

EGG REJECTION BY COWBIRD HOSTS IN GRASSLANDS

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ABSTRACT.—We tested Field Sparrows (*Spizella pusilla*), Vesper Sparrows (*Pooecetes gramineus*), Lark Sparrows (*Chondestes grammacus*), Grasshopper Sparrows (*Ammodramus saviannarum*), Dickcissels (*Spiza americana*), Eastern Meadowlarks (*Sturnella magna*), and Western Meadowlarks (*S. neglecta*) to determine whether the low level (<10%) of observed parasitism by Brown-headed Cowbirds (*Molothrus ater*) on these grassland hosts is a result of egg rejection. Western Meadowlarks rejected 78% of artificial and real cowbird eggs, Eastern Meadowlarks rejected 36% of artificial cowbird eggs, and Dickcissels rejected 11% of artificial cowbird eggs. None of the other hosts regularly rejected cowbird eggs. Thus, egg rejection may account for some, but not all, of the low level of observed parasitism on grassland hosts in the Midwest. Meadowlarks were also tested with nonmimetic eggs, and the remaining hosts were tested with undersized mimetic and nonmimetic eggs when possible. All hosts, with the exception of the Field Sparrow, demonstrated some level of rejection of the nonmimetic eggs. These results suggest that some grassland hosts, which apparently have been in contact with cowbirds the longest, have evolved some form of rejection behavior that might have selected for mimetic eggs in cowbirds. The intermediate levels of rejection by both species of meadowlarks also may indicate that rejection is increasing in these populations. Received 5 April 1998, accepted 20 February 2000.

BROWN-HEADED COWBIRDS (*Molothrus ater*) are known to have parasitized at least 227 host species (DeGeus and Best 1991, Ortega 1998). Despite their generalist nature, cowbirds exhibit considerable geographic variation in parasitism. For example, parasitism frequencies for common hosts such as Red-winged Blackbirds (*Agelaius phoeniceus*), Song Sparrows (*Melospiza melodia*), and Wood Thrushes (*Hylocichla mustelina*) vary widely in different regions of North America (Freeman et al. 1990, Hoover and Brittingham 1993, Smith and Smith 1998). Not only do parasitism frequencies vary for individual hosts, they also vary for entire host assemblages. Most grassland hosts in the midwestern United States (hereafter, “the Midwest”), for example, contain cowbird eggs in less than 10% of their nests (Strausberger and Ashley 1997; Robinson et al. 1999, 2000; see also Hahn and Hatfield 1995), whereas grassland species in the Great Plains often are parasitized at twice this frequency or higher (Hergenrader 1962, Newman 1970, Hill 1976, Elliott 1978, Zimmerman 1983, Davis and Sealy 2000,

Koford et al. 2000). The same grassland hosts in the Midwest are parasitized less frequently than hosts in adjacent habitats: parasitism is highest on forest species, intermediate on shrubland species, and lowest on grassland species (Strausberger and Ashley 1997; Robinson et al. 1999, 2000).

Grassland hosts in the Midwest may experience relatively low levels of parasitism for several reasons. Cowbird densities are highest in the Great Plains (Price et al. 1995), and the Great Plains are dominated by grasslands, whereas shrublands and forests are more available in the Midwest; host nests may be easier for cowbirds to find in these other habitats (Robinson et al. 1999, 2000). Grassland hosts in the Midwest also may have evolved defenses against cowbird parasitism, particularly egg rejection. Rejection could account for the low frequency of cowbird parasitism on grassland hosts in the Midwest (Rothstein 1975b, Scott 1977, Sealy and Neudorf 1995).

In this study, we tested the hypothesis that the relatively low level of cowbird parasitism observed on grassland hosts in the Midwest is a result of egg rejection by hosts. Many grassland hosts have eggs that closely resemble cowbird eggs (Fig. 1), and recognition of cowbird

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eggs by hosts whose own eggs resemble those of cowbirds apparently is difficult (Rothstein 1975b; Burhans and Freeman 1997; see also Peer and Sealy 2000). Therefore, we also tested whether these hosts reject nonmimetic eggs, and in the cases of the smaller hosts, we used both nonmimetic and mimetic undersized eggs. We predicted that nonmimetic eggs should be rejected at higher frequencies than mimetic eggs. We used undersized eggs to facilitate ejection by smaller hosts, because many small hosts seem to be incapable of grasping cowbird eggs in their bills (Rothstein 1975b, Sealy 1996).

METHODS

Study areas.—We experimentally parasitized nests during the 1997 and 1998 breeding seasons. Experiments were conducted at the Savanna Army Depot (42°01'N, 90°02'W), Ayers Sand Prairie Nature Preserve (42°03'N, 90°06'W), and Thompson-Fulton Sand Prairie Research Natural Area (41°57'N, 90°06'W) in northwestern Illinois, and at the Midewin National Tallgrass Prairie in northeastern Illinois (41°03'N, 88°00'W). Eastern Meadowlarks (*Sturnella magna*) and Western Meadowlarks (*S. neglecta*) nested at the Savanna Army Depot; for this reason, species were distinguished by call or song. To increase our sample sizes, we monitored nests that were naturally parasitized by cowbirds at the aforementioned study sites and at Thompson-Fulton Sand Prairie Nature Preserve (41°56'N, 90°06'W) in northwestern Illinois, Nachusa Grasslands (41°08'N, 89°04'W) and Green River Conservation Area (41°06'N, 89°05'W) in north-central Illinois, and Des Plaines Conservation Area (41°03'N, 88°01'W) and Goose Lake Prairie (41°03'N, 88°02'W) in northeastern Illinois. Nests were checked approximately every two to four days. We also report parasitism frequencies that we recorded for hosts at the above sites from 1995 to 1998, although not all sites were monitored every year.

Experimental parasitism.—Nests were parasitized with one of several egg types, with one exception (see below). All hosts were parasitized with artificial cowbird eggs that were made of wood and painted to mimic real cowbird eggs. The artificial eggs effectively mimicked cowbird eggs; hosts responded in the same manner to these eggs as they did to real cowbird eggs, and they accepted artificial wooden eggs that mimicked their own (Peer 1998; Peer and Bollinger 1997, 1998). Western Meadowlarks also were experimentally parasitized with real cowbird eggs that we collected from other host nests, and with Red-winged Blackbird eggs. These eggs were added as controls to ensure that Western Meadow-

larks responded to cowbird parasitism rather than to artificial eggs per se. We used Red-winged Blackbird eggs in addition to real cowbird eggs because Red-winged Blackbird eggs clearly are nonmimetic, whereas cowbird eggs closely resemble meadowlark eggs (Fig. 1).

Hosts also were parasitized with artificial nonmimetic eggs (Table 1). Eastern and Western meadowlarks were parasitized with the same wooden eggs described above, but they were painted indigo blue. Field Sparrows (*Spizella pusilla*), Vesper Sparrows (*Poocetes gramineus*), Lark Sparrows (*Chondestes grammacus*), and Grasshopper Sparrows (*Ammodramus saviannarum*) were parasitized with plastic eggs that were filled with white glue and painted indigo blue. Dickcissels (*Spiza americana*), which lay immaculate eggs (Fig. 1), were parasitized with the same plastic eggs but with white or beige backgrounds with spots. It is possible that the smaller hosts recognized cowbird eggs but were unable to remove them. Therefore, when possible, hosts that rejected the smaller nonmimetic eggs also were experimentally parasitized with smaller plastic eggs that resembled their own eggs. This allowed us to ascertain whether acceptance was due to the large size of cowbird eggs or because hosts could not distinguish cowbird eggs from their own eggs.

Eggs were added to nests during the host's laying or incubation period. The time of parasitism usually has no effect on host response (Rothstein 1975b; Sealy 1996; but see Rothstein 1976) if parasitism occurs after at least one host egg is present (Peer and Bollinger 1997). No host eggs were removed in conjunction with experimental parasitism, and nests were parasitized from 0500 to 1600 CST. Nests were checked for evidence of rejection every one to three days until the cowbird egg was rejected or the host's eggs hatched. Eggs were considered rejected if they disappeared from an active nest (i.e. ejected) or if they were damaged by the host (i.e. pecked). Artificial eggs were checked closely for peck marks. The plastic eggs were soft and could be compressed, so presumably hosts could inflict noticeable damage; in all likelihood, these eggs were small enough to be ejected. Similarly, the wooden eggs were soft enough for Mourning Doves (*Zenaid macroura*) to make peck marks (Peer and Bollinger 1998), despite the delicate bills of this species (Mirarchi and Baskett 1994). Therefore, we assumed that smaller hosts, with stronger bills, could inflict noticeable damage to these eggs as well. At the very least, these hosts should have been able to chip the paint off the eggs. We also noted whether host eggs were missing or damaged. Eggs that remained in nests for at least five days were considered to be accepted because most rejecters remove cowbird eggs within 24 h and nearly always within five days (Rothstein 1975b, Sealy 1996, Peer 1998).

Desertion of parasitized nests, including burial of

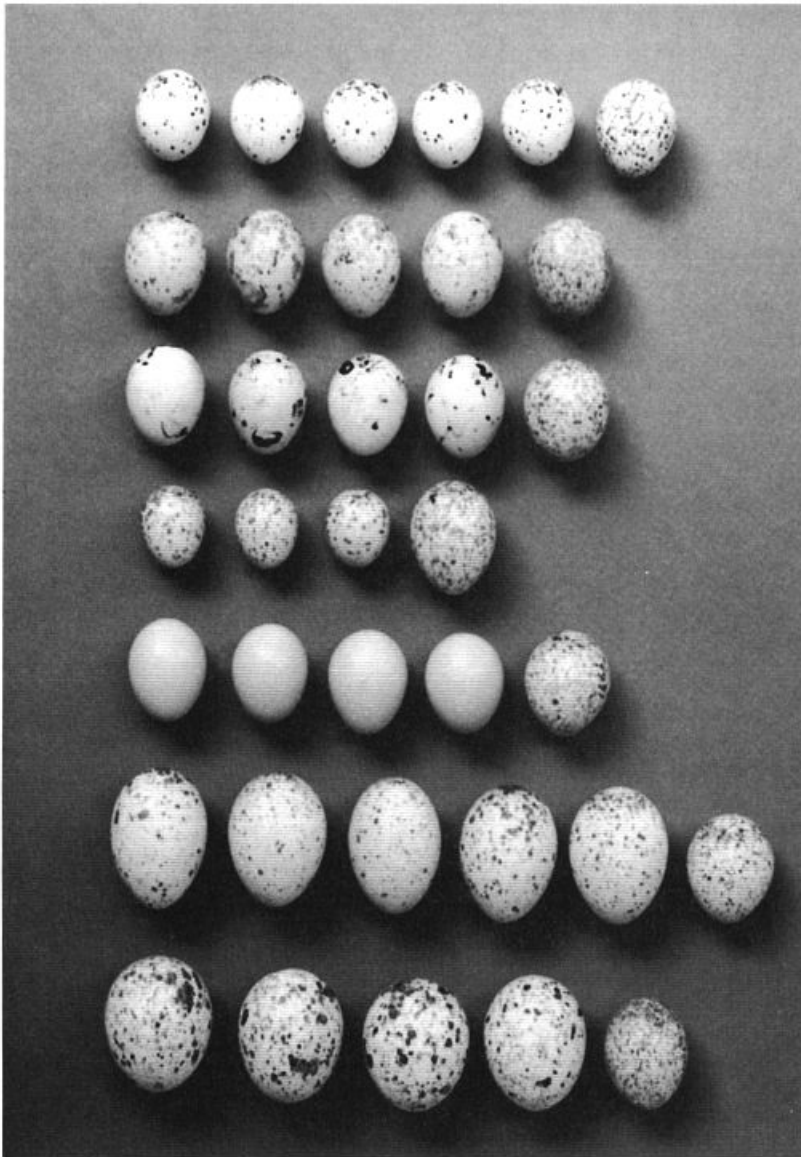


FIG. 1. Clutches of hosts tested for egg-rejection in this study. Host eggs are to the left, and the last egg in each row is a cowbird egg. Clutches are as follows from top to bottom: Grasshopper Sparrow, Vesper Sparrow, Lark Sparrow, Field Sparrow, Dickcissel, Eastern Meadowlark, and Western Meadowlark.

cowbird eggs, sometimes is considered rejection behavior. However, birds desert their nests for a variety of reasons (Rothstein 1975b, Hill and Sealy 1994), and egg burial is usually a continuation of nest building (Rothstein 1975b, Hobson and Sealy 1987; but see Sealy 1995). Thus, we did not consider these behaviors as rejections unless they occurred consistently in response to parasitism. Eggs that were found just outside nests also were not considered rejections because rejecter species usually carry cow-

bird eggs away from their nests (Rothstein 1975b, Peer 1998). It is likely that such eggs were knocked out of nests when females flush from the shallow ground nests typical of grassland species. Indeed, during the course of this study we observed eggs being knocked out of two meadowlark nests when the females flushed (see also Peer and Bollinger 1998).

Statistics.—We used chi-square tests to analyze egg rejection and Fisher exact tests when expected values were less than five. Tests were two-tailed except for

TABLE 1. Observed parasitism frequencies (n = number of nests) on grassland host species in Illinois, 1995 to 1998, and sizes of real (Baich and Harrison 1997) and artificial^a eggs involved in this study.

| Species/egg type | % Parasitism (n) | Mean egg size (mm) |
|-------------------------|------------------|--------------------------|
| Field Sparrow | 13.1 (336) | 18 × 13 |
| Vesper Sparrow | 7.7 (52) | 21 × 15 |
| Lark Sparrow | 20.9 (43) | 20 × 16 |
| Grasshopper Sparrow | 4.0 (318) | 19 × 14 |
| Dickcissel | 13.1 (222) | 21 × 16 |
| Eastern Meadowlark | 1.8 (221) | 28 × 20 |
| Western Meadowlark | 2.2 (46) | 28 × 21 |
| Unknown Meadowlark spp. | 0.0 (15) | — |
| Brown-headed Cowbird | — | 21 × 16 |
| Artificial cowbird | — | 22.4 × 16.5 ^b |
| Artificial undersized | — | 15.4 × 11.8 ^c |

^a Includes both mimetic and nonmimetic egg types.

^b Mean mass = 2.3 ± 0.04 g (n = 18).

^c Mean mass = 1.1 ± 0.03 g (n = 15).

cases where we predicted differences in rejection behavior, in which case we used one-tailed tests. We predicted *a priori* that nonmimetic eggs would be rejected more frequently than mimetic eggs when egg size was held constant. However, when size differed between egg types (e.g. for Grasshopper Sparrows, Lark Sparrows and Vesper Sparrows) we did not predict a difference, because despite the smaller size that may facilitate rejection, smaller eggs also were similar to host egg size, which should make recognition more difficult. Egg measurements are given as $\bar{x} \pm SE$.

TABLE 2. Rejection rates of hosts in response to natural and experimental nest parasitism in Illinois. Mimetic eggs were painted to resemble cowbird eggs and nonmimetic eggs were painted solid indigo blue or with white or beige backgrounds and darker spots (for use only in Dickcissel nests). Values are percentages, with number of nests in parentheses.

| Species | Experimental | | | | |
|---------------------|--------------|------------------------|----------------------|-----------------|------------|
| | Natural | Cowbird-sized eggs | | Undersized eggs | |
| | | Mimetic | Nonmimetic | Mimetic | Nonmimetic |
| Field Sparrow | 0 (28) | 0.0 (3) | — | — | 0.0 (4) |
| Vesper Sparrow | 0 (4) | 0.0 (4) | — | 100 (1) | 75.0 (4) |
| Lark Sparrow | 0 (5) | 0.0 (2) ^a | — | 0.0 (2) | 66.7 (3) |
| Grasshopper Sparrow | 0 (11) | 0.0 (10) | — | 25.0 (8) | 42.9 (14) |
| Dickcissel | 0 (15) | 11.1 (9) | — | — | 100 (3) |
| Eastern Meadowlark | 0 (2) | 35.7 (14) | 40 (10) | — | — |
| Western Meadowlark | 0 (1) | 77.8 (18) ^b | 100 (9) ^c | — | — |
| Unknown Meadowlark | — | 100 (2) | — | — | — |

^a Experimental cowbird parasitism was also accepted at two additional Lark Sparrow nests for four days before the nests were depredated.

^b Includes 11 of 14 rejected artificial cowbird eggs and three of four rejected real cowbird eggs.

^c Includes eight artificial nonmimetic eggs and one real Red-winged Blackbird egg.

RESULTS

Four of the seven hosts we monitored were parasitized in less than 10% of their nests, and the remaining three hosts were parasitized in 13 to 21% of their nests (Table 1).

Western Meadowlark.—The Western Meadowlark was the only host that regularly rejected mimetic and nonmimetic eggs (Table 2). Experimentally added real cowbird eggs and artificial cowbird eggs were rejected at similar frequencies (Fisher exact test, $P > 0.99$; Table 2). Nonmimetic eggs were rejected at a higher frequency than mimetic cowbird eggs (Table 2), but the difference was not significant (Fisher exact test, one-tailed, $P = 0.17$). All rejections for which the time required to reject was known ($n = 19$) occurred within 24 h. One host egg was missing following an ejection of an artificial cowbird egg. Parasitism was accepted at the one known naturally parasitized nest (Table 2).

A nest at which an artificial cowbird egg was ejected within 24 h was subsequently experimentally parasitized with a real cowbird egg that was not ejected, and with a Red-winged Blackbird egg that was ejected within 24 h. These data are not included in the above analyses because this nest was parasitized with more than one egg type.

Eastern Meadowlark.—Eastern Meadowlarks rejected mimetic and nonmimetic cowbird-sized eggs at an intermediate level (Table 2), but the frequency of rejection did not differ be-

tween the two egg types (Fisher exact test, one-tailed, $P > 0.50$; Table 2). More nonmimetic eggs (4 of 4) than mimetic eggs (2 of 5) were rejected within 24 h (Fisher exact test, one-tailed, $P = 0.11$). Two host eggs were missing following the ejection of an artificial blue egg from one nest. Cowbird eggs were accepted at the two known naturally parasitized nests (Table 2).

Dickcissel.—Dickcissels rejected 11.1% of artificial cowbird eggs (Table 2). It is possible that this ejection was a case of partial predation because a host egg was also missing from this nest. All undersized nonmimetic eggs also were rejected (Table 2), and they were rejected more frequently than were normal-sized cowbird eggs (Fisher exact test, one-tailed, $P = 0.02$). A naturally parasitized nest was found with an empty host egg with a hole in it, plus two intact host eggs and a real cowbird egg. The damaged egg was gone when the nest was revisited three days later. Cowbird eggs plus host eggs disappeared from two other naturally parasitized nests, but these appeared to be depredated.

Grasshopper Sparrow.—Grasshopper Sparrows accepted all artificial cowbird eggs and natural cowbird parasitism (Table 2). Undersized eggs of both types were rejected. All undersized eggs combined were rejected more frequently than the normal-sized cowbird eggs (8/22 vs. 0/10, respectively; Fisher exact test, $P = 0.04$), and all nonmimetic eggs combined tended to be rejected more frequently than all mimetic eggs combined (6/14 vs. 2/18, respectively; Fisher exact test, $P = 0.10$).

Vesper Sparrow.—Vesper Sparrows accepted all artificial cowbird eggs and natural cowbird parasitism (Table 2). All undersized eggs combined were rejected more frequently than the normal-sized cowbird eggs (4/5 vs. 0/4, respectively; Fisher exact test, $P = 0.05$), and all nonmimetic eggs tended to be rejected more frequently than mimetic eggs (3/4 vs. 1/5, respectively; Fisher exact test, $P = 0.21$).

Lark Sparrow.—Lark Sparrows accepted all artificial cowbird eggs (Table 2) and seemingly all natural cowbird parasitism. Two of three undersized nonmimetic eggs were rejected, but neither of two undersized mimetic eggs were rejected (Table 2).

Field Sparrow.—Field Sparrows accepted all artificial cowbird eggs and undersized nonmi-

metic eggs (Table 2). A cowbird egg was partially buried in a naturally parasitized nest. Three more parasitized nests had been deserted when found, and a fourth was deserted by the second visit with only the cowbird egg remaining in the nest. We did not consider these rejections.

DISCUSSION

Low frequency of observed parasitism.—Low frequencies of cowbird parasitism are sometimes explained by rejection of cowbird eggs by hosts. Several rejecter species often remove cowbird eggs immediately after they have been parasitized, which leads to an underestimate of actual parasitism (Rothstein 1977, Scott 1977, Sealy and Neudorf 1995). Egg rejection by Western Meadowlarks, and to a lesser extent Eastern Meadowlarks, may contribute to the low levels of observed parasitism on these hosts in the Midwest. Western Meadowlarks rejected most cowbird eggs, and all rejections occurred within a day. Eastern Meadowlarks also rejected cowbird eggs, but less frequently, and only 40% of rejections occurred within a day. Nests must be inspected soon after cowbirds lay their eggs around sunrise to determine whether eggs are being rejected (Scott 1977). Dickcissels also may have rejected cowbird eggs, though this may have been partial predation. Even if it was rejection, it is unlikely that this low level of rejection significantly affected the observed frequency of parasitism.

The parasitism frequencies we observed appear to be very close to actual parasitism frequencies for Field Sparrows, Vesper Sparrows, Lark Sparrows, and Grasshopper Sparrows because all accepted natural and experimental cowbird parasitism. Our results are supported by findings that Vesper Sparrows accept artificial cowbird eggs ($n = 3$; Rothstein 1975b) and that Field Sparrows accept real and artificial cowbird eggs ($n = 27$; Burhans 1996). Instead of rejecting cowbird eggs, Field Sparrows apparently desert nests in response to parasitism, especially when they observe a female cowbird at their nest (Burhans 2000). This may explain the naturally parasitized nests we found that were deserted. Thus, rejection may account for some of the relatively low levels of parasitism on grassland hosts in the Midwest. In addition, it appears that grassland habitats

are simply avoided by cowbirds. Similar to the findings in the Midwest (Strausberger and Ashley 1997; Robinson et al. 1999, 2000), hosts nesting in old-field habitats in New York are also parasitized less frequently than those nesting in adjacent forests (Hahn and Hatfield 1995). The reasons for the avoidance of these grassland habitats remain unclear, but the vegetative structure and secretive behavior of hosts in grasslands may make it more difficult for cowbirds to locate these nests compared with those in shrublands and forests (Robinson et al. 1999, 2000).

Rejection of nonmimetic and undersized eggs.—Western Meadowlarks, Vesper Sparrows, Lark Sparrows, and Grasshopper Sparrows tended to reject nonmimetic eggs more frequently than mimetic eggs (see Fraga 1985, Burhans and Freeman 1997). Apparently, nonmimetic eggs differed enough for these hosts to recognize the difference between their eggs and the foreign eggs, as was evident at the Western Meadowlark nest that was parasitized with three egg types. This meadowlark rejected the Red-winged Blackbird egg and an artificial cowbird egg, but accepted the real cowbird egg. Despite the similar rate of rejection of real and artificial cowbird eggs (Table 2), the spots on real cowbird eggs tended to be somewhat larger than those on the artificial eggs, and the larger spots were very similar to those on meadowlark eggs. As a result, real cowbird eggs appeared more similar to meadowlark eggs than to artificial eggs, which may explain why the real egg was not rejected.

The similarity of Brown-headed Cowbird eggs to those of most of the grassland hosts we tested, in addition to those of many other grassland hosts, is striking (Fig. 1; see Baicich and Harrison 1997). Combining this with our findings that some grassland hosts tended to reject the nonmimetic eggs more frequently than mimetic eggs raises the possibility that the Brown-headed Cowbird evolved a mimetic egg (see Elliott 1977). Grassland hosts, including those in Illinois, apparently have been in contact with cowbirds for the longest period of time (Mayfield 1965); hence, they have had the longest time to evolve antiparasite defenses such as egg rejection. Subsequently, cowbirds may have evolved an egg that mimics those of its hosts, similar to Common Cuckoos (*Cuculus canorus*), although cuckoos parasitize specific

hosts, whereas cowbirds do not (Davies and Brooke 1998, Fleischer 1985; but see Alderson et al. 1999). Nevertheless, several other host species that do not nest in grasslands ostensibly have been in contact with cowbirds for a relatively short time, but they too have eggs that resemble those of cowbirds (e.g. Rose-breasted Grosbeak [*Pheucticus ludovicianus*], Northern Cardinal [*Cardinalis cardinalis*], Eastern Towhee [*Pipilo erythrophthalmus*], Yellow-breasted Chat [*Icteria virens*]). Chats also reject nonmimetic eggs more frequently than mimetic eggs (Burhans and Freeman 1997). Therefore, it is possible that cowbirds simply have a generalized egg morph that fortuitously matches eggs of many of its hosts, making recognition of cowbird eggs by these hosts difficult. We cannot rule out this possibility. However, egg coloration has gone through considerable evolution in different species of cowbirds (Rothstein and Robinson 1998), suggesting that the Brown-headed Cowbird has evolved a mimetic egg.

We had no controls for undersized eggs. Consequently, Vesper Sparrows, Lark Sparrows, Grasshopper Sparrows, and Dickcissels may have removed undersized eggs because the eggs were artificial, or because they viewed them as inviable eggs or as empty eggshells owing to their low masses (see Kattan 1998). This seems unlikely. Rothstein (1975b) also tested four accepter species using undersized cowbird eggs and found no differences in host responses to these eggs and normal-sized cowbird eggs. Acceptor species apparently do not reject runt eggs, which are inviable and weigh less than normal eggs (Rothstein 1973), whereas at least one rejecter species rejects these eggs (Peer 1998).

Most birds remove empty eggshells from their nests (Kemal and Rothstein 1988); however, relatively few species reject cowbird eggs (Peer 1998). Also, Field Sparrows did not reject the undersized eggs (Table 2), and the same is true for Chipping Sparrows (*Spizella passerina*; B. Peer unpubl. data). Yet, both of these species remove eggshells from their nests (Carey et al. 1994, Middleton 1998). If the birds we tested simply responded to the eggs as if they were empty eggshells, then we would expect Field Sparrows and Chipping Sparrows to have removed the eggs. They did not, which is further evidence that Vesper Sparrows, Lark Sparrows,

Grasshopper Sparrows, and Dickcissels demonstrate rejection behavior.

Why did Dickcissels, Vesper Sparrows, Lark Sparrows, and Grasshopper Sparrows rarely reject normal-sized artificial cowbird eggs? Dickcissels should have no difficulty distinguishing cowbird eggs from their immaculate blue eggs; hence, they do not risk making recognition errors. In contrast, eggs of Vesper Sparrows, Lark Sparrows, and Grasshopper sparrows resemble cowbird eggs (Fig. 1), so these species risk rejecting their own eggs. Grasshopper Sparrow eggs typically are smaller than cowbird eggs (Table 1), although they overlap in size with them (Lowther 1993, Vickery 1996). Vesper Sparrow and Lark Sparrow eggs are similar in size to cowbird eggs, but their eggs differ enough in maculation patterns to be distinguished from cowbird eggs by most humans (Table 1, Fig. 1) and presumably by these hosts.

Another factor may be that larger eggs are more difficult to reject for these relatively small hosts. Small hosts often must use puncture ejection to remove cowbird eggs because their bills are too small to grasp the eggs. Bills of smaller hosts sometimes ricochet off thick-shelled cowbird eggs during attempts at puncture ejection, which may damage the host eggs (Rohwer and Spaw 1988, Picman 1989). Warbling Vireos (*Vireo gilvus*) are the smallest hosts known to eject cowbird eggs frequently, and they do so without incurring significant costs (Sealy 1996). Dickcissels, Vesper Sparrows, Lark Sparrows, and Grasshopper Sparrows have shorter bills than that of the Warbling Vireo (Peer 1998), which may be a constraint when the former species attempt to reject the larger cowbird eggs (Rohwer and Spaw 1988).

Geographic variation and microevolution of egg-rejection behavior.—The relatively high parasitism recorded for meadowlarks in the northern Great Plains versus the Midwest implies that egg rejection varies geographically, especially for Western Meadowlarks. Parasitism frequencies for this species range from 43 to 45% in Manitoba, Saskatchewan, and North Dakota (Davis and Sealy 2000, Koford et al. 2000, S. Davis pers. comm.) versus 2 to 22% in Illinois, Kansas, Minnesota, and Wisconsin (Lanyon 1957, Hill 1976, Johnson and Temple 1990, this study), suggesting that northern Great Plains birds exhibit lower levels of egg rejection than

those in the Midwest. This is unusual because the only cowbird hosts known to vary in rejection behavior are American Robins (*Turdus migratorius*; Briskie et al. 1992) and Brown Thrashers (*Toxostoma rufum*; Haas and Haas 1998). Eastern and western Warbling Vireos also differ in rejection frequency, but these taxa may be distinct species (Sealy 1996). Meadowlarks in the northern Great Plains may not reject because they mistakenly treat cowbird eggs laid early in first nests as their own, as may be the case in Brown Thrashers (Haas and Haas 1998). If so, then these examples would not constitute geographic variation in rejection.

The historic range of Brown-headed Cowbirds included the prairies of Illinois where our studies were conducted as well as the Great Plains (Mayfield 1965), so we would expect similar rejection frequencies by species in these two areas. Moreover, we would expect Eastern Meadowlarks and Western Meadowlarks to exhibit similar rejection frequencies, particularly at the Savanna site where populations ostensibly have been in contact with cowbirds for similar lengths of time. Possibly, the necessary mutations and recombinants for rejection behavior arose earlier in Western Meadowlarks than in Eastern Meadowlarks (see Rothstein 1975a, b); hence, the higher rejection rate demonstrated by the former species. Testing the rejection behavior of other populations of Eastern Meadowlarks and Western Meadowlarks is warranted.

The low-to-intermediate levels of true egg rejection demonstrated by the meadowlark species may represent examples of microevolution. Very few North American hosts exhibit intermediate levels of true rejection (Rothstein 1975b), perhaps because rejection behavior has a high selective value and increases rapidly until it reaches fixation, thereby transforming a species from an acceptor to a rejecter (Rothstein 1975a). Meadowlarks may be undergoing such a transformation, making them unique among cowbird hosts. Both species are parasitized throughout most of their ranges and raise fewer young in parasitized versus unparasitized nests (Elliott 1978, Davis and Sealy 2000). As a consequence, rejection may be increasing and approaching fixation in these species (Rothstein 1975a), which would be evidence of microevolutionary change in response to parasitism (see Soler et al. 1994). Alterna-

tively, meadowlarks may be in an evolutionary equilibrium with cowbirds. The similarity between meadowlark and cowbird eggs may increase the likelihood of recognition errors that may make acceptance of cowbird eggs the better strategy in these larger hosts, yet this seems unlikely because such errors rarely occurred in our study. Further investigation is required to resolve these issues.

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LITERATURE CITED

- ALDERSON, G. W., H. L. GIBBS, AND S. G. SEALY. 1999. Determining the reproductive behaviour of individual Brown-headed Cowbirds using microsatellite DNA markers. *Animal Behaviour* 58: 895–905.
- BAICICH, P. J., AND C. J. O. HARRISON. 1997. A guide to the nests, eggs, and nestlings of North American birds, 2nd ed. Academic Press, New York.
- BRISKIE, J. V., S. G. SEALY, AND K. A. HOBSON. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric populations. *Evolution* 46:334–340.
- BURHANS, D. E. 1996. Anti-brood parasite strategies and nest-site selection by forest-edge songbirds in Central Missouri. Ph.D. dissertation, University of Missouri, Columbia.
- BURHANS, D. E. 2000. Morning nest arrivals in cowbird hosts: Their role in aggression, cowbird recognition and host response to parasitism. Pages 161–168 in *Ecology and management of cowbirds and their hosts* (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.
- BURHANS, D. E., AND P. C. FREEMAN. 1997. Partial rejection of immaculate foreign eggs by Yellow-breasted Chats. *Auk* 114:503–506.
- CAREY, M., D. E. BURHANS, AND D. A. NELSON. 1994. Field Sparrow (*Spizella pusilla*). In *The birds of North America*, no. 103 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- DAVIES, N. B., AND M. DE L. BROOKE. 1998. Cuckoos versus hosts: Experimental evidence for coevolution. Pages 59–79 in *Parasitic birds and their hosts: Studies in coevolution* (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, New York.
- DAVIS, S. K., AND S. G. SEALY. 2000. Cowbird parasitism and nest predation in fragmented grasslands of southwestern Manitoba. Pages 220–228 in *Ecology and management of cowbirds and their hosts* (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.
- DEGEUS, D. W., AND L. B. BEST. 1991. Brown-headed Cowbirds parasitize Loggerhead Shrikes: First records for family Laniidae. *Wilson Bulletin* 103: 504–506.
- ELLIOTT, P. F. 1977. Adaptive significance of cowbird egg distribution. *Auk* 94:590–593.
- ELLIOTT, P. F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. *Auk* 95:161–167.
- FLEISCHER, R. C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. *Behavioral Ecology and Sociobiology* 17:91–99.
- FRAGA, R. M. 1985. Host parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. Pages 829–844 in *Neotropical ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithological Monographs No. 36.
- FREEMAN, S., D. F. GORI, AND S. ROHWER. 1990. Red-winged Blackbirds and Brown-headed Cowbirds: Some aspects of a host-parasite relationship. *Condor* 92:336–340.
- HAAS, C. A., AND K. H. HAAS. 1998. Brood parasitism by Brown-headed Cowbirds on Brown Thrashers: Frequency and rates of rejection. *Condor* 100:535–540.
- HAHN, D. C., AND J. S. HATFIELD. 1995. Parasitism at the landscape scale: Cowbirds prefer forests. *Conservation Biology* 9:1415–1424.
- HERGENRADER, G. L. 1962. The incidence of nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) on roadside nesting birds in Nebraska. *Auk* 79:85–88.
- HILL, D. P., AND S. G. SEALY. 1994. Desertion of nests parasitized by cowbirds: Have Clay-coloured Sparrows evolved an anti-parasite defence? *Animal Behaviour* 48:1063–1070.
- HILL, R. A. 1976. Host-parasite relationships of the Brown-headed Cowbird in a prairie habitat of

- west-central Kansas. *Wilson Bulletin* 88:555–565.
- HOBSON, K. A., AND S. G. SEALY. 1987. Cowbird egg buried by a Northern Oriole. *Journal of Field Ornithology* 58:222–224.
- HOOVER, J. P., AND M. C. BRITTINGHAM. 1993. Regional variation in cowbird parasitism of Wood Thrushes. *Wilson Bulletin* 105:228–238.
- JOHNSON, R. G., AND S. A. TEMPLE. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54:106–111.
- KATTAN, G. H. 1998. Impact of brood parasitism: Why do House Wrens accept Shiny Cowbird eggs? Pages 212–220 in *Parasitic birds and their hosts: Studies in coevolution* (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, New York.
- KEMAL, R. E., AND S. I. ROTHSTEIN. 1988. Mechanisms of avian egg recognition: Adaptive responses to eggs with broken shells. *Animal Behaviour* 36:175–183.
- KOFORD, R. R., B. S. BOWEN, J. T. LOKEMOEN, AND A. D. KRUSE. 2000. Cowbird parasitism in grassland and cropland in the northern Great Plains. Pages 229–235 in *Ecology and management of cowbirds and their hosts* (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.
- LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. *Publications of the Nuttall Ornithological Club* No. 1.
- LOWTHER, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). In *The birds of North America*, no. 47 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- MAYFIELD, H. 1965. The Brown-headed Cowbird, with old and new hosts. *Living Bird* 4:13–28.
- MIDDLETON, A. L. A. 1998. Chipping Sparrow (*Spizella passerina*). In *The birds of North America*, no. 334 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- MIRARCHI, R. E., AND T. S. BASKETT. 1994. Mourning Dove (*Zenaida macroura*). In *The birds of North America*, no. 117 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- NEWMAN, G. A. 1970. Cowbird parasitism and nesting success of Lark Sparrows in southern Oklahoma. *Wilson Bulletin* 82:304–309.
- ORTEGA, C. P. 1998. Cowbirds and other brood parasites. University of Arizona Press, Tucson.
- PEER, B. D. 1998. An experimental investigation of egg rejection behavior in the grackles (*Quiscalus*). Ph.D. dissertation, University of Manitoba, Winnipeg.
- PEER, B. D., AND E. K. BOLLINGER. 1997. Explanations for the infrequent cowbird parasitism on Common Grackles. *Condor* 99:151–161.
- PEER, B. D., AND E. K. BOLLINGER. 1998. Rejection of cowbird eggs by Mourning Doves: A manifestation of nest usurpation? *Auk* 115:1057–1062.
- PEER, B. D., AND S. G. SEALY. 2000. Conspecific brood parasitism and egg rejection in Great-tailed Grackles. *Journal of Avian Biology* 31:271–277.
- PICMAN, J. 1989. Mechanisms of increased puncture resistance of eggs of Brown-headed Cowbirds. *Auk* 106:577–583.
- PRICE, J., S. DROEGE, AND A. PRICE. 1995. The summer atlas of North American birds. Academic Press, New York.
- ROBINSON, S. K., J. D. BRAUN, S. MORSE, AND J. R. HERKERT. 1999. Use of different habitats by breeding Brown-headed Cowbirds in fragmented midwestern landscapes. Pages 52–61 in *Research and management of the Brown-headed Cowbird in western landscapes* (M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, Eds.). *Studies in Avian Biology* No. 18.
- ROBINSON, S. K., J. P. HOOVER, AND J. R. HERKERT. 2000. Cowbird parasitism in a fragmented landscape: Effects of tract size, habitat, and abundance of cowbirds and hosts. Pages 280–297 in *Ecology and management of cowbirds and their hosts* (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.
- ROHWER, S., AND C. D. SPAW. 1988. Evolutionary lag versus bill-size constraints: A comparative study of the acceptance of cowbird eggs by old hosts. *Evolutionary Ecology* 2:27–36.
- ROTHSTEIN, S. I. 1973. The occurrence of unusually small eggs in three species of songbirds. *Wilson Bulletin* 85:340–342.
- ROTHSTEIN, S. I. 1975a. Evolutionary rates and host defenses against avian brood parasitism. *American Naturalist* 109:161–176.
- ROTHSTEIN, S. I. 1975b. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250–271.
- ROTHSTEIN, S. I. 1976. Experiments on defenses Cedar Waxwings use against cowbird parasitism. *Auk* 93:675–691.
- ROTHSTEIN, S. I. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. *Wilson Bulletin* 89:21–32.
- ROTHSTEIN, S. I., AND S. K. ROBINSON. 1998. The evolution and ecology of avian brood parasitism: An overview. Pages 3–56 in *Parasitic birds and their hosts: Studies in coevolution* (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, New York.
- SCOTT, D. M. 1977. Cowbird parasitism on the Gray Catbird at London, Ontario. *Auk* 94:18–27.

- SEALY, S. G. 1995. Burial of eggs by parasitized Yellow Warblers: An empirical and experimental study. *Animal Behaviour* 49:877-889.
- SEALY, S. G. 1996. Evolution of host defenses against brood parasitism: Implications of puncture-ejection by a small passerine. *Auk* 113:346-355.
- SEALY, S. G., AND D. L. NEUDORF. 1995. Male Northern Orioles eject cowbird eggs: Implications for the evolution of rejection behavior. *Condor* 97:369-375.
- SMITH, J. N. M., AND I. H. MYERS-SMITH. 1998. Spatial variation in parasitism of Song Sparrows by Brown-headed Cowbirds. Pages 296-312 in *Parasitic birds and their hosts: Studies in coevolution* (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, New York.
- SOLER, M., J. J. SOLER, J. G. MARTINEZ, AND A. P. MØLLER. 1994. Micro-evolutionary change in host response to a brood parasite. *Behavioral Ecology and Sociobiology* 35:295-301.
- STRAUSBERGER, B. M., AND M. V. ASHLEY. 1997. Community-wide patterns of parasitism of a host "generalist" brood-parasitic cowbird. *Oecologia* 112:254-262.
- VICKERY, P. D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*). In *The birds of North America*, no. 239 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- ZIMMERMAN, J. L. 1983. Cowbird parasitism of Dickcissels in different habitats and at different nest densities. *Wilson Bulletin* 95:7-22.

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