

## Measuring Edge Effects on Nest Predation in Forest Fragments: Do Finch and Quail Eggs Tell Different Stories?

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ABSTRACT.—Experiments assessing rates of avian nest predation often find that nests near forest edges are at high risk of predation, suggesting the importance of forest fragmentation in recent population declines of ground-nesting passerines. However, the use of quail (*Coturnix* spp.) eggs in nest predation experiments may confound conclusions about edge effects because only large-mouthed predators are able to consume these relatively large eggs, but both large and small-mouthed predators consume smaller passerine eggs. We directly compared predation rates on artificial nests baited with quail eggs or with zebra finch (*Poephila guttata*) eggs; the latter are similar in size to the eggs of many neotropical passerines. In 1998 and 1999 we placed 392 artificial ground nests at edge and interior locations in two east-central Iowa forest fragments. Predation on these nests varied with egg type (quail or finch) and location (edge or interior) and there was a significant interaction between egg type and location: predation on quail eggs was greater at edges than in the interior, whereas finch egg predation was high in both edge and interior locations. Based on tooth imprints in clay eggs, we determined that large-mouthed predators were six times more active at edges, whereas activity of small-mouthed nest predators was evenly distributed between edge and interior locations. We suggest that the use of only quail eggs can exaggerate edge effects and that finch eggs or clay eggs used in conjunction with quail eggs in artificial nests can be used to estimate relative predation rates by large- and small-mouthed predators.

### INTRODUCTION

Recent declines in populations of neotropical migratory songbirds have received considerable attention from professional and amateur ornithologists and are believed to be related to widespread habitat loss and fragmentation in both breeding and wintering grounds (Terborgh, 1989; Askins *et al.*, 1990; Robinson *et al.*, 1995). Fragmentation not only isolates patches, but also increases the proportion of edge habitat (Hansen and Urban, 1992) which differs from the forest interior in ways that affect the nesting success of many bird species (Hawrot and Niemi, 1996). For example, mixed vegetative nest cover (Johnston and Odum, 1956) and higher abundance of arthropod prey at edges may enhance nesting success, but these advantages could be offset by higher densities of nest predators such as raccoons (*Procyon lotor*), foxes (*e.g.*, *Vulpes fulva*), sciurids and corvids (Andren and Angelstam, 1988; Leimgruber *et al.*, 1994).

Effects of edge on avian nest success have been hotly debated (Donovan *et al.*, 1997) because of mixed results from experimental studies in a wide range of biomes, regions and forest types (Latta *et al.*, 1995; Huhta *et al.*, 1998; Wong *et al.*, 1998). These mixed results may be due in part to the use in many artificial nest experiments of excessively large quail

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(*Coturnix* spp.) eggs (Major and Kendal, 1996; Ortega *et al.*, 1998; Newton and Heske, 2001), which are 30–100% larger than the eggs of most neotropical passerines (Haskell, 1995a). This size difference matters because egg predators include small-mouthed mammals (*e.g.*, shrews, mice, chipmunks and rats; Boag *et al.*, 1984; Haskell, 1995b; Eitel *et al.*, 1998), and these animals may have insufficient jaw gape to grasp a quail egg (Roper, 1992; Rangen *et al.*, 2000). Indeed, small-mouthed mammals such as white-footed mice (*Peromyscus leucopus*; DeGraaf and Maier, 1996), cotton rats (*Sigmodon hispidus*; Eitel *et al.*, 1998), eastern chipmunks (*Tamias striatus*; Haskell, 1995b) and house mice (*Mus musculus*; Marini and Melo, 1998) are often unwilling or unable to consume quail eggs, even after fasting.

The use of large quail eggs in field experiments could produce exaggerated or even spurious edge effects if large mammals (*e.g.*, skunks, raccoons and foxes) and corvids are more abundant at edges than interiors, but small mammals are not. Distributions of large and small nest predators frequently follow this pattern (Wilcove, 1985; Nour *et al.*, 1993; Yahner and Scott, 1988; Dijak and Thompson, 2000). Consequently, predation rates in forest interiors may be underestimated by the use of large quail eggs.

Zebra finch (*Poephila guttata*) eggs are an attractive alternative to quail eggs because they are approximately the same size (16 × 12 mm) as the eggs of neotropical passerines and are readily consumed by small predators (Haskell, 1995a; Eitel *et al.*, 1998). A few studies have deployed finch or similarly-sized eggs in artificial nest studies (King *et al.*, 1998; DeGraaf *et al.*, 1999; Lindell, 2000; Rangen *et al.*, 2000), but only one has compared edge effects estimated using nests baited with quail and finch eggs (Lindell, 2000, for a Costa Rican wet forest). Because egg size is a concern in predation studies using quail eggs, there is a need for direct comparison of predation on quail and finch eggs in a variety of natural habitats.

During the summers of 1998 and 1999 we studied predation on eggs of different sizes, placing mottled quail (*Coturnix coturnix*) and zebra finch eggs into artificial nests at two sites in east-central Iowa. We tested for differences in predation rates between egg types (quail vs. finch) and between locations (forest edge vs. interior), paying particular attention to the possibility of an egg-type-by-location interaction (expected if apparent edge effects are stronger for one egg type than the other). We hypothesized that: (1) predation on nests with quail eggs should be greater at edge locations than interior locations, due to greater activity of large-mouthed predators along the forest edge, (2) the edge effect should be smaller, or even absent, for predation on nests with finch eggs (assuming small-mouthed predators are equally or less abundant at edges) and (3) predation on finch eggs would be greater overall than on quail eggs because they can be consumed by a greater variety of organisms.

#### METHODS

*Study area.*—We measured nest predation at two sites in Iowa County, Iowa, each located in an irregular, 1.5 × 5–7 km complex of upland deciduous forest fragments bounded by pastures and agricultural fields. Individual fragments within these complexes were narrowly separated from, or connected by wooded corridors to, neighboring fragments and were roughly 60–300 ha (although the complex geometry of the fragment complexes makes assigning individual fragment areas difficult). One site was located near Homestead, Iowa (Iowa Co., Iowa Township, Section 2, T-80N, R-9W) and the other near West Amana, Iowa (Iowa Co., Washington Township, Section 13, T-81N, R-10W); the two sites were separated by 10 km and by the Iowa River and its floodplain. These areas are controlled by the Amana Society Inc., which restricts access, so trespassers on the research sites were unlikely. The two sites had similar dominant tree species, including elms (*Ulmus* spp.), hickories (*Carya* spp.) and oaks (*Quercus* spp.).

*Experimental design.*—Each site (Amana and Homestead) included an edge plot and an interior plot. The edge plots were along the southern edges of the fragment complexes, where the forest abruptly ended in very large pastures. Here we laid out five 90 m long transects, just inside and parallel to the edge and separated from each other by 10 m. In interior locations we laid out five 90 m long transects, again 10 m apart, running parallel to the edge transects but at least 450 m from any forest edge. We located sample points along each of the transects at 10 m intervals (10 points/transect); nests were then placed at the point of greatest cover within a 1.5 m radius of each sample point. Thus, the overall distribution of nests within an edge or interior plot was a  $5 \times 10$  grid with neighboring nests (within or between transects) approximately 10 m apart. We used a small piece of flagging within a 2 m radius of, but not directly over, each nest as a location aid. We labeled sample points (nest locations) more than a month before nest trials to reduce human disturbances during the study period. Sample points inevitably differed in available nest cover; this variance contributes to the error term in our analysis but does not affect comparisons among treatments.

Nest spacings of 10–100 m are typical for nest predation experiments (Reitsma, 1992; Vander Haegen and DeGraaf, 1996; Keyser *et al.*, 1998; Ortega *et al.*, 1998; Lindell, 2000; Jobin and Picman, 2002). While nest predation rates in this range of densities can sometimes be density-dependent (Reitsma, 1992; Major and Kendal, 1996; Schmidt and Whelan, 1999), nest spacing was identical across all our experiments and so our comparative results should not be sensitive to our spacing decision. However, spacing between nests is small compared to territory sizes of some nest predators, and so we were concerned that neighboring nests might not provide independent data points (for instance, if predators searched the immediate vicinity after discovering one nest). Therefore, we calculated a single measure of predation (proportion predated) for all nests in each treatment at each subsite (*see Statistical Analysis*, below).

We constructed artificial nests with the common roadside grasses *Elymus canadensis* L. and *Phalaris arundinacea* L. Small bundles of grass stems were twisted into wreaths 10 cm in diameter and secured with twine. These nests were placed on the ground and concealed with leaves to simulate natural nest camouflage (*e.g.*, of ovenbird nests, *Seiurus aurocapillus*; *see Linder, 1995; Sloan et al., 1998*). While we did not attempt to mimic nest construction for any particular species, the size and shape of our nests were typical for ground-nesting passerines. Rangen *et al.* (2000) found little effect of details of nest construction on predation rates for ground nests. However, reduced nest success has been associated with the presence of human scents and perfumes (Whelan *et al.*, 1994), so we wore latex gloves during all stages of nest construction and aired nests outside for at least 5 d before placing them at the study sites. During nest placement and subsequent visits, we refrained from use of artificial scents before fieldwork and wore latex gloves and rubber boots to minimize human scents near nests. In addition, care was taken to avoid producing foot trails along transects and between nests.

Nests contained real eggs for evaluation of nest predation rates and artificial clay eggs for predator identification from tooth and bill imprints. Alternate nests contained two mottled quail eggs or two zebra finch eggs. Typical neotropical migrants lay clutches of more than one egg, but because of egg breakage during shipping and handling, a few randomly-selected nests contained only one finch or quail egg. Differences in egg numbers had no effect on the likelihood of a nest's being predated (G-tests for 1998 and 1999, both  $P > 0.2$ ).

Clay eggs were formed in plaster molds with cream-colored Permaplast<sup>R</sup>, a nontoxic, nonhardening modeling clay. Clay eggs do not artificially attract predators (Major, 1991; Bayne and Hobson, 1999). In 1998 every other nest of each type (quail or finch) contained

a same-sized clay egg. We found no relationship between the presence of a clay egg in a nest and predation on the nest in 1998 ( $G$ -test,  $P > 0.9$ ; see also Bayne and Hobson, 1999), and so in 1999 we placed a clay egg in every nest to acquire more tooth imprints. Because in 1998 predators tended to ingest finch-egg sized clay eggs, in 1999 all clay eggs were formed to the size of quail eggs. To identify predators, we compared dentition patterns left in the clay eggs to those of mammals in the Vertebrate Specimens Collection of the University of Iowa Department of Geosciences. Tooth marks were classified as belonging to small-mouthed predators (squirrel or smaller, similar to Taylor and Ford, 1998) or larger predators (*e.g.*, skunk, raccoon, opossum). Punctures were attributed to avian predators (*e.g.*, corvids: Marini and Melo, 1998). Because a variety of predators are known to remove eggs from the nest before consumption (Boag *et al.*, 1984; Haskell, 1995b), we could make no inferences about the species responsible for missing clay eggs.

The experiment was conducted in late May each year when ground-nesting passerines are likely to be incubating eggs (Bayne and Hobson, 1997). In 1998 we checked nests for evidence of predation after 5 and 10 d, but found that most predation events occurred during the first 5 d. Therefore, in 1999 we checked nests at days 2 and 5. All analyses reported in this paper are based on the 5 d predation surveys. A predation event was defined as damage to, or removal of, one or more eggs from the nest. Some quail eggs were marked with tooth scratches of small-mouthed predators; such eggs were recorded as depredated, making our analysis conservative with respect to the idea that small-mouthed predators are less likely to depredate larger eggs. (Ignoring tooth scratches would not change our overall results.) Broken, removed or damaged eggs were not replaced when noted at the earlier of the two predation surveys.

*Statistical analysis.*—We used a 4-way factorial ANOVA (PROC GLM, SAS 8.2, SAS Institute Inc. Cary, NC) to test the ability of egg type, site, location (edge vs. interior) and year to predict the predation fate of nests. For our dependent variable we used the observed logit corresponding to each type-site-location-year combination, defined as  $\log\{p/(1-p)\}$ , where  $p$  is the observed predation rate (proportion of eggs eaten). Thus, for purposes of analysis our data set consisted of 16 observed logits (2 sites  $\times$  2 locations  $\times$  2 egg types  $\times$  2 years). In order to avoid undefined logits, we defined  $p = 1/n$  if no eggs were eaten and  $p = 1 - 1/n$  if all the eggs were eaten, where  $n$  is the number of eggs. Estimates and confidence intervals for marginal means were computed using the LSMEANS option. We report predation value estimates as percentages; these estimates and the corresponding confidence interval bounds were computed by applying the inverse logit transformation to the estimates and confidence intervals for the expected logit responses.

Since there was only one response per cell, it was not possible to include all possible main effects and interactions in the model. We first fitted a model containing all main effects and 2-way interactions. We then dropped insignificant 2-way interactions, followed by checking if any 3-way interactions were significant when included in the model one at a time. We were particularly interested in the interaction between egg type and nest location because a significant interaction indicates that inferences about edge effects are not independent of the choice of eggs used to bait nests.

## RESULTS

For the model containing all main effects and 2-way interactions, the year-by-location interaction was highly insignificant ( $F_{1,5} = 0.03$ ,  $P = 0.86$ ). We then fitted the model without this interaction (Table 1). Examination of the residual vs. predicted and normal probability plots did not reveal any obvious violation of model assumptions. Furthermore, 3-way interactions were not significant (all  $P > 0.14$ ) when included one at a time with the model

TABLE 1.—ANOVA analysis of nest predation rates

Effect <sup>a</sup>	df	F	P
<b>Egg type</b>	1, 6	45.4	<b>0.0005</b>
<b>Year</b>	1, 6	22.9	<b>0.003</b>
<b>Location</b>	1, 6	22.8	<b>0.003</b>
<b>Site</b>	1, 6	19.4	<b>0.004</b>
<b>Egg type*Location</b>	1, 6	8.9	<b>0.024</b>
Year*Site	1, 6	2.8	0.14
Location*Site	1, 6	1.8	0.23
Egg type*Site	1, 6	1.7	0.24
Egg type*Year	1, 6	1.6	0.25

<sup>a</sup> Variables/interactions in **bold** significant at  $\alpha = 0.05$ . "Egg type", quail vs. finch eggs; "year", 1998 vs. 1999; "location", edge vs. interior; "site", Homestead vs. Amana

containing main effects and 2-way interactions. Even though some of the interactions in this model were not significant, we left them in the model since the power is low with only 6 error degrees of freedom and omitting any of the remaining terms resulted in less satisfactory residual plots.

Across sites and years, nest predation varied significantly with both location and egg type (Fig. 1). Predation rate was significantly higher overall on nests containing finch eggs (88%,  $CI_{95}$  79–93%) vs. quail eggs (37%,  $CI_{95}$  23–53%), and lower in the forest interior than at the edge (46%,  $CI_{95}$  30–62% vs. 83%,  $CI_{95}$  72–91%). There was a significant location-by-egg-type interaction because quail eggs were more likely to be consumed in the edge than interior (71%,  $CI_{95}$  50–86% vs. 12%,  $CI_{95}$  5–25%), whereas predation rates for finch eggs did not differ significantly between locations (91%,  $CI_{95}$  80–96% vs. 84%,  $CI_{95}$  67–93%). We also detected significant differences in nest predation between years and sites with greater predation in 1998 than 1999, and greater predation at the Homestead site than at the Amana site (Fig. 1). However, site and year did not significantly influence comparisons among locations and egg types (no interactions involving site or year were significant; Table 1).

Bite marks suitable for predator identification were present on 95 clay eggs. The principal predators were raccoons and mice (*Peromyscus* spp.). Two clay eggs had avian beak punctures and nine eggs contained marks of multiple predators. Combining data across years and sites, the frequencies of marks made by large and small mammals were not independent of location ( $G = 5.33$ ; 1 df;  $P = 0.021$ ): clay eggs with marks of large predators were nearly six times more common at edges than interiors (23 vs. 4 eggs), whereas eggs with marks of small predators were about equally common at edge and interior sites (39 vs. 38).

## DISCUSSION

Our results show that egg size can significantly (and strongly) influence estimates of differences in nest predation rates between edges and the forest interior. Nests with large quail eggs, but not those with small finch eggs, were attacked more frequently at edges than in interiors (Fig. 1). Because logistical constraints prevented us from studying edge effects at more than two forest fragments, we are hesitant to conclude that egg size will always affect measurements of edge effects on nest predation. Nevertheless, our results confirm and extend those of Lindell (2000), who documented the same pattern in a Costa Rican wet forest, and those of Newton and Heske (2001), who found marked differences in predation rates on quail and finch eggs in grassland nests. Because most songbirds lay small eggs,

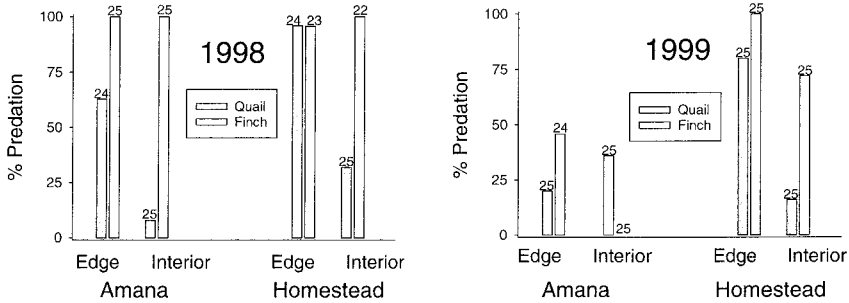


FIG. 1.—Percent of experimental nests depredated during 1998 and 1999. Numbers above bars are sample sizes; where these are less than 25, a few nests were lost or damaged before predation data were available

similar in size to those of zebra finches, use of quail eggs to measure avian nest success is inappropriate, as suggested (but only indirectly tested) by other studies (Haskell, 1995b; Reitsma *et al.*, 1990).

While greater predation on quail-egg nests at the edge (vs. in the interior; Fig. 1) appears to indicate an edge effect, our data suggest this may be an artifact of the distribution of predators able to consume large eggs. Large-mouthed predators are often more abundant at edges (*see* Introduction), but represent only a portion of the predator community threatening real nests. While we did not measure absolute predator abundance, our clay egg data indicate greater activity of large-mouthed nest predators at the edge than in the interior. In contrast, evidence of attack by small-mouthed predators on clay eggs did not differ between edge and interior (and was relatively high compared to evidence of large-mouthed predation).

Studies using quail eggs that have reported edge effects (*e.g.*, references in Paton, 1994; Hartley and Hunter, 1998; Donovan *et al.*, 1997) may suffer from similar problems. If large-mouthed mammals are less likely than small-mouthed mammals to depredate nests in the forest interior, as we found in east-central Iowa, then nests with larger eggs will have greater success in interior locations simply because the small-mouthed mammals active there cannot consume the eggs. In our study, nests with small, more realistically-sized eggs had equally high depredation rates at edge and interior, indicating no edge effect.

Four studies have tested for edge effects on nest predation using eggs small enough to be taken by mice and other small-mouthed predators. In Illinois grassland patches, Newton and Heske (2001) found no edge-interior difference in predation on zebra finch (or quail) eggs. In Massachusetts, DeGraaf *et al.* (1999) found no edge-interior difference in predation on house sparrow (*Passer domesticus*) eggs, but King *et al.* (1998) found higher predation on zebra finch eggs at forest edges. Finally, in Costa Rica, Lindell (2000) found zebra finch eggs attacked equally between edge and interior sites. Unfortunately, none of these studies used clay eggs (or other techniques) to identify predators, so the roles of large- and small-mouthed predators in generating these patterns cannot be distinguished.

Our measurements of overall predation rates are consistent with previous findings (Boag *et al.*, 1984; Reitsma *et al.*, 1990; Roper, 1992) that artificial nests tend to be more extensively depredated than real nests (Major and Kendal, 1996; Sloan *et al.*, 1998; Wilson *et al.*, 1998). Predation rates for both egg types in our nests were higher than rates typical of natural nests of ground-nesting passerines (often 15–55%; *e.g.*, Gates and Gysel, 1978; Wilson *et al.*, 1998; Martin and Martin, 2001; but *see* Ortega *et al.*, 1998). This difference may arise in part

because artificial nests are not defended by incubating adults. Indeed, Bayne and Hobson (1997) suggest that mice may be less important predators when a parent bird is present at the nest than when nests are unprotected. (This does not, however, affect our edge/interior comparisons, because our clay egg data indicated small mammals were equally active in edge and interior locations.) Because measured predation rates differ between artificial and real nests, inferences from artificial nest experiments must be restricted to patterns in relative predation rates among treatments, habitats or locations (assessed with similar methodologies).

Artificial nest experiments remain valuable, nonetheless, because the degree of experimental control they offer allows tests of hypotheses that would be difficult or impossible to address using real nests. The egg-size effects we have demonstrated can even be turned to an investigator's advantage, with finch eggs (and/or clay) eggs used in conjunction with quail eggs in artificial nests to estimate relative predation rates by large- and small-mouthed predators. We concur with others (Sloan *et al.*, 1998; Wilson *et al.*, 1998) that the effects of habitat fragmentation on songbird reproduction may best be elucidated by a combination of artificial and real nest studies—but our results emphasize that artificial nest studies must be carefully designed and analyzed. In particular, the common practice of baiting nests with quail eggs can produce spurious edge effects because such eggs differentially sample large-mouthed relative to small-mouthed nest predators.

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