EGGSHELL REMOVAL AND NEST SANITATION IN RING DOVES

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Avian nest sanitation includes eggshell disposal, inhibition of defecation on the nest, and the ingestion or removal of nestling fecal matter. Such behavior is widespread among birds, although many different adaptions have evolved in the rearing of offspring (e.g. Blair and Tucker, 1941; Nethersole-Thompson and Nethersole-Thompson, 1942; Pettingill, 1970; Yapp, 1970).

A surprising lack of information exists concerning the defecation patterns of birds (Hailman, 1965; Brackbill, 1972), and only a few systematic studies of eggshell removal have been carried out (Beer, 1960; Hailman, 1966; Thompson, 1970; Tinbergen, 1963). Captive Ring Doves (*Streptopelia risoria*) have been reported to defecate away from their nests during incubation and to remove eggshells from their nests (Miller and Miller, 1958). The present investigation was designed to explore systematically the tendencies of captive Ring Doves to remove eggshells from their nests and to keep their nests free of fecal matter throughout the course of a reproductive cycle. An excellent account of the breeding activities of Ring Doves can be found in Lehrman (1964).

METHODS

Thirty-five pairs of Ring Doves from a laboratory colony were used in this study. All doves were reproductively inexperienced when paired in breeding cages ($81 \times 46 \times 36$ cm), which were equipped with a food container, grit container, water dispenser, glass nest bowl (10.8 cm diam., 3.8 cm depth), and straw. Birds were sexed by laparotomy. The pairs were visually but not auditorily isolated from each other, and a photoperiod of 14 hours (06:00–20:00 EST) of artificial light was maintained. Eggshell tests consisted of placing a Ring Dove eggshell in the nest bowl or nest. The eggshells were cracked around the blunter pole to resemble one which remains following the hatching of a squab. The reactions of the doves to the shells were either observed directly through one-way observation windows, or the location of the shell in the breeding cage was checked at 15 minute intervals for a period of one hour. The outcomes of the tests were scored according to the following scale: 1—shell removed within 15 minutes; 2—removal between 15 and 30 minutes; 3—removal between 30 and 45 minutes; 4—removal between 45 and 60 minutes; 5—no removal at the end of the hour test period.

Daily checks were made on the breeding activities of the birds. The tests were administered during the following seven phases of the reproductive cycle: a. prenest test (P)—within approximately 5 days after pairing in the breeding cage (always fewer than 10 straws in the nest bowl); b. nest test (N)—within the period when the depth of straw in the nest bowl was at least 1.25 cm until the first egg was laid (the modal amount of nest material in the nest bowl at test was approximately 2.00 cm); c. early incubation test (E)—counting the day on which the first egg was laid as day 1 of incubation, from day 1 through and including day 5 of incubation; d. mid-incubation

TABLE 1

EGGSHELL REMOVALS AND REMOVAL SCORES OVER THE BREEDING CYCLE[1]

	Prelaying		Incubation			Posthatch	
	P	N	E	M	L	B	O
Number of pairs tested	26	24	23	16	14	20	26
Number of removals	8	9	12	9	8	14	17
Percentage of removals	31	38	52	56	57	70	73
Median removal score	5.0	5.0	3.0	2.5	2.5	2.0	1.0

[1] See methods for explanation of breeding cycle components.

test (M)—from day 6 through and including day 10 of incubation; e. late incubation test (L)—from day 11 through and including day 14 (or the day prior to the hatching of the first egg); f. posthatch brooding test (B)—anytime from the hatching of the first egg (posthatch day 1) until the parents were first observed not brooding the squabs on the nest (approximately day 7 posthatch); g. posthatch nonbrooding test (O)—from the day on which the squabs were first seen unattended on the nest until approximately day 15 posthatch. Most pairs were tested in approximately five of the reproductive phases; successive tests were administered with an interval of at least three days between them. Records of the fecal droppings on the tops of each of the nests were collected during each of these seven reproductive phases.

RESULTS

The percentages of tests during which Ring Doves removed eggshells from their nests increased through successive phases of the breeding cycle (Table 1). Thus, a smaller percentage of the pairs tested in the prelaying periods removed eggshells from their nests than did those tested during the incubation periods, while a greater percentage of the pairs tested during the posthatch periods removed eggshells than did those tested during the incubation periods. The percentage of pairs removing shells during the early, mid, and late parts of the incubation period were very similar. The median removal scores also decreased over the seven successive phase of the reproductive cycle (Table 1).

If an eggshell was removed, removal most often occurred during the first 15 minutes interval (Fig. 1). Observations indicated that most such removals occurred within the first 5 minutes of the test. Sixty-five, sixteen, thirteen and six percent of the removals occurred during the first, second, third and fourth 15 minute interval of the test, respectively. This frequency distribution is significantly different from a random distribution ($P < .01$, Kolmogrov-Smirnov one sample test, Siegel, 1956). The distances to which the shells were removed were found to be least during the prenest period and greatest during the posthatch brooding phase. The severe spatial constraints

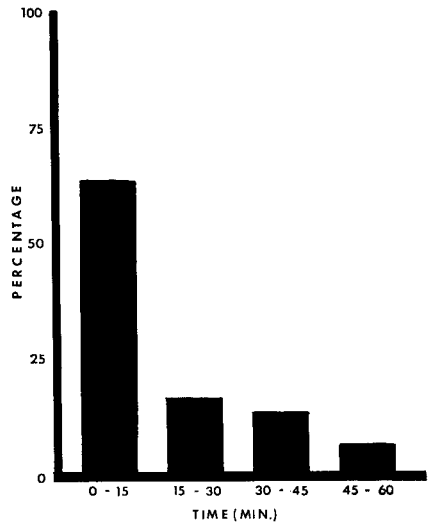

FIG. 1. Percentages of eggshell removals occurring during the different 15 minute intervals of the test.

of the breeding cages precluded any meaningful interpretations from being drawn. Eggshells were flown, walked, and dropped from the nest.

The mean number of fecal droppings in the nest bowl and on the nest varies over the breeding cycle in a manner which may be described as a U shaped function (Fig. 2). A one way nonparametric analysis of variance revealed a significant difference among these seven groups ($F = 7.498$, $df = 6$, $P < .01$). Subsequent Duncan's multiple range tests indicated that the defecation count posthatch phase was significantly greater than those of each of the other six reproductive stages and that the defecation count of the posthatch brooding phase was significantly greater than those of the mid and late incubation phases; all other paired comparisons were nonsignificant.

DISCUSSION

Ring Doves exhibited an increasing tendency to remove eggshells from their nests over the course of the reproductive cycle. The removal of eggshells increased most markedly around the time of egg-laying, and some evidence exists suggesting a further change in responsiveness toward removal at hatching. The tendency remained remarkably stable throughout the incubation period.

In the prenest tests most doves paid least attention to the nest bowls or to the shell within them, while during the nest tests the doves often incubated

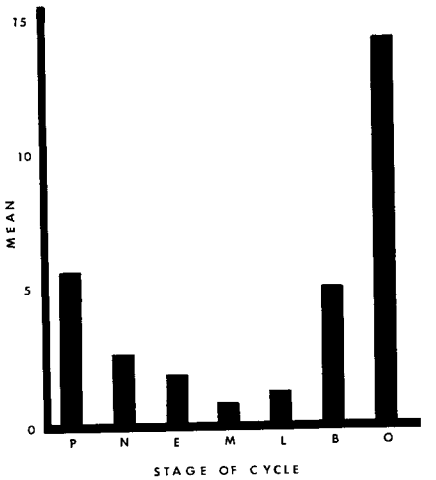

FIG. 2. Mean number of fecal droppings in Ring Dove nests at different stages of the reproductive cycle. Abbreviations explained in text.

the eggshell (seemingly indicative of an increasing tendency to incubate as laying approached). Once a dove laid an egg(s) in the nest, the shell was more apt to be removed. The eggshells were apparently better "differentiated" from eggs, when eggs were present in the nest. The responsiveness of Ring Doves to other sources of external stimulation (eggs, newly hatched squabs) also changes markedly around egg-laying (Hansen, 1966; Moore, 1970). The "tight" sitting behavior of incubation gradually gives way to "looser" sitting patterns of brooding around hatching, and these behavioral changes may be responsible for changes in responsiveness to eggshells in the nest around this time. Doves brooding newly hatched squabs are more likely to arise, look down, and resettle than incubating doves, behavior that may increase the probability of detection and removal of an eggshell. It is well documented that the presence or absence of eggs and/or young in the nest has profound influences upon the responsiveness of birds to many sources of external stimulation (e.g. Lehrman, 1961; Emlen and Miller, 1969; Impekoven, 1973; Cheng, 1973).

The eggshell removal tendency of Black-headed Gulls (*Larus ridibundus*) has been found to increase at laying and to remain high and constant throughout the laying and incubation periods (Beer, 1960:395–408). Beer has also reported that this tendency begins to decline early in the posthatch period of the gulls. Part of the difference between the eggshell removal tendencies of the doves and the gulls in the posthatch period can be attributed to the different patterns of nest attentiveness which species producing altricial and

semi-precocial young exhibit during this phase of the reproductive cycle. Within a few days after hatching Black-headed Gull chicks begin making excursions from the nest; the parents, while still strongly attached to the chicks, become less and less attached to the nest site (Beer, 1966). The doves by comparison remain strongly attached to the nest, until the squabs have fledged. Therefore, differences in the nest proximity maintained by Ring Doves and Black-headed Gull families in the posthatch period may account for the differential eggshell removal tendencies seen between these species during this phase. It should also be noted that the laboratory breeding cages confined *both* Ring Dove parents to the immediate vicinity of the nest, and therefore may have contributed to the species difference reported.

If the doves removed an eggshell during a test, they tended to do so relatively rapidly following the introduction of the shell into the nest. This phenomenon may be widespread among birds; a similar effect has been obtained in eggshell removal experiments conducted with Laughing Gulls (*Larus atricilla*) and Oystercatchers (*Haematopus palliatus*) (Montevecchi, in prep.). This effect is probably due in part to short term habituation process of the birds to a novel stimulus object in the nest.

The adaptive significance of removing eggshells (and other foreign objects) from the nest throughout the reproductive cycle, and particularly at the time of hatching, may differ from species to species. Numerous selective advantages have been postulated to account for the evolution of this behavior, e.g. maintenance of nest camouflage among birds which produce cryptic eggs and young; prevention of interference with effective incubation and brood care; elimination of possible bacteria growth, injury to nestlings, and interference with the hatching success of subsequent other eggs. Ring Dove eggs are white and are continuously incubated (covered) by one parent or the other, which sits tight rather than flees at the approach of an alarming stimulus. Nest camouflage does not seem to have played a significant role in the evolution of the eggshell disposal patterns of Ring Doves.

On the other hand, an unremoved eggshell probably reduces the hatching success of an unhatched egg in the nest. In five of the 24 instances during which eggshells were not removed during incubation period tests, these were found to have fitted over an unhatched egg in the nest by the end of the hour test period. Unremoved eggshells have also been found to entrap unhatched eggs of Tree Swallows (*Iridoprocne bicolor*) (E. H. Burtt, Jr., pers. comm.) and Laughing Gulls (Montevecchi, in prep.).

Once their nests take shape, adult Ring Doves show an inhibition of defecation at the nest which is generally maintained until the squabs vacate the nest. Numerous other species also refrain from defecating at their nests during the incubation period, but Mourning Doves (*Zenaida macroura*)

(Snyder, 1923) and Inca Doves (*Scardafella inca*) (Johnston, 1960) are exceptions. The defecation by those doves on their nests may have adaptive significance, in that the excrement may strengthen their flimsy nests (Skutch, 1964). Fecal droppings occurring on the nest of Ring Doves in this study were due primarily to the excretory activities of the squabs, although adult doves also began to defecate at the nest after the eggs hatched. Adult Ring Doves have been observed eating the feces of nestling squabs, and excrement has been removed from the crops of parental doves (J. Buntin, pers. comm.). Many species of dove are known to eat the fecal matter of their young, and this substance may in turn be fed back to the squabs (Skutch, 1964). As the squabs develop, the amount of feces they excrete increases considerably, and the parent doves make no attempt to deal with this nest fouling.

Like numerous passerines (Yapp, 1970) and other nonpasserines (Nice, 1962), Ring Dove and Rock Dove (*Columba livia*) squabs have been observed to erect their hind ends and defecate over the nest rim (C. Barbiere, pers. comm.). The glass bowls in which the Ring Doves built their nests may have interfered with such behavior in this study. Early in incubation the straw nests often overflowed the bowls, yet by hatching this was matted down and usually contained within the bowl—leaving a glass lip about the nest perimeter. Squab droppings were always found forming a tight circle around the nest edge and on the outer surface of the nest bowl, but never in the center of the nest cup. In a more naturally situated nest, "over the edge" defecation by squabs may have been enhanced.

The study of nest sanitation adaptions in other avian species that remove eggshells from their nests might reveal the generality of the findings that the eggshell removal tendency increases at laying and remains constant throughout the incubation period. Such investigations might also focus upon species whose young show differing degrees of precocity at hatching (thus remaining in close proximity to the nest for different periods after hatching), and on how these adaptions influence eggshell removal and defecation behavior.

SUMMARY

The tendency of Ring Doves to remove introduced eggshells from their nests was investigated over the course of the reproductive cycle. This tendency increased markedly around egg laying, remained constant through the incubation period and showed evidence of a further increase just after hatching. If an eggshell was removed from the nest, it was most likely to have been removed within 15 minutes of its introduction. Comparisons with the eggshell removal tendencies of Black-headed Gulls are made, and the possible adaptive significance of eggshell removal behavior is discussed.

The incidence of defecation at the nest was studied throughout the reproductive cycle. Adult doves refrained from defecating at the nest during the incubation period, although they exhibited a slight tendency to do so during other reproductive phases. Adults

did little to keep their nests clean of the excrement of their young. The squabs showed some evidence of nest sanitation behavior, defecating over the nest rim.

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