

**/THE ROLE OF HOST EGG COLOR
IN HOST NEST SELECTION BY THE BROWN-HEADED COWBIRD/**

(Molothrus ater)

by

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A review of the literature reveals many reports of avian brood parasitism- a female bird laying her eggs in the nests of other species and leaving the rearing of her young to foster parents. This characteristic has been documented in members of five families: *Anatidae*, *Cuculidae*, *Indicatoridae*, *Icteridae*, and *Ploceidae*. This behavior holds many advantages for the parasite. She incurs none of the time and energy expense of building a nest, incubating a clutch, feeding the nestlings and fledglings, and runs none of the risk of predation that the nesting bird does; she increases her individual fitness largely at the expense of the host. The expenses for the host can be heavy; often, the young parasite is the sole survivor in a clutch (Hann 1937, Berger 1951, Hofslund 1957, Mayfield 1960, Walkinshaw 1961, Wiens 1963, Elliott 1978).

The foster parent is not without defense against brood parasitism. Experiments have shown that host species possess abilities to detect foreign objects and eggs placed in their nests (Swynnerton 1918, Ali 1931, Baker 1942, Rothstein 1970 and 1974, Victoria 1972). Many potential foster parents reject an intruder's egg in their nests by ejecting the egg, by abandoning the nest, or by burying the foreign egg under a new nest floor (Friedmann 1929, Leathers 1956, Rothstein 1970, Kendeigh 1942). It is therefore logical to conclude that any aspect of the parasite egg's appearance that reduces its chances of being detected, and subsequently rejected, by the foster parent is adaptive.

Probably as a result of host discrimination of foreign eggs, counterselection has driven the Old World Cuckoos (*Cuculidae*) to produce eggs that are highly mimetic of those of the host species

upon which they specialize. The cuckoo eggs exhibit a remarkable resemblance to the color pattern and in some cases, size, of their models (Ali 1931, Baker 1942, Southern 1954).

The Icterid cowbirds exhibit several degrees of development of parasitic behavior, ranging from the nonparasitic Bay-winged Cowbird (*Molothrus badius*) to the specialized parasitical relationships of the Screaming Cowbird (*M. rufoaxillaris*) and of the Giant Cowbird (*Scaphidura oryzivora*), (Friedmann 1929, Smith 1968).

The North American Brown-headed Cowbird (*Molothrus ater*) is completely parasitic, and is known to victimize over 200 species (Friedmann 1929, 1963, and 1971). Selection in this system operates strongly on the host's ability to detect and reject the cowbird eggs. In some species one or two cowbird eggs in a nest are sufficient to cause complete failure of the host's clutch (Rothstein 1970) and most species suffer reduced fledging rates for their own offspring if the offspring had a cowbird nestmate (Hann 1937, Berger 1951, Hofslund 1957, Nice 1957, Mayfield 1960, Walkinshaw 1961, Wiens 1963, Elliott 1978). Rothstein (1970) stated that birds known to regularly reject cowbird eggs, and those known to be poor foster parents, have eggs that differ markedly from the size range and the marking range of species most often victimized by cowbirds. He also stated that color and spotting seemed to be the most important factors in determining whether a foreign egg is accepted or rejected by the nesting bird. Elliott (1976), working in eastern Kansas, noted a "remarkable similarity between appearances, i.e. markings, of the host eggs in a clutch and the first cowbird egg laid in the nest."

This study was conducted in an attempt to partially answer the question of whether cowbirds specialize on certain host species by asking specifically: if given a free choice between clutches that differ only in color of the eggs, do female cowbirds preferentially select clutches composed of eggs most like her own?

The findings of the previously cited investigations would indicate that it is in the cowbird's best interest to choose a host clutch that minimizes the chance that her own egg would be detected and subsequently rejected by the host. Specifically, the cowbird should select a host nest with speckled eggs of a similar size to her own eggs preferentially to host clutches of dissimilar egg color and size.

METHODS

This study was conducted from 3 May 1981 to 13 July 1981, in Riley and Geary counties, Kansas. The study area was the Konza Prairie Research Natural Area, 8600 acres of tallgrass prairie purchased by the Nature Conservancy and administered by Kansas State University for research.

A series of eight experiments were run. All experiments involved either a grid or a transect arrangement of Redwinged Blackbird (*Agelaius phoeniceus*) nests mounted on special support devices. These devices were 5/16-inch diameter dowel sticks, sharpened to a point on one end. The unsharpened end of the dowel had one hole drilled through it; a 13-gauge wire was threaded through each of these holes and wrapped tightly around the top end

of the dowels to form a spiral basket for holding the nest. See Fig.1.

The eggs used in the experiments were all artificial. These were made of plaster of Paris cast in latex rubber molds. The molds were made by painting liquid latex rubber over 10 House Sparrow (*Passer domesticus*) eggs, one thin layer at a time. Each coat was allowed to dry before successive coats were applied. Between layers of latex rubber, strips of gauze were added to provide reinforcement. When the mold was complete and dry, a small hole was cut in the bottom of the molds to allow removal of the sparrow eggs. The artificial eggs were produced by pouring a thin stream of water mixed with plaster through the cut holes in the bottom of the mold. The mold was gently shaken to remove air bubbles from the plaster, then the plaster was left to set. The artificial eggs were easily removed from the mold via the cut holes. The eggs were then sanded with garnet paper and smoothed with the wooden handle of a paint brush (Rothstein, 1970). Robin (*Turdus migratorius*) eggs were used as the models for the mold for the large egg types used in experiments 3 and 4. The mold was prepared in the method described above.

The sanded eggs were then painted in one of two color/markings patterns: either a pale blue-green, or a neutral gray background with fine brown spotting and flecking. The blue eggs received several coats of a blend of bright aqua green and titanium white acrylic paint. The speckled eggs received several coats of neutral gray (value 8) acrylic paint. The speckles were added to the gray base color by dipping a stiff-bristled tooth brush into raw umber acrylic paint which had been thinned with water, then running a

finger over the brush bristles, spraying paint over the eggs in a mist. This applied a fairly even flecking with some irregular small blotches of irregular shape. All of the large eggs were of the gray speckled type.

In each of the eight experiments, each nest received a "clutch" of eggs of a randomly assigned color type. Half the clutches in a given experiment were of the blue type and half of the gray speckled type.

The eggs comprising each clutch were "laid", one of the assigned type per nest per day, at dawn or shortly after. An additional egg was laid in each nest on subsequent days until the clutches were completed.

The nests were then checked daily for signs of cowbird activity. Evidence of activity was supplied by either the presence of a cowbird egg in the nest, or by a single host egg vanishing from the nest. Incidences where there was damage to the nest or to the contents of the nest were taken to be evidence of predation. If a single dummy egg was discovered missing from the nest, a thorough search was made of the ground and vegetation within a circle ($r=5m$) with its center at the nest. If the missing egg was found undamaged and unmarked by teeth or by beak, it was replaced in the nest and counted as accidental displacement. If the egg was found with damage from teeth, it was recorded as predation. If the egg was not found, it was counted as evidence of cowbird activity.

Eastern Kansas experienced much stormy weather and rain in May and early June of 1981. As nests were damaged or destroyed by weather, they were replaced with fresh nests. As much as possible, the nests used in any one experiment exhibited roughly the same

degree of weathering.

EXPERIMENT 1. This experiment was conducted 3 May 1981 to 10 May 1981 on unburned south Konza pasture WB. The 42 nests were arranged in a 6-nest by 7-nest grid. Each nest was approximately 15m from its nearest neighbors. A completed clutch consisted of 4 eggs. I spent two mornings and part of a third in a blind observing the grid for cowbird activity. The nests in the grid were 1m above the ground surface, which put them just below the top of the grass.

EXPERIMENT 2. This experiment was conducted 13 May 1981 through 18 May 1981 on a recently burned pasture, Konza 20C. The 38 nests were arranged in an 8-nest by 5-nest grid, each nest being approximately 15m from its neighbors. All nests were .4m above ground surface to place them near the top of the recovering vegetation and to avoid putting them directly on the ground in order to minimize the impact on the results of rodent and reptile predation. A completed clutch consisted of 4 eggs. These nests were checked twice daily, at dawn and at dusk. The study site was upland vegetation bordered on three sides by gullies containing trees, brush and some water.

EXPERIMENT 3. This experiment was conducted 20 May 1981 through 26 May 1981 on the same site as Experiment 2. The 40 nests were again arranged in an 8-nest by 5-nest grid, with each nest approximately 15m from its neighbors. The egg types used in this experiment were the House Sparrow-sized gray speckled eggs previously described, and the larger gray speckled egg type. Clutch size was 3 because the nests would not readily accommodate 4 of the larger egg type.

Weather was extremely stormy during this experiment. Nests were checked twice daily, at dawn and at dusk. Nests were .4m above the ground surface.

EXPERIMENT 4. This experiment was conducted 29 May 1981 through 1 June 1981 on unburned Konza pasture 4E. This experiment was a replicate of Experiment 3, using the small and large egg types. In addition to the twice daily nest checks, I observed the grid from a blind on the mornings of 30 May, 31 May, and 1 June. This experiment was terminated on 1 June due to complete absence of bird activity at the nests.

EXPERIMENT 5. This experiment was conducted 2 June 1981 through 7 June 1981 on Konza's White Pasture. The 40 nests were set out in an 8 nest by 5 nest grid with each nest being approximately 15m from its neighbors. The site was upland vegetation. The egg types used in this experiment were the small-sized blue and the small gray speckled. A clutch consisted of 4 eggs. Nests were at dusk for activity.

EXPERIMENT 6. This experiment was conducted 19 June 1981 through 29 June 1981. The 34 nests were set out in 6.4km-long line along the eastern boundary of the Konza Prairie, along Kansas highway 177. The nests were approximately 30m apart. Clutch size was 4. The line of nests passed through both upland and lowland sites. Egg types were the small blue and small gray speckled. Nests were checked each morning.

EXPERIMENT 7. This experiment was conducted 29 June 1981 through 5 July 1981. The 34 nests were again set out in a transect, in the

same location as the transect described in Experiment 6, but the nests were each moved approximately 10m further south from their previous locations. Again, a completed clutch contained 4 eggs. Egg types were the same as in Experiment 6. Nests were checked each morning for activity.

EXPERIMENT 8. The final experiment was conducted 6 July 1981 through 13 July 1981. The 34 nests were set out along the previously described transect, each nest was moved an additional 10m south of its original location (20m south of location in Exp.6, 10m south of location in Exp. 7). A complete clutch contained 4 eggs. The egg types were as in Experiments 6 and 7. Nests were checked each morning for activity.

RESULTS AND DISCUSSION

Table 1 illustrates the distribution of cowbird activity between clutches of the blue and speckled egg types for the entire 1981 breeding season. When the experiments were subjected to Chi-square analysis using a 2 by 2 contingency table, the data in experiment 2 show that speckled eggs were taken from host nests in preference to blue eggs. The discrepancy between the numbers of each egg type taken in this experiment is too large to be due to chance alone ($X^2 = 14.63$, d.f. = 1, $P < 0.001$). The results of the other experiments show no preference by female cowbirds for one egg type over another. I gathered data on cowbird reactions to large versus small eggs of the same color type in one experiment only

(Table 2). Of the 60 large eggs set out in clutches, 7 were removed by cowbirds. Of the 60 small eggs set out, 9 were removed by cowbirds. The hypothesis that host egg size is unimportant in host nest selection by the cowbird cannot be refuted by the data presented in Table 2.

Table 3 and Table 4 show the distribution of cowbird activity between blue egg clutches and speckled egg clutches for early season and late season, respectively. Combined data from Experiments 1 and 2, treated with the Chi-square analysis described above, show a strong preference on the part of the cowbirds for speckled clutches ($X^2 = 11.292$, d.f. = 1, $P < 0.001$) early in the breeding season. The combined data for Experiments 6, 7, and 8 treated in the same manner as previously described, show no preference by cowbirds for one egg type over the other ($X^2 = 0.051$, d.f. = 1, $P < 0.9$) late in the breeding season.

These results may demonstrate a seasonal shift of preference for speckled clutches early in the season to no preferential use of blue or speckled host clutches late in the season, but can not be demonstrated by these data without testing for consistency of trend between experiments before pooling the results. As mentioned above, Experiments 1 and 2 had nests arranged in a grid configuration, Experiments 6, 7, and 8 in a line or transect configuration. It could be argued that the discrepancies in the X^2 values for these two sets of experiments is an artifact of experimental design, that it is possible that any one grid of nests lay entirely within the breeding territory of one female cowbird who may have exhibited individual specialization on a particular host egg type. The line or transect experiments were arranged over

6.4km of prairie and more than likely intersected more than one female cowbird's domain, therefore reducing the likelihood that the results from these experiments were biased by the idiosyncratic behavior of any one female cowbird.

I feel that the discrepancy between the high X^2 value in experiment 2 and the low X^2 values of experiments 6 through 8 is not an artifact of experimental design. The cowbird is generally regarded as not territorial (Elliott 1980, Laskey 1950, McGeen and McGeen 1962). During the time I spent observing these grids, it was a common sight to see several female cowbirds inspecting the nests in a grid at the same time without any signs of aggressive or display behavior. It seems logical that subsequent removal of eggs from the nests in these grids was the work of more than one cowbird.

Clearly, the most acceptable evidence of cowbird activity at a host nest would be the deposition of one or more cowbird eggs in the nest. In this study, this type of evidence was obtained in only four instances- too small a sample size from which to draw conclusions.

Direct evidence of cowbird activity at a host nest can also be obtained by actually observing the activities of female cowbirds at the nest. This approach allows the observer to state with certainty whether or not a missing egg was removed by a cowbird or by predation or by some other agent. This approach was not feasible in this study, as the maximum number of nests visible from a stationary blind at any one time was 25, and the smallest of my grids had 38 nests; only 3 nests were visible at any one time from a stationary blind in the line configuration. Data gathered from

twice-daily nest checks in some of these experiments showed that the majority of eggs were removed from the nests during the period between dawn and dusk. In order to obtain firsthand observations of all of these egg removals would have required two observers in separate blinds to keep watch on the nests for as long as 17 hours each day that the experiment was in progress.

The literature contains reports of cases in which a single egg was removed from a nest, with no signs of predation, by an unknown agent and in which the nest received no parasitism. Hann (1937) reports that during his season-long observation of Ovenbird (*Seiurus aurocapillus*) and cowbird interactions, he only found one instance in which an ovenbird egg disappeared from an unparasitized nest, and he suggests that a cowbird may have been responsible for its removal. Rothstein (1970) recorded the disappearance of an egg from an unparasitized Mockingbird (*Mimus polyglottos*) nest as partial predation. Lowther (1979), in recording events at 20 nests with "dummy" clutches (composed of real eggs) "laid" by the author, saw 22 instances of a single egg vanishing from a nest; in 11 of these cases, the missing egg was the solitary occupant of the nest, and in the other 11 the missing egg was part of a clutch. He regarded these disappearances as suggestive of cowbird activity; he had one dummy clutch, composed of one cowbird-like egg and one similarly sized less spotted egg, from which only the less cowbird-like egg disappeared. Lowther (pers. comm.) also observed seven additional cases of a single egg disappearing from nests he had under observation in 1982.

In all the time I spent on the study site during the 1981 breeding season, I never saw or heard any Blue Jays (*Cyanocitta*

cristata) , known to rob eggs from the nests of other birds. In the clutches from which single eggs disappeared, I only recorded the missing eggs as evidence of cowbird activity if there was no sign of damage to the nest or its remaining contents, and if the egg had disappeared completely from the vicinity of the nest (i.e., there was little possibility of accidental displacement). These disappearances continued throughout the breeding season , declining markedly in occurrence towards the end of the breeding season. If these disappearances were due to egg robbing and/or predation, the data should show no such phenology. I therefore feel justified in regarding these disappearances as indicative of cowbird activity.

An interesting question arises at this point: if these eggs were removed by cowbirds as part of normal parasitical behavior (Friedmann 1929, Hann 1937), why were so few cowbird eggs subsequently laid in these nests? Hann (op. cit.) found that the number of host eggs removed from Ovenbird nests was only 75% of the number of cowbird eggs laid in these nests. Hann records watching a female cowbird remove an ovenbird egg from a nest and then eat it. Olson (1943) reports seeing a female cowbird fly out of a field with an egg in her beak, which she proceeded to drop on the road surface and thence to sip the albumin, eat the yolk, and consume every scrap of the shell. Stephen Fretwell (pers. comm.) postulates that cowbirds usually remove an egg from a potential host nest prior to parasitizing the nest and possibly consumes this egg as a means of assessing the quality of the eggs laid by the host. If this removal of eggs by cowbirds prior to the laying of their own eggs and the consumption of these eggs are common phenomena, then Fretwell's idea seems reasonable. If the female

cowbird decides whether or not to parasitize a given nest on the basis of the quality of the egg she consumed, then this may explain the scarcity of cowbird eggs actually laid in my nests. A plaster egg cannot be readily consumed and digested, and it is difficult to imagine such an egg being assessed as high quality by any cowbird that tried to consume it. In the four instances that a cowbird actually did lay an egg in the nests of this experiment, 2 of these eggs were laid after a plaster egg was removed from the clutches that they were deposited in, and 2 were deposited in clutches that experienced no egg removal at all. It is possible that the nests in the transect were far enough apart that from any one nest, neighboring nests were not visible to the visiting cowbird- no free choice of egg types was presented and she therefore "dumped" in any available unparasitized nest.

Elliott (1976) found the tall-grass prairie of eastern Kansas to be an area of high cowbird density; he stated that "dissimilarity between host and parasite eggs seem[ed] to be favored due to the high frequency of multiple parasitism and the resulting opportunity for mistaken egg ejections."

However, the data gathered in this study in the same habitat indicate that cowbirds do, at least in one instance, express a preference for host clutches composed of eggs that resemble their own eggs when given a free choice of egg types from which to choose.

SUMMARY

Cowbird activity was monitored at dummy nests containing artificial clutches in eastern Kansas in order to determine whether or not cowbirds preferentially selected nests containing "host" eggs that resembled their own over clutches with "host" eggs unlike their own.

In only one experiment did female cowbirds exhibit a marked preference for host nests containing eggs like their own over eggs unlike their own. In this case, nests containing gray speckled eggs were preferred over those containing solid pale eggs.

Two experiments tested for preference by cowbirds for nests containing large gray speckled eggs or small grey speckled eggs. The large size was 20 x 28 mm, the small size 16 x 23 mm. Cowbird eggs are typically 16 x 21 mm. If female cowbirds were preferentially selecting host eggs most like their own, they should have shown a preference for the small egg type. One experiment was abandoned due to total absence of cowbird activity, the other yielded no significant preference.

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exp	Number of Clutches			Eggs Removed from Nests			Eggs Remaining in Nests			Chi Squared (2 by 2 table)
	blue	spk	tot	blue	spk	tot	blue	spk	tot	(1 D.F.)
1	21	21	42	11	15	26	73	69	142	$P(X > 0.728) < 0.25$
2	19	19	38	6	25	31	70	51	121	$P(X > 14.63) < 0.001$
5	20	20	40	1	0	1	79	80	158	$P(X > 1.006) < 0.25$
6	17	17	34	9	8	17	59	60	119	$P(X > 0.067) < 0.90$
7	17	17	34	1	3	4	67	65	132	$P(X > 1.030) < 0.50$
8	17	17	34	1	0	1	67	68	135	$P(X > 1.008) < 0.50$
Totals				29	51	80	415	393	808	

Table 1. Chi-square analysis of data by experiment using a 2 x 2 contingency table, each experiment with 1 degree of freedom.

exp	Number of Clutches			Eggs Removed from Nests			Eggs Remaining in Nests			Cowbird Eggs Deposited		
	blue	spk	tot	blue	spk	tot	blue	spk	tot	blue	spk	tot
1	21	21	42	11	15	26	73	69	142	1	2	3
2	19	19	38	6	25	31	70	51	121	0	0	0
Totals				17	40	57	143	120	163	1	2	3

Table 2. Early season distribution of cowbird activity between blue egg clutches and speckled egg clutches. For each experiment there are 4 eggs per clutch. The "blue", "spk", and "tot" notation indicates blue eggs, speckled eggs, and the total, respectively.

exp	Number of Clutches			Eggs Removed from Nests			Eggs Remaining in Nests			Cowbird Eggs Deposited		
	blue	spk	tot	blue	spk	tot	blue	spk	tot	blue	spk	tot
6	17	17	34	9	8	17	59	60	119	0	1	1
7	17	17	34	1	3	4	67	65	132	0	0	0
8	17	17	34	1	0	1	67	68	135	0	0	0
Totals				11	11	22	193	193	386	0	1	1

Table 3. Late season distribution of cowbird activity between blue egg clutches and speckled egg clutches. The clutch size, in all experiments equals 4. The "blue", "spk", and "tot" notation indicates blue eggs, speckled eggs, and the total, respectively.

exp	Number of Clutches			Eggs Removed from Nests			Eggs Remaining in Nests			Cowbird Eggs Deposited		
	large	small	tot	large	small	tot	large	small	tot	large	small	tot
3	20	20	40	7	9	16	53	51	104	0	1	1
4	20	20	40	0	0	0	60	60	120	0	0	0
Totals				7	9	16	113	111	224	0	1	1

Table 4. Distribution of cowbird activity between clutches of large eggs and clutches of small eggs. The clutch size in both experiments equals 3. Eggs of both sizes were of the speckled type.

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ABSTRACT - Host nest selection behavior of the parasitic Brown-headed Cowbird (*Molothrus ater*) was studied during the 1981 breeding season. Eight experiments were conducted in the tallgrass prairie community of northeastern Kansas to determine the importance of host egg appearance in host nest selection by female cowbirds.

Each experiment involved an arrangement of Red-winged Blackbird (*Agelaius phoeniceus*) nests mounted on nearly identical substrates. The nests received clutches of artificial eggs; each experiment tested for preference by the cowbirds by presenting two types of clutches that differed only in either color or size. Two experiments tested for a size preference, six for color preference.

A significant preference for gray speckled eggs over pale blue eggs was found in only one experiment, $P(X > 13.129) < .001$. No preference for small or large gray speckled eggs was demonstrated.

Several North American bird species are known to reject cowbird eggs in their nests by ejecting it, burying it under a new nest floor, or by deserting the nest. The female cowbird can best avoid this rejection if her egg is like enough to the host eggs to make its detection difficult. The small gray speckled egg type is very similar to the cowbird's own egg. The cowbirds were expected to prefer host clutches of this type over pale blue clutches or large gray speckled clutches. The results of this experiment indicate no consistent preference.