The Auk 113(3):703–705, 1996

Occurrence of Egg-capping in Birds' Nests

NICOLAAS A. M. VERBEEK
Department of Biology, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

Most parent birds remove eggshells from the nest shortly after hatching. Eggshells may be carried away (e.g. American Pipit [*Anthus rubescens*]; Verbeek and Hendricks 1994), tossed from the nest (e.g. Indigo Bunting [*Passerina cyanea*]; Morgan 1976), left in the nest and sometimes trampled (e.g. Blue Grouse [*Dendragapus obscurus*]; Zwickel 1992), or various combinations of these behaviors (e.g. Gray Catbird [*Dumetella carolinensis*]; Zimmerman 1963). Species that remove eggshells do so soon after hatchlings have freed themselves from the eggs. In some species, removal of eggshells can have considerable survival value for the as yet unhatched eggs (e.g. Black-headed Gull [*Larus ridibundus*]; Tinbergen et al. 1962). Tinbergen et al. listed five possible functions for eggshell removal and concluded that predator avoidance was the most important. As Derrickson and Warkentin (1991) pointed out, however, predator avoidance is not a convincing reason for eggshell removal in species with hidden nests. Another function listed by Tinbergen et al. was prevention of shells from slipping over unhatched eggs (which could interfere with the hatching of those eggs). This phenomenon may be widespread but rarely reported because it is easily overlooked or considered trivial. A recent paper by Derrickson and Warkentin (1991), who coined the term "egg-capping," prompted me to report the following observations.

Study area and methods.—I observed egg-capping during studies of: Glaucous-winged Gulls (*Larus glaucescens*) on Mitlenatch Island, British Columbia (49°57'N, 125°00'W) in 1985 and 1986; Northwestern Crows (*Corvus caurinus*) on Mitlenatch and Mandarte (48°38'N, 123°17'W) islands, British Columbia from 1976 to 1995; and American Pipits at Beartooth Pass, Wyoming (45°00'N, 109°30'W) in 1963 and 1964. Nests of these species were checked daily during the egg-laying and hatching periods.

Results.—Less than 2% of nests with at least one egg that survived to the time of hatching contained a capped egg, and less than 0.4% of all eggs laid that survived to the time of hatching were capped (Table 1). Among the various causes that resulted in eggs failing to hatch (e.g. predation and infertility), egg-capping made up less than 3% (Table 1). In all five cases of egg-capping that I observed, none of the eggs hatched.

Discussion.—When reporting on egg-capping, it seems most useful to express its occurrence based on nests that hatch at least one egg and in terms of all eggs that survive to the time of hatching, regardless of whether they hatched. Using these criteria, useful comparative data are scarce. Derrickson and Warkentin (1991) reported single instances of egg-capping in 2 (1.4%) of 145 Merlin (*Falco columbarius*) nests and two cases in 1 (1.3%) of 79 Northern Mockingbird (*Mimus polyglottos*) nests that hatched eggs. Arnold (1992) found single cases of egg-capping in 6 (2.6%) of 234 American Coot (*Fulica americana*) nests "visited during the hatching stage." It is unclear from Arnold's report how many of these 234 nests did not hatch at least one egg. The results of Derrickson and Warkentin (1991) are similar to mine for American Pipit and Northwestern Crow nests (Table 1). The total numbers of eggs contained in the Merlin, Northern Mockingbird, and American Coot nests were not provided.

Egg-capping appears to be an extremely rare event. In the nine cases reported here (including four in Derrickson and Warkentin [1991]), none of the affected eggs hatched. Arnold (1992) was not able to follow the fate of capped American Coot eggs. For this and possibly other reasons (Tinbergen et al. 1962), one would expect strong selection in favor of diligent and prompt removal of empty shells. Arnold (1992) experimentally capped 35 fertile American Coot eggs and compared them with 35 fertile, uncapped eggs. When put in an incubator, capped eggs had lower hatching success than controls, but the difference was not significant. Arnold (1992) calculated that his sample size was too small for an adequate test, but nevertheless, it appears that egg capping in American Coots is less harmful than in the other species mentioned above. It would be interesting to repeat this experiment by comparing the hatching success of capped and uncapped eggs incubated by the coots themselves, rather than by an incubator.

A survey of the first 160 accounts (omitting the two cowbirds [*Molothrus*]) in the *Birds of North America* series (see citations of individual accounts) showed that 25 species (15.6%) either routinely (11 species) or occasionally (14 species) left eggshells in the nest. If the risk of egg-capping has selected for removal of eggshells, why do 15.6% of the species leave eggshells in the nest? Three of the 25 species lay single-egg clutches, so egg-capping is not a problem. Of the remaining 22 species, 16 have shallow (i.e. saucer-shaped, scrape, or platform) "ground" nests (Ehrlich et al. 1988), except the Black Rail (*Laterallus jamaicensis*), which has a cup-shaped nest. Of the remaining six species, two have platform nests in trees and four nest in cavities (two build saucer-shaped nests). Eggshells in shallow nests are less likely to gravitate to the center of the nest than in cup-shaped nests (which

TABLE 1. The occurrence of egg-capping in nests of Glaucous-winged Gulls, Northwestern Crows, and American Pipits.

	Glaucous-winged Gull	Northwestern Crow	American Pipit
No. nests examined[a]	501	263	69
No. eggs laid[b]	1,164	765	314
No. capped eggs	1	3[c]	1
Percent of nests with capped eggs	0.20	1.14	1.45
Percent of eggs laid that were capped	0.09	0.39	0.32
No. eggs not hatched	113	106	44
Percent of unhatched eggs that were capped	0.88	2.83	2.27

[a] All nests having one or more eggs that survived to potential time of hatching.

[b] Total eggs laid minus those that disappeared before potential time of hatching.

[c] One egg in each of three nests.

are typical of passerine nests). In addition, almost all the species are medium to large in size. Large size makes trampling of eggshells easier. Fragments of eggshells could injure nestlings, but among the 22 species, 14 are precocial and downy at hatching, and 8 are altricial or semialtricial, of which 5 are downy and 3 naked. Notably, none of the 22 species is a passerine. Being covered in down may reduce the chance of injury by eggshell fragments. Only 63 passerines have been dealt with in the first 160 *Birds of North America* accounts. These passerines are not known to leave eggshells in the nest or trample them, most likely because they build cup-shaped nests and have naked young. The only option left to passerines is to dispose of the shells.

Species that carry eggshells away from the nest will have difficulty doing so at night unless they see well in low light, as do owls and caprimulgids. Shells of eggs that hatch at night can be disposed of by leaving them in the nest and trampling them (only medium to large birds appear to do this), tossing them out of the nest, or eating them. Few species (19 of 160; 11.9%) toss eggshells from the nest, either habitually or in combination with eating, carrying, or leaving them in the nest. Those that do, typically nest in safe sites (e.g. Cliff Swallow [*Hirundo pyrrhonota*]; Brown and Brown 1995) or are large (e.g. White Ibis [*Eudocimus albus*]; Kushlan and Bildstein 1994). Only 20 of 160 species (12.5%) are reported to eat eggshells habitually or in combination with other ways of removing them; this total includes nine passerines.

For species that carry eggshells from the nest, and which cannot do this at night, shells from eggs that hatch at night must remain in the nest until dawn, thus increasing the chance of egg-capping. I suggest that the potential risk of egg-capping in such species may contribute to selection in favor of eggs hatching during the day. We know almost nothing about when eggs hatch in a 24-h day. A survey of the first 160 species accounts in *The Birds of North America* series showed that we do not know the hatching times of 129 species. Hatching times are given for the remaining 31 species, but many of these are vague, such as "early in the morning," which could mean before or after sunrise.

At present, we know very little about the frequency of occurrence of egg-capping, whether it is more prevalent in some species than in others, the possible role played by the type of nest, its prevalence in species with synchronous versus asynchronous hatching eggs (Derrickson and Warkentin 1991), or its occurrence relative to the 24-h day. There is clearly a need for more information and more accurate reporting.

Acknowledgments.—I thank the British Columbia Department of the Environment, Lands and Parks for permission to do my research on Mitlenatch Island. The manuscript benefitted greatly from the comments of F. Zwickel and two anonymous referees. My research was supported by the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

ARNOLD, T. W. 1992. The adaptive significance of eggshell removal by nesting birds: Testing the egg-capping hypothesis. Condor 94:547–548.

BROWN, C. R., AND M. B. BROWN. 1995. Cliff Swallow (*Hirundo pyrrhonota*). *In* The birds of North America, no. 149 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

DERRICKSON, K. C., AND I. G. WARKENTIN. 1991. The role of egg-capping in the evolution of eggshell removal. Condor 93:757–759.

EHRLICH, P. R., D. S. DOBKIN, AND D. WHEYE. 1988. The birder's handbook. Simon and Schuster, New York.

KUSHLAN, J. A., AND K. L. BILDSTEIN. 1994. White Ibis (*Eudocimus albus*). *In* The birds of North America, no. 9 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

MORGAN, F. D. 1976. Nesting sites of the Indigo Bunting at Thornhill, Indiana. Proceedings of the Indiana Academy of Sciences 86:461–465.

TINBERGEN, N., G. J. BROEKHUYSEN, F. FEEKES, J. C. W. HOUGHTON, H. KRUUK, AND E. SZULC. 1962. Egg shell removal by the Black-headed Gull, *Larus ridibundus* L.: A behaviour component of camouflage. Behaviour 19:74–117.

VERBEEK, N. A. M., AND P. HENDRICKS. 1994. American Pipit (*Anthus rubescens*). *In* The birds of North America, no. 95 (A. Poole and F. Gill, Eds.). Acad-

emy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

ZIMMERMAN, J. 1963. A nesting study of the Catbird in southern Michigan. Jack-Pine Warbler 41:142–160.

ZWICKEL, F. C. 1992. Blue Grouse (*Dendragapus obscurus*). *In* The birds of North America, no. 15 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Received 10 July 1995, accepted 25 September 1995.

The Auk 113(3):705–708, 1996

Influence of Lunar Cycle on Laying Dates of European Nightjars (*Caprimulgus europaeus*)

C. M. PERRINS[1] AND H. Q. P. CRICK[2,3]

[1] *Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom; and*

[2] *British Trust for Ornithology, The National Centre for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, United Kingdom*

Mills (1986) suggested that the timing of laying by crepuscular or nocturnal birds, such as caprimulgids, might be related to the amount of ambient light with different phases of the moon. He argued that such birds might be able to collect food more easily at times when the moon was near to full than when it was new. As part of a study of the Whip-poor-will (*Caprimulgus vociferus*), he looked at a combined sample of breeding records of five caprimulgid species, including the European Nightjar (*Caprimulgus europaeus*), and showed that there was indeed a nonrandom distribution of laying dates. More clutches were started in the half-month prior to full moon than in the other half. Furthermore, he found that Whip-poor-wills foraged more (see also Brigham and Barclay 1992), sang more, and fed their nestlings more frequently on moonlit than on dark nights. Mills suggested that the timing of laying was synchronized with the lunar cycle so that the first two weeks of the nestling period would coincide with the greatest amount of moonlight. He also noted that this schedule would result in high levels of moonlight five to six weeks after hatching when the young gain independence from their parents. Similar results have been found for the Fiery-necked Nightjar (*C. pectoralis*), which concentrates egg laying in the week following a full moon (Jackson 1985). However, data for two species of nighthawk—the Common Nighthawk (*Chordeiles minor*) and the Lesser Nighthawk (*C. acutipennis*)—showed no such correlation between laying date and phase of lunar cycle, which Mills (1986) thought was because these species are partially diurnal. The Common Poorwill (*Phalaenoptilus nuttallii*), another nocturnal caprimulgid, nests without relation to the lunar cycle, which Brigham and Barclay (1992) suggest is related to their propensity to attempt two broods within a limited season.

In a brief report by Cresswell (1992), a relatively small sample ($n = 30$) of European Nightjars in southern England were shown to start egg laying around the time of the full moon in the first half of June, but not if the full moon occurred in late May (and so also in late June). He suggested that there might be some advantage for egg laying to occur during a full moon in early June, but that to delay laying until a full moon in late June would limit the chances of successfully rearing a second brood.

The sample sizes in Cresswell's and Mills' papers were not very large (the latter had to combine data from 79 records of five species of *Caprimulgus*, ranging from North America and Europe to South Africa). In this paper we examine the relationship between laying and the lunar cycle for the European Nightjar using a much larger sample of records from Britain ($n = 464$).

Methods.—Our analysis makes use of the Nest Record Card data available from the British Trust for Ornithology. Nest Record Cards are completed by volunteer observers who record details of the nest contents on each visit made to a nest (Mayer-Gross 1970). The information is coded and computerized and, for many records, laying date can be back-calculated on the basis of the nest contents at later stages of nesting. The analysis is based on 464 records with sufficient data for us to estimate the date of clutch initiation to an accuracy of ± 5 days. Most (454, or 98%) of the records come from England, and the rest come from Wales; they were recorded from 1921 to 1991. The English records come mainly from three

[3] Address correspondence to this author.