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POSSIBLE MANIPULATION OF EGGSHELL CONDUCTANCE OF HOST EGGS BY BROWN-HEADED COWBIRDS[1]

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Key words: Eggs; avian parasitism; cowbirds; water-vapor conductance; Red-winged Blackbirds.

Avian parasites, such as Brown-Headed Cowbirds (*Molothrus ater*) use several methods that minimize the competitive advantage of host nestlings and that maximize survival of their own young to fledging (Friedmann 1929, Payne 1977). Ejection of one or more host eggs can reduce the number of host nestlings competing with the parasite nestlings for food, but sometimes this behavior can cause the host to abandon the nest (Payne 1977). Alternatively, the competitive advantage of parasite nestlings can be enhanced without removal of host eggs from the nest by any mechanism that disrupts the structural integrity of the eggshell of host eggs to a sufficient degree that host embryos do not hatch.

The shell thickness and pore area are two features of avian eggs which must meet a set of mutually antagonistic requirements within narrow limits; otherwise, the development of the embryo is disrupted and hatching will not occur. The eggshell must be sufficiently thick to support the mass of the egg contents and weight of the incubating adult, yet thin enough to permit the embryo to pip and hatch successfully. Additionally, the shell thickness and pore area together comprise the conductance (*G*) of the eggshell to gaseous diffusion (see Ar et al. 1974). The conductance must be sufficiently great that enough O_2 can diffuse into the egg to meet the needs of the embryo, yet it must be small enough that excessive losses of CO_2 and water vapor are prevented and invasion of bacteria and other infectious agents is minimized (see Carey 1983).

Blankespoor et al. (1982) recently observed that Red-winged Blackbird (*Agelaius phoeniceus*) eggs are more frequently cracked during egg laying and incubation than are cowbird eggs in the same nest. Since Red-winged Blackbird eggs have a thinner shell than cowbird eggs, those authors speculated that Red-winged Blackbird eggs were more likely to become cracked when eggs were jostled against one another in the nest. Further, they hypothesized that the thicker eggshell of cowbird eggs conferred a competitive advantage over Red-winged Blackbird eggs, since cracked eggs were more likely to break and to be removed from the nest by the incubating host. It is also possible that embryos in cracked eggs might not develop and hatch successfully because of excessive loss of water and CO_2 and/or invasion of bacteria, fungi, etc.

The phenomenon documented by Blankespoor et al. (1982) may result from differences in thickness and strength

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TABLE 1. Water-vapor conductance (G_{H_2O}) and daily water loss ($\dot{M}_{H_2O}$) of eggs with a hole in the shell compared with G_{H_2O} and $\dot{M}_{H_2O}$ of intact host eggs in the same nest. Values are for individual eggs; see Methods for details about the measurements. Values in parentheses represent mass of freshly laid egg (in g).

Species	Nest No.	Intact egg	Egg with hole
		$\dot{M}_{H_2O}$ (g·day^{-1})	
Red-winged Blackbird	514	0.059 (4.089)	0.098 (4.108)
	526	0.054 (3.916)	0.063 (4.158)
	550	0.053 (4.474)	0.252 (4.549)
House Finch	3	0.028 (2.152)	0.148 (2.138)
Eastern Phoebe	5	0.014 (2.531)	0.072 (2.645)
		G_{H_2O} (mg·day^{-1}·torr^{-1})	
Red-winged Blackbird	514	0.96	1.41
	526	1.01	1.13
	550	0.91	4.19

between Red-winged Blackbird and cowbird eggs, rather than from behavioral attempts by cowbirds to crack host eggs. However, cowbirds may also play a more active role in disrupting the integrity of the eggshells of host eggs, with the result that the competitive advantage of host embryos is decreased. During another study on cowbird parasitism of nests of Red-winged Blackbirds, Eastern Phoebes (*Sayornis phoebe*), and House Finches (*Carpodacus mexicanus*), I noted a small, triangular hole in the side of a few eggs of host species in nests that had been parasitized by cowbirds. In each case, only one host egg per nest contained a hole. The holes averaged approximately 1 mm in diameter. Since the embryos in eggs with holes were dead, while those of host eggs with intact shells in the same nests were viable, it appeared that the presence of holes caused embryonic mortality. The purpose of this study was to determine how the hole affected eggshell water-vapor conductance (G_{H_2O}) and daily water loss ($\dot{M}_{H_2O}$) and to evaluate whether the hole increased rates of water loss beyond the limits lethal to the embryo.

MATERIALS AND METHODS

Nests of Red-winged Blackbirds and House Finches were studied near Boulder, Boulder County, Colorado. The Eastern Phoebe nest was found near Lawrence, Douglas County, Kansas. Since G_{H_2O} and $\dot{M}_{H_2O}$ of many small avian eggs, including those of Red-winged Blackbirds, increase during the first few days of incubation (Carey 1979, 1983), measurements were not made until the eggs had been incubated for at least five days. Then, each host egg containing a hole and one intact host egg from the same nest were marked individually with waterproof ink and were weighed to the nearest 0.05 g on a portable Torbal balance. They were replaced in the nest and were weighed again 24 hr later, the difference in mass representing the daily water loss ($\dot{M}_{H_2O}$) in g·day^{-1} (Drent 1970, Ar and Rahn 1980). Verification that the adult had incubated the eggs normally during the 24-hr period was obtained by comparing the rate of water lost by the intact egg with average rates measured concurrently in the same population. After the final weighing, the eggs were transported to the University of Colorado in Boulder, where G_{H_2O} (mg·day^{-1}·torr^{-1}) was measured according to methods described by Carey et al. (1983). Values reported here were standardized to 760 torr.

RESULTS AND DISCUSSION

When results from Red-winged Blackbird, House Finch, and Eastern Phoebe eggs with holes are compared with those of intact eggs within the same clutch, the presence of a hole clearly results in an increase in both $\dot{M}_{H_2O}$ and G_{H_2O} (Table 1). To determine if such increases could have proven lethal to the embryos, the G_{H_2O} and $\dot{M}_{H_2O}$ of the three Red-winged Blackbird eggs were plotted (Fig. 1) against the ranges of variability of these characteristics in naturally incubated eggs and the ranges within which all Red-winged Blackbirds would be expected to hatch (Carey, in press). The $\dot{M}_{H_2O}$ and G_{H_2O} of two of these eggs fall within the limits within which hatching should occur; therefore, it is unlikely that embryonic death was caused by variation in gas exchange due to the hole. The values for the other Red-winged Blackbird egg fall outside these limits due to a slightly larger hole in the eggshell than in the other eggs. Therefore, disruption of gas exchange could have proven lethal to that embryo.

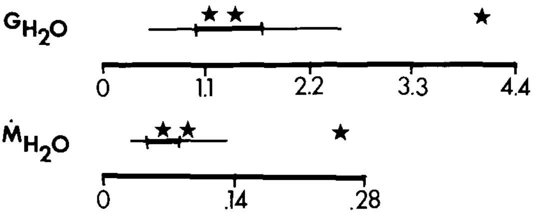

FIGURE 1. Eggshell water-vapor conductance (G_{H_2O}, mg·day^{-1}·torr^{-1}) and daily water loss ($\dot{M}_{H_2O}$, g·day^{-1}) of three Red-winged Blackbird eggs with holes in the shell (stars) in relation to the range of natural variation in G_{H_2O} and $\dot{M}_{H_2O}$ of Red-winged Blackbird eggs (thick line) and to the range of G_{H_2O} and $\dot{M}_{H_2O}$ in which all Red-winged Blackbird embryos should be capable of hatching (thin line). Ranges were obtained from eggs in the same population as the eggs with holes. More information about these ranges is located in Carey (1986).

At this time, the full implications of these findings are difficult to assess for several reasons. First, no data on tolerance limits of embryonic House Finches and Eastern Phoebes are available. Therefore, we can't determine if the holes could have disrupted gas exchange enough to lead to embryonic death. Second, the actual cause of death was unclear. Disruption of normal patterns of gas exchange may be a primary factor if the hole is large. However, invasion of bacteria, fungi, or other infectious agents through the hole may be the primary cause of death regardless of the size of hole, with disruption of gas exchange being only a contributory factor. Further study is necessary to clarify why a hole in the shell invariably leads to embryonic death.

While no proof exists that cowbirds made the holes, no holes were found in eggs in over 500 Red-winged Blackbird nests that were not parasitized by cowbirds. Assuming that cowbirds did make the holes, it is unclear whether the action might have occurred by accident as a corollary of egg-laying, or by a deliberate attempt to render the host egg inviable without having to remove it from the nest and risk nest abandonment by the host. Whether due to accident or to deliberate behavior, the holes occurred only infrequently (in less than 20% of the parasitized nests of these three species). However, since embryos invariably died in eggs with holes, the enhancement of survival of cowbird offspring could possibly select for greater prevalence of this phenomenon in the future.

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CHANGES IN WATER-VAPOR CONDUCTANCE OF COMMON CANARY EGGS DURING THE INCUBATION PERIOD[1]

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Key words: Common Canary; Serinus canarius; *chorioallantois; water-vapor conductance; incubation period.*

Drent (1970) and Rahn and Ar (1974) postulated some time ago that the conductance of the avian eggshell to water ($G_{\mathrm{H_2O}}$) was constant throughout incubation and indeed that seems to be the case for large precocial eggs. However, the $G_{\mathrm{H_2O}}$ increases nearly 50% during the first few days of incubation in several altricial species of songbirds including Red-winged Blackbirds *Agelaius phoeniceus* and American Robins *Turdus migratorius* (Carey 1979), Cliff Swallows *Hirundo pyrrhonata* (Sotherland et al. 1980), and Yellow-headed Blackbirds *Xanthocephalus xanthocephalus* (Hanka et al. 1979). The reasons for the increase are still unclear, although they may be related to the development of the chorioallantoic membrane (Sotherland et al. 1979, 1980; Birchard and Kilgore 1980), abrasion of the shell during incubation (Carey 1983), or the small size of the eggs of altricial birds (Birchard and Kilgore 1980).

In this paper, I describe changes in the $G_{\mathrm{H_2O}}$ of Common Canary (*Serinus canarius*) eggs during the 13-day incubation period. Because I used fertile and sterile eggs in this study and because some were incubated by canaries and others were incubated artificially, I was able to determine if embryonic development and/or abrasive changes in the shell were responsible for changes in the $G_{\mathrm{H_2O}}$ of the eggs.

MATERIALS AND METHODS

I collected freshly laid eggs from the nests of canaries in my colony each morning during the nesting season, within 1 to 5 hr of laying. The eggs were marked with a felt-tipped pen for identification and were weighed on a Sartorius balance accurate to 0.1 mg. Their $G_{\mathrm{H_2O}}$ was determined by the method of Ar et al. (1974). They were kept in small sealed containers over silica gel at an average constant temperature of 23.85°C (range: 23.3 to 24.4°C) for five days during which they were weighed at roughly 24-hr intervals. Conductance values were corrected to 25°C and 760 torr. I have assumed, as others apparently have (Carey 1979, Hanka et al. 1979, Sotherland et al. 1980), that the egg's $G_{\mathrm{H_2O}}$ remains constant during the period of calibration. This assumption is supported by the fact that daily changes in each egg's mass during these five-day periods of calibration were nearly constant.

Once calibrated, the eggs were placed either in the nest of an incubating hen with three other noncalibrated eggs (clutch size was maintained at four eggs) or on a bed of fine sand in sealed containers kept in a water bath at 34°C (typical egg temperature during incubation by birds in my study). The calibrated eggs were incubated under the hen or in the water bath for 3, 6, 9, or 12 days. At that time, I removed and reweighed them and then recalibrated them for an additional five days as above. Finally, I candled them and then blew them to ascertain if they were fertile, i.e., I checked for the presence of embryos and extraembryonic membranes. I examined changes in the conductance of 79 sterile eggs and 16 fertile ones.

The data within each group (eggs incubated artificially; eggs incubated by a canary) were analyzed by paired *t*-tests and Student-Newman-Keuls tests. Student's *t*-tests and analysis of variance (*ANOVA*) were used to compare data between groups. Percentages were converted to their arcsin equivalents for analysis (Zar 1974).

RESULTS

STERILE EGGS

The $G_{\mathrm{H_2O}}$ of sterile eggs increased 65 to 66% in the first three days of incubation, irrespective of whether they were incubated by canaries or in a water bath. This change was very highly significant ($P < 0.001$, paired *t*-test). Thereafter the $G_{\mathrm{H_2O}}$ was relatively constant through Day 9 of incubation (percent changes in $G_{\mathrm{H_2O}}$ for Days 3, 6, and 9 were not significantly different; Table 1). The conductance then declined appreciably (but the decrease was significant only in the group of eggs incubated by canaries) so that on Day 12 it approached the $G_{\mathrm{H_2O}}$ of freshly laid eggs (Day 0 in Table 1).

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