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THE ADAPTIVE SIGNIFICANCE OF EGGSHELL REMOVAL BY NESTING BIRDS: TESTING THE EGG-CAPPING HYPOTHESIS[1]

Todd W. Arnold
Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan N6A 5B7, Canada

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Many birds remove empty eggshells from their nests soon after their nestlings have hatched (reviewed by Nethersole Thompson and Nethersole Thompson 1942, Tinbergen et al. 1963). Tinbergen et al. (1963) suggested five possible reasons why birds might remove hatched eggshells from the nest: (1) sharp shell edges could injure newly hatched chicks, (2) unhatched eggs could become trapped inside hatched shells, thereby reducing hatchability, (3) hatched shells could interfere with brooding, (4) hatched shells could reduce nest hygiene and increase the risk of bacterial infection, and (5) hatched shells could reduce nest camouflage, thereby increasing the risk of predation by visually-oriented predators. Through an elegant series of experiments on eggshell removal in Common Black-headed Gulls (*Larus ridibundus*), Tinbergen (1963) and colleagues (Tinbergen et al. 1963) found considerable support for the nest-camouflage hypothesis, but they did not test any of the other four hypotheses.

Removal of hatched eggshells has been observed in a variety of birds where nest camouflage seems to be an unlikely selective advantage. Common Ringed Plovers (*Charadrius hiaticula*) and Red Knots (*Calidris canutus*) have precocial offspring that leave the nest soon after hatching, yet they remove hatched eggshells from their nests (Tinbergen et al. 1963, Whitfield and Brade 1991). Hatched eggshells are also removed by a variety of cup- and cavity-nesting passerines (Nethersole Thompson and Nethersole Thompson 1942; Arnold, pers. observ.), but empty shells are unlikely to increase the conspicuousness of these birds' nests. Thus, it seems unlikely that the nest-camouflage hypothesis can account for eggshell removal in all species of birds.

Derrickson and Warkentin (1991) recently reported several instances in which unhatched eggs became trapped inside the shells of previously-hatched eggs, a phenomenon that they referred to as "egg-capping." They suggested that egg-capping could lower hatchability by reducing embryonic gas exchange or by interfering with the pipping process, and that egg-capping might be an important and unappreciated factor affecting the evolution of eggshell removal in birds. Derrickson and Warkentin (1991) reported that two of two capped eggs in a single Northern Mockingbird (*Mimus polyglottos*) nest failed to hatch, and that two of two capped Merlin (*Falco columbarius*) eggs from two different nests failed to hatch (but both of these eggs turned out to be infertile). Although their data are suggestive of a hatchability cost to egg-capping, their limited observations constitute insufficient evidence of such a cost.

In this note, I attempt to test the egg-capping hypothesis as it relates to eggshell removal by American Coots (*Fulica americana*). American Coots usually remove newly-hatched eggshells from their nests within an hour of hatching (Arnold, pers. observ.). This is probably not related to nest camouflage because hatched eggshells are relatively inconspicuous in comparison to the large overwater nest bowls used by coots. Moreover, American Coots suffer very low rates of nest predation during hatching (ca. 0.2% daily loss rate; Arnold, unpubl. data), and losses are mostly caused by

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nocturnal mammals (i.e., olfactory predators). However, I have observed several coot nests where an unhatched egg became entrapped inside the shell of a previously hatched egg. Egg-capping was detected at 2 of 61 nests (3.3%) in 1987, 3 of 119 nests (2.5%) in 1988, and 1 of 54 nests (1.9%) in 1990, for an overall rate of 2.6% (only those nests visited during the hatching stage have been included in these estimates). In the absence of egg removal by the parents, egg-capping seems especially likely among coots because nest bowls are often crowded, hatch is highly asynchronous, and (with the exception of the first three to four eggs) egg size declines with laying sequence (Arnold 1991), so late-laid eggs can fit readily inside the empty shells of earlier-hatching eggs. I was unable to determine the fates of these naturally capped eggs because eggshells are fairly opaque (and hence difficult to candle), chicks leave the nest in response to an approaching human (and hence hatching success cannot be inferred by counting nestlings), hatch is asynchronous and may be spread over as long as 10 days (necessitating numerous nest visits), and most importantly, parents often remove unhatched eggs from the nest bowl (Arnold, unpubl. data). Therefore, to better evaluate the effects of egg-capping on hatchability of coot eggs, I conducted an incubator experiment where I could positively ascertain hatching success.

Field and lab work were conducted at the Minnedosa Substation of the Delta Waterfowl and Wetlands Research Station in southwestern Manitoba during the summers of 1988 and 1991. I collected 70 coot eggs from 23 nests in which at least one egg had already hatched. Eggs were candled to verify that they were fertile and that normal development had begun (embryo development ranged from approximately 14 days to pipping). Eggs were then randomly assigned to two groups. One group of eggs was designated as controls; each egg from the other group was encased in a previously hatched eggshell. The inner membranes of these eggshells were dry and had to be moistened to allow the unhatched eggs to be slipped inside them. Capped and control eggs were then placed in a Petersime® Model 4 rotary incubator where temperature and relative humidity were set at 37.5°C and 70%.

Among controls, 29 of 35 eggs hatched (83%), whereas 27 of 35 capped eggs hatched (77%). This slight (6%) reduction in hatchability was not significant (Fisher's exact test, 1-tailed, $P = 0.38$), and I was therefore unable to reject the null hypothesis that egg-capping has no effect on hatchability. However, it is important to assess the power of a statistical test whenever the null hypothesis is not rejected, because nonsignificant results may be due to lack of statistical power rather than absence of the effect being tested (Toft and Shea 1983). Assuming that 83% accurately reflects the hatching success of control eggs, observed hatching success of capped eggs would have had to decline to ≤60% in order to obtain a significant 1-tailed test at $P \leq 0.05$. Simulation results suggest that "true hatchability" of capped eggs would have had to be ≤48% in order to have a ≥80% chance of detecting a significant difference between capped and control eggs, given the sample sizes used in this experiment. In order to have an 80% chance of detecting a 10% difference in hatchability between capped and control eggs (assuming ~85% hatching success among controls), sample sizes would have had to include approximately 200 eggs per treatment group (McDonald 1977). Such samples would have been impossible for me to justify in my study, and probably would be difficult to justify for other investigators that work with wild birds. Adequate sample sizes to test for small effect sizes can probably best be obtained from domestic birds (e.g., Japanese Quail or chickens). Thus, although I observed no cost to egg-capping in my experiment with American Coots, I concede that my experiment could not easily have detected reductions in hatchability of ≤30%. It is impossible to guess how small the effect of egg-capping must be before it becomes evolutionarily insignificant, but for American Coots egg-capping is clearly not as deleterious as Derrickson and Warkentin's (1991) observations might suggest.

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