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PARASITISM AND EGG PUNCTURE BEHAVIOR BY BRONZED AND BROWN-HEADED COWBIRDS IN SYMPATRY

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Abstract. We monitored parasitism by the sympatric Bronzed (*Molothrus aeneus*) and Brown-headed (*M. ater*) cowbirds in south Texas to determine whether the two cowbird species avoid overlap in host use. We also investigated egg puncture behavior by Bronzed Cowbirds. Nests of 11 potential host species were found and 5.1% of 1256 nests were parasitized. Brown-headed Cowbirds parasitized seven host species, whereas Bronzed Cowbirds parasitized three species. The two cowbirds demonstrated overlap in host use. Punctured eggs were found in the nests of three host species. Nearly 81% of nests where egg puncture was observed were subsequently deserted. Egg puncture may force hosts that have escaped parasitism to renest, thereby creating additional opportunities for parasitism.

Key Words: Bronzed Cowbird, brood parasitism, Brown-headed Cowbird, egg puncture, *Molothrus aeneus, Molothrus ater.*

The Brown-headed Cowbird (scientific names given in Appendix) is the only obligate brood parasite that occurs throughout most of North America. Its range overlaps that of the Bronzed Cowbird in the southwestern United States and northern Mexico (see Lowther 1993, 1995). Scant information exists on host use by Brown-headed and Bronzed cowbirds in areas of sympatry (but see Carter 1986). Other species of brood parasites that are sympatric, particularly the cuckoos (*Cuculus, Chrysococcyx, Clamator, Eudynamis, Oxylophus, Scythrops*), reduce competition by partitioning their primary hosts (Friedmann 1928, 1967a; Payne and Payne 1967; Brooker and Brooker 1989a, b, 1992).

Little is known concerning the parasitic behavior of Bronzed Cowbirds in general. Bronzed Cowbirds puncture host eggs (Friedmann 1929, Carter 1986), behavior that differs from egg removal by Brown-headed Cowbirds. Brown-headed Cowbirds often pierce eggs in their open beaks and remove them from nests (Blincoe 1935, Sealy 1992), whereas Bronzed Cowbirds puncture holes in eggs but leave them in the nests (Friedmann 1929, Carter 1986, this study). Egg removal by Brown-headed Cowbirds appears to enhance incubation of the parasite's eggs (Sealy 1992, McMaster and Sealy 1997; Peer and Bollinger 1997, in press; see also Davies and Brooke 1988). The function of egg puncture by Bronzed Cowbirds, however, is unclear. Carter (1986) hypothesized that Bronzed Cowbirds puncture eggs to decrease competition with host nestlings or other cowbird nestlings. Shiny Cowbirds also puncture eggs (Friedmann 1929), and Mason (1986) suggested this behavior serves the same function in Shiny Cowbirds. Other researchers have suggested egg puncture by Shiny Cowbirds is spiteful behavior (Post and Wiley 1977), or that it is a general habit that is unrelated to brood parasitism (Hoy and Ottow 1964). Recent evidence, however, indicates Shiny Cowbirds puncture eggs to force hosts to desert and renest, thus providing the cowbirds with future opportunities for parasitism (Nakamura and Cruz in press). In the present study we tested two hypotheses. First, that sympatric Bronzed and Brown-headed cowbirds parasitize different host species to reduce competition, and second, that Bronzed Cowbirds puncture eggs to force hosts to desert and renest in order to obtain additional opportunities for parasitism.

METHODS

We conducted this study at the Welder Wildlife Refuge in San Patricio County, Texas (28°0′N, 97°5′W), from 1994–1996. The refuge is 3156 ha and is characterized by a mesquite-mixed grass community interspersed with chaparral (Drawe et al. 1978). Cattle were present and grazed throughout most of the refuge. Brown-headed and Bronzed cowbirds occur at the refuge in approximately equal numbers during the breeding season (B. Peer, pers. obs.). To the south of this region of Texas, Bronzed Cowbirds predominate with very few Brown-headed Cowbirds present during the breeding season, and in areas of Texas to the north, the Brown-headed Cowbird predominates with very few Bronzed Cowbirds present (Oberholser 1974, Carter 1986, Price et al. 1995).

One of us (B. Peer) searched for nests throughout most of the refuge almost daily in all three years, and one assistant also searched in 1996. The only vegetation type not searched was grassland where Eastern Meadowlarks nested in all years and Dickcissels in 1994. This area was not searched due to the low densities of these hosts and time constraints. We did not census birds, but the number of nests found were generally reflective of overall passerine densities. The exceptions, in addition to the two afore-

FIGURE 1. Northern Cardinal nest containing one punctured host egg and one Brown-headed Cowbird egg.

mentioned grassland species, were the Painted Bunting and White-eyed Vireo, both of which were more common than the number of nests found.

Only suitable hosts in terms of body mass, diet, and nest accessibility were included in the analyses. Unsuitable hosts (e.g., Killdeer, Mourning Dove, Common Ground-Dove, Yellow-billed Cuckoo, Greater Roadrunner, and Ash-throated Flycatcher) were excluded because such species are typically avoided by cowbirds (Friedmann 1963, Friedmann and Kiff 1985; but see Rothstein 1976, Clotfelter and Brush 1995), and indeed we found no parasitism on these species. The Great-tailed Grackle is too large to be a suitable host for the Brown-headed Cowbird, but it is suitable for the Bronzed Cowbird (Peer 1998), which is the largest of the molothrine cowbirds (males = 67 g, females = 57 g; Dunning 1993). We included species that reject cowbird eggs (e.g., Scissor-tailed Flycatcher, Northern Mockingbird, Great-tailed Grackle, and Bullock's Oriole [Rothstein 1977, Carter 1986, Regosin 1994; Peer 1998, unpubl. data]), because rejecters are sometimes parasitized (Scott 1977; see below).

Nests were marked with flagging tape and subsequently inspected every one to three days for evidence of parasitism and egg puncture. Our estimates of egg puncture are conservative because some punctured eggs may have been removed by hosts before nests were inspected. Only eggs that had holes poked through the eggshells (see Fig. 1) were considered as punctured by Bronzed Cowbirds. We used this criterion to reduce the risk of including damage that was caused by other predators (see also Nakamura and Cruz in press and below).

RESULTS

Bronzed and Brown-Headed Cowbird Parasitism

There was no apparent partitioning of hosts by Bronzed and Brown-headed cowbirds. Bronzed Cowbirds parasitized three host species, and Brown-headed Cowbirds parasitized seven species, including all three parasitized by Bronzed Cowbirds (Table 1). The Northern Cardinal was the most frequently parasitized host overall (59 of 115 nests parasitized vs. 7 of 1151 for all other hosts; $G = 272.7$, $P < 0.001$), and individually by both Bronzed (31 of 115 vs. 2 of 1139; $G = 141.9$, $P < 0.001$) and Brown-

TABLE 1. FREQUENCY OF BRONZED AND BROWN-HEADED COWBIRD PARASITISM ON HOSTS AT THE WELDER WILDLIFE REFUGE, TEXAS FROM 1994–1996

Host species	Total nests N (%)	Nests parasitized: Bronzed Cowbird N (%)	Nests parasitized: Brown-headed Cowbird N (%)
Parasitized by both cowbirds			
Northern Cardinal	115 (9.2)	31 (27.0)	32 (27.8)
Painted Bunting	2 (0.2)	1 (50.0)	1 (50.0)
Olive Sparrow	3 (0.2)	1 (33.3)	1 (33.3)
Subtotal	120 (9.6)	33 (27.5)	34 (28.3)
Parasitized by Bronzed Cowbird only			
None	—	—	—
Parasitized by Brown-headed Cowbird only			
Verdin	4 (0.3)	—	1 (25.0)
White-eyed Vireo	2 (0.2)	—	2 (100)
Red-winged Blackbird	8 (0.6)	—	1 (12.5)
Bullock's Oriole	4 (0.3)	—	1 (25.0)
Subtotal	18 (1.4)	—	5 (12.8)
Not parasitized			
Scissor-tailed Flycatcher	279[a,b] (22.2)	—	—
Northern Mockingbird	40 (3.2)	—	—
Lark Sparrow	2 (0.2)	—	—
Great-tailed Grackle	797 (63.4)	—	—
Subtotal	1118 (89.0)	—	—
Total	1256 (100)	33 (2.6)	39 (3.1)

[a] Includes unpublished data from F. Guerrero.
[b] One nest containing a Mourning Dove egg.

headed (32 of 115 vs. 7 of 337; G = 62.5; P < 0.001) cowbirds (Table 1). Four cardinal nests, one Painted Bunting nest, and one Olive Sparrow nest were parasitized simultaneously by both cowbird species. There was no evidence that Bronzed and Brown-headed cowbirds partition the nests of cardinals as four of 31 nests parasitized by Bronzed Cowbirds were also parasitized by Brown-headed Cowbirds, and four of 32 nests parasitized by Brown-headed Cowbirds were parasitized by Bronzed Cowbirds (Fisher's exact test, P > 0.99). The 66 parasitized nests we found contained an average of 1.4 cowbird eggs per nest. Forty-five Bronzed Cowbird eggs were found in 33 nests, and 49 Brown-headed Cowbird eggs were found in 39 nests.

EGG PUNCTURE BEHAVIOR

Punctured eggs were found in nests or on the ground below nests of three species (Table 2), with cardinals having the most number of nests with punctured eggs (N = 24 nests). Nests that had eggs punctured were more likely to be deserted (80.8% of 26 nests) than nests that did not have eggs punctured for these three species (10.7% of 103 nests; Fisher exact test, P <

TABLE 2. FREQUENCY OF EGG PUNCTURE ON HOSTS NESTING AT THE WELDER WILDLIFE REFUGE, TEXAS FROM 1994–1996

Host species	Total no. nests	No. unparasitized nests with punctured eggs	Nests parasitized by Bronzed Cowbird: N (%)	Nests parasitized by Bronzed Cowbird: No. with punctured eggs	Nests parasitized by Brown-headed Cowbird: N (%)	Nests parasitized by Brown-headed Cowbird: No. with punctured eggs
Northern Cardinal	115	10	27 (27)	8[a]	32 (28)	6[b]
Olive Sparrow	3	0	1 (33)	1	1 (33)	1
Yellow-billed Cuckoo	11	1	0 (0)	0	0 (0)	0

[a] One Bronzed Cowbird egg was removed prior to puncture.
[b] Two Brown-headed Cowbird eggs were removed prior to puncture.

0.001). The stage of the nesting cycle at which eggs were punctured was known for 10 nests: six nests that had eggs punctured during incubation were deserted, whereas only one of four nests that had eggs punctured during laying was deserted (Fisher's exact test, $P = 0.03$). Four nests that had eggs punctured during the laying stage were also parasitized, and puncture occurred the same day as parasitism or later.

Parasitized nests contained punctured eggs more frequently than unparasitized nests (15 of 66 parasitized nests vs. 11 of 1190 unparasitized nests; $G = 57.4$, $P < 0.001$; Table 2). Single cowbird eggs were removed from four of these nests for other experiments, three of which were removed before puncture occurred (two brown-headed eggs and one bronzed egg) (Peer 1998). Taking these three nests into account, parasitized nests still had eggs punctured more frequently (12 of 63 vs. 11 of 1193; $G = 43.2$, $P < 0.001$). Nests parasitized by Bronzed Cowbirds were no more likely to have eggs punctured than were those parasitized by Brown-headed Cowbirds (9 of 33 nests vs. 7 of 39, respectively; $G = 0.90$, $P = 0.34$).

Host eggs were punctured more frequently (37 punctured vs. 14 not punctured) than cowbird eggs (6 vs. 10; $G = 6.3$, $P = 0.01$) in all nests that had eggs punctured. However, host eggs were punctured at the same frequency as cowbird eggs of both species combined in parasitized nests (9 of 13 vs. 6 of 14, respectively; Fisher exact test, $P = 0.25$). Bronzed Cowbird eggs were also punctured at the same frequncy as host eggs in parasitized nests (7 of 8 vs. 5 of 8; Fisher's exact test, $P = 0.57$). However, Brown-headed Cowbird eggs were punctured less often than host eggs (0 of 7 vs. 6 of 6, respectively; Fisher exact test, $P < 0.001$), and Bronzed Cowbird eggs in parasitized nests (0 of 7 vs. 7 of 8, respectively; Fisher's exact test, $P = 0.001$).

DISCUSSION

Bronzed and Brown-Headed Cowbird Parasitism

Friedmann (1967b) coined the terms "homoxenia" to designate the situation where two or more brood parasitic species use the same hosts in areas of sympatry, and "alloxenia" where parasites use different hosts in areas of sympatry. It should be to the advantage of sympatric parasites to avoid using the same hosts to reduce competition. Indeed African and Australian cuckoos avoid overlap of their primary hosts (Friedmann 1928, Brooker and Brooker 1989b). In southern Texas, however, Bronzed and Brown-headed cowbirds are seemingly homoxenic. All three species parasitized by Bronzed Cowbirds were also parasitized by Brown-headed Cowbirds. The fact that Brown-headed Cowbirds used a wider variety of host species reflects the host use by these two cowbirds in general. Brown-headed Cowbirds have parasitized about 220 host species (Friedmann and Kiff 1985), whereas Bronzed Cowbirds are known to have parasitized only 87 species (Lowther 1995, Sealy et al. 1997). Possibly, some of the hosts we observed parasitized only by Brown-headed Cowbirds were also parasitized by Bronzed Cowbirds, but escaped our detection because our samples were small for those four species. However, only two of these species, the Red-winged Blackbird and Bullock's Oriole, are known hosts of the Bronzed Cowbird (Friedmann and Kiff 1985). We also have no data on parasitism of Eastern Meadowlarks or Dickcissels. Both are hosts of the Brown-headed Cowbird, but neither has been observed to be parasitized by Bronzed Cowbirds (Friedmann and Kiff 1985, Lowther 1995, Sealy et al. 1997).

Our small samples for some hosts limit our conclusions somewhat. However, our findings are similar to those of Carter (1986) at the Santa Ana refuge, a semi-arid forest-brushland area of southernmost Texas. Carter found that all nests parasitized by Brown-headed Cowbirds ($N = 6$) were also parasitized by the more common Bronzed Cowbirds. Perhaps the best explanation for the overlap in host use is that the two cowbird species have just recently come into contact in this area of Texas. The Bronzed Cowbird was not known to occur in Texas until the late 19th century (Merrill 1876), thus there may not have been sufficient time for competition between the two species to force differences in host utilization.

Egg Puncture Behavior

Our data support the hypothesis that egg puncture forces hosts that have escaped parasitism to desert and renest, thereby creating additional opportunities for parasitism (Nakamura and Cruz in press; see also Arcese et al. 1996). Female cowbirds may not be ready to lay, or they may find nests during the incubation stage or later. Such nests are too advanced to be successfully parasitized because the parasite's eggs must often hatch before or at the same time as host nestlings if they are to fledge (Carter 1986, Peer and Bollinger 1997). Although we were often unaware of what stage of the nesting cycle at which egg puncture occurred, 81% of nests that had eggs punctured were deserted. Nests that had eggs punctured during the laying stage were less likely to be deserted than those that had eggs punctured during incubation. Eggs that

were punctured during the laying stage may have been punctured by females who were not ready to lay, but were unsuccessful at forcing desertion. These results concur with studies of the Shiny Cowbird in which nests that had eggs punctured were also frequently deserted (Post and Wiley 1977, Fraga 1985, Nakamura and Cruz in press). Similarly, Arcese et al. (1996) found that nest failure in Song Sparrows increased when Brown-headed Cowbirds were present and they suggested Brown-headed Cowbirds depredate nests to create additional opportunities for parasitism.

Nakamura and Cruz (in press) further suggested that egg puncture by Shiny Cowbirds may reflect competitive interactions between cowbirds for parasitism opportunities because punctured eggs were more common in areas with higher cowbird densities. We have no data on cowbird densities at the Welder Wildlife Refuge. Parasitized nests were, however, more likely to have eggs punctured than nonparasitized nests, which may indicate that cowbirds puncture eggs in nests that have already been parasitized. This would require that cowbirds recognize cowbird eggs in the nests of their hosts. Presumably, Bronzed Cowbirds should be able to recognize the immaculate eggs of other Bronzed Cowbirds in the nests of the most frequently parasitized host, the cardinal, which has spotted eggs (Baicich and Harrison 1997). However, it seems unlikely that they can recognize Brown-headed Cowbird eggs in cardinal nests because cowbird eggs closely resemble cardinal eggs (see Baicich and Harrison 1997). Inexperienced researchers frequently mistake Brown-headed Cowbird eggs for cardinal eggs (B. Peer, pers. obs.); thus, it is possible that cowbirds cannot distinguish between the two egg types. If so, we would expect that nests parasitized by Bronzed Cowbirds would be more likely to have eggs punctured than those nests parasitized by Brown-headed Cowbirds, but there was no difference. The fact that parasitized nests were more likely to contain punctured eggs may be a result of cowbirds keying in on the nests of these frequently parasitized hosts, particularly the cardinal.

Similar to Nakamura and Cruz (in press), we found no evidence that egg puncture helps cowbirds fledge from nests by reducing competition with host nestlings or other cowbird nestlings (e.g., Carter 1986, Mason 1986). Hosts clearly deserted their nests in association with puncture behavior in our study and this would make the elimination of host or other cowbird nestlings superfluous. Moreover, the contents of punctured eggs often leaked into nests and caused the remaining eggs to stick to the bottom of the nest, and this also attracted ants (B. Peer, pers. obs.; see also Nakamura and Cruz in press). This would prevent the remaining eggs including the cowbird eggs from being turned, which would result in the death of the embryos (Gill 1990). Thus, this behavior would actually decrease the likelihood of a cowbird fledging.

Great Spotted Cuckoos damage host eggs indirectly as a result of their eggs hitting host eggs during laying (Soler 1990, Soler et al. 1997). Soler et al. (1997) suggested that damage to host eggs decreases competition from host nestlings and increases the chances of late-laid eggs hatching. Indeed, one of us witnessed an incident where a Bronzed Cowbird laid her egg in a cardinal nest and, upon inspection, we found that one of the cardinal eggs had been cracked (see Peer and Sealy 1999). The egg was subsequently removed, presumably by the adult, and the nest was later depredated. Soler et al. (1997) state that this sort of damage is beneficial because it makes host eggs inviable and decreases the risk of attracting insects and bacteria. However, if as they suggest this change in the egg is so subtle that the host does not notice it, the host may not remove the egg. Eggs that are cracked or dented often hatch; the inner membrane must be damaged for the egg to become inviable (Røskaft et al. 1993; S. Sealy, pers. obs.). Therefore, this would not reduce competition. Soler et al. (1997) also incorrectly state that when brood parasites damage eggs they do so without breaking them. The references they list (Hoy and Ottow 1964, Post and Wiley 1977, Carter 1986) refer to Bronzed and Shiny cowbirds and these parasites puncture holes in the eggs making them inviable (see above and Nakamura and Cruz in press).

Egg puncture also does not appear to be of a generalist nature in Bronzed Cowbirds, nor does it appear to be spiteful (e.g., Hoy and Ottow 1964, Post and Wiley 1977). Egg puncture was clearly associated with Bronzed Cowbird parasitism. Punctured eggs were found only in the nests of species that were parasitized by Bronzed Cowbirds, or are known hosts of this cowbird (Table 1; Clotfelter and Brush 1996). In addition to being the most frequently parasitized host, the cardinal also suffered the highest frequency of egg puncture, which indicates that this behavior is associated with parasitism (see also Nakamura and Cruz in press). Thus, despite the fact that we did not witness Bronzed Cowbirds puncture eggs, we are confident the eggs were indeed punctured by Bronzed Cowbirds rather than other predators. Furthermore, egg predators typically consume eggs, i.e., they do not puncture eggs and leave them in the nests. Eastern Meadowlarks puncture eggs (Picman 1992) and

they nested at the refuge; however, meadowlarks were not present in the habitats where egg puncture was observed. Red-winged Blackbirds puncture eggs (Sealy 1994) and they also nested at the refuge, but they were relatively rare and we did not observe punctured eggs at the lake where they nested.

We are also confident that Brown-headed Cowbirds were not responsible for egg puncture in our study. Instead of puncturing eggs, Brown-headed Cowbirds may depredate host nests (Arcese et al. 1996), but it is unclear how widespread this behavior is in Brown-headed Cowbirds. It is possible that Brown-headed Cowbirds depredated some nests in our study. However, only hosts that were parasitized or are known hosts of the Bronzed Cowbird suffered egg puncture (see Clotfelter and Brush 1995 and below), and none of the hosts that were parasitized by only Brown-headed Cowbirds suffered egg puncture.

Egg puncture also differs from the "mafia" behavior described in Great Spotted Cuckoos. Mafia cuckoos (Zahavi 1979, Soler et al. 1995) purportedly depredate some or all the eggs or nestlings of their Black-billed Magpie hosts to punish them for rejecting cuckoo eggs. The three hosts that experienced egg puncture in our study are not known to reject cowbird eggs, although the cardinal is the only one that has been tested experimentally (Rothstein 1975a; see also Carter 1986). Furthermore, we found no evidence of egg puncture in the nests of the four rejecter species that nested at the refuge. Thus, it appears that egg puncture by Bronzed Cowbirds, similar to Shiny Cowbirds, functions to force hosts to renest to provide the cowbirds with future opportunities for parasitism.

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APPENDIX. SCIENTIFIC NAMES OF BIRDS MENTIONED IN TEXT OR TABLES.

Killdeer	*Charadrius vociferus*
Mourning Dove	*Zenaida macroura*
Common Ground-Dove	*Columbina passerina*
Great-spotted Cuckoo	*Clamator glandarius*
Yellow-billed Cuckoo	*Coccyzus americanus*
Greater Roadrunner	*Geococcyx californianus*
Scissor-tailed Flycatcher	*Tyrannus forficatus*
Ash-throated Flycatcher	*Myiarchus cinerascens*
Black-billed Magpie	*Pica pica*
Verdin	*Auriparus flaviceps*
Northern Mockingbird	*Mimus polyglottos*
White-eyed Vireo	*Vireo griseus*
Northern Cardinal	*Cardinalis cardinalis*
Painted Bunting	*Passerina ciris*
Olive Sparrow	*Arremonops rufivirgatus*
Song Sparrow	*Melospiza melodia*
Lark Sparrow	*Chondestes grammacus*
Dickcissel	*Spiza americana*
Eastern Meadowlark	*Sturnella magna*
Red-winged Blackbird	*Agelaius phoeniceus*
Brown-headed Cowbird	*Molothrus ater*
Bronzed Cowbird	*Molothrus aeneus*
Shiny Cowbird	*Molothrus bonariensis*
Great-tailed Grackle	*Quiscalus mexicanus*
Bullock's Oriole	*Icterus bullockii*