

PREDATION OF ARTIFICIAL GROUND NESTS AT TWO TYPES OF EDGES IN A FOREST-DOMINATED LANDSCAPE¹

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Abstract. Artificial ground nests were placed in medium-age or older forests adjoining (a) stands of regenerating forest (vegetation < 2 m high) where 'hard' edges were created, and (b) stands of young forest (vegetation 2-8 m high) where 'soft' edges were created. Nests were placed at three distances from the forest edge (0 m, 50 m, and 100 m). Two Northern Bobwhite Quail (*Colinus virginianus*) eggs were placed in each nest and monitored after 7 and 14 days of exposure between late May and mid-July, 1994. Overall nest predation was 72% after 7 days and 85% after 14 days of exposure. Predation near soft edges was significantly higher than near hard edges after both 7 and 14 days of exposure. Predation near the edges was significantly higher than away from the edges after both 7 and 14 days of exposure. Two motion-sensitive cameras were used to record the identity of predator species. Cameras documented 28 predation events during 1,728 hours of operation, caused by eight species of mammals. The predators included, in order of decreasing predation: fisher (*Martes pennanti*), Eastern chipmunk (*Tamias striatus*), red-backed vole (*Clethrionomys gapperi*), red squirrel (*Tamiasciurus hudsonicus*), deer mouse (*Peromyscus maniculatus*), black bear (*Ursus americanus*), gray squirrel (*Sciurus carolinensis*), and striped skunk (*Mephitis mephitis*). The relationship between edges, predator assemblages, and nest success is complex; more studies at the landscape level are required to better understand the effects of these factors on avian population dynamics.

Key words: predation, artificial nest, edges, fragmentation, camera, Minnesota, birds, forests.

INTRODUCTION

Avian nest loss in forested environments may be attributed to numerous factors, including nest predation, nest parasitism, death of an adult, inclement weather, infertile eggs, and nest desertion. Predation is the most significant of these factors (Hahn 1937, Nolan 1963, Thompson and Nolan 1973, Gates and Gysel 1978, Loiselle and Hoppes 1983, Martin 1988a, Tomialojc and Wesolowski 1990, Hanski et al. 1996). The degree of nest loss is of interest because fecundity is the primary demographic parameter influencing population dynamics of songbirds (Temple and Cary 1988). Determining how nest predation is related to habitat characteristics within a managed landscape, especially those characteristics that may affect predator abundance and behavior,

provides information useful in determining how future management practices will affect the breeding success of forest bird species. With the current interest in declining population trends of Neotropical migrants (see Brittingham and Temple 1983, Wilcove 1985, Robinson 1987, Askins et al. 1989, Terborgh 1989, Porneluzi et al. 1993) and the importance of insectivorous birds on the health and growth of trees (Holling 1988, Marquis and Whelan 1994), it is important to understand which predator species influence avian breeding success and how this influence varies within the forest environment.

Numerous studies have shown a statistically significant correlation between nest predation and proximity to habitat edges, but the majority of this information is based on landscapes dominated by agriculture (see Paton 1994). Logging practices in northern Minnesota and other forest-dominated landscapes have created many habitat edges that are less abrupt than those in the agricultural areas typical of a large portion of the eastern United States. Most studies in forest-dominated areas have not shown a relationship between nest predation and edges

¹ Received 8 December 1995. Accepted 19 August 1996.

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(Boag et al. 1984, Yahner and Wright 1985, Small and Hunter 1988, Storch 1991, Yahner 1991, Rudnicky and Hunter 1993, Hanski et al. 1996), although some have found predation to be higher near edges (Chasko and Gates 1982). There currently is a great need to have a better understanding of the nesting success of forest birds in relation to different types of forest management practices, especially in regard to edges and patch sizes (e.g., Robinson et al. 1995).

Our null hypothesis is that predation rates of artificial nests within mature forest stands are not different within two different edge types. Alternative hypotheses are that predation rates are negatively associated with the distance from an edge and are higher at more abrupt edges. As structural similarity increases between two adjacent stands, the edge created between the stands becomes less abrupt and the area may be more like a forest interior.

METHODS

STUDY AREA

Artificial nests were located in the Walker Ranger District of the Chippewa National Forest (47°00'N, 94°30'W) in north-central Minnesota on a site approximately 14 km southeast of Walker, MN. Logging practices in the area have produced a mosaic of openings ranging from 2 to 42 ha at varying stages of regeneration within the forest matrix. Natural features such as beaver ponds and lowland swamps and bogs also contribute openings to the forest matrix. These natural openings range from 0.1–3.5 ha. For purposes of this study the forest cover was divided into three categories representing different canopy height classes: <2 m regenerating forest, 2–8 m young forest, and >8 m medium-age or older forest. The overall study area, an area described by placing a 500 m buffer around all the nest study sites, was comprised of 62% medium-age or older forest, 9% young forest, and 29% regenerating forest (Fig. 1). Upland stands of medium-age forest were selected for the placement of artificial nests. The forest was dominated by quaking aspen (*Populus tremuloides*) or a mixture of aspen and paper birch (*Betula papyrifera*). Several northern hardwood stands existed, consisting mostly of red maple (*Acer rubrum*), basswood (*Tilia americana*), and red oak (*Quercus rubra*), but also containing small areas with white spruce



FIGURE 1. Vegetation map of the study site. Numbers represent the general locations of the 10 nest groups.

(*Picea glauca*), balsam fir (*Abies balsamea*), and red pine (*Pinus resinosa*). Hazel (*Corylus* sp.) dominated the shrub layer, while alder (*Alnus* sp.), mountain maple (*Acer spicatum*), and viburnum (*Viburnum* sp.) also were common.

ARTIFICIAL NESTS

The artificial nests were woven, straw-colored avicultural nests similar to those used by Wilcove (1985). Nests were immersed in boiling water prior to use to help remove any odors. Eggs were obtained from captive Northern Bobwhite Quail (*Colinus virginianus*) and rinsed in distilled water to aid in the removal of any odors. Two eggs were placed in each nest. Rubber gloves were used to handle eggs and nests at all times, and rubber boots were worn when placing and monitoring nests in the field. A small depression was made on the ground and each nest was placed with its rim level with the surface of the ground litter. The inside of each nest was lined with leaf litter from the area surrounding each nest location. Each nest location was marked with a short (0.2 m) piece of flagging tape at a distance of approximately 3 m

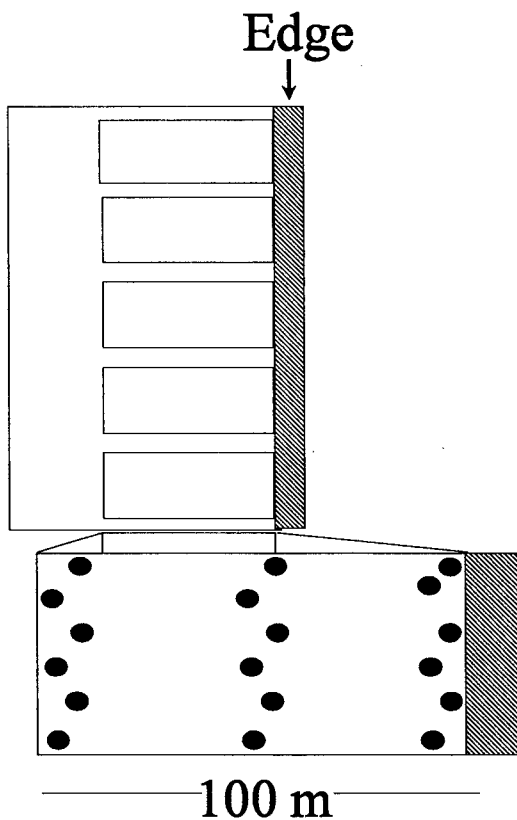


FIGURE 2. Schematic diagram of the experimental unit and nest groups. Each of five nest groups was adjacent to a hard or soft edge. Each nest group contained three nest lines with one each at 0 m, 50 m, and 100 m from either the hard or soft edge. Individual nests were offset from the nest line by 3 m and were approximately 14 m from the next nest in the nest line.

from the nest. When monitoring nests, observers avoided approaching and leaving the nest area by the same path, as recommended by Martin and Guepel (1993), to prevent the creation of dead end trails leading to each nest.

EXPERIMENTAL DESIGN

There were 10 distinct areas within the forest where groups of artificial nests were placed (nest group). Five of these nest groups (1–5) were in medium-age or older forest adjacent to stands of regenerating forest (2–4 year old aspen), and five nest groups (6–10) were in medium-age or older forest adjacent to stands of young forest (13–19 year old regenerating aspen) (Fig. 1). Medium-age or older forest bordering regenerating forest created a ‘hard’

edge, whereas medium-age or older forest bordering young forest created a ‘soft’ edge. Each of the 10 nest groups consisted of three lines of nests (nest lines) with six nests in each line. Each nest line was parallel to the treatment edge and was positioned either at the edge (0 m), or at 50 m or 100 m from the edge. No nest was less than 100 m from an edge other than the treatment edge, including edges with roads or natural openings in the forest. Few possibilities existed in this landscape to place nests at distances greater than 100 m from a treatment edge while still maintaining the required 100 m distance from other edges. Individual nests were offset from the nest lines by approximately 3 m, in alternating directions perpendicular to the direction of the nest line (Fig. 2), to avoid the creation of a straight line of nests which may lead predators more readily from one nest to another. Each nest was approximately 14 m from the adjacent nest in the nest line.

The experiment was repeated three times (trials) between late May and mid-July, 1994, coinciding with the breeding season of Neotropical migrants in the area (Janssen 1987). During each of the three trials, 180 individual nests were exposed. Before data were collected, simulated data sets were used to help choose the number of nests necessary to be able to detect a 20% difference in predation between edge types and a 15% difference in distances from the edge with a power level of 0.8 and an alpha level of 0.05. Simulated data sets were based on predation levels from a previous artificial nest predation study in the Chippewa National Forest (Manolis et al. 1994).

Predation was monitored after 7 and 14 days during all three trials. Nests were collected after they were monitored on day 14. The 2-week exposure period approximately simulated the incubation period of Ovenbirds (*Seiurus aurocapillus* Ehrlich et al. 1988), the most common ground-nesting Neotropical migrant in forested areas on the study site (G. Niemi, unpubl. data). The 7-day exposure period allowed for comparison with results from other studies (e.g., Wilcove 1985). A predation event was considered to have occurred if the nest or any number of eggs were missing, damaged, or displaced.

STATISTICAL ANALYSIS

The data were analyzed with a split-plot analysis of variance using the general linear model

procedure and repeating on the variable trial (SAS Institute, Inc. 1992). All *P*-values less than 0.05 were considered statistically significant. The proportion of the six nests preyed upon in each nest line represented the experimental unit. Proportions were logit transformed for purposes of analysis with the following equation:

$$\text{logit} = (\text{predation rate} + \text{constant}) / (1 - \text{predation rate} + \text{constant})$$

The effects considered were edge type, distance from the edge, nest group, and trial, as well as, interactions between edge type and distance from the edge, trial and edge type, trial and distance from the edge, and trial and nest group. The power of this model to detect the observed differences between edge type and distance levels was calculated using SOLO Software (BMDP Statistical Software, Inc. 1991).

PREDATOR IDENTIFICATION

Two motion-sensitive cameras were employed at artificial nests similar to, but separate from, the main group of nests to record the specific identity of predators in the area. Nests monitored by cameras were not combined with the main group of nests for analysis of predation rate. Yashika AW-mini cameras, with built-in 32 mm 1:3.5 lenses, were used. Each camera was equipped with an automatic flash, a motor to advance the film, and was wired to a passive infrared motion/heat detector (DEERFINDER, Non Typical Engineering) and mini-computer which triggered a photograph every time a heat source moved within the range of the detector. The unit was manufactured to detect a $\pm 0.1^\circ\text{F}$ difference from the background temperature (Non Typical Engineering 1991). The detector units were placed within 1.2 m of the artificial nests to ensure that even the smallest potential predators would be detected. Time and date were automatically recorded with each triggering of the camera. A programmed delay period of 15 sec after each triggering event was included.

Nests monitored by cameras were exposed for an average of 2.8 days at 26 of the 30 nest lines. Mechanical problems with the camera equipment prevented uniform camera exposure at all 30 nest line locations. Cameras were checked daily between 07:00 and 11:00 CDT,

and any missing or damaged eggs were replaced.

The definition of 'predation event' used with the main group of nests was modified for nests monitored by cameras because the flash from the camera may have frightened predators from the nest before they had adequate time to consume, damage, or displace the eggs. Any individual photographed in direct contact with an egg (regardless of subsequent damage to the egg) constituted a predation event. Additional photographs of that species only needed to show that an individual was in the proximity of the nest for a predation event to be recorded. Furthermore, to avoid biases resulting from a predator's potential ability to learn the location of a food source, only one predation event was recorded at any given camera location for a given predator species, unless it was clear from the photographs that more than one individual of the same species preyed on the same nest.

RESULTS

Total predation on all 90 nest lines exposed during the entire study period increased from 72% after 7 days to 85% after 14 days of exposure, including nests at both edge types and at all three distance levels. For a list of predation values at each nest line see Fenske (1995).

EDGE TYPE

Predation was higher near soft edges than it was near hard edges after both 7 ($P < 0.01$) and 14 ($P = 0.02$) days of exposure. Predation near hard edges after 7 days of exposure was 48%, 80%, and 54% during the early, mid, and late trials, respectively; at the same time predation near soft edges was 74%, 93%, and 88% during the early, mid, and late trials, respectively. Predation near hard edges after 14 days of exposure was 82%, 89%, and 68% during the early, mid, and late trials, respectively; at the same time predation near soft edges was 79%, 99%, and 96% during the early, mid, and late trials, respectively. An interaction was found between edge type and trial after 14 days of exposure ($P < 0.01$).

DISTANCE FROM THE EDGE

Predation was highest near the edge after both 7 ($P = 0.02$) and 14 ($P = 0.02$) days of exposure (Fig. 3). After 7 days of exposure, there were only three of 30 nest groups in which the

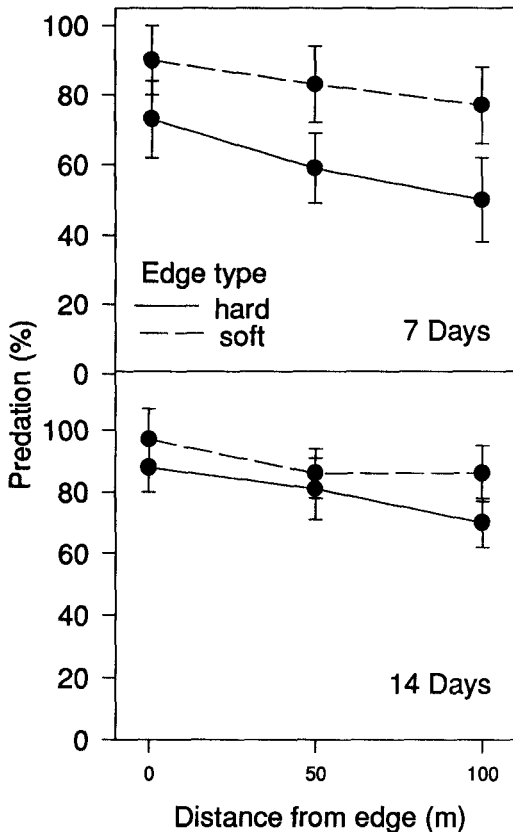


FIGURE 3. Mean predation rates (\pm SE) at increasing distances from the habitat edge at 7 (top) and 14 (bottom) days of exposure.

0 m nest line did not experience predation greater than, or equal to, predation at the 50 m and 100 m nest lines. After 14 days of exposure there were only two of 30 nest groups in this same situation.

NEST GROUP

There was a difference in predation rates among the 10 nest groups, nested within each edge type, after both 7 ($P < 0.01$) and 14 ($P < 0.01$) days of exposure. The greatest variation was recorded during the early trial. During this trial, after 7 days of exposure, predation ranged from 5% to 94% among the five nest groups near hard edges. At the same time, it ranged from 33% to 100% among the five nest groups near soft edges. An interaction was found between nest group and trial after both 7 ($P < 0.01$) and 14 ($P < 0.01$) days of exposure. This interaction indicates that the significance of these two

main effects should be interpreted with caution. When considering predation effects caused by mobile predators it is not surprising that space (nest group) and time (trial) are related.

TRIAL

There was a difference in predation rates between the three trials after both 7 ($P < 0.01$) and 14 ($P < 0.01$) days of exposure. After 7 days of exposure overall predation was 61%, 87%, and 71% during the early, mid, and late trials, respectively. After 14 days of exposure predation was 81%, 94%, and 82%, during the early, mid, and late trials, respectively.

PREDATOR IDENTIFICATION

A total of 28 predation events was recorded by the motion-sensitive cameras during 1,728 hr of operation. This is equivalent to one predation event every 62 hr. A positive identification of the predator species was possible for 27 of the 28 predation events. Eight species of mammals were responsible for the 27 predation events: fisher (*Martes pennanti*; eight predation events), Eastern chipmunk (*Tamias striatus*; five), red-backed vole (*Clethrionomys gapperi*; four), red squirrel (*Tamiasciurus hudsonicus*; three), deer mouse (*Peromyscus maniculatus*; three), black bear (*Ursus americanus*; two), gray squirrel (*Sciurus carolinensis*; one), and striped skunk (*Mephitis mephitis*; one). In one case two individuals of the same species (deer mouse) could be differentiated from photographs taken at the same camera location, so two predation events were recorded. In all other cases multiple photographs of a species at each camera location were considered to be the same individual and only one predation event was recorded per species. This may underestimate the total number of predation events that occurred at camera-monitored nests.

Of the eight predator species, only two (red-backed vole, deer mouse) never removed or damaged eggs, although they were photographed in direct contact with the eggs. These same two species, in addition to gray squirrel, were the only species which never stayed at a nest longer than 15 sec, the required time to trigger a second photograph.

Of the 28 photographed predation events, there were data on the date and time of predation for 23 events. Data for the remaining five

events were lost due to the mechanical problems (discussed above) that prevented deploying cameras at all locations. Nine predation events occurred during night hours (21:00–05:00) and 14 during daylight hours (05:00–21:00). This is equivalent to one predation event every 64 hr during the night, and one predation event every 82 hr during the day. These same data can be used to determine predation rates after nests are visited by observers. Five predation events occurred within 5 hr after an observer visited a nest, four occurred 5–10 hr after a visit, four occurred 10–15 hr after a visit, five occurred 15–20 hr after a visit, and the remaining five occurred more than 20 hr after a visit.

DISCUSSION

Most nest predation studies conducted in a forest matrix have not recorded the specific identity of nest predator species; Storch (1991) provides a rare exception. Many include lists of potential predators observed within the study areas as the only indication of what the predator assemblage might be (Chasko and Gates 1982, Boag et al. 1984, Yahner and Wright 1985, Small and Hunter 1988, Yahner 1991, Rudnicki and Hunter 1993), but these data may be misleading. Within our study area we observed seven species of birds and mammals in addition to those photographed that have been recorded as nest predators in other studies: flying squirrel (*Glaucomys* sp), raccoon (*Procyon lotor*), Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), Black-billed Cuckoo (*Coccyzus erythrophthalmus*), Broad-winged Hawk (*Buteo platypterus*) and Cooper's Hawk (*Accipiter cooperii*) (Dwernychuck and Boag 1972, Thompson and Nolan 1973, Picozzi 1975, Marzluff 1985, Reitsma et al. 1990, Leimgruber et al. 1994, Picman and Schriml 1994, Sealy 1994).

The most common predator photographed at the nests (fisher) was never observed on the site. One of the most common potential predators observed on the site, the Blue Jay, was never photographed at a nest. Because the entire assemblage of potential predators may not affect a certain group of nests equally (e.g., ground nests or nests in mature forest), it is important to have detailed information on which predator species are preying on the specific type of nests being studied. Although it is possible that cameras did not record all species depredate nests

within the study area, they most likely did record the common predator species and provided a more accurate estimate of the predator assemblage than that based exclusively on sightings of animals within a study area.

Even if the predator assemblages of the different studies conducted in forested landscapes (see Introduction) are similar, there are differences in the design of these studies which may provide advantages to different species within the respective predator assemblages and cause the conflicting patterns of nest predation discussed above. These differences may alter the percentage of predation caused by different component species of an assemblage, subsequently altering predation patterns if hunting strategies vary among the species of the predator assemblages (Martin 1987, Moller 1989, Yahner 1991). One difference that may affect predation patterns is the height of the nests studied. All of the artificial nest studies conducted within a forest matrix have used ground nests (Yahner and Wright 1985, Small and Hunter 1988, Storch 1991), but studies that used real nests had varying combinations of ground, shrub, and canopy nests (Chasko and Gates 1982, Boag et al. 1984, Yahner 1991, Rudnicki and Hunter 1993, Hanski et al. 1996). The vertical layer of the forest in which a nest is located can affect the predation rate (Loiselle and Hoppes 1983, Yahner and Cypher 1987, Martin 1988b, Yahner and Scott 1988, Yahner 1991, Rudnicki and Hunter 1993). For example, Hanski et al. (1996) found no edge effects in a study of real nests on a site directly adjacent to ours in which more than 90% of the real nests were above the ground.

The type of egg used to bait an artificial nest is another difference between studies that may alter the percentage of predation events caused by different species within the predator assemblage. Artificial nest studies conducted within a forest matrix have used several types of eggs to bait nests (e.g., domestic hen, Yahner and Wright 1985, and Japanese Quail *Coturnix coturnix*, Small and Hunter 1988). Several species of mice (*Peromyscus* sp.) have been recorded as predators on both real nests (Maxson and Oring 1978, Guillory 1987) and artificial nests baited with quail eggs (Reitsma et al. 1990, Leimgruber et al. 1994, Picman and Schriml 1994). However, these small animals may not depredate the larger chicken (or even

quail) eggs as effectively as the smaller eggs of warblers (Parulidae) and thrushes (Muscicapidae), which are the most common ground-nesting birds in the area (G. Niemi, unpubl. data). Of the seven photographed predation events caused by deer mice and red-backed voles in this study, none resulted in damage to the eggs. Small mammals also may be influenced by the camera flash (see below). An inability, or limited ability, of small predators to damage the bait may underestimate the role of these predators within an assemblage and alter the nest predation patterns observed. This bias was minimized in our study by recording displaced (but undamaged) eggs as predation events. Among the main group of nests, 5% of the predation events recorded the displacement of at least one egg, while recording no damage to either egg. Although it is not certain that all displaced eggs were the result of attempted predation events by small mammals, it is probable that a natural nest disturbed in this manner would fail and it is therefore reasonable to record this activity at an artificial nest as a predation event.

DISTANCE FROM EDGE

In agricultural areas high nest predation near edges has been attributed to the relative abundance of generalist predators which penetrate the perimeter of forest patches from the surrounding field matrix (Angelstam 1986). In forested landscapes, open areas are not as extensive as they are in agricultural landscapes (Fig. 1). There is no evidence that predators penetrate the forest from young or regenerating forest the same way they penetrate forest patches from a field matrix (Angelstam 1986). This does not preclude the existence of edge effects in forested areas. Forest-dwelling predators may show increased activity near edges; this is the case with two of our predator species, Eastern chipmunk (Bider 1968, Chasko and Gates 1982) and red squirrel (Bider 1968). Some animals may be more active near edges because of the increased cover available there (Chasko and Gates 1982), while others may be using edges as travel routes (Bider 1968, Bowman and Harris 1980). Increased activity near edges should increase the probability of a predator discovering a nest.

There is evidence that human observers may play a role in attracting predators to nests

(Dwernychuck and Boag 1972, Bart 1977, Major 1990, Whelan et al. 1995). If so, this may create, or enhance, an edge effect if visual and/or olfactory cues left by humans are greater in the heavier shrub and ground cover found near edges (Dwernychuck and Boag 1972). However, there also is evidence that human observers do not influence predation rates (Nolan 1963, Gottfried and Thompson 1978, Reitsma et al. 1990). Identification of the predator assemblage may provide some insight into the extent of observer effects; birds are more likely than mammals to respond positively to human cues (Dwernychuck and Boag 1972, Major 1990). A predator assemblage dominated by mammals, such as the one recorded on our site, may be less influenced by human cues than one dominated by birds. Additionally, daily nest mortality is highest within the first day after an observer visits a nest (Bart 1977), indicating that visual and/or olfactory cues dissipate quickly. Based on the limited sample of photographed predation events which included data on the time of predation, predation events were evenly distributed after human visits.

EDGE TYPE

There is evidence from agricultural areas that edge effects caused by predators from outside of the forest increase as the difference in productivity between two adjacent habitats increases (Angelstam 1986). However, this same pattern may not be expected at different stages of a successional gradient (Storch 1991). Predation on our site was higher near soft edges than near hard edges, which does not agree with the conclusions of Angelstam (1986), based on edges in agricultural areas. Higher predation near soft edges may reflect a tendency of forest predators to avoid the open canopy of the regenerating forest stands. An additional consideration is that regenerating aspen stands in the study area were mostly larger than young aspen stands (Fig. 1). It may be possible that forest predators avoided these large, relatively open areas of regenerating forest.

Although this may explain why predation was higher near soft edges, it is not consistent with the distance effect observed. If forest predators are avoiding openings in the forest canopy, or using them less frequently, a positive relationship between predation and distance from an edge would be expected, especially near hard

edges where the difference in canopy height is greater. This was not observed. We cannot assume that all component species of a predator assemblage exhibit similar responses to edges, therefore, contrasting predation patterns may be observed. For example, with two predator species in an assemblage, one species may prefer a closed canopy and avoid hard edges but have no preference regarding proximity to edges. The other species may use habitat edges as travel routes and spend less active time in the forest interior, but have no preference for the abruptness of an edge. In this case both edge type and distance may be significant. As the diversity of the predator assemblage increases, these combinations become more complicated.

Storch (1991) monitored nest predation within forest stands at varying stages of successional development. He found predation rates to be highest in medium-aged forest, and lower in both young and mature forest. If certain predator species are more active or abundant within intermediate age classes such as the young forest here, this would lead to the type of edge effect we observed.

Some caution must be used with the interpretation of edge type effects. There was a significant interaction between edge type and trial after 14 days of exposure, although no interaction was observed after only 7 days of exposure. This may be related to the interaction of trial effects with nest group effects, discussed below.

TEMPORAL AND SPATIAL VARIATION IN PREDATOR DISTRIBUTION

Trial and nest group effects were both significant, but there also was a significant interaction between the two effects after both 7 and 14 days of exposure. Overall predation was lowest early in the season and highest at mid-season, but this pattern varied considerably when the overall predation was divided into the ten nest group components. Only four of the 10 nest groups exhibited the same seasonal pattern after 7 days of exposure, and only two of the 10 after 14 days of exposure. Within one nest group, after 7 days of exposure, predation rates varied by as much as 89% from one trial to another. Within each trial there also was variation in the predation rate between nest groups.

This spatial and temporal variation may be the result of predation by animals with relatively large home ranges. A male fisher has a

home range of up to 50 km² (Racey and Hesse 1989, Powell 1993) and a black bear has a range of up to 112 km² (Amstrup and Beecham 1976), while our study area occupied 3.7 km². The entire study area could fall within the range of a single male fisher and still occupy as little as 8% of its range, or it may fall within the range of a black bear and occupy as little as 4% of its range. These two predators were responsible for 36% of all photographed predation events. If these animals do not move throughout their ranges in a uniform manner, predation rates will show spatial variation. Similarly, if a predator concentrates its foraging within the study area during one trial but not during another, predation rates may show considerable temporal variation.

This same phenomenon also may explain the interaction between edge type and trial effects discussed above. If an animal has a large range it may spend a different amount of time in the study area during each trial. Whatever effects this animal has on predation patterns within the study area should vary according to the amount of time it spends there. A predator with a large range, whose foraging behavior leads to higher predation near one type of edge, may cause temporal variation in predation patterns related to edge type. We cannot explain why this would be evident after 14 days of exposure, but not after 7 days of exposure.

Microregional differences in the distribution of predators with relatively small ranges also may be responsible for spatial fluctuations. Reitsma et al. (1990) found a patchy distribution of predators including Eastern chipmunk and red squirrel by trapping, whereas Leimgruber et al. (1994) found a patchy distribution of predators based on nest predation patterns.

PREDATOR IDENTIFICATION

Predation events at camera-monitored nests were widely distributed across the study site; predation events were recorded at 19 of the 26 nest lines monitored by cameras, encompassing all nine of the nest groups which were monitored. Fishers were the most frequently photographed predator on our study site, but they accounted for less than 30% of all photographed predation events. The combined effects of five predator species were required to account for 75% of all recorded predation events. Other studies which have used cameras (Leimgruber

et al. 1994, Picman and Schriml 1994) or grease boards (Angelstam 1986) to record the specific identity of predator species have found that only one or two species account for at least 70% of observed predation events. This diversity within the predator assemblage, and the associated diversity of foraging behavior, may complicate interpretation of the mechanisms influencing predation patterns.

Together fisher and red-backed vole account for 43% of the photographed predation events. To our knowledge red-backed voles have not previously been recorded as nest predators. Although birds have been recorded in the diet of fisher (Racey and Hessey 1989), we found no mention of eggs in their diet since Seton (1929). The fisher spends most of its time on the ground (de Vos 1951, Quick 1953, Racey and Hessey 1989, Powell 1993) and often travels in a zigzag pattern when hunting (Powell 1993). This type of foraging behavior would seem to bring fisher into contact with many ground nests during the breeding season. If the hunting strategies of fisher or red-backed vole differ from those of more commonly recorded nest predator species, predation patterns observed on our site could be expected to differ from those observed on other sites. These potential differences encourage edge effects to be considered on a site-by-site basis as recommended by Murcia (1995).

The motion-sensitive cameras used to record the identity of predator species may bias the relative abundance of the predator species depredated nests, although Leimgruber et al. (1994) found cameras had no effect on predation rates. Because logistical constraints required camera-monitored nests to be set up and checked during morning hours, diurnal predator species had access to all nests while nocturnal predator species only had access to those nests not depredated by diurnal predators earlier each day. Ideally, camera-monitored nests would be checked at random times throughout the day and night. Nocturnal predation may therefore be under represented in the limited sample of nests monitored by cameras.

A negative response to the cameras' flash may have reduced the amount of time some animals spent at nests. In each of the seven photographed predation events caused by red-backed voles and deer mice, the animals did not remain at a nest for more than 15 sec after the initial flash was triggered and they never damaged any

eggs. Most other species except for gray squirrels stayed at nests for more than 15 sec and experienced multiple flashes. This short interval at the nest may not have given these animals whatever handling time they required to penetrate the egg shells, if they were even capable of doing so.

CONCLUSIONS

Based on these data, the effects of edges on nest success in forest-dominated areas of northern Minnesota appear to differ from agricultural areas. Predation on our site decreased as the productivity gradient between adjacent habitats increased, contradictory to the patterns recorded in agricultural areas (Angelstam 1986). This indicates that different mechanisms may be associated with edge effects in forested areas. Differences in predator assemblages and the corresponding hunting behavior associated with these species will influence predation patterns. If different predators within an assemblage respond differently to edges, contradictory predation patterns may be observed. The large range of some predator species may cause temporal and/or spatial variation in predation rates measured on a relatively small spatial scale. Detailed information about the response of predator species to edges is necessary to help interpret nest predation patterns.

With the increasing human population and the subsequent demand for greater timber harvest, it is important to continue investigating changes in edge effects over successional gradients. Although clearcuts regenerate quickly, edge effects may persist for a decade or more. The size and shape of openings created in the forest, as well as the rotation period between harvest events, may influence nest success. We are only beginning to understand the various factors associated with nest success in forest-dominated landscapes, but the role of edges in these landscapes cannot be ignored.

ACKNOWLEDGMENTS

Funding for the project was appropriated by the Minnesota State Legislature from the Environmental Trust Fund as recommended by the Legislative Commission on Minnesota Resources. Additional funding and support was provided by the U. S. Department of Agriculture - Forest Service through cooperative agreement USDA/23-91-16. Comments on earlier versions of this manuscript and insights in the study were greatly appreciated from Don Christian, Ilpo

Hanski, JoAnn Hanowski, Ann Lima, and Ron Regal. This paper represents contribution number 184 of the Center for Water and the Environment, University of Minnesota, Duluth.

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