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ARE COWBIRD EGGS UNUSUALLY STRONG FROM THE INSIDE?

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ABSTRACT.—The shells of Brown-headed Cowbird (*Molothrus ater*) eggs are unusually strong from the outside, presumably to reduce chances of puncture ejection by small hosts. To evaluate the potential effects of "outside" eggshell strength on inside strength, I measured the force required to puncture the inside of eggshells. When the confounding effects of variation among species in egg size were controlled, cowbird eggshells tolerated 1.7 times greater pressure than eggs of nine control species from several families. Within-species analyses of cowbirds and two nonparasitic blackbirds indicated that most of the variation in the inside strength of eggshells is related to their thickness. Analyses among species demonstrated that the greater inside strength of cowbird eggs could be explained mostly by their unusually thick eggshells. However, because cowbird eggshells were stronger than expected for their thickness, other eggshell characteristics also must play a role in inside strength. These results suggest that hatching from cowbird eggs is more difficult than would be expected for eggs of their size. *Received 17 January 1996, accepted 18 September 1996.*

AVIAN EGGSHELLS must fulfill several functions: (1) provide mechanical protection from outside pressures exerted by the incubating parent; (2) prevent excessive dehydration; (3) allow adequate gas exchange; and (4) protect the egg contents from detrimental microorganisms (Romanoff and Romanoff 1949, Burley and Vadehra 1989). In addition, eggshells also act as a storage place for inorganic constituents required by the developing embryo (Romanoff and Romanoff 1949).

Incubation-related risks of egg breakage should favor strong eggshells, but egg strength must have an upper limit that is probably set by the hatching process (a young bird must open the eggshell without assistance from its parents) and by the cost to the laying female of providing extra material for thick shells. Therefore, the strength of avian eggshells must present an evolutionary compromise between opposing selective forces.

Four studies recently demonstrated that some birds lay stronger eggs than would be expected for their size. First, the Brown-headed Cowbird (*Molothrus ater*), a brood parasite laying in nests of many hosts (Friedmann et al. 1977, Friedmann and Kiff 1985), forms eggs that are approximately twice as strong as those of other nonparasitic blackbirds of similar size (Picman 1989a). Second, several brood-parasitic cuckoos lay eggs with shells that are unusually thick and hence presumably stronger than expected for their size (Lack 1968, Gaston 1976, Brooker and Brooker 1991, Picman and Pribil unpubl. data). The unusual egg strength of these brood parasites apparently is an adaptation to parasitism, with several possible advantages. A strong eggshell may reduce chances of egg damage at laying (Lack 1968) and during incubation (Blankespoor et al. 1982), and it also may prevent puncture ejection by small hosts (Spaw and Rohwer 1987, Rohwer et al. 1989, Picman 1989a). In addition, in brood parasites, the unusually strong eggshell may reduce hatching success of the host, thereby reducing the number of competing host nestlings (Blankespoor et al. 1982). Cavity-nesting species of waterfowl (Anseriformes) also lay unusually strong eggs, but in this case strong eggs probably reduce chances of accidental breakage in tight and irregularly shaped nesting cavities (Mallory and Weatherhead 1990). Lastly, Marsh Wrens (*Cistothorus palustris*) lay eggs that are almost three times stronger than would be expected for their size. The greater strength of Marsh Wren eggs presumably reduces chances of egg breakage by conspecific attackers (Picman et al. 1996).

The evolution of eggs with unusually high outside strength also probably makes them structurally stronger from the inside. If hatching is a physically demanding process even for birds with eggs of normal strength, then successful hatching from unusually strong eggs may require special adaptations. However, before such adaptations are addressed, we need to establish how outside strength affects inside strength of eggs.

This study has two goals. The first is to establish if eggshells of the parasitic Brown-headed Cowbird are stronger from the inside than would be expected for their size. Greater inside strength of cowbird eggs relative to that of control eggs indicates that hatching may be a more demanding process for young cowbirds. The second goal is to establish the relative contributions of eggshell thickness, egg shape, and egg volume to the inside strength of cowbird eggs. Although the role of these characteristics in outside-eggshell strength has been examined in the Brown-headed Cowbird (Picman 1989a), their relative importance for inside-eggshell strength is likely to differ. Surface curvature theoretically should increase the outside strength of an egg but not its inside strength because only the convex curvature increases the load-bearing capacity and hence the outside strength of the eggshell (e.g. Bernadou and Boisserie 1982). Therefore, any variation in shape among conspecific eggs should have an effect on their outside strength but should be unimportant for their inside strength. Consequently, eggshell thickness should be a stronger predictor of the inside strength than of the outside strength of eggs.

METHODS

Egg collections.—Freshly laid eggs (i.e. eggs that sank to the bottom of a 50-ml container of water) were collected in May, June, and July of 1993 and 1994 near Ottawa, Ontario in Canada. Twenty cowbird eggs were obtained from parasitized nests of Red-winged Blackbirds (*Agelaius phoeniceus*), Yellow Warblers (*Dendroica petechia*), Song Sparrows (*Melospiza melodia*), and Purple Finches (*Carpodacus purpureus*). For a comparative study, I collected eggs of nine species that covered a wide range of egg sizes: Mourning Dove (*Zenaida macroura*; $n = 2$), Tree Swallow (*Iridoprocne bicolor*; $n = 41$), Black-capped Chickadee (*Parus atricapillus*; $n = 14$), Yellow Warbler ($n = 40$ eggs), American Robin (*Turdus migratorius*; $n = 13$), Cedar Waxwing (*Bombycilla cedrorum*; $n = 29$), Purple Finch ($n = 16$), Red-winged Blackbird ($n = 29$), and Common Grackle (*Quiscalus quiscula*; $n = 14$). I kept the eggs in a refrigerator (4°C) at 100% humidity until eggshell analyses were performed.

Eggshell measurements.—The length (L) and breadth (B) of all eggs were measured with calipers to the nearest 0.05 mm. I used the ratio of L:B as an index of egg shape. Size is an important egg characteristic that must be taken into consideration in the analysis of egg strength. Therefore, for all eggs I calculated their volume (V) using the equation provided by Spaw and Rohwer (1987):

$$V = 0.498\,LB^2 \qquad (1)$$

I used egg volume to: (1) establish if egg size had an effect on egg strength, and (2) control for the confounding effects of egg size in analyses of the role of eggshell thickness and egg shape in determining eggshell strength.

I measured eggshell thickness with a micrometer to the nearest 0.001 mm at three uniformly distributed points (see Picman 1989a for details). From these measurements I calculated the mean eggshell thickness for each egg. To measure eggshell strength from inside the egg (henceforth, "inside strength"), I estimated puncture resistance of each egg with a mechanical puncture tester (see Picman 1989b). I measured the inside strength of eggshells (i.e. the pressure in g required to puncture the eggshell from inside the egg) at three uniformly distributed points along the widest circumference of each egg as follows. First, I punctured a given egg from outside as described in Picman (1989b). When puncturing the eggshells from outside, I restricted the penetration of the steel punch to about 2.0 mm inside the tested egg (this reduced the damage to the tested shell to a small hole created during the test). I adjusted the puncture-resistance tester for the inside strength measurements by: (1) placing a new egg support (i.e. a round disk of hard rubber 10 mm thick, with an outside diameter of 19 mm and a circular hole inside it with a diameter of 10 mm) on the egg-support stand, and (2) by selecting the appropriate capacity balance (50 or 100 g) that was used to generate the pressure in tests of the inside strength (puncture resistance) of eggshells. I estimated the inside strength of eggshells by inserting the steel punch through the puncture made from outside the egg, resting it against the inside surface of the eggshell along its widest circumference (perpendicular to its surface), and then gradually increasing the pressure through the Pesola balance until the steel punch broke through the eggshell (see Picman 1989b). The inside puncture resistance of an egg is defined as the minimum pressure (in g) required to break through the eggshell from inside the egg. I calculated the mean inside puncture resistance for each egg by averaging the three measurements of the inside puncture resistance.

Statistical evaluation of puncture resistance.—To establish the magnitude of increase in the inside strength of cowbird eggs relative to the control eggs, I compared cowbird eggs with eggs of nine control species. Because egg size is positively correlated with eggshell thickness and egg strength (Romanoff and Romanoff 1949, Thompson et al. 1981, Picman 1989a), egg size is an important confounding variable that must be controlled. Therefore, I compared the observed inside puncture resistance of cowbird eggs to their expected inside puncture resistance as follows. First, I regressed the inside puncture resistance on egg volume for the control species. Second, I calculated the expected puncture resistance for cowbird eggs (i.e. control eggs of the same volume) from the regression equation obtained for the control species. I calculated vertical deviation from the regression line (henceforth, residual puncture resistance of inside strength) for each bird species and then compared the residual puncture resistance of cowbird eggs with those of the control species (one-sample t-test) to establish whether the inside strength of cowbird eggs differs significantly from that of control species.

Mechanisms of increased eggshell strength.—I conducted statistical analyses at both the within-species and among-species levels to establish which eggshell characteristics are responsible for the greater inside strength of cowbird eggs. The goals of the within-species analyses were to determine the role of selected eggshell characteristics in puncture resistance of eggs and to establish if the examined eggshell characteristics play a similar role in eggshell strength in different species. Because the dependent variable (inside puncture resistance) was normally distributed and its variance was homoscedastic, I performed forward stepwise multiple regression (Zar 1984) for each of three species (Brown-headed Cowbird, Red-winged Blackbird, Common Grackle) to establish the relative importance of egg shape, eggshell thickness, and egg volume in determining the inside puncture resistance of eggs and to estimate the combined effect of these predictor variables on within-species variation in puncture resistance of eggs.

The goal of the among-species analyses was to establish which of the eggshell characteristics that play a role in egg strength (as determined by the within-species analyses) natural selection has favored to produce stronger eggs in cowbirds. To achieve this, I compared cowbird eggs with eggs of control species (i.e. eggs of "normal" strength). A shift in a predicted direction along with a corresponding result from the within-species analyses would indicate that a given eggshell characteristic plays a role in the greater inside strength of cowbird eggs. To provide a more accurate estimate of differences in eggshell thickness and egg shape, I controlled for the confounding effects of egg size in two ways: (1) by using the regression approach; and (2) by directly comparing eggshell thickness and egg shape between the cowbird and other passerines that lay eggs of the same size, while taking into account the relationship between shape and thickness (henceforth, the direct approach).

The regression approach is based on a comparison of residuals calculated for a given eggshell characteristic between the cowbird and control species (in the manner described above). In the control group, which was used to establish a relationship between selected eggshell characteristics, I included 11 passerines (the nine species used to estimate the inside strength of cowbird eggs plus Bobolink [*Dolichonyx oryzivorus*; $n = 30$] and Yellow-headed Blackbird [*Xanthocephalus xanthocephalus*; $n = 46$], for which data were available in Picman [1989a]). The regression approach allows control of only one variable at a time.

The direct approach is based on direct comparison of cowbirds with control species laying eggs of the same size with respect to the two eggshell characteristics. This approach also considers a possible interaction between egg shape and shell thickness. I performed this analysis as follows. First, I selected from Schönwetter (1979, 1984) all passerine species ($n = 99$) whose eggs were similar in mass (3.05–3.20 g) to Brown-headed Cowbird eggs (3.12 g). For polytypic species I selected the taxon with the largest sample size (i.e. each species was represented by only one subspecies). Then, I regressed egg shape on eggshell thickness for all control species to establish if the two traits are correlated. Finally, I compared cowbird eggs with eggs of control passerines with respect to eggshell thickness and egg shape (one-sample t-test). The lack of a significant correlation between eggshell thickness and egg shape for the control species would allow a direct comparison between the cowbird and control species by a one-sample t-test. A significant correlation between the two egg characteristics would require that the one-sample t-test between the cowbird and control species be performed on residuals obtained for all species from the regression established for the control species as described earlier. All statistical analyses were performed using SigmaStat Software (Jandel Scientific Software 1992–1994).

RESULTS

Inside strength of cowbird eggs.—The observed inside puncture resistance of cowbird eggs was 45.1 g (Table 1). For nine control species, the inside puncture resistance (R) increased with egg volume ($R = 11.27 + 5.20V$; $r^2 = 0.96$, $P < 0.001$; Fig. 1). The expected inside puncture resistance of cowbird eggs calculated from this regression equation is 26.3 g. Thus, when the confounding effects of egg volume were controlled, the observed puncture resistance of cowbird eggs was 1.71 times greater than that of nine control species (Fig. 1). Differences between the residual puncture resistance of cowbird eggs and eggs of nine control species were highly significant ($t = -23.43$, $P < 0.001$).

Mechanism of increased eggshell strength: Within-species analyses.—The eggs of cowbirds and two nonparasitic icterids used in the within-species analyses differed in all four eggshell characteristics examined (Table 1). Despite these differences, the multiple regression analysis established that shell thickness was most important for all three species, accounting for 41–65% of the variation in the inside puncture resistance

TABLE 1. Comparisons ($\bar{x} \pm$ SD) of inside puncture resistance, egg volume, egg shape, and eggshell thickness between Brown-headed Cowbirds and two nonparasitic blackbirds.

	Species				
Egg variable	Brown-headed Cowbird	Common Grackle	Red-winged Blackbird	F	P
Puncture resistance (g)	45.13 ± 7.07	45.26 ± 6.94	27.53 ± 3.75*	74.27	<0.001
Volume (ml)	2.902 ± 0.311	6.292 ± 0.583*	3.826 ± 0.324*	319.83	<0.001
Shape (L:B)	1.309 ± 0.046	1.366 ± 0.057*	1.377 ± 0.067*	8.51	<0.001
Thickness (mm)	0.120 ± 0.008	0.129 ± 0.006*	0.106 ± 0.008*	46.53	<0.001
No. of eggs	20	14	29		

*, $P < 0.05$; Dunnett's test comparing cowbird versus the other two species.

of their eggs (Table 2). Egg shape entered the regression equation only for the cowbird but explained a small amount of variation in the inside puncture resistance of cowbird eggs (Table 2). Finally, egg volume consistently was unimportant. Overall, these variables explained 41-72% of the observed variation in the inside puncture resistance in the three species (Table 2). In conclusion, the within-species analyses established that eggshell thickness consistently was a strong predictor of the inside strength of eggs.

Mechanism of increased eggshell strength: Among-species analyses.—I estimated how much the cowbird eggs differed in eggshell thickness (T) from control species because thickness was consistently the best predictor of puncture resistance of eggshells. The regression approach demonstrated that, based on data from 11 control species, egg volume (V) is a strong predictor of eggshell thickness ($r^2 = 0.98$, df = 9, $P < 0.001$; Fig. 2). From the regression equation describing the relationship between these variables ($T = 0.058 + 0.11V$; $F = 373.97$, $P < 0.001$), the expected thickness of cowbird eggshells is 0.09 mm. The observed thickness (0.120 mm) is 1.33 times greater than the expected thickness for this species. Residual eggshell thickness of cowbirds differs significantly from the 11 control species ($t = -26.74$, $P < 0.001$).

The direct approach, based on a large-scale comparison of cowbird eggs and similarly sized control eggs from 99 passerine species, established that: (1) egg shape and eggshell thickness were not significantly correlated for control species ($r = 0.037$, $P = 0.72$; Fig. 3), thereby allowing direct comparison with cowbird eggs; (2) cowbird eggshells were significantly thicker than those of the control species ($t = -35.04$, $P < 0.001$; Fig. 3); and (3) cowbird eggs were significantly rounder than eggs of control species ($t = 9.37$, $P < 0.001$; Fig. 3). Comparison of the mean eggshell thickness and egg shape between eggs of cowbirds and the control passerines indicated that cowbird eggs have shells that are 1.404 times thicker but whose shape index is 0.959 of that of the control group. The difference in eggshell thickness was still greater for the sample of cowbird eggs analyzed in this study (Fig. 3).

Is the greater thickness of cowbird eggshells the sole cause of their greater strength?—If the greater thickness of cowbird eggshells was the sole cause of their greater inside strength, then eggs of other birds with eggshells of the same thickness

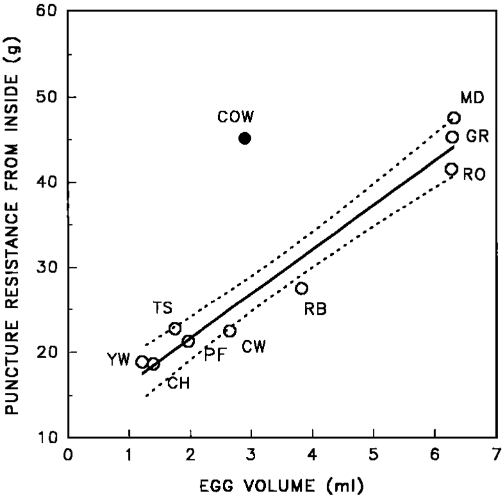

Fig. 1. Puncture resistance from inside the egg of Brown-headed Cowbird (COW) and a sample of nine control species (MD = Mourning Dove, TS = Tree Swallow, YW = Yellow Warbler, CH = Black-capped Chickadee, PF = Purple Finch, CW = Cedar Waxwing, RO = American Robin, RB = Red-winged Blackbird, GR = Common Grackle). Dashed lines indicate 95% confidence intervals around the regression line (see text for regression equation).

TABLE 2. Summary of forward stepwise multiple regression on the effect of egg volume, egg shape (S), and eggshell thickness (T) on puncture resistance measured from inside eggs of Brown-headed Cowbird, Common Grackle, and Red-winged Blackbird. P is the probability that puncture resistance of eggs of a given species can be predicted from a linear combination of the predictor variables. Sample sizes as in Table 1.

	Step 1		Step 2			
Species	Variable	r	Variable	r	Total r^2	P
Brown-headed Cowbird	T	0.808	S	0.850	0.722	<0.001
Common Grackle	T	0.637	—	—	0.405	0.014
Red-winged Blackbird	T	0.802	—	—	0.644	<0.001

should be of the same strength, regardless of their size. To establish the relative importance of the increased thickness of cowbird eggshells in their greater inside strength, I characterized the relationship between eggshell thickness and inside puncture resistance for nine control species. The relationship between these variables was highly significant ($r = 0.97$, $P < 0.001$; Fig. 4), explaining most of the observed variation ($r^2 = 0.95$) in the inside puncture resistance between these species. This relationship can be described as: $R = -15.018 + 454.34T$ ($F = 141.61$, $P < 0.001$). The expected inside puncture resistance of cowbird eggs calculated from this equation is 39.5 g. Therefore, the actual inside puncture resistance of cowbird eggs (45.1 g) is 1.14 times greater than the expected puncture resistance. The comparison of the residual inside puncture resistance between cowbird and control eggs demonstrated that cowbird eggs are significantly stronger from inside than would be expected from the thickness of their shells ($t = -6.481$, $P < 0.001$). Therefore, in addition to eggshell thickness, some other eggshell characteristic(s) must play a role in the greater inside strength of cowbird eggs.

DISCUSSION

Puncture-resistance tests demonstrated that the inside strength of cowbird eggs is 1.7 times greater than would be expected for their size. Although this estimate is based on a small sample of control species, it is likely to be reasonably accurate because the relationship between the inside strength and volume of eggs of control species was strong (almost all variation in the inside strength of eggs was explained by

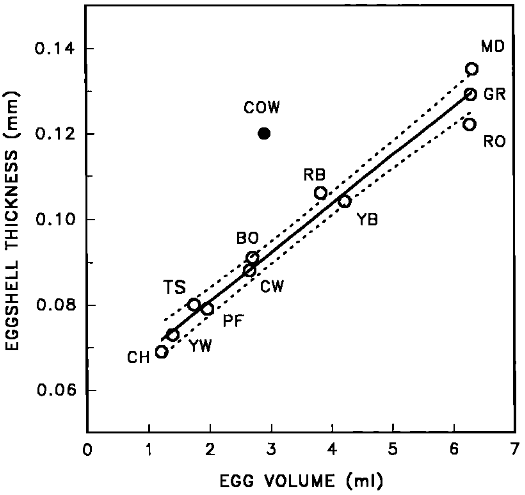

Fig. 2. Eggshell thickness of the Brown-headed Cowbird and 11 control species. Species are same as in Figure 1 with the addition of Bobolink (BO) and Yellow-headed Blackbird (YB). Dashed lines indicate 95% confidence intervals around the regression line (see text for regression equation).

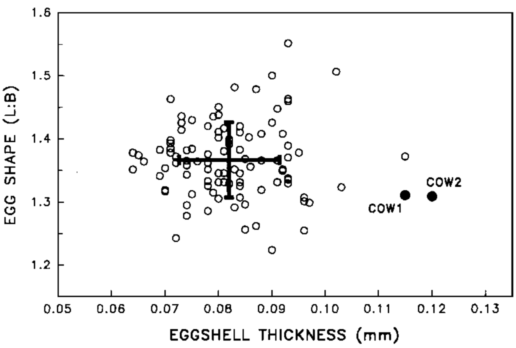

Fig. 3. Eggshell thickness and egg shape for eggs of the Brown-headed Cowbird and 99 other passerines laying eggs of similar mass to cowbird eggs. The cross denotes mean and standard deviation for eggshell thickness and egg shape of the 99 control passerines. Cow 1 refers to Schönwetter's (1979) data on cowbird eggs, Cow 2 to the sample of cowbird eggs examined in this study. Cow 1 was used for the statistical comparisons.

variation in volume; Fig. 1). It is highly likely that eggs of other species (e.g. parasitic cuckoos, cavity-nesting waterfowl, and Marsh Wrens) that are unusually strong from the outside also are unusually strong from the inside.

The within-species study of mechanisms of inside egg strength indicated that in three blackbird species, eggshell thickness was a strong predictor of inside strength of eggs, regardless of differences in egg shape, volume, and eggshell thickness. The role of these same characteristics in determining the outside egg strength has been examined in two blackbird species (Picman 1989a). In both cases, eggshell thickness was a stronger predictor of inside strength than of outside strength (in Red-winged Blackbirds, eggshell thickness accounted for 50.0% and 64.3% of the variation in outside and inside puncture resistance, respectively; in the cowbird, it accounted for 44.0% and 65.3%). This is consistent with the prediction that eggshell thickness is a stronger predictor of inside- than of outside-eggshell strength.

Of the remaining eggshell characteristics, only shape seemed to affect inside strength of eggs. In cowbird eggs, a positive regression coefficient between egg shape and inside puncture resistance implies that the inside strength of cowbird eggshells increases as they become more elongated (i.e. less curved in the region tested). In contrast, the outside strength of cowbird eggs decreases as they become more elongated (Picman 1989a). Thus, although the more rounded shape of cowbird eggs increases their outside strength (Picman 1989a), it may actually decrease their inside strength. This result is consistent with the initial prediction that surface curvature (egg shape) should play different roles in outside and inside strength of an egg. However, the evidence for the decreasing inside-eggshell strength with increasing surface curvature of an egg must be interpreted with caution for two reasons: (1) in cowbird eggs, the contribution of egg shape to the final r^2 in the multiple regression was very small (Table 2); and (2) egg shape did not have a statistically significant effect on inside strength of eggshells of the two nonparasitic blackbirds (Table 2). The lack of a significant effect of egg shape on inside strength of eggs of Common Grackles and Red-winged Blackbirds cannot be explained by a smaller amount of within-species variation in this egg characteristic in the two species as compared with the cowbird (Table 1). In fact, the coefficient of variation is somewhat higher for grackle and red-wing eggs (4.17% and 4.87%, respectively) than for the cowbird eggs (3.57%). Therefore, establishing the role of egg shape in the inside strength of cowbird eggs will require another study specifically designed to address this problem.

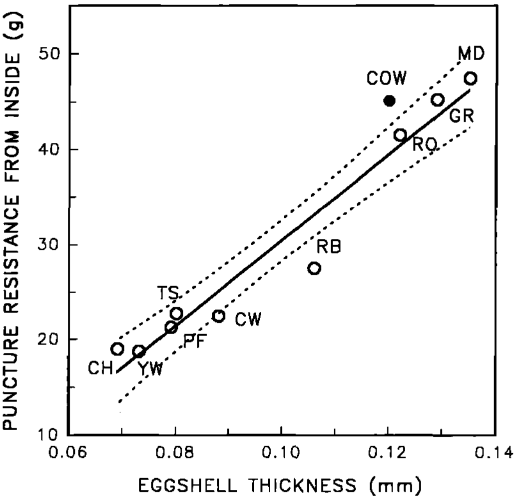

Fig. 4. Puncture resistance from inside the egg as a function of eggshell thickness between the Brown-headed Cowbird and nine control species. Species abbreviations as in Figure 1. Dashed lines indicate 95% confidence intervals around the regression line (see text for regression equation).

Among-species analyses demonstrated that eggshells of cowbird eggs were significantly thicker than expected for their size. The regression approach and the direct comparison approach indicated that cowbird eggshells are 1.3 times and 1.4 times thicker, respectively, than expected for their size. The direct comparison of cowbird eggs with those of other passerine species with eggs of similar size probably yielded a more accurate result because this approach more effectively controlled for effects of confounding variables and because it involved a much larger group of control species. These results are similar to those of Spaw and Rohwer (1987), who concluded that cowbird eggshells are 30% thicker than expected for their size. However, because cowbird eggshells are significantly stronger than expected from their thickness, the greater eggshell thickness is not the sole cause of their greater inside strength. This view is further supported by the finding that in the three blackbird species, a large amount of variation (Table 2) in the inside puncture resistance among conspecific eggs could not be explained by differences in eggshell thickness. Therefore, in addition to eggshell thickness, some other eggshell characteristic(s), such as different chemical composition, higher eggshell density, and possibly different size and spatial organization of pores, must play a role in the increased strength of cowbird eggs.

The finding that cowbird eggshells are unusually strong from inside the egg suggests that young cowbirds must put more effort into hatching than young of other birds with eggs of the same volume. However, the strength that a hatching cowbird must generate to break open the eggshell is likely to be smaller than puncture tests suggest for the following reason. Most (about 80%) of the calcium needed for the formation of bones during embryogenesis is derived from the eggshell, whereas the rest originates from yolk (Burley and Vadehra 1989). Because calcium (the main cation of the crystalline layer of avian eggshells) is responsible for the mechanical strength of an egg (Romanoff and Romanoff 1949, Burley and Vadehra 1989), its removal from the eggshell during embryogenesis is likely to reduce the strength of an egg, thereby facilitating hatching. The role of the decalcification process in reducing the inside strength of eggshells has not been examined, but young of all species presumably remove from their eggshell only that amount of calcium needed for skeleton formation during embryonic development. Therefore, in theory, differences among species in eggshell strength observed in this study should persist throughout all stages of embryogenesis. Consequently, compared with control species, cowbird eggs are likely to have stronger eggshells at hatching, and the young hatching from these eggs presumably experience greater difficulty in breaking open their eggs. These assertions, however, will have to be verified by directly examining the effect of eggshell decalcification on the inside strength of cowbird eggs.

The finding that freshly laid cowbird eggs are unusually strong from the inside suggests that cowbirds have been under strong selection for mechanisms allowing them to overcome costs related to hatching (this argument could be extended to all species that lay unusually strong eggs). The increased hatching difficulty due to an unusually strong eggshell potentially could favor two basic types of adaptations: (1) hatching-related adaptations that would allow the young to break open the egg, such as a highly specialized hatching behavior, stronger egg tooth, and increased strength of musculature required for successful hatching; and (2) adaptations that would reduce the strength of the eggshell. The latter could be achieved, for example, by concentrating calcium removal on the hatching zone of an egg and through a generally increased rate of calcium removal from the eggshell by the embryo. The relative importance of these adaptations could be established by examining the effect of embryonic development on the strength and quality of the eggshell and through a comparative study of young birds hatching from eggs of "normal" versus unusually high strength. The finding that freshly laid cowbird eggshells are unusually strong from inside the egg suggests that a study of these potential adaptations is required.

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