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NEST CONCEALMENT AND PREDATION IN HOODED WARBLERS: EXPERIMENTAL REMOVAL OF NEST COVER

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ABSTRACT.—It is commonly assumed that passerine birds with open nests reduce the risk of predation by concealing their nests. At a forest study site in northwestern Pennsylvania, about 50% of the Hooded Warbler (*Wilsonia citrina*) nests were depredated—the primary cause of reproductive failure. To test the hypothesis that concealed nests are less likely to be depredated than conspicuous nests, we examined seven characteristics of the warbler's nest and nest microhabitat in relation to nest predation: nest visibility, vegetation density surrounding the nest, height of nest, height of nest substrate, nest-substrate species, height of cryptic dead-leaf base of nest, and proximity of nest to a microedge. Successful and depredated nests ($n = 97$) did not differ in any of these variables. In addition, we performed a vegetation-removal experiment in which manipulated nests ($n = 15$) with surrounding vegetation removed were on average 86% more visible overall than control nests ($n = 15$). The highly visible manipulated nests did not suffer higher predation than control nests. Contrary to our hypothesis, our results show that nest concealment is not an important factor in predator avoidance for Hooded Warblers. This outcome would be expected if nest predation is the result of nonspecialist predation that occurs by chance and is based on the location of available food in general. *Received 19 September 1994, accepted 25 April 1995.*

THE MAJOR FACTOR influencing reproductive success of open-nesting birds is nest predation (Skutch 1949, Nice 1957, Ricklefs 1969, Gates and Gysel 1978, Martin 1992). Consequently, there should be selective pressure for birds to place their nests in sites that deter predation. It is clear that birds select nest sites nonrandomly (e.g. Peterson and Best 1985, Bekoff et al. 1987), and there is evidence that they can identify nest sites with characteristics that reduce the risk of predation (Stauffer and Best 1986, Martin and Roper 1988, Marzluff 1988, Møller 1988). Nest concealment and characteristics of nest microhabitat, such as vegetation density and height

of nest from the ground, have been related to predation risk (Caccamise 1977, Murphy 1983, Martin and Roper 1988, Yahner and Scott 1988, Kelly 1993, Martin 1993) and, thus, could serve as criteria in nest-site selection.

Although concealment of a nest by selecting an inconspicuous site is commonly assumed to reduce the risk of predation, there have been conflicting results in testing this hypothesis. Martin (1992) concluded in a review of 56 studies that dense foliage reduces the probability of predation by concealing a nest. However, of the 11 studies on passerines, 7 reported a negative correlation between predation and nest concealment, and 4 reported no correlation.

Pertinent research, including those studies reviewed by Martin (1992), was conducted by Nice (1937), Nolan (1978), Martin and Roper

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(1988), Norment (1993), and Gregg et al. (1994), who found that concealment of nests of Song Sparrow (*Melospiza melodia*), Prairie Warbler (*Dendroica discolor*), Hermit Thrush (*Catharus guttatus auduboni*), Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*), and Sage Grouse (*Centrocercus urophasianus*), respectively, was significantly related to low predation rates. However, Roseberry and Klimstra (1970), Gottfried and Thompson (1978), Best and Stauffer (1980), Holway (1991), and Schieck and Hannon (1993) did not find a significant difference in levels of concealment between successful and depredated nests of Eastern Meadowlarks (*Sturnella magna*), Black-throated Blue Warblers (*Dendroica caerulescens*), Willow Ptarmigan (*Lagopus lagopus*), and additional songbird species. In the only published study of experimental vegetation removal, Bengtson (1972) reported that losses of vegetational cover increased predation on waterfowl nests. The lack of substantial experimental evidence and the inconclusive results of studies on avian anti-predator strategies in nest-site selection calls into question basic assumptions about the selective value of nest concealment.

The natural variability of Hooded Warbler (*Wilsonia citrina*) nest sites within forest interior shrubbery (Evans Ogden and Stutchbury 1994) makes these warblers ideal subjects for testing the prediction that there is a negative relationship between nest concealment and nest predation. In addition, we performed a vegetation-removal experiment on a separate set of nests to evaluate the critical prediction that nests with experimentally increased visibility as a result of vegetation removal will have a higher rate of predation compared to control nests.

STUDY AREA AND METHODS

The study site was 100 ha of a forest fragment of about 180 ha surrounded by farmland in Rockdale Township, Crawford County, Pennsylvania. It is located in the Millers Station, Pennsylvania Quadrangle of the U.S. Geological Survey (41°46'N, 79°56'W). The study area is continuous, uninhabited forestland interrupted only by the sites (ca. 50 m²) of four gas wells and a narrow, dirt road connecting the wells. There are several stream ravines that run through the forest. Selective logging has created openings in the canopy, as well as dense, stratified shrub and forb layers. The major overstory trees (>7.5 cm dbh and ≥1.5 m tall) were American beech (*Fagus grandifolia*),

sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), and eastern hemlock (*Tsuga canadensis*). The principal understory trees and shrubs included saplings of overstory trees, blackberry (*Prunus* spp.), prickly gooseberry (*Ribes cynosbati*), maple-leaf viburnum (*Viburnum acerifolium*), and common spicebush (*Lindera benzoin*).

We conducted fieldwork during the spring and summer of 1992 and 1993 in conjunction with other ongoing studies of this breeding population of Hooded Warblers (Mark and Stutchbury 1994, Stutchbury et al. 1994). Upon arrival in May, the adult warblers were netted, measured, weighed, bled for DNA fingerprinting, and banded with aluminum U.S. Fish and Wildlife Service bands. We also banded them with uniquely color-coded bands.

Nests were located primarily by following vocalizing females and were found during construction, egg laying, or early incubation. Aside from vegetation removal, all nests used were treated essentially the same when active. We checked them every three to five days. When the nestlings were approximately five days old, we banded them and took blood samples. The nests were videotaped during the last few days of the nestling stage for studies of parental care (Evans Ogden 1994, Stutchbury et al. 1994). A nest was considered successful if at least one nestling fledged.

We do not know the extent to which nest visitation by us affected predation patterns. Investigator visits to nests have reduced nest success in several studies (Bengtson 1972, Lenington 1979, and Westmoreland and Best 1985), but in many other studies frequent nests visits have not been found to increase nest predation (Willis 1973, Gottfried and Thompson 1978, Wray and Whitmore 1979, Sugden and Beyersbergen 1986, Martin and Roper 1988). In our study, overall predation rates were not unusually high for a forest fragment (see Results), and visitation at all nests was equivalent. Furthermore, our experimental removal of vegetation specifically tests whether severe disturbance around a nest increases predation risk.

Nest concealment and predation.—Measurements of nest and vegetation characteristics were taken within three weeks of a nest becoming inactive. Characteristics measured were: (1) plant species that served as nest substrate; (2) height of nest substrate from ground to tallest point of plant; (3) height of nest from ground to top of nest rim; and (4) height of base of nest constructed from dead leaves from lowest leaf to bottom of inside of cup (dead leaves appear to serve as camouflage in that they mimic natural dead leaves that get caught in branches of shrubs). We also measured the distance to the forest edge (interface with a field) or a microedge (interruption of forest shrubbery by a deer trail, old logging road, stream, gas well road, or patch edge) within 10 m of the nest. We defined a habitat patch as a distinct group of shrubs

and defined a patch edge to be where there was a change in dominant shrub species or a change in the average height of shrubs greater than 0.5 m.

Additionally, vegetation density and visibility of nests were measured within a circle with a 1-m radius (3-m² area) centered around the nest (see Petit et al. 1988). To quantify the vegetation density, we counted stems (>3 mm diameter and >20 cm tall) at ground level and branches at nest height within the circle and calculated the stems and branches per square meter.

We determined visibility scores using methods similar to Holway (1991). All visibility scoring was done by J.S.H. to ensure consistency. She made estimates of the percentage of the nest that was visible to the nearest 20%. These estimates were taken 1 m from the nest at ground level, at nest height, and at 1.5 m above ground; they were taken at every 45° compass interval (eight points) around the circle. One estimate was made from directly over the nest at a height of 1.5 m. The overall visibility of the nest was calculated as the average of the 25 estimates. In addition, we calculated the average visibility at each height of viewing (ground, nest, 1.5 m).

Vegetation-removal experiment.—A vegetation-removal experiment, using a paired design, was conducted in 1993 with 30 nests that were not included in the general analysis of nest concealment and predation. Nests were chosen and paired *a priori* using the following criteria: proximity to each other; stage of nesting; time of season; and initial visibility of nest. Nests selected for the experiment were judged to be less than 50% visible overall (more concealed than average) upon initial inspection. We paired nests that were active at the same time of the season from nearby territories (within 200 m) so they shared similar habitat features. We repeated the use of some territories later in the season.

The vegetation-removal experiment began at all nests in early incubation. Measurements were taken and the experimental treatment conducted for each nest in a pair on approximately the same day of incubation. For a few nests, the first day of incubation was unknown, and the day of incubation when experimentation occurred was an estimate based on the known activity of the female.

Nests within a pair were randomly designated to the manipulated or control treatment. On corresponding days of incubation, we estimated visibility scores as described previously for our general analysis of concealment and predation. After scoring visibility, we clipped vegetation from within a 1-m radius of manipulated nests so that the nests appeared as natural as possible and approached 80% visibility, the maximum of the natural range of overall visibility (see Results).

The control nests were given a mock vegetation-removal treatment. The mock treatment included vis-

ibility scoring and consisted of a visitation of 25 min, about the same time required to do an actual manipulation. Stems were sorted and held just like they would have been if they were actually cut.

Within a week of the manipulated nests becoming inactive, we estimated postvegetation removal visibility in the same manner as previously described. Also, after the nests were inactive, we recorded for all 30 nests the other nest-site data measured at non-experimental nests.

Statistical analyses.—The nest-site variables of concealment were not normally distributed and our sample sizes in the vegetation-removal experiment were relatively small ($n = 15$); therefore, we primarily used nonparametric statistics (sign test, Spearman rank-order correlations, Mann-Whitney *U*-test). We computed the statistics using *CSS: Statistica* computer software (Statsoft 1991).

RESULTS

Predation.—We collected data from 97 nests (71 in 1992 and 26 in 1993). In 1993, 30 additional nests were used for the vegetation-removal experiment. The average overall nest visibility (excluding experimental nests) for each year was the same at 50%.

All nest failures were due to predation. There was very little Brown-headed Cowbird (*Molothrus ater*) parasitism as a result of a cowbird control program (Mark and Stutchbury 1994). Nest-predation rates did not differ between years: 51% (36/71) of the nests were depredated in 1992; and 50% (13/26) in 1993 ($X^2 < 0.01$, $P > 0.95$). Therefore, we combined nests for subsequent analysis; the combined predation rate was 51% (49/97).

Of the 97 nests, 57 were first nests, 31 were second nests, and 9 were third nests due to re-nesting and double brooding. The frequency distribution of depredated and successful nests did not differ between the first nesting attempt and the second and third nesting attempts combined ($X^2 = 0.11$, $df = 1$, $P = 0.74$). We therefore included all nesting attempts in our analysis of the relationship of nest concealment and predation.

A related variable that potentially could bias our testing of the concealment hypothesis is nonrandom predation among territories. There were 30 territories with more than one nest. The frequency of predation of the first two nests within these 30 territories did not differ significantly from expected based on a random

TABLE 1. Variability and means of characteristics of Hooded Warbler nests and nest sites that could affect nest concealment ($n = 97$).

	$\bar{x} \pm SE$ (range)
Nest-substrate height (cm)	102.4 \pm 3.1 (48.0–184.0)
Nest height (cm)	53.5 \pm 1.8 (29.0–146.0)
Dead-leaf nest base height (cm)	7.6 \pm 0.3 (3.0–20.0)
Stem density (stems/m ²)	23.7 \pm 1.3 (0.3–58.0)
Branch density (branches/m ²)	19.7 \pm 1.1 (0.0–85.0)
Visibility (%)	
At ground level	56.9 \pm 1.7 (12.5–97.5)
At nest height	57.9 \pm 1.9 (2.5–92.5)
At height of 1.5 m	39.0 \pm 1.6 (7.5–75.0)
From above	31.0 \pm 2.9 (0.0–100.0)
Overall	50.4 \pm 1.3 (9.6–78.4)

probability of predation: 5 territories had two successful nests; 16 had a successful and a depredated nest; and 9 had two depredated nests ($X^2 = 0.76$, $df = 2$, $P > 0.68$). Typically, third clutches are laid only when the first two have been lost; therefore, there were only nine third nests.

Nest concealment and predation.—The nest and nest-site characteristics of nest substrate height (NSH), nest height (NH), height of cryptic dead-leaf base of nest (LH), stem density (SD), branch density (BD), visibility at ground level (VG), visibility at nest height (VN), visibility at height of 1.5 m (V1.5), visibility from above (VA), and visibility overall (VO) ranged considerably between their minimum and maximum values, although height of cryptic dead-leaf base of nest was less variable than the other factors (Table 1). On average, visibility from above was significantly lower (sign test; $P < 0.01$) than vis-

ibility at ground level, at nest height, and at 1.5 m (Table 1). Visibility at 1.5 m was also significantly lower (sign test; $P < 0.01$) than visibility at ground level and at nest height.

As expected, many of the characteristics were significantly correlated (Table 2). Overall visibility and stem density were negatively correlated. Stem and branch density were positively correlated. Positive correlations also existed between nest-substrate height and nest height, and nest-substrate height and visibility at 1.5 m. And finally, nest height was negatively correlated to both stem and branch density. Since these variables are interrelated, they should reinforce each other in discriminating between successful and depredated nests.

Contrary to our prediction, Mann-Whitney U -tests clearly showed no significant differences between successful and depredated nests for all 10 variables of nest concealment (Fig. 1; $U = 962.5$ to $1,171.0$, all $P > 0.05$). Additionally, the least visible nest overall (10% visible) was depredated and the most visible (78%) was successful.

We recorded 15 species of shrubs that were used for nest substrates; in five nests, stems from two species were used together. We assumed that the height of the plant and the density of foliage and stems, which we have shown to be related to visibility, were characteristic of the plant species. The dominant species used, which corresponded to dominant shrub species in the forest, were blackberry, American beech, prickly gooseberry, and black cherry. The frequency distribution of substrate species for successful nests did not differ significantly from that of depredated nests (Fig. 2; $X^2 = 5.16$, $df = 4$, $P = 0.27$).

While edges and microedges might not al-

TABLE 2. Spearman rank order correlations for NSH (nest-substrate height), NH (nest height), LH (cryptic dead-leaf nest base height), SD (stem density), BD (branch density), VG (visibility at ground level), VN (visibility at nest height), V1.5 (visibility at height of 1.5 m), VA (visibility from above), and VO (visibility overall).

	NSH	NH	LH	SD	BD	VG	VN	V1.5	VA
NH	0.59***								
LH	-0.08	-0.12							
SD	-0.29**	-0.28**	-0.12						
BD	-0.23*	-0.31**	-0.13	0.66***					
VG	-0.08	-0.09	0.17	-0.45***	-0.41***				
VN	0.16	0.12	0.13	-0.29**	-0.44***	0.55***			
V1.5	0.28**	0.06	-0.02	-0.11	-0.24*	0.02	0.23*		
VA	0.13	0.01	0.11	-0.12	-0.12***	0.13	0.10	0.24*	
VO	0.16	0.05	0.13	-0.40***	-0.49	0.70***	0.85***	0.54***	0.27**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

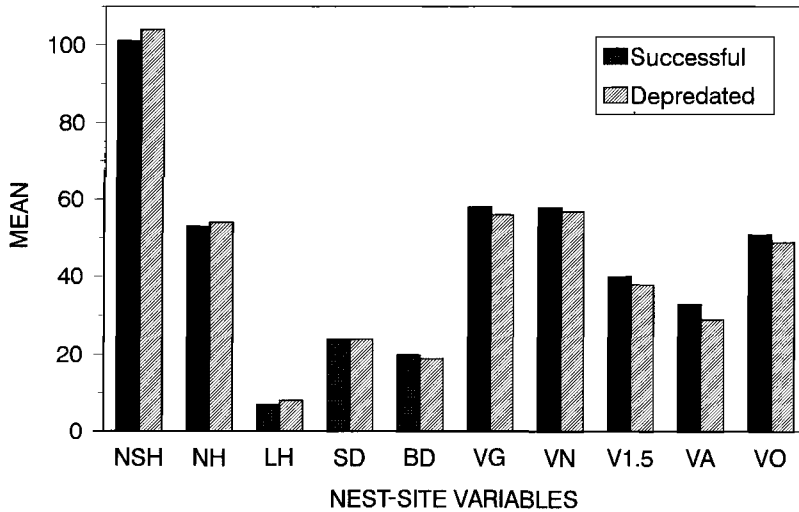


Fig. 1. Means of successful ($n = 48$) and depredated ($n = 49$) nests for variables of nest concealment. Identifications of variables (with units and SE for successful and depredated nests, respectively, in parentheses) are: **NSH**, nest-substrate height (cm; 3.62, 4.95); **NH**, nest height (cm; 2.27, 2.87); **LH**, cryptic dead-leaf nest base height (cm; 0.54, 0.40); **SD**, stem density (stems/m², 1.82, 1.88); **BD**, branch density (branches/m², 1.81, 1.28); **VG**, visibility at ground level (%; 2.35, 2.54); **VN**, visibility at nest height (%; 2.58, 2.85); **V1.5**, visibility at height of 1.5 m (%; 2.21, 2.34); **VA**, visibility from above (%; 4.36, 3.69); and **VO**, visibility overall (%; 1.72, 1.82).

ways affect the visibility of a nest, they potentially could influence predation rates by increasing the probability that a predator will be found in the vicinity of the nest (Angelstam 1986, Andren and Angelstam 1988, Yahner et

al. 1989, Santos and Telleria 1992). Only one nest was located within 10 m of a forest and field edge, but 75 (77%) nests were near microedges (e.g. deer trails, old logging roads, patch edges, and gas well road). We decided to consider only the effects of the microedges and eliminated the one nest adjacent to the field for this comparison. The frequency distribution of microedges for successful nests did not differ significantly from that of depredated nests (Fig. 2; $X^2 = 3.92$, $df = 4$, $P = 0.42$).

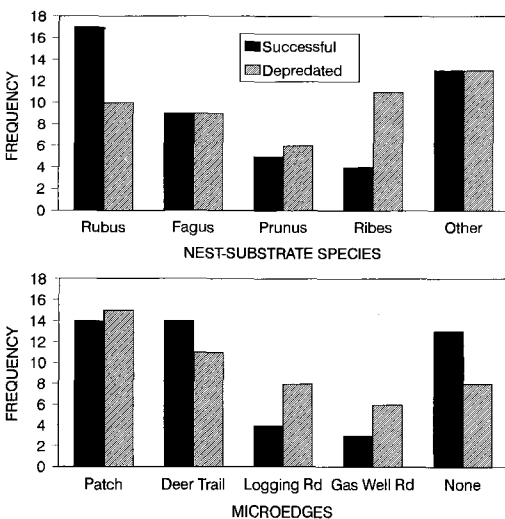


Fig. 2. Frequencies of successful and depredated nests for nest-substrate species (top, $n = 97$) and for nearby microedges (bottom, $n = 96$).

Vegetation-removal experiment.—Before removal of vegetation, there was no significant difference in the visibility of the manipulated and control nests (Fig. 3). Mann-Whitney U -tests were used to compare the means of premanipulated and control nests for the five visibility factors ($U = 82.0$ to 110.0 , all $P > 0.05$). After removal of vegetation there were highly significant differences ($P < 0.01$) in the visibility of control and manipulated nests (Fig. 3; VG [$U = 16.0$]; VN [$U = 6.0$]; V1.5 [$U = 1.0$]; VA [$U = 14.0$]; VO [$U = 0.0$]).

The difference between the predation rate for control nests and those nests with the surrounding vegetation removed was not significant (Fig. 4; $X^2 = 0.14$, $P > 0.71$). Neither of these predation rates was significantly different from the

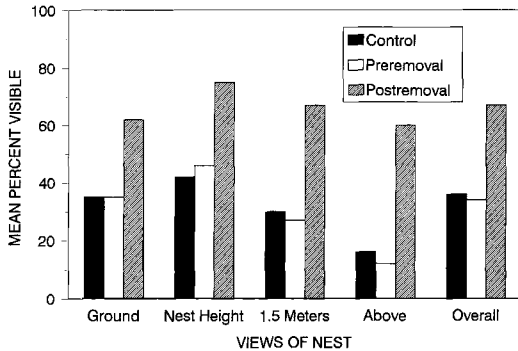


Fig. 3. Mean visibility (%) of control nests ($n = 15$) compared to that of manipulated nests ($n = 15$) before and after vegetation removal. Standard errors in parentheses for control, preremoval, and postremoval nests, respectively, are: at ground level (3.07, 3.86, 3.41); at nest height (4.23, 3.76, 2.85); at height of 1.5 m (2.94, 5.09, 2.45); from above (2.90, 2.62, 6.48); and overall (2.02, 3.18, 2.22).

rate of 51% for the general analysis of concealment and predation (control, $X^2 = 0.03$, $P > 0.87$; manipulated, $X^2 = 0.21$, $P > 0.65$). Results of the vegetation-removal experiment confirm those of our general analysis of concealment and predation, and do not support the prediction that there is a positive correlation between the visibility of manipulated nests and predation.

DISCUSSION

Our study demonstrates that Hooded Warbler nest sites vary considerably in microhabitat features (Table 1), but that the variability in visibility of the nest, vegetation density, nest height, and nest-substrate height had no influence on the probability of fledging young. Nest success also was not affected by the plant species used for nesting, nor by proximity to various microedges. None of these factors exhibited a significant statistical association with predation rate despite the fact that predators (Blue Jays [*Cyanocitta cristata*], American Crows [*Corvus brachyrhynchos*], eastern chipmunks [*Tamias striatus*], three squirrel species [*Sciurus* and *Tamiasciurus*], raccoons [*Procyon lotor*], striped skunks [*Mephitis mephitis*], three weasels [*Mustela*], opossums [*Didelphis virginiana*], and black rat snakes [*Elaphe obsoleta*]) were abundant (pers. obs.). Furthermore, experimental vegetation manipulations to increase the visibility of nests did not increase predation (Fig. 4).

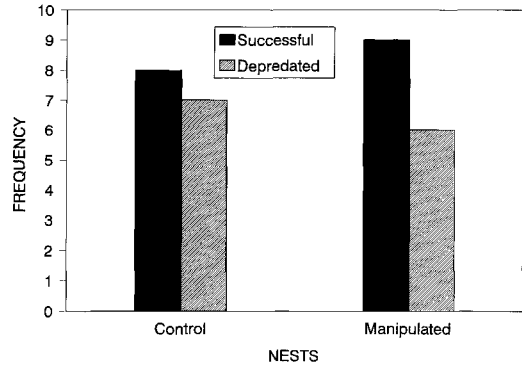


Fig. 4. Frequency of success and predation of control ($n = 15$) and manipulated ($n = 15$) nests.

We did not investigate the frequency of predation from each species of predator. However, video cameras monitoring parental behavior recorded single predation events by a Blue Jay, eastern chipmunk, and red squirrel (*Tamiasciurus hudsonicus*). Nests were not altered visibly by any of these events. In fact, only 8% of all depredated, nonexperimental nests were damaged or destroyed as a result of predation. This indicates that the larger nocturnal mammals (e.g. skunks and raccoons) that rip apart nests also were likely predators (Best 1978, Nolan 1978, Best and Stauffer 1980, Small and Hunter 1988, Yahner and Voytko 1989), but less abundant than visually oriented diurnal predators. In studies comparing the abundance of predator species with the relative importance of these species as nest predators, nests were depredated by predator species in proportion to their abundance (Loman 1977, Muller 1985, Angelstam 1986). Angelstam (1986) suggested that this indicates that individuals of different predator species are on average equally efficient at finding nests.

In addition to visual cues from nests, various predators may respond to: visual and auditory clues of parents (Skutch 1949, Willis 1973, Holway 1991); olfactory clues from nests, parents, or young (Henry 1969, Lill 1974, Reitsma et al. 1990); or begging calls of nestlings (Skutch 1949, Perrin 1965). Nest predators also may be nonspecialists that use such clues only during random, close encounters with nests (Zimmerman 1984).

In support of the idea of nonspecialist nest predators are studies on the foraging habits of chipmunks, crows, skunks, and raccoons. Devenport and Devenport (1994) have established

that foraging search patterns of least chipmunks (*Tamias minimus*) are visual, but generally based on the identity of patches that consistently yield food. Sugden and Beyersbergen (1986) concluded that American Crows also return to areas of past successes, where they search at random, before they move to new foraging areas. Skunk predation on nests of grassland birds occurred when nests were found accidentally while skunks foraged for invertebrates (Vickery et al. 1992). In a study with raccoons, Bowman and Harris (1980) found that spatial heterogeneity of vegetation decreased foraging efficiency significantly more than nest concealment. Our results would be expected if nest predation is the result of nonspecialist predation that is based on the location of available food in general, and not specifically on the location and conspicuousness of nests.

Nest predation also can be affected by factors other than methods used by predators when finding nests. The frequency of predation may vary with densities of nest predators. High densities of nest predators typically are found in small forest fragments (Wilcove 1985, Small and Hunter 1988, Robinson 1992), at forest edges (Gates and Gysel 1978, Wilcove 1985, Yahner and Scott 1988), and in forests that have complex and heterogeneous vegetational structure (Brooks 1990, Martin 1993). Bird densities also can be high in these habitats (Willson 1974, Ambuel and Temple 1983, Litwin and Smith 1992, Robinson 1992), but there is little research comparing nest-predation rates to actual predator-prey ratios. Extremely high (80% or more) predation rates found in some small forest fragments (Robinson 1992) could mask any concealment effect. In our study, however, the predation rate was 51%, not out of the ordinary for open-nesting species (Nice 1957, Martin 1992, Robinson 1992); therefore, our results cannot be attributed to artificially high predation rates from landscape effects.

In conclusion, we tested the effect of the variability of nest concealment on nest success of Hooded Warblers in a forest fragment with complex, heterogeneous vegetation where predators that orient visually (e.g. Blue Jays and eastern chipmunks) were present. We did not find any effect of nest concealment on nest predation from either our correlative or experimental data. Other factors may be more important in determining the risk of nest predation than physical characteristics of particular nest-

ing sites. We recommend that the effects of nest concealment be tested in other species using experimental manipulation of vegetation cover.

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