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THE ROLE OF EGG-CAPPING IN THE EVOLUTION OF EGGSHELL REMOVAL[1]

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Key words: Behavior; eggs; nest; egg-capping; eggshell removal.

The adaptive value of removing eggshells from the nest after hatching has been interpreted as an antipredator function, based solely on the classic experiments of Tinbergen and his colleagues on Black-headed Gulls (*Larus ridibudundus*; Tinbergen et al. 1963, Tinbergen 1963). Although Tinbergen et al. briefly mentioned several other potential costs that may have favored eggshell-handling behaviors, these costs have been ignored. While predation may explain eggshell-removing behavior in species whose nests are relatively exposed, it is more difficult to accept predation as an explanation in species with well-concealed nests, especially cavity nests. For these species, the other adaptive reasons may be valid and should be reconsidered. Here, we present evidence implicating one of the other potential costs, "egg-capping." Egg-capping occurs when the empty eggshell from a recently hatched egg slips over an unhatched egg, thereby preventing the "capped" egg from hatching, either by mechanically interfering with pipping or with gas transport across the eggshell. That egg-capping was found to occur, even at a low frequency, despite the existence of eggshell-handling behaviors, strongly implicates egg-capping as a selective force favoring the evolution of eggshell-handling behaviors. We briefly describe instances of egg-capping in six species: Gadwall (*Anas strepera*), Merlin (*Falco columbarius*), Purple Martin (*Progne subis*), Tree Swallow (*Tachycineta bicolor*), Clay-colored Robin (*Turdus grayi*), and Northern Mockingbird (*Mimus polyglottos*). We speculate on the absence of other such observations from the literature and further discuss the significance of these observations in relation to the evolution of eggshell handling.

Egg-capping was observed in one Northern Mockingbird nest during studies conducted from 1979–1990. In this nest, the halves from the first egg that hatched each slid over respective parts of the two other eggs in the nest. Although cracks were evident on these two eggs, egg-capping was missed during a quick inspection of the nest. That egg-capping had occurred became apparent when, during a subsequent nest check, the background color of the eggs was noted to change abruptly at the cracks and, furthermore, egg dimensions were noted to be larger than measurements taken shortly after laying. One egg, initially measured 25.2 × 17.4 mm, was now 26.6 × 17.6 mm, and the other egg, initially 25.9 × 17.8 mm, was now 27.8 × 17.9 mm. Neither of the capped eggs hatched. The egg that hatched was the first egg laid and did not differ in dimension or mass from the other eggs.

A total of 144 nests have been examined in the mid-Atlantic region of the United States. Of these nests, 129 eventually contained eggs and 79 reached the nestling stage. Thus, egg-capping occurred in 0.8% of the nests with eggs and 1.3% of the nests in which it potentially could have been observed. Northern Mockingbirds are multi-brooded, potentially producing 2–

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3 broods per season (Sprunt 1964, Logan 1983, Breitwisch 1988, Derrickson 1989). Clutch size is typically 3–5 eggs, averaging between 3.5 and 3.9 eggs/nest depending upon geographical area (Laskey 1962; Graber et al. 1970; Means and Goertz 1983; Breitwisch, unpubl. data; Derrickson, unpub. data). Generally, adults remove eggshells from the nest.

Two instances of egg-capping were discovered in Merlins during examination of nests in Saskatoon, Saskatchewan, from 1985–1990. Interestingly, in both cases, one member of the pair had previous breeding experience and, yet, egg-capping occurred. In the first case, a 6 + year-old male who had bred successfully in a minimum of three other years paired with a female who was new to the population and presumably inexperienced. In the second instance, a two-year-old male who had not bred previously paired with an eight-year-old female who had bred successfully at least four times. In both instances, only one egg was capped. The positioning of the eggshell on the intact egg differed. One capped egg was almost indistinguishable from a normal egg because of the similar color and pattern of the intact egg and cap, and also because of the tight fit of the cap over the intact egg. However, in the second instance, the cap was much lighter in color than the intact egg, and was positioned on the egg at an angle, making its presence obvious. Neither capped egg hatched, but subsequent examination determined that they were infertile.

A total of 149 nests were examined and of these 145 hatched young. Thus, egg-capping occurred in 1.3% of nests that contained eggs and 1.4% of nests in which it potentially could have occurred. Merlins produce one clutch per year, and in the Great Plains region of North America generally lay four or five eggs per nesting attempt (Fox 1971, Hodson 1976, Becker and Sieg 1985).

Discussion with other researchers at the National Zoological Park revealed that egg-capping had been observed in four additional species: single instances in Gadwalls (S. Derrickson, pers. comm.), Tree Swallows (E. S. Morton, pers. comm.) and Clay-colored Robins (E. S. Morton, pers. comm.), and three times in Purple Martins (E. S. Morton, pers. comm.). In robins, it occurred in 0.3% of the approximately 350 nests found. Based on examination of approximately 550 nests at several breeding colonies around Severna Park, Maryland, egg-capping frequency in Purple Martins is 0.5%.

DISCUSSION

We could not find any reports of egg-capping in the ornithological literature, except those alluded to by Tinbergen et al. (1963). There are several potential explanations for this paucity. First, egg-capping appears to be a rare event, necessitating the inspection of hundreds of nests. Second, even when egg-capping has occurred, it may be difficult to detect. It can be easily overlooked during quick nest checks because of the similarity in appearance of eggs within a clutch and the close fit between the intact egg and cap. Third, individual researchers may have information on egg-capping in only a single species, which by itself may not seem significant or publishable. General patterns and interesting questions, such as the influence of age or nesting experience on the incidence of egg-capping, will be revealed only by combining observations from several species.

Even in this incomplete survey, it is apparent that egg-capping occurs in several taxa, and may be a problem encountered by almost all birds with clutches larger than one. The six species discussed above are from three orders, Anseriformes, Falconiformes and Passeriformes. Further, it was observed in species that construct open nest-cups and species that nest in cavities.

Despite its appearance in a broad range of species, egg-capping is presently a rare event. Rates were limited to approximately 1% of the nests inspected in all species considered here, thereby representing only a small loss in fitness. But, if eggshell-handling behaviors had not evolved, egg-capping would probably be more common, resulting in a greater loss of fitness. The extent of this cost would depend upon clutch size and the frequency of renesting, but regardless would favor the evolution of eggshell-handling behaviors.

How a species circumvents egg-capping, i.e., evolved eggshell-handling behaviors, likely depends upon its breeding biology, and factors such as the conspicuousness of nests, predatory pressure, social spacing, and intraspecific aggression directed towards newly hatched nestlings (see Tinbergen 1963, Tinbergen et al. 1963). For example, if predation pressures are lower on cavity nests as compared to open nests, then eggshell removal may occur later in those species that nest in cavities. As Tinbergen et al. (1963) proposed for species with closely-spaced nests and high intraspecific aggression towards newly hatched nestlings, eggshell removal will be delayed until the young can escape such a threat. The frequency of egg-capping is likely to be positively correlated with the extent of asynchrony in the hatching of young, both within and among species. S. Derrickson (pers. comm.) has provided details about an interesting behavior that Tinbergen et al. (1963) only briefly mentioned. He observed Northern Pintail (*Anas acuta*) hens treading while moving about in the nest. Microphones placed near the nest picked up the sound of eggshells from recently hatched eggs being crushed. This behavior eliminates the possibility that one of these eggshells will cap an unhatched egg, although it may not be the only explanation for the behavior.

As more information about the frequency of egg-capping and the species involved becomes available, the selective forces that favored the evolution of eggshell-handling, an important yet poorly appreciated behavior, will be more apparent.

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HATCHING SUCCESS IN ROOF AND GROUND COLONIES OF LEAST TERNS[1]

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Key words: *Least Tern;* Sterna antillarum; *hatching success; roof-nesting; Florida.*

Least Terns (*Sterna antillarum*) were first reported nesting on gravel-covered roofs in Florida more than 30 years ago (Goodnight 1957). Roof-nesting colonies have since become increasingly common in the southeastern United States (Fisk 1975, 1978; Jackson and Jackson 1985), and in some areas of Florida Least Terns nesting on roofs outnumber those on the ground (Hovis and Robson 1989; Gore, unpubl. data). Despite the increasing proportion of Least Terns nesting on roofs, little is known about the productivity of roof colonies relative to those on the ground. Here we compare hatching success in ground and roof colonies of Least Terns and discuss the importance of roof-nesting to local populations and to the conservation of Least Terns.

STUDY AREA

We studied eight colonies of Least Terns in northwest Florida in 1989; four were on roofs and four on the ground (Table 1). Five colonies were located in Bay County, in or near Panama City. The East Pass colony was located in Okaloosa County 75 km west of Panama City; the Phipps colony was approximately 115 km east, at the tip of Alligator Point, in Franklin County; and the Publix colony was 135 km northwest in Tallahasee, Leon County. For logistical reasons, study colonies were not randomly selected from all available Least Tern colonies in northwest Florida. However, the study colonies represent about 20% of the region's colonies and are found across >75% of the range of nesting habitat in the area (Gore, unpubl. data). Thus, we believe the study colonies are likely to be representative of Least Tern colonies in northwest Florida.

Each site supported nesting terns in 1988 and most had been active each year since 1985. Of the four colonies nesting on the ground, three were within 100 m of the Gulf of Mexico and either on the beach in front of the dunes or, in the case of the East Pass colony, some nests were upon or behind high open dunes. The Highway 98 colony was located 800 m north of the beach, on a barren site that was cleared for construction several years ago. To deter people from entering the colonies on the ground, we posted signs and surrounded each site with string and colored flagging.

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