

- R. King, and K. C. Parkes, Eds.). Academic Press, Orlando, Florida.
- OLSON, S. L. 1992. *Neogaeornis wetzeli* Lambrecht, a Cretaceous loon from Chile (Aves: Gaviidae). *J. Vertebr. Paleontol.* 12:122-124.
- OLSON, S. L. 1994. A giant *Presbyornis* (Aves: Anseriformes) and other birds from the Paleocene Aquia Formation of Maryland and Virginia. *Proc. Biol. Soc. Wash.* 107:429-435.
- OLSON, S. L., AND D. C. PARRIS. 1987. The Cretaceous birds of New Jersey. *Smithson. Contrib. Paleobiol.* 63:1-22.
- WETMORE, A. 1926. Fossil birds from the Green River deposits of eastern Utah. *Ann. Carnegie Mus.* 16: 391-402.
- WOOD, D. S., AND G. D. SCHNELL. 1986. Revised world inventory of avian skeletal specimens, 1986. American Ornithologists' Union and Oklahoma Biological Survey, Norman, Oklahoma.
- ZUSI, R. L. 1984. A functional and evolutionary analysis of rhynchokinesis in birds. *Smithson. Contrib. Zool.* 395:1-40.

Received 21 February 1994, accepted 17 April 1994.

*The Auk* 112(3):767-770, 1995

## Forest Fragmentation and Nest Predation: Are Experiments with Japanese Quail Eggs Misleading?

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There is recent concern over the status of many Neotropical migrant bird populations. Reports of declining numbers and the continuing loss and degradation of breeding and overwintering habitats have prompted an upsurge of interest in the conservation biology of these birds (review papers in Hagan and Johnston 1992). Fragmentation of the breeding habitat in North America often is cited as one of the factors contributing to the decline of many species. Fragmentation is thought to act in two ways. First, brood-parasitic Brown-headed Cowbirds (*Molothrus ater*) thrive in fragmented landscapes, decreasing the productivity of many species (Brittingham and Temple 1983). Second, fragmentation is widely believed to increase rates of nest predation, further decreasing productivity (e.g. Wilcove 1985, Terborgh 1989, 1992).

The evidence that fragmentation of forests in eastern North America increases rates of nest predation is based on the results of experiments in which artificial nests baited with Japanese Quail (*Coturnix coturnix*) eggs are used to compare rates of predation in fragments of different sizes (Wilcove 1985, Small and Hunter 1988; see also Yahner and Scott [1988] who used chicken eggs). There is some evidence for the fragmentation effect based on studies of real nests in Europe (Møller 1988) and in grassland habitats in North America (Paton's [1994] reanalysis of Best 1978, Gates and Gysel 1978, Johnson and Temple 1990; Gates and Gysel's [1978] analysis included 10 nests of forest-dwelling birds). Despite the absence of data on the effects of fragmentation on the nesting success of real nests of forest-dwelling birds, the results of quail-egg studies have been widely accepted as reflecting relative trends for rates of predation on real bird nests

(e.g. Sieving 1992, Terborgh 1992, Böhning-Gaese et al. 1993).

The lack of parental and nestling activity and the potentially unnatural positioning and appearance of artificial nests complicates the interpretation of artificial-nest experiments. Studies that have investigated these, and other, potential biases (Boag et al. 1984, Martin 1987, Storaas 1988, Yahner and Voytko 1989, Götmark et al. 1990, Reitsma et al. 1990, Roper 1992) have reached conflicting conclusions as to the utility of artificial-nest experiments. Based on the scratch marks found on many of the quail eggs in artificial nests, Reitsma et al. (1990) suggested that small mammals may have attempted to consume the eggs, but failed to break them because of the animals' small mouths. Roper (1992) used a similar line of reasoning to account for the difference between predation rates on his real and artificial nests in the tropics, and concluded that quail-egg experiments were inappropriate for making comparisons between rates of nest predation in tropical and temperate habitats.

In this paper, I report the results of an experiment testing the suggestions of Reitsma et al. (1990). I discuss whether quail-egg experiments are an appropriate tool for investigating among-fragment differences in the rate of predation on Neotropical migrant bird nests. The potential inappropriateness of using quail eggs to estimate differences in rates of predation on the nests of Neotropical migrant birds becomes evident when the egg sizes of forest-nesting Neotropical migrant birds are compared to the size of quail eggs (Fig. 1). All Neotropical migrant passerines nesting in forests or scrub in eastern North America have eggs that are much smaller than quail eggs. I tested

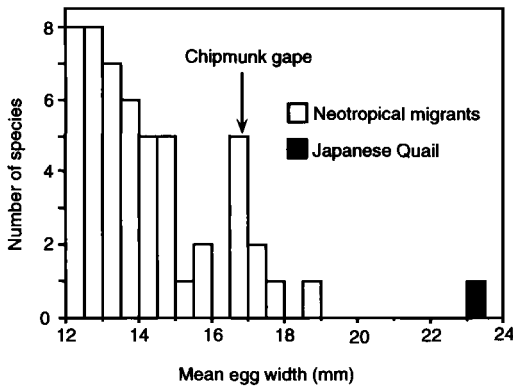


Fig. 1. Frequency distribution of mean egg widths for Japanese Quail and for passerines. Egg-size data from Harrison (1975). All eastern forest- and scrub-nesting Neotropical migrant passerine birds listed in Sauer and Droege (1992: table 2, forest and scrub habitat) are included in figure. Mean jaw gape of chipmunk is shown by arrow.

the hypothesis that eastern chipmunks (*Tamias striatus*) cannot eat the relatively large quail eggs used to bait artificial nests. If chipmunks cannot eat quail eggs, and if they are major nest predators in some habitats but not in others, then the results of artificial-nest experiments will not reflect differences in rates of nest predation in different habitats. I will address both these points in turn.

In November 1992, I trained wild chipmunks to feed at a pile of seeds 3 m away from the window of my house 10 km north of Ithaca, New York. The area in upstate New York is dominated by eastern hemlock (*Tsuga canadensis*). I counted six chipmunks at one time around the seed pile. After three days of training, the chipmunks were regularly visiting the area around the pile, so I removed the seeds and began the experiments, which involved presenting eggs to chipmunks as a possible food resource. Throughout the experiments, I provided no extra seeds for the chipmunks, so the only sources of food at the feeding site were the eggs that I presented. Each trial lasted until an egg was eaten or for 30 min after the first appearance of a chipmunk. In the first set of trials, which ran for five consecutive days, I placed one Japanese Quail egg and one Zebra Finch (*Poephila guttata*) egg on the site of the former seed pile. The average width of quail eggs was  $23.5 \pm \text{SD of } 1.24$  mm ( $n = 15$ ), whereas the average width of Zebra Finch eggs was  $10.8 \pm 0.56$  mm ( $n = 15$ ). From inside the house, I noted which eggs the chipmunks ate. In all 20 trials, the chipmunks quickly ate the Zebra Finch egg, but never consumed the quail egg. These results demonstrate that chipmunks can and do eat small eggs, even when presented outside of a nest, and suggest that they cannot eat quail eggs.

These results (and Roper's [1992] observations on a caged mouse-opossum [*Micoureus cinereus*]) cannot rule out the possibility, however, that the mammals being observed were inexperienced individuals and did not recognize the large eggs as food. In order to evaluate this possibility, I trained the chipmunks to associate quail eggs with food by placing broken quail eggs (with contents exposed) on the former seed pile every day for five days. During the next five days, I again placed whole quail eggs on the seed pile, observing the behavior of the chipmunks. All seven broken quail eggs were readily consumed. Despite seeming to search for food and pushing the whole eggs with their noses, the chipmunks never ate any of the 15 whole quail eggs, even though the same chipmunks had eaten broken quail eggs.

Another line of evidence suggesting that chipmunks cannot eat quail eggs comes from inspection of chipmunk skeletons in Cornell University's Vertebrate Collections. I measured the tooth-tip-to-tooth-tip gape of 10 adult specimens by placing the coronoid process of the lower jaw into its articulation, then opening the jaw until the angular process abutted onto the auditory bulla. Because these measurements were made on skeletons, they probably slightly overestimate the actual gape of the chipmunks. The mean gape size was  $17.0 \pm 1.79$  mm ( $n = 10$ ). Given the average width of quail eggs (23.5 mm), it would have been very difficult for the chipmunks to break or carry a quail egg with their teeth. In contrast, Zebra Finch eggs are well within the maximum gape of the chipmunks.

These experiments and observations suggest that chipmunks, at least in central New York, cannot consume quail eggs. Considered alongside data on the egg sizes of Neotropical migrant birds (Fig. 1), it is likely that artificial-nest experiments using quail eggs will underestimate predation rates wherever these relatively small-mouthed nest predators live. If small-mouthed nest predators rarely ate bird eggs, or if they were responsible for the same proportion of nest predation in all forest fragments, this underestimation of predation rates would not have much effect on the interpretation of artificial nest experiments used to compare rates of nest predation in different forest fragments.

Unfortunately, neither of these conditions appears to hold. Eastern chipmunks and other small-mouthed mammals (e.g. *Peromyscus*) are known to be egg and chick predators (Maxson and Oring 1978, Weeks 1978, Wells-Gosling and Heaney 1984, Guillory 1987, Reitsma et al. 1990), and they are common throughout much of the northeastern forests where many Neotropical migrant bird species breed. Furthermore, the relative importance of small mammals may vary according to the size of forest fragments. In Europe, Nour et al. (1993) used small artificial eggs and found that, as fragment size increased, the abundance of large-mouthed predators declined, but this decline

was compensated for by an increase in the abundance of small-mammal nest predators. Thus, they found no consistent effect of fragmentation on rates of nest predation. Although there have been no thorough studies of the effects of fragmentation on the abundance of nest predators in North American forests, it is clear that forest fragmentation profoundly changes the spectrum of nest predators that breeding birds have to face (cf. Yahner and Cypher 1987, Yahner et al. 1989; see also Robbins et al. 1989, Reitsma et al. 1990, Andr en 1992, Haskell 1995). The studies just cited suggest that in North America, as in Europe, large-mouthed nest predators such as American Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), raccoons (*Procyon lotor*) and feral house cats may be the dominant nest predators in small fragments, while small-mouthed mammalian nest predators may be relatively more common in large tracts of forest. The results of the study by Nour et al. (1993), combined with my observations, suggest that the negative correlation observed between fragment size and rates of nest predation in North America may be an artifact of the large quail eggs used to measure rates of nest predation.

Other factors may further confound the interpretation of quail-egg experiments. For example, if over time chipmunks could learn how to break quail eggs, the results of quail-egg experiments would be influenced by different levels of "quail-egg experience" in different chipmunk populations. C. Whelan (pers. comm.) noted that chipmunks in some populations in Illinois may be able to break quail eggs, whereas chipmunks in upstate New York (my study) do not. We might not be justified in using the results of quail-egg experiments to compare the relative rates of nest predation in Illinois and New York (cf. Wilcove 1985). Variations in levels of neophobia (e.g. Greenberg 1990) could exert another bias. If predators in fragmented or urban areas show reduced neophobia, or are more accustomed to human smell, they may be more likely to prey upon artificial nests that look and smell unusual than predators in areas far removed from human disturbance.

In conclusion, some small-mouthed mammals appear to be unable to eat the relatively large quail eggs that have been used to compare rates of predation in forest fragments of different sizes. Quail-egg experiments, therefore, may not accurately reflect predation by small-mouthed mammals in populations of birds with small eggs. In addition, given that the relative importance of small-mammal nest predators seems to be changed by forest fragmentation, the extent of this bias may vary across forest fragment sizes. Quail-egg experiments should not, therefore, be accepted as reflecting the true differences in relative rates of predation on the nests of Neotropical migrant birds living in fragmented landscapes.

*Acknowledgments.*—I thank C. R. Freeman, F. G tmark, J. P. McCarty, R. T. Holmes, S. K. Robinson, G.

D. Schnell, P. W. Sherman, S. A. Vance, and D. W. Winkler for helpful discussions, comments, and reviews of the manuscript. J. P. McCarty supplied the Zebra Finch eggs, K. J. McGowan helped with the museum specimens, and C. Hip and D. Ale helped with the experiments.

#### LITERATURE CITED

- ANDR EN, H. 1992. Corvid density and nest predation in relation to forest fragmentation. *Ecology* 73: 794-804.
- BEST, L. B. 1978. Field Sparrow reproductive success and nesting-ecology. *Auk* 95:9-22.
- BOAG, D. A., S. G. REEBS, AND M. A. SCHROEDER. 1984. Egg loss among Spruce Grouse inhabiting lodgepole pine forests. *Can. J. Zool.* 62:1034-1037.
- B HNING-GAESE, K., M. L. TAPER, AND J. H. BROWN. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? *Conserv. Biol.* 7:76-86.
- BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31-35.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- G TMARK, F., R. NEERGAARD, AND M. AHLUND. 1990. Predation of artificial and real Arctic Loon nests in Sweden. *J. Wildl. Manage.* 54:429-32.
- GREENBERG, R. 1990. Feeding neophobia and ecological plasticity: A test of the hypothesis with captive sparrows. *Anim. Behav.* 39:375-379.
- GUILLORY, H. G. 1987. Cavity competition and suspected predation on Prothonothary Warblers by *Peromyscus*. *J. Field Ornithol.* 58:425-427.
- HAGAN, J. M., III, AND D. W. JOHNSTON (EDS.). 1992. Ecology and conservation of Neotropical migrant birds. Smithsonian Institution Press, Washington, D.C.
- HARRISON, H. H. 1975. A field guide to the birds' nests. Houghton Mifflin, Boston.
- HASKELL, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of predation on bird nests. *Conserv. Biol.* 9:1316-1318.
- JOHNSON, R. G., AND S. A. TEMPLE. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *J. Wildl. Manage.* 54:106-111.
- MARTIN, T. E. 1987. Artificial nest experiments: Effects of nest appearance and type of predator. *Condor* 89:925-928.
- MAXON, S. J., AND L. W. ORING. 1978. Mice as a source of egg loss in ground-nesting birds. *Auk* 95:582-584.
- M LLER, A. P. 1988. Nest-site selection across field-woodland ecotones: The effect of nest predation. *Oikos* 56:240-246.
- NOUR, N., E. M. MATTHYSEN, AND A. A. DHONDT. 1993. Artificial nest predation and habitat fragmenta-

- tion: Different trends in bird and mammal predators. *Ecography* 16:111-116.
- PATON, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conserv. Biol.* 8:17-26.
- 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.
- ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds in the middle Atlantic states. *Wildl. Monogr.* 103.
- ROPER, J. J. 1992. Nest predation experiments with quail eggs: Too much to swallow? *Oikos* 65:528-530.
- SAUER, J. R., AND S. DROEGE. 1992. Geographical patterns in population trends of Neotropical migrants in North America. Pages 26-42 in *Ecology and conservation of Neotropical migrant birds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- SIEVING, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of central Panama. *Ecology* 73:2310-2328.
- SMALL, M. F., AND M. L. HUNTER. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76:62-64.
- STORAAS, T. 1988. A comparison of losses in artificial and naturally occurring Capercaillie nests. *J. Wildl. Manage.* 52:123-26.
- TERBORGH, J. 1989. *Where have all the birds gone?* Princeton Univ. Press, Princeton, New Jersey.
- TERBORGH, J. 1992. Perspectives on the conservation of Neotropical migrant landbirds. Pages 7-12 in *Ecology and conservation of Neotropical migrant birds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- WEEKS, H. P. 1978. Clutch-size variation in the Eastern Phoebe in southern Indiana. *Auk* 95:654-666.
- WELLS-GOSLING, N., AND L. R. HEANEY. 1984. *Glaucomys sabrinus*. Mammalian species 229. American Society of Mammalogists, New York.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- YAHNER, R. H., AND B. L. CYPHER. 1987. Effect of nest location on depredation of artificial arboreal nests. *J. Wildl. Manage.* 51:178-181.
- YAHNER, R. H., AND D. P. SCOTT. 1988. Effects of forest fragmentation on depredation of artificial nests. *J. Wildl. Manage.* 52:158-161.
- YAHNER, R. H., T. E. MORRELL, AND J. S. RACHAEL. 1989. Effect of edge contrast on depredation of artificial avian nests. *J. Wildl. Manage.* 53:1135-1138.
- YAHNER, R. H., AND R. A. VOYTKO. 1989. Effects of nest-site selection on depredation of artificial nests. *J. Wildl. Manage.* 53:21-25.

Received 5 April 1994, accepted 16 May 1994.

*The Auk* 112(3):770-774, 1995

## A Prairie Warbler with a Conspecific and Heterospecific Song Repertoire

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Song in most oscine passerines is suspected to develop through imitative learning (Kroodsma 1982, Spector 1992). In the genus *Dendroica*, it has been shown that both song and the context of its use are learned from adult tutors (Kroodsma et al. 1983, Spector 1992). The learning of heterospecific song may be constrained by many factors, including species-specific (genetic) auditory templates for learning (Marler

1975), limitations of the vocal apparatus (Thorpe 1961), and behavioral and ecological aspects that may isolate birds during critical learning periods (e.g. Lanyon 1957). Despite these constraints, learning of heterospecific song has been observed in both the field and the laboratory, particularly in the subfamily Parulinae (see Spector 1992).

In many reported cases of interspecific song learning, the learned songs differ structurally from those of the mimicked species, or are simply incorporated as components of conspecific song (e.g. Baptista 1972, Kroodsma 1972, Kroodsma et al. 1983, Payne et al. 1984). Aspects of singing behavior associated with heterospecific song are not often described in the wild.

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