

IMPACT OF NEST-SITE SELECTION ON NEST SUCCESS AND NEST TEMPERATURE IN NATURAL AND DISTURBED HABITATS

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Abstract. Nest-site selection behavior is a maternal effect that contributes to offspring survival and variation in offspring phenotypes that are subject to natural selection. We investigated nest-site selection and its consequences in the snapping turtle, *Chelydra serpentina*, in northwestern Illinois. We evaluated nest-site selection at both the microhabitat and habitat patch levels. Turtles selected nest sites with shorter vegetation, more open sand, and fewer cacti than random locations. These microhabitat characteristics described sandy patches where both nest density and success were higher compared to grassy patches in 1999. We subsequently investigated nest-site selection within two discrete subdivisions of the study area that varied in the degree of human disturbance to determine if nesting behavior, nest success, or nest temperatures were affected. The tendency to nest in sandy patches was much stronger at the natural site due to habitat modifications at the residential site that have blurred the distinction between sandy and grassy patches. Additionally, the residential site had a high density of nests within 5 m of houses and a fence (both areas with disturbed habitat similar to sandy patches), compared to the overall density. Thus, nest success associated with sandy patches may be compromised at the residential site; an ecological trap may result in lower nest success in areas with preferred microhabitat characteristics. Despite a similar basis for nest-site selection in terms of microhabitat characteristics at both sites, nest temperatures were correlated with microhabitat characteristics used to select nest sites only at the natural site. Nest temperatures at the residential site were instead correlated only with the percentage overstory vegetation cover and therefore averaged 2°C lower than at the natural site, a temperature difference that influenced offspring sex. The higher percentage overstory vegetation cover at the residential site was due to human alterations of the habitat, and may serve to extend the ecological trap biasing the sex ratio of this population. This study illustrates the importance of (1) nest-site selection as a substantive maternal effect, (2) understanding habitat use during crucial life-history events, and (3) the potential for human disturbance to modify offspring phenotypes and negatively impact nest success despite adaptive nesting behavior.

Key words: *Chelydra serpentina*; ecological trap; human-altered habitat; maternal effects; microhabitat; Mississippi River shoreline, Illinois; nest microenvironments; nest-site selection; offspring survival; turtles.

INTRODUCTION

Habitat selection often results in nonrandom patterns of organism distribution, which are assumed to be the result of natural selection (Southwood 1977, Martin 1998, Clark and Shutler 1999). These patterns result from selection of environmental cues, such as patches in a habitat mosaic or specific microhabitats, by organisms. Especially useful in identifying patterns of selection is the comparison of measurements taken at selected sites to those at random locations within the same habitat (e.g., Wilson 1998). This method can detect habitat selection and help identify important environmental cues. In particular, evaluating maternal nest-site selection offers a tangible way to track habitat

selection during an important life-history event with implications for offspring and maternal fitness.

Maternal effects are widespread and may play an important adaptive role in evolution (Bernardo 1996a, Mousseau and Fox 1998a, b). Key life-history traits such as propagule number and size are the focus of most research on maternal effects (Bernardo 1996b, Roff 1992, Stearns 1992). Less understood is the role maternal behavior plays in life-history evolution (Resatits 1996). Maternal effects, such as oviposition-site choice, may have important ramifications for offspring survival and offspring phenotypes. If a female's choice of a nest site leads to differences in offspring survival, fitness-related phenotypes, or key demographic factors, then nesting behavior warrants consideration as a substantive evolutionary force. For nest-site selection to be considered an important maternal effect, it must be identified in natural populations and variation in nest success or fitness-related offspring phenotypes documented. In this study, we determine

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how maternal nest-site selection influences nest success and nest temperature in a mosaic habitat. Consequently, we evaluate nest-site selection as a potentially important cross-generational maternal effect; maternal behavior in one generation has far-reaching implications for offspring of the next generation.

Oviposition decisions may result in important life-history, phenotypic, and survival consequences for the offspring of many oviparous animals. Selection of nest sites with specific characteristics leads to higher nest and offspring survival in many birds (e.g., Dunk et al. 1997, Martin 1998, Hatchwell et al. 1999). Maternal oviposition preference is also widely studied in insects (Rauscher 1983, Bernardo 1996a), and influences development time, size of offspring, and other fitness components in some insects (e.g., Janz et al. 1994, Sadeghi and Gilbert 1999). Less is known about oviposition-site choice in natural populations of reptiles (Bernardo 1996a). Reptile oviposition decisions have implications beyond nest success; variable developmental environments influence gas and water exchange and the temperature experienced by eggs (e.g., Packard et al. 1987, Ratterman and Ackerman 1989, Deeming and Thompson 1991, Cagle et al. 1993). During incubation, these microenvironments influence developmental rate, offspring size, offspring sex, locomotor speed, thermoregulation behavior, and growth rate (e.g., Miller et al. 1987, Packard et al. 1987, Plummer and Snell 1988, Janzen et al. 1990, Roosenburg and Kelley 1996, Shine and Harlow 1996, O'Steen 1998). Additionally, some of these traits are linked to offspring survival in the field (Janzen 1993, 1995, Janzen et al. 2000a, b). Only a few studies have considered whether natural variation in reptile nest-site selection can result in variation in nest success (Temple 1987, Wilson 1998) or how offspring phenotypes are mediated by the nest microenvironment (Schwarzkopf and Brooks 1987, Shine and Harlow 1996, Madsen and Shine 1999, Packard et al. 1999).

Understanding what environmental cues organisms use to select nest sites and the subsequent consequences for offspring is also important for conservation. Identifying areas or particular microhabitat variables associated with higher nest density and success within a nesting area provides clues for the habitat needs of a species. Additionally, this knowledge may aid in understanding the consequences of human alterations of habitat for critical life-history events such as nesting. Under some circumstances, negative consequences of seemingly adaptive nesting behavior may result because of human modifications of habitat (Gates and Gysel 1978, Misenhelter and Rotenberry 2000).

We studied the common snapping turtle to evaluate the potential importance of maternal nest-site selection. First, we documented that nest-site selection was occurring and identified characteristics that turtles used to select nest sites. We took both a microhabitat and a habitat patch level perspective, comparing nest density

and nest success in sandy and grassy patches. We also compared two discrete sites at the study area with substantially different levels of human disturbance to determine if human habitat alterations influenced nest-site selection or nest microenvironments. For nest-site selection to evolve through natural selection on maternal behavior, variation that results in differential offspring fitness must be present. We quantified the range of nest-site characteristics in this population of snapping turtles and determined how these factors related to nest success and offspring phenotypes. We found that nest location strongly influenced nest success and nest temperature, and that human disturbances have disrupted the seemingly adaptive nesting behavior of this population.

METHODS

Study organism

The snapping turtle, *Chelydra serpentina*, is an aquatic species with a wide distribution across the eastern two-thirds of North America (Conant and Collins 1991). Snapping turtles inhabit permanent bodies of fresh water and use the land adjacent to these waters for nesting. In addition, snapping turtles nest in large numbers in some areas (Hammer 1969, Congdon et al. 1987, Janzen 1993), making it an excellent species for assessing habitat selection during nesting. Previous studies of the nesting ecology of freshwater turtles in northern North America described nest sites as being in open areas with little surrounding vegetation (e.g., Petokas and Alexander 1980, Christens and Bider 1987, Ewert et al. 1994, Plummer et al. 1994, Butler and Hall 1996), but few studies have quantified multiple microhabitat characteristics of nests (see Schwarzkopf and Brooks 1987, Roosenburg 1996, Wilson 1998). Snapping turtles also exhibit pattern II temperature-dependent sex determination, such that females are produced at low and high incubation temperatures and males at intermediate temperatures (Janzen and Paukstis 1991, Ewert et al. 1994).

Study sites

We conducted this research on U.S. Army Corps of Engineers and U.S. Fish and Wildlife Service land along the eastern bank of the Mississippi River in Carroll and Whiteside Counties, Illinois. The study area consisted of relic sand-prairie habitat. Dominant vegetation was *Stypa* sp., *Opuntia humifusa*, and *Rhus aromatica* (Warner 1998). Ground cover was heterogeneous with a mixture of distinct grassy and sandy patches. We used two discrete sites within the study area that differed substantially in the amount of human disturbance. The residential (RES) site consisted of ~1100 m of shoreline extending ~75–150 m inland to a boundary fence that ran the length of the site (Fig. 1A). This site was composed of grassy patches, sandy patches, houses, several continuous tree stands, and

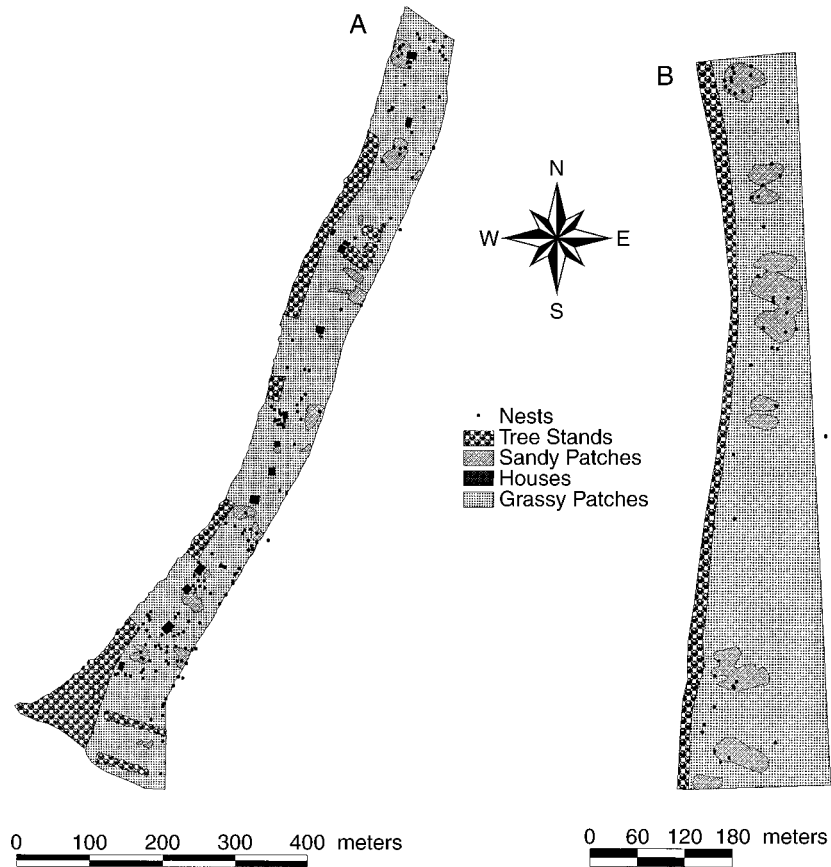


FIG. 1. Maps of the habitat types in (A) the residential (RES) site and (B) the National Wildlife Refuge (NWR) site showing the grassy areas, sand patches, houses, continuous tree stands, and nest sites of snapping turtles in (A) 1990–1999 and (B) 1997–1999. The Mississippi River is located to the west of both study sites, and a fence runs along the eastern boundary of the RES.

many isolated trees interspersed throughout the site (Table 1). The RES site was a highly disturbed site with frequent mowing, sand roads throughout, fire suppression, houses, and many isolated trees resulting in a heterogeneous overstory. The National Wildlife Refuge (NWR) site was located ~750 m north of the RES and consisted of ~900 m of shoreline extending ~100–175 m inland (Fig. 1B). This site was composed of grassy patches, sandy patches, a continuous strip of trees along the shoreline, and, in contrast to the RES site, virtually no isolated trees (Table 1). The NWR site

had limited disturbance except for fire suppression and upland hunting, and we consider it representative of native nesting habitat. The two sites differed primarily in the amount of sandy area and the presence/absence of houses and isolated trees (Table 1).

GIS model

From May to July 1990–1999, snapping turtle nests were located during morning surveys (0600–1200) (Table 2). From 1990–1996 we measured the location of each nest relative to known landmarks at the RES site only and from 1997 to 1999 we marked each nest with a flag at both the RES and NWR sites. We used a Global Positioning System (GPS) to obtain the coordinates of all nests (± 3 m). Nest coordinates were converted into Geographic Information Systems (GIS) coverages using ArcView software (ESRI 1998). We digitized landscape features (i.e., houses, fences, continuous tree stands, sandy patches, and the site boundary) from an aerial photograph (U.S. Army Corps of Engineers) for the RES site (Fig. 1A). GPS coordinates were used to verify the location of RES landscape features and to create the landscape map (i.e., site boundary, contin-

TABLE 1. Areas (m²) for each habitat patch type and houses at the RES and NWR study areas in Illinois taken from the Geographical Information System (GIS) coverage.

Habitat type	Study area	
	RES	NWR
Grassy patch	80 155	94 105
Tree stands	20 026	13 171
Sandy patch	7 636	13 871
Houses	1 513	...
Total	109 330	121 147

TABLE 2. Number of snapping turtle nests laid at the RES and NWR sites by year 1990–1999.

Year	Number of nests		Total
	RES	NWR	
1999	30	18	48
1998	12	17	29
1997	4	11	15
1996	3	16	19
1995	14	8†	22
1994	15	22†	37
1993	17	16†	33
1992	10	...	10
1991	28	28†	56
1990	30	21†	51
Total	163	157	320

† Not included in analyses where exact location data are needed.

uous strip of trees along the shoreline, and sandy patches) for the NWR site (Fig. 1B). The GIS model consisted of nest locations for 1990–1999 and the landscape features at both the RES and NWR sites.

Nest-site selection at the patch level

To analyze the spatial distribution of nests and determine if nest-site selection was occurring, we first employed a conservative first-order nearest-neighbor index (Clark and Evans 1954, Shaw and Wheeler 1985). This index evaluates how nests are spaced compared to the null hypothesis of complete spatial randomness. The ratio (R) is the average observed nearest-neighbor distance to the expected nearest-neighbor distance. The expected distance is calculated using the area of the study site and the number of nests. $R = 1$ indicates a random pattern, $R < 1$ suggests a clustered pattern, and $R > 1$ means regular spacing of nests. Significance was tested by calculating the standard error and a z score (Shaw and Wheeler 1985).

A 2×2 contingency test was used to determine if there was an excess of nests in sandy or grassy patches at the two sites. We then used the GIS model to determine the area of each patch feature for both study sites (Table 1). We calculated the expected number of nests in grassy and sandy patches based on the area of each patch divided by the total area available for nesting (i.e., the area of the continuous tree stands and houses for the RES site and continuous tree stand for the NWR site were subtracted from the respective total areas). No turtle nests were found in the areas under continuous tree stands, thus we excluded these areas from calculations of the total area available for nesting. Nest densities in sandy and grassy patches for the RES and NWR sites were compared using an ANOVA in JMP (SAS Institute 1997). For the RES site, we also calculated the expected number of nests in buffer areas within 0–5 m and 5–10 m of each house (excluding the area of the houses) and of the west side of the boundary fence using the GIS coverage. The observed

vs. expected number of nests in the area of sandy patches and buffers around houses and the fence were evaluated using chi-square tests (Sokal and Rohlf 1995).

Nest-site selection at the microhabitat level

To determine if turtles selected microhabitat characteristics, we evaluated 48 nest sites and 100 random locations in 1999 (50 random locations at each study site). Random locations were determined by generating two random numbers, one number each for the length and width of the study site in meters. For each nest or random location, we measured slope, aspect, distance from the water, and percentage overstory vegetation cover (see Janzen 1994a). The maximum vegetation height, modal vegetation height, presence/absence of cacti, and percentages of bare ground, litter, herbaceous vegetation, and succulent vegetation were measured in a 1×1 m quadrat (Daubenmire 1959) placed directly over the random points or 0.5 m in a random cardinal direction from each nest site. We shifted the quadrat at nest sites because nesting females disturbed the vegetation such that measures representative of pre-nest conditions could not be obtained. The total percentage of ground cover at a nest site could equal more than 100% because some categories occupied different layers of the same space. For example, Nest 23 had 20% bare ground, 60% litter, 45% herbaceous vegetation, and 20% succulent vegetation for a total of 145%. The presence or absence of cacti in the $1 \text{ m} \times 1 \text{ m}$ quadrat placed over the nest site was also recorded. Surface vegetation was cut in a $0.25 \text{ m} \times 0.25 \text{ m}$ quadrat placed in a random cardinal direction within the $1 \text{ m} \times 1 \text{ m}$ quadrat. The dried sample gave the vegetation dry mass.

Many of the microhabitat variables measured were intercorrelated so we used a principal components analysis (PCA) of the correlation matrix to generate new variables (SAS Institute 1997). All percentages were arcsine transformed and the other microhabitat variables were square root transformed except modal vegetation height, which was log transformed. Aspect was not included in the PCA, and was analyzed separately instead, because some nests and random locations had a slope of zero, thus no aspect. We used the brokenstick model, which compares eigenvalues from the data to random ones, to determine the number of principal components to use in analyses (Jackson 1993, McGarigal et al. 2000). Nontrivial principal component variables and aspect were then used in ANOVAs to determine if there was a difference in microhabitat between random locations and nest sites overall and within each site separately. Additionally, potential differences between the two sites in microhabitat characteristics of nests and random locations were evaluated using ANOVAs.

Nest success

Nests in 1999 were followed from the date laid until either the nest was destroyed by a predator ($2.07 \pm$

3.33 d [mean \pm 1 SD], range = 0–10 d) or hatchling emergence was completed (i.e., the nest was successful). We determined hatch date by checking the top tier of eggs for each nest once or twice daily beginning 60–65 d into incubation. If a pipped egg or hatchling was found, the nest was no longer disturbed and was monitored only for emerging hatchlings. We erected a 15 cm tall drift fence around nests to collect hatchlings as they emerged. Drift fences were checked 2–3 times per day for emerged hatchlings. From these data, we tested for differences in nest success between sandy and grassy patches using chi-square tests (Sokal and Rohlf 1995). We evaluated the relationship between microhabitat characteristics and probability of nest success using logistic regression for both sites combined and each separately. We also analyzed the relationship between microhabitat characteristics and the percentage of eggs that hatched and percentage of hatchlings that emerged from nests with linear regression in JMP (SAS Institute 1997). Hatching and emergence percentages were arcsine transformed before the analyses. We also determined if there was a difference in nest survival between sandy and grassy patches using chi-square tests (Sokal and Rohlf 1995).

Nest temperature and offspring sex ratio

Temperatures were recorded in 16 snapping turtle nests in 1999 with HOBO XT and HOBO-TEMP temperature loggers (Onset Computer Corporation, Pocasset, Massachusetts) (see Weisrock and Janzen 1999). Dataloggers were placed just outside the nest cavity at a depth corresponding to the middle of each nest (mean \pm SD = 17.5 \pm 2.18 cm, range 15–21.5 cm) within 2 wk of oviposition and remained until hatchling emergence. We used the overall mean temperature (i.e., the mean of the average daily temperature) during the middle third of incubation to characterize nest temperatures because this corresponds roughly to the thermosensitive period during which sex determination occurs (Yntema 1979). By so doing, we standardized comparisons by developmental period. The overall mean temperature during the middle third of incubation was positively correlated with the mean temperature for the entire incubation period ($r = 0.99$, $P < 0.0001$). We used a two-factor ANOVA to determine if there was a difference in nest temperatures between patch types (i.e., sandy and grassy) and between sites (i.e., RES and NWR), and linear regression to determine if overall mean nest temperatures were correlated with microhabitat characteristics. Because percentage overstory vegetation cover was highly skewed, we used the non-parametric Wilcoxon test to determine if there was a difference between the RES and NWR sites (SAS Institute 1997).

To evaluate the relationship between nest temperature and offspring sex ratio, we determined the sex of 10 randomly chosen individuals from each clutch after hatchling emergence. Sex was determined by macro-

scopic examination of gonads (Yntema 1976). The effect of nest temperature on sex ratio, measured as the percentage of males, was evaluated using linear regression. Sex ratios were arcsine transformed before the analysis.

RESULTS

Nest-site selection at the patch level

Nests were clustered at both the NWR ($R = 0.84$, $P = 0.02$) and RES ($R = 0.85$, $P = 0.02$) sites, indicating nonrandom nest-site selection. Clustering at the NWR site was in sandy patches, but at the RES site, nests seemed to be clustered around houses and the fence, not in sandy patches (Fig. 1A, B). The 2×2 contingency analysis indicated an excess of nests in sandy patches at the NWR site (1996–1999) and an excess of nests in grassy patches at the RES site (1990–1999) ($\chi^2 = 43.14$, $df = 1$, $P < 0.0001$). More than half of nests laid at the NWR site in the four years were in sandy patches (58.1% and 36 of 62 nests), while the opposite was true for the RES site, where the vast majority of nests over the 10-yr span were in grassy patches (82.7% and 115 of 139 nests). A similar result was obtained when accounting for the proportion of each patch type; many more nests were located in sandy patches than expected at the NWR site ($\chi^2 = 150.02$, $df = 1$, $P < 0.0001$), but not at the RES site ($\chi^2 = 1.86$, $df = 1$, $P = 0.17$) during 1996–1999. However, when all 10 years (1990–1999) of available data were included for the RES site, more nests were located in sandy patches than expected based on the area proportions ($\chi^2 = 7.41$, $df = 1$, $P = 0.006$), but the tendency was not nearly as strong as in just four years at the NWR site. For the NWR site (1996–1999), the density of nests in sandy patches was significantly higher ($F_{1,6} = 38.55$, $P = 0.0008$) than in grassy patches (Table 3). In contrast, the density of nests at the RES site between sandy and grassy patches was not significantly different in 1996–1999 ($F_{1,6} = 0.43$, $P = 0.54$) nor in 1990–1999 ($F_{1,18} = 2.99$, $P = 0.10$). Thus, when considering nest-site selection at the habitat patch level, nests at the NWR site had a much stronger tendency to be in sandy patches than nests at the RES site.

More nests were located within 0–5 m of houses ($\chi^2 = 6.99$, $df = 1$, $P = 0.008$) and the fence ($\chi^2 = 16.74$, $df = 1$, $P < 0.0001$) than expected at the RES site (Fig. 1A). No such relationship existed, however, for the 5–10 m buffer around houses ($\chi^2 = 0.22$, $df = 1$, $P = 0.64$) or 5–10 m from the boundary fence ($\chi^2 = 0.01$, $df = 1$, $P = 0.92$). The density of nests within 0–5 m of houses was 3.45×10^{-3} nests/m² and the fence was 4.07×10^{-3} nests/m² compared to an overall nest density of 1.82×10^{-3} nests/m² at the RES site. These higher densities around houses and the fence were likely the cause of the significant clustering at the RES site while nests were concentrated in sandy patches at the NWR site (Fig. 1A and B).

TABLE 3. Density of snapping turtle nests (nests/m²) for sandy and grassy patches by year for the RES (1990–1999) and the NWR (1996–1999) sites.

Year	RES				NWR			
	Sandy patches		Grassy patches		Sandy patches		Grassy patches	
	<i>N</i>	Density	<i>N</i>	Density	<i>N</i>	Density	<i>N</i>	Density
1999	4	5.24×10^{-4}	26	3.24×10^{-4}	10	7.21×10^{-4}	8	0.85×10^{-4}
1998	3	3.93×10^{-4}	9	1.12×10^{-4}	12	8.65×10^{-4}	5	0.53×10^{-4}
1997	0	0.00	4	0.50×10^{-4}	6	4.33×10^{-4}	5	0.53×10^{-4}
1996	0	0.00	3	0.37×10^{-4}	8	5.77×10^{-4}	8	0.85×10^{-4}
1995	2	2.62×10^{-4}	12	1.50×10^{-4}				
1994	5	6.55×10^{-4}	10	1.25×10^{-4}				
1993	2	2.62×10^{-4}	15	1.87×10^{-4}				
1992	0	0.00	10	1.25×10^{-4}				
1991	5	6.55×10^{-4}	23	2.87×10^{-4}				
1990	4	5.24×10^{-4}	26	3.24×10^{-4}				
Mean	2.5	3.27×10^{-4}	13.8	1.72×10^{-4}	9	6.49×10^{-4}	6.5	0.69×10^{-4}

Note: The area of each habitat type is given in Table 1.

Nest-site selection at the microhabitat level

Based on the broken-stick method, which compares eigenvalues to those from random data, PC1 and PC2 were different from random (Table 4). We considered both PC1 and PC2 non-trivial and describe them here. Ground vegetation characteristics, that is, maximum and modal vegetation height, percentages of bare ground, litter, herbaceous vegetation, succulent vegetation, dry vegetation mass, and cacti presence/absence uniformly comprised PC1. As PC1 values decreased, they described decreasing amounts of vegetation, more open sand, and fewer cacti. PC2 was primarily a contrast between values of slope and percentage overstory vegetation cover, and distance from the water with positive values indicating shadier areas (Table 4).

In the overall comparison of nest sites ($N = 48$ sites) vs. random locations ($N = 100$ locations), only PC1 ($F_{1,146} = 43.76$, $P < 0.0001$) differed significantly (Fig. 2). Nest sites were characterized by shorter maximum and modal vegetation height, a greater percentage of bare ground, a lesser percentage of litter, herbaceous

vegetation, and succulent vegetation, less dry vegetation mass, and fewer cacti than random locations. Similar results were obtained when considering the RES nest sites ($N = 30$ sites) and random locations ($N = 50$ locations) ($F_{1,78} = 22.37$, $P < 0.0001$) and NWR nest sites ($N = 18$ sites) and random locations ($N = 50$ locations) ($F_{1,66} = 18.76$, $P < 0.0001$) separately. PC2 ($F_{1,78} = 11.50$, $P = 0.001$) was also significantly different between nest sites and random locations at the RES site, with nest sites on less of a slope, with a smaller percentage overstory vegetation cover, and farther from the water. Univariate analysis of microhabitat differences between random locations and nest sites gave similar results to the principal components scores and aspect did not influence nest-site selection ($F_{1,133} = 0.11$, $P = 0.74$). Thus, nest-site selection was based on similar microhabitat characteristics at the two sites despite differences in nest-site selection tendencies at the habitat patch level, where NWR nests were in sandy patches and RES nests were in grassy patches.

To investigate these site differences further, we ex-

TABLE 4. Factor loadings for principal components analysis (PCA) of 11 microhabitat variables measured at $N = 48$ nest sites and $N = 100$ random locations in 1999.

Variable	PC1	PC2
Slope	-0.103	0.737
Percentage vegetation cover	-0.048	0.624
Maximum vegetation	0.707	0.140
Modal vegetation	0.659	0.185
Percentage bare ground	-0.914	-0.168
Percentage litter	0.821	0.325
Percentage herbaceous vegetation	0.787	0.030
Percentage succulent vegetation	0.610	-0.378
Dry vegetation mass	0.800	-0.023
Cacti presence	0.642	-0.420
Distance from water	0.054	-0.752
Eigenvalue	4.5035	2.0062
Percentage of variation	40.94	18.24

Note: Aspect was not included in PCA because many of the sites had zero slope (hence, no aspect).

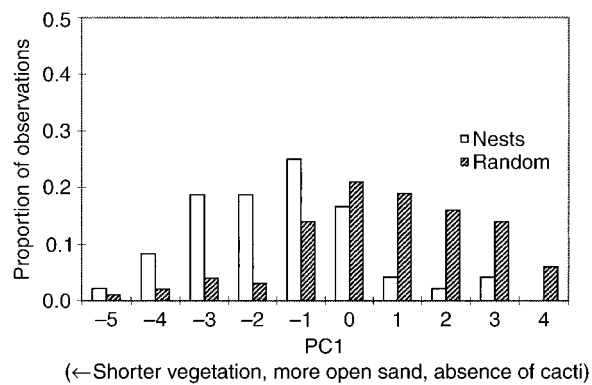


FIG. 2. Distribution of PC1 for random locations compared to nest sites of snapping turtles at the RES and NWR study sites combined. Nest sites were characterized by shorter vegetation, more open sand, and fewer cacti than random locations.

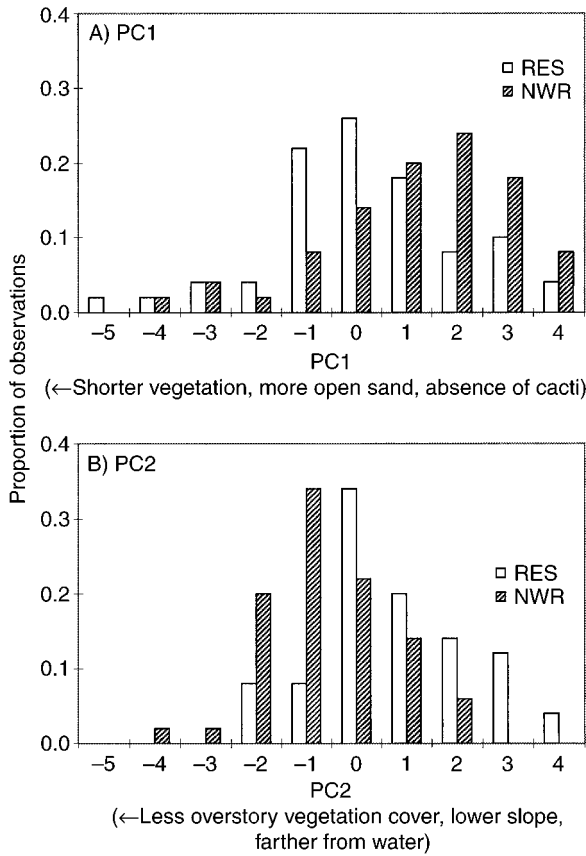


FIG. 3. Distribution of (A) PC1 and (B) PC2 for random locations at the RES and NWR study sites. In general, the RES sites had less ground vegetation but more overstory vegetation cover than the NWR.

explored differences between microhabitat characteristics of nests and random locations at the two sites. Nests at the RES and NWR sites differed mostly in the percentage overstory vegetation cover ($F_{1,46} = 6.02, P = 0.02$). Nests at the RES site were in shadier areas than those at the NWR site. Differences in random locations illustrate the background habitat available for nesting at the two sites. The NWR site had more ground vegetation overall (PC1: $F_{1,98} = 8.73, P = 0.004$) and less overstory vegetation cover (PC2: $F_{1,98} = 23.28, P < 0.0001$) than the RES site (Fig. 3). Examination of the differences between sandy and grassy patches within each site provided some insight into these site differences. Though sandy and grassy patches were different in PC1 at the NWR site ($F_{1,48} = 33.25, P < 0.0001$) and nearly so at the RES site ($F_{1,48} = 3.73, P = 0.06$), a more pronounced difference between the patch types was observed at the NWR site (Fig. 4). Sandy patches had similar PC1 values at each site (i.e., PC1 ranging from -4 to 0), but the range of PC1 values for grassy patches at the RES site overlaps with the sandy patch values more. The difference between sandy and grassy patches at the RES site, although nearly significant, was much less distinct than at the NWR site.

Nest success

Overall success for the 48 nests laid in 1999 was 35.4%. Nest success, defined here as survival until hatchling emergence was completed, was significantly higher in sandy patches ($\chi^2 = 11.07, df = 1, P = 0.0009$) than in grassy patches. Nests in sandy patches had a 71.4% success rate (10 of 14 nests) and nests in grassy areas had 20.6% success (7 of 34 nests). For the sites considered separately, there were more successful nests in sandy patches and unsuccessful nests in grassy patches than expected by chance (NWR, $\chi^2 = 3.74, df = 1, P = 0.05$; RES, $\chi^2 = 4.84, df = 1, P = 0.03$). Overall, the probability of nest success was significantly higher with decreasing values of PC1 ($\chi^2 = 7.65, df = 1, P = 0.006$) (Fig. 5). That is, the probability of nest success increased with decreasing amounts of vegetation, more open sand, and fewer cacti. Additionally, PC1 showed a similar relationship at both sites when considered separately, with a significant result at the NWR site ($\chi^2 = 7.72, df = 1, P = 0.006$) and a nearly significant result at the RES site

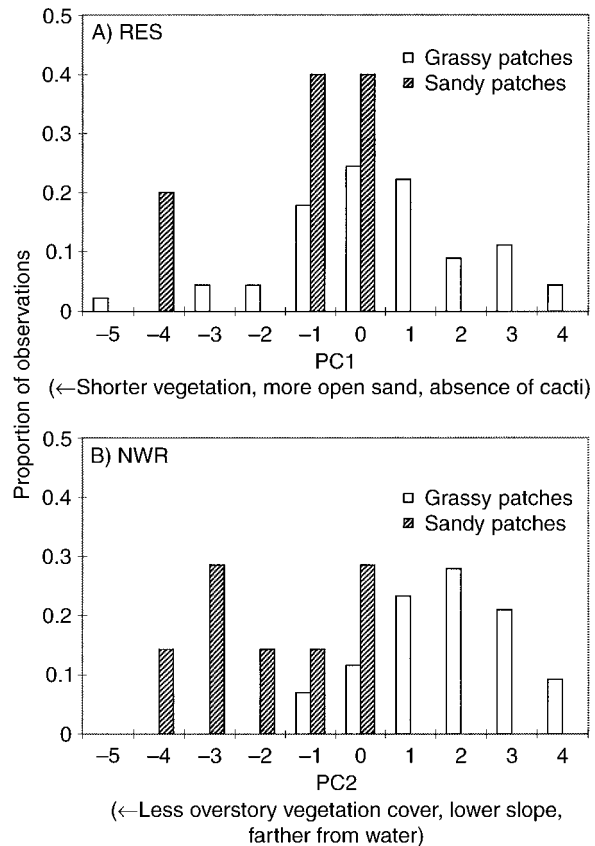


FIG. 4. Distribution of PC1 for random locations from sandy and grassy patches at the (A) RES and (B) NWR study sites, separately. Sandy patches were characterized by the same range of PC1 scores in both sites. In contrast, grassy patches were distinct from sandy patches at the NWR site, while at the RES site, PC1 scores of grassy patches strongly overlapped with scores of sandy patches.

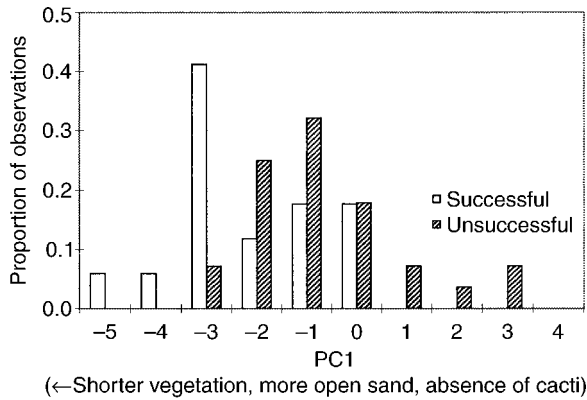


FIG. 5. Distribution of PC1 for successful and unsuccessful nest sites of snapping turtles at the RES and NWR study sites combined. Successful nests were characterized by shorter vegetation, more open sand, and fewer cacti than unsuccessful nests.

($\chi^2 = 3.46$, $df = 1$, $P = 0.06$). Univariate analysis of the probability of nest success gave similar results to the principal components scores. Nest success was comparable at the habitat patch level for both sites with sandy patches having more successful nests; however, there was a higher probability of nest success with decreasing vegetation, more open sand, and fewer cacti at the NWR site than at the RES site.

There was no difference in the percentage hatching ($F_{1,12} = 0.03$, $P = 0.86$) or hatchlings emerging ($F_{1,12} = 0.64$, $P = 0.44$) between sandy and grassy patches. No microhabitat characteristics (PCs) had an effect on the percent hatching or hatchlings emerging either. In addition, no univariate analyses of microhabitat characteristics showed significant relationships with hatching percentage or percentage emergence.

Nest temperature and offspring sex ratio

Temperatures for nests in sandy patches ($28.94 \pm 0.93^\circ\text{C}$ [mean \pm 1 SD], $N = 7$ nests) were significantly higher ($F_{1,13} = 6.03$, $P = 0.03$) than those recorded for nests in grassy patches ($27.33 \pm 1.72^\circ\text{C}$, $N = 9$ nests); temperatures were also nearly significantly different ($F_{1,13} = 4.12$, $P = 0.06$) between the RES and NWR sites (Table 5). Overall, nest temperatures were negatively correlated with PC2 ($r = -0.63$, $P = 0.009$). Nest temperatures at the RES site were also negatively correlated with PC2 ($r = -0.75$, $P = 0.02$). At the NWR site, however, nest temperatures were correlated with PC1 only ($r = -0.91$, $P = 0.004$). Univariate analyses were consistent with these results. Percentage overstory vegetation cover was the only microhabitat characteristic significantly correlated with nest temperature at the RES site ($r = -0.97$, $P < 0.0001$). Relatively unshaded nests had higher temperatures. Percentage overstory vegetation cover was significantly higher (Wilcoxon score = -5.59 , $P < 0.0001$) at the RES site ($15.11 \pm 24.45\%$, range = 0–81.90%,

$N = 80$ nests and random locations) than at the NWR site (mean = $1.77 \pm 4.91\%$, range = 0–25.74%, $N = 68$ nests and random locations) (Fig. 3B). At the NWR site, nest temperatures depended on ground characteristics (PC1), such that nest temperatures were higher for nests in less vegetated areas, while at the RES site, percentage overstory vegetation cover affected nest temperatures.

Overall, 8.6% of the hatchlings sexed were male (Table 5). One clutch was all male, 11 were all female, and two clutches had mixed sex ratios. Overall mean nest temperature was inversely correlated with nest sex ratio (% male) ($r = -0.73$, $P = 0.003$). This result was heavily influenced by the one all-male nest.

DISCUSSION

To evaluate the ecological and evolutionary importance of a behavioral maternal effect like nest-site selection, several criteria must be fulfilled. Nest-site selection must occur along some measurable axis. Then, nest success, offspring survival, or another fitness-related phenotype must be linked to the same variables used by the organism to select nest sites for natural selection to shape behavioral choices. Finally, some component of nest-site selection must have a genetic basis to permit evolution.

We established that nest-site selection occurs in snapping turtles. Female turtles selected nonrandom nest sites based on ground characteristics such as shorter vegetation, more open sand, and the absence of cacti (Fig. 2), and sandy patches were selected far more often at the NWR site. These microhabitat characteristics described sandy patches at the NWR site within which both nest density and success were higher (Table 3 and Fig. 5). Similar nest-site selection for microhabitat characteristics was observed for the RES site, except the tendency to nest in sandy patches was much weaker and likely due to a human-related increase in sandy (e.g., roads) and sparsely vegetated (e.g., mowed lawns) areas. Nest-site selection behavior may influence offspring success by shaping fitness-related phenotypes during development. Differences in nest temperatures between sandy and grassy patches may affect hatchling phenotypes, such as sex or body size, influencing survival and other key demographic features of the population. Although a genetic basis for nest-site selection in this population of snapping turtles was not evaluated, it likely exists to some extent. Insects show a genetic basis for oviposition preference (e.g., Via 1986, Singer et al. 1988), and a significant repeatability of nest-site selection on a microhabitat variable was found in painted turtles (F. Janzen, unpublished data). Repeatability provides an estimate of the upper bound for the heritability of a trait (Lynch and Walsh 1998). Thus, nest-site selection in this population has substantial ecological and evolutionary importance.

TABLE 5. Conditions in snapping turtle nests along the shores of the Mississippi River in Illinois in 1999 during the middle third of incubation (i.e., the thermosensitive period for sex determination).

Nest no.	Daily max temp	Daily min temp	Overall temp	Incubation length (d)	Date laid	Sex ratio
A) RES						
1	31.01 ± 1.99	25.80 ± 1.19	28.20 ± 2.38	64	1 Jun	0.0
2	29.80 ± 1.86	25.98 ± 1.38	27.83 ± 2.00	67	31 May	0.0
4	31.85 ± 1.87	26.31 ± 1.39	28.80 ± 2.48	66	1 Jun	0.1
10	31.57 ± 1.97	25.08 ± 1.53	28.06 ± 2.74	69	2 Jun	0.0
23	35.10 ± 3.37	23.08 ± 1.96	28.04 ± 4.50	66	5 Jun	...
29	26.31 ± 1.31	22.72 ± 1.23	24.30 ± 1.66	70	6 Jun	1.0
30	27.46 ± 1.51	23.68 ± 1.14	25.37 ± 1.69	66	6 Jun	...
31	28.44 ± 1.64	24.28 ± 1.22	26.18 ± 1.95	70	6 Jun	0.0
47	29.82 ± 1.85	26.00 ± 1.36	27.85 ± 1.98	68	31 May	0.0
Mean	30.15 ± 2.63	24.77 ± 1.37	27.18 ± 1.52	67.33 ± 2.69		
B) NWR						
5	32.57 ± 2.03	27.47 ± 1.44	29.94 ± 2.45	64	1 Jun	0.0
7	34.05 ± 2.42	25.97 ± 1.63	29.79 ± 3.35	66	1 Jun	0.0
12	33.06 ± 1.95	26.79 ± 1.48	29.82 ± 2.77	65	2 Jun	0.0
15	33.28 ± 1.98	26.18 ± 1.60	29.67 ± 2.96	68	2 Jun	0.0
17	31.61 ± 1.81	25.74 ± 1.32	28.54 ± 2.54	63	3 Jun	0.0
18	31.07 ± 1.73	24.39 ± 1.24	27.33 ± 2.68	68	3 Jun	0.1
37	31.02 ± 1.63	26.78 ± 1.26	28.80 ± 2.07	63	7 Jun	0.0
Mean	32.38 ± 1.17	26.19 ± 0.99	29.13 ± 0.96	65.29 ± 2.14		

Notes: Temperature data are means ± 1 SD. Incubation length and date laid are also given for each nest. Boldface type indicates nests in sandy patches, and lightface type indicates nests in grassy patches. Sex ratio was based on 10 random hatchlings from each nest except Nests 23 and 30, for which hatchlings emerged before a capture fence was erected.

Adaptive nest-site selection

Clark and Shutler (1999) identified three steps for studying how the process of natural selection can result in adaptive patterns of habitat use. To evaluate these steps, we focused on nesting at the NWR, the site with natural nesting habitat. We first addressed how available habitat differed from habitat used for nests by comparing random locations to nest sites. We showed that nest-site selection was based on ground vegetation characteristics (Fig. 2), and that nests occurred in sandy patches disproportionately more than the availability of that habitat patch type.

Second, do unsuccessful and successful nests differ in some quantitative or identifiable way? As with nest sites overall, successful nests were more often in areas with shorter vegetation, fewer cacti, and more open sand (Fig. 5). That is, sandy patches had higher nest success and the probability of nest success increased with decreasing amounts of vegetation (i.e., decreasing PC1). Clark and Shutler (1999) caution, however, that characteristics of successful nests may vary over time and space, and nest-site selection could reflect long-term optima that are neutral or maladaptive in the short term. Still, far more nests than expected were located in sandy patches at the NWR site from 1997 to 1999, and nest success in 1999 was entirely consistent with criteria for natural selection to have shaped nest-site choice.

Finally, if habitat selection and nest success are to be considered adaptive, then an increase in nest density in areas with above-average success rates should be observed. Such a pattern is much easier to detect in

annual insects or short-lived birds as compared to turtles, which have long generation times (e.g., 12 yr in snapping turtles; Congdon et al. 1987). Thus, a substantial time lag may be involved in studies of organisms with long generation times that makes observing an increase in nest density in successful areas very difficult. The definitive answer to this particular question must therefore await long-term investigation. Still, some evidence exists for adaptive nest-site selection at the NWR site where nest density and success are higher in sandy patches.

Nest temperature and offspring sex ratio

Variation in nest temperatures similar to that measured in this study (Table 5) has an important influence on offspring phenotypes and survival (e.g., Janzen 1995, Wilson 1998, Packard et al. 1999). Maternal nest-site selection not only affects nest success because of nest location, but may also influence embryo survival via nest temperature differences. For example, survival of striped mud turtle embryos in Florida was higher at sites located close to vegetation because of lower nest temperatures due to shade (Wilson 1998). Hatching success was not strongly influenced by microhabitat characteristics or nest location in this study, but other years with warmer or cooler summer temperatures may impact embryo survival (E. Janzen, unpublished data for *Chrysemys picta*).

Nest temperature differences may also influence offspring sex ratios. The 2°C difference in mean nest temperatures between sandy and grassy patches in 1999 spanned the pivotal temperature (i.e., 27.6°C) for sex

determination in this population (Janzen 1992, Janzen et al. 1998). This modest temperature difference could thus profoundly influence offspring sex ratios. For example, the percentage of male hatchlings in snapping turtle nests in Nebraska went from 0% at a mean nest temperature of 25.8°C to 97% at 23.9°C (Packard et al. 1999). Painted turtle nests in Illinois showed a similar pattern, going from 0 to 100% male when the mean nest temperature decreased from 26.6°C to 24.5°C (Weisrock and Janzen 1999). There was an inverse relationship between mean nest temperature and percentage of male hatchlings in both of these studies ($r = -0.47$, $P = 0.07$, $N = 15$ snapping turtle nests and $r = -0.66$, $P = 0.04$, $N = 10$ painted turtle nests). A similar inverse relationship between nest temperature and percentage of male hatchlings ($r = -0.73$) was detected in this study despite a heavily female biased sex ratio for the cohort (Table 5). In 1999, with its above average summer temperatures, only nests in grassy areas produced male hatchlings in this population. In addition, the only all-male clutch had the highest percentage overstory vegetation cover of any nest in 1999 at 66%. Years with more moderate summer temperatures would likely yield more nests with mixed sex ratios. Regardless, nest-site selection in this population had a significant impact on nest temperatures and sex ratios.

Other microclimate characteristics of nests, such as water potential, may also vary among nest sites and subsequently influence offspring phenotypes. Though we did not assess water potentials in this study, the availability of water influenced survival, metabolism, and growth of embryos in a population of painted turtles (Cagle et al. 1993), and environmentally induced variation in body size of hatchling snapping turtles was attributed primarily to variation in water potentials among nests in a Nebraska population (Packard et al. 1999).

Influence of human-altered habitat

Nest-site selection at both sites was mechanistically similar, that is, female turtles selected nest sites based on the same microhabitat characteristics. Differences in the sites unrelated to nest-site selection may, however, result in important differences in nest success and offspring phenotypes that affect population demography. The most striking differences were the greater range of grassy patch habitat, the high proportion of nests within 0–5 m of houses and the fence, and lower nest temperatures at the RES site (Fig. 4 and Table 5). While sandy patches were similar at the RES and NWR sites, the grassy patches at the RES site had much less vegetation than at the NWR site (Fig. 4). Human alterations of the RES habitat, such as roads and mowing, have likely produced a site with less vegetation overall (Fig. 3) and no clear distinction between sandy and grassy patches.

Houses and the fence may act as barriers to females

in the nesting area. Females may simply stop when they encounter such a barrier and then construct nests. In addition, the vegetation around houses and the boundary fence was shorter and sparser than other available areas because homeowners mow their yards and other human activity keeps vegetation short and sparse. Thus, turtles may have selected these areas for nest sites based on microhabitat choices. Though we cannot distinguish between turtles selecting sites near houses and the fence because of microhabitat preferences or simply because these structures acted as barriers, either scenario implicates human alterations of habitat in modifying nest-site selection patterns. Nests at the NWR site were more heavily concentrated in the sandy areas than nests at the RES site (Fig. 1A, B). The higher proportion of nests in the grassy areas at the RES site may be the result of humans converting grassy areas to habitat more similar in composition to sandy patches. Thus, turtles nesting in these human-altered areas may suffer higher nest predation rates and a loss of the connection between ground vegetation characteristics and nest temperatures observed at the NWR site.

Houses and interspersed trees contributed to the lower nest temperatures detected because only percentage overstory vegetation cover was correlated with nest temperatures at the RES site. Thus, a variable not used for nest-site selection was the only microhabitat variable correlated with nest temperatures. Mrosovsky et al. (1995) observed similar cooling of nesting areas for sea turtles in Florida; condominiums shading nest sites lowered nest temperatures an average of 1°C and as much as 2°C. For nests laid earlier in the season, this shade reduced nest temperatures below the pivotal temperature of sex determination, presumably producing more males in these nests. Additionally, three of the four loggerhead sea turtle nests most heavily shaded by vegetation and buildings on another Florida beach were the only nests predicted from nest temperatures to produce <100% females (Hanson et al. 1998). The effect of shading on nest temperatures and sex ratios is well known (e.g., Janzen 1994a), but the impact of human modifications (i.e., buildings and unnatural vegetation) is only beginning to be understood.

This scenario of habitat modification lowering nest success and nest temperatures despite adaptive nesting behavior constitutes an ecological trap (Gates and Gysel 1978). An ecological trap exists when human modifications of the habitat in which populations evolved occur at a rate faster than the populations can respond, resulting in populations somewhat poorly adapted to cope with the altered habitat. In this study, habitat modifications at the RES site have resulted in a reduced tendency for turtles to nest in sandy patches, even though sandy patches at the RES site exhibit higher nest success. Additionally, nest temperatures at the RES site were no longer correlated with ground vegetation characteristics as at the NWR site. The reduc-

tion in nest success due to more nests in grassy areas at the RES site is similar to the standard ecological trap scenario. For example, Misenhelter and Rotenberry (2000) found that sage sparrows preferred territories in which nest predation was high, and that the decoupling of habitat attractiveness and suitability for nest success was the result of human caused landscape-level changes. Additionally, the ecological trap in the present study may result in sex ratio bias. Microhabitat characteristics used by turtles to indicate favorable nest sites were no longer valid at the RES site, and human modifications (i.e., houses and trees) have severed the connection between ground vegetation characteristics and nest temperatures observed at the NWR site.

Consistent skewing of offspring sex ratios at the RES site caused by shade from houses and trees may ultimately alter adult sex ratios in this population, due not to adaptive nest-site selection, but to an ecological trap set by human modifications of nesting habitat. Such sex ratio biases are particularly critical for vertebrates with temperature-dependent sex determination that have long generation times. Given that snapping turtles take ~12 yr to reach reproductive age (Congdon et al. 1987), only eight snapping turtle generations have occurred in the last 100 yr. This is probably not enough generations for an evolutionary response to changes in habitat even under strong selection pressure. Furthermore, turtles nesting at these two sites and their mates are likely part of an interbreeding population and may even switch nesting sites. Thus, even with strong selection pressure and high heritability for nest-site selection, adaptive evolutionary change may be swamped out by gene flow.

Conservation implications

Declines in turtle populations worldwide are becoming more apparent, particularly in Asia (Behler 1997). Long-term studies are needed to understand the population dynamics of long-lived organisms such as turtles (e.g., Congdon et al. 1987). Life tables allow theoretical manipulation of key demographic factors to determine the impact on population size, age-specific survival, and other demographic features. For example, the stability of a Michigan population of snapping turtles is putatively most sensitive to changes in adult and juvenile survival (Congdon et al. 1994). Integration of life table analysis with primary sex ratio data may aid in determining the impact of changing sex ratios on population viability (Caswell and Weeks 1986). To what extent could sex ratios biased by human modifications of nesting habitat endanger populations? Any deviation from a 1:1 sex ratio lowers the effective population size, and a primary sex ratio bias effectively induces sex-specific mortality in the adult population. Efforts to understand the impact of maternal nest-site selection behavior on population dynamics are thus crucial for conservation (Roitberg 1998).

CONCLUSIONS

We showed that nest-site selection occurs in a population of snapping turtles and produces variation in nest locations, thereby influencing nest success. Additionally, this behavioral maternal effect results in nest temperature variation that has ramifications for the population sex ratio and possibly for other fitness-related offspring phenotypes. Human modifications of the nesting habitat at the RES site have altered the consequences of adaptive nest-site selection, leading to an ecological trap that lowers nest temperatures (which may produce more males) and overall nest success. Because snapping turtles are long-lived, their evolutionary response to natural selection exerted by a rapidly changing environment will be slow; this is compounded by time lags due to maternal effects and ecological traps set by humans. Long-lived organisms present an urgent challenge for conservation biologists in a world that is undergoing rapid modification by humans and facing global climate change (Janzen 1994b, Mrosovsky 1994, Vitousek et al. 1997).

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