

- delity in relation to breeding success in Cory's Shearwater *Calonectris diomedea*. *Bird Study* 41: 25–28.
- WINK, M., P. HEIDRICH, U. KAHL, AND I. SWATSCHKE. 1993. Inter- and intraspecific variation of the nucleotide sequence of the cytochrome *b* gene in Cory's Shearwater (*Calonectris diomedea*), Manx Shearwater (*Puffinus puffinus*) and the Fulmar (*Fulmarus glacialis*). *Zeitschrift Naturforschorschung* 48:504–509.
- WOLFF, J. O. 1993. What is the role of adults in mammalian juvenile dispersal? *Oikos* 68:173–176.
- WOOLLER, R. D., J. S. BRADLEY, AND J. P. CROXALL. 1992. Long-term population studies of seabirds. *Trends in Ecology and Evolution* 7:111–114.

Received 28 January 1997, accepted 11 August 1997.

Associate Editor: R. M. Zink

*The Auk* 115(2):486–489, 1998

## Chipmunks Use Leverage to Eat Oversized Eggs: Support for the Use of Quail Eggs in Artificial Nest Studies

DAVID P. CRAIG<sup>1</sup>

*Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Colorado 80309, USA*

Several authors have questioned the use of Japanese Quail (*Coturnix japonica*) eggs as bait in artificial nests (Roper 1992, Haskell 1995a, DeGraaf and Maier 1996, Major and Kendal 1996). Based on observations at a feeding station, Haskell (1995a) concluded that the gape of eastern chipmunks (*Tamias striatus*) was not sufficiently wide to open quail eggs. Consequently, Haskell (1995a,b) questioned the validity of studies that use quail eggs in artificial nests to evaluate the relationship between nest predation and forest fragmentation. In this paper, I focus on the behavior of least chipmunks (*Tamias minimus*) eating quail eggs in artificial nests in the Colorado Front Range. Observations of other sciurids also are described to add to the general understanding of rodent predation behavior (Callahan 1993). I also comment on possible biases in Haskell's (1995a) observations of chipmunk egg predation and the weak support of his critical view of quail-egg experiments (1995b). Finally, I suggest a protocol for evaluating a potential predator's ability to consume eggs.

**Methods.**—I used two sources of data. First, 10 predation events by sciurids were observed without a blind during the summers of 1993 to 1996 in the foothills of Boulder County, Colorado. Observations were collected opportunistically from artificial nests as part of a broader study of nest predation by corvids (Craig 1997). Artificial nests resembling nests of American Robins (*Turdus migratorius*) were constructed from mud, grass, and a wicker basket and

placed 1 to 2 m above the ground in conifers. Each nest had a fine-grass lining, one or two *Coturnix* quail eggs, and a color-matched plasticene egg (hereafter "clay" egg) wired to the nest. Predators often were startled during observations, and I never observed the initial attack on artificial nests.

Second, I observed predator behavior during the entire predation event from a blind by staging predation events in July and August of 1995. An artificial nest (with one clay egg and two quail eggs) was placed on a porch rail 3 m from a platform feeder that was visited frequently by a variety of birds, least chipmunks, and fox squirrels (*Sciurus niger*). A total of 15 separately constructed nests (30 quail eggs and 15 clay eggs) was used. Nests were placed on the porch railing repeatedly and were not independent of each other. This may have facilitated habituation by the predators to the nests and eggs. Nevertheless, Steller's Jays (*Cyanocitta stelleri*) and Black-billed Magpies (*Pica pica*) regularly nested in the study area (pers. obs.), and their eggs are about the same size and shape as quail eggs (Harrison 1979).

**Results.**—During four years of opportunistic observations, I observed chipmunks (*T. minimus* and *T. quadrivittatus*) eating eggs from artificial nests three times. Twice the chipmunks were recorded eating an egg in the nest and once on the ground directly below the nest. It is possible that the egg on the ground fell out of the nest, broke open, and then was consumed. Nevertheless, in all three cases the egg was opened through its small end. During the same period, one golden-mantled ground squirrel (*Spermoph-*

<sup>1</sup> E-mail: dcraig@columbia-center.org

*ilus lateralis*) with an egg in its mouth was observed on a tree trunk below an artificial nest. Red squirrels (*Tamiasciurus hudsonicus*) were observed eating eggs twice in the nest, twice on a branch immediately above the nest, and once at the base of the artificial nest tree. An Abert's squirrel (*Sciurus aberti*) with an egg in its mouth was seen on the trunk of a tree 2 m above an artificial nest. With the exception of the Abert's squirrel, all eggs eaten by squirrels were opened on the small end or on a side near the small end.

From the blind, I observed at least four different chipmunks (distinct pelage patterns) eat 17 quail eggs. Each chipmunk approached the nest hesitantly and initially probed the eggs with its nose from outside the nest. The chipmunks then entered the nest and pushed the eggs around, occasionally mouthing the sides of the egg. It appeared that a chipmunk's gape was not wide enough to bite an egg from the side or the large end. However, once an egg was lodged between a chipmunk's body and the inside edge of the nest (which took 3 s to 2 min), the chipmunk bit through the small end of the egg with little apparent difficulty. If no other animals approached the nest, the chipmunk ate the eggs in or immediately adjacent to the nest. On seven occasions when another chipmunk, squirrel, or bird approached, the chipmunk ran to the cover of a nearby wood pile with the opened egg in its mouth. Twice a chipmunk dropped an egg but then immediately picked it up by the opening made from previous bites. Nests depredated by chipmunks always contained eggshell fragments. Chipmunks also probed the bottom of the nest with their nose and scratched with their paws, which generally dislodged the fine-grass lining.

Chipmunks that initially failed to open a quail egg ( $n = 9$ ) tried the other quail egg ( $n = 5$ ) or the clay egg ( $n = 4$ ). In four cases chipmunks tried a clay egg first. In contrast to the quail eggs, chipmunks immediately drove their teeth into the clay eggs. The bite orientation on a clay egg depended on the egg's position when the chipmunks tried to bite. Chipmunks had no apparent trouble biting at the clay egg's greatest circumference. On 6 of 15 clay eggs, the chipmunks chewed at least 50% of the clay, but never more than 75%. Chipmunks apparently did not ingest any clay because all of the eggs could be reformed to their original size. In all cases, the chipmunks again attempted to open a real egg and eventually broke through the small end.

Of the remaining 13 eggs, 8 were taken by at least two different fox squirrels. In five of eight observations, the fox squirrel initially bit a real egg. After the first real egg was consumed, fox squirrels started on either the second real egg or the clay egg. In all cases, the clay egg eventually was marked by a bite. In two cases, fox squirrels chewed more than 75% of the clay egg. A real egg was removed from the nest and moved more than 1 m twice, but the clay egg wired

to the nest never moved. Eggshell fragments were left behind following seven of the eight fox squirrel predation events, and in five of the nests the fine-grass lining was disturbed.

*Discussion.*—In contrast to eastern chipmunks in New York (Haskell 1995a), least chipmunks in Colorado consumed quail eggs consistently. Chipmunk predation on quail eggs also was documented by Reitsma (1990) in New Hampshire and C. Whelan (in Haskell 1995a) in Illinois. Haskell (1995a) presented eggs of Zebra Finches (*Taeniopygia guttata*) and quail at a feeder where chipmunks had been trained to visit a seed pile. Chipmunks ate the Zebra Finch eggs but not the quail eggs, unless the latter were broken open by a human and placed on the seed pile (Haskell 1995a). Haskell noted that chipmunks pushed unbroken eggs around as if they were searching for food, and he estimated that an eastern chipmunk's gape ( $17.0 \pm \text{SD of } 1.79 \text{ mm}$ ) was not large enough to break or carry a quail egg.

The diameter of quail eggs was near or larger than the gape size of the chipmunks that I studied. Nevertheless, chipmunks in Colorado consumed and carried quail eggs by biting through the small end of the eggs. Least chipmunks measured in the University of Colorado Museum had a gape of  $16.0 \pm 1.68 \text{ mm}$  ( $n = 10$ ), which is the same size or smaller than that of eastern chipmunks (Haskell 1995a). Having eaten the more easily handled sunflower seeds, Zebra Finch eggs, and broken quail eggs, eastern chipmunks may not have been motivated to pursue the more difficult-to-handle unbroken quail eggs. Zebra Finch eggs are smaller, and presumably easier to manipulate, than are eggs of the 51 species of Neotropical migrant passerines referenced by Haskell (1995a: figure 1). Perhaps more importantly, because quail eggs were not placed in a nest in Haskell's (1995a) study, the chipmunks may not have had the physical leverage they needed to attack the small end of the egg.

The concern that predation rates may be underestimated when bait eggs are significantly larger than those of the species of interest is valid. Although quail eggs have a larger diameter than eggs of many passerines, my observations suggest that the shape of the small end of the eggs, coupled with a chipmunk's ability to use the nest for leverage, make quail eggs useful for identifying predators as small as chipmunks. Thus, the maximum gape size of a predator being smaller than the width of an egg may not be sufficient to eliminate that animal as a potential predator.

Nonetheless, small mammals sometimes break into or distinctly mark eggs larger than their gape size by attacking the small end of the egg. Reitsma (1990) documented a deer mouse (*Peromyscus maniculatus*) in a nest and reported a small number of unbroken quail eggs with scratch marks that he believed came from chipmunks, mice, and shrews.

Maxson and Oring (1978) reported mouse scratches on Spotted Sandpiper (*Actitis macularia*) eggs and also observed eggs with two small punctures about 8 mm apart. Deer mice have been observed biting the small ends of quail eggs and leaving scratch marks (V. Lewin in Boag et al. 1984). Leimgruber et al. (1994) also documented predation by a white-footed mouse (*Peromyscus leucopus*) and a gray squirrel (*Sciurus carolinensis*) on quail eggs. Boag et al. (1984) found that red squirrels that chewed the small end of quail eggs invariably left scratch marks and punctured the egg a least half of the time.

DeGraaf and Maier (1996) tested the ability of captive white-footed mice to consume eggs of different sizes. White-footed mice consumed Zebra Finch eggs but not Japanese Quail eggs. Because eggs were placed in wicker nests, the mice probably were below a gape-size or dexterity threshold for which a nest was of assistance (i.e. provided leverage). White-footed mice did not leave scratch marks on quail eggs (DeGraaf pers. comm., Leimgruber pers. comm.).

The chipmunks in my study broke open quail eggs and also left tooth marks on large fragments of eggshell that remained in or near the nest. In another Colorado study using 800 artificial nests (Craig 1997), I found similar scratches on unbroken quail eggs in five nests where the clay eggs were distinctly bitten by chipmunks. Eggs in an additional two of the 800 artificial nests had mouse tooth marks (probably deer mice) in the clay, as well as scratches on the quail eggs.

It appears that although some small mammals may have difficulty opening quail eggs, the presence of a quail egg is sufficient to attract these predators to artificial nests. If an appropriate predator identification system such as fastened clay eggs (Nour et al. 1993, Craig 1997) or automatic cameras (Reitsma et al. 1990, Leimgruber et al. 1994) also is present, quail eggs can be useful as bait for artificial nests. Quail eggs may not be appropriate if used alone because unsuccessful depredation attempts would not be detected.

It is not known whether eggs smaller than quail eggs provide a more accurate assessment of predation on songbird eggs. However, Sieving and Willson (unpubl. data) found no significant differences between predation and disturbance rates of ground nests with *Coturnix* eggs versus the much smaller buttonquail (*Turnix* sp.) eggs. In contrast, other field experiments have been conducted in which removal rates were higher on finch eggs than on quail eggs (T. Martin unpubl. data, R. DeGraaf unpubl. data). A stronger test of Haskell's suggestion of a quail-egg bias would have been to compare predation rates of clay eggs against those of quail eggs. At my study sites, such tests indicated no differences when I included scratch marks as evidence of attempted predation (Craig 1997).

It is important to secure clay eggs to a nest. Ro-

dents often transport eggs for distances that would make it difficult to discover the eggs' remains (e.g. Maxson and Oring 1978, Boag et al. 1984). In my study, 7 of 17 and 3 of 8 eggs eaten by chipmunks and fox squirrels, respectively, were removed from the nest. Because they were wired to nests, no clay eggs were removed. In separate field trials, clay eggs with red squirrel tooth marks occasionally were found a few meters up the nest tree with only the wire and a few traces of clay left behind (Craig 1997). In one case, the wicker basket was chewed apart, separating the wire and clay egg, which were found 5 m away with red squirrel tooth marks. An advantage of having both attached clay and real eggs in an artificial nest is that eggshell fragments may be left behind in the rare cases when the clay is removed. In a field test of the quail-egg size bias, Haskell (1995b) suggested that all missing eggs resulted from corvid predation. Although corvids typically remove eggs before consuming them (Hill 1988, Haskell 1995b), Haskell's nests with unsecured clay eggs do not provide dependable data for discriminating between predators that may remove eggs from the nest. Raccoons (*Procyon lotor*), which depredated some of Haskell's (1995b) nests, also may remove eggs from a nest before consuming them (Rearden 1951, Leimgruber unpubl. data).

When choosing eggs to use in an artificial nest, the ultimate goal should be to use an egg that closely resembles the species of interest (Sieving 1992). Pragmatically, however, Japanese Quail and Northern Bobwhite (*Colinus virginianus*) eggs are among the only commercial eggs available in large quantities (pers. obs.). Zebra Finch eggs are possible substitutes for bait in artificial nests, especially if mice are important predators (DeGraaf and Maier 1996, T. Martin pers. comm.). Because Zebra Finch eggs are smaller than the eggs of many birds of interest (Harrison 1975, 1979, Haskell 1995b), researchers should be aware that these eggs may experience higher predation rates because of the relative ease with which they are handled and consumed. The fundamental problem of using quail or finch eggs is not necessarily the size of the egg, but a general ignorance of predator behavior at the nest and predator abundance in different habitats. Therefore, it may be premature to reject quail-egg experiments in studies of the relative predation rates on bird nests.

A more informative approach would be to continue in the spirit of Haskell (1995a) and further evaluate the biases of quail eggs in artificial nests. DeGraaf and Maier (1996) provide an excellent model for such studies using captive animals. Wild animals also should be observed to determine: (1) how eggs are handled (e.g. rolled on ground, wedged against side of nest, carried in mouth unbroken or by a puncture); (2) where eggs are eaten (i.e. in the nest or cavity, above the nest, away from the nest); (3) how eggs are consumed (e.g. broken at the small end

or side, scratch marks made by teeth on outside of shell); (4) size of eggs (i.e. length, width, shell thickness); (5) predator handling ability (e.g. mouth gape, dexterity of feet and/or mouth, age or experience); (6) utility of using clay eggs for predator identification (e.g. frequency of predator bites, type of marks); and (7) behavior in response to automatic cameras and other measuring equipment at the nests. These types of observations will enhance the interpretation of field sign at and around both artificial and natural nests and also will help define the limits of artificial nest data. More importantly, however, these data will contribute to a better understanding of the variation in behavior within and among nest predators.

*Acknowledgments.*—I thank T. Martin, L. Reitsma, K. Sieving, and an anonymous reviewer for useful reviews of the manuscript. M. Bekoff, M. Berry, C. Bock, K. Collis, D. M. Craig, and K. Veirling also made substantial comments. Additional thanks to M. Bekoff for the use of his home study site. M. Tracy, R. Fletcher, and E. Byram helped in the field.

#### LITERATURE CITED

- BOAG, D. A., S. G. REEBS, AND M. A. SCHROEDER. 1984. Egg loss among Spruce Grouse inhabiting lodge-pole pine forests. *Canadian Journal of Zoology* 62:1034–1037.
- CALLAHAN, J. R. 1993. Squirrels as predators. *Great Basin Naturalist* 53:137–144.
- CRAIG, D. P. 1997. An experimental analysis of nest predation in western coniferous forests: A focus on the role of corvids. Ph.D. dissertation, University of Colorado, Boulder.
- DEGRAAF, R. M., AND T. J. MAIER. 1996. Effect of egg size on predation by white-footed mice. *Wilson Bulletin* 108:535–539.
- HARRISON, H. H. 1975. A field guide to birds' nests. Houghton Mifflin, Boston.
- HARRISON, H. H. 1979. A field guide to western birds' nests. Houghton Mifflin, Boston.
- HASKELL, D. G. 1995a. Forest fragmentation and nest predation: Are experiments with Japanese Quail eggs misleading? *Auk* 112:767–770.
- HASKELL, D. G. 1995b. A reevaluation of the effects of forest fragmentation on rates of predation on birds nests. *Conservation Biology* 9:1316–1318.
- HILL, G. 1988. Age, plumage brightness, territory quality, and reproductive in the Black-headed Grosbeaks. *Condor* 90:379–388.
- LEIMGRUBER, P., W. MCSHEA, AND J. RAPPOLE. 1994. Predation on artificial nests in large forest blocks. *Journal of Wildlife Management* 58:254–260.
- MAJOR, R. E., AND C. E. KENDAL. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: A review of methods and conclusions. *Ibis* 138:298–307.
- MAXSON, S. J., AND L. W. ORING. 1978. Mice as a source of egg loss in ground-nesting birds. *Auk* 95:582–584.
- NOUR, N., E. M. MATHYSEN, AND A. A. DHONDT. 1993. Artificial nest predation and habitat fragmentation: Different trends in bird and mammal predators. *Ecography* 16:111–116.
- REARDEN, J. D. 1951. Identification of waterfowl nest predators. *Journal of Wildlife Management* 15:386–395.
- REITSMA, L. R. 1990. Importance of nest predation to avian population regulation and community structure in a northern hardwood forest. Ph. D. dissertation, Dartmouth College, Hanover, New Hampshire.
- 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.
- ROPER, J. J. 1992. Nest predation experiments with quail eggs: Too much to swallow? *Oikos* 65:528–530.
- SIEVING, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of central Panama. *Ecology* 73:2310–2328.

Received 24 March 1997, accepted 19 August 1997.

Associate Editor: T. E. Martin