The Adaptive Value of Thick-shelled Eggs for Brown-headed Cowbirds

PATRICK J. WEATHERHEAD
Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada

As generalist brood parasites (Friedmann et al. 1977), Brown-headed Cowbirds (*Molothrus ater*) have not evolved the specialized adaptations such as egg mimicry typical of brood parasites that parasitize single species. However, there are some attributes that may benefit cowbirds regardless of which host species they parasitize. The evolution of disproportionately thick eggshells is one such potential adaptation. Brown-headed Cowbirds do have significantly thicker eggshells than predicted for the size of their eggs (Blankespoor et al. 1982, Spaw and Rohwer 1987, Picman 1989). Two hypotheses have been proposed to explain the functional value of thicker shells. First, because some host species recognize cowbird eggs and attempt to eject them from their nests (Rothstein 1975), thicker shells may be more resistant to attempts by the host to puncture the eggs (Spaw and Rohwer 1987, Rohwer et al. 1989). In many small host species, puncturing the egg is the only way a cowbird egg can be grasped because of the hosts' small bills (Rohwer and Spaw 1988). Picman (1989) demonstrated that Brown-headed Cowbird eggs are more puncture resistant than the eggs of three closely related but nonparasitic species.

The second hypothesis proposes that thicker shells protect cowbird eggs from cracking due to being stepped on by the female or due to bumping host eggs during laying or incubation (Blankespoor et al. 1982). If cowbird eggs crack less often than host eggs, then cowbird nestlings will face reduced competition because of smaller host broods. Blankespoor et al. (1982) showed that Red-winged Blackbird (*Agelaius phoeniceus*) eggs in parasitized nests cracked more often than those in unparasitized nests. Although these data supported the hypothesis that cowbirds gain an advantage from having thicker eggshells, they did not elucidate the mechanism by which the advantage is realized. Red-winged Blackbird eggs may crack more often than cowbird eggs because of the normal bumping of eggs that occurs during incubation, or female cowbirds may accidentally or even purposefully bump eggs together when parasitizing a nest. Another possibility is that the damage to host eggs has nothing to do with cowbird eggs having thick shells. Cowbirds often remove a host egg by piercing it with their beak (Spaw and Rohwer 1987), so damaged host eggs could represent failed puncture attempts by cowbirds. Here I use data collected as part of another study (Weatherhead 1989) to provide some insight into these possibilities.

To differentiate the effects of passive egg bumping during incubation and active bumping or attempted puncturing by the female cowbird requires an experiment in which the fate of host eggs in naturally parasitized nests is compared with that of host eggs in nests artificially parasitized with cowbird eggs. I inadvertently conducted that experiment when I salvaged cowbird eggs from abandoned host nests and placed them in active host nests. This was done to maximize the data I obtained on cowbird growth rates and sex ratios. Because I wanted salvaged cowbird eggs to hatch at the same time as the hosts' eggs, I salvaged only cowbird eggs that had not been incubated and placed them only in host nests that were still in the egg-laying stage or were at the onset of incubation. In parasitized nests that remained active, I removed cowbird eggs to photograph them, and then I replaced them. Therefore, in both naturally and artificially parasitized nests, cowbird eggs were handled by a human observer. Host eggs were not handled in any nests. Thus, the only difference between the two types of nests was the involvement of female cowbirds at naturally parasitized nests.

These data were collected in southern Manitoba in 1983 and 1984. The two host species were Red-winged Blackbirds and Yellow Warblers (*Dendroica petechia*). Details of the study locations and general methods are presented in Weatherhead (1989). For the analyses here I used all nests found before the onset of incubation and in which I did not manipulate the host clutch. For the hatching analysis I used only nests in which at least one egg hatched. For the egg-loss analysis I also included nests that failed because of predation during incubation; I used only those egg losses that preceded complete nest failure. Although I did not examine host eggs for evidence of cracking, I assumed that cracked eggs would either be detected by the host female and removed (Kemal and Rothstein 1988) or would fail to hatch. If female cowbirds bump eggs together to crack host eggs or crack host eggs when attempting to remove them, then host eggs should disappear during incubation or fail to hatch in naturally parasitized nests more often than in artificially parasitized and unparasitized nests. By contrast, if host egg loss occurs because of inadvertent bumping with cowbird eggs during incubation, then naturally and artificially parasitized nests should lose similar numbers of host eggs and both should lose more eggs than unparasitized nests. I restricted the analysis of egg disappearance to the period between the onset of incubation and hatching to avoid including the removal of host eggs by female cowbirds at the time they parasitized nests (Weatherhead 1989).

There was no evidence that cowbird eggs reduced the hatching success of Red-winged Blackbird eggs (Table 1). There was no difference in hatching success between unparasitized and naturally parasitized nests ($\chi^2 = 0.53$, $P = 0.47$) or between unparasitized and

TABLE 1. The fate of host eggs in naturally and artificially parasitized nests.

	Red-winged Blackbird			Yellow Warbler		
	Unparasitized	Naturally parasitized	Artificially parasitized	Unparasitized	Naturally parasitized	Artificially parasitized
Hatching success						
No. of nests	82	33	21	139	21	20
Host eggs hatched	290	94	68	531	63	65
Host eggs unhatched[a] (%)	37 (11.3)	16 (14.4)	6 (8.1)	58 (9.8)	16 (20.3)	9 (12.2)
Egg disappearance						
No. of nests	89	40	22	146	22	21
Host eggs not disappearing	355	136	77	617	85	79
Host eggs that disappeared (%)	19 (5.0)	8 (6.0)	8 (9.0)	22 (3.0)	3 (3.0)	11 (12.0)

[a] Does not include eggs that disappeared.

artificially parasitized nests ($\chi^2 = 0.36, P = 0.55$). However, Yellow Warbler eggs in unparasitized nests had higher hatching success than eggs in naturally parasitized nests (Table 1, $\chi^2 = 6.64$, $P = 0.01$) but not higher than eggs in artificially parasitized nests (Table 1, $\chi^2 = 0.17$, $P = 0.68$).

There was also no evidence that cowbird parasitism increased the rate of egg disappearance in Red-winged Blackbird nests (Table 1). The number of eggs lost from unparasitized nests did not differ significantly from naturally parasitized ($\chi^2 = 0.00$, $P = 1.00$) or artificially parasitized nests ($\chi^2 = 1.63$, $P = 0.20$). Yellow Warblers did show an effect of parasitism on egg loss, but the pattern was different from the hatching analysis (Table 1). More eggs disappeared from artificially parasitized nests than unparasitized nests (Fisher exact test, $P = 0.001$) while there was no difference between unparasitized and naturally parasitized nests (Fisher exact test, $P = 0.64$).

My results for Red-winged Blackbirds appear inconsistent with those of Blankespoor et al. (1982). In my study, cowbird eggs did not increase the number of blackbird eggs that either failed to hatch or that disappeared. I suggest that the presence of a cowbird egg was not associated with increased cracking of blackbird eggs. However, differences in the methods used in the two studies may explain the different outcomes. Blankespoor et al. (1982) closely examined eggs for evidence of cracking to determine that blackbird eggs in parasitized nests were cracked more than those in unparasitized nests. I did not examine cowbird eggs for cracks. If cracked eggs sometimes hatch, then it is possible to have increased incidence of cracking without a significant reduction in hatching success. Blankespoor et al. (1982) showed that blackbird eggs disappeared more often than cowbird eggs. However, they did not show that blackbird eggs from parasitized nests disappeared more than those from unparasitized nests. Therefore, it is possible that blackbird eggs disappear from nests more often than cowbird eggs, independent of whether they are in parasitized nests. Although this may reconcile my results with those of Blankespoor et al. (1982), it leaves unexplained the reason for the higher rate of disappearance of blackbird eggs.

The results for Red-winged Blackbirds indicate that the actions of female cowbirds at host nests (e.g. puncture attempts) do not damage host eggs because there was no difference in loss or hatching failure of host eggs between naturally and artificially parasitized nests.

My results showed that Yellow Warbler eggs suffered reduced hatching and higher disappearance because of the presence of cowbird eggs. Curiously, reduced hatching was observed only in naturally parasitized nests, while increased disappearance was observed only in artificially parasitized nests. This latter result demonstrates that some host egg losses were due to the cowbird egg alone and not to the action of the female cowbird. Although these data collectively illustrate an additional cost to parasitism that may be associated with cowbird eggs having thicker shells, the results could have been due solely to the fact that warbler eggs were in a nest that had a much larger and therefore stronger egg. One would have to do experiments with cowbird-sized eggs of normal shell thickness to determine whether it is large size or thick shells that causes cowbird eggs to break warbler eggs.

My experiment with Red-winged Blackbirds did not support the hypothesis that thicker shells cause cowbird eggs to reduce competition in host nests by damaging host eggs. However, this hypothesis was supported in Yellow Warblers, a much smaller species with more fragile eggs, although the specific role of eggshell thickness remains to be determined. Although the results were ambiguous, they indicate that female cowbirds appeared not to contribute directly to the damage their eggs caused.

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