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DOES BROWN-HEADED COWBIRD EGG COLORATION INFLUENCE RED-WINGED BLACKBIRD RESPONSES TOWARDS NEST CONTENTS?[1]

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In North America, the Brown-headed Cowbird (*Molothrus ater*) is known to parasitize 221 species (Friedmann et al. 1977, Friedmann and Kiff 1985). In Colorado, Brown-headed Cowbirds parasitize Red-winged Blackbirds (*Agelaius phoeniceus*) to varying degrees depending upon year, location, and habitat (Hanka 1979, Ortega and Cruz 1988, Ortega 1991).

Brood parasites often are detrimental to the reproductive efforts of their hosts; therefore, natural selection should favor host behaviors that deter brood parasitism (Rothstein 1975, 1990; Rohwer and Spaw 1988). Such behaviors or defense mechanisms include: (1) aggression toward adult parasites, (2) abandoning parasitized nests, (3) constructing a new nest over parasitized clutches, (4) puncturing parasitic eggs, and (5) removing parasitic eggs (Rothstein 1975, 1990; Ortega and Cruz 1988; Rohwer and Spaw 1988). Although brood parasitism by Brown-headed Cowbirds can significantly decrease the reproductive output of host species (Mayfield 1965, Walkinshaw 1972, Marvil and Cruz 1989, but see Weatherhead 1989, Ortega 1991), Red-winged Blackbirds are nevertheless an "accepter" species of cowbird eggs and also readily accept cowbird egg models (Rothstein 1975, Ortega and Cruz 1988). That is, in contrast to "rejecter" species (see Rothstein 1975), "accepter" species are those species in which nearly all individuals accept eggs that are nonmimetic (Rothstein 1975).

Examining how various parameters (e.g., egg shape, size, color, and maculation) influence responses towards cowbird eggs is basic to understanding the evolution of host-parasite interactions and could aid in the potential management of cowbirds. Ortega and Cruz

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TABLE 1. Number (and percent) of acceptance/rejection responses of Red-winged Blackbirds to objects (painted to either mimic Brown-headed Cowbird egg coloration, or simply white) added to nests during the egg laying or early incubation stages in Boulder County, Colorado, 1991.

Model added	Hole in model	Accept	Reject	P*
Cowbird dowel	No	11 (100%)	0 (0%)	0.001
White dowel	No	10 (83.3%)	2 (16.7%)	0.039
Cowbird large bead	Filled in	11 (100%)	0 (0%)	0.001
White large bead	Filled in	12 (100%)	0 (0%)	0.0005
Cowbird large bead	Yes	2 (16.7%)	10 (83.3%)	0.039
White large bead	Yes	4 (28.6%)	10 (71.4%)	0.18
Cowbird large bead	Filled in, painted[a]	15 (100%)	0 (0%)	0.00006
White large bead	Filled in, painted[a]	14 (100%)	0 (0%)	0.00012
Cowbird small bead	Filled in	11 (55%)	9 (45%)	0.82
White small bead	Filled in	6 (35.3%)	11 (64.7%)	0.33
Cowbird star	Yes	1 (9.1%)	10 (90.9%)	0.012
White star	Yes	0 (0%)	11 (100%)	0.001

* Binomial probability.
[a] Signifies a bead in which a large black "hole" had been painted over the original, now filled with wood puddy, central hole.

(1988) investigated the importance of egg size and shape, object size and shape, and to some degree coloration, on the acceptance into nests of Red-winged Blackbirds of various eggs and objects. Here, we report on the potential importance of Brown-headed Cowbird egg coloration and maculation in the acceptance or rejection of various objects into the nests of Red-winged Blackbirds.

METHODS

The acceptance/rejection of various objects placed into the nests of Red-winged Blackbirds was studied at three cattail (*Typha latifolia* and *T. angustifolia*) marshes in Boulder County, Colorado, from 14 May to 8 August 1991. Red-winged Blackbird nests were located and marked with coded flagging tape. Objects were painted to either simulate the color and maculation of Brown-headed Cowbirds eggs (i.e., off-white background with brown speckles [see Harrison 1978]) or they were painted immaculate white. Objects were added to nests during the egg-laying and early incubation stages because this is when Brown-headed Cowbirds normally lay their eggs in Red-winged Blackbird nests (Ortega and Cruz 1988). Nests were typically examined every 2–5 days, and objects were classified as "accepted" if they were not damaged and still remained in active Red-winged Blackbird nests after five days (Ortega and Cruz 1988). Each experimentally manipulated nest received only one object (Ortega and Cruz 1988).

The various objects added to Red-winged Blackbird nests included: dowels (23.5 mm in length by 15.5 mm in width, 3.3 g), large round beads (14.8 by 16.2 mm, 1.6 g), large hollow round beads with 6.2 mm holes drilled through center (14.8 by 16.2 mm, 1.4 g), small round beads (9.0 by 9.8 mm, 0.4 g)—all made of wood, and plastic stars (18.2 by 18.2 by 7.7 mm, 0.6 g). Dowels were added to nests because similar-shaped objects are known to be accepted by Red-winged Blackbirds in California (Rothstein, pers. comm.) and because such dowels are relatively similar in shape to blackbird eggs, but they differ in having an edge. Large and small beads and plastic stars were used as experimental objects because similar or the same (plastic stars) objects were rejected in previous research (Ortega and Cruz 1988). Similar objects painted to mimic cowbird eggs, if accepted, may show the importance of cowbird egg color and maculation to acceptance by hosts. Holes in one set of large and in all small round beads were filled with wood puddy so that the surface of these objects had no edges. For a second set of large round beads, we did not fill the holes in order to offer the blackbirds an object whose surface was interrupted by edges. Finally, for a third set of large round beads, we filled the holes with wood puddy, but after painting the bead the color and maculation of Brown-headed Cowbird eggs, or simply white, we painted "black holes" over the original now-filled holes in the beads. This allowed us to examine the potential importance of both tactile and visual cues to the discriminatory abilities of Red-winged Blackbirds with respect to their acceptance of objects into their nests. All wooden models were sanded smooth to minimize the chance that surface texture influenced responses. For comparison, Red-winged Blackbird eggs are typically 25.0 by 18.0 mm, 4.0–4.4 g (Ortega 1991), and Brown-headed Cowbirds eggs are 21.1 by 16.3 mm, 3.0 g (Ortega and Cruz 1988, pers. observ.).

To examine whether a particular object of a particular color was accepted or rejected, we used the binomial test (Zar 1984). To examine whether there was a significant difference in the acceptance or rejection of an object based upon color, we used a Fisher exact test (Zar 1984). All statistical tests were two-tailed, and values of $P \leq 0.05$ were considered significant.

RESULTS

Successful experiments were completed in 160 (63.5%) of 252 nests to which we added an object. Dowels and large beads with filled-in holes were nearly always accepted by blackbirds irrespective of color or maculation (Table 1); this also includes the large beads in which we painted visual "holes" over the filled-in original holes. However, both the large beads with large central holes and the stars were generally rejected irrespective of color or maculation (Table 1). Small beads were the only objects in which a clear pattern of acceptance/rejection behavior by blackbirds was not apparent based on object size, color, and maculation (Table 1). However, for each object, there was no significant difference in the frequencies of acceptance or rejection based upon color (Table 1, $P \geq 0.32$, two-tailed Fisher exact tests).

DISCUSSION

We tested the hypothesis that the color and maculation of Brown-headed Cowbird eggs influences Red-winged Blackbird responses toward objects placed into their nests. The logic behind this hypothesis is that the color and maculation of Brown-headed Cowbird eggs does not contrast strongly with the background coloration of a nest bottom and, therefore, such eggs might not be readily perceived by a potential host. However, we found no statistical evidence that cowbird egg coloration helps to conceal objects so that they are eventually accepted by Red-winged Blackbirds (Table 1). Our observations that color is of little importance to the acceptance or rejection of objects into the nests of Red-winged Blackbirds supports earlier conclusions by Ortega and Cruz (1988).

In contrast to earlier work (Ortega and Cruz 1988), we found that Red-winged Blackbirds accepted some nonegg-shaped objects (Table 1). Dowels and large beads without holes were generally accepted. However, two white dowels were rejected during our study. This demonstrates that Red-winged Blackbirds can at least grasp-eject objects of 15.5 mm in width. Ortega and Cruz (1988) similarly observed that Red-winged Blackbirds were able to grasp-eject objects of 15.3 mm (round bumpy beads) and 20.1 mm in width (large, round, smooth beads). This further supports the claim of Ortega and Cruz (1988) that Red-winged Blackbirds are capable of grasp-ejecting cowbird eggs which are typically 16.3 mm in width.

In contrast to the observations of Ortega and Cruz (1988), we found that some nonegg-shaped objects were accepted by Red-winged Blackbirds. We suggest that some of our nonegg-shaped objects were accepted by Red-winged Blackbirds because none of these had holes. The beads utilized by Ortega and Cruz (1988) had holes of only 1.5 mm in diameter, which were not large enough holes to allow spiking by blackbirds (Ortega and Cruz 1988); however, such holes might have indicated to the birds that the "eggs" (objects) were damaged and should be removed. During the first nine days of incubation, Kemal and Rothstein (1988) similarly found that Red-winged Blackbirds generally remove "broken" or damaged eggs from their nests.

The purpose of our experiments was to investigate whether blackbirds use tactile or visual cues to discriminate among objects placed into their nests. Large beads with holes were usually rejected while those with painted simulated holes were not (Table 1). However, we cannot definitively conclude that tactile stimuli are completely responsible for the acceptance/rejection behavior because we cannot be certain that our painted holes realistically suggested a hole to the Red-winged Blackbirds. Therefore, the importance of tactile versus visual stimuli in promoting rejection behavior in blackbirds requires further research. Interestingly, Kemal and Rothstein (1988) found that visual cues were important in eliciting the rejection response by Red-winged Blackbirds on "broken" eggs after tactile cues indicated a broken egg.

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