18.0) to determine mean differences in nest predation counts during the two periods of nest construction. A Fisher's Exact Test was run to determine if nest treatment had an effect on the type of predator digging up artificial nests.

Experiment 2: Effects of Nest Distance from River on Nest Predation

Artificial nests were constructed at three distances from the river to examine the effects of this variable on nest predation. These distances were ≤ 5 m (close), 7-10 m (medium) and ≥ 20 m (far). Due to the nature of the nesting areas, nests were created in sand or vegetation. This confounding variable was noted to determine microhabitat (sand vs. vegetated) effects on predation of artificial nests. Nests were considered in sand habitat if 50% or more sand was observed in 0.5 m² plots.

Transects (a line of 3 nests, one at each distance, and perpendicular to the river) were created in areas that had evidence of nesting turtle activity and nest predators. These areas are typically sand or cobble near the river and have vegetation increasing as distance from the river increases. All transects were created in areas with an open canopy.

Although variable, vegetation usually became dense at about 10-15 m distance from the river, which was likely an effect of elevation above the flood line.

Sixteen transects were constructed on May 22 - June 10, 2010. Nests were made along the river and transects were separated by a minimum of 10 m. For each nest, vegetation was cleared if necessary and a hole was dug with a trowel. One chicken egg was placed in the hole and sand was replaced. Sand plots (cardboard with 1 cm deep, wet sand) were placed around each nest to verify the type of predator disturbing the nest. Sand plots were constructed of 4 pieces of cardboard 23 cm in length arranged in a square to surround each nest. Wet sand, gathered near the river, was placed 1 cm deep on top of the cardboard to record predator tracks. Rocks were placed at the four corners to secure sand plots in place. Strickland et al. (2010) found that researcher-associated cues (e.g., rocks, flags) did not attract or deter turtle nest predators (i.e., raccoons). Nests were checked on three consecutive mornings for predation, and tracks were identified using a field guide (Elbroch, 2003). The dependent variable was nest fate (depredated or non-depredated) and the independent variable was nest distance from the river.

A Pearson's Chi-square Test was run to determine effects of distance from the river on artificial nest predation ($N = 16$). The frequency of depredated and non-depredated nests was compared for each level of the distance variable (close, medium, far). A Bonferroni correction test was applied to the alpha value for post hoc comparisons between groups (Neu, 1974). Additionally, data on natural nests from Experiment 1 were used to determine effects of distance from the river on predation of natural nests ($N = 5$ depredated nests). Natural nests were categorized similar to simulated nests and a Fisher's Exact Chi-square test was applied. Additionally, a Chi-Square Test was used to

determine microhabitat effects on nest predation. The dependent variable, nest predation, was dichotomous (1 = predation, 0 = no predation). All analyses were performed using PASW Statistics (18.0) software.

RESULTS

Natural History Observations

Predation of Natural Nests. Seven natural nests were marked and monitored for predation. Three of those nests were depredated less than 24 hours after construction, one was depredated two days after construction, one was unsuccessful due to environmental factors (dry, hot weather caused eggs to desiccate) and two nests were successful (i.e., at least one egg from each nest hatched). Thus, 29% of nests were successful and a predation rate of 57% was found for this Wood Turtle population (N =7).

Nest Predation Counts and Predator Activity. Twenty-five depredated nests were found in the study area in 2009 and 12 were found in 2010. Raccoon and River Otter (*Lontra canadensis*) were the only predators of natural nests detected in the study area. Mean number of predator tracks on beaches was significantly greater during nesting season ($\bar{x} = 8.6$, $SD \pm 1.14$, $N = 5$) than prior to nesting ($\bar{x} = 1.2$, $SD \pm 1.3$, $N = 5$) ($t = -10.752$, $df = 8$, $P < 0.001$) in 2009. There was a significant difference in mean number of artificial nests depredated (mean = 3 vs 9, $N = 18$) between the two periods of nest construction ($t = -2.449$, $df = 16$, $P = 0.026$). Tracks of White-tailed Deer (*Odocoileus virginianus*), Gray Wolf (*Canis lupus*), American Mink (*Mustela vison*), Coyote (*Canis latrans*), Black Bear (*Ursus americanus*) and Bobcat (*Lynx rufus*) were also seen on the river banks, but there was no evidence of natural nest predation by these species.

Nesting Ecology. Female Wood Turtles were observed digging on eight nesting areas in 2009, seven of which had signs of oviposition (i.e., depredated or hatched nests).

Beach six did not have evidence of oviposition, even though it was large and exposed with a sandy substrate. This was probably due to its northeast facing aspect. Beaches used for nesting were primarily facing south, southwest or northwest (Table 2) and had a slope less than 15°. Oddly, one Wood Turtle nested on a northeast facing cut bank that had a 35° slope and a hard, clay substrate (this nest was depredated). The average slope of natural nests was $11.6^\circ \pm 9.5^\circ$ (N = 19, range = 1-35°). The mean aspect of natural nests was $218.6^\circ \pm 57.7^\circ$ (N= 18, range = 60-295°). Mean distance from vegetation was 1.64 ± 1.19 m (N = 13, range = 0.01-3.7 m). Mean distance from river of natural nests was 5.5 m, $SD \pm 3.23$ (N = 18, range = 1.5-12 m).

Wood Turtles were seen digging on nesting beaches most commonly in the evening (\bar{x} time = 19:52, $SD \pm 163$, N = 12, range = 16:00-21:33) and early morning hours (\bar{x} time = 06:75, $SD \pm 150$, N = 4, range = 06:00-09:00). In the summer of 2009, nesting began June 14 at 16:00 after a thunderstorm. Nesting continued until June 24, 2009. In the summer of 2010, nesting season was considerably earlier and of longer duration than in 2009. Nesting started on May 22, 2010 (32 days before nesting started in 2009) and lasted until June 15.

Turtles were observed digging nests with their hind legs and faced up-slope. Mean interval between deposition of individual eggs was 90.4 seconds ($SD \pm 3.64$, N = 5) and mean clutch size was 7.4 ($SD \pm 3.18$, range = 1-15, N = 18). After oviposition, turtles covered their eggs with loose sand/gravel using alternating movements of their back legs and proceeded to move their whole body in a “U.” Turtles packed down the gravel or sand by lifting their rear end and slamming it down (as described by Harding and Bloomer, 1979). Turtles retreated to the river immediately after nesting.

No-see-ums or biting midges (Family: Ceratopogonidae), a common ectoparasite of Wood Turtles (Wirth and Hubert, 1962), were often observed on nesting Wood Turtles at my study site. Ceratopogonids covered turtle's faces, limbs and in between scutes on the carapace. To date, there are no data on the affects of Certapoginids on Wood Turtles' well-being. After turtles finished nesting, Certapogonids remained on top of the recently made nests for about 5-10 minutes.

Table 2. Characteristics of nesting beaches used by female Wood Turtles in June, 2009.

Beach	Size (m)	Substrate	Slope (°)	Aspect
1	120 x 10	Mixed	15	NW
2	100 x 15	Gravel	5	W
3	110 x 10	Mixed	15	SW
4	50 x 15	Sand	2	SW
5	15 x 10	Gravel	15	SW
6	200 x 15	Sand	10	NE
7	15 x 10	Gravel	15	NW
8	40 x 20	Clay	35	NE

Dominance Behavior. On June 17, 2009 I observed three female Wood Turtles digging on a 15x10 m gravel bar at my study site. During peak nesting season, female Wood Turtles emerge from the river to investigate potential nest sites (e.g., sand or gravel bars along the river). Turtles dig in several places before depositing eggs in a nest cavity. At approximately 2130 h, I observed one female (Turtle 1) on a nesting beach digging in the gravel with her front feet. At 2131 h another female (Turtle 2) emerged from the river, crawled onto the same nesting beach, and started digging about a meter and a half from Turtle 1. At 2133 h, a third female (Turtle 3) emerged from the river, approached Turtle 1, then bit and lunged toward Turtle 1. Turtle 1 moved to another spot on the

beach. Turtle 3 moved toward Turtle 2 and repeated the behaviors that she had just directed toward Turtle 1. Turtle 2 moved to a different spot on the beach as well. Both of the submissive turtles retreated to areas of the beach that were lower and closer to the river and resumed digging. Turtle 3 started digging at 2140 h where Turtle 1 was seen digging at 2130 h. Turtles stayed in these positions until dark and I could no longer observe them.

Mating and Site Fidelity. I observed a pair of Wood Turtles in copulation on three consecutive days on June 20-22, 2009. Mating occurred in the same location, near a popular nesting beach on all three days. The pair was mostly in water during copulation, but sometimes they were half in water and half on shore. As part of a larger study, individual turtles were marked (notched with a file) at my study site, allowing for identification of individual turtles. Hence, I am certain that it was the same individuals in copulation on all three days.

Some Wood Turtles exhibited site fidelity. For example, I observed one female turtle basking in the same location on the river bank on five consecutive days. A seven year old Wood Turtle was seen basking on the same log above the river daily for two consecutive weeks and a hatchling was found basking on the same log three days in row.

Experiment 1: Effects of Artificial Nest Treatment on Predation

In total, only 8% (18/224) of all simulated nests were depredated (Table 3). Twenty percent (11/56) of nests with soil disturbance were depredated and 12% (7/56) of nests with soil disturbance plus turtle-scented water were depredated. There was a significant difference in predation between nest treatments. Specifically, nest predation

was significantly higher in D than T ($Z = 2.299$, $df = 3$, $P = 0.02$) and C ($Z = -2.299$, $df = 3$, $P = 0.020$). Nest predation was not significantly different between D and B ($Z = 0.512$, $df = 3$, $P = 0.318$). Nest predation was not significantly different between B and T ($Z = -1.928$, $df = 3$, $P = 0.054$) or C ($Z = -1.928$, $df = 3$, $P = 0.054$) (see Table 4).

Nests with only turtle water or control water were not depredated. River Otter and raccoon were the main nest predators, but one American Mink was also detected. If just raccoon and otter are considered, then nest treatment did not have a significant effect on the type of predator that depredated the nest, but sample sizes were relatively small (Fishers Exact Test $P = 0.134$).

Table 3. Proportion and number of nests depredated for each treatment and predator elicited. D=soil disturbance, B=soil disturbance plus turtle-scented water, T=turtle-scented water, C=control water. N = 56 for each treatment.

Treatment	Proportion of Depre- dated Nests	No. of Depredated Nests	Predator
D	20%	11	6 otter, 4 raccoon, 1 mink
B	12%	7	1 otter, 6 raccoon
T	0%	0	
C	0%	0	
Total	8%	18	

Table 4. Loglinear Logit Saturated Model results of nest treatments effects on predation.

D = soil disturbance, B = soil disturbance and turtle-scented water, T = turtle-scented water, C = control ($\alpha = 0.05$, * = significant).

Treatment	Z-value	df	P-value
D*T	-2.299	3	*0.02
D*C	-2.299	3	*0.02
D*B	0.512	3	0.318
B*C	-1.928	3	0.054
B*T	-1.928	3	0.054

Experiment 2: Effects of Distance from River on Nest Predation

Forty-eight percent of artificial nests at all distances were depredated (23/48) (Table 5). Sixty-nine percent (11/16) of close nests were depredated, 56% (9/16) of medium distance nests were depredated and 19% (3/16) of nests far from the river were depredated. Most such nests were depredated 1 day after creation (78%, 18/23). No nests were depredated on day 2 and 22% (5/23) were depredated on day 3. Interestingly, all of the nests depredated on day 3 were in the “close” (<5 m from the water) category.

Table 5. Number and proportion of nests depredated at close, medium and far distances for each day. There was a significant difference between predation rates of nests at various distances from the river (Pearson’s $X^2 = 8.682$, $df = 2$, $P = 0.013$, $N = 16$)

Distance	# of Predated			Day 1	Day 2	Day 3
	Nests	% Predated				
Close	11	69%		6	0	5
Medium	9	56%		9	0	0
Far	3	19%		3	0	0
Total	23	48%		18	0	5

There was a significant difference ($\alpha = 0.05$) between predation rates of artificial nests at various distances from the river (Pearson's $X^2 = 8.682$, $df = 2$, $P = 0.013$, $N = 16$) (Figure 1). A post-hoc comparison of groups showed there was a significant difference between predation at close and far nests ($P = 0.002$) (Bonferonni correction $P = 0.008$). There was not a significant difference between predation of close and medium nests ($P = 0.212$) nor medium and far nests ($P = 0.050$). Artificial nests created in non-vegetated areas were depredated most. Specifically, there was a significant difference in predation between nests made in open sand and vegetated areas (16 vs. 7) (Pearson's X^2 with continuity correction = 12.023, $df = 1$, $P = 0.001$). Eighty percent (16/20) of nests created in sand were depredated and only 25% (7/28) of nests created in vegetated areas were depredated. This variable was not included in the original model because it had a

Raccoon, Otter and White-tailed Deer tracks were detected on sand plots. Usually only tracks from one species were recorded on sand plots, which simplified predator identification. Eighty-seven percent (20/23) of nests were depredated by raccoon, 4% (1/23) of nests were depredated by River Otter. Nine percent (2/23) of nest predators were unidentified due to rain or tracks of different species on sand plots. When tracks of two species (e.g., deer and raccoon) were present on sand plots, I could not be certain as to what species depredated the nest. Although there are no accounts that deer depredate turtle nests, deer are known to prey upon grassland bird nests (Pierce and Pobprasert, 2007).

Natural nests in medium and far categories were combined because there were no natural nests found further than 12 m from the river. There was not a significant difference between predation rates of natural nests at close and medium distances from

the river (Fisher's Exact Test $X^2 = 3.600$, $df = 1$, $P = 0.103$, $N = 5$) (Figure 2). There was no evidence of turtles nesting more than 12 m from the river. All nests were found in sandy or rocky substrate with little vegetation. Two successful nests were 3.5 m and 7 m from the river.

Figure 1. The number of artificial nests that were depredated at close (≤ 5 m), medium (7-10 m) and far (≥ 20 m) distances from the river. A Chi-square test showed that there was a significant difference between nest predation at various distances from the river (Pearson's $X^2 = 8.682$, $df = 2$, 60 , $P = 0.013$, $N = 16$).

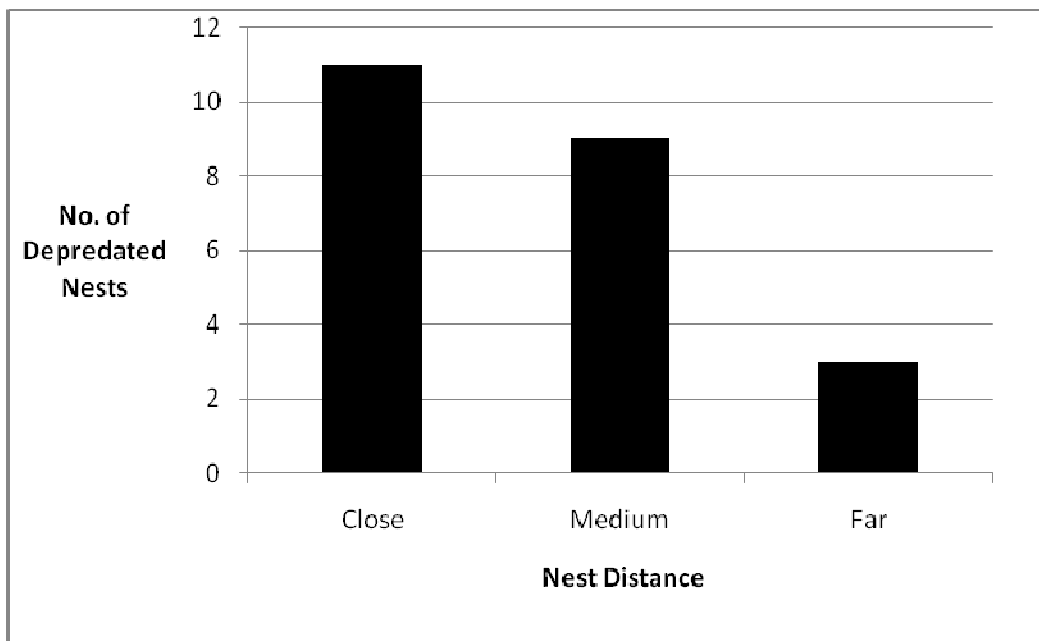
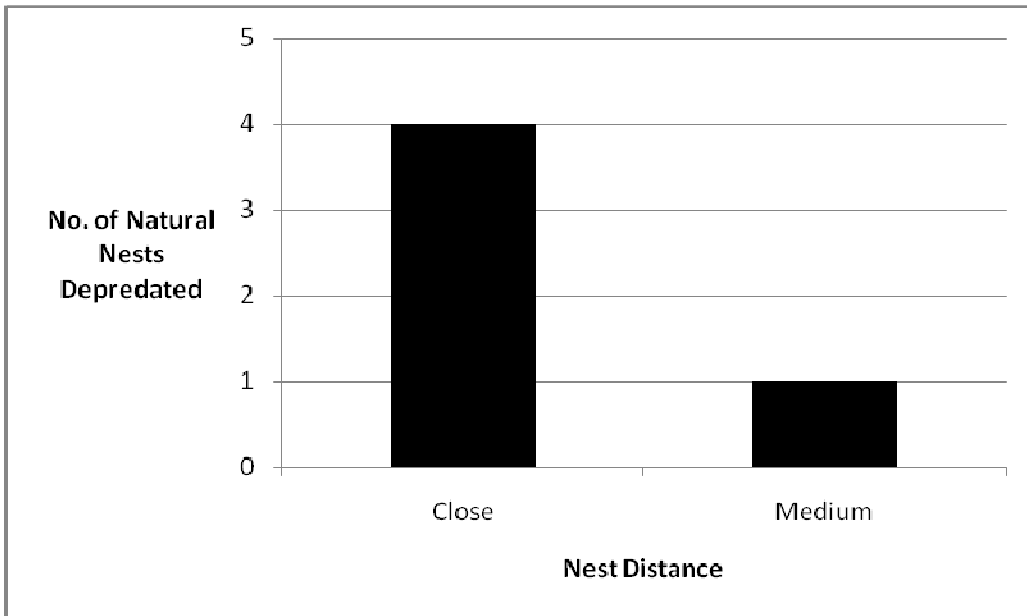


Figure 2. The number of natural nests that were depredated in close (≤ 5 m), medium (6-19 m) distance categories. There was not a significant difference between predation on natural nests at close and medium distances from river (Fisher's Exact Test $X^2 = 3.600$, $df = 1$, $P = 0.103$, $N = 5$).



DISCUSSION

Natural History Observations

Predation of Natural Nests. Wood Turtles retreated to the river whenever they felt threatened, making observations of nesting difficult. Consequently, a small number of natural nests were detected. A predation rate of 57% was calculated at my study area, which is low compared to similar studies on Wood Turtles (Table 6). One exception is Walde et al. (1997), who found no nest predation despite the presence of predators in the study area. Nest predation reached 100% in Schoolcraft County, Michigan (Harding, 1991) and in a New Hampshire study area (Tuttle and Carroll, 1997). Nest predation was 88% in a study area in Ontario (Brooks et al., 1992).

Table 6. Comparison of Wood Turtle nest predation rates for 5 populations.

Nest predation	Source	State
100% (n=4)	Tuttle and Carrol, 1997	New Hampshire
88% (n=17)	Brooks et al., 1992	Ontario
0%	Walde et al., 2007	Quebec
near 100%	Harding, 1991	Michigan (Schoolcraft Co.)
57% (n=7)	*This Study*	Michigan

Three out of the five nests that were monitored, were depredated less than 24 hours following oviposition. One nest was depredated two days after nest construction and, oddly, one nest was dug up 79 days after construction, although turtle embryos were not consumed. It was hot and dry with no rain for 14 consecutive days during the first two weeks in September, and I think this contributed to nest mortality. It is likely that the

hot, dry weather conditions desiccated turtle eggs making them malodorous, and these rotting eggs attracted a predator. However, the embryos were so desiccated that they were not palatable and not consumed.

Turtle populations tolerate relatively high nest and juvenile predation rates so long as adult mortality remains low. This results from life history traits, which include long adult life spans and fecundity increasing with age (Congdon et al., 1993). However, when human disturbance, and consequently predator abundance, is high, predation rates increase dramatically (Harding, 1991). Rates nearing 100% are common in disturbed areas and may be detrimental to populations (Harding and Bloomer, 1979; Harding, 2008), especially when adult mortality is high (Burger and Garber, 1995). A relatively low predation rate was found in my study. This may be an artifact of the small sample size ($N = 7$), or the presence of wolves at my study site may have helped to keep raccoon and otter numbers low. A more important influence may have been that human disturbance was absent.

A good indication of Wood Turtle population stability is the presence or absence of human activity (Walde et al., 2003). Garber and Burger (1995) reported that Wood Turtle populations declined by 100% in 10 years, because Wood Turtle habitat was opened for human recreational use (i.e., hiking and fishing). There was no human activity at my site, except for researchers, during the summers of 2009 and 2010. Additionally, a high percent of juveniles indicates that recruitment rate may be high and thus nest predation low. Numerous juveniles were detected at my study area in 2009 or 2010. Thirty-two percent (6/19) of turtles detected in 2009 were juveniles and 27% (5/18) of turtles detected in 2010 were juveniles. Saumure and Bider (1998) estimated a juvenile

detection rate for two populations of Wood Turtles in Quebec, Canada. One population was near an agricultural field and the other near a forest. The percent of juveniles in each population was 12% juveniles and 36% juveniles, respectively. In a study area in West Virginia, age structure was 46% juveniles and 54% adult (Niederberger and Seidel, 1999). Farrell and Graham (1991) reported 61% of turtles captured in a New Jersey population were juveniles and 31% of Wood Turtles in a Quebec population were juveniles (Walde et al., 2003).

Nest Predation Counts and Predator Activity. The number of depredated nests detected was higher in 2009 than 2010. Twenty-five and 12 depredated nests were detected in 2009 and 2010, respectively. Variability in nest predation between years may be due to several factors. For example, predator numbers could have decreased from 2009 to 2010, egg production may have been lower or females may have nested somewhere else (although Walde et al. (2007) reported that 95% of females returned to the same nest site in his two year study). Another theory is that the early and longer nesting period of 2010 produced lower predation rates because nests were not clumped temporally or spatially. Spatially clumped nests generally experience higher predation rates than scattered nests (Spencer and Thompson, 2003).

In 2009, raccoon and otter tracks were seen on nesting beaches before peak nesting activity started and predator trails were observed on beaches more often during nesting season than any other time during the summer. In 2010, there were no tracks seen on the nesting beaches before nesting, or even several days after nesting began. Interestingly, there was no indication that predators foraged on beaches until June 2, 11 days after nesting began. I think that either the majority of turtles nested early, before

predators were foraging for turtle nests, or predator numbers were low. It was warm in early-May, 2010 which may have resulted in optimum temperatures for egg development, thus, expediting egg development and oviposition. In addition to predator tracks on the river bank, there were raccoon digs on beaches. I suspect raccoons were strategically searching for turtle nests where they had been rewarded with turtle eggs in previous years. For example, I observed a raccoon dig in the exact location that a nest was created (and then depredated) the year previous.

Nesting Ecology. Female Wood Turtles started to dig on beaches about a week before actual nesting began (a behavior that is thought of as “testing” the soil for appropriate nesting conditions; Harding and Bloomer, 1979). In my study, Wood Turtles nested most commonly in the evening and morning hours. Walde et al. (2007) found similar results for a population of Wood Turtles in Quebec. Also, my study corroborates previous observations of nesting occurring just after rain events (Farrell and Graham, 1991; Walde et al., 2007) and that such behavior starts in early to mid-June (Harding and Bloomer, 1979; Farrell and Graham, 1991; Kaufman, 1992; Walde et al., 2007). However, a recent study observed the start of nesting in late-May (Smith, 2002), as I found for 2010. Variation in the start of nesting is likely due to annual weather patterns resulting in variable timing of appropriate temperatures for incubation (Walde et al., 2007). Congdon et al. (1987), who studied Snapping Turtles in southern Michigan, found that high ambient temperatures during the three months prior to nesting significantly correlated with the start of nesting activity. Heat availability was quantified as the number of days with daily mean temperatures above 18.3°C at Lansing, Michigan for March, April and May. Nesting behavior was similar to that described by Harding and Bloomer

(1979). Mean clutch size (7.4 eggs) was slightly lower than reported in previous studies of Wood Turtles (generally 9-10) (Harding and Bloomer, 1979; Farrell and Graham, 1991; Kaufman, 1992; Walde et al., 2007). Variation in clutch size is thought to be related to body size and latitudinal differences (Hughes et al., 2009).

Dominance Behavior. Male Wood Turtles are known to form a linear dominance hierarchy, which functions to determine access to females (Kaufmann, 1992). Males determine dominance by ritualistic fighting (biting, lunging and mounting) that can last up to 3.5 hours (Kaufmann, 1992). Dominance is not known to occur in female Wood Turtles (or any freshwater turtle). However, Walde et al. (2007) reported that female Wood Turtles by-passed suitable nesting beaches used by other Wood Turtles. My observations suggest that a dominance/subordination relationship may exist among female Wood Turtles.

The behavior of the three turtles that I observed may function to determine access to favored nesting sites. Fighting over nesting sites makes sense when nesting sites are limited, but there were ample nesting sites on this particular gravel bar. However, a particular site on a nesting area may be more suitable for oviposition than others. Substrate, soil temperature, elevation and moisture are important factors in nest site selection (Buech et al., 1997; Hughes et al., 2009). Females could have been fighting over the highest point on the nesting beach, which may provide greater nest success than areas lower on the beach due to the chance of periodic flooding. Buech et al. (1997) studied a Wood Turtle population in Minnesota and found that suitable nesting sites were at least one meter above the river.

Mating and Site Fidelity. My observations of mating are supported by Harding

and Bloomer (1979). Mating usually occurred on the edge of water and with less frequency in summer months than in the spring and fall. There are no previous observations of mating on three consecutive days. I also observed site fidelity in Wood Turtles, which has been reported by other studies (Harding and Bloomer, 1979; Arvisais et al., 2002).

Experiment 1: Effects of artificial nest treatment on predation

My hypothesis, that predators would preferentially depredate nests with both turtle-scented water and soil disturbance chemical cues, was rejected. Nests with soil disturbance plus turtle-scented water were not depredated significantly more than nests with soil disturbance alone. However, nests with soil disturbance were depredated more than nests without disturbance (turtle-scented water and control treatments). It is perhaps an anomaly that nests with soil disturbance plus turtle-scent were not depredated more than nests without disturbance (turtle-scented water or control treatments). In total, my results suggest that soil disturbance is an important factor in nest location. In a similar study of Painted Turtle nesting ecology, Strickland et al. (2010) reported that soil disturbance was the only determinant in predation on artificial nests.

Only 20% (11/56) of artificial nests that had soil disturbance were depredated. If soil disturbance cues alone are used by predators to find turtle nests, then I would have expected higher rates of predation with soil disturbance, because predation rates of natural turtle nests have been reported as high as 90-100% (Harding, 1991). It seems likely that a soil disturbance cue may be the primary determinant of nest predation, but

additional cues, such as turtle tracks and egg-derived chemical cues, may also be important in nest detection.

A low percentage (8%) of artificial nests was detected by predators. This low response may be due to multiple factors, but is probably largely explained by the absence of eggs in artificial nests. This is supported by the fact that 48% of nests, which contained eggs in Experiment 2, were depredated. With the absence of eggs, predators had no food reward for their search efforts. Hence, a predator was expending energy with no energy gain. This negative reinforcement may have deterred predators from nest searching, resulting in minimum effort searches over a smaller area. However, Strickland et al. (2010) stated that eggs buried in Painted Turtle nests do not affect predator behavior. An alternative theory is that predator abundance was low or predator activity was low during at least half of the time when artificial nests were constructed. Predator and prey activity noticeably increased during the period of June 11 - 23, which was when peak nesting activity began. Twice as many artificial nests were depredated during peak nesting (6 vs. 12). Conversely, Wilhoft (1979) found that simulated turtle nests made in June were no more vulnerable than nests made in April. Artificial nests made during the low activity period were still used in data analyses because date should not have an effect on which nest treatment elicited a predator response. However, if predator activity was low, then the probability of detecting an artificial nest dramatically decreased. Thus, explaining the low predation observed in Experiment 1.

Raccoon and River Otter were the primary predators on artificial nests in my study. Both predators were able to locate artificial nests without turtle-derived chemical cues, as suggested by other studies of raccoon predation on turtle nests (Wilhoft et al.,

1979; Hamilton et al., 2002; Strickland and Janzen, 2008; Strickland et al., 2010).

The abundance of raccoons in this study area is difficult to assess because of their relatively large home ranges (60.5 ha; Barding and Nelson, 1986) and long distance movements (1.5 km - 11.5 km; Greenwood, 1982), but based on predator activities and remoteness of the study area, raccoon density was probably low. Thus, it is possible that only one or two raccoons were depredating artificial nests. However, based on variation in track sizes, I estimate that 4-5 raccoons were involved in predation of artificial nests.

River Otters have not been previously studied as nest predators. Their diets are specialized for piscivorous feeding, but they opportunistically feed on invertebrates and berries (Sheldon and Toll, 1964). They also feed on turtle eggs during nesting season as observed in this study, although River Otters fed mainly on crayfish at my study site, based on analysis of scat. This study showed that River Otters responded to soil disturbance cues and, therefore, probably used visual cues or chemical cues associated with disturbed soil in locating nests. Interestingly, there was one incident in which River Otter tracks were observed going to each treatment on a single beach, but predation never occurred. Perhaps this otter was primarily using visual soil disturbance cues to locate potential nests and then used a secondary cue, such as a turtle-derived chemical cue (i.e., eggs) to determine if artificial nests were actual turtle nests. River Otters mainly use vision and vibrissae to capture aquatic prey with their mouths (Green, 1977). Therefore, I would expect visual cues to be important for River Otters to locate turtle nests. Gittleman (1986) states that olfactory bulb size is reduced in otters (because of their aquatic foraging habitats) compared to other mammalian carnivores.

Nests with only turtle-scented water were never detected by predators. However,

this does not mean that they did not detect the chemical cue applied. They may have detected it, but were deterred by the turtle scent (which was malodorous) or perhaps the turtle-scented water masked a chemical produced from soil disturbance that predators typically use in nest location. It is possible that turtle-scented water deposited on artificial nests did not mimic the authentic scent left behind from egg-laying turtles and predators did not associate this smell with turtle nests. Other studies have shown that applying chemical cues, such as turtle urine or water taken from a source that turtles live in, also do not affect nest predation (Hamilton et al., 2002; Strickland and Janzen, 2008; Strickland et al., 2010). Strickland et al. (2010), who studied a population of Painted Turtles, applied slough water onto artificial nests the same way that I applied turtle-scented water and also had zero nest predation.

Soil disturbance produces multiple cues that predators could utilize in nest detection, including visual, tactile and chemical. Tactile cues seem likely when foraging in the dark, but the efficiency of this strategy would be poor in a large nesting area. Visual and chemical cues offer advantages over tactile cues, because nests at long distances could be located with minimal energy. It is likely that predators use a combination of cues produced from soil, because this would increase the probability of locating nests. Galois (1996) found that raccoons learn to discriminate between tactile and chemical cues and that both are important in nest localization.

It is unclear what soil-derived cue triggered a predator response, because multiple cues may be associated with soil disturbance, but nests with only turtle-scented water applied were never depredated. This indicates that soil disturbance is the primary cue eliciting predator response. Therefore, in future empirical studies, it may not be necessary

to apply a turtle chemical cue to artificial nests. Furthermore, soil disturbance cues are ephemeral, which may explain why nest predation rates are lower after rainfall (Bowen and Janzen, 2005) and why nest predation usually occurs 24-48 hours after nest construction (Tinkle et al., 1981; Congdon et al., 1983).

Experiment 2: Effects of Distance from River on Nest Predation

My hypothesis, that nest predation increases as nest distance from the river decreases, was supported. Marchland et al. (2002) and Spencer and Thompson (2003) report similar findings with nests of other turtle species. Marchland et al. (2002) studied a population of Painted Turtles and found that nest predation, primarily by raccoons, decreased as distance from pond edge increased. Spencer and Thompson (2003) studied the turtle *Emydura macquarii*, which inhabits rivers in Australia, and found that predation rate decreased as the distance between nest and water increased. Strickland et al. (2010) found that predation rates of artificial nests were higher near habitat edges (e.g., water and forest) than in the middle of the study area for a population of Painted Turtles. While my study showed that predation was higher near water, I did not investigate predation near forest edge.

Nests made closer to the river shoreline were likely more susceptible to predation because raccoons followed the corridor of the river while foraging. This is supported by observations of numerous raccoon tracks following the river bank. Raccoons usually forage along water sources, because they are able to find food in water as well as on land (Cagle, 1949). This behavior is consistent with optimal foraging theory; predators act to minimize energy output while maximizing energy expenditure (Charnov, 1976).

Therefore, it seems likely that predators expend less energy while foraging in a relatively straight line than in zigzag patterns along rivers. Also, the lack of vegetation along rivers allows animals to move with minimal energy expenditure, compared to animals moving through thickly vegetated areas. Track patterns also revealed that raccoons searched primarily for nests along the shorelines and on beaches that were used by nesting turtles.

Most predation on artificial nests occurred one day after nest construction, which is when predation commonly occurs for natural nests (Tinkle et al., 1981; Congdon et al., 1983). Interestingly, no predation occurred on day two, but five nests were depredated on day 3. This is likely the result of predators primarily foraging closer to the river's edge than more inland. Thus, increasing encounter rates of nests in close proximity to the water.

Nests less than 19 m from the river were most susceptible to predation, compared to nests greater than 19 m distance from the river. Congdon et al. (1987) found that nests less than 30 m from water were more susceptible to raccoon predation than nests greater than 30 m from the water. However, distance from water is confounded with vegetation density. Hence, nests created in sandy open areas were found by predators more often than nests in vegetated areas. This may be because raccoons primarily forage along habitat edges (Greenwood, 1982; Temple, 1986; Barding and Nelson, 2008). Greenwood (1982) found that raccoon activity was concentrated near wetlands and was greatest in spring and early summer. In another study on *P. lotor* in Illinois, it was found that 79 % of raccoon activity occurred near linear edges and habitat used was predominately forest edge.

A higher proportion of nests (48%) were depredated in this experiment than Experiment 1 (8%), probably because chicken eggs were buried under nests to elicit predators. The addition of eggs may have provided a reward or an egg-derived chemical cue which facilitated nest localization. Another possibility is that sand plots, which encircled eggs, provided a visual cue. Predators may have exploited these sand plots by finding one and associating the sand plot with a food reward. However, in one case, I observed a raccoon track on top of a sand plot of a nest that was not disturbed (i.e., a raccoon walked over a sand plot without detecting the nest. This same nest was depredated two days later.

Project Implications

The relatively low predation rate, high percent of juveniles detected and no adult mortality suggests a low effect of predators on this population. This may be an ideal population to make comparisons with other studies in which turtles could be declining. Wood Turtle populations exposed to human recreation, agriculture, logging and roads should be monitored and compared to populations that are not exposed to such threats. Predator numbers at such sites should also be compared and monitored to prevent further decline of Wood Turtle populations. Also, a conservation management plan should be enacted for Wood Turtle populations in the Upper Peninsula of Michigan.

In future studies that seek to investigate predation rates of turtle populations by using artificial nests may not need to apply a turtle-derived chemical cues to nests. However, the addition of eggs to artificial nests may increase predator search efforts and produce more accurate predation rates. Thus, burying eggs in artificial nests may be

necessary to obtain more accurate results. I also suggest creating artificial nests (with no eggs) in nesting habitat to deter predators from searching for natural nests. If predators dig up artificial nests and gain no reward, then predators will be less likely continue nest searching and this may decrease predation on natural nests.

Additionally, future management projects should implement a plan to increase nest success and recruitment in declining Wood Turtle populations by creating artificial nesting habitat at least 20 m distance from heavily used corridors, such as rivers and roads. Suitable nesting habitat is critical for population persistence (Bowen and Gillingham, 2004). When nesting habitat is limited, female turtles are more likely to travel long distances in search of suitable nesting grounds. Female Wood Turtles have been known to travel up to 3.7 km in Quebec (Walde et al., 2003) to nesting sites. However, increased nest success rates could be counteracted by increased adult female mortality due to road crossings and predator exposure. Creating artificial nesting habitat away from high traffic corridors could potentially decrease the number of female Wood Turtles hit by motorized vehicles because they would be less likely to travel long distances. However, nest site fidelity, which is common in Wood Turtles, may prevent turtles from using new nesting areas. I recommend a pilot study to determine if artificial nesting habitat would be utilized by females.

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