MECHANISM OF INCREASED PUNCTURE RESISTANCE OF EGGS OF BROWN-HEADED COWBIRDS

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ABSTRACT.—Spaw and Rohwer (1987) proposed that thick shells of the Brown-headed Cowbird (*Molothrus ater*) eggs are a response to puncture ejection by some hosts. I provide evidence for puncture resistance of eggs of the Brown-headed Cowbird and of a sample of nonparasitic icterids. I attempted to establish the relative role of the eggshell shape and inorganic constituents in determining puncture resistance of cowbird eggs. I found that the cowbird eggs tolerated approximately twice as much pressure during puncture resistance tests than eggs of three nonparasitic icterids. The greater strength of cowbird eggs is due mainly to thicker eggshells and a more rounded shape. These variables play a similar role in variation in puncture resistance among conspecific eggs. Cowbird eggshells have a higher content of inorganic constituents than those of nonparasitic icterids. However, the hypothesis that inorganic content further increases strength of cowbird eggs requires additional testing.

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THE BROWN-HEADED Cowbird (*Molothrus ater*) is an opportunistic brood parasite known to lay in nests of 221 species (Friedmann et al. 1977, Friedmann and Kiff 1985). Brood parasitism exhibited by this species is a highly specialized reproductive activity which involves a number of adaptations. For example, to reproduce successfully, a female cowbird must find a suitable host nest and then lay her egg in it at an appropriate time (e.g. Clark and Robertson 1981). The success of this behavior may be greatly affected by the tendency of some hosts to reject cowbird eggs (e.g. Rothstein 1982). Most rejecter species remove cowbird eggs through grasp ejection (Rothstein 1975, 1982), but Spaw and Rohwer (1987) suggested that puncture ejection should be characteristic of small birds which have small beaks and cannot grasp the cowbird egg.

The evolution of host tendency to reject parasitic eggs by puncture ejection might elicit new responses by a parasite. For instance, parasitic cowbirds may lay thick-shelled eggs (Hoy and Ottow 1964, Blankespoor et al. 1982, Spaw and Rohwer 1987). Because shell thickness and shell strength are strongly correlated (Romanoff and Romanoff 1949), thicker eggshells should reduce chances of egg breakage. For this reason, Spaw and Rohwer (1987) proposed that thicker cowbird eggshells may be an adaptation to puncture ejection by small hosts.

To determine the effect of eggshell thickness on puncture resistance, Spaw and Rohwer (1987) examined the ability of a small puncture specialist, the Marsh Wren (*Cistothorus palustris*), to break eggs of cowbirds and several nonparasitic passerines. In this experiment Marsh Wrens broke all eggs, but apparently had greater difficulty puncturing the cowbird eggs. On the basis of this qualitative evidence, Spaw and Rohwer (1987) concluded that thicker eggshells increase puncture resistance of cowbird eggs. However, to understand the role of a thicker shell and to establish its relative importance in the susceptibility of cowbird eggs to puncture ejection by small hosts, quantitative data are required.

In addition to eggshell thickness, I hypothesized that the strength of eggshells could be influenced by the egg shape and the chemical composition of the shell. Egg shape might play a role because a curved shape will increase the load bearing capacity of the shell (e.g. Bernadou and Boisserie 1982). I predicted that greater puncture resistance should also favor a rounder shape in cowbird eggs. The test of this prediction required that the shape (i.e. roundness) of eggs of parasitic cowbirds and nonparasitic icterids be compared and its role in determining puncture resistance established. Further, various minerals (especially calcium) determine the breaking strength of chicken eggs (Romanoff and Romanoff 1949). Therefore, a trend towards stronger eggs in parasitic cowbirds might also favor a higher proportion of inorganic eggshell constituents. The test of this prediction re-

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TABLE 1. Comparison of eggshell thickness ($\bar{x} \pm$ SD) in 4 icterid species.

Species	Shell thickness (mm)	Eggs (*n*)	*t*[a]
Cowbird	0.125 ± 0.006	25	—
Red-wing	0.107 ± 0.007	46	11.08*
Yellow-head	0.104 ± 0.006	32	13.08*
Bobolink	0.091 ± 0.003	17	24.00*

[a] Student's *t* test; * = $P < 0.001$.

TABLE 2. Comparison of volume of eggs ($\bar{x} \pm$ SD) of cowbirds with 3 blackbird species.

Species	Egg volume	Eggs (*n*)	*t*[a]
Cowbird	2.838 ± 0.24	25	—
Red-wing	3.868 ± 0.359	68	−15.89*
Yellow-head	4.225 ± 0.272	45	−22.06*
Bobolink	2.697 ± 0.231	30	2.20**

[a] Student's *t* test; * = $P < 0.001$, ** = $P < 0.05$).

quired comparison of the content of inorganic constituents in eggshells of cowbirds with a sample of nonparasitic icterids.

METHODS

I obtained 25 freshly laid cowbird eggs from 19 parasitized Red-winged Blackbird (*Agelaius phoeniceus*) nests (1 cowbird egg was found in 14 Red-wing nests, 2 in 4 nests, and 3 in 1 nest) between 25 and 27 May 1987 at the Delta Marsh located at the south end of Lake Manitoba, Manitoba, Canada. Although it is impossible to establish how many female cowbirds laid the 25 eggs, I believe that most were laid by different individuals. The reasons are that many cowbirds were present in the area, a large area was searched, and all eggs were collected in 3 days at the start of the cowbird laying period. Eggs were stored in a refrigerator at 100% humidity until they could be analyzed ca. 6 weeks later. I used another 31 cowbird eggs (collected by K. Hobson and J. Friskie in the same area) for size measurements. To establish the relative role of different features of eggshells for the strength of eggs, I compared cowbird eggs with those of Red-winged Blackbirds (a total of 44 eggs from 22 clutches), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus;* 30 eggs from 15 clutches), and Bobolinks (*Dolichonyx oryzivorus;* 16 eggs from 8 clutches). In these three nonparasitic icterids, two eggs were selected randomly from freshly laid clutches. Red-wing and Yellow-head eggs were collected at the same time as the cowbird eggs at Delta Marsh. The Bobolink eggs were collected 1-7 June 1987 near Ottawa, Ontario. All eggs were stored as described above.

Eggshell measurements.—The length (L) and breadth (B) of all eggs were measured with calipers to the nearest 0.05 mm. The ratio L:B was used as an index of egg roundness (shape index). Egg size could affect puncture resistance of eggs if it varied systematically with eggshell thickness or egg shape (e.g. larger eggs should have thicker shells and thus be harder to puncture). To establish whether or not egg size is a confounding variable that biased the results on puncture resitance of eggshells, I used egg volume as an index of size in the analyses. Egg volume (V) was calculated from the equation: $V = 0.498LB^2$ (Spaw and Rohwer 1987). I measured eggshell thickness with a micrometer at three points along the widest area of each egg, where puncture resistance tests were performed previously. During each test a small disk was usually punched out of the shell. This small shell chip with egg membranes (ca. 2 mm^2) was removed with pincers from each of the three marked areas where a puncture test was done, and the thickness of the shell fragment was measured to the nearest 0.001 mm (each shell fragment was measured at least twice). I calculated the mean shell-thickness score for each egg. The puncture resistance of eggs was measured with a mechanical puncture tester (Picman in press). The instrument consists of a spring-loaded Pesola balance which generates accurate pressure on an egg, a metal bar hinged to a stand which transmits the pressure generated by a balance to the egg through a small punch (diameter: 1.2 mm), an egg support stand on which an egg is laid, and a bell assembly to signal when an eggshell is punctured. I used the instrument to determine the pressure required for a punch to break the shell at the widest point of an egg. Usually three (sometimes two to four) measurements for each egg were made along the widest egg area (points evenly spaced). Mean egg puncture resistance score was then calculated for each egg and used for statistical analyses.

Determination of inorganic constituents in eggshells.—The egg contents were removed and shells were washed in water. Numbered ceramic dishes for use in a combustion chamber were first dried (30 min in a drying oven at 60°C), cooled to room temperature in a desiccator, and then weighed to the nearest μg (weight of empty dish A). Clean eggshells (with egg membranes) in ceramic dishes (1 eggshell/dish) were dried for 60 min at 60°C. The shells were then allowed

TABLE 3. Comparison of egg-shape index (egg length divided by egg breadth) for eggs of cowbirds, Red-wings, Yellow-heads, and Bobolinks

Species	Length : breadth ($\bar{x} \pm$ SD)	Eggs (*n*)	*t*[a]
Cowbird	1.296 ± 0.082	56	—
Red-wing	1.410 ± 0.079	68	−7.78*
Yellow-head	1.444 ± 0.052	46	−11.03*
Bobolink	1.351 ± 0.037	30	−4.23*

[a] Student's *t* test; * = $P < 0.001$.

TABLE 4. Data on egg shape (length : breadth) and egg volume for 16 nonparasitic icterids and 5 parasitic cowbirds.

Species	Computed volume	Egg-shape index	n	Source
Bobolink (*Dolichonyx oryzivorus*)	2.59	1.342	77	Bent 1958
Eastern Meadowlark (*Sturnella magna*)	5.72	1.364	201	Bent 1958
Western Meadowlark (*S. neglecta*)	5.99	1.375	206	Bent 1958
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	4.13	1.441	134	Bent 1958
Red-winged Blackbird (*Agelaius phoeniceus*)	3.80	1.413	380	Bent 1958
Tri-colored Blackbird (*A. tricolor*)	3.76	1.394	40	Spaw & Rohwer 1987
Orchard Oriole (*Icterus spurius*)	2.16	1.408	133	Bent 1958
Hooded Oriole (*I. cucullatus*)	2.50	1.417	93	Bent 1958
Altamira Oriole (*I. gularis*)	4.81	1.478	10	Spaw & Rohwer 1987
Scott's Oriole (*I. parisorum*)	3.43	1.405	25	Bent 1958
Northern Oriole (*I. g. galbula*)	2.74	1.491	56	Bent 1958
Rusty Blackbird (*Euphagus carolinus*)	4.45	1.387	50	Bent 1958
Brewer's Blackbird (*E. cyanocephalus*)	4.39	1.370	245	Bent 1958
Boat-tailed Grackle (*Quiscalus major*)	8.85	1.461	62	Bent 1958
Common Grackle (*Q. quiscula*)	6.33	1.414	40	Bent 1958
Montezuma Oropendola (*Psarocolius montezuma*)	12.58	1.402	19	Spaw & Rohwer 1987
Brown-headed Cowbird (*Molothrus ater*)	2.88	1.306	127	Bent 1958
Nevada Brown-headed Cowbird (*M. a. artemisiae*)	3.06	1.298	40	Bent 1958
Dwarf Brown-headed Cowbird (*M. a. obscurus*)	2.16	1.288	37	Bent 1958
Bronzed Cowbird (*M. aeneus*)	3.85	1.264	38	Bent 1958
Shiny Cowbird (*M. bonariensis*)	3.89	1.284	12	Spaw & Rohwer 1987

to cool to room temperature in a desiccator for 30 min and weighed to the nearest μg (weight B). The ceramic dishes with shells were then exposed to 600°C for 16 h in a combustion chamber. Dishes with remaining shell material (inorganic constituents) were transferred to a desiccator where they cooled for 60 min to room temperature. The dishes were then weighed to the nearest μg (weight C). The inorganic content of an eggshell was expressed for each egg as a proportion of its total weight [i.e. $(C - A)/(B - A)$].

To establish the accuracy of this method to determine inorganic content of eggshells, I placed known amounts of organic and inorganic constituents (a protein, serum bovine albumin, and calcium carbonate, respectively) in 10 ceramic dishes. The two chemicals were combined in a ratio of 0.4 organic to 0.6 inorganic constituents, which approximates natural eggshells (the weight of the mixture also approximated that of an eggshell). After the above procedures, I estimated the inorganic content. Comparison of inorganic content based on the actual proportion of $CaCO_3$ in the mixture and the proportion of $CaCO_3$ estimated by combustion of serum bovine albumin in a mixture of two chemicals demonstrated that the combustion data were always within 10% of the mixtures of known proportions.

Statistical analyses.—I examined the relationships among eggshell thickness, egg roundness, inorganic content, egg volume, and puncture resistance of eggs at two levels. First, the between-species comparisons should indicate if a shift in a given eggshell feature occurred in a predicted direction (e.g. more rounded eggshells with higher inorganic content in parasitic cowbirds as compared to nonparasitic icterids). Conversely, the within-species analyses should establish if selected eggshell parameters have the predicted effects on eggshell strength (puncture resistance).

RESULTS

Between-species comparison of thickness, shape, and inorganic constituents.—Cowbird eggs have significantly thicker eggshells than Red-wings,

TABLE 5. Comparison of egg-shape index ($\bar{x}$ ± SD) of 5 parasitic cowbirds and 16 nonparasitic icterids (see Table 4) by Student's t test.

Category	Egg-shape index	99% CI[a]	Statistical comparison
Nonparasitic icterids (5)	1.410 ± 0.041	1.380–1.440	$t = 9.776$ $P < 0.001$
Parasitic cowbirds (16)	1.288 ± 0.016	1.270–1.306	

[a] Confidence interval.

TABLE 6. The amount of inorganic constituents in eggshells of cowbirds, Red-wings, Yellow-heads, and Bobolinks.

Species	Proportion of inorganic constituents ($\bar{x} \pm$ SD)	No. eggs analyzed	t[a]
Cowbird	0.707 ± 0.112	25	—
Red-wing	0.571 ± 0.094	44	5.106*
Yellow-head	0.600 ± 0.116	30	3.523*
Bobolink	0.556 ± 0.056	16	5.697*

TABLE 7. Puncture resistance tests with eggs of 4 icterid species. The value in parentheses is the percentage of puncture resistance of the cowbird eggs for eggs of a given species.

Species	Pressure to puncture egg in g ($\bar{x} \pm$ SD)	Eggs (n)	t[a]
Cowbird	245.72 ± 38.39	25	—
Red-wing	135.25 ± 25.99 (55.0%)	44	12.82*
Yellow-head	130.53 ± 18.61 (53.12%)	30	13.72*
Bobolink	105.13 ± 6.79 (42.8%)	16	17.94*

[a] Student's t test; * = $P < 0.001$.

Yellow-heads, and Bobolinks (Table 1). The difference in shell thickness is even more striking because Red-wing and Yellow-head eggs are significantly larger than cowbird eggs (Table 2). Egg size is thus an important confounding variable. Similar difference in eggshell thickness of cowbirds and other icterids was reported earlier by Spaw and Rohwer (1987), who concluded that the cowbird eggshells were 30% thicker than expected for their size.

Cowbird eggs are significantly more rounded than the eggs of Red-wings, Yellow-heads, and Bobolinks (Table 3). To further test the hypothesis that cowbird eggs should be more rounded, I calculated the egg-shape index for 16 nonparasitic and 5 parasitic icterids (Table 4). However, egg size, as measured by egg volume, varied greatly among the species (Table 4). Because egg volume and egg shape could be correlated, differences in the size of parasitic and nonparasitic icterids could mask the predicted effect of reproductive behavior on egg shape. To determine if egg volume was a confounding variable, I correlated egg shape with egg volume for 16 nonparasitic icterids. The two variables were not correlated ($r = 0.003$, $n = 16$, $P > 0.5$), which allows the direct comparison of the egg-shape index for nonparasitic and parasitic icterids. Eggs of parasitic cowbirds are significantly more rounded that those of nonparasitic icterids (Table 5). This supports the hypothesis that a trend towards stronger eggshells may also influence the egg shape of parasitic cowbirds.

In comparison with eggs of nonparasitic species, cowbird eggshells have a significantly higher inorganic content (Table 6). This is consistent with the hypothesis that a higher proportion of inorganic constituents produces stronger eggshells in cowbirds.

Puncture resistance of eggs.—Cowbird eggs tolerated significantly more pressure in puncture tests than eggs of the nonparasitic icterids (Table 7). This supports the proposition that parasitic cowbirds have stronger shells. Cowbird eggs differ from nonparasitic icterids in their thicker shells, rounder shape, and also in their greater inorganic content (Tables 1, 3, 6).

Within-species correlations of shell thickness, egg shape, and inorganic content.—If these eggshell variables determine eggshell strength, they should be correlated within species with the puncture-resistance score obtained for individual eggs. Shell thickness had a significant positive correlation with puncture resistance of eggs of all four species (Table 8). The egg-shape index correlated negatively with puncture resistance for cowbird, Red-wing, and Yellow-head eggs (Table 8). A negative trend for Bobolink eggs is not significant, presumably because of a smaller sample size. In these species puncture resistance increased as egg roundness increased. Inorganic content was not correlated significantly with puncture resistance of eggs of any of the icterids (Table 8). Finally, egg volume (a potentially confounding variable) had a significant negative correlation with puncture resistance of Red-wing eggs, but there was no significant relationship between these variables for eggs of the other species (Table 8).

The examination of correlations among independent variables could indicate between-species differences in correlations between puncture resistance and the three independent variables. Second, correlations among shell thickness, egg shape, inorganic content, and egg volume might further improve our understanding of the role of eggshell physical properties which, in turn, determine their strength. The egg-shape index was not significantly correlated with shell thickness for any of the species

TABLE 8. The effect of eggshell variables on puncture resistance of cowbird, Red-wing, Yellow-head, and Bobolink eggs.[a]

Species (n)	Egg shape	Shell thickness	Inorganic constituents	Egg volume
Cowbird (25)	−0.64***	0.67***	0.10	0.16
Red-wing (44)	−0.30*	0.71***	0.07	−0.47**
Yellow-head (30)	−0.40*	0.63***	−0.08	−0.09
Bobolink (16)	−0.19	0.59**	−0.01	−0.42

[a] Pearson correlation; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

(Table 9). However, the shape index was correlated positively with inorganic content for Yellow-head and Bobolink eggs. In these species, the loss of strength caused by flatter surfaces in more elliptical eggs appears to be compensated by a higher proportion of eggshell inorganic constituents. The shape index correlated positively with egg volume in Red-wing eggs (Table 9), and implies that larger Red-wing eggs tend to be more elliptical. This correlation and a negative correlation between shell thickness and volume of Red-wing eggs (Table 9) could explain the negative correlation between puncture resistance of Red-wing eggs and their volume (Table 6). In contrast, shape and volume of cowbird eggs are negatively correlated; larger cowbird eggs tend to be more rounded. Furthermore, volume of cowbird eggs and shell thickness are not correlated (Table 7). In such cases, selection for strong eggshells will favor more rounded shape in larger eggs. This view is supported by the fact that cowbird eggs of different sizes exhibit similar resistance to puncture (Table 6).

I used a stepwise multiple regression to estimate the relative role of eggshell variables in puncture resistance of icterid eggs. The eggshell thickness accounted for 35–50% of the variation in puncture resistance of eggs of individual species (Table 10). The egg shape entered the regression equation in two species, but not in the Red-wing and Bobolink. Egg shape explained 26% (cowbird) and 13% (Yellow-head) of the observed variation in puncture resistance. Thus, in cowbirds, the eggshell thickness and egg shape explained 70% of the observed variation in puncture resistance of eggs (Table 10).

The relative importance of independent variables can be more accurately assessed from partial correlations which provide a single measure of association between two variables while adjusting statistically for the effects of another variable. For cowbird eggs, the partial correlations between eggshell thickness (T) and puncture resistance (P; egg shape (S) controlled) and between egg-shape index and puncture resistance (eggshell thickness controlled) are $r_{\mathrm{TP.S}} = 0.706$ and $r_{\mathrm{SP.T}} = -0.68$, respectively (for both partial correlations $P < 0.001$). I conclude that eggshell thickness and egg shape have similar effects on puncture resistance of cowbird eggs. Eggshell thickness explains 48%, and egg shape 46%, of variation in puncture resistance of cowbird eggs.

DISCUSSION

Spaw and Rohwer (1987) proposed that the greater thickness of cowbird eggs was a response to puncture ejection exhibited by some cowbird hosts. Eggs with thicker shells should be more difficult to puncture. They argued that Marsh Wrens had greater difficulty puncturing eggs of cowbirds than those of other nonpar-

TABLE 9. Intercorrelations between independent variables egg shape (S), shell thickness (T), proportion of inorganic constituents (I), and egg volume (V) for four icterids.[a]

Species	S × T	S × I	S × V	T × V	I × V	T × I
Cowbird	−0.22	0.07	−0.44*	−0.04	0.30	−0.01
Red-wing	−0.19	−0.20	0.42**	−0.30*	−0.25	−0.06
Yellow-head	−0.05	0.36*	0.19	0.01	0.04	0.11
Bobolink	−0.33	0.77***	0.09	−0.44	0.02	−0.13

[a] Significance levels are given for 2-tailed tests; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

TABLE 10. Stepwise multiple regression analyses on the effect of egg shape (S), shell thickness (T), proportion of inorganic constituents (I), and calculated egg volume (V) on puncture resistance (PR). Only statistically significant predictor variables ($P < 0.05$) are included in equations.

Species	Regression equation	r^2 T	S	V	Total	F (P)
Cowbird	PR = 56.38 + 3482.55T − 188.90S	0.44	0.26	—	0.70	25.61 (0.0001)
Red-wing	PR = −50.25 + 2594.62T − 24.65V	0.50	—	0.07	0.57	27.37 (0.0001)
Yellow-head	PR = 65.11 + 2373.55T − 126.50S	0.40	0.13	—	0.53	15.47 (0.0001)
Bobolink	PR = −17.89 + 1350.84T	0.35	—	—	0.35	7.39 (0.02)

asitic passerines (Spaw and Rohwer 1987). My results also demonstrated that cowbird eggs are much stronger. The Red-wing, Yellow-head, and Bobolink eggs tolerated 55, 53, and 43% of the pressure required to puncture cowbird eggs, respectively. However, Red-wing and Yellow-head eggs are substantially larger than cowbird eggs, while Bobolink eggs are slightly smaller (Table 2). If the effect of egg size is taken into account, then cowbird eggs resisted approximately twice the pressure during puncture resistance tests. This evidence strongly supports Spaw and Rohwer's (1987) hypothesis that thicker eggshells may reduce chances of puncture ejection of cowbird eggs by small hosts.

The greater puncture resistance of cowbird eggs is derived mostly from thicker eggshells and more rounded eggs. The fact that these two variables explain most of the observed variation in puncture resistance suggests that other features (e.g. inorganic content, and density and porosity of eggshell) play only a minor role.

In addition to egg strength, increased roundness may be related to egg-shape mimicry. This hypothesis predicts that the shape of eggs of cowbirds and their hosts should be similar. To test this hypothesis, I compared the shape of eggs of cowbirds with that of 50 frequently parasitized cowbird hosts (Friedmann 1963). The cowbird eggs are significantly rounder than eggs of their common hosts (Table 11). This argues against the egg-shape mimicry hypothesis.

A greater proportion of inorganic constituents in cowbird eggs than in the three nonparasitic species is consistent with the hypothesis that higher inorganic content produces stronger eggshells. Inorganic content, however, was not a significant predictor of puncture resistance in eggs of any of the four species. This result could be explained by low variability in inorganic content between conspecific eggs, the low accuracy of estimates of inorganic constituents, and the small sample of eggs examined. However, the proportion of inorganic constituents varied sufficiently within cowbird eggs (range 0.53–0.88) and the estimates of inorganic constituents were reasonably accurate (see Methods). Alternatively, the small number of experimental eggs was a problem because inorganic content is only a weak predictor of puncture resistance of cowbird eggs. Most of the observed variation in puncture resistance of eggs can be explained by their different eggshell thickness and shape. The predicted effect of inorganic content is thus presumably masked by the combined effects of eggshell thickness, egg shape, and egg size. A stronger test of the role of the inorganic content in determining greater strength of cowbird eggshells will require analysis of a larger sample of eggs.

TABLE 11. Shape of eggs (length : breadth) of parasitic cowbirds and frequently parasitized hosts.[a] Data on eggs of host, from which the egg-shape index was calculated, were obtained from Harrison (1978). The parasitic cowbirds and their hosts were compared by Student's t-test.

Category	Egg shape index ($\bar{x} \pm$ SD)	99% CI	n	Statistical comparison
Parasitic cowbirds	1.288 ± 0.016	1.270–1.306	5	$t = 4.107$ $P < 0.001$
Cowbird hosts	1.331 ± 0.054	1.311–1.350	50	

[a] Fifty host species are listed in Friedmann (1963: 7). Only species for which at least 25 cases of cowbird parasitism were documented are included. These 50 species account for 7,800 records (87%) of a total of ca. 9,000 cases of parasitism by *Molothrus ater*.

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