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PREDATION OF SMALL EGGS IN ARTIFICIAL NESTS: EFFECTS OF NEST POSITION, EDGE, AND POTENTIAL PREDATOR ABUNDANCE IN EXTENSIVE FOREST

RICHARD M. DEGRAAF,[1,3] THOMAS J. MAIER,[1] AND TODD K. FULLER[2]

ABSTRACT.—After photographic observations in the field and laboratory tests indicated that small rodents might be significant predators on small eggs, we conducted a field study in central Massachusetts to compare predation of House Sparrow (*Passer domesticus*) eggs in artificial nests near to (5–15 m) and far from (100–120 m) forest edges and between ground and shrub nests. As in earlier studies in managed northeastern forest landscapes that used larger quail eggs, predation rates on small eggs in nests at the forest edge did not differ ($P > 0.05$) from those in the forest interior for either ground nests (edge = 0.80 vs interior = 0.90) or shrub nests (edge = 0.38 vs interior = 0.28) after 12 days of exposure. However, predation rates on eggs in ground nests were significantly higher ($P < 0.001$) than in shrub nests at both the edge and interior. There were no significant ($P > 0.05$) differences in the frequency of capture of the 6 most common small mammal species between forest edge and interior. Logistic regression analyses indicated a highly significant ($P < 0.001$) nest placement effect but very little location or small mammal effect. Predation of small eggs by small-mouthed ground predators such as white-footed mice (*Peromyscus leucopus*) has not been documented as a major factor in egg predation studies, but use of appropriately-sized eggs and quantification of predator species presence and abundance seems essential to future studies. *Received 31 March 1998, accepted 5 Jan. 1999.*

Previously published evidence for elevated nest predation rates at forest edges in the northeastern U.S. is not consistent. For example, in Maine, predation rates were higher for artificial nests placed in shrubs at edges than in forest interiors, but the distance to edge had no effect on predation of ground nests (Rudnicky and Hunter 1993). Also, neither the edge:area ratio of forest patches nor the distance from edge affected artificial ground nest predation rates (Small and Hunter 1988). Predation rates of artificial nests were higher in extensive industrial forests than in fragments, but within fragments, shrub nests near edges were depredated at a higher rate than those farther from edges. Furthermore, the predation rate in clearcuts was lower than that in forest fragments or plantations, and within plantations, predation rates increased with increasing distance from the edge (Vander Haegen and DeGraaf 1996). In Pennsylvania, Yahner and Scott (1988) reported a direct relationship between amount of forest fragmentation caused by clearcutting and predation rates on artificial nests, yet Yahner and coworkers (1993) did not find greater predation rates on such nests despite greater fragmentation resulting from additional clearcutting on the same study area. In sum, the results of previous studies in the northeastern U.S. are inconsistent, perhaps because the large quail (*Coturnix* sp.) or chicken (*Gallus* sp.) eggs used do not sample the entire predator community (Haskell 1995). Would the use of eggs of approximately the same size as most forest passerines shed light on patterns of predation on artificial nests in relation to forest edge?

White-footed mice (*Peromyscus leucopus*) were frequently recorded by remotely-triggered cameras at ground and shrub nests containing eggs of Japanese Quail (*Coturnix japonica*); many of these same nests appeared to be undisturbed at the end of the exposure period and thus were not classified as visited by predators (Danielson et al. 1997). Similarly, Northern Bobwhite (*Colinus virginianus*) eggs at artificial nests in Minnesota that were visited (as determined by photographs) by red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) were not damaged, although those nests were classified as depredated by Fenske-Crawford and Niemi (1997). Small mammalian predators are clear-

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[1] USDA Forest Service, Northeastern Research Station, University of Massachusetts, Amherst, MA 01003 USA.

[2] Department of Forestry and Wildlife Management and Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA 01003-4210.

[3] Corresponding author; E-mail: rdegraaf@forwild.umass.edu

ly able to locate artificial nests, but have limited ability to destroy quail eggs in these nests. Quail eggs are not representative of the sizes of eggs of most temperate forest passerines, especially those of Neotropical migratory species (Haskell 1995, DeGraaf and Maier 1996). If appropriately-sized eggs were not available to potentially common predators, then results of previous studies to estimate nest predation rates for forest songbirds may have been biased, contributing to the inconsistency of results in extensive northeastern forests.

Egg size is potentially important in nest predation studies; even though small rodents such as mice and eastern chipmunks (*Tamias striatus*) may be egg predators (e.g., Maxon and Oring 1978, Reitsma et al. 1990, respectively), they apparently cannot readily open and consume the larger eggs of quails and chickens (Roper 1992, Haskell 1995; but see Craig 1998). Roper (1992) showed that predators did not respond to quail eggs as they did to native birds' eggs in Panama because most mammalian nest predators were too small to eat quail eggs. Such eggs, however, are virtually the only ones that have been used in artificial nest predation studies (Major and Kendal 1996).

These facts led us to conduct a laboratory experiment of mouse predation on large (*C. japonica*) and small (Zebra Finch, *Taeniopygia guttata*) eggs (DeGraaf and Maier 1996). Mouse predation on small eggs was immediate but did not occur on the large eggs. Similar laboratory trials (Maier and DeGraaf, unpubl. data) indicated that white-footed mice, including juveniles, could open House Sparrow (*Passer domesticus*) eggs; we conducted a field study to evaluate egg predation in artificial nests containing such eggs.

We attempted to assess the effects of nest location (edge vs interior), placement (shrub vs ground), and the relative abundance of small mammals on the predation of small eggs. We hypothesized that small mammals were equally abundant at edges and in forest interiors (Heske 1995), that no edge-related differences in nest predation would be found for either ground or shrub nests (Major and Kendall 1996), and that predation would be greater on ground nests than on shrub nests because small mammals such as mice and chipmunks spend the majority of their foraging time on the ground (Madison 1977, Elliot 1978, Graves et al. 1988).

METHODS

We placed artificial nests near (5–15 m) and far (100–120 m) from stand edges in 40 mature stands in an extensive managed mixed-wood forest in central Massachusetts during June to 15 July 1997. All stands were at least 80 years old and of the red oak (*Quercus rubra*)-white pine (*Pinus strobus*)-red maple (*Acer rubrum*) forest-cover type (Eyre 1980); edges were formed by small (2–4 ha) clearcuts 1–6 years old. We placed two ground nests and two shrub nests in each stand, one of each type near and far from the edge and at least 100 m from each other (Fig. 1). Nests (160 total) were wicker baskets 10 cm in diameter and 6 cm deep, weathered for 3 weeks before use, and contained one fresh House Sparrow egg. To minimize human scent at nests, we wore rubber boots and clean cotton gloves during nest placement (Whelan et al. 1994). Ground nests were set into the surface litter; shrub nests were wired 1–1.5 m above the ground in crotches or forks of branches of shrubs or small saplings. All nests were checked after 12 days, approximately the mean incubation time for small forest passerines. Eggs found out of the nest, destroyed in the nest, or missing were classified as predations.

We analyzed the nest predation data as paired-sample nest types within stands (Zar 1996:163) and performed statistical tests using SYSTAT 7.0 for Windows. Sign tests were used to detect differences in the number of nest predations among edge and interior nests on the ground and in shrubs (Zar 1996:536).

We assessed the relative abundance of small mammal species at edge and interior sites using 3-day removal trapping (Miller and Getz 1977) at each site immediately after the nest predation experiments. Two circular trapping arrays (20 traps/20 m diameter array) were set in each of the 40 stands, one midway between edge nests and one between interior nests (Fig. 1). Different types of small mammal traps are more efficient for trapping certain species under varying conditions, e.g., weather (Williams and Braun 1983, Bury and Corn 1987, Mengak and Guynn 1987); we used four types of traps in an attempt to more completely sample the small mammal community (Pelikan et al. 1977). Small Victor snap traps with expanded pedals, Museum Special snap traps with expanded pedals, large (approx. 8 × 8 × 24 cm) Sherman traps, and modified large Sherman live traps with circular glass windows (5.5 cm diameter) in the rear door were used at each array in equal numbers. All traps were baited with a mixture of peanut butter, oatmeal, bacon, and black sunflower seed and were checked daily. All small mammals collected were deposited in the Vertebrate Museum of the University of Massachusetts, Amherst, Massachusetts. We followed the guidelines for the capture and handling of mammals approved by the American Society of Mammalogists (American Society of Mammalogists 1998).

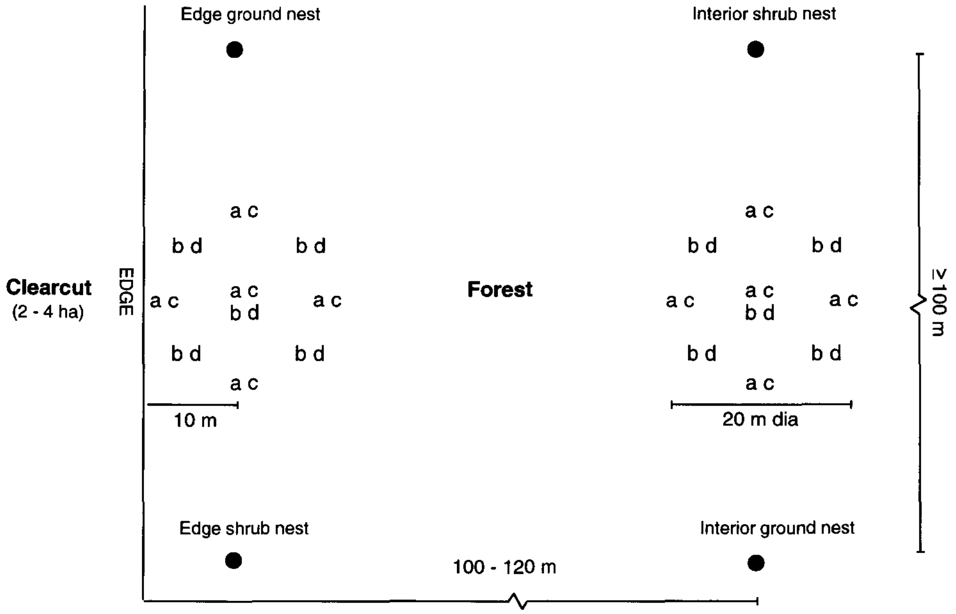

FIG. 1. Placement of small mammal trapping arrays and artificial nests in central Massachusetts, June–August. 1997. Four types of traps include: (a) small Victor snap, (b) Museum Special, (c) large Sherman, (d) large Sherman with glass window. (Figure not to scale.)

Small mammal capture counts were compared by species between edge and interior using the Wilcoxon paired-sample test for species with sufficient n (Zar 1996:167). Logistic regression (PROC LOGISTIC, SAS 1989) was used to assess the relationship between small mammal counts and nest predation; we used a model with nest placement (ground or shrub), location (edge or interior), and small mammal abundance effects; the first two were treated as categorical variables and the third as a continuous variable. The tests for whether a coefficient is zero were carried out using Z = (estimated coefficient/standard error) with the P-value obtained using the standard normal distribution (Hosmer and Lemeshow 1989:17).

RESULTS

We did not detect any significant differences between the number of nest predations at the forest edge and those in the forest interior for either ground nests (Sign test: ties = 28, 4 "+", 8 "−", critical value = 2, $P > 0.05$) or shrub nests (Sign test: ties = 24, 10 "+", 6 "−", critical value = 3, $P > 0.05$). However, the number of nest predations on ground nests at both the edge (Sign test: ties = 15, 21 "+", 4 "−", critical value = 7, $P < 0.001$) and interior (Sign test: ties = 15, 25 "+", 0 "−", critical value = 7, $P < 0.001$) were significantly higher than those on shrub nests.

Twelve species of small mammals were detected; six species represented 99% of captures at both forest edge and interior. The distributions of the 6 most commonly detected small mammal species did not differ significantly (Wilcoxon paired-sample tests: $P > 0.05$) between stand edges and interiors (Table 1). White-footed mice were detected more than all other species combined in both stand edges and interiors and were the only small mammal species detected in all 40 stands. Logistic regression analyses confirmed nest placement (ground, shrub) effects but showed no effect of small mammal abundance or location (edge, interior) on nest predation rate (Table 2).

DISCUSSION

Because this is the first study that we know of to systematically evaluate artificial nest predation in relation to forest edge using small eggs, comparison with other studies where larger eggs were used is difficult. In a recent review of studies in both agricultural and settled landscapes in North America and Europe, Major and Kendal (1996) showed that egg predation (on large eggs) was higher near the

TABLE 1. Numbers of small mammals captured near edges and interiors of 40 stands in extensive forest in central Massachusetts, July and August 1997. Wilcoxon paired-sample results for most commonly detected species; N = stands species detected in, n = differences (N minus ties), T = smallest sum of ranks, $T_{0.05(2),n}$ = critical value (Zar 1996: table B.12).

Species[a]	Edge	Interior	Total	N	n	T	$T_{0.05(2),n}$	P
White-footed mouse (*Peromyscus leucopus*)	251	235	486	40	34	262.5	182	>0.05
Red-backed vole (*Clethrionomys gapperi*)	74	63	137	25	21	90.5	58	>0.05
Northern short-tailed shrew (*Blarina brevicauda*)	61	65	126	35	28	202.0	116	>0.05
Masked shrew (*Sorex cinereus*)	16	22	38	17	15	44.0	25	>0.05
Eastern chipmunk (*Tamias striatus*)	14	5	19	15	15	28.5	25	>0.05
Smoky shrew (*Sorex fumeus*)	7	3	10	9	9	13.5	5	>0.05

[a] Species detected in ≤3 stands: woodland jumping mouse (*Napaeozapus insignis*), flying squirrel (*Glaucomys* sp.), long-tailed weasel (*Mustela frenata*), red squirrel (*Tamiasciurus hudsonicus*), pine vole (*Microtus pinetorum*), meadow vole (*Microtus pennsylvanicus*).

forest edge in three studies, higher away from the edge in one study, and equal in seven studies. Predation of artificial nests containing Northern Bobwhite eggs in Wisconsin pine barrens savannah patches was correlated with proximity to the edge (Niesmuth and Boyce 1997). Predation on artificial nests containing small chicken, Japanese Quail, and plasticine eggs in Alberta was highest in larger woodlots and showed no edge effect (Hannon and Cotterill 1998). Two additional studies (which used Japanese Quail eggs) in the northeastern U.S. did not detect any difference in predation rates between edges and interiors of extensive-managed forests (Table 3; Vander Haegan and DeGraaf 1996) or suburban/agricultural/forest landscapes (Danielson et al. 1997). Along with our current results, these variable findings suggest either that the "edge" effect as related to egg predation (Andrén and Angelstam 1988) is not a widespread phenomenon or that not all forest edges are the same; i.e., forest-clearcut, forest-agriculture, and forest-suburb edges differ in the predators present (Danielson et al. 1997).

TABLE 2. Parameter estimates and statistics from logistic regression analysis of placement (ground/shrub), location (edge/interior), and small mammal abundance in relation to predation of small eggs in artificial nests in central Massachusetts, 1997. The tests for whether a coefficient is zero were carried out using Z = (est. coefficient/SE) with the P-value obtained using the standard normal distribution (equivalent to $C = Z^2$ with the P-value based on χ^2 distribution with 1 df).

Variable	Estimated coefficient	Standard error	P
INTERCEPT	−1.7320	0.5080	0.0007
LOCATION	0.0002	0.3805	0.9996
W-F MICE	−0.0005	0.0602	0.9940
PLACEMENT	2.4655	0.3937	0.0001

Equally variable are the results of nest placement studies (i.e., ground vs shrub/elevated nests). Major and Kendal (1996) reported higher predation at elevated nests in six studies, higher predation at ground nests in four studies, and equal predation rates in three studies. Ground nests containing Japanese Quail and plasticine eggs had increased predation along farm edge and interior in Saskatchewan, but there were no detectable differences in predation rate between ground and shrub nests at logged edge, logged interior, or contiguous forest (Bayne and Hobson 1997). Although two studies in the northeastern U.S. did not detect any difference in predation rates between ground and shrub nests (Vander Haegan and DeGraaf 1996, Danielson et al. 1997), we found a strong placement effect (high predation on ground nests) using small eggs.

Where edge or nest placement effects occurred, generalist predators commonly were presumed to depredate specific nest types disproportionately. The variability in results among studies may reflect differences in nest predator guilds or the abundance of particular species in study areas (e.g., Picman 1988). Attempts to identify individual egg predators include characterizations of predation remains of real eggs (Gottfried and Thompson 1978, but see Marini and Melo 1998), impressions in plasticine (Bayne et al. 1997), and clay eggs (Donovan et al. 1997), hair catchers (Baker 1980), and remotely triggered cameras (DeGraaf 1995). Nevertheless, egg predation

TABLE 3. Predation rates (%) on eggs in artificial nests exposed for 12–14 days at forest edge and interior (>50 m) in the northeastern U.S.

Nest placement	Egg size	Edge		Interior			Study location	Reference
		Rate	*n*	Rate	*n*	*P*		
Ground	Sparrow	0.80	40	0.90	40	>0.05	Massachusetts	This study
	Quail	0.45	20	0.41	80	>0.05	Massachusetts	DeGraaf, unpubl. data[a]
		0.20	50	0.25	48	>0.05	Maine	Vander Haegan and DeGraaf 1996[b]
		0.29	42	0.21	42	>0.05	Maine	Rudnicky and Hunter 1993
Shrub	Sparrow	0.38	40	0.28	40	>0.05	Massachusetts	This study
	Quail	0.60	20	0.51	80	>0.05	Massachusetts	DeGraaf, unpubl. data[a]
		0.16	50	0.14	50	>0.05	Maine	Vander Haegan and DeGraaf 1996[b]
		0.55	42	0.29	42	0.015	Maine	Rudnicky and Hunter 1993

[a] Recalculated from data used by Danielson et al. 1997.
[b] From Table 1; edge = 5 m and interior = 200 m from edge.

studies almost never include surveys of the predator community in the study area or index predator abundance (Yahner 1996). We indexed small mammal abundance; the overall abundance and distribution of small mammals at forest edge and interior were similar, as were the distributions of depredated ground and shrub nests, but the abundance of small mammals was not related to nest predation for either nest type or location in one season. Either the small mammals that we detected were not major nest predators, or they did not vary sufficiently in abundance in a homogeneous landscape in one season to show a relationship with nest predation. A relationship between nest predation and small mammal abundance may be detectable only over time; small mammals vary greatly from year to year with food abundance (Elkinton et al. 1996). Long-term studies are needed to determine if this is the case.

Small-mouthed nest predators such as *Peromyscus* were abundant in our study area (10–40/ha; Elkinton et al. 1996) compared to larger generalist predators such as fishers (*Martes pennanti*; 21/100 km^2 in central Massachusetts; York 1996) that have been shown to depredate artificial nests in northern New England (DeGraaf 1995). If small eggs that are susceptible to depredation by all potential predators are used in artificial nests, then ubiquitous, abundant predators (e.g., small mammals) may swamp the effect of larger generalist predators, even if the latter are more abundant along forest edges (apparently not the case in the northeastern U.S.). Moreover, our data suggest that ground nests may be particularly vulnerable to predators such as mice and chipmunks (Haskell 1995, Bayne et al. 1997), which spend more time foraging on the ground than in shrubs or trees (Madison 1977, Elliot 1978, Graves et al. 1988). Hence, the hypothesis that egg predation rates are elevated at forest edges may, in large part, be an artifact of egg size. Virtually all studies to date have used quail eggs (see Paton 1994, Major and Kendal 1996; but see George 1987) which apparently cannot be opened by the most abundant small-mouthed predators in temperate forests.

Do natural nests containing small eggs show edge related predation in the extensively forested northeastern U.S.? In a 2-year study of ground nesting Ovenbird (*Seiurus aurocapillus*) reproductive success in New Hampshire (King et al. 1996), nests, territories, and territorial males were equally distributed in edge (0–200 m) and forest interior (201–400 m); nest survival was higher in the forest interior in year 1, but not in year 2. The proportion of pairs fledging at least 1 young, fledgling weight, and fledgling wing chord did not differ between edge and interior over the course of the study.

In extensive mixed-wood forests in New England, edge related differences in artificial nest predation rates have not been consistently demonstrated. In our study predation rates were substantially higher on artificial ground nests that contained small eggs than those in studies that used quail eggs (Table 3). All potential predators can open small eggs, and their use should result in higher predation rates because small-mouthed predators are more abundant than large nest predators. Predation rates of artificial nests often have been assumed to track those of natural nests (Major and Kendal 1996), but they may not unless egg sizes closely approximate those of the species of concern. For example, nest survival of natural nests was lower than that of experimental nests containing quail eggs in Panama because of the abundance of small-mouthed nest predators (Roper 1992). Predation rates in quail egg experiments (e.g., Loiselle and Hoppes 1983; Martin 1987, 1988) may be useful to compare local habitats, but may be inappropriate for estimating natural predation rates or for comparing areas inhabited by different predators (Roper 1992). Nest predation is a dominant factor in avian reproductive success (Ricklefs 1969, Martin 1988); results of experiments that exclude major sources of mortality (i.e., small-mouthed predators) may not be representative (Roper 1992).

Only if appropriate egg sizes are used can predation rates in relation to habitat edge or placement be generalized or approximated for natural nests. Even then, effects such as nest defense and appearance (Martin 1987) are difficult to address. Our data suggest that egg predation rates may be strongly related to egg size, other factors being equal, because the most abundant predators can only open small eggs.

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