Effects of Forest Fragment Size, Nest Density, and Proximity to Edge on the Risk of Predation to Ground-Nesting Passerine Birds

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Abstract: *Many species of Neotropical migrant songbirds are experiencing population declines. Degradation of habitat on breeding grounds, particularly the fragmentation and isolation of forest habitats, has been suggested as an important factor in the decline of these populations. Using artificial ground nests containing quail and clay eggs, we compared risk of predation relative to the size of forest fragments, the proximity of nests to forest edge, and the density of nests. Because small predators rarely can damage or remove quail eggs, the loss of these eggs reveals activity by large predators. Small predators, however, often leave identifiable claw and tooth marks on artificial eggs, and we used such marks to assess the importance of small predators as nest predators. We found a negative correlation between predation rate and fragment size. Nest clustering increased predation by large predators but did not affect small predator activity. No significant edge effects on predation were apparent. The relative threat to nesting songbirds posed by small and large predators changed with forest fragmentation. Large predator activity increased as forests become more fragmented. Historically, interior forest-dwelling birds have been subjected primarily to small predator activity. The increased large predator activity we documented, against which songbirds have no defense, could be partially responsible for recent population declines.*

Efectos del Tamaño de Fragmento de Bosque, Densidad de Nidos y Proximidad al Borde en el Riego de Depredación de Aves Paserinas que Anidan en el Suelo.

Resumen: *Muchas de las especies de aves canoras neotropicales migratorias están experimentando disminuciones poblacionales. La degradación del hábitat en las áreas de reproducción, particularmente la fragmentación y el aislamiento de los hábitats boscosos han sido sugeridos como factores importantes en la disminución de estas poblaciones. Mediante el uso de nidos artificiales con huevos de codornices y barro, comparamos el riesgo de depredación relativa al tamaño del fragmento de bosque, la proximidad de los nidos al borde del mismo y la densidad de nidos. Debido a que los depredadores pequeños raramente pueden dañar o remover huevos de codorniz, la pérdida de éstos revela la actividad de depredadores grandes. Sin embargo, los depredadores pequeños dejan frecuentemente marcas de garras y dientes en huevos artificiales porloque utilizamos éstas para evaluar la importancia de estos como depredadores de nidos. Encontramos una correlación negativa entre la tasa de depredación y el tamaño del fragmento de bosque. El hacinamiento de nidos incrementó la depredación por depredadores grandes pero no afectó la actividad de los depredadores pequeños. De manera aparente, no se encontraron efectos de borde significativos con respeto a la depredación. La amenaza relativa a las aves canoras por depredadores pequeños y grandes cambia con la fragmentación del bosque. La actividad de los depredadores aumenta a medida que el bosque se encuentra*

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más fragmentado. Históricamente, las aves que habitan en el interior del bosque han estado primordialmente sujetas a la actividad de depredadores pequeños. El incremento en la actividad de depredadores grandes en contra de aves canoras indefensas, podría ser parcialmente responsable de disminuciones poblacionales recientes.

Introduction

Many species of Neotropical migrant land birds are experiencing population declines (Robbins et al. 1989; Terborgh 1989, 1992; Hagan & Johnston 1992). Degradation of habitat on the breeding grounds, particularly the fragmentation and isolation of forest habitats, has been suggested as an important factor in the decline of these populations (Robbins et al. 1989; Hagan & Johnston 1992). Large tracts of contiguous forest are broken into smaller fragments through urbanization, logging, and road building. The amount of forest edge increases, core forest area decreases, and vegetation composition and structure change. Habitat loss of this kind has been implicated in most studies addressing avian population declines (Hagan & Johnston 1992; Robinson et al. 1995). There is some question about whether bird populations are most threatened by habitat alteration on breeding grounds or wintering grounds (Rappole & McDonald 1994), but forest fragmentation on breeding grounds appears to have a multitude of negative effects (Hagan & Johnston 1992; Böhning-Gaese et al. 1993).

Loss of forest area and concomitant vegetation alteration may reduce the availability of suitable nesting sites and cause crowding of nests in remaining habitat fragments (Hagan & Johnston 1992; Holmes et al. 1996). Increased nest density has been shown to reduce nesting success (Van Horn et al. 1995; Hagan et al. 1996). Fragmentation also creates avenues by which brood parasites can access the nests of potential hosts. Brown-headed Cowbird (*Molothrus ater*) parasitism severely affects the reproductive success of many passerines (Wilcove 1985; Terborgh 1989; Robinson et al. 1995).

It has been suggested that many of the changes associated with forest fragmentation alter the rate of nest predation, a major cause of reproductive failure in birds (Ricklefs 1969). Several studies have found that decreased forest fragment size results in increased nest predation (Wilcove 1985; Møller 1988; Small & Hunter 1988; Yahner & Scott 1988; Hoover et al. 1995; also see review by Paton 1994). This negative association between forest fragment size and rate of nest predation has been attributed to increased nest density, edge-related effects, or a combination thereof.

Gates and Gysel (1978) proposed that increased nest density in small habitat patches, perhaps due to an influx of birds displaced by deforestation, results in increased predation. Hogstad (1995) found that clustered nests were advantageous to Fieldfares (*Turdus pilaris*) when avian predator density was high but disadvantageous when mammalian predators were the primary threat. The defenses of colonially nesting Fieldfares were effective against corvids but not against mustelids. Major et al. (1994) concluded that clustered nests experienced higher predation (see also Picman 1988). Recently, Martin (1996) demonstrated that when the microhabitat nesting requirements of several species overlap, those species face increased nest predation.

Bider (1968) found high utilization of ecotone habitat by many different species. He suggested that forest edges acted as "biological barriers" along which animals forage. Preferential use of edge habitat by nest predators may lead to increased nest loss in these "ecological traps" (Gates & Gysel 1978). In a recent review, Paton (1994) reported that 10 of 14 studies found a significant edge effect on predation rates. This has important conservation implications because the size of habitat buffer zones is a key element of management plans. Vander Haegen and DeGraaf (1996) suggested that a riparian buffer zone of at least 150 m is necessary to mitigate increased predation along edges.

When addressing the effects of forest fragmentation on nest predation, some researchers have examined directly the rates of predation on active songbird nests (Hoover et al. 1995; Van Horn et al. 1995; Holmes et al. 1996). Most studies, however, have focused on indices of predation risk using artificial nests containing quail or chicken eggs. Recently there has been debate over the appropriateness of using relatively large galliform eggs to assess the risk of predation to passerine bird nests (Roper 1992; Haskell 1995*a*, 1995*b*).

Small-mouthed predators such as mice (e.g., *Peromyscus* sp.) and chipmunks (e.g., *Tamias* sp.), which are effective nest predators on small passerine birds such as parulid warblers, are unable to break the substantially larger quail eggs (Roper 1992; Haskell 1995*a*, 1995*b*). In some cases, small rodents may be more important predators of passerine bird nests than are larger carnivores (Maxson & Oring 1978; Reitsma et al. 1990; Leimgruber et al. 1994; DeGraaf & Maier 1996). Thus, experiments that use quail eggs test only risk of predation due to predators larger than chipmunks and may provide an unrealistic measure of the true risk of predation for ground-nesting passerines. Results from these studies may lead to spurious negative correlations between forest fragment size and nest predation rates. Haskell (1995*b*) found that nest predation by small-mouthed predators increased with fragment size, whereas predation by large predators decreased. When predation by both small and large predators was considered, there was no correlation between fragment size and predation rate.

As an alternative to artificial nest experiments that use quail eggs, some researchers have used artificial nests with eggs constructed from clay (Møller 1988, 1989; Haskell 1995*b*). Clay eggs have advantages over quail eggs in artificial nest experiments in that they closely match the size of passerine eggs and they retain tooth, bill, and claw marks from which predators can be identified. Some problems associated with clay eggs are that they do not provide the same visual, tactile, or olfactory cues as real eggs, and some potential predators such as snakes may not respond to clay eggs. Thus, the design of artificial nest experiments may seriously undermine the validity of the results.

Another potential bias in studies of forest fragmentation and nest predation is that such studies have been conducted almost exclusively in the midwestern and northeastern portions of North America. Findings from these studies have then been extrapolated to other areas of the continent. The southeastern United States contains a large proportion of the forested acreage of eastern North America (Alig et al. 1990), but no studies of the effect of fragmentation on passerine nest predation have been conducted in the southeastern United States.

We examined the relationship between forest fragment size and relative rates of nest predation in a southern Appalachian forest in Alabama. In our study, we attempted to circumvent the egg-size problems discussed above by using both quail and clay eggs. Our goal was to study nest predation risk relative to forest fragment size, with the realization that this sort of artificial nest experiment yields only an index of relative nest predation risk. We addressed three questions: (1) Does the rate of nest predation increase as forest fragment size decreases? (2) Does increased nest density lead to higher predation rates? (3) Do nests close to forest edges experience higher predation than nests in the forest core?

Methods

Forest Fragments

We conducted our study at Fort McClellan in northeastern Alabama. Fort McClellan lies in the southern Appalachian region and supports stands of native hardwood and mixed pine-hardwood forests (Shankman & Wills 1995). In a recent study at Fort McClellan by Soehren (1995), point counts of Neotropical migrant songbirds were conducted during the breeding season in 12 forest fragments ranging in size from 4 to 849.4 ha. We used the same 12 forest fragments identified by Soehren (1995) plus four additional fragments.

The edge structure of forest fragments differed slightly. Edges of the larger fragments were defined by two-lane roads clearly visible on aerial photographs taken during the summer, when the forest canopy is at its most dense. Traffic along these roads was minimal and often limited to troop movement. Large fragments contained remnant dirt roads from World War II training activities. Trees and understory plants had begun to colonize the roadbeds. These were not visible on aerial photos and were not counted as edges. The smaller fragments were bounded by power line servitudes, roads, fields, parking lots, and residential neighborhoods. Even though edge structure differed between fragment sizes, however, the internal vegetative structure was nearly homogeneous among fragments (Soehren 1995).

Within each fragment, points of known location (determined by a global positioning system) established by Soehren (1995) were used to position transects of 30 artificial nests along which nests were placed 20 m apart. Our transects were located in areas where Soehren conducted breeding bird point counts. Transects were oriented toward the center of the fragment, and locations were not used repeatedly.

Artificial Nests

We made a small ground scrape (~10 cm in diameter) in the leaf litter to serve as a nest. Each artificial nest contained two fresh Northern Bobwhite (*Colinus virginianus*) eggs and two gray plasticine (Roma Italian Plastilina) eggs (average width 11.8 mm). Nests were constructed and all eggs were handled with gloved hands to minimize human scent (Whelan et al. 1994). All nests were far enough from surrounding shrubbery to be clearly visible.

The majority of nests were checked 7 days after placement. Several transects in large fragments were checked after 8 days because troop activities prohibited our access on the seventh day. If this extra day of exposure in large fragments had any effect, it made our test of decreased nest predation in larger fragments more conservative. Missing or damaged eggs were noted, along with any signs left by predators.

We were concerned only with categorizing predators as small-mouthed or larger, and we used clues in the depredated nests to implicate small-mouthed predators, larger predators, or both (Fig. 1). To verify that some small claw and tooth marks were likely made by small-mouthed predators, we gave clay eggs to captive mice (*Peromyscus* sp.). Claw and tooth marks left by small rodent predators were compared to these samples. Bill marks were compared to the bill dimensions of Blue Jay (*Cyanocitta cristata*) and American Crow (*Corvus*

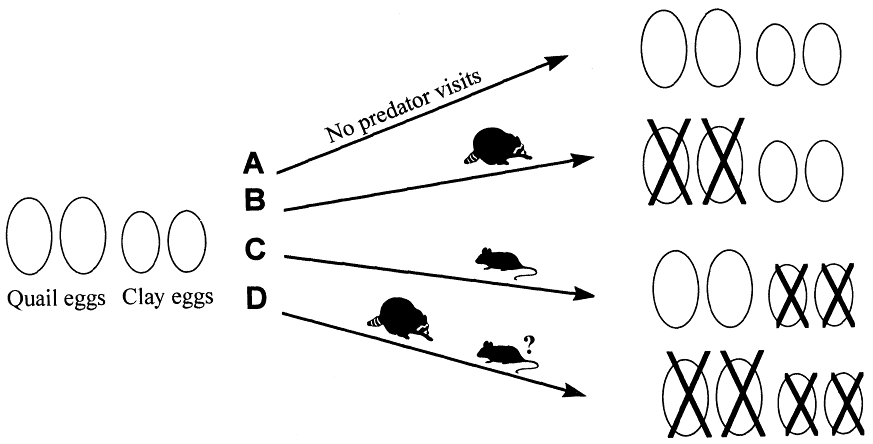

Figure 1. Possible fate of eggs in artificial nests. An X indicates eggs that were missing or damaged. In the last scenario, in which both types of eggs are missing or damaged, there are three possible options: (1) large predator damaged all eggs; (2) small predator visited first and then large predator visited, obscuring small predator signs; (3) large predator visited first and then small predator visited, leaving distinct signs.

brachyrhynchos) specimens. Larger canine and incisor marks were compared to skulls of gray fox (*Urocyon cinereorgenteus*), raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis virginiana*). White-tailed deer (*Odocoileus virginianus*) left extremely large, apparent molar impressions.

We did not attempt to identify predator species from marks left in clay eggs. Instead we coded the damage as left by small-mouthed predators (defined as gapes as small or smaller than a chipmunk) or large predators (defined as anything larger than a chipmunk, including Blue Jay, American Crow, gray fox, raccoon, Virginia opossum, and white-tailed deer. No index of snake visitation could be estimated.

We calculated the proportion of nests depredated for each transect. If either quail or clay eggs were damaged or missing, we considered the nest depredated. Of the damaged nests, some had both quail and clay eggs damaged, some had only quail eggs damaged, and some had only clay eggs damaged. Of the damage to clay eggs, some was attributable to small-mouthed predators (Fig. 1). Overall nest fate was the independent measure. Considered separately, quail and clay egg fates were subsets of overall nest fate, and obvious damage by small-mouthed predators was nested within the clay egg subset. These subsets were not independent.

The total proportion of depredated nests per transect yields an index to predation rates within that fragment. Only large predators are capable of damaging quail eggs (Haskell 1995*a*). This means that analyzing quail egg loss per transect yields an index to the activity of these predators. Likewise, analyzing damage attributable to small-mouthed predators (as determined by tooth and claw marks) yields an index to their activity rates within fragments. Both of these indices are subsets nested within the total predation index. As a result, they should not be considered independent measures of the activities of large and small predators. Instead they can be interpreted as measures of relative change in predator activity levels in different-sized forest fragments. The fates of quail and clay eggs are intentionally correlated via experimental design. All mammalian predators, large or small, probably search for prey items using olfactory cues. The scent of the real eggs is necessary to attract small predators to artificial nests, but clay eggs are necessary to record their visits. The egg-fate subsets jointly contribute information regarding the total risk of predation to passerine bird nests, but they do not allow us to make reliable inferences about the true composition of the predator community.

Effect of Forest Fragment Size on Nest Predation Rates

To test the prediction that the rate of nest predation increases with decreasing forest fragment size, we placed 22 linear transects, each consisting of 30 nests placed 20 m apart in 10 fragments (Table 1). Five of these transects were deliberately placed near the edge of large fragments so that edge effects could be examined. The other transects within large fragments were all located in the interior. Each transect was a single unit of analysis (Table 1). We used Spearman rank correlations to compare forest fragment size in hectares and the proportion of nests depredated in each transect.

Four fragments contained several transects. We consider these transects independent because they were separated by at least 500 m and a ridge. It is unlikely that individual predators ranged widely enough to have affected two transects. Many small fragments were closer to one another than were transects within the large fragments. Ideally we would have placed one transect per fragment, but there were too few large fragments of forest remaining in the study region. We also report the results of Spearman rank correlations in which the fragment is the unit of analysis and the predation rate was calculated as the number of nests depredated divided by the total number of nests within the fragment.

Table 1. Distribution of transect types in 16 forest fragments containing artificial nests.[a]

	Transect type		
Fragment (ha)	*Linear*	*Grid*	*Edge*
849.4	3 (90)		1 (30)
586.2	3 (90)	2 (60)	1 (30)
457.5	2 (60)	2 (60)	3 (90)
90.0	3 (90)		
48.3		1 (30)	
44.0		1 (30)	
40.0	1 (29)[b]		
36.0	1 (30)		
23.0	1 (30)		
23.0	1 (30)		
18.0		1 (30)	
11.5	1 (30)		
11.0		1 (30)	
9.9		1 (30)	
9.0	1 (30)		
4.0		1 (29)[b]	
Totals	17 (509)	10 (299)	5 (150)

[a] *Number of nests in parentheses.*

[b] *When checking the transects, we were able to locate only 29 out of 30 nests in these fragments. Proportion of nests depredated was calculated out of 29 instead of 30 for these two instances.*

Effect of Nest Density on Rate of Nest Predation

We predicted that increased nest density would increase the rate of nest predation. To simulate clustered nests, we placed 30 nests in a grid formation with 5 rows, each 20 m apart, and consisting of 6 nests that were 20 m apart. These grid transects were in eight different forest fragments (Table 1). As above, the unit of analysis was the transect (Table 1). Using Wilcoxon rank sums, we compared the proportion of nests depredated in these 10 transects to the proportion of nests depredated in the 22 linear transects described above.

Effect of Proximity to Edge on Rate of Nest Predation

Each of the 22 linear transects described above was located on aerial photographs (scale 1 inch = 122 m) using global positioning information from Soehren (1995). From the photographs, we calculated distance to the nearest edge for each nest. Five of these transects were placed 10 m from the edge of large fragments (Table 1). This was done because all of the nests in small fragments were closer to the edge than any of the nest transects in the interior of large fragments. Using edge transects in large fragments means that both the edge and the core area were sampled for small and large fragments.

The fate of an individual nest is not independent of the fate of neighboring nests because of the potential for predator trap-lining. Thus it is not appropriate to use nests as independent sampling points, but it is also not meaningful to discuss mean distance from edge for an entire transect.

To address this question, we used the first, tenth, twentieth, and thirtieth nest in each 30-nest transect as the sample units for the analysis. For a single predator to depredate two of these nests, it would have had to travel at least 180 m and eat 20 quail eggs. Only nests from linear transects were included in this analysis. For one transect we relocated only 29 of the 30 nests. As a result, a total of 87 nests were considered (22 transects × 4 nests per transect minus one missing value). The mean distance from edge of depredated nests was compared to the mean distance from edge of intact (untouched) nests with a two-tailed, unpaired *t* test.

For all hypotheses, we performed statistical analyses for total nest fate (if one egg was damaged in any way, the nest was considered depredated), quail egg fate, and damage attributable to small-mouthed predators (assessed by marks left on clay eggs as described above).

Results

Effect of Forest Fragment Size on Nest Predation Rates

There was a significant, negative correlation between the total predation rate per transect (loss of either quail or clay eggs within the nest) and fragment size ($R_s = -0.50$, $n = 22$, $p = 0.02$, Fig. 2a). Predation of quail eggs was also significantly negatively correlated with fragment size ($R_s = -0.54$, $n = 22$, $p = 0.01$; Fig. 2b). There was no correlation between predation events attributable to small-mouthed predators and fragment size ($R_s = 0.16$, $n = 22$, $p = 0.48$, Fig. 2c).

If transects are not independent within large fragments, the appropriate unit of analysis is the fragment (data from all transects combined). When each fragment was used as the unit of analysis, the trends remained: total predation rate versus fragment size ($R_s = -0.60$, $n = 10$, $p = 0.07$), quail egg loss versus fragment size ($R_s = -0.52$, $n = 10$, $p = 0.12$), and loss to small-mouthed predators versus fragment size ($R_s = 0.39$, $n = 10$, $p = 0.27$). The effect size of these tests remained the same, but the much-reduced sample size and consequent reduction in statistical power caused the probability of making a type 2 error to increase. In addition, nonparametric tests are generally more conservative than parametric tests. Thus, the results of this second analysis still appear biologically meaningful.

Whether the results of the first or second analysis are more valid depends on the independence of transects within fragments. There are so few transects in each large fragment (Table 1) that a statistical test for independence of transects is not possible. Visual inspection of the data (Fig. 2) does not suggest greater correlation within fragments than between fragments. To be an adequate test of our hypothesis, the transects should be independent in terms of predators. In other words, each

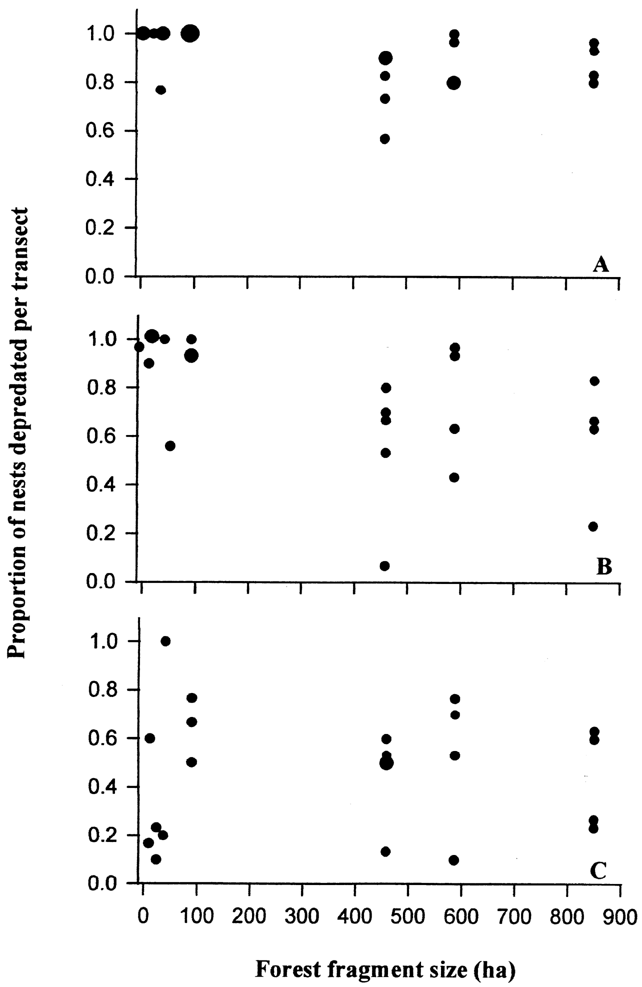

*Figure 2. Forest fragment size in relation to proportion of artificial nests depredated in each transect, with the calculations based on combined quail and clay egg fates, which provide an overall index of predation (a); quail egg fate, which provides an index of large predator activity (b); and clay egg fate, which provides an index of small-mouthed predator activity (c) (*n *= 22 for all comparisons). Circles are proportional to the number of overlapping data points (1, 2, or 3).*

transect should sample a completely separate set of individuals. If effects of fragment size are strong, however, predation on each transect should be similar in similiarly sized fragments. The lack of obvious pattern in the data (Fig. 2) suggests that transects are independent in terms of predators and that the analysis that uses the transect as the sample unit is appropriate. It also suggests that there may be a threshold fragment size above which a large fragment is "large enough," and predation rate will not drop any lower no matter how large the fragment gets.

Effect of Nest Density on Rate of Nest Predation

We compared predation rate in linear transects ($n = 22$) to the total predation rate in grid transects ($n = 10$) using Wilcoxon rank sums (Table 2). There was no significant difference in total predation rate between the clustered and unclustered nests (mean rank = 15.30, linear; 19.15, grid; $z = 1.13, p = 0.26$). Predation rate on quail eggs, however, was significantly higher in the grid transects than in the linear transects (mean rank = 14.25, linear; 21.45, grid; $z = 2.03, p = 0.04$). Losses attributable to small-mouthed predators were greater in linear transects than grids, the reverse of the pattern for quail eggs, but this was not statistically distinguishable (mean rank = 17.93, linear; 13.35, grid; $z = -1.26, p = 0.21$). Because both the quail egg fate and the clay egg fate contributed information to the overall index of predation, the combination of these opposing trends explains the lack of pattern in the overall analysis.

Effect of Proximity to Edge on Rate of Nest Predation

When total nest loss was analyzed, there was no significant difference between the mean distance from edge for intact and depredated nests (intact: $\bar{x} = 234.5$ m, $n = 10$; depredated: $\bar{x} = 219.2$ m, $n = 77$; $t = 0.18, p = 0.86$). A more pronounced trend was apparent when quail egg loss was considered. Intact nests tended to be deeper within the forest than depredated nests (intact: $\bar{x} = 282.5$ m, $n = 30$; depredated: $\bar{x} = 188.6$ m, $n = 57$), but this trend was not significant ($t = 1.64, p = 0.11$). There was no discernible effect of edge on small predator activity (nests depredated by small-mouthed predators: $\bar{x} = 233.7$ m, $n = 43$; nests where no small-mouthed predator activity was evident: $\bar{x} = 208.6$ m, $n = 43$; $t = 0.44, p = 0.65$).

Discussion

As has been found in the northeastern and midwestern United States (Wilcove 1985; Small & Hunter 1988; Yahner & Scott 1988; Hoover et al. 1995), nest predation increased as forest fragment size decreased in our southern Appalachian study site. Our experimental design allowed us to determine how the activity patterns of both small and large predators contributed to the overall pattern of nest predation that we observed. Small predator activity remained constant regardless of forest fragment size, but large predator activity increased as forest fragments decreased in size. Thus, songbirds nesting in small fragments bear an increased predation burden. Obviously this has important conservation implications. In addition, the data suggest that there is a threshold fragment size above which predation rates level off.

Table 2. Wilcoxon rank sums test comparing proportion of nests depredated in linear versus grid transects.*

Predation	*First quartile*	*Median*	*Third quartile*	$\bar{x}$	z	p
Total						
linear	7.0	14.0	24.5	15.30	1.13	0.26
grid	15.0	24.5	24.5	19.15		
Large predators						
linear	8.5	13.5	20.5	14.25	2.03	0.04
grid	20.5	27.5	27.5	21.45		
Small predators						
linear	11.5	18.5	25.0	17.93	−1.26	0.21
grid	5.5	11.5	20.0	13.35		

**Median, quartiles, mean,* z *statistic, and* p *value given for three comparisons: total predation in linear versus grid transects, predation by large predators in linear versus grid tansects (large predators), and predation by small predators in linear versus grid transects (small predators).*

We found that large predator activity was increased among clustered nests. One short-term result of forest patch reduction is increased avian density as northbound migrants settle into available breeding habitat (Hagan & Johnston 1992; Holmes et al. 1996). For nest predators this means an increase in available resources and potentially a reduction of foraging effort. Clustered nests should be equally advantageous to large and small predators, but we found increased predator activity for large predators only. The lack of clustering effects on small predators may be due to a sampling artifact. Increased large predator activity is likely to mask small predator activity and inhibit our ability to discern whether or not small predators visited artificial nests. When predation rates are high, saturation occurs (everything is eaten within a transect), and small predator activity is obscured.

Another element of the experimental design may have influenced these results. A large predator that encounters an experimental nest with quail eggs is likely to continue to search the surrounding area for more such rewards. Small predators get no food reward (they cannot break quail eggs), however, so they may not be as likely to keep searching. This may explain the nonsignificant results of nest clustering on predation by small predators.

Although there was a trend toward increased large predator activity closer to the edge of fragments, we found no significant effects of edge on predation rates. Several previous studies also failed to demonstrate a significant edge effect on nest predation (Yahner & Wright 1985; Angelstam 1986; Hanski et al. 1996; King et al. 1996), whereas other studies have noted a strong effect (Gates & Gysel 1978; Andren & Angelstam 1988; Small & Hunter 1988; Møller 1989; Linder & Bollinger 1995). This lack of consistency seems to be the rule rather than the exception when edge effects are considered (reviewed by Murcia 1995). The ability to discern edge effects is confounded by the difficulty of differentiating between edge types and between kinds of edge-matrix interfaces, as well as by imprecise experimental design (Paton 1994). We have not yet begun to quantify the many different biotic and abiotic factors that characterize edge habitats (Murcia 1995) and that will allow us to elucidate the effect of edges on nest predation (but see Hawrot & Niemi [1996] and Hanski et al. [1996] for a consideration of vegetation characteristics and Angelstam [1986] for a discussion of edge-matrix effects).

Our study did not control for edge type. Although edge structure was similar in all fragments, the habitat matrix surrounding fragments included forest, fields, large roads, residential neighborhoods, and parking lots. A forest cut into patches by roads exists in a very different matrix than does a patch surrounded by suburban backyards. The effects of edge structure (i.e., abrupt versus gradual) and edge-matrix type have not been well studied, and yet it seems likely that they have profound effects on local fauna. In our opinion, the lack of discernable edge effects in this study is due to these confounding factors. We are currently investigating the effects of edge-matrix type on nest predation rates in this study area.

We conclude that reduced forest size increases predation on ground nests and that nest clustering increases predation of ground nests by large predators. Our results suggest a causal link between increased predation rate, fragment size, and the observed abandonment of small forest fragments by Neotropical migrant songbirds. The mechanisms behind this relationship will depend on how avian activity is affected by changes in fragment size and on how the predator community is influenced. There are several possible mechanisms for future study: (1) Decreased core forest area may lead to a proportional increase in edge habitat in which predators preferentially forage. (2) Packing predators into remaining forest fragments may increase their densities. (3) Fragmentation may change habitat structure and vegetation, altering the composition of the predator community. (4) Birds attempting to nest in whatever forest patch remains after fragmentation may lead to increased nest density and thus increased predator efficiency. Mechanisms 1–3 propose that forest fragmentation affects predators, which in turn affect breeding birds. We concur with Yahner (1996) that further studies should directly investigate predator density, community composition, and habitat usage.

We found that the use of both quail and clay eggs in the experimental design helped separate the activities of small and large predators. This supports the contention of Haskell (1995*a*) and Roper (1992) that experiments that use only large eggs sample only large predators. We did not find any significant trends in small predator activity. This may be because small predator activity remains constant regardless of fragment size. Our method underestimates predation by small-mouthed predators, however, and differences in the densities of small-mouthed predators associated with fragment size may have gone undetected. Clay eggs often showed the marks of more than one species of predator. Tooth impressions left by large predators can mask marks left in the clay by small predators. Moreover, large predators often completely removed clay eggs from the artificial nests, leaving no evidence by which predator identity could be determined. Future experiments should attempt to obviate this problem by excluding large predators with exclosures that contain both quail and clay eggs. Saturation effects can be reduced if transects are checked after a shorter period of time (perhaps 3–4 days). There would then likely be fewer multiple visitations (activity at a nest by more than one predator), and it would be possible to find more nests that only small predators had visited.

We advocate the continued use of both quail and clay eggs in artificial nest experiments to differentiate the activity patterns of small predators from those of large predators under different kinds of habitat change. Modified methods are required to distinguish with confidence nest losses due to small predators from those due to large predators.

Point-count data from the same forest fragments that we used in this study indicate that most Neotropical migrant land birds have abandoned small forest fragments (Soehren 1995). Whether or not this decline is causally linked to increased nest predation remains to be resolved, but the patterns between nest predation risk and forest fragmentation documented in our study suggest that it is, at least, a contributing factor. The causal mechanisms behind avian responses to changes in landscape structure, including fragmentation and alteration of edge-matrix composition, need to be elucidated. The composition of other trophic levels within habitat patches may explain the variation in avian productivity and patterns of abundance.

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Literature Cited

Alig, R., W. G. Hohenstein, B. C. Murray, and R. G. Haight. 1990. Changes in area of timberland in the United States, 1952-2040 by ownership, forest type, region, and state. General report SE-64.1. Southeastern Forest Experiment Station, U.S. Forest Service, Asheville, North Carolina.

Andren, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology **69:**544–547.

Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos **47:**365–373.

Bider, J. R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecological Monographs **38:**269–308.

Böhning-Gaese, K., M. L. Taper, and J. H. Brown. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biology **7:**76–86.

DeGraaf, R. M., and T. J. Maier. 1996. Effect of egg size on predation by white-footed mice. Wilson Bulletin **108:**535–539.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology **59:**871–883.

Hagan, J. M., and D. W. Johnston, editors. 1992. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C.

Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology **10:**188–202.

Hanski, I. K., T. J. Fenske, and G. J. Niemi. 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. Auk **113:**578–585.

Haskell, D. 1995*a*. Forest fragmentation and nest predation: are experiments with Japanese Quail eggs misleading? Auk **112:**767–770.

Haskell, D. 1995*b*. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. Conservation Biology **9:**1316–1318.

Hawrot, R. Y., and G. J. Niemi. 1996. Effects of edge type and patch shape on avian communities in a mixed conifer-hardwood forest. Auk **113:**586–598.

Hogstad, O. 1995. Do avian and mammalian nest predators select for different nest dispersion patterns of Fieldfares *Turdus pilaris*? A 15-year study. Ibis **137:**484–489.

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. Journal of Animal Ecology **65:**183–195.

Hoover, J. P., M. C. Brittingham, and L. J. Goodrich. 1995. Effects of forest patch size on nesting success of Wood Thrushes. Auk **112:** 146–155.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in forested landscapes. Conservation Biology **10:**1380–1386.

Leimgruber, P., W. J. McShea, and J. H. Rappole. 1994. Predation on artificial nests in large forest blocks. Journal of Wildlife Management **58:**254–260.

Linder, E. T., and E. K. Bollinger. 1995. Depredation of artificial Ovenbird nests in a forest patch. Wilson Bulletin **107:**169–174.

Major, R. E., G. H. Pyke, M. T. Christy, G. Gowing, and R. S. Hill. 1994. Can nest predation explain the timing of the breeding season and the pattern of nest dispersion of New Holland Honeyeaters? Oikos **69:**364–372.

Martin, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. Nature **380:**338–340.

Maxson, S. J., and L. W. Oring. 1978. Mice as a source of egg loss among ground-nesting birds. Auk **95:**582–584.

Møller, A. P. 1988. Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. Oikos **53:**215–221.

Møller, A. P. 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos **56:**240–246.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution **10:**58–62.

Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology **8:**17–26.

Picman, J. 1988. Experimental study of predation on eggs of ground-nesting birds: effects of habitat and nest distribution. Condor **90:**124–131.

Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. Auk **111:**652–660.

Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. Oikos **57:**375–380.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology **9:**1–48.

Robbins, C. S., J. R. Sauer, R. Greenburg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Science **86:**7658–7662.

Robinson, S. K., F. R. Thompson, III, and T. M. Donovan. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267:**1987–1990.

Roper, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? Oikos **65:**528–530.

Shankman, D., and K. M. Wills, Jr. 1995. Pre-European settlement forest communities of the Talladega Mountains, Alabama. Southeastern Geographer **35:**118–131.

Small, M. F., and M. L. Hunter. 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia **76:**62–64.

Soehren, E. C. 1995. Effects of forest fragmentation on breeding populations of Neotropical migratory birds on Fort McClellan, Alabama. M.S. thesis, Jacksonville State University, Jacksonville, Alabama.

Terborgh, J. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey.

Terborgh, J. 1992. Why American songbirds are vanishing. Scientific American **266:**98–104.

Van Horn, M. A., R. M. Gentry, and J. Faaborg. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. Auk **112:**98–106.

Vander Haegen, W. M., and R. M. DeGraaf. 1996. Predation on artificial nests in forested riparian buffer strips. Journal of Wildlife Management **60:**542–550.

Whelan, C. J., M. L. Dilger, D. Robson, N. Hallyn, and S. Dilger. 1994. Effects of olfactory cues on artificial-nest experiments. Auk **111:** 945–952.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66:**1211–1214.

Yahner, R. H. 1996. Forest fragmentation, artificial nest studies, and predator abundance. Conservation Biology **10:**672–673

Yahner, R. H., and D. P. Scott. 1988. Effects of forest fragmentation on depredation of artificial nests. Journal of Wildlife Management **52:** 158–161.

Yahner, R. H., and A. L. Wright. 1985. Depredation on artificial ground nests: effects of edge and plot age. Journal of Wildlife Management **49:**508–513.