

SHORT COMMUNICATIONS

Eggshell Strength and Cowbird Parasitism of Red-winged Blackbirds

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Recently, there has been much interest in avian brood parasitism (review by Payne 1977). Its study provides a unique opportunity to gain some understanding of how two distinct and different lineages coevolve (Robertson and Norman 1977). Rothstein (1975) suggests that, during the egg-laying period, host species for the Brown-headed Cowbird (*Molothrus ater*) fall into two mostly nonoverlapping categories: some species, "rejecters," exhibit behaviors that, at least in part, negate the efforts of the parasite, while others, "accepters," appear to tolerate the presence of cowbird eggs.

In 1975 and 1976 we monitored cowbird parasitism in populations of an accepter species, the Red-winged Blackbird (*Agelaius phoeniceus*), in Lincoln County, South Dakota. Rates of parasitism measured at the beginning of incubation were 14 out of 19 nests (21 out of 90 eggs) in 1975 and 14 out of 34 nests (23 out of 136 eggs) in 1976. These results confirm other published reports that Red-winged Blackbirds are common cowbird hosts on the Great Plains (Hergensdörfer 1962, Hill 1976, Facemire 1980). The higher rate of parasitism in 1975 might have resulted from a drought-induced reduction in the number of available host nests.

Apparently, Brown-headed Cowbird nestlings show few adaptations for the parasitic habit. They do not hatch significantly sooner than host nestlings, their growth rates are similar to those of related species (Payne 1977), and they do not evict nest mates. Recently, Eastzer et al. (1980) have shown that cowbird nestling survival in Barn Swallow (*Hirundo rustica*) nests was no better than four of five nonparasitic species, although a fledgling cowbird was successful in eliciting feeding behavior from Barn Swallow foster parents.

Cowbird nestlings often do enjoy a competitive advantage, however, because they typically occur in the nests of smaller host species. Another strategy for gaining a disproportionately large share of food resources involves a reduction in the number of competing host nestlings. One way cowbirds accomplish this is by removing host eggs. We examined our 1975 and 1976 samples of Red-winged Blackbird nests for evidence of host-egg removal (Table 1). If one assumes a normal clutch size of four, then cowbirds at 10 of the 37 parasitized nests showed no ejection behavior. Because in the remaining nests a number of Red-winged Blackbird eggs may have disappeared for other reasons (see below), we conclude that cowbirds quite often fail to eject Red-winged Blackbird eggs.

We suggest that cowbirds have evolved an additional kind of indirect strategy to reduce the number of competing Red-winged Blackbird nestlings. This strategy involves eggshell strength and egg survivorship. We suggest that Red-winged Blackbird eggs are structurally weaker and more likely to be broken (and subsequently removed) during egg-laying and incubation than are cowbird eggs. As part of a 1979 and 1980 study of egg porosity in these two species, we used the scanning electron microscope to measure shell thickness in eggs collected before the onset of incubation. The thickness measurement for each egg was the mean of five shell fragments near the equator of the egg. Thickness measurements did not include the shell membranes. Thirty Red-winged Blackbird eggs (mean fresh weight = 4.03 g \pm 0.43 SD) had a mean thickness of 41.38 μ m \pm 3.56 SD, while 30 cowbird eggs (mean fresh weight = 3.26 g \pm 0.24) had a mean thickness of 58.79 μ m \pm 2.67. Thus, using thickness as one measure of shell strength, we conclude that cowbird eggs are clearly stronger. The fact that the heavier Red-winged Blackbird eggs had thinner eggshells runs counter to the usual relationship between egg weight and shell thickness in birds (Ar et al. 1974).

But, in fact, are Red-winged Blackbird eggs more likely to be cracked and broken? During the porosity study, a number of eggs of both species had unexpectedly high rates of water loss. Upon close examination, these eggs were determined to have cracks. Because all eggs were wrapped in cotton wadding before being transported from the field to the laboratory, we are confident that most of these eggs were already cracked in the nest. The numbers of cracked eggs in parasitized nests were as follows: 1979, 23 of 65 (35.4%) Red-winged Blackbird eggs and 14 of 81 (17.3%) cowbird eggs; 1980, 35 of 89 (39.3%) Red-winged Blackbird eggs and 19 of 151 (12.6%) cowbird eggs. Pooling the data for both years, the proportion of cracked eggs in Red-winged Blackbirds was significantly higher ($\chi^2 = 36.41$, $df = 1$, $P < 0.005$).

Presumably, an individual egg is cracked either by being stepped on by the female or by being jostled against other eggs. In both cases, eggs with thicker, stronger shells (i.e. cowbird eggs) would enjoy a distinct advantage. With regard to egg jostling, it is expected that, when a Red-winged Blackbird egg is jostled against a thicker-shelled cowbird egg, it is more likely to crack than when it is jostled against another Red-winged Blackbird egg. This idea can be tested by comparing the numbers of cracked Red-winged Blackbird eggs in parasitized and nonpar-

TABLE 1. Nest contents at the beginning of incubation or at the time of nest discovery.

Nest contents ^a	Number of nests	
	1975	1976
5 RW	—	1
4 RW	4	17
4 RW, 1 CB	5	3
4 RW, 2 CB	—	1
4 RW, 3 CB	1	—
3 RW	3	7
3 RW, 1 CB	4	4
3 RW, 2 CB	4	5
3 RW, 3 CB	—	1
2 RW	—	2
2 RW, 1 CB	1	2
2 RW, 2 CB	1	2
2 RW, 4 CB	1	—
1 RW, 1 CB	—	1
1 RW, 4 CB	1	—

^a RW = Red-winged Blackbird eggs; CB = Brown-headed Cowbird eggs.

asitized nests. Ideally, only eggs from clutches of equal size should be used for such comparisons. Because no sample for a single clutch-size category was sufficiently large, we included eggs from all clutch-size categories in our analysis. The numbers of cracked eggs were as follows: 1979, 35 of 89 (39.3%) in parasitized nests and 33 of 120 (27.5%) in nonparasitized nests; 1980, 58 of 154 (37.6%) in parasitized nests and 50 of 230 (21.7%) in nonparasitized nests. Pooling the data for both years, the number of cracked eggs was significantly higher in parasitized nests ($\chi^2 = 11.57$, $df = 1$, $P < 0.005$).

We have demonstrated that by the time incubation begins a significantly larger number of Red-winged Blackbird eggs sustains cracks than do cowbird eggs. It remains to be demonstrated that Red-winged Blackbird eggs actually survive less well in the field during incubation. Our assumption is that most cracked eggs subsequently break and are removed from the nest. In 1975 and 1976 during incubation, we visited parasitized and nonparasitized nests almost every day and were able to compare egg survivorship in the two species. Eggs that were lost because of whole-nest predation were not included in the comparison. Typically, single eggs would disappear from a nest between one visit and the next. In 1975, 14 Red-winged Blackbird eggs were lost during 580 egg-days, while no cowbird eggs were lost during 245 egg-days. In 1976, disregarding two cowbird eggs that were laid maladaptively during incubation, 13 Red-winged Blackbird eggs were lost during 691 egg-days while 1 cowbird egg was lost during 181 egg-days. The difference between rates of egg loss for the two species was tested by using a test of proportions (Ferguson 1966: 176). Pooling

data across 1975 and 1976 and using a one-tailed test, egg loss was significantly greater in Red-winged Blackbirds ($Z = 2.65$; $P < 0.01$). Eighteen of the 27 eggs lost (66.7%) were in parasitized nests.

We believe this differential egg loss was due to a greater tendency for Red-winged Blackbird eggs to break and to be subsequently ejected by female Red-winged Blackbirds. There are alternative explanations, however, that need to be examined. Because cowbird eggs are better camouflaged, it could be argued that differential egg survivorship was due to a greater probability of Red-winged Blackbird eggs being preyed upon during partial predation. Picman (1977) demonstrated that the Long-billed Marsh Wren (*Cistothorus palustris*), a common breeding species in the study area, does break and remove Red-winged Blackbird eggs. His results, however, indicate that Marsh Wrens respond equally to eggs of a different color. It may also be argued that female cowbirds remove some Red-winged Blackbird eggs after incubation has begun. Although such behavior has been observed by Mayfield (1961) in the Kirtland's Warbler (*Dendroica kirtlandii*), it apparently occurs only rarely, because cowbirds usually lay an egg of their own after removing a host egg and such eggs laid after incubation essentially would be wasted.

From the parasite's point of view, it is surprising that the Red-winged Blackbird is used so often as a host, because cowbird nestlings would be expected to do better in the nests of smaller hosts. The negative effect of large host size, however, can be countered by reducing the number of host eggs (and therefore host nestlings). Cowbirds often do this by ejecting host eggs. An additional, favorable change in the ratio of host to parasite eggs would occur if host eggs had lower survival rates during incubation. This study indicates that such is the case when Red-winged Blackbirds serve as hosts, primarily because Red-winged Blackbird eggs are structurally weaker.

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Evidence of a Boreal Avifauna in Middle Tennessee during the Late Pleistocene

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A faunistically significant, stratified cave deposit was discovered during an archaeological site survey of the proposed Tennessee Valley Authority (TVA) Columbia Dam reservoir that will impound approximately 30 km of the Duck River in middle Tennessee. This small cave, known as Cheek Bend Cave (40MU261), is in a limestone bluff 20 m above the river bed, 13 km east-southeast of Columbia, Maury County. Testing for the presence of aboriginal occupation began in September 1978 and, as a result of encountering huge quantities of animal bone and shell at considerable depths that appeared not to be attributable to man, was continued until May 1979. Three 1 × 2-m excavation units placed along the east wall revealed stratified deposits of animal remains to a depth of about 4.5 m.

On the bases of the species composition within and among strata, differing fill zones, and certain other stratigraphic features, the deposit reflects two distinct and well-defined major episodes of fill. The top 2 m represent the Holocene epoch and contain remains of only extant modern species. In contrast, the faunal assemblage in the bottom 2 m, although it includes some species that still inhabit the cave area (presently a deciduous Western Mesophytic Forest), contains many that are now extirpated and reflect a prairie habitat (Prairie Chicken, *Tympanuchus cupido*; 13-lined ground squirrel, *Spermophilus tridecemlineatus*, pocket gopher, *Geomys* sp.) or a boreal environment (e.g. arctic shrew, *Sorex arcticus*; water shrew, *Sorex palustris*; red-backed vole, *Clethrionomys gapperi*; yellow-cheeked vole, *Microtus xanthognathus*; red squirrel, *Tamiasciurus hudsonicus*; northern flying squirrel, *Glaucomys sabrinus*; and heather vole, *Phenacomys intermedius*). Recovery of a partial carapace of a wood turtle (*Clemmys insculpta*) also suggests, based on the present center of distribution of the wood turtle, a well-established boreal

environment for an extended period of time in this area during the Late Wisconsinan (Parmalee and Klippel 1981).

The avifauna from Cheek Bend Cave is extremely diversified and reflects both open grassland or savanna and forest habitat. Remains of aquatic birds (e.g. Pied-billed Grebe, *Podilymbus podiceps*, and at least three species of ducks) are rare in the deposit, although several species associated with riverine or marsh habitats are represented. Most notable among these are the Yellow Rail (*Coturnicops noveboracensis*) and the Black Rail (*Laterallus jamaicensis*), both probably rare transients in Tennessee, although their modern distribution in the Midsouth is poorly known. We identified a minimum of approximately 60 species, representing 28 families, from the avian sample. Elements of numerous passerine species of the families Parulidae and, particularly, Fringillidae comprised 75-95% of the avian samples from the Holocene levels. Except for the Passenger Pigeon (*Ectopistes migratorius*) and the Ruffed Grouse (*Bonasa umbellus*), all of the identified species represented in the Holocene levels are still a part of the avifauna of middle Tennessee. A comprehensive report dealing with the stratigraphy and chronology of Cheek Bend Cave, its archaeological component, and the total faunal assemblage is being prepared for the Tennessee Valley Authority.

Several species of birds identified from elements recovered in the bottom 2 m of the deposit are especially significant, because they not only represent new state or regional records but also because they suggest a boreal climate and habitat in this region during the Wisconsinan. Five species worthy of special comment are the Hawk Owl (*Surnia ulula*), Boreal Owl (*Aegolius funereus*), Saw-whet owl (*Aegolius acadicus*), Gray Jay (*Perisoreus canadensis*), and Pine Grosbeak (*Pinicola enucleator*). In addition to these