

# A COMPARATIVE STUDY OF EGG SHELL THICKNESS IN COWBIRDS AND OTHER PASSERINES<sup>1</sup>

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**Abstract.** We directly measured the eggshell thickness of the three brood parasitic *Molothrus* cowbirds, 17 other icterids, and 13 additional passerines. By correcting these shell thickness measurements for variation attributable to interspecific differences in egg volume, we show that the *Molothrus* cowbirds lay eggs with shells that are 30% thicker than expected for their size. Our samples of nonparasitic icterids and of other passerines do not differ significantly in shell thickness values corrected for differences in egg volume. We evaluate two hypotheses for the evolution of unusually thick-shelled eggs in cowbirds. The first, an old idea proposed for parasitic cuckoos, is that thick shells resist damage to the parasite's egg at laying. From indirect tests we could find little or no evidence that the thin-shelled eggs of the hosts of cowbirds were damaged by impact when cowbird eggs were laid in their nests; thus, we tentatively conclude that resistance to laying damage has not been critical in favoring the evolution of thick shells in cowbird eggs. As an alternative hypothesis we propose that thick shells have evolved in cowbird eggs to resist puncture ejections by hosts that are too small to grasp whole cowbird eggs for ejection. We show that a puncture specialist, the Marsh Wren (*Cistothorus palustris*), has greater difficulty puncturing cowbird eggs than the thinner-shelled eggs of various other passerines. Implications of our hypothesis concerning resistance to puncture ejections are discussed.

**Key words:** Shell thickness; cowbirds; puncture ejections; brood parasites; icterids; *Molothrus ater*.

## INTRODUCTION

At least some brood parasitic cuckoos are known to lay particularly thick-shelled eggs (Baker 1942, Lack 1968, Gaston 1976) and some data indicates that the brood parasitic cowbirds also lay unusually thick-shelled eggs (Hoy and Ottow 1964, Blankespoor et al. 1982). Good comparative data on the relative eggshell thickness for both parasitic and nonparasitic species of these families are, however, largely lacking. In this paper we compare the eggshell thickness of parasitic cowbirds with that of other icterids and other, nonparasitic passerines. After establishing that the eggs of the parasitic *Molothrus* cowbirds are unusually thick-shelled, we use Brown-headed Cowbirds (*Molothrus ater*) to evaluate two hypotheses for the evolution of thick eggshells: resistance to laying damage and resistance to puncture ejection. The first was proposed for parasitic cuckoos but seems not to apply to cowbirds; the second is developed here for cowbirds, and may also apply to parasitic cuckoos.

Because of the variety of our methods and the diversity of our results, we present our data as a series of separate studies, each with its own methods, results, and discussion sections.

## EGGSHELL THICKNESS IN COWBIRDS AND OTHER PASSERINES

### METHODS

In this part of our study our purpose was simply to provide descriptive data on the thickness of eggshells for parasitic cowbirds and other nonparasitic passerines. We measured eggshell thickness directly with a Model 35 Bench Comparator thickness gauge, modified for use on small eggs. With this device, a narrow pin is lowered through the blow hole of an "egg" specimen until it rests on the inner surface of the eggshell; shell thickness is then measured as the perpendicular distance between the end of the pin and the surface upon which the egg rests. Readings are provided to the nearest 5  $\mu$  and may be estimated to the nearest micron. When so measured shell thickness includes the thickness of the shell itself and the thickness of the membranes which always

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adhere to the eggshell when the egg contents are blown out.

Since the thickness of eggshells declines during incubation (Taylor 1970), we measured only eggs that were indicated by the collector to have been fresh when collected. To maximize variance among individual females, only one egg was measured from a clutch for eggshell thickness; similarly only a single cowbird egg was measured from any host nest. With three exceptions, noted in Table 1, every egg set from which an egg was measured was chosen from a different geographic locality, or, at least, from different years.

C. D. Spaw and S. Sumida made the measurements of eggshell thickness. Measurement error, estimated by a nested ANOVA on repeated measurements, accounted for only about 10% of the variance in measurements within subspecies.

Before the shell thickness of eggs of various species could be related to whether or not they are brood parasites, the more fundamental effect of egg mass had to be eliminated statistically. We used the interior volume of eggs as an index of their mass, and estimated volume with the equation  $V = 0.498LB^2$ , where  $V$  is interior volume,  $L$  is length, and  $B$  is breadth. The constant 0.498 was derived from direct measurements of the length, breadth, and volume for 18 passerine eggs, varying from 1.19 to 8.89 ml in volume; each was from a different species but the eggs were dataless and not identified to species. Using a Mettler Balance, these 18 eggs were weighed empty, then filled with distilled water and weighed again; the difference between these weights represents egg volume. Volume for these eggs was then regressed on  $LB^2$  to find the constant 0.498. For this sample of 18 eggs of various shapes (Harrison 1979), mean percent errors (measured volume - estimated volume/measured volume  $\times$  100) were 1.85 for elliptical eggs ( $n = 3$ ), 2.05 for short oval eggs ( $n = 5$ ), 1.30 for oval eggs ( $n = 5$ ), and 2.90 for long oval eggs ( $n = 5$ ).

This study is based on measurements for 20 icterids and 13 additional passerines. A diversity of passerines exclusive of icterids was measured to determine how nonparasitic icterids compared with other passerines and to expand the egg size axis of our regression line, thus increasing its accuracy. Among these other passerines we included the European Magpie (*Pica p. pica*) even though it is not specifically distinct from

the Black-billed Magpie (*P. p. hudsonia*), which was also included. We did so because the European Magpie added a data point for an egg size considerably larger than that for the Black-billed Magpie.

To compute egg volume for the full sample of eggs (Table 1) we always used our derived constant of 0.498 and usually used the length and breadth estimates given by Bent (1942 to 1968). For the European Magpie we used the measurements in Harrison (1975) and for the Boat-tailed Grackle (*Quiscalus major*) and the Great-tailed Grackle (*Q. mexicanus*) we used measurements provided by Selander and Giller (1961). For the following species and subspecies, we measured length and breadth directly from egg specimens because the measurements either were not available in Bent or were obviously erroneous: Shiny Cowbird (*Molothrus bonariensis bonariensis*)  $L = 23.43 \pm 1.86$ ,  $B = 18.25 \pm 0.73$  (12 eggs from seven clutches); *M. b. minimus*,  $L = 20.31 \pm 0.47$ ,  $B = 15.90 \pm 1.32$  (six eggs from four clutches); Tricolored Blackbird (*Agelaius tricolor*)  $L = 24.47 \pm 1.23$ ,  $B = 17.56 \pm 0.82$  (40 eggs from 10 clutches); Lichtenstein's Oriole (*Icterus gularis*)  $L = 27.66 \pm 1.15$ ,  $B = 18.71 \pm 0.34$  (10 eggs from 10 clutches); and Montezuma Oropendola (*Psarocolius montezuma*)  $L = 36.80 \pm 2.41$ ,  $B = 26.24 \pm 1.14$  (19 eggs from eight clutches).

Because the effect of mass on shell thickness is multiplicative, the data were transformed to logs. To control for the effect of egg volume on eggshell thickness, we regressed log mean shell thickness on log mean volume. Vertical deviations from this regression were then used to measure the relative shell thickness for each species. Species lying above the line (positive deviations) have thicker shells than expected by the effect of mass alone and species lying below the line (negative deviations) have thinner shells than expected. The average deviation of shell thickness in log microns was calculated for various subgroups. The antilog of this average deviation represents the geometric mean of the ratio of observed shell thickness to expected shell thickness (expected based on the log-log regression). This geometric mean of observed to expected values is unitless and represents the percent that a group (or an individual) lies above or below the expected value of 1.0 from the log-log regression line.

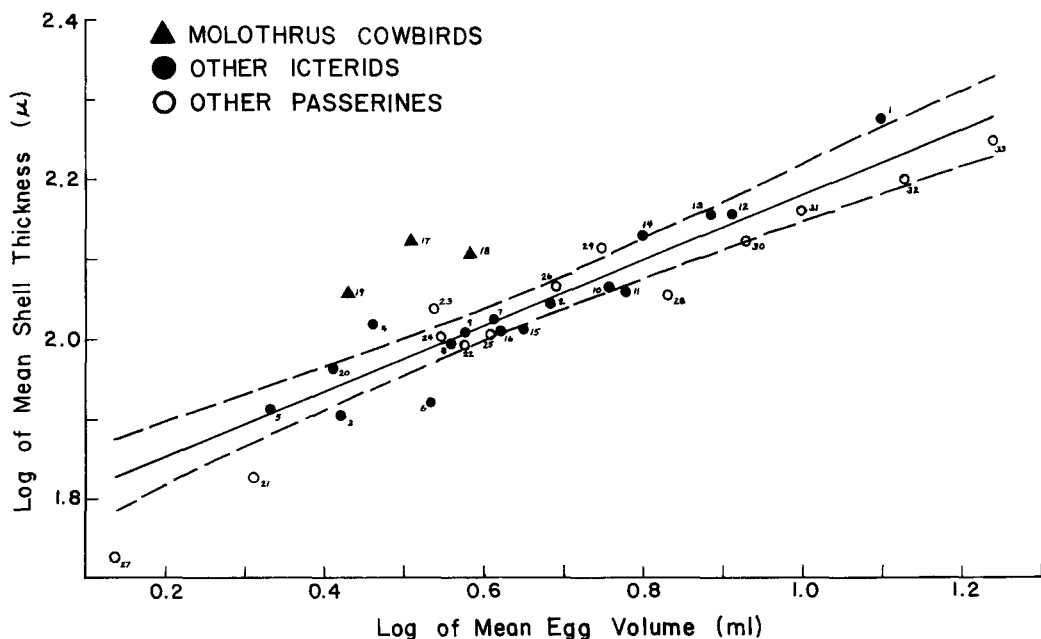


FIGURE 1. Log-log regression and 95% confidence belts of eggshell thickness on egg volume for the three brood parasitic *Molothrus* cowbirds, 17 other icterids, and 13 additional passerines.

## RESULTS AND DISCUSSION

In our entire sample of 20 icterids and 13 other passerines, there is a strong correlation between log egg volume and log eggshell thickness ( $r = 0.889$ ,  $P < 0.001$ ; Fig. 1). Egg volume explains 79% of the variation in eggshell thickness among these 32 species. The shell thickness for the parasitic cowbirds (*Molothrus bonariensis*, *M. aeneus*, and *M. ater*) was 30% greater than predicted by the regression whereas shell thickness for the other 17 icterids was 0.4% lower than predicted ( $P < 0.005$ ,  $df = 16$ , 1-tailed  $t$ -test on the deviations measured in logs). The 13 other passerines, which fall an average of 5.4% below the line, were not significantly different from the 17 nonparasitic icterids ( $P > 0.10$ ,  $df = 26$ , 2-tailed  $t$ -test). These comparisons suggest that the extreme shell thickness of *Molothrus* cowbirds is associated with their parasitic habits and not with their membership in the subfamily Icterinae. We should note that our finding that cowbird eggs are 30% thicker than expected by that volume is conservative because we included cowbird eggs in the regression of shell thickness on egg volume. Blankespoor et al. (1982) found the eggs of Brown-headed Cowbirds to be more than 40% thicker

than Red-winged Blackbird (*A. phoeniceus*) eggs even when the effect of the larger volume of red-winged eggs was ignored.

Numerous tests, both within and among species, show that eggs with thicker shells can withstand more external pressure before breaking (Tyler 1969, Ar et al. 1979). In the next two sections we evaluate two hypothetical sources of damage to cowbird eggs that could have selected for their remarkably thick shells.

## HAVE THICK SHELLS EVOLVED TO PREVENT BREAKAGE AT LAYING?

Lack (1968:85) proposed that the thick shells of the eggs of parasitic cuckoos evolved to protect the egg when it falls into the nest. The speed with which parasitic cuckoos lay together with their unusually extensible cloaca and habit of laying in nests in niches or holes that female cuckoos cannot enter make this a plausible explanation for the evolution of thick shells in cuckoo eggs (Lack 1968). Gaston (1976) provided a confirming anecdote for the laying damage hypothesis when he observed a Pied-billed Cuckoo (*Clamator jacobinus*) lay an egg in a babbler's (*Turdoides* sp.) nest while perched on a twig 15 cm

TABLE 1. Data on egg volume and eggshell thickness for the 33 passerines included in Figure 1.

Species/subspecies	Computed volume (ml)	Sample size for egg dimensions	Shell thickness (mm)		Sample size for shell thickness
			Mean	SD	
Icterids:					
1. Montezuma Oropendola <i>Psarocolius montezuma</i>	12.58	19	0.187	0.022	8
2. Lichtenstein's Oriole <i>Icterus gularis</i>	4.81	10	0.112	0.010	5
3. Hooded Oriole <i>Icterus cucullatus sennetti</i>	2.64		0.080		
<i>I. c. californicus/nelsoni</i>	2.50	93	0.080	0.002	5
<i>I. c. trochiloides</i>	2.50	—	0.078	0.008	6
	2.93	10	0.082	0.001	6
4. Northern Oriole <i>Icterus g. galbula</i>	2.88		0.104		
<i>I. g. bullocki</i>	2.74	56	0.106	0.004	5
	3.01	144	0.101	0.008	6
5. Orchard Oriole <i>Icterus spurius</i>	2.16	133	0.082	0.004	5
6. Scott's Oriole <i>Icterus parisorum</i>	3.43	25	0.083	0.008	5
7. Yellow-headed Blackbird <i>Xanthocephalus xanthocephalus</i>	4.13	134	0.105	0.008	9
8. Red-winged Blackbird <i>Agelaius phoeniceus littoralis</i>	3.61		0.099		
<i>A. p. californicus</i>	3.42	50	0.101	0.011	5
<i>A. p. phoeniceus</i>	3.61	44	0.101	0.013	5
	3.80	380	0.094	0.004	6
9. Tri-colored Blackbird <i>Agelaius tricolor</i>	3.76	40	0.102	0.006	5
10. Eastern Meadowlark <i>Sturnella magna</i>	5.72	201	0.116	0.008	5
11. Western Meadowlark <i>Sturnella n. neglecta</i>	5.99	206	0.114		
<i>S. n. confluenta</i>			0.112	0.006	5
			0.118	0.010	5
12. Great-tailed Grackle <i>Quiscalus mexicanus prosopidicola</i>	8.20	29	0.143	0.007	12
13. Boat-tailed Grackle <i>Quiscalus major</i>	7.70	21	0.147	0.013	5
14. Common Grackle <i>Q. q. quiscula</i>	6.32		0.134		
<i>Q. q. versicolor</i>	6.33	40	0.132	0.009	8
	6.31	40	0.135	0.008	8
15. Rusty Blackbird <i>Euphagus carolinus</i>	4.45	50	0.103	0.004	6
16. Brewer's Blackbird <i>Euphagus cyanocephalus</i>	4.39	45	0.102	0.004	5
17. Shiny Cowbird <i>Molothrus b. bonariensis</i>	3.23		0.132		
<i>M. b. minimus</i>	3.89	12	0.138	0.011	7
	2.56	6	0.126	0.004	4
18. Bronzed Cowbird <i>Molothrus a. aeneus</i>	3.85	38	0.128		
<i>M. a. milleri</i>			0.130	0.005	7
			0.125	0.006	5
19. Brown-headed Cowbird <i>Molothrus ater obscurus</i>	2.70		0.114		
<i>M. a. ater</i>	2.16	37	0.110	0.011	27
<i>M. a. artemesia</i>	2.88	127	0.115	0.009	22
	3.06	40	0.116	0.012	12
20. Bobolink <i>Dolichonyx oryzivorus</i>	2.59	77	0.092	0.005	14

TABLE 1. Continued.

Species/subspecies	Computed volume (ml)	Sample size for egg dimensions	Shell thickness (mm)		Sample size for shell thickness
			Mean	SD	
Other passerines:					
21. Eastern Phoebe <i>Sayornis phoebe</i>	2.04	50	0.067	0.003	5
22. Eastern Kingbird <i>Tyrannus tyrannus</i>	3.78	50	0.097	0.009	5
23. Great-crested Flycatcher <i>Myiarchus crinitus</i>	3.46	40	0.109	0.006	5
24. Gray Catbird <i>Dumetella carolinensis</i>	3.55	50	0.100	0.013	5
25. Northern Mockingbird <i>Mimus polyglottis</i>	4.05	50	0.100	0.011	5
26. Crissal Thrasher <i>Toxostoma dorsale</i>	4.92	50	0.116	0.008	5
27. Clay-colored Sparrow <i>Spizella pallida</i>	1.37	50	0.053	0.002	5
28. Pinyon Jay <i>Gymnorhinus cyanocephalus</i>	6.85	50	0.113	0.007	5
29. Blue Jay <i>Cyanocitta c. cristata</i>	5.62	40	0.129	0.006	6
30. Black-billed Magpie <i>P. pica hudsonia</i>	8.47	201	0.132	0.011	10
31. European Magpie <i>P. p. pica</i>	9.95	—	0.114	0.007	5
32. Fish Crow <i>Corvus ossifragus</i>	13.46	46	0.158	0.008	5
33. Common Crow <i>Corvus b. brachyrhynchus</i>	16.49	292	0.177	0.016	5

above the nest. One of the four babbler eggs present in the nest showed a circular depression "which was probably caused by the cuckoo's egg falling on it."

The idea that thick shells evolved to resist damage at laying is less plausible for cowbirds than for cuckoos because the asymmetry in size between cowbirds and their hosts is considerably less than that between cuckoos and their hosts. Although cowbirds can settle fully into the nest of most of their hosts, they have been reported to do so with difficulty for some hosts with small nests (Hann 1937, Norris 1947). Like cuckoos, cowbirds deposit their eggs very rapidly, typically spending considerably less than 1 min on the nest, while nonparasitic passerines usually spend over 30 min on the nest when they lay (Friedmann 1929, Hann 1937, Mayfield 1960, Nolan 1978).

If cowbirds have evolved thick eggshells to prevent impact damage at laying, then the following two predictions should hold when cowbirds lay in nests that already contain host eggs. First, cowbird eggs should rarely sustain any damage when they are laid. Second, impact damage should, not infrequently, be reported for the thin-shelled eggs of the host. The first prediction should hold regardless of the selective reason for the thick shells of cowbird eggs, so only confirmation of the second prediction will support the hypothesis that thick shells evolved to prevent damage at laying. The assumption underlying this test is that the thin shells of host eggs adequately represent the ancestral condition of cowbird eggs. Thus, if host eggs show evidence of impact damage, but cowbird eggs do not, then we can infer that ancestral cowbird eggs—prior to the evolution of thick shells—would also have

TABLE 2. Records of individual nests in which condition of the eggs was evaluated before and after each cowbird laying.

Host nest	Min. possible no. of host eggs present when parasitized	Min. possible no. of cowbird layings	Source
Indigo Bunting	1	1	Norris (1947)
American Robin	4	1	Friedmann (1929)
Song Sparrow	1	1	Norris (1944)
Red-eyed Vireo	2	1	Howell (1914)
Kirtland's Warbler	1 and 2	2	Mayfield (1960)
Kirtland's Warbler	1 and 1	2	Mayfield (1960)
Gray Catbird	1 and 2	2	Mengel and Jenkinson (1970)
Bell's Vireo (nest no. 1)	1	1	Pitelka and Koestner (1942)
Bell's Vireo (nest no. 2)	1 and 1	2	Pitelka and Koestner (1942)
Ovenbird (nest no. 5)	1 and 1	2	Hann (1937)
Ovenbird (nest no. 31-2)	1 and 1	2	Hann (1937)
Ovenbird (nest no. 37-2)	2	1	Hann (1937)
Ovenbird (nest no. 23-2)	1	1	Hann (1937)
Ovenbird (nest no. 23-4)	1 and 2	2	Hann (1937)
Rufous-sided Towhee <sup>1</sup>	1 and 1	2	Walkinshaw (1949)
Field Sparrow (nest no. 17) <sup>1</sup>	1	1	Walkinshaw (1949)
Field Sparrow (nest no. 19)	1	1	Walkinshaw (1949)
Brewer's Blackbird	1	1	Rohwer (unpubl.)
Bullock's Oriole <sup>1</sup>	1	1	Spaw (unpubl.)
Bullock's Oriole <sup>2</sup>	3	1	Spaw (unpubl.)

<sup>1</sup> A small puncture reported in one host egg.

<sup>2</sup> A small puncture reported in two host eggs.

sustained impact damage at laying and that selection would have favored eggs with thicker shells.

#### METHODS AND INTERPRETATIVE ASSUMPTIONS

Our data relevant to these predictions came from examinations of eggs in individual nests prior to and after the appearance of cowbird eggs, and from monographic studies of certain hosts of Brown-headed Cowbirds. We reviewed data from these latter monographic studies if the authors themselves had related damage (or its absence) of host eggs to the appearance of cowbird eggs and, thus, seemed to have been checking eggs for obvious breaks.

Data from observations at single nests (Table 2) were included or excluded from this analysis according to the following criteria. First, the nest had to have been examined on the day before laying by the cowbird and at least within 24 hr after the cowbird had laid. The prior examination provided an evaluation of the minimum number and condition of host eggs present in the nest when the cowbird laid. The nest check after the appearance of the cowbird egg provided an assessment of damage that could be attributable to the cowbird egg having been laid in the nest.

Second, empty nests that received a host and a cowbird egg on the same day were excluded. Because cowbirds usually lay earlier in the day than their hosts, such nests usually would not have contained a host egg to have been damaged (Hann 1937, Mayfield 1960, Nolan 1978). Third, nests that contained only one host egg prior to and after the appearance of the cowbird egg were also excluded because cowbirds often remove a host egg prior to laying their own egg (Hann 1937, Nolan 1978). Again, such nests could well have been empty when the cowbird egg was laid. Finally, we included in our sample nests from which a single host egg disappeared. In doing so we assumed that the missing egg had been removed by the cowbird; therefore, we did not record the missing egg as one that had been damaged by impact when the cowbird egg was laid and, subsequently, removed by the host. While this convention will inevitably underestimate the number of broken host eggs, the alternative of attributing the disappearance of single eggs to impact damage when the cowbird laid would produce a far greater error because cowbirds remove host eggs more than 50% of the time (Hann 1937, Hofslund 1957, Mayfield 1960, Nolan 1978).

While much of our data from the examination

of individual nests (Table 2) comes from published accounts, we think the sample of nests chosen represents one in which the eggs were carefully being examined. Most of these studies must have involved detailed inspections of the host eggs because they were often individually numbered. Furthermore, our own three observations were made in conjunction with other studies which involved a careful and thorough inspection of all eggs in the nest for damage.

## RESULTS AND DISCUSSION

We were able to find 28 cases, involving 20 nests of 12 species, in which the condition of eggs had been assessed before and after the appearance of a cowbird egg. In every case, neither the host egg(s) nor the cowbird egg was reported to have sustained any damage that could be attributed to impact. Small punctures found in host eggs in several nests suggested that aborted removals, presumably of host eggs by cowbirds, were responsible for the only damage observed for the relatively thin-shelled host eggs. In most of these nests the clutches were incomplete, thus the likelihood of egg collisions occurring was less than 100%. Of the 28 layings, 19 occurred in small nests which conceivably could have been difficult for the female cowbird to settle into. These data provide no evidence supporting the hypothesis that cowbird eggs have thick shells to survive impact damage at laying.

Data from several monographic studies of single host species confirm this result. Two of 98 nests of Song Sparrows (*Melospiza melodia*) and six of 20 nests of Common Yellowthroats (*Geothlypis trichas*) that were parasitized had host eggs with tiny punctures; but no host egg had damage suggestive of impacts with other eggs (Nice 1937, Hofslund 1957). For Ovenbirds (*Seiurus aurocapillus*), Hann (1937, 1941) found six broken eggs in a sample of 161 eggs (in parasitized nests). While he did not describe the damage itself, Hann reported that none of the broken eggs could be attributed to the cowbird entering the nest to lay.

A particularly valuable set of data is provided by Mayfield (1960) for 12 Kirtland's Warbler (*Dendroica kirtlandii*) nests that were parasitized after clutches were complete. Most of these nests contained four or five warbler eggs when the cowbird eggs were laid in them; thus, the probability of the cowbird egg striking a warbler egg at laying

should have been high. In these nests there were 14 cowbird layings and no report of impact damage. At four nests (five layings) no host egg disappeared, so no impact damage could have been missed. At eight nests (nine layings) 25 of 35 host eggs were lost, and it is highly unlikely that these nine cowbird layings resulted in an average destruction of 2.8 warbler eggs each. The contrast between this high loss rate in nests where a removal by the cowbird presumably occurred and the absence of loss in nests where no removal by the cowbird occurred suggests that the losses were related to acts of egg removal by the cowbirds rather than impact damage associated with laying by the cowbirds.

In a sample of 83 nests of Prairie Warblers (*Dendroica discolor*) that contained warbler eggs when parasitized, Nolan (1978) associated five of 12 damaged warbler eggs with cowbird layings because host egg removals by the cowbirds did not occur on the day of laying at these nests. Punctures, cracks, and dents were associated with this "laying" damage. The punctures can reasonably be attributed only to aborted egg removals, presumably by cowbirds; however, the dents and possibly the cracks could have represented damage caused by cowbird eggs striking the warbler eggs at laying.

In summary, neither the detailed histories of individual nests (Table 2) nor the larger data sets from several monographs suggest much impact damage to host eggs caused by cowbird eggs dropping into their nests. We think it highly unlikely that dents in host eggs of the sort that have been found after cuckoo layings (see Gaston 1976) would have been missed by these field workers, and Hann (1937:220) specifically notes he found no broken eggs attributable to the cowbird entering the nest to lay. Most reported damage for host eggs seems to be the result of cowbirds piercing eggs to remove them. Since host eggs are rarely if ever damaged by being struck by cowbird eggs at laying, it is not at all surprising that the detailed histories at individual nests revealed no evidence of cowbird eggs, themselves, being damaged at laying (Table 2). From these negative data we tentatively reject the hypothesis that cowbirds have thick-shelled eggs to prevent damage at laying. We are tentative because Nolan's (1978) observations of dents in eggs of the Prairie Warbler—a very small species whose nests may be difficult for a cowbird to enter—could be indicative of impact damage that ancestral cow-

birds may have suffered when their eggs had thinner shells.

#### HAVE THICK SHELLS EVOLVED TO PREVENT PUNCTURE EJECTIONS?

Despite the costs of being parasitized by cowbirds, numerous species accept their eggs and rear their young. Given the general lack of resemblance between cowbird eggs and those of their hosts and the fact that a number of species do remove cowbird eggs from their nests (Rothstein 1975, 1982; Friedmann et al. 1977), the acceptance of cowbird eggs is perplexing. We propose that an important factor contributing to the acceptance of cowbird eggs by small hosts is their very thick shells.

Most rejecter species remove the eggs of Brown-headed Cowbirds from their nest by grasping them in their mandibles. Based on limited data comparing bill length and the width of cowbird eggs, Rothstein (1975, 1982) argues that most accepter species should be able to remove cowbird eggs from their nests. His data on this point are weak, however, because he fails to maintain a consistent distinction between grasp and puncture ejections. Thus, Rothstein (1975) compares the bill length to egg width ratio for a series of accepter species (using cowbird egg widths) and for a series of birds that were known to have rejected relatively large eggs (of various kinds, so various widths). While this index is relevant to grasp ejections, in each of Rothstein's cases of known ejection, the mode of removal either was by puncture or was not specified (Rohwer and Spaw, unpubl.).

Rothstein (1975:264) recognizes that some small accepters may have difficulty "handling" or "manipulating" cowbird eggs as easily as rejecters, but he suggests that his analyses (involving bill size and egg widths and bird size and egg weight) "indicate that all or nearly all accepters can eject cowbird eggs." Our own work suggests small bills are a significant constraint. Most accepters have small bills while most grasp ejecters have large bills, suggesting that small beaks prohibit the evolution of grasp ejection in many hosts (Rohwer and Spaw, unpubl.). We further hypothesize that selection favoring puncture ejections by small hosts has been stopped by cowbirds evolving thick-shelled eggs, which, even if they are not impossible to break, render the cost of puncture ejection higher than the cost of acceptance. This puncture resistance hypothesis

has been advanced at least once before by Swynerton (1918:151) who wrote that the thick shells of the cuckoo's egg "may also protect it from being pierced by such weak birds as warblers," which in Swynerton's egg addition experiments sometimes pierced thinner-shelled eggs.

In the following preliminary test of this puncture resistance hypothesis, we presented Marsh Wrens with cowbird eggs and the eggs of various other passerines. We chose to initiate this testing with Marsh Wrens because they are well known for puncturing eggs (Picman 1977). Our experiment had two possible outcomes. First, forced acceptance would be strongly confirmed if Marsh Wrens proved incapable of puncturing cowbird eggs. Such a result would be particularly significant because Marsh Wrens are puncture specialists and because they have a very thin and sharply pointed beak. Thus, if a Marsh Wren could not pierce a cowbird egg, neither should other small hosts be able to do so. Second, the puncture resistance hypothesis would be weakly confirmed if the wrens succeeded in puncturing the cowbird eggs but experienced difficulty in doing so.

#### METHODS

Unfortunately, Marsh Wrens nest before cowbirds commence laying in Washington. Consequently, we resorted to using old and dateless museum specimens for this work. The eggs were filled with water and their blow holes were then glued over with Duco Cement. Our use of these old specimens was unfortunate. Some had been collected over 100 years earlier and, undoubtedly, had become brittle through the dehydration of the hydrated proteins which contribute to shell strength (Vincent 1982). Before filling these eggs with water, the empty shells were weighed on a Mettler Balance. Their weight (in mg) was then divided by  $LB^2$ , an index of the volume of the egg in cc, to provide an index of shell thickness for each experimental egg (see Table 3).

Our experiments were conducted in mid-May 1982 at the Skagit Wildlife Recreation Area in western Washington. For presentation to the wrens, eggs were placed in the bottom of a Red-winged Blackbird nest that had been placed in a stand on a short length of conduit pipe. A pair of eggs was presented on each territory, but they were presented separately with the cowbird egg presented first on about half of the territories and second in the other half (see Table 3 for se-



TABLE 3. Eggs presented to Marsh Wrens for ejection, their thickness index, and the number of pecks and number of holes made by the wrens.

Wren territory	Eggs <sup>1</sup>	Shell thickness index	No. pecks/no. holes <sup>2</sup>	Data for sign test <sup>3</sup>
1	Northern Oriole	26	7/6	
	Brown-headed Cowbird	38	17/1	+
2	Brown-headed Cowbird	33	30/4	
	Gray Catbird	34	29/6	+
3	Brown-headed Cowbird	39	22/1	
	Field Sparrow	25	3-5/1	+
4	Red-winged Blackbird	29	2/1	
	Brown-headed Cowbird	39	24/2	+
5	Brown-headed Cowbird	37	14/?	
	Northern Mockingbird	30	—	0
	Brown Thrasher	32	3/2	
	Brown-headed Cowbird	38	3/2	—
6	Tricolored Blackbird	26	6/1	
	Brown-headed Cowbird	43	—	0
7	<i>Myiarchus</i> sp.	28	8/1	
	Brown-headed Cowbird	34	10/1	+
8	House Sparrow	33	5/1	
	Brown-headed Cowbird	38	11/1	+
9	Song Sparrow	27	5/1	
	Brown-headed Cowbird	40	27/2	+
10	Brown-headed Cowbird	36	11/3	
	Field Sparrow	24	5/3	+
11	Logger-headed Shrike	28	—	
	Brown-headed Cowbird	39	—	0

<sup>1</sup> For each territory the eggs are listed in the sequence in which they were presented.

<sup>2</sup> Dashes signify eggs that could not be found; the question mark signifies an egg that split into halves.

<sup>3</sup> + = Cowbird egg has more pecks per hole; — = cowbird egg has same or fewer pecks per hole; 0 = no difference established.

quences and identities of the noncowbird egg). Once the wren arrived at the nest we counted the number of pecks it made and then retrieved the egg to count the number of holes. Some of the ejected eggs could not be found in the dense cattails.

#### RESULTS AND DISCUSSION

In all but one of our paired comparisons, the thickness index was greater for the cowbird egg than for its control (Table 3). We were able to retrieve both eggs in nine of 11 paired presentations. In eight of these nine cases the cowbird egg received more pecks per hole than did its control ( $P = 0.004$ ; 1-tailed sign test). In the one exception both eggs were punctured with ease.

All of these punctures and ejections were performed by territorial male wrens. They responded to the nest immediately upon discovering it by approaching its position low in the cattails, and then, when immediately below the nest, by flying directly up to its rim. Without exception, the egg present in the nest was immediately at-

tacked. Not evident in Table 3 is the fact that in several trials, the wrens showed obvious difficulty in breaking the cowbird eggs. Their first blows were typically quite weak and, particularly for the control eggs, were often sufficient to puncture the egg for removal. For the cowbird eggs that received many pecks, the wrens soon switched from calmly poking at the egg to standing tall on their legs and swinging their entire head and body down with comical force as they pounded the egg. No egg survived this treatment, but some received a remarkably large number of blows before they were picked up and removed (Table 3).

The strong confirmation that we had hoped for failed. Marsh Wrens were able to puncture our water-filled cowbird eggs and, thus, eject them from the red-wing nests in which they were presented. In some cases, they showed obvious difficulty in doing so; and the data clearly show that the thicker shells of cowbird eggs make them harder to puncture than thinner-shelled control eggs (Table 3;  $P = 0.004$ , sign test).

While these results support our hypothesis that the thick shells of cowbird eggs have evolved to resist puncture ejections, they do so only weakly. From our direct observations of these Marsh Wrens struggling so hard to puncture some of our cowbird eggs, we doubt that small birds with sparrow-like or flycatcher-like beaks could puncture cowbird eggs at all. But this supposition should be tested directly by operant conditioning experiments.

We should also note, however, that a complete inability to reject cowbird eggs is not necessary for our hypothesis to be true. It may well be the case that cowbird eggs are hard enough that damage caused to the host's own egg in the rejection process would be sufficient to select against attempts at rejection. Blows that do not pierce the cowbird egg must cause it to bounce around in the nest or cause the bird's beak to ricochet off the egg; either of these reactions could cause some of the host's own eggs to be broken. Such indirect damage to the host's eggs may well be more costly than accepting the cowbird egg and raising a mixed brood.

#### GENERAL DISCUSSION

Blankespoor et al. (1982) suggest that Brown-headed Cowbirds may have evolved thick-shelled eggs to resist accidental damage by the attending host. They found numerous damaged red-wing eggs in nests that had been parasitized by cowbirds but very few damaged cowbird eggs. Why they presumed that the damage to such eggs accrues "by being stepped on by the (host) female or by being jostled against other eggs" is unclear to us. Cowbirds are known to be puncture ejectors, Marsh Wrens were common in their study area, and the egg shells of any species should be sufficiently strong to resist damage during normal incubation.

Blankespoor et al. (1982) tested their prediction by comparing the numbers of damaged host eggs in nests of Red-winged Blackbirds that either did or did not contain cowbird eggs. This test is based upon the implausible assumption that when two red-wing eggs are jostled against one another, a break in *either* of them is less likely to occur than is a break in a single red-wing egg, when it is jostled against a cowbird egg. We doubt this assumption because it implies that thinner shells are more resilient and that sharing this (implicitly assumed) resilience between two thin-shelled eggs will result in less total incubation damage.

Furthermore, by using naturally parasitized nests the (likely) possibility that the damage was caused in return visits by the female cowbird cannot be precluded (see Hann 1941, Walkinshaw 1949, Nolan 1978). To exclude the cowbird as the cause of the damage they recorded, Blankespoor et al. (1982) should have compared the incidence of damage in two groups of *unparasitized* red-wing nests. Nests of the experimental group should have been artificially parasitized with a cowbird egg and nests of the control group should have been given another red-wing egg.

The "puncture resistance" and the "laying damage" hypotheses are not mutually exclusive explanations for the thick shells of cowbird eggs. However, the rarity of host eggs exhibiting dents that would suggest impact damage at laying leaves us with no reason to invoke the laying damage hypothesis as the cause for cowbirds evolving thick-shelled eggs. This idea may still be very important for parasitic cuckoos because many of them are much larger than their hosts and should, therefore, have much more difficulty settling into the nests of their hosts. Comparative testing of this idea on cuckoos should be most instructive. The laying damage hypothesis predicts that cuckoos that cannot readily enter the nests of their hosts should produce eggs with relatively thicker shells than should those cuckoos that can readily enter the nests of their hosts. Added shell thickness for resistance to puncture ejections should only occur when the parasitized species cannot grasp-eject the egg. Thus, thick shells should not evolve for cuckoos that specialize on hosts large enough to be capable of grasp ejections, providing that the nests of these are large enough for the cuckoo to enter for laying.

Our hypothesis that the thick shells of the eggs of brood parasites force acceptance on small hosts suggests an inverse correlation between shell thickness of the eggs of brood parasites and the degree to which their eggs mimic those of their hosts in appearance. If thick shells effectively resist puncture ejections, then mimicry of the host's eggs is unnecessary providing, of course, that the host profits more, on average, from rearing a mixed brood than from abandoning the parasitized nest. Thus, certain brood parasites, such as cowbirds, that specialize on hosts that are similar or smaller to them in size may benefit little from the evolution of egg mimicry. This should be true when the eggs of the parasite are sufficiently thick-shelled to render attempted

puncture-ejections of their eggs maladaptive. In contrast, brood parasites that specialize on hosts that are large enough to evolve to be grasp ejecters may not benefit from evolving thick-shelled eggs, but should benefit strongly from the evolution of mimetic eggs. Finally, mimicry of the hosts' eggs but not thick shells should always evolve in brood parasites that cause the death of all host chicks, for in this circumstance abandoning a parasitized nest should always pay.

In sum, our puncture resistance hypothesis renders the acceptance by large numbers of hosts of the nonmimetic eggs of *Molothrus* cowbirds somewhat less puzzling. Rothstein (1975, 1982) has interpreted such behavior as maladaptive. But we would argue, instead, that a choice between acceptance and nest desertion is forced upon these small birds and that they are merely making the best of a bad situation. The real challenge to our hypothesis will be to explain why most small hosts do not abandon parasitized nests in favor of renesting (some do, e.g., Cedar Waxwing, *Bombycilla cedrorum* [Rothstein 1976]; Yellow Warbler, *Dendroica petechia* [Clark and Robertson 1981]; Prairie Warbler [Nolan 1978]; Field Sparrow, *Spizella pusilla*). Perhaps part of the answer to this question lies in the fact that young fledging early in the season survive much better than young fledging late in the season (Perkins 1963). Another part may be the seasonal increase in cowbird parasitism. At least in eastern Washington, early nests are rarely parasitized by cowbirds, but late nests are heavily parasitized (e.g., Brewer's Blackbird, *Euphagus cyanocephalus* [Furrer cited in Friedmann et al. 1977]; Northern Orioles, *Icterus galbula* [Røskaft, Spaw, and Rohwer, unpubl.]). The critical experiment will be to determine whether more host young are fledged by individuals that invest in parasitized nests or by an experimental group of parasitized hosts forced to renest by the experimental destruction of their parasitized clutch. By our puncture resistance hypothesis we predict that renesting will be the worse of these two options in small species which have long been exposed to cowbird parasitism.

It is also worth considering the effects of eggshell thickness on the conditional strategy "attempt to eject and desert only if too many eggs fail," which Rothstein (1982:553) considers an "optimal and reasonable" strategy for small hosts. We point out that the invasion of this conditional strategy requires that ejection attempts result, on

average, in a higher net gain than does abandoning a parasitized nest in favor of renesting. Only *after* this were the case could selection favor the fine tuning adjustment of renesting if damage were unusually high. Thus we return again to the critical, and entirely unevaluated, empirical question: Will small accepters which are experimentally forced to abandon their nests have higher successes in their renests than controls which are left with their cowbird egg?

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