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Effects of landscape composition, habitat features, and nest distribution on predation rates of simulated turtle nests

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Abstract

We investigated predation of simulated turtle nests in an effort to understand how land-use patterns and the availability of nesting habitat may affect turtle recruitment in a region where human populations and associated development are increasing. Simulated nests were patterned after those created by painted turtles (*Chrysemys picta*), a common aquatic turtle in our study area, and distributed in four patterns (clustered and near pond, scattered and near pond, clustered and far from pond, and scattered and far from pond) around 36 ponds. Landscape composition (500–2000 m from pond perimeters) and habitats surrounding pond edges (an area extending 250 m from the shore of each pond) were then compared with rates of predation at each pond. Nest-site characteristics also were compared to the fate of individual nests. Landscape composition and habitats surrounding ponds apparently had little influence on predation rates. Nest distribution and the immediate habitat features associated with each nest did affect vulnerability to predation. Clumped nests were preyed upon at a higher rate than scattered nests, and nests close to ponds (within 50 m) were more vulnerable to predators than those created far (100–150 m) from a pond. Counter to our expectations, proximity to edge habitats (other than the shore of a pond) reduced the probability that a nest would be detected by predators. Also, nests placed near roads and suburban lawns had a reduced likelihood of predation whereas those placed in agricultural areas or disturbed sites had a greater probability of being preyed upon. Our results suggest that predation of simulated turtle nests may be a consequence of their distribution and location relative to the foraging activities of common nest predators, especially raccoons (*Procyon lotor*). Efforts to enhance recruitment among declining populations of turtles should consider the abundance and distribution of nesting habitat. Providing additional nesting sites away from predator foraging habitats may reduce nest predation and increase the recruitment of hatchlings into a population.

Keywords: Turtle nest predation; Habitat fragmentation; Landscape composition; Spatial scale

1. Introduction

Worldwide, populations of many species of turtles are declining (Gibbons et al., 2000). Although survival of adults has been demonstrated to be crucial to long-term viability of turtle populations (Brooks et al., 1991; Congdon et al., 1993), all life stages should be considered in efforts to stabilize or restore declining populations. Among the factors that affect recruitment, predation is recognized as a major cause of turtle egg mortality (Congdon et al., 1983). Nest predation can approach 100% in some populations (Congdon et al., 1987), presenting obvious limitations to any recovery effort. Intense predation may be especially problematic in human-dominated landscapes where recent studies have demonstrated that populations of generalist predators can increase and limit the populations of some prey species (Wilcove, 1985; Robinson and Wilcove, 1994; Brown and Litvaitis, 1995). Predators, including raccoons (*Procyon lotor*), corvids, and canids (e.g., *Vulpes vulpes* and *Canis latrans*) benefit from supplemental foods associated with agriculture and suburban developments (Oehler and Litvaitis, 1996; Pedlar et al., 1997; Dijak and Thompson, 2000). As a result, increased predator abundance may be a major proximate factor causing the declines of some prey in these modified landscapes (Oehler and Litvaitis, 1996).

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Turtles are known to exploit modified habitats (Linck et al., 1989; Joyal et al., 2001) because they contain features (e.g., open canopy and exposed soil that can be easily excavated) that may be less abundant in undisturbed areas. However, modified habitats may serve as 'ecological traps' (sensu Gates and Gysel, 1978) if nest predation is substantially greater in these areas (Kolbe and Janzen, 2002). To evaluate the factors that may limit populations of turtles in a region undergoing substantial human population growth and development, we initiated a comprehensive study of the demography of painted turtles (*Chrysemys picta*). Although this species is among the most abundant turtles in the northeastern United States (Conant and Collins, 1991), we suspected that some of the factors limiting this species also would affect populations of rare species in the region [e.g., spotted (*Clemmys guttata*), wood (*Clemmys insculpta*) and Blanding's turtles (*Emydoidea blandingii*)]. By studying an abundant species, we hoped to avoid the limitations of small samples that characterize investigations of rare species. As part of our effort, we considered how landscape composition and habitat features influenced the vulnerability of simulated painted turtle nests to predators.

Based on previous research (Brown and Litvaitis, 1995), we speculated that nest vulnerability would be influenced by features that were expressed at three spatial scales. Landscape composition would influence the abundance and distribution of resources used by predators, and therefore, would affect local predator abundance. At a patch or pond-specific scale, predator activity may be concentrated in particular areas where life requisites (e.g., prey, water, den sites) were concentrated (especially habitat edges and disturbed patches). If these sites were used by nesting turtles, increased incidental encounters with turtle nests (Vickery et al., 1992) would result in substantial predation (Hamilton et al., 2002). Furthermore, habitat features immediately surrounding a nest may affect the detection by a predator. Robinson and Bider (1988) reported that snapping turtle (*Chelydra serpentina*) nests had higher survival when they were at least partially concealed by vegetation, whereas Kolbe and Janzen (2002) found that the probability of snapping turtle nests surviving in Illinois increased with decreasing vegetation, more open sand, and fewer cacti. Finally, changes in nesting habitat configuration and nest distributions may affect foraging success of predators. Nesting areas that are small or linear may concentrate nests and lead to increased predation (Jackson and Walker, 1997). In a pilot study, we found nest predation was greater among simulated nests that were clumped and near water than nests that were scattered or far from a pond (Marchand et al., 2002).

To expand on those findings, we constructed nests in several distribution patterns surrounding ponds and investigated the effects of habitat features on rates of nest predation at several spatial scales. Simulated nests have been used to investigate relative predation rates among avian species in a variety of habitats (review by Major and Kendal, 1996), and may provide insight into factors limiting recruitment in turtle populations (Hamilton et al., 2002; Marchand et al., 2002). Specifically, we predicted that: (1) nest predation would be greater in human-altered landscapes (e.g., large amount of agricultural land or urban development); (2) nests located in heavily disturbed patches of habitat (e.g., roadside and lawns) would suffer greater predation than nests in less disturbed habitat patches; (3) nests located near ponds and other habitat edges would have increased rates of predation; and (4) nests that were clumped would be preyed upon at a greater rate than nests that were scattered.

2. Methods

2.1. Study area

Thirty-six ponds that ranged in size from 0.3 to 5.2 ha in a ~1400 km^2 portion of southeastern New Hampshire were used in our experiment (Fig. 1). Habitat mosaics that surrounded ponds included forests, agricultural fields, and suburban and urban developments. New Hampshire is the second most forested state in the country (ca. 83%; Sundquist and Stevens, 1999), but southern counties have undergone rapid development and increases in human populations (Vogelmann, 1995), making New Hampshire the fastest growing state in the northeastern United States from 1990 to 1998 (7% population increase). Because we wanted ponds surrounded by a range of land uses, we selected ponds along a gradient of forest continuity where the intensity of development changed from west (less developed) to east (more developed), as summarized by Vogelmann (1995). Dominant overstory species in the area included American beech (*Fagus grandifolia*), maples (*Acer* spp.), oaks (*Quercus* spp.), eastern white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*).

Semiaquatic and aquatic turtles in the region included painted, snapping, musk (*Sternotherus odoratus*), spotted, wood, and Blanding's (Taylor, 1993). The latter three species are currently considered rare in New Hampshire (Kanter et al., 2001). Painted turtles were the most abundant species occurring within the study area (Marchand, 2002). Identified nest predators in our study area included raccoon (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), fisher (*Martes pennanti*), and red squirrel (*Tamiasciurus hudsonicus*) (Marchand et al., 2002). Other potential predators included striped skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), opossums (*Didelphis virginiana*), and minks (*Mustela vison*), eastern chipmunk (*Tamias striatus*).

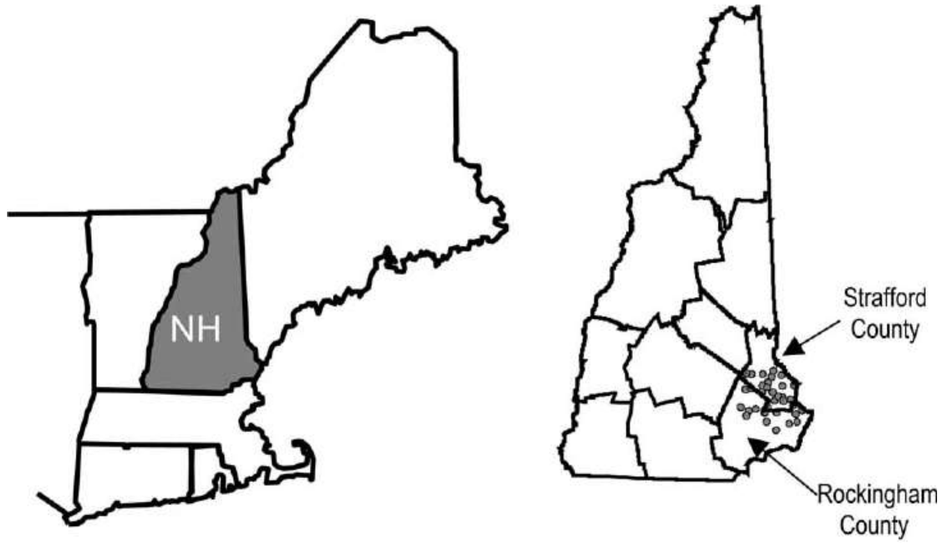

Fig. 1. Distribution of 36 ponds that were sampled in southeastern New Hampshire used to study predation rates on simulated turtle nests. Ponds are illustrated with a 2000 m buffer that was used to investigate surrounding landscapes.

2.2. Rates of predation and influence of nest distribution

We positioned 40 nests in the habitat surrounding each of 36 ponds. Nests were placed in four distribution patterns: near edge of pond in a scattered distribution ($n = 10$), near edge of pond in a clumped distribution ($n = 10$), far from pond in a scattered distribution ($n = 10$), and far from pond in a clumped distribution ($n = 10$). Nests 'near' ponds were within 50 m of the pond shore and 'far' nests were placed 100–150 m from shore. Scattered nests were separated from each other by at least 30 m, whereas nests in a clumped distribution were approximately 2 m from the closest nest within the clump of 10 nests. Sites where nests were placed included small canopy gaps, dirt trails, roadside banks, fields, lawns and other open or disturbed areas. These habitats represented the type of sites in which we observed turtles nesting. All nests were created during 1–28 June 2001, corresponding to the peak nesting period observed the previous year (Marchand, 2002).

For each nest, a hole approximately 10 cm deep was excavated with a trowel, and three commercially-obtained bobwhite (*Colinus virginianus*) eggs were placed in the hole and covered with soil (Marchand et al., 2002). Nesting turtles often release bladder water while excavating a nest (Ernst et al., 1994; Kinney et al., 1998), so we attempted to mimic this by utilizing water from a tank that held female painted turtles. This water was sprayed onto the eggs within the nest and on the surface of the completed nest. To minimize human scent left at nests, we wore rubber boots and gloves while creating nests (Whelan et al., 1994). The location of each nest was recorded with a handheld GPS unit and plastic flagging was placed within 3 m to enable our quick relocation of the nest. Plastic flagging has been used with previous investigations of turtle nests with no apparent effect on rates of predation by mammalian predators (Tuberville and Burke, 1994).

All nests at a pond were created on the same day, and nest fate was recorded after 7 and 14 days of exposure. Each nest was recorded as depredated (at least 1 egg was consumed), disturbed, or survived. Disturbed nests sometimes resulted in exposed eggs, increasing their vulnerability to predation, desiccation, or drowning from rainwater accumulating in the nest. We used a 2×2 contingency table with a Fisher's exact test (Zar, 1999) to determine if nests disturbed after 7 days were more likely to be depredated after 14 days than were nests that survived the first 7 days. All other analyses used nest fate from the 14-day sample, because it included a larger segment of the actual nesting period. Because real turtle nests usually suffer the greatest predation during the first several days after excavation (Tinkle et al., 1981; Congdon et al., 1983; Christens and Bider, 1987; but see Snow, 1982), our 14-day sampling period should have included most predation.

2.3. Landscape composition and pond-specific features

The landscape scale included information at three distances from pond perimeters (500, 1000, and 2000 m). These distances corresponded to the daily cruising range of several local predators (Barbour and Litvaitis, 1993). We used a geographic information system in conjunction with a land cover map produced by the Complex Systems Research Center at the University of New Hampshire to determine the land cover surrounding each pond. The land cover map was produced from Landsat thematic mapper imagery (spatial resolution ca. 0.09 ha) taken between 1990 and 1996 (Rubin et al., 2001). We collapsed the 19 cover types to six because of superior accuracy of the data (Rubin et al., 2001). For example, the seven forest cover types that were classified in the 19-class land cover map were condensed into a single cover type (forest). Other land cover categories included in our assessment were developments, agricultural fields, open or disturbed areas, open water, and wetlands. Because each pond had a unique shape, the area within a buffer of equal distance from pond edges was different. Therefore, each cover type was calculated as the percentage of total area consisting of that particular cover type.

For the pond-specific scale, a distance of 250 m from pond perimeters was used. This distance included all simulated nests in this study and also corresponded to distance most painted turtles were likely to nest from pond perimeters (Ernst et al., 1994). In our study area, the maximum distance that transmitter-equipped female painted turtles were observed from ponds during the nesting season was 273 m ($n=20$; Baldwin et al., 2004).

2.4. Nest-site features

We measured habitat characteristics in the immediate vicinity of nests because these features likely affect predator detection of nests. Nest-site features were sampled for all scattered nests. Among clumped nests, we measured variables for only three nests (one nest near the center of the clump and two nests on extreme ends of the clump) because habitat characteristics among clumped nests were similar. We averaged the measurements for these three nests and used that value for the other seven nests in each clump.

The immediate habitat in which a nest was located was recorded as forest gap, lawn, roadside, agriculture area, and disturbed or open areas. Forest gaps were small, human-created breaks in the forest canopy (e.g., trails) or natural openings [e.g., beaver (*Castor canadensis*) flowages]. Nest sites among lawns often were associated with residential or urban buildings. Roadside nest sites were within 5 m of roads or other paved surfaces. Agricultural areas included pastureland and hay fields, cornfields, and blueberry barrens. Disturbed areas included dams, abandoned railroad beds, and open areas with sparse shrubbery or grasses that were not used for agriculture.

We also measured the distance from nest sites to the nearest edge because some predators that are known to prey on turtle nests have an affinity for edge habitats (Temple, 1987). Edge habitat consisted of any transition between forest, roads, lawns, water, and other open habitats. Slope and aspect of a nest site were described because these parameters affect the amount of sunlight exposed to nest sites, surface temperatures, and possibly rates that odors are dissipated from nests. Natural nests are frequently located on south-facing slopes (Schwarzkopf and Brooks, 1987) and south-facing slopes tend to be warmer than other cardinal directions; as a result, we estimated aspect as the number of degrees deviating from south. For example, a north aspect deviated 180° from south (Table 1).

Understory was described by counting woody stems along four 10×1 m transects. All transects originated at the nest site and continued in the four cardinal directions. Stems included in the tally were less than 7.5 cm in diameter. The percentage of canopy closure was estimated by looking up through a 23.5×7.5 cm cylinder. Canopy closure was measured at the end of each 10 m transect and also directly above the nest, and the average of the five estimates was used for subsequent analyses. Finally, litter depth was measured 1 m from nests in the four cardinal directions and averaged. Litter included leaves, needles, and dead grass.

2.5. Data analysis

SPSS statistical software (2001) was used for all analyses. We used backwards elimination linear regression to assess if landscape composition and pond-specific features varied with the rate of nest predation at individual ponds (sample unit = pond). This comparison was based on the rate of predation of all nests associated with a specific pond. Prior to this analysis, variables were screened for normality, skewness, and kurtosis and transformed if necessary (Zar, 1999). The rate of predation at each pond and all landscape and pond-specific variables were transformed by calculating the arcsine square root of each proportion (Zar, 1999). To eliminate redundant variables, a correlation matrix was created for all independent variables (Marchand, 2002). One variable among a highly correlated pair ($r\geqslant0.7$) was retained to enter the regression model. For the landscape scale, each habitat variable was included at the distance (500, 1000, or 2000 m) that explained the most variation in the dependent variable (i.e., the largest Pearson r among correlations).

We then used logistic regression to compare the fate of individual nests (survived or preyed upon) to the immediate nest-site features we sampled (sample unit = individual nest). We did not include landscape or pond-specific features in this comparison because all the nests associated with a pond shared these characteristics. Logistic regression allows for the use of both continuous and categorical independent variables, and does not assume variables are normally distributed (Tabachnick and Fidell, 2001). Nest fate was the dichotomous dependent variable and was coded as survived = 0 or depredated/disturbed = 1. Understory stem density, litter depth, nest-site aspect, and canopy closure were included as continuous predictor variables (Table 1). Distance to an edge and slope were included as ranked independent variables. Habitat types were

Table 1
Habitat features sampled at simulated turtle nests used to investigate predation in southeastern New Hampshire. Time of nest construction (WEEK) also was included

Variable	Description
DISTANCE	= distance from pond perimeter, dummy coded as near = 0 or far = 1
TYPE	= distribution of nest, dummy coded as scattered = 0 or clumped = 1
EDGE	= distance to the nearest edge habitat, ranked as: 1 (0–4 m), 2 (5–9 m), 3 (10–19 m), 4 (20–29 m), 5 (30–99 m), and 6 (> 100 m)
SLOPE	= slope of ground surface at nest site, ranked as 1 (⩽5°), 2 (6–10°), 3 (11–20°) and 4 (>20°)
ASPECT	= degrees deviation from south (0–180°)
CANOPY	= percentage of canopy closure
STEM	= woody stem abundance measured along four 10×1 m transects
LITTER	= litter depth, average of four measurements at each nest
LAWN	= mowed grass, dummy coded as no = 0 or yes = 1
ROAD	= nest within 5 m of roadside, dummy coded as no = 0 or yes = 1
AG	= nest within agricultural area, dummy coded as no = 0 or yes = 1
DISTRBED	= nest within disturbed habitat, dummy coded as no = 0 or yes = 1
GAP	= nest within opening in forest canopy, dummy coded as no = 0 or yes = 1
WEEK	= week when nest was created, ranked as 1 (1–7 June), 2 (8–14 June), 3 (15–21 June), and 4 (22–28 June)

dummy coded (0 = absent, 1 = present). Because the assumption of multicollinearity is violated when all dummy coded habitat variables are entered (Tabachnick and Fidell, 2001), we eliminated canopy gaps from further analysis. Gaps largely represented habitats not influenced by intense human activity and corresponded to the elimination of forests within local and landscape scale analyses. Nest position (near = 0, far = 1) and distribution (scattered = 0, clumped = 1) also were included as dummy variables. Because the date nests are created can influence predation (Burger, 1977), we included a ranked variable that described the week a nest was created (Table 1). The probability of *F*-to-remove in the backwards regression models (linear and logistic) was set at 0.1. An α larger than 0.05 helps ensure that important variables aren't excluded (Tabachnick and Fidell, 2001). Final models were assessed at $P < 0.05$.

Finally, a repeated-measures ANOVA was performed using MANOVA to test if rates of nest predation differed among the four nest distribution patterns. Differences among groups were assessed using paired samples *t*-tests with a Bonferroni corrected α of 0.008 ($\alpha = {}^{0.05}/_{6}$).

3. Results

The proportion of nests depredated at 14 days was greater for nests disturbed at day 7 than for nests that survived through day 7 (40 versus 11%; Fisher exact test, $P < 0.001$). Therefore, we combined disturbed and depredated nest data for all analyses. Five nests were eliminated from analyses because their fate was unknown after both 7 and 14 days of exposure. Four of these nests were buried with dirt (i.e., road grading, landscaping) and the fifth nest could not be located. For an additional nine nests, the fate after 14 days of exposure was unknown, but the fate after 7 days of exposure was known and used in analyses. The fate of all other nests is reported for the 14-day sample period. Overall, 42% of simulated nests were depredated or disturbed and rates of predation at ponds ranged from 0 to 93%.

3.1. Effects of landscape and pond-specific habitat composition on rates of nest predation

Composition of landscapes surrounding individual ponds varied considerably. At the largest scale (2 km radius), forest coverage ranged from 10 to 87% ($\bar{x} = 61\% \pm 18$ S.D.), development ranged from 1 to 55% ($\bar{x} = 8\% \pm 10$ S.D.), and agricultural land ranged from 0 to 27% ($\bar{x} = 6\% \pm 6$ S.D.). The amount of forest habitat was highly correlated with other habitat variables. Previous research in our study area indicated that populations of raccoons, coyotes, and foxes increase as forests are replaced by agriculture and suburban developments (Oehler and Litvaitis, 1996). Because nest predators in our area are most likely influenced by human-altered habitats, forest habitat was eliminated from regression analyses rather than eliminate urban and open habitats. At the landscape scale, the amount of open, urban, wetlands, and water had the highest correlation with rates of nest predation at the 2-km buffer distance. Agricultural lands showed the highest correlation within the 500 m buffer. The amount of agricultural and urban habitats within 250 m was eliminated from consideration because they were highly correlated with agricultural habitat within 500 m and urban habitat within 2 km of ponds. As a result, eight predictor variables were considered eligible to enter the regression.

Only one variable was retained in the final two-scale regression model ($F = 8.539$, df = 1, $P = 0.006$). Nest predation at a pond (pond = sample unit) was inversely related to the amount of wetland habitat within 2 km ($\beta = -0.448$, $t = -2.922$, $P = 0.006$). However, this model only explained 18% of variation in rates of nest predation at ponds (adjusted $R^2 = 0.177$). In addition, univariate correlations of the probability of nest depredation were not associated with any human-altered habitats at the pond-specific or landscape scale.

3.2. Nest-site feature associated with predation

Considering nests as the sample unit, eight predictor variables were retained in the final model that explained predation ($\chi^2 = 295.2$, df = 8, $P < 0.001$, Nagelkerke $R^2 = 0.250$, $N = 1435$, Table 2). Nests far from pond perimeters were less likely to be depredated than nests near pond perimeters. Clumped nests were more likely to be depredated than scattered nests. Nests in agriculture or disturbed habitats were more vulnerable to predation whereas those located in lawns or roadsides were less likely to be depredated. Nests established late in the season were slightly more vulnerable. Counter to our expectation, nest vulnerability increased with distance from a habitat edge, but this was a weak relationship. Overall classification accuracy was 69% and varied from 77% for nests that survived to 58% for nests that were depredated.

3.3. Implications of nest distribution

Nests near pond perimeters in a clumped distribution were depredated at the highest rate (68%), compared with nests near ponds in a scattered distribution (40%), nests far from ponds in a clumped distribution (34%), and nests far from ponds in a scattered distribution (26%). The repeated-measures ANOVA assumption of sphericity (structure of the variance/covariance matrix) was violated (Mauchly's $W = 0.30$, $\chi^2_5 = 40.6$, $P < 0.001$), so a MANOVA was used to assess whether distributions differed. The predation rate was different among the four distributions (Wilks' $\lambda = 0.464$, $F = 12.69$, df = 3, $P < 0.001$). Within clumped distributions, predation was greater near pond perimeters ($t = 3.25$, $P = 0.003$, Fig. 2). Within scattered distributions, predation was greater near pond perimeters at the standard α level ($P < 0.05$), but these distributions did not differ when the conservative Bonferroni adjustments were applied ($t = 2.54$, $P = 0.016$). Within 50 m of a pond, predation on clumped nests was greater than among scattered nests ($t = -5.15$, $P < 0.001$). There was no difference between clumped and scattered nests at distances > 100 m from a pond ($t = -1.38$, $P = 0.176$).

Table 2
Nest-site features measured at simulated turtle nests that were retained in the final model of a backwards elimination logistic regression ($\chi^2 = 295.2$, df = 8, $P < 0.001$, Nagelkerke $R^2 = 0.250$)[a]

Variable	Coefficient	Wald	P	Odds ratio
DISTANCE	−1.238	86.051	<0.001	0.290
AG	1.013	24.288	<0.001	2.755
ROAD	−0.909	15.408	<0.001	0.403
LAWN	−0.839	25.385	<0.001	0.432
TYPE	0.833	45.864	<0.001	2.301
DISTRBED	0.410	4.610	0.032	1.507
WEEK	0.178	10.206	0.001	1.195
EDGE	0.085	3.945	0.047	1.089
CONSTANT		7.929	0.005	

[a] Overall classification accuracy was 69% and varied from 77% for nests that survived to 58% for nests that were depredated or disturbed. See Table 1 and text for a description of each feature.

4. Discussion

4.1. Landscape features and nest-site characteristics

The lack of association between predation rates and landscape features was unexpected. Based on a previous study in the same area (Oehler and Litvaitis, 1996), we initially speculated that predation rates would be greater among ponds surrounded by human-modified habitats (especially agricultural and urban areas) than those in more continuous forests because populations of generalized predators are greater in disturbed landscapes. Raccoons were the most frequent predator of simulated nests in our study area, accounting for 74% of predation by identified carnivores (Marchand et al., 2002). However, if raccoons concentrated their activity near ponds, then predation rates might be independent of raccoon abundance and our speculation would be incorrect. Raccoons are known to forage intensively near ponds (Llewellyn and Uhler, 1952); therefore, nests near ponds may be at risk regardless of the composition of surrounding landscapes and thus explain the observed patterns.

We suggest that high rates of predation near pond edges resulted from increased predator activity in these

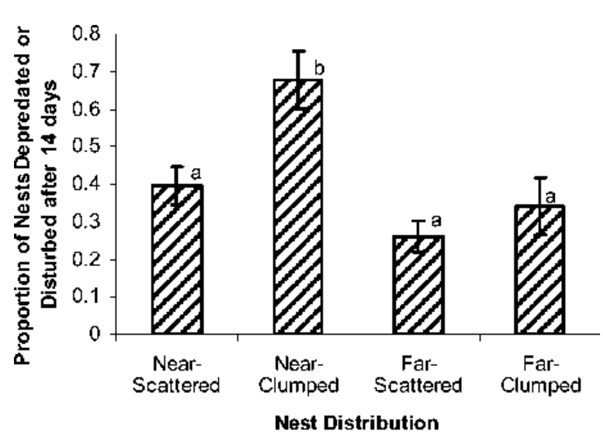

Fig. 2. Rates of nest predation for four distribution patterns. Bars with different letters represent differences in predation rates ($P < 0.008$).

areas, making nests especially vulnerable to incidental encounters (Vickery et al., 1992). The increased predation near pond edges is consistent with predation on painted turtle nests (Legler, 1954; Christens and Bider, 1987). However, a distance effect was not detected by investigators examining predation on other species of turtles (Congdon et al., 1987; Robinson and Bider, 1988; Burke et al., 1988). Incidental encounters of nests by predators could lead to more intense searches. Where suitable nesting habitat is limited, the likelihood of nests being clumped probably increases. The frequency of naturally occurring clumped nests (Christens and Bider, 1987; Robinson and Bider, 1988; Kolbe and Janzen, 2002) might be a consequence of limited nesting habitats and thus may explain the high rates of predation that often are reported.

At the nest-site scale, the low rates of predation on nests within lawn and roadside habitats also were unexpected. Nests within lawn habitats may have benefited from frequent activity by humans or domestic dogs (*Canis familiaris*) that predators avoided. Domestic dogs were not identified as nest predators in our study area (Maier et al., 2002). Additionally, mowed lawns where we placed nests may have had lower visual and olfactory cues, reducing nest detection by predators. Although some investigators have reported elevated rates of nest predation along roadsides for birds (Paton, 1994) and turtles (Gemmell, 1970; Jackson and Walker, 1997), Hamilton et al. (2002) found that simulated turtle nests along roadsides had a lower predation rate than those in forests or edge habitats. Predation along roads may be influenced by the presence of other habitat features, especially ponds. For example, all simulated nests along a road in Pawtuckaway State Park were depredated and these were ~5 m from a pond edge. It is important to note that roadside nests may encounter other risks to survival, such as road grading and hatchlings emerging near roadsides may suffer considerable mortality (Standing et al., 1999). Adult turtles utilizing roadside areas for nesting also are vulnerable to vehicle-related mortality, and the fate of adults is often more influential to population stability than nest success (Congdon et al., 1993).

4.2. Implications of nest distribution on predation

In addition to distance from water, nest distribution had a substantial influence on vulnerability to predation (Fig. 2). Clumped nests were depredated at a greater rate than scattered nests, especially when near pond perimeters. These results are consistent with a pilot study we conducted in the same area (Marchand et al., 2002). Because individual nests are closer together when clumped, a predator obviously had an increased probability of detecting a second nest once one nest was located. Predation of snapping turtle (Robinson and Bider, 1988) and diamondback terrapin (*Malaclemys terrapin*) nests (Burger, 1977) was greater when nests were clustered (within 1 m of other nests). On the other hand, Burke et al. (1998) found no relationship between predation and nest density, and density-dependent predation also was not detected among green sea turtles (*Chelonia mydas*; Fowler, 1979). The later two studies, however, were restricted to single sites and their results may have been influenced by local factors.

Although the distance to pond edges was influential, the distance to other edges did not have a strong effect on vulnerability to predation. These results run counter to those reported by Temple (1987) where turtle nests near the edge of a field were more likely to be depredated than nests further from edge habitat. Similarly, Linck et al. (1989) noted that *C. serpentina* nests in cornfields often survived but those nests along the perimeter were frequently destroyed. Our results regarding the influence of proximity to an edge may have been influenced by the high survival of nests along roadsides where the edge distance was low. The type of edge likely influences predator activity and thus rates of predation (Heske et al., 1999; Dijak and Thompson, 2000).

4.3. Management implications

We acknowledge that our results may not apply directly to other species of turtles because some species (e.g., Blanding's, spotted, and wood) tend to utilize terrestrial habitats more extensively than painted turtles that we patterned our nests after (Joyal et al., 2001; Compton et al., 2002). However, other turtles are known to exploit human-modified habitats for nesting (Joyal et al., 2001), making them vulnerable to generalist predators.

Abundant populations of generalist predators have become a concern among conservation biologists and controls may be necessary in some areas (Garrott et al., 1993; Congdon et al., 1993). Removing predators has had some success and may be appropriate in certain circumstances. For example, nest success and recruitment of yellow mud turtles (*Kinosternon flavescens*) were enhanced after the removal of raccoons (Christiansen and Gallaway, 1984). However, Schneider (2001) noted that long-term predator management may be problematic and is not a viable solution in landscapes where predator densities are high and subsidized by human activity. Furthermore, some investigators have questioned whether removal of these predators will have adverse ecosystem implications (Stancyk et al., 1980; Ratnaswamy and Warren, 1998). Transplanting nests, where nests are moved from natural to man-made nests to reduce visual and olfactory cues, has had some success with sea turtles (Stancyk et al., 1980), but limited application with freshwater species of turtles. Wire cages have been used to protect turtle nests (especially rare species) from predators (Butler and Graham, 1995; Kiviat et al., 2000). Although the above methods have had some success, they can require intense effort. An alternative approach is the active management of landscapes in order to reduce predator impacts (Schneider, 2001).

Results from our study indicate that local habitat manipulations also could be implemented to potentially reduce nest predation. For example, artificial nesting habitat has been created to enhance recruitment (Kiviat et al., 2000). Habitat manipulations (e.g., patch cuts to open the canopy and tilling small areas) might be most beneficial in areas with limited nesting opportunities and chronically high rates of nest predation. Nesting habitats should be created away from road crossings and other potentially hazardous sites. Our results indicate that the location and size of nesting habitats are important parameters to consider. If nesting habitats are created near ponds, they should be large enough to minimize nests being clumped. Otherwise, nesting sites should be available at distances of at least 50 m from pond or wetland edges. In some instances, management may include the revegetation of existing nesting habitats where nests are concentrated. To ensure maximum recruitment into populations of turtles, nesting habitat should be managed to incorporate habitat preferences of turtles (Wilson, 1998; Kolbe and Janzen, 2002), maximize embryonic survival (Cagle et al., 1993) and minimize predation (Kolbe and Janzen, 2002; this study).

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