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Does Egg Rejection Account for the Low Incidence of Cowbird Parasitism in Chestnut-collared Longspurs (*Calcarius ornatus*)?

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ABSTRACT.—We experimentally parasitized Chestnut-collared Longspur (*Calcarius ornatus*) nests with mimetic and nonmimetic Brown-headed Cowbird (*Molothrus ater*) eggs to determine whether the low frequency of parasitism reported for that grassland host is due to egg rejection behavior. Longspurs accepted all 23 mimetic eggs (real and wooden) and rejected 9 of 22 blue nonmimetic eggs. Our results suggest longspurs accept cowbird eggs even though they are physically capable of ejecting them from their nest. Thus, the low parasitism frequency reported for that species is not a result of egg rejection behavior, but may be due to antiparasite strategies that reduce their chances of being parasitized (e.g. nest defense behavior).

RESUMEN.—Parasitamos experimentalmente nidos de *Calcarius ornatus* con huevos miméticos y no miméticos de *Molothrus ater* para determinar si la baja frecuencia de parasitismo reportada para este hospedero se debe al comportamiento de rechazo de los huevos. Individuos de *C. ornatus* aceptaron el total de los 23 huevos miméticos (verdaderos y artificiales) y rechazaron 9 de los 22 huevos azules no miméticos. Nuestros resultados sugieren que *C. ornatus* acepta los huevos de *M. ater* a pesar de que son físicamente capaces de expulsarlos de sus nidos. En consecuencia, la baja frecuencia de parasitismo documentada para esta especie no resulta del comportamiento de rechazo, sino que puede deberse a estrategias antiparasitarias (e.g. defensa de los nidos) que reducen la probabilidad de ser parasitados.

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The Chestnut-collared Longspur (*Calcarius ornatus*; hereafter “longspur”) is a grassland specialist of the northern Great Plains (Mengel 1970) most commonly associated with native mixed-grass prairie

pastures (Stewart and Kantrud 1972, Davis and Duncan 1999). Similarly, the brood parasitic Brown-headed Cowbird (*Molothrus ater*; hereafter "cowbird") is most abundant within its historic range on the northern Great Plains (Peterjohn et al. 2000) and typically uses pastures for both foraging and breeding (Davis and Sealy 2000). Despite the current and historic overlap of longspur and cowbird populations, longspurs are parasitized infrequently by cowbirds (Hill and Gould 1997). Davis and Sealy (2000), for example, found that longspurs were parasitized 2–3× less frequently than most other grassland hosts in southern Manitoba.

Species infrequently parasitized by cowbirds may be poor-quality hosts due to their nonoverlapping laying seasons (Carey 1982), incompatible nestling diets (Middleton 1977), aggressive nest-defense behavior (Sealy et al. 1998), or their ability to recognize and reject cowbird eggs (Rothstein 1975). Longspurs, however, should be suitable hosts because they (1) nest during the cowbird's laying season (Davis 1994, S. K. Davis unpubl. data), (2) feed their young mostly invertebrates (Maher 1979), (3) have similar incubation periods as cowbirds (Lowther 1993, Hill and Gould 1997), (4) have less-concealed nests than those of most grassland species (Davis 1994) and therefore may be easier for cowbirds to locate (Rothstein 1975), and (5) are known to have successfully reared cowbird young (Friedmann and Kiff 1985, Davis and Sealy 2000).

Mayfield (1965) suggested grassland hosts were more likely to evolve antiparasite behaviors because of their longtime association with cowbirds. Thus, it is reasonable to predict that the low incidence of parasitism observed in longspurs is a result of evolved traits that allow them to reject cowbird eggs or deter parasitism. To address that, we experimentally parasitized longspur nests with real and wooden cowbird eggs to determine whether longspurs eject cowbird eggs. Because the color and maculation of cowbird eggs closely resemble longspur eggs (S. K. Davis pers. obs.), we also added blue eggs (nonmimetic) to nests to determine whether longspurs might accept cowbird eggs because they are unable to distinguish cowbird eggs from their own (see Davies and Brooke 1988).

Methods.—We located and monitored nests from early May to mid-August 1999 and 2000 on 13 native prairie pastures in the eastern portion of the mixed-grass ecoregion of southern Saskatchewan (see Davis et al. 1999 for a description of the region). Different pastures were used in each year of the study. Female longspurs were flushed from their nests with a weighted 25 m nylon rope that was dragged across the vegetation. We marked nests using 30 cm bamboo stakes placed 5 m away and inspected nests every 2–5 days until the young fledged or the nesting attempt failed. Eggs were candled (Lokemoen and

Koford 1996) to determine stage of incubation and to estimate hatching dates.

Although hosts typically respond similarly to experimental parasitism using artificial or real eggs (Rothstein 1975), we used real eggs and wooden eggs because we were unsure whether longspurs could remove the latter. Thus, we parasitized nests with one of four egg types: mimetic and nonmimetic wooden and real eggs. Wooden eggs were coated with a water-based wood finish and then sanded prior to painting with acrylic paint. Wooden eggs were similar in size to real cowbird eggs, but slightly lighter in mass (22.2 ± 0.03 SE $\times$ 16.5 ± 0.09 mm, and 2.1 ± 0.04 g [$n = 13$], vs. 21.4×16.4 mm and 3.0 g, respectively; Lowther 1993). Wooden mimetic eggs were painted to resemble real cowbird eggs (white background with brown and gray splotches and specks) and nonmimetic eggs were painted blue. Real mimetic eggs were Brown-headed Cowbird eggs collected from Brewer's Blackbird (*Euphagus cyanocephalus*) nests, whereas real nonmimetic eggs were House Sparrow (*Passer domesticus*) eggs painted blue. House Sparrow eggs were painted instead of cowbird eggs because of our concern that the acrylic paint would increase the overall thickness of cowbird eggs making it more difficult for longspurs to remove them from their nest. Because House Sparrow eggs have thinner shells than cowbird eggs (Lowther and Cink 1992, Lowther 1993), we assume that longspurs were equally able to eject real cowbird eggs and painted House Sparrow eggs.

Between 0900 to 1900 CST, we added one experimental egg (type chosen at random) to each of 62 longspur clutches that were at the laying or early incubation stage. No host eggs were removed during the experiment. Nests were checked every one to three days for evidence of rejection until an experimental egg was rejected or the longspur's eggs hatched. During each visit, we closely examined host and experimental eggs for signs of damage. Although egg loss may be attributed to partial predation by small mammals (Pietz and Granfors 2000), we considered experimental eggs rejected if they had disappeared by a subsequent visit (i.e. ejected) or if an egg(s) was apparently damaged by the host. We searched for ejected eggs within 5 m of each nest from which an experimental egg was missing. Experimental eggs were considered accepted if they were present in active nests for at least five days. We removed experimental eggs after five days and monitored nests until the nesting attempt was complete. A five-day trial was used because most rejecter species remove cowbird eggs within 24 h and nearly always within five days (Rothstein 1975, Sealy 1996). We also include in our analyses data for three nests (two wooden mimetic eggs and one real cowbird egg) that were inadvertently collected after four days because all rejections in this study occurred within two days of parasitism. Two-tailed Fisher's exact

TABLE 1. Chestnut-collared Longspurs accept mimetic cowbird eggs added to their nests but reject nonmimetic eggs.

Egg type	Eggs rejected (%)
Mimetic	0/23 (0)
Real cowbird	0/12 (0)
Wooden cowbird	0/11 (0)
Nonmimetic	9/22 (41)
Blue House Sparrow	7/13 (54)
Wooden blue ^a	2/9 (22)

^a Does not include two deserted eggs.

tests (PROC FREQ; SAS Institute 1989) were used to test for differences in rejection frequencies among egg types.

Results.—Natural parasitism was recorded at 12.3% of the 170 longspur nests located, and six of the 21 (28.6%) parasitized nests received more than one cowbird egg (range = 1–3).

We experimentally parasitized 62 longspur nests but excluded 17 nests from subsequent analyses due to predation ($n = 11$), desertion ($n = 2$), hatching ($n = 2$), cattle trampling ($n = 1$), and investigator error ($n = 1$). Although we did not include the two deserted nests in our analyses, it is worth noting that both desertions occurred in nests parasitized with blue wooden eggs, and may represent possible rejection responses (Rothstein 1975). Longspurs accepted all mimetic eggs (real and wooden) and rejected 7 of 13 blue House Sparrow eggs and 2 of 9 blue wooden eggs (Table 1). Four of the blue House Sparrow eggs ejected from the nests were not relocated, but three eggs were found within 50 cm of the nest; two eggs appeared to be puncture-ejected whereas the third egg may have been grasped-ejected, because there were only two scratch marks at the narrow end of the egg. One of the two rejected blue wooden eggs was not recovered, whereas the second egg was found in the nest with scratch marks and flecks of paint missing. We interpreted that as evidence of an attempted ejection. None of the wooden or real cowbird eggs were rejected in our experiment. Although no significant difference was detected between real and wooden eggs ($P > 0.20$), rejection of blue House Sparrow eggs was noticeably greater than wooden blue eggs (Table 1). Overall rejection frequency was significantly higher for nonmimetic eggs than mimetic eggs ($P < 0.001$; Table 1). No host eggs were damaged or missing at nests where an experimental egg was ejected.

Discussion.—Our results indicate that longspurs can be classified as an “accepter” species (Rothstein 1975) because they accepted all cowbird eggs placed in their nests. Other grassland species in the northern Great Plains such as Clay-colored Sparrows (*Spizella pallida*; Hill and Sealy 1994) and Lark Buntings (*Calamospiza melanocorys*; Sealy 1999) also accept

cowbird eggs added to their nests, and Vesper (*Pooecetes gramineus*), Field (*Spizella pusilla*), Lark (*Chondestes grammacus*), and Grasshopper (*Ammodramus savannarum*) sparrows have been found to be accepters in other parts of their range (Rothstein 1975, Peer et al. 2000). Rejection of cowbird eggs by grassland hosts has been demonstrated only for Eastern (*Sturnella magna*) and Western (*S. neglecta*) meadowlarks and Dickcissels (*Spiza americana*) in Illinois (Peer et al. 2000). Rothstein (1975), however, found that Eastern Meadowlarks accept cowbird eggs. Furthermore, Western Meadowlarks in the northern Great Plains are frequently and intensely parasitized by cowbirds (Davis and Sealy 2000, Koford et al. 2000, S. K. Davis unpubl. data) and thus are likely accepters in that region.

The acceptance of cowbird eggs by longspurs appears to contradict Mayfield’s (1965) contention that the low incidence of parasitism observed in grassland species is due to antiparasite behaviors that evolved during their long period of sympatry with cowbirds. Mayfield’s hypothesis may still be valid because many grassland hosts, including longspurs, recognize and reject nonmimetic eggs (Peer et al. 2000, this study). The rejection of nonmimetic eggs in this study suggests that longspurs may possess coarse levels of egg recognition. Although longspur eggs are smaller than cowbird eggs, we found that eggs of many longspur clutches were virtually identical to cowbird eggs. Thus, longspurs may accept cowbird eggs because they cannot differentiate them from their own eggs. Additionally, Mayfield’s hypothesis may be supported if longspurs evolved other traits to reduce the risk of parasitism. Experimental studies have shown that several host species respond aggressively towards cowbird models and that host aggression may lower the chances of being parasitized (reviewed by Sealy et al. 1998).

The acceptance of cowbird eggs by longspurs may be explained by two hypotheses, the evolutionary lag and the equilibrium hypotheses. The evolutionary-lag hypothesis postulates that hosts have not yet evolved antiparasite defenses (Rothstein 1975, 1990). Although we would expect that the long period of sympatry between cowbird and longspur populations would be sufficient for longspurs to develop egg-rejection behavior, this hypothesis cannot be discounted. Cowbird parasitism may not have been a strong selective force prior to human settlement when longspurs and other grassland hosts would have bred on large contiguous tracts of prairie. Cultivation of grasslands has fragmented the prairie landscape such that grassland hosts are often forced to nest closer to edge habitat where they are at greater risk to parasitism (Johnson and Temple 1990, Winter et al. 2000). Thus, the costs of parasitism may have only recently been great enough to exert selection pressure on grassland hosts for evolution of egg rejection behaviors. Indeed, recent studies have doc-

umented high parasitism frequencies in grassland hosts of the northern Great Plains (Davis and Sealy 2000, Koford et al. 2000). Longspurs may also accept cowbird eggs because the cost of rejection is greater than acceptance. That forms the basis of the equilibrium hypothesis (Rohwer and Spaw 1988). Hosts may not only mistakenly eject one of their own eggs, but they might also damage their own eggs when ejecting cowbird eggs from their nest (Rohwer and Spaw 1988, Rohwer et al. 1989). Davis and Sealy (2000) found that longspurs fledge as many host young from parasitized nests as nonparasitized nests, suggesting that the cost of acceptance is relatively small for longspurs.

We caution against using wooden eggs in egg rejection studies, particularly for small passerines. The higher rejection frequency of blue House Sparrow eggs compared to blue wooden eggs (54 vs. 22%, respectively) and the desertion of only blue wooden eggs suggests that longspurs may have difficulty ejecting those eggs from their nest, possibly due to their inability to puncture wooden eggs. Nevertheless, the ejection of nonmimetic eggs by longspurs suggests they are physically capable of removing cowbird eggs, yet they accepted all cowbird eggs added to their nests. Thus, the low incidence of parasitism reported for longspurs cannot be attributed to egg-rejection behavior. Further experiments are required to determine (1) whether longspurs possess true egg recognition (Rothstein 1975), (2) why longspurs ejected nonmimetic eggs at only moderate frequencies, (3) whether the presence of a female cowbird at the nest prior to parasitism influences rejection frequency (see Davies and Brooke 1998, Burhans 2000), (4) whether longspurs possess other antiparasite behaviors (e.g. nest defense), and (5) whether the evolutionary-lag or equilibrium hypothesis best explains why longspurs accept cowbird eggs.

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