EGGSHELL REMOVAL BEHAVIOR OF AMERICAN AVOCETS AND BLACK-NECKED STILTS

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Abstract.—Eggshell removal behavior of American Avocets (*Recurvirostra americana*) and Black-necked Stilts (*Himantopus mexicanus*) was studied in northern Utah. Both species removed eggshells from their nests soon after hatching or whenever they found them there. Both male and female avocets exhibited this behavior; female stilts exhibited it (and males probably did also). Although some shells were disposed of by dropping them over land, both species tended to carry shells to nearby water and submerge them. Eggshell removal is probably an antipredator behavior in avocets and stilts. Shell removal behavior occurred throughout the incubation period (documented on day 3 through hatching in avocets and day 7 through hatching in stilts). Observations of avocets indicated shell removal at a partially depredated nest, removal of one or more entire damaged eggs, and removal of a dead chick.

CONDUCTA DE REMOCIÓN DEL CASCARÓN DEL HUEVO POR PARTE DE RECURVIROSTRA AMERICANA Y HIMANTOPUS MEXICANUS

Sinopsis.—Se estudió la conducta de remoción del cascarón del huevo por parte de individuos de avoceta (*Recurvirostra americana*) y de viudas (*Himantopus mexicanus*) en una localidad de Utah. Ambas especies remueven el cascarón del nido tan pronto eclosionan los huevos o tan pronto lo encuentran. Ambos sexos de avocetas exhibieron dicha conducta, al igual que dos hembras de viuda y un individuo de sexo desconocido. Aunque algunos cascarones fueron desechados dejándose caer sobre tierra firme, ambas especies tienden a llevar éstos a lugares con agua y sumergirlos. La remoción de huevos es probablemente una conducta anti-depredador. Dicha conducta se llevó a cabo virtualmente a través de todo el periodo de incubación (del tercer día hasta el eclosionamiento en avocetas y del séptimo día hasta el eclosionamiento en las viudas). En las avocetas se observó la remoción de huevos rotos y de un polluelo muerto, en un nido que fue parcialmente depredado.

Many birds remove empty eggshells from the nest shortly after their young hatch (Nethersole-Thompson and Nethersole-Thompson 1942, Skutch 1976). The urge to remove eggshells near the nest is so strong that Stilt Sandpipers (*Calidris himantopus*) can be captured in a trap baited with an empty shell (Parmelee et al. 1968). At least five hypotheses for the adaptive value of eggshell removal behavior have been proposed (Tinbergen et al. 1962): (1) eggshells that are externally cryptic are white inside, and may be conspicuous enough to lead predators to the nest; (2) later-hatching eggs might become encapsulated, the egg-young thus becoming trapped inside a double shell; (3) sharp edges of shells might injure chicks in the nest; (4) organic material associated with eggshells might lead to growth of bacteria and mold in the nest; (5) hatched shells could interfere with brooding in the nest.

In this paper I report observations and field experiments on the eggshell removal behavior of American Avocets (*Recurvirostra americana*) and Black-necked Stilts (*Himantopus mexicanus*), two members of the family Recurvirostridae. Eggshell removal in these two species was inferred by Hamilton (1975) because he never observed shells in the nest during or after hatching. Gibson (1971) stated that American Avocets removed shells as soon as a chick freed itself from the egg and dropped them 5–50 m from the nest. Eggshell removal has also been reported for the Eurasian Avocet (*R. avosetta*) (Cramp and Simmons 1983, Makkink 1936).

STUDY AREA AND METHODS

I studied avocets and stilts in northern Utah during 1977 and 1978, and made additional observations in 1974–1976, 1979–1980, and 1987, totalling >2000 h of field observation. My study sites, the Barrens Company Hunting Club (41°52'N, 111°55'W) in Cache County and the Bear River National Wildlife Refuge (approx. 41°26'N, 112°10'W) in Box Elder County, are described in Sordahl (1982). The Barrens supported breeding populations of about 85 avocet and 25 stilt pairs (Sordahl 1981), while the Bear River Refuge had much larger populations of about 2500 avocet and 1000 stilt pairs (refuge personnel, pers. comm.).

I nest-trapped and color-marked 19 adult avocets and seven adult stilts (Sordahl 1980). In the field, I determined the sex of adult avocets by bill curvature and of adult stilts by color of the dorsal plumage (Hamilton 1975). In addition to numerous observations of nests and chicks during routine field work, I monitored 122 nests at the Barrens and made observations around the time of hatching at 24 avocet and six stilt nests. Between 21 May and 6 Jul. 1978, using shells from depredated nests, I conducted 13 eggshell removal experiments at 12 different nests on 9 d. Quarter or half shells were placed in nests, and the parents' behavior upon returning was observed with 7×35 binoculars or a $20 \times$ spotting scope from an automobile or blind at least 100 m away.

RESULTS

Parent avocets and stilts removed shells soon after hatching. Even though broods usually abandoned the nest permanently within 24 h after hatching, I often was able to distinguish successful and depredated nests because of parental shell removal behavior. A successful nest cup contained a few tiny shell fragments that were produced during pipping and hatching; the parents apparently removed all fragments ≥ 1 cm in diameter. Depredated nests had yolk stains and/or large shell fragments nearby, or else nothing at all if the eggs were carried away by predators (see also Green et al. 1987). Parent avocets and stilts, however, probably also remove shells from some depredated nests, as several shell fragments were removed from an avocet nest after a cow stepped on three of four eggs.

In 10 experiments at avocet nests, all shells were removed immediately, before incubation was resumed. Five removers were males, one was a female, and four were of unidentified sex. Of these 10 birds, four carried shells to the nearest water and submerged them (sometimes repeatedly picking them up and resubmerging them), two dropped them over salt flats, and four deposited them in unknown places. It appeared that those that were dropped over salt flats were dropped accidentally during flight. In three experiments at stilt nests, one shell was removed immediately

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and submerged in water, one was removed immediately and deposited in an unknown place, and one was not removed. Two females and one bird of unidentified sex were involved. The shell that was not removed had slid down between two eggs so that it was inconspicuous, and perhaps was unnoticed by the parent.

Eggshell removal behavior apparently occurs throughout the incubation period, which is about 24 d in both species (Gibson 1971, Hamilton 1975). For the 10 avocet nests in my removal experiments the approximate day of incubation was: 3, 3, 5, 18, 19, 19, 19, 19, 20 and 24. The day of incubation at the three stilt nests was: 7, 10 and 14. As noted above, shells were removed at one avocet nest after a cow stepped on the eggs. At another avocet nest a female punctured an egg while caught in my nest trap. Less than 1 h later, when I returned her to the nest after banding, the damaged egg was gone, presumably removed by her mate. It was approximately day 11 of incubation. The day after hatching at another avocet nest, I found a dead chick, only halfway out of its egg, about 20 m from the nest. As this chick was second in the hatching order and the other three chicks hatched successfully, I believe this chick died during hatching and was removed by a parent before the brood was ready to leave the nest.

DISCUSSION

Eggshell removal has usually been interpreted as an antipredator behavior, based largely on the classic experiments of Tinbergen and his colleagues (Tinbergen et al. 1962, Tinbergen 1963) on Common Blackheaded Gulls (*Larus ridibundus*). The importance of other explanations for this behavior is much less clear (e.g., Arnold 1992, Derrickson and Warkentin 1991). Benefits of eggshell removal predicted by all five of the hypotheses listed above may have contributed to the evolution of this behavior, depending on the nesting ecology of a species.

I suggest that hypothesis 1 (antipredator) is most important in accounting for eggshell removal in recurvirostrids. Avocets and stilts are subject to intense predation in their breeding areas (Sordahl, unpubl. data), and exhibit a variety of antipredator adaptations (e.g., Sordahl 1982, 1986, 1988a, 1988b, 1990). Hypothesis 2 (encapsulation) is weakened by the fact that avocets and stilts remove the shell of the last-hatched chick, which poses no danger of encapsulation to other eggs. Edges of eggshells (Hypothesis 3) might injure chicks, but this hypothesis does not require that the shells be carried far from the nest; avocets and stilts dispose of shells thoroughly. Hypothesis 4 (growth of bacteria and mold) seems weak for nidifugous birds such as recurvirostrids, and any organic material would probably soon be washed off by young shorebirds. Similarly, Hypothesis 5 (interference with brooding) seems less likely to be important for nidifugous birds whose young are brooded in the nest only briefly than to nidicolous species whose young are brooded in the nest much longer; this hypothesis also does not require that the shells be carried far from the nest.

My experiments indicate that avocets and stilts tend to deposit removed shells in nearby water. Hamilton (1975:86) reported finding two eggshells in shallow water near a nesting dike. I have found several recurvirostrid shells in the water and only a few on dry ground. Makkink (1936:53) reported that Eurasian Avocets walked or flew with eggshells to the water, and dropped them, sometimes "nibbling" at them (this seems similar to the repeated lifting and submerging I observed).

The function of sinking eggshells in water is not clear. An analogous behavior in nidicolous birds is the dropping of fecal sacs in water, which has been reported in several species (Petit et al. 1989:481 and references therein). Submerged shells probably are less likely to be found by predators than shells lying on the ground. Thus predators that have learned to associate eggshells with food would not intensify search efforts near the nest of an eggshell-submerging parent. For avocets and stilts needing to avoid attracting predators to their nests, nearby water may be a better disposal site than a distant land site because it permits a shorter unattended period for the hatching eggs. Makkink (1936:53) stated that Eurasian Avocets remove eggshells that they find anywhere in the colony. This behavior, along with the apparently deliberate sinking of shells, would be adaptive only in the context of an antipredator hypothesis for eggshell removal.

I also found removal behavior to be present throughout incubation, which may be true for most birds (Montevecchi 1976). This has likely been selected for in a context of removing damaged eggs. My observations suggested shell removal at a partially depredated nest, removal of one or more entire damaged eggs, and removal of a dead chick. Nethersole-Thompson (1951:183) also reported an instance of removal of a dead chick, by a Common Greenshank (*Tringa nebularia*). Removal behavior in these situations could be explained by several of the five hypotheses listed above.

ACKNOWLEDGMENTS

I thank K. L. Dixon for helpful suggestions throughout my studies. K. J. Larsen, D. F. Parmelee, D. R. Petit and K. Yasukawa kindly provided comments on the manuscript. I appreciate the cooperation of the members of the Barrens Company Hunting Club and the staff of the Bear River National Wildlife Refuge. My work was supported by the Utah State University Biology Department, the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and by Sigma Xi, The Scientific Research Society.

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Received 9 Aug. 1993; accepted 21 Oct. 1993.