

EGG-CAPPING AND EGG SHELL REMOVAL BY WESTERN AND SEMIPALMATED SANDPIPERS¹

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water (Sandercock, unpubl.); nests were revisited daily close to the expected hatching date.

Parents of birds with nidicolous young that remain in the nest after hatching generally remove eggshells from the nest after the chicks emerge from the eggs. In contrast, birds with nidifugous young usually leave eggshells and unhatched eggs in the nest when the brood departs on the day of hatching. Shorebirds (Suborder Charadrii) are a curious exception to this pattern. Despite having well-developed precocial young that leave the nest soon after hatching, many shorebirds will remove the shells of hatched eggs from the nest (e.g., Red Knot *Calidris canutus*, Whitfield and Brade 1991; White-rumped Sandpiper *C. fuscicollis*, Parmelee 1992; Buff-breasted Sandpiper *Tryngites subruficollis*, Lantot and Laredo 1994; Black-necked Stilt *Himantopus mexicanus*, American Avocet *Recurvirostra americana*, Sordahl 1994).

Tinbergen et al. (1962) suggested five reasons that parents might remove eggshells: (1) if sharp shell edges injure chicks, (2) if shells from hatched eggs interfere with brooding, (3) if material on remaining shells increases the risk of bacterial infection, (4) if the white linings of eggshells from hatched eggs increase the conspicuousness of the nest to a predator (here called the predation hypothesis), or (5) if the shells from a hatched egg become affixed to a later-hatching egg, forming a double shell layer that a pipping chick cannot break through (here called the egg-capping hypothesis, Derickson and Warkentin 1991, Arnold 1992). The first three explanations seem unlikely for shorebirds because the young do not remain long in the nest. In this note, I evaluate the predation and egg-capping hypotheses as explanations for parental removal of eggshells at hatching by Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*C. pusilla*).

METHODS

Observations on eggshell removal and egg-capping were conducted as part of an ongoing study of the reproductive biology of Western and Semipalmated Sandpipers near Nome, Alaska (64°20'N, 164°56'W). Field workers intensively searched for nests by walking on the tundra and observing the behavior of flushed birds. Stage of incubation was estimated by floating eggs in

RESULTS

Eggs that were known to have been broken during incubation disappeared from the nest ($n = 3$ nests); presumably because the parents removed them. Repeated visits to the nests during hatching showed that eggshells were sequentially removed from the nestcup as the young emerged from the eggs. A few tiny fragments produced during pipping were usually left in the debris of the nest. Eggshells were never found near the nestcup; parents observed removing eggshells ($n = 4$ nests) flew with them at least 20 m from the nest. Shells from hatched eggs were occasionally found on the study area, but not near known nest locations. Eggs that failed to hatch (possibly infertile) were abandoned in the nestcup by Western (21 of 248 eggs [8.5%] in 19 of 66 nests [28.8%]) and Semipalmated Sandpipers (16 of 238 [6.7%] eggs in 14 of 62 nests [22.6%]).

In the three years of this study (1993–1995), egg-capping was observed in both Western (2 of 248 eggs [0.8%] in 2 of 66 nests [3.0%]) and Semipalmated Sandpipers (1 of 238 eggs [0.4%] in 1 of 62 nests [1.6%]). In a six-year study (1976–1979, 1994–1995) at Cape Espenberg, Alaska (66°30'N, 163°30'W), D. Schamel (unpubl.) detected egg-capping in Semipalmated Sandpipers (1 of 202 eggs [0.5%] in 1 of 55 nests [1.8%]) but not Western Sandpipers (0 of 208 eggs in 59 nests). Only nests that were known to have hatched eggs are included in the totals. In one Western Sandpiper nest, the rounded end of an eggshell from a hatched egg was attached to the rounded end of a later-hatching egg. In the two Semipalmated Sandpiper nests, a fragment from the conical end of an egg adhered to the rounded end of another hatching egg. In these three cases, the chicks had reached an advanced stage of hole-pipping but failed to hatch, presumably because the presence of the additional shell fragment smothered the emerging young. In the second Western Sandpiper nest, the capping shell fragment was removed by an observer from the encapsulated egg; the egg subsequently hatched normally.

DISCUSSION

Removal of eggshells has been previously observed in both Western (Wilson 1994) and Semipalmated Sandpipers (Gratto-Trevor 1992) but egg-capping has not been reported for any shorebird. Arnold (1992) found that egg-capping had little effect on the hatchability of

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American Coot (*Fulica americana*) eggs, but in this study it clearly had a detrimental effect because it killed three sandpiper chicks.

The rates of egg-capping I observed are similar to those reported for other birds (ca. 2% of nests; Derrickson and Warkentin 1991, Arnold 1992). It is possible that I could have underestimated the rates of egg-capping if parents had perceived a capped egg to be broken and removed it from the nest. This seems unlikely because rejection of broken eggs declines close to hatching in other birds (Kemal and Rothstein 1988) and because failed eggs were left in the nest. Although rates of egg-capping appear to be low, this phenomenon could act as a selective pressure because it directly affects parental fitness.

If the egg-capping hypothesis was the sole explanation for removal of eggshells, parents might move the shells just a short distance from the nestcup. Instead, shorebirds remove eggshells far from the nest (Whitfield and Brade 1991, Parmelee 1992, Sordahl 1994, this study), which is consistent with the predation hypothesis. Nonetheless, many ground-nesting birds that do not remove eggshells from their nests use the same habitats as shorebirds and are exposed to the same predators. For example, Willow Ptarmigan (*Lagopus lagopus*) nest sympatrically with Western and Semipalmated Sandpipers, and all of these birds can suffer high rates of nest depredation (Martin et al. 1989, Sandercock, unpubl.).

The predation hypothesis does not seem sufficient to explain why eggshell removal has evolved in shorebirds but not in other birds with nidifugous young. Predation risk increases close to nest departure in some birds (Redondo and Castro 1992), but usually as a function of increased begging by the young. It is unlikely that predation risk at hatching is higher for shorebirds. Shorebird young are similar to grouse and waterfowl young in that they usually remain in the nest for no more than 24 hours, and escape the risk of the site by leaving quickly. Like most precocial young, sandpiper chicks have a large cloacal yolk sac (Sandercock, pers. observ.) which probably minimizes their activity because they do not need to feed immediately. Further, although shorebirds generally react to humans as if they are a potential threat to their nest (Reid and Montgomerie 1985), some sandpipers have been observed to remove eggshells in the presence of an observer (Parmelee 1992, this study).

Risk of egg-capping could influence eggshell removal. If parents did not remove eggshells, the rate of egg-capping would presumably increase with clutch size and the degree of hatching asynchrony (Derrickson and Warkentin 1991). If the rate of egg-capping is a function of number of eggs, grouse and waterfowl would be more likely to remove eggshells because they lay larger clutches than shorebirds (Winkler and Walters 1983). In these three groups of birds, the young hatch relatively synchronously because incubation is usually initiated close to the completion of laying.

Shorebirds may be more susceptible to egg-capping because they differ from grouse and waterfowl in the shape of their eggs and mode of hatching. Grouse and waterfowl have eggs that are typically ovate. Their chicks hatch as follows: from a holepup the chick chips a lateral ring in the side of the shell by rotating its head, once

it has broken about two-thirds of the shell the egg cap is pushed away (Bond et al. 1988). This mode of hatching has been termed symmetrical because the resulting eggshell fragments are round. In contrast, shorebirds have conical pyriform eggs, a shape that may be an adaptation for incubation efficiency (Andersson 1978). Scolopacid shorebird chicks have egg teeth on both the upper and lower mandible (Jehl 1968). From a holepup, the chick does not rotate but produces a longitudinal slit which it rips by convulsing; the eggshell fragments are asymmetrical and irregular in shape (Wetherbee and Barlett 1962, Bond et al. 1988).

I suggest that the risk of both egg-capping and predation have contributed to the evolution of eggshell removal in shorebirds. The large irregular-shaped eggshell fragments left from hatched shorebird eggs could pose a higher risk of interference than the small neatly piped caps from grouse and waterfowl eggs. In this study, different portions of eggshell were responsible for hatching mortality in each of the capped sandpiper eggs. Risk of predation may contribute to eggshell removal by compelling the parents to carry the fragments far from the nest.

Additional reports of eggshell removal in other shorebirds and experimental manipulation of this behavior are necessary to further assess the relative importance of egg-capping and predation. Red-necked Phalaropes (*Phalaropus lobatus*) leave large eggshell fragments in the nest after hatching (Sandercock, pers. observ.); the risk of egg-capping could be lower if the mode of hatching is different. Moreover, Black Oystercatchers (*Haematopus bachmani*) remove eggshells only a short distance (<25 m) from the nest (Andres and Falxa 1995), in this species the risk of predation may be low. To test the egg-capping and predation hypotheses in shorebirds, eggshells could be placed at varying distances from artificial nests and natural nests during hatching; control nests could be sham-visited. The predation hypothesis suggests that artificial nests with eggshells should be depredated more often than controls; the egg-capping hypothesis would be supported by no difference between treatments. If a shorebird's propensity to remove eggshells declined slowly with increasing distance, the predation hypothesis would be strengthened. Alternately, the egg-capping hypothesis predicts that parents should quickly remove eggshells put in the nestcup but ignore those placed any distance from the nest.

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NESTING PHENOLOGY OF KITTLITZ'S MURRELET¹

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The Kittlitz's Murrelet (*Brachyramphus brevirostris*) is a small, solitary nesting alcid that nests near the sub-arctic North Pacific and the more arctic Bering and Chukchi Seas (American Ornithologists' Union 1983). Because of its low nesting density and the extreme difficulty of finding its nests, it truly is one of the most poorly known species regularly breeding in North America; only 18 definite nests of this species have

ever been located (Day et al. 1983, Naslund et al. 1994, Day 1995). Most of the little information that is available lists those few nests that have been found and summarizes the scattered data on characteristics of nest-sites and eggs (Day et al. 1983, Naslund et al. 1994, Piatt et al. 1994, Day 1995). This paper summarizes the available information on nesting phenology of this species and speculates on reasons for the observed patterns.

METHODS

I surveyed both published literature and unpublished information for data on the timing of particular aspects of nesting phenology of Kittlitz's Murrelets: eggs in oviducts, egg-laying dates, eggs in nests, hatching dates,

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