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Daniel Moore '96
Illinois Wesleyan University

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HABITAT EDGE AND NEST PREDATION IN HOUSE WRENS

Daniel Moore

Thesis for Research Honors in Biology

Dr. R. Given Harper, Advisor

Department of Biology

Illinois Wesleyan University

Bloomington, Illinois 61702-2900

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Abstract.---I studied the effect of habitat edge on nest predation rates in a population of House Wrens (Troglodytes aedon) which bred in nest boxes in central Illinois from 1986-1994. Each nest box was classified according to its distance from the nearest habitat edge, and edges were classified into either abrupt, gradual or riverine edge-types. Nest predation rates varied significantly annually for the the two major nest predator classes, apparent avian and snake, and Raccoon (Procyon lotor). Neither predator class showed significant differences in nest predation rates in relation to distance from the nearest edge. There was no significant effect of edge-type on nest predation rates by birds and snakes, but nests along riverine edges incurred significantly higher Raccoon nest predation rates. Although nest predation rates did not differ significantly for either predator class between gradual and abrupt edge-types, the potential importance of this variable warrants further studies in open- and ground-nesting species.

Introduction

The effect of habitat fragmentation on avian nest predation has received little scrutiny until the last twenty years (Gates and Gysel 1978, Kroodsma 1984, Andrén et al. 1985, Angelstam 1986, Small and Hunter 1988, Yahner and Scott 1988, Andrén 1992, Burkey 1993, Paton 1994, Bollinger and Peak 1995, Robinson et al. 1995). Habitat fragmentation has been implicated in the recent population decline in many woodland bird species, because birds nesting in smaller tracts of forest suffer increased nest predation and/or parasitism compared to those nesting in larger tracts (Loiselle and Hoppes 1983, Wilcove 1985, Askins et al. 1990, Brawn and Robinson 1996). Smaller plots have more habitat edge than interior habitat compared to larger plots, where nest predation and parasitism rates are higher (Gates and Gysel 1978). The tendency for population densities to increase near habitat transitions is well established for many organisms (Odum 1971). Several avian species have been shown to have higher nest densities in mixed habitats characteristic of habitat edges compared to homogenous habitats (Beecher 1948, Johnston and Odum 1956). One explanation is that habitat edges incorporate individuals from populations in each adjoining habitat, as well as individuals from populations localized only along the habitat edge itself (Gates and Gysel 1978). Mammalian nest predators also tend to be localized along the habitat edges for the same reason, in addition to the fact that they also use habitat edges as movement corridors (Hoffmeister 1991). Thus, habitat edges become 'ecological traps' for nesting birds, where increased nest densities may result in increased nest predation rates (Gates and Gysel 1978).

Much of the research on nest predation rates near habitat edges is based on work with artificial nests; however, results from such studies must be interpreted with caution as they may be biased towards predators using only visual cues, since others factors such as nest scent and nestling

vocalizations are omitted (Paton 1994). In addition only a few studies have investigated the possible relation between habitat edge-types (e.g. Ratti and Reese 1988, Yahner et al. 1989, Gates and Giffin 1991, Bollinger and Peak 1995) and nest predation rates. The purpose of this study was to test the hypothesis that nest predation rates in House Wrens (*Troglodytes aedon*) are higher on nests along habitat edges than nests in the forest interior. I also tested the hypothesis that habitat edge-type may influence predation rates. I predicted that nests along gradual edge transitions should incur less nest predation than nests along abrupt edge transitions and riverine edges, because gradual edges mimic more closely the interior nest sites.

This study was conducted on a population of House Wrens that bred in nearly identical nest boxes, which may eliminate some of the variation in nest site characteristics that often confound the results of studies of nest predation along habitat edges (Martin 1995). Although the House Wren is not a threatened species, patterns of nest predation found in the study may be important to understanding the population declines of many woodland bird species. The conservation of species of woodland birds with declining populations is dependent upon understanding those factors that impact negatively their reproductive success (Martin 1993).

Methods

Study organism.—The House Wren is a territorial, non-excavating, cavity nesting, insectivorous passerine. In the population of nest box-breeding House Wrens used in this study in central Illinois, 70% of females are doubled-brooded (Drilling and Thompson 1988). Clutch size varies from 3-8 eggs, with first (early-season) and second (late-season) modal clutch sizes of 7 and 6 eggs, respectively (Finke et al. 1987). The eggs hatch after an average of 13 days of incubation. The nidicolous nestlings become homeothermic approximately six days after hatching, and leave the nest

between 15-17 days after hatching (Finke et al. 1987).

Study area.---Data for this study were collected from May-September 1986-1994 on the 108-ha Mackinaw Study Area in central Illinois, USA (40°40' N, 88°53' W) (Fig. 1; see Finke et al. 1987, Drilling and Thompson 1988, Harper et al. 1992). The 585 nest boxes, located in north-south lines, were separated within each line by 30 m, and between lines by 60 m. The nearly identical nest boxes (floor: 8.4 x 9.0 cm; diameter of entrance: 3.2 cm; distance from bottom of box to bottom of entrance: 13.0 cm) were placed on steel poles (with a diameter of approximately 2.54 cm) 1-1.5 m above the ground. The removable lids were attached with Velcro. Many of the poles (48.4% in 1993 and 1994) were coated with axle grease to reduce predation rates so that other studies could be conducted (e.g. Harper et al. 1992, 1993, 1994). Possible effects of greasing poles are discussed in the Results and Discussion. Each box was checked twice weekly between 05:00-11:00 CST, except for daily visits near times of hatching and fledging.

Habitat and predator types.---Each box was categorized by distance from the nearest edge. We defined edge as any area where the forest canopy was interrupted, followed by a transition into another type of habitat. Nest boxes adjacent to habitat edges were considered 0 m from the edge, although the actual distance from the edge ranged from approximately 5-20 m. Habitat edges were further classified as abrupt, gradual, or riverine. Abrupt edges were characterized by sudden transition of the forest into either cropland or a roadway, while gradual edges were characterized by forest located adjacent to oldfield habitat. The Mackinaw river ran through the study area, and nest boxes adjacent to it were classified as riverine edge. Paton's (1994) criterion of using in edge analyses only those forest canopy openings with a diameter three times or more the height of the adjacent trees were met for abrupt and gradual edges. However, this was not met for riverine edges, which, in most places, had a canopy

opening approximately equal to the height of adjacent trees.

The disappearance or destruction of eggs or nestlings was considered predation. When predation occurred, the appearance of the nest was noted. Five major predator types were documented during the study; however, the major predators were likely birds (mostly other House Wrens) and snakes, and mammals [mostly Raccoons, but possibly also by Virginia Opposums (Didelphus virginia)]. Raccoons (Procyon lotor) were implicated as the predator if hair or tracks were present on or near the nest box, and/or if the nest was destroyed (i.e. pulled partially or completely out of the nest box). If the eggs or nestlings had holes pecked in them the predator was considered to be a bird (Neill and Harper 1990), likely another House Wren (Belles-Isles and Picman 1986). Snakes were implicated as predators only if they were observed in the nest or if there was evidence (scales or markings in grease) they had climbed over the greased poles. If the nest was undisturbed with the eggs and/or nestlings missing, we considered the predator as either another bird or a snake (Pogue and Carter 1995). Further analyses are divided into the two major predator classes: (1) apparent avian and snake and (2) Raccoon. Over the course of the study some nests ($n = 22$) were depredated by mustelids (likely Mustela frenata), mice (Leucopus spp.), and possibly Eastern Chipmunks (Tamias striatus), and these nests were all excluded from further analyses.

Statistical analyses.---I used the Statistical Analysis System (SAS; SAS Institute 1994) for all analyses. The CATMOD procedure was employed to compare predation rates in habitat edge versus interior. We assigned a value of 0.001 to cells that had frequencies of 0 to avoid inconclusive results (SAS Institute 1994). In some instances we were unable to incorporate certain variables into statistical models because of small sample sizes, and interactions between variables were analyzed only when sample sizes were sufficiently large. In addition, years with very low predation rates were dropped

from the analyses (see Table 1). Broods in which eggs or nestlings were added or removed for experimentation were omitted from the analyses. In all following analyses, the proportions given are the number of nests depredated by the particular predator type in relation to the total number of nests which could have been depredated (i.e. the denominator is the total number of nests minus the nests depredated by all other predators).

Selective logging occurred on the study site in 1982 (Drilling and Thompson 1984). It took five years before the forest canopy closed and resembled the pre-logging and adjacent unlogged areas condition (C.F. Thompson, pers. comm.). As a result, we deleted data from 149 nest boxes in that portion of the study area from the analyses in 1986, and included them in analyses starting in 1987.

Results

Effects of greased poles on predation rates.---Applying axle grease to the steel poles upon which the nest boxes were mounted significantly reduced predation rates in 1993 (depredated nest boxes with ungreated poles = 45.0%; depredated nest boxes with greased poles = 33.1%, $G = 5.19$, $df = 1$, $p = 0.023$) and 1994 (depredated nest boxes with ungreated poles = 66.7%; depredated nest boxes with greased poles = 33.0%, $G = 45.79$, $df = 1$, $p < 0.0001$). There were no significant differences in the distribution of greased poles in relation to distance from habitat edges in 1993 ($G = 9.47$, $df = 6$, $p = 0.149$) or in 1994 ($G = 4.73$, $df = 6$, $p = 0.579$). However, significantly more poles were greased along abrupt edge-types (69.4%) compared to riverine (6.5%) and gradual edge-types in 1993 (24.2%, $G = 21.33$, $df = 2$, $p < 0.0001$) and in 1994 (abrupt = 64.4%, riverine = 16.44%, gradual = 19.2%; $G = 15.82$, $df = 2$, $p < 0.0001$).

House Wrens and edge.---I first determined whether House Wrens preferred to nest along habitat edges over interior nest sites. In all years of the study, there were significantly more nest boxes

that contained one or more nests per year in the edge habitat (69.7%) compared to nest boxes with one or more nests in the interior habitat (56.4%, $G = 107.38$, $df = 1$, $p < 0.0001$).

Distance from nearest edge and nest predation.---Apparent avian and snake nest predation rates varied significantly over the course of the study (Table 1; $G = 42.12$, $df = 6$, $p < 0.00001$). There was no significant effect of distance from the habitat edge on apparent avian and snake nest predation rates (Fig. 2, $G = 4.62$, $df = 8$, $p = 0.7971$). Likewise, there was a highly significant difference in Raccoon nest predation rates among years (Table 1; $G = 103.95$, $df = 7$, $p < 0.00001$), and there was no significant difference in Raccoon nest predation rates in relation to distance to the nearest edge (Fig. 2; $G = 4.26$, $df = 8$, $p = 0.8329$).

I also analyzed for the effect of brood size on Raccoon nest predation rates separately from the distance to nearest edge analysis because the added variable gave inconclusive results. I classified brood sizes of 3, 4, or 5 as small broods, while brood sizes of 6, 7, or 8 were considered large broods. Larger broods were depredated by Raccoons significantly more frequently than smaller broods (large broods = 6.02%, small broods = 4.06%, $G = 3.78$, $df = 1$, $p = 0.0518$).

Edge-type and nest predation.---Only nest boxes immediately adjacent to habitat edges were included in the following edge-type analyses. There was a significant year effect on apparent avian and snake predation rates in relation to habitat edge-types (Table 1; $G = 13.63$, $df = 6$, $p = 0.034$). However, there were no significant differences between abrupt, gradual, and riverine edge-types for apparent avian and snake nest predation rates (Fig. 3, $G = 3.22$, $df = 2$, $p = 0.2003$). Likewise, there was not a significant interaction between edge-type and year ($G = 18.18$, $df = 12$, $p = 0.1103$).

The interaction between year and edge type was not significant in the analysis of Raccoon predation on nests immediately adjacent to the edge ($G = 10.71$, $df = 14$, $p = 0.7085$). Therefore, I

report the analysis without an interaction in the model. There was a significant year effect on Raccoon nest predation rates ($G = 45.36$, $df = 7$, $p < 0.00001$), and significantly higher Raccoon nest predation rates were found along riverine edges than along abrupt and gradual edge-types (Fig 3, $G = 9.28$, $df = 2$, $p = 0.0097$).

Discussion

Greasing poles.---Greasing poles upon which nest boxes were mounted reduced, but did not totally prevent predation. However, there were no significant differences in the distribution of these greased poles in relation to habitat edges in 1993 or 1994. Although I do not have data on which poles were greased in other years of the study, I believe the distribution of greased poles in the study area was similar in all years. Therefore, greasing poles may not have affected predation rates in relation to distance from habitat edge, although they did likely affect predation rates in relation to edge-type. Because greased poles would not affect avian nest predation, the result would be an underestimation of the overall rate of mammalian and snake predation in this study.

Predator types.---The most abundant egg and nestling predators were other birds, snakes, and mammals. I believe that the majority of the avian nest predation was a result of other House Wrens, because the size of the opening of the nest box prevented most other avian predators from gaining access to the House Wren nest. Although the House Wren is well known as a nest destroyer (Belles-Isles and Picman 1987, Pribil and Picman 1991), the extent of intraspecific nest predation in our study was unexpected. Other studies have estimated House Wren nest destruction to be low (Belles-Isles and Picman 1986, Quinn and Holroyd 1989, Young 1994). My high rates of House Wren nest predation may be an artifact of the numerous nesting sites available on the study area. However, the densities of breeding wrens in our study area are not unusually high (Kendeigh 1941), and House

Wren nest destruction may be an underestimated phenomenon. Other potential avian predators include Blue Jays (*Cyanocitta cristata*) sometimes kill fledglings (Harper pers. observation), Red-Bellied Woodpeckers (*Melanerpes carolinus*) prey on nestlings (Neill and Harper 1990), and Black-capped Chickadees (*Parus atricapillus*), which occasionally nest in some of the nest boxes (Harper pers. observ.), are known nest destroyers (Picman and Belles-Isles 1988).

Raccoon nest predation was expected to be high since Raccoons were commonly seen foraging on the study area. Moreover, many studies have found mammals, particularly Raccoons, to be major nest predators in forests (e.g. Yahner and Morrell 1991, Schaub et al. 1992). Adjacent agriculture land used for cropland [e.g. soybeans (*Glycine max*) and maize (*Zea mays*)] may serve as a food source and contribute to large Raccoon populations in the study area, particularly along its edges. Raccoon populations increase near human homes (Hoffmeister 1991); those few homes near the study area may have helped support elevated Raccoon populations.

Distance from nearest edge and nest predation.---The significant year effect on apparent avian and snake nest predation rates was unexpected and has not been observed in other studies (e.g. Morton et al. 1993), but it could be the result of fluctuating House Wren densities from year to year (Thompson pers. comm.). An inverse relationship between distance from the edge and nest predation rates has been supported in some studies (e.g. Rudnicki and Hunter 1993, Linder and Bollinger 1995, Robinson et al. 1995), but not in others (e.g. Small and Hunter 1988, Yahner 1991). A possible factor may be due to the House Wrens being a cavity nesting species. Most studies of the edge effect have been conducted on ground- or open-nesting birds (e.g. Latta et al. 1995, Brawn and Robinson 1996), which often experience higher rates of nest predation than cavity-nesting species (Ricklefs 1969, Martin and Li 1992, Bollinger and Linder 1994). Kroodsma (1984) found that nest predation rates

were influenced by habitat edge more frequently in open-nesting than in cavity nesting passerines.

The significant year effect on Raccoon nest predation rates may be due to fluctuating Raccoon populations between years (Hoffmeister 1991). Another possible explanation may be learning or conditioning by Raccoons to the sight and/or odor of the nest boxes, and of the scent of researchers walking between nest boxes. For example, it was common for several adjacent boxes in north-south lines to be depredated by Raccoons between visits by field workers (Harper pers. observ.). This pattern of predation could be due to Raccoons forming a search image or following the scent of the investigators. Such learned foraging techniques could be retained from year to year, gradually increasing nest predation, which may explain why the Raccoon nest predation rates generally increased throughout the years of the study. The lack of a significant effect of distance to the edge on Raccoon predation was unexpected, since many studies have shown an inverse relationship between distance from edge and mammalian nest predation rates (reviewed by Paton 1994) and since edges are often sites of increased predator activity (e.g. Gates 1991).

The higher Raccoon nest predation rates in the larger broods was expected, since nestling vocalizations, odor, parental time spent foraging away from the nest, and parental trips in and out of the nest box would all likely increase with increased brood size. All of these factors may contribute to decreased nest concealment and increased Raccoon nest predation rates.

An explanation for the lack of edge effect in both predator classes could be the irregular shape of our study area, which had a relatively large edge-length-to-area ratio of 90.6 m/ha. If our 108 ha study area had been square, it would have had an edge length to area ratio of 38.5 m/ha, and would have contained more interior habitat than our actual study area. The entire study area may, in essence, have functioned as a large edge, as approximately one-third of our nest boxes (31.4%) were located

along the edges, while the median distance from nest boxes to the nearest edge was 60 m. Many studies of the effect of edge and nest predation rates have only considered patch size. Based solely on this aspect, my study area would have been classified as large compared to other studies that found significant effects of patch size on nest predation rates (Hoover et al. 1995). However, as has been documented previously (Patton 1975, Small and Hunter 1988), the edge-length-to-area ratio (i.e. shape) may also be important factor in the considering edge effect and nest predation rates.

Edge type and nest predation.---The significant year effect on apparent avian and snake nest predation rates of edge boxes was not suprising since similar variations in annual nest predation rates were seen for the entire study area. I had hypothesized that gradual edge transitions between adjoining habitats would incur less avian and snake predation than abrupt or riverine edges, since the edge would more closely resemble an interior habitat. A possible reason why no differences were seen between edge types could relate to spatial considerations. Avian predators forage mainly by sight, and the nest boxes in our study area are spaced at constant intervals; the resulting pattern of nest boxes could therefore be learned by birds and prevent any possible trends in predation rates from occurring in the study area. It was also possible that the vegetation surrounding the boxes may have been insufficient to conceal them adequately.

In terms of Raccoon predation rates, the year effect on the edge boxes was similar to that for the entire study area. I expected higher Raccoon nest predation rates along riverine edges, as Raccoons are known to utilize waterways as corridors between fragmented habitats (Forman and Godron 1986, Hoffmeister 1991), and would be expected to be localized along riverine edges. However, our results may have been influenced by the fact that significantly fewer poles were greased along riverine edges. No differences in nest predation rates by mammals between forest-field and forest-lake ecotones have

been found in other species (Bollinger and Peak 1995). I also expected Raccoon nest predation rates to be higher along abrupt edges than gradual edges, but this was not the case. It could be that Raccoons tend to follow ecotones regardless of whether the edge is well-defined, and therefore do not prey on nests preferentially in either abrupt or gradual edge habitats.

Although nest predation rates did not differ significantly for either predator in relation to edge-type, few studies have compared nest predation rates within one fragmented forest tract (Bollinger and Peak 1995), and these studies have used artificial nests. The potential importance of the variable to conservation practices for declining bird populations warrants future studies of real nests in open- and ground-nesting species.

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Table 1. Annual House Wren nest depredation rates (%) by predator type.

Depredation rates including all nest boxes.

Predator Class	Predation rates								
	Year								
	1986	1987	1988	1989	1990	1991	1992	1993	1994
Apparent avian and snake	15.1	10.0 ^a	12.3 ^a	20.2	16.6	25.9	16.7	26.1	33.2
Raccoon	8.9	6.0	7.1	15.9	2.5 ^a	16.3	13.4	22.6	34.4

Depredation rates (%) including only nest boxes adjacent to habitat edges.

Predator Class	Predation rates								
	Year								
	1986	1987	1988	1989	1990	1991	1992	1993	1994
Apparent avian and snake	15.3	6.7 ^a	12.1 ^a	22.5	18.6	23.0	16.1	22.5	36.0
Raccoon	7.7	4.6	10.4	16.2	2.5 ^a	20.6	7.1	24.0	34.9

^aNot included in the analyses due to small values or too many zero frequencies in cells

Fig. 1. The Mackinaw study area. Each dot represents one nest box.

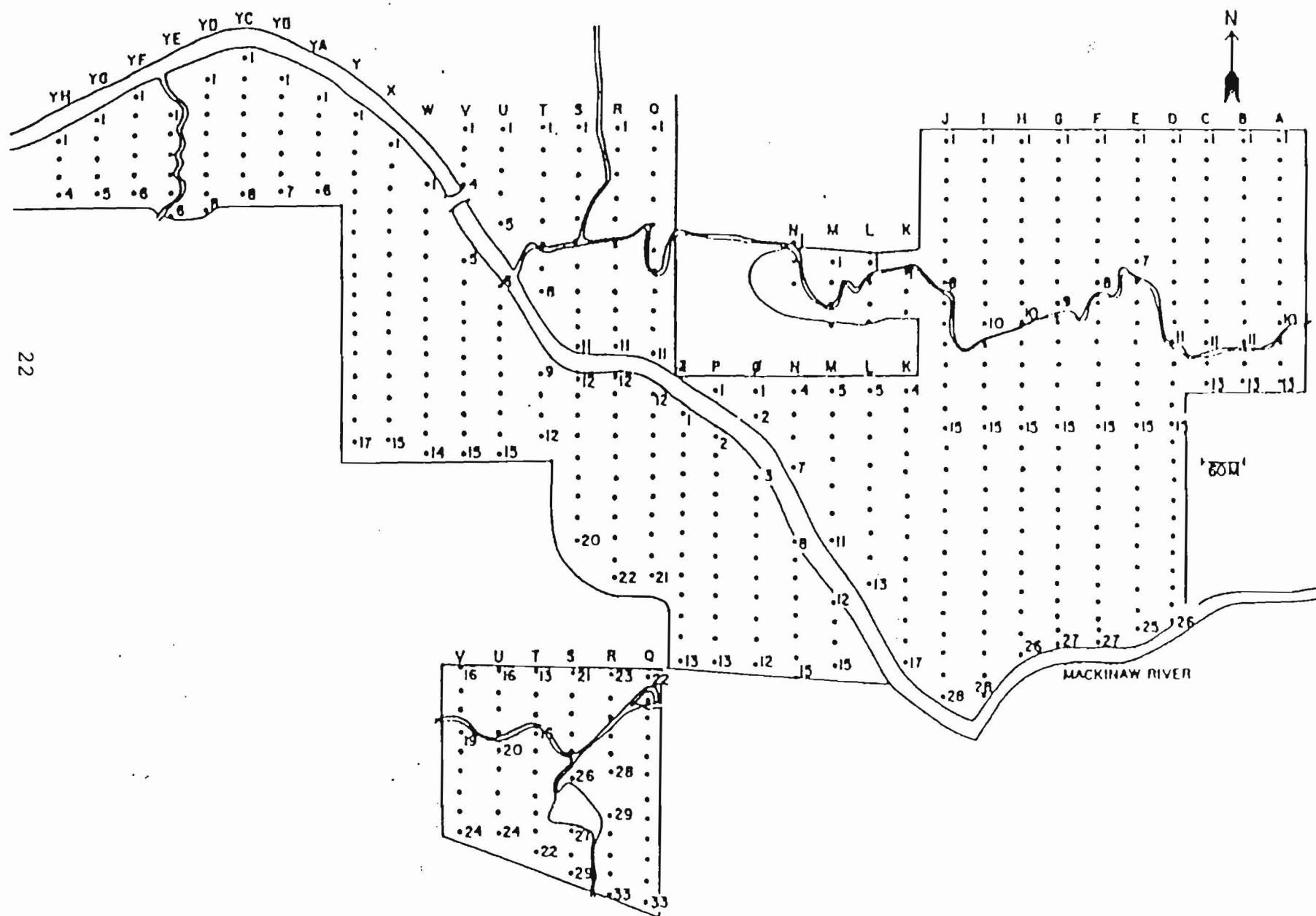
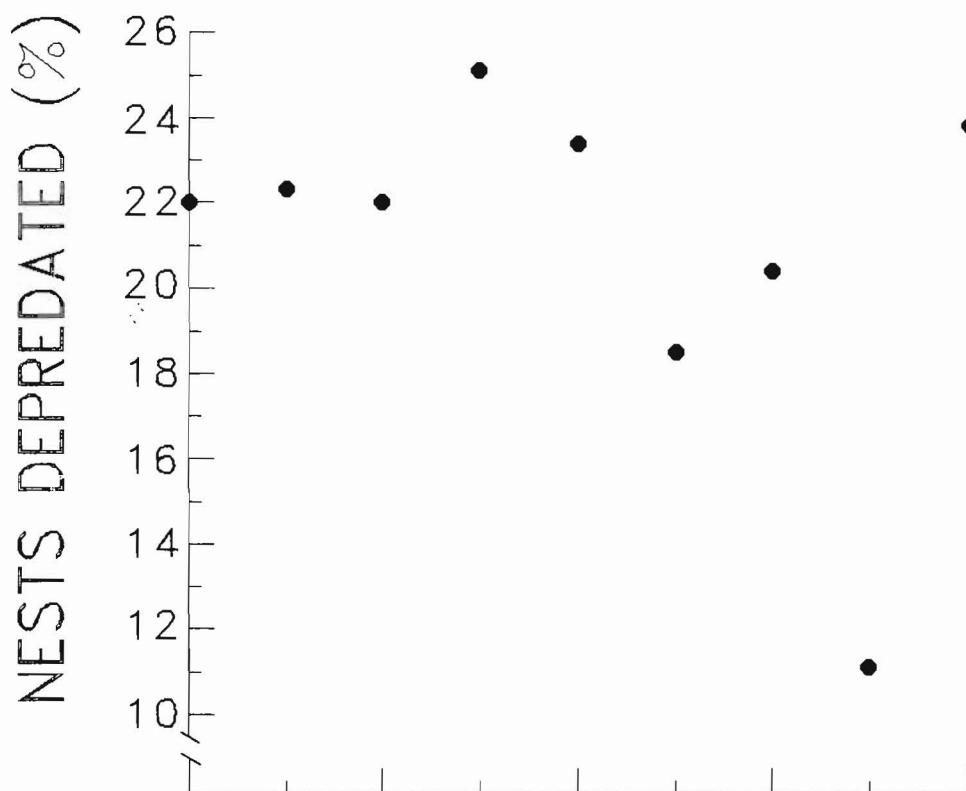


Fig 2. A. Percentage of House Wren nests likely depredated by birds and snakes in relation to distance to nearest habitat edge. B. Percentage of House Wren nests depredated by Raccoons in relation to distance to nearest habitat edge.

A



B

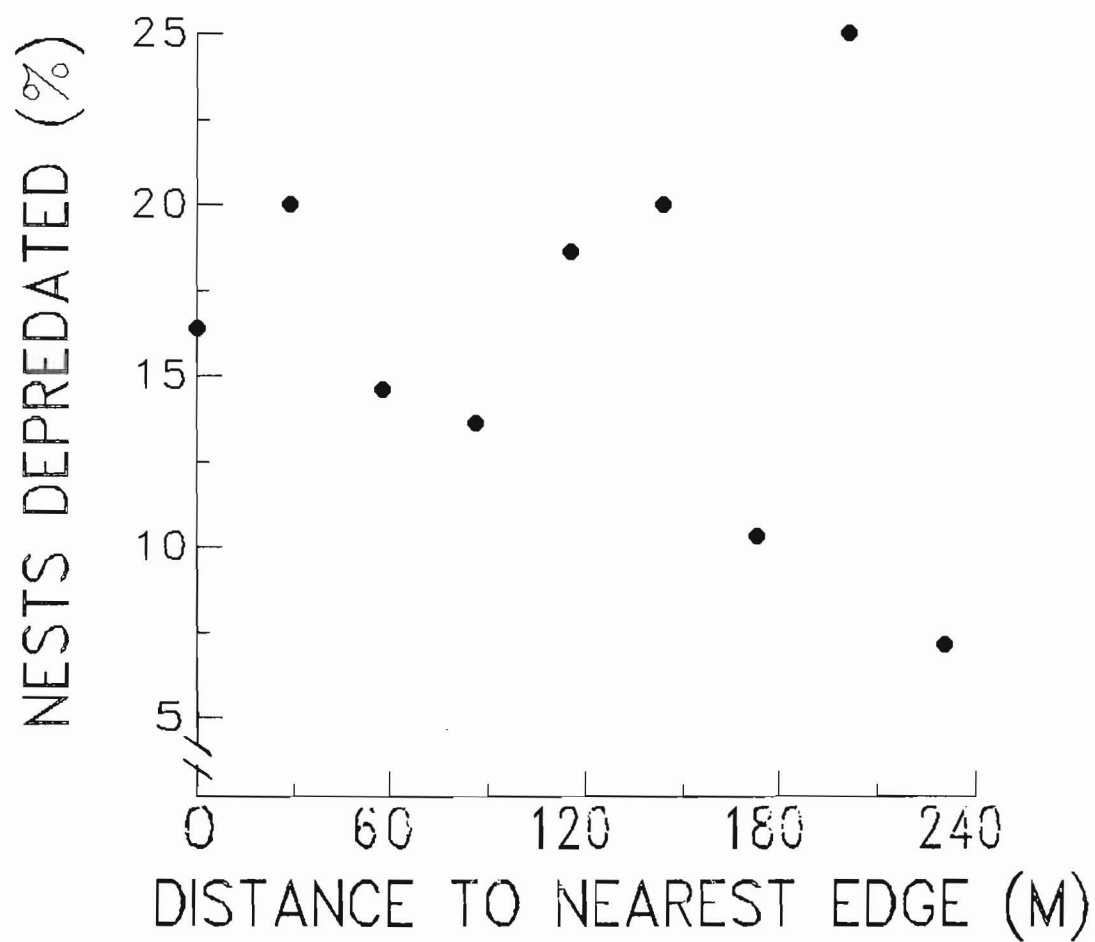


Fig. 3. Percentage of House Wren nests depredated for the two predator categories by edge-type.

Edge-type: A=Abrupt; R=Riverine; G=Gradual.

