PREDATION ON ARTIFICIAL NESTS ALONG THREE EDGE TYPES IN A NORTH CAROLINA BOTTOMLAND HARDWOOD FOREST

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ABSTRACT.—Many researchers have reported high rates of nest predation near forest edges. However, edges may be of various types (e.g., interior or exterior, abrupt or gradual), which may not always result in elevated predation. We compared predation rates on artificial arboreal nests along three types of edges in a bottomland forest in North Carolina during the 1996 breeding season. Edge types were forest–farm, forest–river, and the transition zone between the two dominant forest types in the floodplain (cypress-gum swamps–natural levees). We tested for differences in predation rates using two egg types: Northern Bobwhite (*Colinus virginianus*) and clay eggs. Predation rates were higher (P < 0.05) along forest–farm edges than along the other two edges. Predation rates did not differ between forest–river and transition zone edges. Patterns of predations may have exerted more predation pressure along these edges. These results are consistent with other studies, which suggest that encroachment by agriculture into forested landscapes may negatively affect breeding bids. Our findings also suggest that not all edge types are equivalent in terms of predation rates. This is important in assessing the conservation value of bottomland forests, which may contain various edge types resulting from natural processes (e.g., hydrodynamics). *Received 19 Feb. 1999, accepted 6 July 1999.*

Predation is the primary cause of nest loss for a wide range of passerine birds (Martin 1992) and may be the most important factor affecting their population dynamics (Temple and Cary 1988). Forest birds nesting in highly fragmented landscapes or near edges may experience higher rates of nest predation than birds nesting in contiguous forests (Paton 1994, Andrén 1995, Robinson et al. 1995). However, forest edges occur in a variety of contexts which may not always lead to increased predation levels. For example, edges may be in the interior (e.g., clearcuts within contiguous forest) or along the exterior (e.g., agricultural encroachment from outside) of forests and they exhibit varying degrees of contrast from subtle to abrupt (Ratti and Reese 1988, Yahner et al. 1989, Hawrot and Niemi 1996, Fenske-Crawford and Niemi 1997, Suarez et al. 1997). Most researchers reporting high predation rates near edges have examined abrupt exterior edges (reviewed by Andrén 1995). Those that have considered interior and more subtle edges have reported less consistent results (e.g., Ratti and Reese 1988, Yahner et al. 1989, Fenske-Crawford and Niemi 1997, Suarez et al. 1997). Further investigation into the characteristics of edges that influence levels of predation is clearly needed. Such information could be used to assess the conservation value of complex landscapes, such as bottomland hardwood forests that support diverse breeding bird communities (e.g., Wharton et al. 1981, Mitchell and Lancia 1990, Mitchell et al. 1991, Pashley and Barrow 1992). These forested wetlands may contain a variety of edge types that result from the patchwork of plant communities whose arrangement is influenced by site-specific hydrodynamics and sediment deposition rates along floodplains (Wharton et al. 1982).

We compared predation rates on artificial arboreal nests among three edge types in bottomland hardwood forests along the Roanoke River in North Carolina. The three edge types were: (1) forest-farm edge (an abrupt exterior edge), (2) forest-river edge (an abrupt interior edge), and (3) levee-swamp edge (a gradual interior edge where the two dominant plant communities in the floodplain meet). We used artificial nests primarily because of the logistic and experimental advantages afforded by their use. We do not claim that predation rates on artificial nests represent those experienced by natural nests, only that the pattern of predation among edge types are likely to be similar for the two. For example, the few studies that have compared patterns of predation among habitats using both artificial and nat-

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ural nests as well as studies comparing similar habitats using either of these methods have typically found a close match in predation patterns for the two nest types (see Andrén 1995). To our knowledge, this is the first study to examine predation rates at an edge between two relatively undisturbed forested plant communities and only the third to examine a forest edge abutting water (Bollinger and Peak 1995, Vander Hagen and DeGraff 1996). Differences in predator communities among the three edge types were assessed by comparing patterns of predation on two egg types and the abundance of likely avian nest predators.

STUDY AREA AND METHODS

This study was conducted within a contiguous forest corridor along the lower Roanoke River between the towns of Palmyra and Jamesville, North Carolina (36° 9′ N to 35° 50′ N, 77° 20′ W to 76° 53′ W). The forested areas we studied have been undisturbed for more than 60 years. Loss and alteration of forests in the floodplain have come primarily from crop (e.g., peanuts, cotton, wheat) and timber production. The lower Roanoke ecosystem is comprised of 20 vegetative community types (Schafale and Weakley 1990), 2 of which are clearly dominant: cypress-gum swamp and coastal plain levee forests (hereafter swamps and levees, respectively). Swamps are flooded for extended periods throughout the year. The dominant canopy species are water tupelo (Nyssa aquatica) and bald cypress (Taxodium distichum); Carolina ash (Fraxinus caroliniana) is common in the understory (Lynch et al. 1994). Levees occur at slightly higher elevations and are comprised of a diverse mixture of canopy species including American elm (Ulmus americana), green ash (Fraxinus pennsylvanica), hackberry (Celtis laevigata), boxelder (Acer negundo), water hickory (Carya aquatica), and sweetgum (Liquidambar styraciflua). The understory of levees is characterized by pawpaw (Asimina triloba), ironwood (Carpinus caroliniana), and various vines (Lynch et al. 1994). Although the sizes and shapes of patches of the two forest types are variable, levees generally occur as linear patches close to the river channel formed by the deposition of sediment following flooding events. Farther from the river channel, these forests grade into swamps. Levee-swamp edges are comprised of a mixture of species typical of the two forest types. Forestriver edges are comprised of species typical of levees. Forest-farm edges are dominated by swamp trees, with red maple (Acer rubrum) also a dominant species.

Artificial nests were placed along two 1.5 km transects established within each edge type. Survey tape was used to mark 59 25-m intervals (nest site locations 1-60) along each transect. Nests were placed at 50 m intervals beginning at the first survey flag (nest site 1) during trials one and three and beginning at the second survey flag (nest site 2) during trial two. Thus, 30 nests

were placed along each transect during each trial. All nests were placed on a suitable substrate within 15 m of the survey flag. Transects along forest-river and forest-farm edges ran parallel to the river and fields, respectively, and were approximately 15 m inside the forest. Levee-swamp edge transects ran along the estimated center of the levee-swamp transition zone. Transition zones were characterized by the presence of bald cypress and water tupelo, wetter soils (often with standing water), and a noticeable opening of the understory. This design resulted in all nests being within 30 m of a habitat boundary. Paton (1994) found that edge effects on nest predation are typically found within 50 m of a habitat boundary; the 30 m distance cutoff we used was well within this range. All transects were separated by at least 2 km and were at least 100 m from any other edge type.

Because predators may respond to artificial nests differently than to natural nests (Major and Kendal 1996), we attempted to mimic as closely as possible the size, color, and locations of nests of Acadian Fly-catchers (*Empidonax virescens*), a common breeding species in the floodplain. Several other common breeding species place their nests in similar locations (Lynch et al. 1994). Artificial nests were constructed from commercially available miniature grape vine wreaths (approximately 8 cm outside and 5 cm inside diameters) with bottoms of dried grass or leaves lining wire mesh frames (approximately 4 cm deep). Nests were attached with wire to the fork of a low hanging tree branch, sapling, or shrub at a height of approximately 2.5 m.

Three 15 day trials were run over the course of the 1996 nesting season (30 May-24 July). Fifteen days approximates a typical incubation period for opennesting passerines in the area. Two egg types were placed in each nest: one Northern Bobwhite egg (Colinus virginianus) and one smaller white clay egg ("Plastalina", Van Aken International; approximately 20×10 mm) to account for potential biases associated with egg type (Roper 1992; Haskell 1995a, b; Major and Kendal 1996). Eggs were placed in each nest 3-5 days after nests were placed in the field. This was intended to mimic the interval between nest building and egg laying (Marini et al. 1995). We minimized human scent at nest sites by wearing rubber boots and gloves while placing nests and eggs, and while checking nests (Nol and Brooks 1982). Nests were checked for signs of predation on three occasions during each trial (day 5, 10, and 15). We considered a nest to be depredated if either egg was damaged or missing. Predation was attributed to a bird if the clay egg was found with bill imprints and/or the bobwhite egg was found with punctures suggestive of a bill (e.g., as described for crows by Rearden 1951). We considered a nest to be depredated by a large mouthed mammal if bobwhite eggs were found half eaten from one end [suggesting raccoon, Procyon lotor (Rearden 1951), or gray squirrel, Sciurus carolinensis (C. J. Whelan, pers. comm.)], if chewed up clay eggs were found, or if nests were destroyed (e.g., nest ring gone or pulled apart; Best and Stauffer 1980). Nests for which tooth imprints or scratches were found on clay eggs, or for which both eggs were found still in the nest or in the immediate vicinity and the clay egg was scratched, were considered to have been depredated by small-mouthed mammals (e.g., *Peromyscus* mice; Major 1991, Haskell 1995b). Although snakes may have also contributed to predation, we were unable to attribute predation events to snakes based on evidence at nest sites.

Birds were censused at 10 count stations located at 150 m intervals along each transect. All birds seen or heard within a 50 m radius and more than 50 m but within the area of interest, over a 10 min interval were recorded (Hutto et al. 1986). One census was conducted along each transect during the morning hours (06:30-09:45 EST) between 20 May and 6 June. Abundance of species likely to depredate nests [American Crow (Corvus brachyrhynchos), Fish Crow (Corvus ossfragus), Blue Jay (Cyanocitta cristata) and Common Grackle (Quiscalus quiscula)] was expressed as total detections per point (i.e., all detections, unbounded radius). Although some independence among sampling stations may have been sacrificed by using detections at all distances, each of these were "highdetection-ratio" species (i.e., each had a high proportion of the total detections recorded outside of the 50 m radius count circle), suggesting that detections at all distances within the edge and immediately adjacent habitats were more appropriate for comparisons (Hutto et al. 1986).

Univariate repeated measures ANOVA was used to test for differences in predation rates among edge types (Proc GLM, SAS Institute 1990; Winer et al. 1991). The response variable was the proportion of the 30 nests depredated on each transect. The independent variable was edge type (forest-farm, levee-swamp, and forest-river); trial (1, 2, and 3) and days of exposure (5, 10, and 15) were repeated measures. Prior to analyses the response variable was square root-arcsine transformed to meet homogeneity of variance assumption (Levene's test: P > 0.05; JMP, SAS Institute 1994). In order to test for potential biases associated with egg type, we used McNemar's tests conducted separately for each edge type (Proc FREQ, SAS Institute 1990). We tested for differences in selected avian predator abundance among edge types using nested-ANOVA (Proc NESTED, SAS Institute 1990). The response variable was the number of detections of selected avian predators per point. Model terms were edge type and transect [edge type]. Data met homogeneity of variance assumption (Levene's test: P >0.05; JMP, SAS Institute 1994). Differences in abundance of individual species of avian predators among edge types were assessed using Kruskal-Wallis tests (Proc NPAR1WAY, SAS Institute 1990). For species where a significant edge effect was found, a posteriori contrasts were computed using the nonparametric alltreatments multiple contrast test described in Hollander and Wolfe (1999). An $\alpha \leq 0.05$ was used for all analyses and values presented are means \pm SE. Statistical analyses were performed with JMP (version 3.2.2) and SAS (version 7.0) for Windows.

RESULTS

Predation rates differed significantly among edge types (F = 11.33, df = 2, 3; P = 0.04) and were higher along the agricultural fieldforest edges than along the other two edge types (F = 22.31, df = 1, 3; P = 0.01; Fig. 1). Predation rates did not differ between forest-river and levee-swamp edges (F = 0.35, df = 1, 3; P > 0.05). There was no difference in predation rate among trials (F = 0.05, df = 2, 6; P > 0.05). Within trials, predation rate increased with day of exposure (F = 94.54), df = 2, 6; P < 0.001). Interaction between day of exposure and edge type was nearly significant (F = 3.55, df = 4, 6; P = 0.08). This nearly significant interaction was likely caused by differences in response pattern (slope) between levee-swamp and forest-river edges from 5-10 days of exposure (Fig. 1). The difference among these two edges at 5 days of exposure was not significant (F =5.23, df = 1,3; P > 0.05). Predation rates were highest along forest-farm edges regardless of exposure time.

The number of nests for which the bobwhite egg was damaged or missing was highest on forest-farm edges, while the number of nests for which only the clay egg was depredated was similar among edge types (Fig. 2A). Bobwhite eggs were preyed upon more frequently on forest-farm edges than on the other two edge types (Fig. 2B). Conversely, the percentage of depredated nests in which only the clay egg was preyed upon was lowest on forest-farm edges and highest on levee-swamp edges. For each edge type, the clay egg was depredated significantly more often than the bobwhite egg in nests where only one egg was depredated (Forest-farm: $G_{adi} = 9.49$, df = 1; P < 0.01; Forest-river: $G_{adj} = 19.15$, df = 1; P < 0.001; Levee-swamp: $G_{adj} = 45.83$, df = 1; P < 0.001). Despite this egg type bias, the pattern of predation, higher on forest-farm edges than on the other two edge types, was the same regardless of whether predation was on bobwhite or clay eggs (Fig. 2A).

We identified nest predators for 30% of depredated nests (114/368). Of these, 69% (79) were birds, 22% (25) were smaller mouthed mammals, and 9% (10) were larger

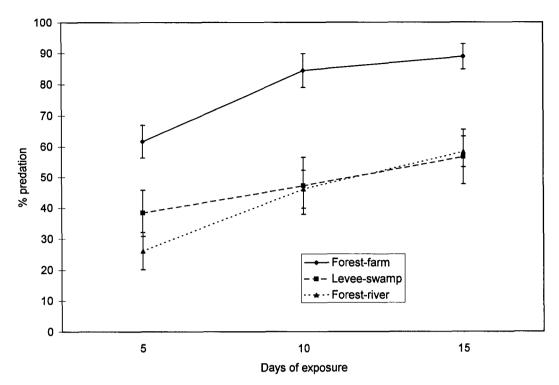


FIG. 1. Predation rates on artificial nests at three edge types in bottomland hardwood forest along the Roanoke River floodplain, North Carolina during the 1996 breeding season. Predation rates were significantly higher along the forest-farm edges than on the other two edges (P < 0.05).

mouthed mammals. Although measurements of bill imprints in clay eggs were not taken, the size and shape of these imprints suggested that crows, Blue Jays, and Common Grackles were among the avian predators. The abundance of these nest predators differed by edge type (F = 36.84, df = 2, 3; P < 0.01) and was higher on forest-farm edges than along forest-river and levee-swamp edges (F =65.79, df = 1, 3; P < 0.01; Fig. 3). Avian predator abundance did not differ significantly between forest-river and levee-swamp edges but tended to be higher along the forest-river edge (F = 7.89, df = 1, 3; P = 0.07; Fig. 3). Considered individually, the four predator species were not consistent in their responses to edge type (Fig. 3). The numbers of American and Fish Crows detected differed significantly among edge types (American Crow: χ^2 = 11.21, df = 2, P < 0.01; Fish Crow: χ^2 = 12.27, df = 2; P < 0.01), and both of these species were significantly more abundant along forest-farm edges than along leveeswamp edges (American Crow q = 4.28, Fish

Crow q = 4.42; P < 0.01). American Crows were also significantly more abundant on forest-farm edges than along forest-river edges (q = 3.65; P < 0.05). Fish Crows tended to be more abundant along forest-farm edges than along forest-river edges, although this difference was not significant (q = 3.06; 0.05) < P < 0.10). In contrast, Blue Jays, which also showed a significant edge effect (χ^2 = 6.05, df = 2; P < 0.05), were more abundant along forest-river edges than on levee-swamp edges (q = 3.33; P < 0.05). Contrasts between forest-farm edges and the other two edge types for this species were not significant (P > 0.05). Common Grackle abundance did not differ significantly among edge types (χ^2 = 3.74, df = 2; P > 0.05).

DISCUSSION

Our findings are consistent with most previous studies that have reported high rates of nest predation along abrupt exterior edges (our forest-farm edge type; see Andrén 1995). The presence of more avian predators along

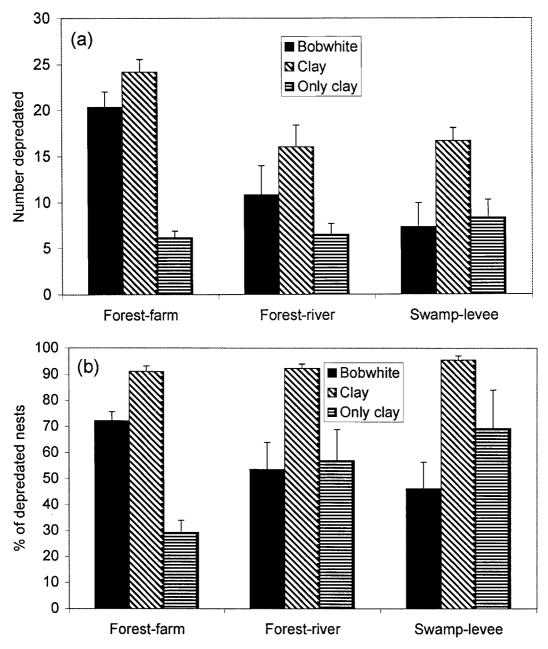


FIG. 2. (A) Absolute number of depredated nests and (B) the percentage of depredated nests for which the bobwhite egg, clay egg, or only the clay egg was preyed upon. Results of McNemar's tests conducted for each edge type (n = 180 nests) suggested a significant egg type bias (P < 0.01 for each edge type); however, the same pattern of predation (highest on forest-farm edges) was apparent regardless of whether bobwhite or clay eggs were considered.

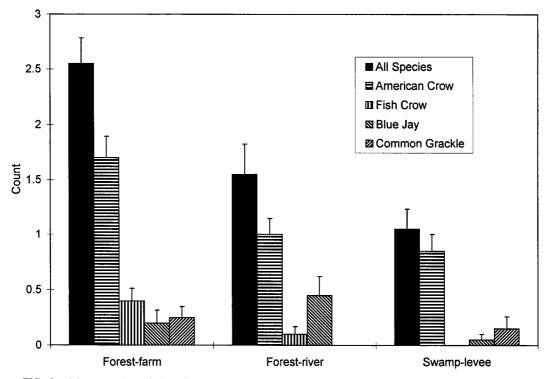


FIG. 3. Mean number of detections per point for selected avian nest predators at three edge types in a bottomland hardwood forest along the Roanoke River floodplain, North Carolina. The pooled abundance for all species was significantly higher on forest-farm edges than on the other two edge types (P < 0.01); the responses of individual species were not consistent among edge types.

forest-farm edges may have contributed to the higher predation rates we observed along these edges. Marini and coworkers (1995) found a positive correlation between avian predator abundance (American Crows, Blue Jays, and Common Grackles) and predation levels on artificial nests in forest saplings, as well as significantly higher predation rates on these nests at forest-farm edges. Other researchers have also related avian nest predator abundance (e.g., corvids) to forest-farm edges or shown predation on artificial nests by these predators to be higher near such edges (e.g., Whitcomb et al. 1981, Angelstam 1986, Andren 1992, Nour et al. 1993).

Our finding that nests at forest-river edges experienced lower predation rates than forestfarm edges is in accordance with Vander Haegen and DeGraff (1986) who found no effect of distance from a river edge on predation rate. In contrast, Bollinger and Peak (1995) found predation rates to be uniformly high on artificial ground nests along a forest edge bordering water and a forest-farm edge in one forest fragment in an agricultural setting. Small forest fragments in agricultural landscapes such as this may become inundated with certain mammalian predator species (e.g., raccoons; gray squirrels, *Sciurus carolinensis*; and opossums, *Didelphis marsupialis*; Bider 1968, Matthiae and Stearns 1981). The relatively wide and heavily forested river corridor in our study may have alleviated any such packing effects by predators.

The levee-swamp edges we studied are unique in that they are naturally occurring boundaries between plant communities rather than edges resulting from human activities (e.g., agriculture, forestry practices). As such, they may not be perceived as edges by some predators that may move freely between levees and swamps rather than concentrating activities along the edge or using it as a travel lane (Bider 1968, Chasko and Gates 1982). This could explain the relatively low predation rates we observed at these edges.

It is difficult to determine the relative impact of different predators at the three edge types because predators were only identified for 30% of depredated nests. The greater abundance of avian predators at forest-farm edges may have contributed to the higher predation rates there: however, some mammalian predators and snakes might also be abundant and concentrate their activities or travel along abrupt edges (Bider 1968, Chasko and Gates 1982, Durner and Gates 1993; but see Heske 1995). Unfortunately, we were unable to assess the relative abundance of non-avian predators or their relative contribution to predation on artificial nests. Nonetheless, there was some indication that the predators responsible for depredating nests may have differed among edge types. For example, because small mouthed predators may have been unable to damage the Northern Bobwhite eggs [as has been reported for Japanese Quail (Coturnix coturnix) eggs; Roper 1992, Haskell 1995a], our finding that the proportion of nests for which only the clay egg was depredated was higher at the forest interior edges suggests that small mouthed predators (e.g., mice) may have been more important at these edges. In contrast, both the proportion and absolute number of depredated nests for which the bobwhite egg was preved upon was highest at forest-farm edges. This supports the contention advanced by Haskell (1995b) and Nour and coworkers (1993) that avian and larger mammalian predators increase in importance in small forest patches or at the edges of forests. Smaller mouthed predators, although possibly more frequent at the interior edges, appear to have depredated similar proportions of nests along the three edge types. Finally, differential predation rates at different types of edges could also be influenced by factors other than the types of predators involved and their abundance. Future studies should be designed to consider factors influencing nest site selection (e.g., number of potential nest sites) and nest densities of avian community members (Martin 1993).

Bottomland hardwood forests of the southeastern U.S. are being destroyed and fragmented at high rates (Turner et al. 1981, Abernathy and Turner 1987). These areas provide important breeding habitats for many migratory and resident birds (Wharton et al. 1981, Mitchell and Lancia 1990, Mitchell et al. 1991, Pashley and Barrow 1992). Understanding how edges resulting from natural processes (e.g., hydrodynamics), as well as from anthropogenic modifications, affect breeding bird communities is important to their conservation and management. Our results suggest that encroachment by agriculture may negatively affect breeding birds through higher predation rates along forest-farm edges. Natural edges between adjacent plant communities and at the forest-river interface may not affect breeding birds in the same way.

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