The Condor 102:629–634
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INTERACTIVE EFFECTS OF VEGETATION AND PREDATORS ON THE SUCCESS OF NATURAL AND SIMULATED NESTS OF GRASSLAND SONGBIRDS[1]

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Abstract. We examined the influence of vegetation and predator community on nesting success of songbirds in the grasslands of eastern North Dakota, USA. Each year, eight sites were chosen: four were subject to predator removal, and four were non-removal sites. On each site, nests of grassland songbirds were monitored, and simulated nests were used to examine how vegetation characteristics at nests affect nest success. Vegetative characteristics at simulated nests did not differ from those at natural nests, but successful natural nests had greater forb and lesser grass cover than unsuccessful nests, whereas no differences in vegetation were detected between successful and depredated simulated nests. On non-removal sites, small mammals and ground squirrels (*Spermophilus* sp.) depredated nests in taller and denser cover when compared to nests destroyed by medium-sized mammals and birds. On removal sites, we found no difference in vegetation characteristics of nests depredated by different predator types. However, each group of mammalian predators depredated simulated nests with different vegetation characteristics on removal versus non-removal sites. On sites where predators were removed, small mammals and ground squirrels preyed on simulated nests in shorter vegetation containing fewer forbs, ground squirrels preyed on nests with higher grass cover and lower vertical density, and medium-sized carnivores preyed on nests in taller vegetation. These results support the hypothesis that high predator diversity may reduce the chance of "safe" nest sites, and suggest that the behavior of low-level predators may change when top-level predators are removed.

Key words: *grasslands, nest concealment, nest predation, predator removal.*

INTRODUCTION

Nest predation is the most important proximate cause of reproductive failure in birds (Martin 1995). Because of its evolutionary importance (Bosque and Bosque 1995), adaptations by birds to counteract predation are numerous and include nesting in areas not easily accessed by predators (Martin 1988), spacing nests away from neighbors (Tinbergen et al. 1967), using cryptic nest sites (Schieck and Hannon 1993), or nest defense (Cresswell 1997). Notably, most defenses used by nesting birds rely on decreasing either nest detection or nest accessibility (Martin 1995).

Vegetative characteristics at the nest site can help reduce predation by providing either visual concealment of the nest (DeLong et al. 1995), or by impairing the movements or foraging efficiency of predators (Sugden and Beyersbergen 1986). However, numerous studies have reported no influence of vegetation on nesting success (Donovan et al. 1997). This discrepancy may be related to linkages between the effects of vegetation on the survival of bird nests and the composition of local predator communities (Clark and Nudds 1991). For example, dense cover around a nest may increase nesting success of ducks and grouse when the primary predators are birds (Stokes and Boersma 1998), but not when they are mammals (Schieck and Hannon 1993). The effect of vegetation on nest success may differ for smaller songbirds; dense vegetation may harbor more small mammals which also depredate nests, and thus dense vegetation may lead to higher predation than sparse vegetation (Johnson and Temple 1990). Undoubtedly, the type of predator or predator community involved is critical in determining the influence of cover on nest fate.

Few studies have addressed the interactive effects of vegetation and predator communities on

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the survival of passerine nests (Johnson and Temple 1990). As part of a larger study designed to evaluate the effects of predator removal on waterfowl nesting success (Garretson et al. 1996), we were able to simultaneously evaluate the effects of vegetation and predator assemblage on nesting success of grassland songbirds. The recent decline of grassland songbirds in the United States (Knopf 1994), and the possibility of mesopredators impacting songbirds following removal of higher-level predators, prompted this study. Our objective was to assess whether vegetation influences the fate of both natural and simulated songbird nests in areas with experimentally-altered predator communities.

METHODS

STUDY AREA

We conducted studies during the breeding seasons of 1995 and 1996 in grasslands of eastern North Dakota, USA. This region has little topographic relief and is dominated by small-grain agriculture (Garretson et al. 1996).

Each year, we chose eight sites (all sites > 6 km apart) with numerous potholes and 10–30% of their surface as Conservation Reserve Program, Water Bank Program, or Waterfowl Production Areas. Each site was 41 km^2 in size, and was randomly assigned as "removal" or "non-removal"; each site was used only once during the study. Removal sites were subjected to intensive predator trapping whereas non-removal sites were left untreated (Garrettson et al. 1996). Within each site, we chose five 200 × 200-m plots and three 500-m transects for a total of 40 plots and 24 transects each year. Plots and transects were positioned independently and did not overlap. Plots were used for nest searching, and transects were used for placement of simulated nests. Distance between any two plots or transects was > 1.6 km.

Predator removal was performed from March through July, using similar legal removal methods (box-traps, snares, foothold traps, and shooting) on all removal sites. Red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and American badger (*Taxidea taxus*) were targeted for removal.

NATURAL NESTS

In 1995 and 1996, we found nests of grassland songbirds incidentally to other field procedures such as vegetation measurements and simulated nest experiments. In 1996, we also searched plots by dragging a 30-m rope with aluminum cans attached every meter. Each plot was searched twice between early June and early July. Each nest was marked with a 1-m bamboo pole placed 5 m from the nest. Nests were visited every 4 days to determine fate (Dion et al. 1999). At each visit, we examined nests for signs of predation including missing, dead, or partially consumed young, broken eggs, or disturbed nest bowl, but given difficulties with interpretation, we did not attempt to identify predators from nest remains (Larivière 1999). We assumed young had fledged if signs of predation were absent and if nestlings were close to fledging during the previous visit (Johnson and Temple 1990).

SIMULATED NESTS

Simulated nests consisted of a commercial wicker nest (9-cm in diameter and 5-cm deep) lined with grass and other natural vegetation. We placed each nest in locations that appeared similar to those of the natural nests we found. In each nest, we placed one Japanese Quail (*Coturnix japonica*) egg, and one painted modeling-clay egg. Modeling-clay eggs were used to help detect and identify predators from beak and tooth marks, whereas quail eggs provided predators with a reward. We wore rubber boots and gloves while handling nests and eggs to reduce human scent.

We deployed nests on the ground at 20-m intervals, and at random distances (5–25 m) from transect lines, alternating sides of transect for consecutive nests. Twenty-five nests were deployed per transect, for a total of 75 nests per site. Simulated nests were exposed for 12 days, and were visited every 4 days. We considered a nest destroyed if at least one egg was missing or destroyed, or if marks of predators were left on clay eggs. Each year we conducted two trials (early June and early July) to mimic the peak nesting and renesting period, respectively, of grassland songbirds in North Dakota (Stewart and Kantrud 1972).

We identified predator species using teeth and beak marks left in the modeling-clay eggs. We compared tooth marks to dental patterns and measurements from 10–15 skulls of small mammals and ground squirrels (*Spermophilus* sp.) from the Biology Museum, University of Saskatchewan. Because many species have overlapping measurements (N. Dion, unpubl. data), we did not attempt to identify species, but instead grouped predators according to ecological relatedness: small mammals (*Peromyscus, Microtis, Clethrionomys*), ground squirrels, medium-sized carnivores including badger, raccoon, red fox, and striped skunk, and birds (primarily Sedge Wren, *Cistothorus platensis,* and Brown-headed Cowbirds, *Molothrus ater*).

VEGETATION SAMPLING

As each nest fledged young or was depredated, we positioned horizontally on the ground four 1-m bamboo poles to serve as sampling sticks around the nest. The angle of the first sampling stick was determined at random, and the other three sticks were placed at 90° increments from that angle, with the nest at the center. We also positioned one bamboo pole vertically at the nest, and one at the end of each horizontal sampling stick.

We followed methods of Wray and Whitmore (1979) and recorded six indicators of nest-site vegetation: vertical density, height of vegetation at nest site, mean vegetation height around the nest site, cover of grass, cover of forbs, and litter depth. Vertical vegetation density was determined at the nest by recording the number of times a plant was in contact with the pole (referred to as a "hit") in each 10-cm height class (Wray and Whitmore 1979). Height of vegetation at the nest was determined as the last hit on the pole placed vertically in the nest bowl. Mean vegetation height was obtained from the average of the highest hits from the four vertical poles away from the nest. We visually estimated (to the nearest 5%) the percentage of cover provided by grasses and forbs (mostly alfalfa *Medicago sativa*) along each of the four horizontal sampling sticks positioned around the nest. The average value was used as cover of grass and cover of forbs. Finally, we measured litter depth (in mm) directly at the nest site.

STATISTICAL ANALYSES

We first tested whether vegetation characteristics differed as a function of nest fate (successful vs. depredated), nest type (natural vs. simulated), and treatment (removal vs. non-removal) using a multivariate analysis of variance based on vegetation variables (density, cover of grass, cover of forbs, mean vegetation height, height of vegetation at nest, and litter depth). We added year as a blocking factor, and used Julian date within year as a covariate. Treatment (removal vs. non-removal) was considered a site-level predictor. Vegetation variables were log-transformed to meet the assumptions of homogeneity of variances (Sokal and Rohlf 1981).

We also used a multivariate analysis of variance to examine whether different predators depredated nests with different vegetation characteristics. Using only depredated simulated nests, we simultaneously considered the effects of predator type (small mammal, ground squirrel, medium mammal, bird), treatment (removal or non-removal), and interactions on vegetative characteristics of depredated nests. Because we could not predict the direction of the results, we performed all analyses using two-tailed tests.

RESULTS

Trappers removed 1,166 and 908 medium-sized predators from the experimental sites in 1995 and 1996, respectively (Garretson et al. 1996). During both years, trappers removed primarily raccoons (42%), striped skunks (31%), and red foxes (24%). American badgers and American mink (*Mustela vison*) comprised the remaining 3%. Because predator densities were not monitored, it is unknown to what degree removal operations affected predator densities or communities. However, because of the high effort and number of animals removed, we suspect most of the resident target animals were removed.

INFLUENCE OF VEGETATION ON NEST FATE

We located 40 natural songbird nests in 1995 and 113 in 1996 (Dion et al. 1999). Nests belonged to Clay-Colored Sparrow (*Spizella passerina,* 52.3%), Savannah Sparrow (*Passerculus sandwichensis,* 16.3%), Le Conte's Sparrow (*Ammodramus leconteii,* 7.8%), Bobolink (*Dolichonyx oryzivorus,* 7.2%), Red-winged Blackbird (*Agelaius phoeniceus,* 5.2%), Grasshopper Sparrow (*Ammodramus savannarum,* 0.7%), Vesper Sparrow (*Poocetes gramineus,* 0.7%), Western Meadowlark (*Sturnella neglecta,* 0.7%), and unknown passerines (9.2%). Only nests of Clay-Colored Sparrow and Red-winged Blackbird were found above ground but always ≤ 30 cm high. Because natural nests on and above ground experienced similar success (Dion et al. 1999), we pooled all natural nests for analyses.

The effects of date ($F_{6,913} = 148.8$, $P < 0.001$) and year ($F_{6,8} = 6.4$, $P < 0.01$) were significant.

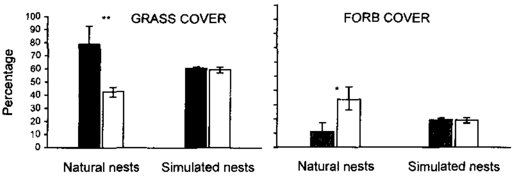

FIGURE 1. Characteristics of vegetation for depredated (shaded bars) or successful (open bars) natural nests of grassland songbirds in North Dakota, USA, 1995–1996. Values represent back-transformed least-square means and control for date and year. * and ** indicate significant differences at $\alpha = 0.05$ and 0.01, respectively. Error bars indicate standard error.

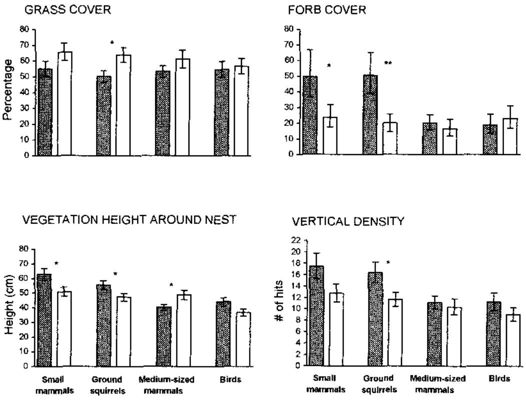

FIGURE 2. Characteristics of vegetation for nests depredated by different predator types on non-removal (shaded bars) and removal (open bars) sites. Values represent back-transformed least-square means. * and ** indicate significant differences at $\alpha = 0.05$ and 0.01, respectively. Error bars indicate standard error.

Once we controlled for date and year, vegetation characteristics did not differ among nests according to treatment ($F_{6,8} = 0.2$, $P = 0.97$) or nest type ($F_{6,913} = 1.7$, $P = 0.11$), but differed among nests according to fate ($F_{9,913} = 2.9$, $P < 0.01$); the interaction between fate and nest type was significant ($F_{6,913} = 2.3$, $P < 0.05$). All other interactions were nonsignificant (all $F < 1.6$, all $P > 0.14$).

We examined the fate and nest-type interaction by considering each nest type separately. For natural nests, successful nests had less grass cover ($F_{1,918} = 11.0$, $P < 0.001$) and greater forb cover ($F_{1,918} = 4.3$, $P < 0.05$) than depredated nests (Fig. 1). Conversely, we detected no difference in vegetation variables between successful and depredated simulated nests.

INTERACTIVE EFFECTS OF PREDATOR TYPE AND VEGETATION

Among depredated simulated nests, vegetation characteristics did not differ according to treatment ($F_{5,11} = 1.5$, $P = 0.26$), but differed according to predator type ($F_{15,1063} = 3.4$, $P < 0.001$). Multiple comparisons of least square means revealed that small mammals depredated nests in denser vegetation than did birds ($P < 0.01$) or medium-sized mammals ($P < 0.01$), and in lesser cover of forbs ($P < 0.001$), and overall shorter vegetation ($P < 0.001$) compared to nests destroyed by medium mammals. In addition, nests destroyed by birds were located in areas of shorter vegetation than nests preyed upon by either ground squirrels ($P < 0.001$) or small mammals ($P < 0.001$).

The interaction between treatment and predator type approached significance ($F_{15,1063} = 1.6$, $P = 0.08$). Thus, we compared vegetation characteristics of nests depredated by the same species, but for removal versus non-removal sites. Overall, nests destroyed by ground squirrels on removal sites were located in sparser vegetation ($F_{1,389} = 5.4$, $P = 0.02$), shorter vegetation around the nest ($F_{1,389} = 4.3$, $P = 0.04$), greater grass cover ($F_{1,389} = 5.0$, $P = 0.03$), and lesser forb cover ($F_{1,389} = 9.3$, $P < 0.01$) compared to non-removal sites. Small mammals also depredated nests located in shorter vegetation ($F_{1,389} = 5.8$, $P = 0.02$), and lesser forb cover ($F_{1,389} = 3.9$, $P = 0.05$) on removal sites compared to non-removal sites (Fig. 2). Finally, nests lost to medium-sized mammals on removal sites were located in taller vegetation ($F_{1,389} = 5.4$, $P = 0.02$) compared to non-removal sites (Fig. 2).

DISCUSSION

There has been conflicting evidence about the relative influence of nest-site vegetation on nesting success of birds (Martin 1995). Differences in local predator communities, and interacting effects of vegetation and predator type have complicated the interpretation of field data (Clark and Nudds 1991). In our study, we considered these aspects simultaneously, and used natural and simulated nests to corroborate our findings. Although our simulated nests were located in vegetation similar to that chosen by grassland songbirds, only for natural nests did we observe a difference in vegetative characteristics between successful and unsuccessful nests.

Simulated nests can provide a convenient tool for identifying nest predators (Bayne et al. 1997), or for comparing predation among experimental treatments. However, the use of simulated nests for assessing the effects of vegetation requires caution, as vegetative characteristics of simulated nests may not reflect those of natural ones (Ortega et al. 1998, Wilson et al. 1998). Although we found no differences in vegetative characteristics between the two nest types, the effects of vegetation on nest fate differed for both nest types, suggesting that predators may have perceived both nests differently. This could explain why natural nests in our study experienced lower nest survival than simulated nests during both years (Dion et al. 1999). Several factors may have contributed to this difference. First, parental activity at nests may have attracted some predators (Roper and Goldstein 1997). Second, some vegetation differences perceived by birds and/or predators may have been undetected by our sampling. For these reasons, we concur with others that simulated nests should be used only to compare the relative effects of treatments among areas, and not to estimate survival of natural nests (Ortega et al. 1998, Wilson et al. 1998).

Our data also indicate that different predators depredated nests with different vegetation characteristics. Small rodents use vegetative cover for protection against aerial predators, and this may explain why they encounter more nests in such areas (With 1994). Alternately, birds rely on vision for detecting nests, so they primarily detect nests in open areas, especially simulated nests that lack parental activity. Dense vegetation may also impede the movements of medium-size mammals, which may choose easier paths for traveling and foraging (Larivière and Messier 1998).

Most predators depredated nests with different vegetation characteristics after medium-sized carnivores were removed. For example, small mammals and ground squirrels depredated more nests in sparser vegetation (less forb cover, lower density and litter depth) on sites where carnivores were removed. Small mammals either became more abundant, or perceived changes in predation risk (Lima and Dill 1990) and altered their foraging behavior to use more open areas when larger predators were removed (Ritchie et al. 1994). If so, this could help explain why nest success of grassland songbirds did not improve significantly following removal of duck nest predators (Dion et al. 1999). Interestingly, the removal of mammalian carnivores did not affect the relationship between avian predators and vegetation; birds continued to destroy nests primarily in short vegetation. Thus, predation of simulated nests by birds appeared largely opportunistic and probably depended on the visibility of nests from the air (DeLong et al. 1995).

In summary, our study indicates that the nature and diversity of the local predator community can interact with vegetative cover at nests and that these two factors are closely linked. If nesting songbirds could recognize dangerous habitats (i.e., those most susceptible to predation), then we would expect strong selection for specific nest-site microhabitats (Martin 1998). However, the diverse predator community that exists on mixed prairie and agricultural grasslands probably precludes the existence of safe nest sites for songbirds, and any remaining patterns of nest-site selection likely reflect other constraints such as thermoregulation, or previous evolutionary pressures.

ACKNOWLEDGMENTS

This study was financed primarily by the Delta Waterfowl Foundation through the Delta Waterfowl and Wetland Research Station. Additional funding was obtained from the Canadian Wildlife Service through an operating grant to K. A. Hobson, and from the University of Saskatchewan through a graduate scholarship to N. Dion. We thank S. Fischer, C. McLaren, N. Kemptf, W. Johnson, M. Holt, M. Schmoll, J. Kreilich, M. Hoff, B. Luse, K. Pontesso, and J. Jordan for field assistance. We are grateful to F. C. Rohwer and J. Scarth who encouraged our participation in this project. L. Armstrong (Ducks Unlimited Canada) provided invaluable help with statistical analyses. L. R. Walton, G. C. Sutter, and one anonymous reviewer helped improve earlier versions of this manuscript. Our research was approved by the Louisiana State University Institutional Animal Care and Use Committee (#A96-11).

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