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WITHIN-SEASON DISPERSAL, NEST-SITE MODIFICATION, AND PREDATION IN RENESTING HOODED WARBLERS

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ABSTRACT.—To test the hypothesis that within-season dispersal and nest-site modification (e.g., changes in nest concealment) occur in Hooded Warblers (*Wilsonia citrina*) as a result of predation of the previous nest, we examined differences in nest height, vegetation density surrounding the nest, nest visibility, and distances between first and second nests. The average distance between successful nest sites and renesting sites was significantly greater than the average distance between unsuccessful nest sites and renesting sites. The concealment variables of renesting sites were not significantly different from either successful or unsuccessful first nest sites. The probability of success of a Hooded Warbler's renest after predation was the same as the probability of success of all first nests (approximately 50%). Our data suggest that predation does not play a role in the selection of renesting sites in Hooded Warblers. We propose that the greater dispersal of successful females was due to their avoidance of fledglings that remained near the nest with the male. *Received 30 Oct. 1996, accepted 10 May 1997.*

Birds that raise multiple broods in a season, or suffer predation and renest, can locate a new nest close to the original site or they can disperse. The factors selecting for within-season dispersal are not well known, but it has long been assumed that nest predation may have an influence (Darley et al. 1971, Greenwood and Harvey 1982). In this case, dispersal is viewed as a predation-avoidance tactic.

Several open nesting species move long distances and/or abandon territories and mates after nest failure (e.g., White-crowned Sparrow [*Zonotrichia leucophrys*, Blanchard 1941]; Gray Catbird [*Dumatella carolinensis*, Darley et al. 1971]; Prairie Warbler [*Dendroica discolor*, Nolan 1978]; Red-winged Blackbird [*Agalaius phoeniceus*, Monnett and Rotterman 1980]). Conversely, in other species, mated pairs do not normally separate or move great distances after nest predation (e.g., European Blackbird [*Turdus merula*, Ribaut 1964]; Song Sparrow [*Melospiza melodia*, Tompa 1964]; Eurasian Skylark [*Alauda arvensis*, Delius 1965]; and Scrub Jay [*Aphelocoma coerulescens*, Woolfenden and Fitzpatrick 1984]). However, there have been only a few studies that have attempted to confirm statistically that within-season dispersal after nest predation is farther or more frequent than within-season dispersal after a successful nesting attempt. Wunderle (1984) found that female Bananaquits (*Coer-*

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eba flaveola) were less likely to abandon their territories and mates if they had a successful nest. On the other hand, Shields (1984) found that Barn Swallows (*Hirundo rustica*), that are colonial and reuse nests, were more likely to change nests if the first nest was successful. Jackson et al. (1989) found that Prairie Warblers were equally likely to leave their mate's territory after successful or unsuccessful nests. Monnett and Rotterdam (1980) correlated distances female Red-winged Blackbirds moved after nest predation to the size of home ranges of predators.

In addition to within-season dispersal, nest concealment could be a factor in predation avoidance. For open nesting birds, a new nest site could differ from the original site in variables such as height, visibility, and cover that affect nest concealment. In Pinyon Jays (*Gymnorhinus cyanocephalus*), Marzluff (1988) found that nest height following predation was significantly lower (nest more concealed) than the height of the nest that was depredated. He also found that the jays' second nests after successful first nests were not significantly more concealed.

In this study, we tested the hypothesis that within-season dispersal and nest-site modification (e.g., changes in nest concealment) occur in Hooded Warblers (*Wilsonia citrina*) as a result of predation of previous nests. Hooded Warblers make good subjects for examining the effects of predation on within-season dispersal and subsequent nest site selection since they are often double brooded and will renest as many as three times in a season. In a previous study on nest concealment in Hooded Warblers (Howlett and Stutchbury 1996), we performed a vegetation-removal experiment to test if nest concealment affected nest predation. Nests manipulated to be highly visible did not suffer higher predation than control nests that remained concealed. Therefore, based on our previous findings, we made the prediction that females that suffer nest predation will not make their subsequent nests more concealed. Based on the tactic of moving a nest away from the site of predation to avoid the immediate presence of predators, we made two additional predictions: (1) females that suffer nest predation will renest farther away from their original nest compared with females that do not suffer predation; and (2) renests after predation will have a greater chance of success than all first nests combined.

METHODS

We conducted fieldwork during May–August of 1992–1995 in conjunction with other ongoing studies of this breeding population of Hooded Warblers (Mark and Stutchbury 1994, Stutchbury et al. 1994, Stutchbury and Howlett 1995, Howlett and Stutchbury 1996, Neudorf 1996, Tarof 1996, Evans Ogden and Stutchbury 1997). The study site was a mixed forest of approximately 150 ha in northwestern Pennsylvania (41°46′N, 79°56′W). We marked grids every 50 m with flagging tape and aluminum markers on nearest trees. Territories were mapped on metric graph paper by observing border disputes, sighting banded males, or observing individuals that responded to playbacks of male song. We banded adult warblers with uniquely color-coded bands and aluminum U.S. Fish and Wildlife bands.

Nests were located primarily by following vocalizing females during nest construction, egg laying, or early incubation. Their open cup nests are made of bark and fine grasses with a base of dead leaves and are placed 0.29–1.46 m above the ground in a shrub (Howlett and Stutchbury 1996). A nest was considered successful if at least one nestling was fledged.

Measurements of nest and vegetation characteristics were taken within three weeks of a nest becoming inactive. We measured distances between first and second nests with a 50-m tape. We also determined distances and exact compass directions from nests to nearest grid markers and mapped the nests on graph paper.

The nest-site characteristics of nest height, stem density, and overall visibility of nest were used as variables of nest concealment. Stem density and visibility of nest were measured within a circle with a 1-m radius (3-m^2 area) centered around the nest (see Petit et al. 1988). To quantify stem density, we counted stems (>3 mm diameter and >20 cm tall) at ground level within the circle and calculated the stems per square meter.

We determined visibility scores using methods similar to those of Holoway (1991). All visibility scoring was done by J.S.H. to ensure consistency. Estimates of the percentage of the nest that was visible were made 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, and they were taken 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 was calculated as the average of the 25 estimates (see Howlett and Stutchbury 1996).

Nests included in this study were pairs of first nests and subsequent renests. Nest site variables were measured during the 1992 and 1993 seasons primarily for another study on nest concealment (Howlett and Stutchbury 1996). Distances between nests were measured in 1994 and 1995 as well as in 1992 and 1993.

Nest predators common at the study site were Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), eastern chipmunks (*Tamias striatus*), red squirrels (*Tamiasciurus hudsonicus*), gray squirrels (*Sciurus carolinensis*), fox squirrels (*Sciurus niger*), raccoons (*Procyon lotor*), striped skunks (*Mephitus mephitus*), weasels (*Mustela spp.*), opossums (*Didelphis virginiana*), and black rat snakes (*Elaphe obsoleta*). There was little Brown-headed Cowbird (*Molothrus ater*) parasitism as a result of a cowbird control program (Stutchbury 1997).

RESULTS

All nest failures were due to predation. None of the females deserted a territory or mate to renest. The average distance from all first nests (N = 47) to their subsequent renests was 48 m (range of 4–160 m). However, contrary to our prediction, renesting Hooded Warblers that were previously successful moved significantly farther away from their original nest sites compared with females who suffered predation (Fig. 1; Mann-Whitney *U*-test, $U = 146.5$, $P < 0.01$).

The size of a territory and the location of the first nest with relation to territory boundaries could affect dispersal distance since there was no territory desertion. We, therefore, estimated territory sizes and nearest distances from first nests to territory boundaries. Territories (N = 47) ranged from 4000 m^2 to 25,000 m^2. The mean territory size (8800 m^2) of territories with successful first nests (N = 22) was not significantly dif-

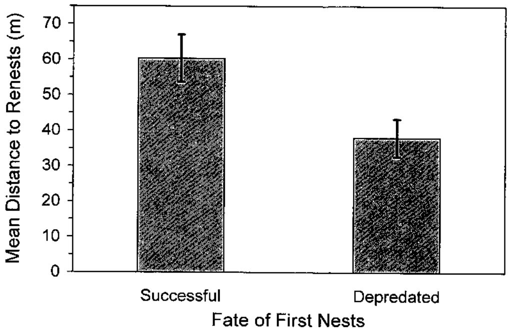

FIG. 1. Mean dispersal distances from successful (N = 22) and depredated (N = 25) first nests to subsequent renests. Error bars show ±SE.

ferent (Mann-Whitney U-test, $U = 266.0$, $P = 0.84$) from the mean territory size (8100 m^2) of territories with depredated first nests (N = 25). Also, the mean nearest distance to territory boundaries (19.2 m) for successful first nests (N = 22) was not significantly different (Mann-Whitney U-test, $U = 198.5$, $P = 0.10$) from the mean nearest distance (16.9 m) for depredated first nests (N = 25).

Each of the nest-site variables of concealment for all measured nests (N = 58) varied considerably (nest height, mean = 51.4 cm, range = 31.0–95.0 cm; stem density, mean = 24.3 stems-m^2, range = 4.1–58.0 stems-m^2; visibility overall, mean = 50.9%, range = 9.6–78.4%). Wilcoxon matched pairs tests clearly showed no significant differences between depredated nests (N = 19) and renests (Fig. 2; $Z = 0.65–1.52$, all $P > 0.05$). These variables also remained the same for successful nests (N = 10) and renests (Fig. 2; $Z = 1.17–1.78$, all $P > 0.05$).

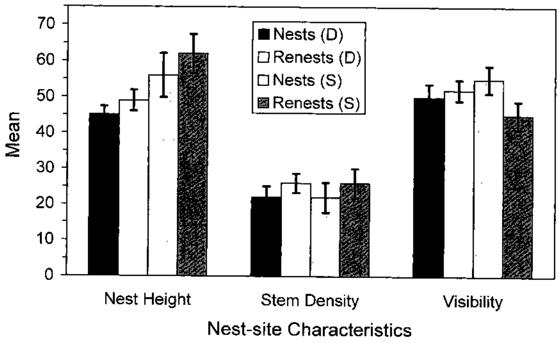

FIG. 2. Means of nest height (cm), stem density (stems-m^2), and overall visibility (% visible) for first nests and subsequent renests. On legend, (D) indicates depredated first nests (N = 19); (S) indicates successful first nests (N = 10). Error bars show ±SE.

The normal frequency of nest predation (all nests per year) of Hooded Warblers at our study site has been approximately 50% (Howlett and Stutchbury 1996). For nests included in this study, the frequency of predation was also 50% (49/98). The frequency of predation was 51% (25/49) for all first nests, 48% for renests following predation, and 50% for renests following successful first nests. Contrary to our prediction, a renest following predation was not more likely to be successful than a first nest ($X^2 = 0.06$, df = 1, $P = 0.81$), nor was a renest after a successful nest more likely to be successful than a first nest ($X^2 = 0.01$, df = 1, $P = 0.93$).

DISCUSSION

Our study examined the effects of nest predation in renesting Hooded Warblers. We expected nest predation to result in within-season dispersal but not greater nest concealment. Opposite to our prediction, females from successful first nests dispersed farther for their second nests than did unsuccessful females. We found no relationship between nest predation and subsequent nest concealment. In addition, renests after predation were no more successful than all first nests.

Why did successful females move their renests significantly farther away compared to females that suffered predation? An alternative hypothesis to explain within-season dispersal could be that this movement could be used by one member of the pair to terminate care of the fledglings, thus improving the probability of raising a subsequent brood elsewhere (Jackson et al. 1989). Indeed, female Hooded Warblers that have successful first nests usually help feed the fledglings with the male only until they begin incubating their second brood (Evans Ogden and Stutchbury 1997). The first egg date for the second clutch is often within a week of the first brood fledging date when the fledglings are still near their nest. Thus, females may be actively avoiding their fledglings in order to improve their success in renesting.

The avoidance of fledglings could serve to isolate a renest from fledgling activities that might attract predators. It could also serve to reduce competition for food resources. In support of the idea of reduced competition for food, Greig-Smith (1982) found that local food depletion was a factor in within-season dispersal of Stonechats (*Saxicola torquata*) and that nestling growth in second broods was better in nests that were at the greatest distances from previously successful nests.

Why do females not disperse or better conceal their nests in response to nest predation? One explanation could be that in Hooded Warblers nest-site selection is instinctual or based on imprinting on characteristics of the natal nest (Sargeant 1965, Cink 1976) and not affected by learning from recent experiences. Another explanation could be related to the fact that females rarely desert their territories or mates to renest. From 1991 to 1995 we observed approximately 184 pairs of Hooded Warblers. We noted only 3 cases of territorial desertion by females (<2%). When females limit renesting to within the same territories, the area of the territories may not be large enough to avoid previous predators.

A third explanation could be that nest predation occurs by chance, regardless of placement or variations in characteristics of specific nest sites. When variations in nest-site characteristics are not factors in predation, they should also not be important factors in nest-site selection after predation. In this study, we found that depredated nest sites were no different from successful nest sites (Fig. 2) and that all nests and renests had about a 50% chance of success. Indeed, nest predation in Hooded Warblers at our study site appears to be random no matter the degree of nest concealment, the location of the nest, the age and plumage of the female, or the time of year (see Stutchbury and Howlett 1995 and Howlett and Stutchbury 1996).

In conclusion, we found that predation did not cause female Hooded Warblers to disperse or alter nest-site selection. Other variables may be more important in determining the location of renesting sites, such as the presence of fledglings and the availability of food resources, in the case of a successful first nest. We recommend that the predation-avoidance hypothesis be tested further on other species and in other habitats.

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