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Brian D. Peer, *Western Illinois University*
Lyndon R. Hawkins
Edwin P. Steinke
Patricia Blair Bollinger, *Eastern Illinois University*
Eric K. Bollinger, *Eastern Illinois University*

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Author(s): Brian D. Peer, Lyndon R. Hawkins, Edwin P. Steinke, Patricia Blair Bollinger, Eric K. Bollinger

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EASTERN BLUEBIRDS EJECT BROWN-HEADED COWBIRD EGGS

BRIAN D. PEER[1,5], LYNDON R. HAWKINS[2], EDWIN P. STEINKE[3], PATRICIA BLAIR BOLLINGER[4], AND ERIC K. BOLLINGER[4]

[1]*Department of Biological Sciences, Western Illinois University, Macomb, IL 61455*
[2] *2645 210th St., Mount Ayr, IA 50854*
[3] *2015 W. Fulliam, Muscatine, IA 52761*
[4]*Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920*

Abstract. The relationship between the Brown-headed Cowbird (*Molothrus ater*) and its cavity-nesting hosts has received little attention because of the assumption that cowbirds rarely parasitize these hosts. We tested the Eastern Bluebird (*Sialia sialis*), a host that is sometimes heavily parasitized by cowbirds, for egg ejection behavior. Bluebirds ejected 65% of experimentally added cowbird eggs (n = 20), but ejected no experimentally added conspecific eggs (n = 66). This suggests that cowbird parasitism, not conspecific brood parasitism, is the selective pressure responsible for egg ejection in this species. This level of rejection may be conservative because bluebirds nest in dark cavities, which may make cowbird eggs difficult to detect by bluebirds.

Key words: brood parasitism, Brown-headed Cowbird, Eastern Bluebird, egg rejection, Molothrus ater, Sialia sialis.

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[5] E-mail: BD-Peer@wiu.edu

Sialia sialis Rechaza los Huevos de *Molothrus ater*

Resumen. La relación entre *Molothrus ater* y sus hospederos que nidifican en cavidades ha recibido poca atención como resultado de la suposición de que *M. ater* rara vez parasita a estos hospederos. En este estudio probamos si *Sialia sialis*, un hospedero que algunas veces es parasitado intensamente por *M. ater*, exhibe comportamiento de rechazo de huevos. Los individuos rechazaron el 65% de los huevos de *M. ater* puestos experimentalmente en los nidos (n = 20), pero no rechazaron ninguno de los huevos coespecíficos añadidos (n = 66). Esto sugiere que el parasitismo por parte de *M. ater* es la presión selectiva responsable por el rechazo de huevos en esta especie, no el parasitismo intraespecífico. Este nivel de rechazo de huevos podría ser conservador, pues *S. sialis* anida en cavidades oscuras, lo que podría hacer que los huevos de *M. ater* sean difíciles de detectar.

Avian brood parasites such as the Brown-headed Cowbird (*Molothrus ater*) must lay their eggs in the nests of suitable hosts for their young to survive. Suitable hosts include those that have incubation periods and nestling growth rates similar to or longer than the cowbird, and those that feed their young an appropriate diet. Species that nest in cavities are usually considered inappropriate hosts, because the parasites cannot fit into the cavities to lay, or they simply avoid these nests for reasons that are unclear (Davies and Brooke 1998, Ortega 1998). There are exceptions, for example Prothonotary Warblers (*Protonotaria citrea*) are frequently parasitized by Brown-headed Cowbirds (Petit 1991), House Wrens (*Troglodytes aedon*) are parasitized by Shiny Cowbirds (*M. badius*, Kattan 1998), and Redstarts (*Phoenicurus phoenicurus*) are parasitized by Common Cuckoos (*Cuculus canorus*, Rutila et al. 2002). In addition, Honeyguides (*Heteronetta* spp.) specialize on parasitizing hole-nesting species (Friedmann 1955).

Because of the assumption that cavity-nesters are avoided by Brown-headed Cowbirds, little attention has focused on antiparasite behaviors of such hosts. Peer and Sealy (2004a) reviewed the correlates of egg rejection behavior in hosts of the Brown-headed Cowbird and reported that the only cavity-nesters tested for rejection were the House Wren, Mountain Bluebird (*Sialia currucoides*), and Prothonotary Warbler. Of these three species, only the Mountain Bluebird rejected cowbird eggs, albeit at a low frequency (20%; Hébert 1999).

Another cavity-nesting species in North America that is parasitized and capable of raising cowbird nestlings is the Eastern Bluebird (*S. sialis*, Woodward and Woodward 1979). Bluebirds possess several traits that are correlated with egg rejection in cowbird hosts (Peer and Sealy 2004a): they nest in open habitats, they are relatively large hosts with correspondingly large nests, and rejection also occurs in closely related Mountain Bluebirds (Hébert 1999). Low levels of conspecific brood parasitism have also been detected in Eastern Bluebirds (Gowaty and Bridges 1991, Meek et al. 1994), and conspecific brood parasitism may occasionally select for egg rejection in non-passerine species (Sorenson 1995, Lyon 2003). However, little compelling evidence exists that passerine species have evolved egg rejection in response to conspecific brood parasitism (Jackson 1998, but see Victoria 1972, Rothstein and Robinson 1998, Lahti 2005). Recognition of conspecific eggs is extremely rare, perhaps because females of the same species typically lay eggs that closely resemble one another (Peer and Sealy 2000). This is especially likely in Eastern Bluebirds, which lay immaculate blue eggs.

We tested whether Eastern Bluebirds eject cowbird eggs and conspecific eggs by experimentally parasitizing bluebird nests. We predicted that Eastern Bluebirds would eject cowbird eggs, but that they would accept conspecific eggs because of the lack of interclutch variation in the appearance of bluebird eggs.

METHODS

Cowbird egg experiments were conducted in Warren and Dallas Counties, Iowa in May and June of 2005. Conspecific egg experiments were conducted in Coles County, Illinois from 1993 to 2005. While it is possible that these geographically separated populations demonstrate variation in their response to parasitism, there is little evidence of geographic variation in egg rejection behavior in hosts that have been tested (Rothstein 1975, Peer and Sealy 2004a, but see Haas and Haas 1998). All nests were located in nest boxes with varying designs. Some had standard, 4 cm diameter, round entrances, and others had elongated oval or rectangular entrances that were >4 cm in diameter. Nests were experimentally parasitized with plaster eggs painted to simulate real cowbird eggs (Rothstein 1975). A sample of these eggs measured (mean ± SE) 20.9 ± 0.4 mm × 16.4 ± 0.2 mm and weighed 3.6 ± 0.1 g (n = 9). Real cowbird eggs measure 21.4 ± 0.2 mm × 16.1 ± 0.2 mm (Peer and Sealy 2004b) and weigh 3.0 g (range: 2.6–3.4 g; Wetherbee and Wetherbee 1961). Nests were parasitized during the laying and incubation stages of the nesting cycle. Nests were checked for evidence of egg ejection every one to two days after parasitism. Eggs were considered ejected if they were missing from nests following parasitism. Only a single egg was added to each nest and no host eggs were removed in conjunction with parasitism because female Brown-headed Cowbirds do not always remove host eggs (Peer 2006). We parasitized nests with cowbird eggs in relatively disparate areas to avoid parasitizing the same individuals more than once, and to our knowledge, only one pair was parasitized more than one time (see below). Individual nests were only tested once a year with conspecific eggs and thus were not likely reparasitized in a given year. It is possible that the same pairs were parasitized in successive years, although, given the low annual survival of Eastern Bluebirds (Gowaty and Plissner 1998), the likelihood of parasitizing the same individuals was likely minimal.

Artificial bluebird eggs were used to test for conspecific egg recognition. These eggs were made of wood and painted to mimic bluebird eggs. A subset of the artificial eggs measured (mean ± SE) 21.9 ± 0.1 mm × 16.1 ± 0.1 mm and weighed 2.0 ± 0.1 g (n = 10). Real bluebird eggs measure (mean ± SD) 20.9 ± 0.9 mm × 16.4 ± 0.6 mm (Pinkowski 1979) and weigh 3.1 ± 0.3 g (range: 2.2–3.8 g; Gowaty and Plissner 1998). Despite the differences in weight, these eggs effectively simulate real eggs (Peer and Bollinger 1997, 1998). A single bluebird egg was removed from each nest and replaced with an artificial bluebird egg. These experiments differ from the cowbird egg experiments in which host eggs were not removed because the conspecific egg experiments were also part of another study examining hatching asynchrony in bluebirds. However, because egg removal does not appear to influence egg rejection this should not have influenced our results (Peer 2006). Nests were checked daily to determine host response, and this also allowed us to detect conspecific brood parasitism. Evidence of conspecific brood parasitism included the appearance of more than one egg in a nest on a given day, because no birds are known to lay more than a single egg per day, and the appearance of eggs after laying had stopped (Peer and Sealy 2000).

We also measured the length of female bluebird bills, from the tip of the upper mandible to the commisure, to the nearest 0.1 mm, using dial calipers (Peer and Sealy 2004a). This served as a comparison with other species known to reject cowbird eggs to determine whether bluebird bills were large enough for egg rejection (Peer and Sealy 2004a).

RESULTS

Bluebirds ejected 65% (13 of 20) of experimentally introduced artificial cowbird eggs. There was no difference in response in relation to the timing of parasitism; 62% of eight eggs that were introduced during laying were ejected, and 67% of 12 eggs that were introduced during incubation were ejected (Fisher exact test, P = 1.0). Twelve of 13 ejections occurred within 24 hr of parasitism; the other took four days. No bluebird eggs were missing or damaged following cowbird egg ejections.

Cowbird eggs were ejected from nine of 10 nests with larger openings (i.e., >4 cm), whereas only four of 10 eggs were ejected from nests with smaller openings (i.e., 4 cm), with perhaps less light penetrating them (Fisher exact test, one-tailed, P = 0.03). One pair of bluebirds was parasitized at two different nests on private property. While we did not band the birds and cannot be certain it was the same pair, this pair successfully fledged one brood from a nest box we erected, maintained their territory, and built a nest and reared a second brood in a nest box we erected ~4–5 m from the first box. This pair accepted parasitism in the first nest box with a small entrance hole. The second box had the same-sized entrance, but we drilled vent holes on either side of it to increase the amount of light entering the box and the cowbird egg was ejected from this nest. We observed no instances of natural cowbird parasitism on bluebirds.

Bluebirds accepted all conspecific eggs (n = 66), thus the rate of rejection of cowbird eggs was significantly greater than that for conspecific eggs (Fisher exact test, P < 0.001). There were unusual responses at two nests, but both were considered as acceptance. In one case, a nest box was deserted after one bluebird egg had been replaced with an artificial egg. Birds desert nests for a number of reasons (Rothstein 1975, Peer and Bollinger 1997), thus it is unclear whether this was a response to the parasitic egg. At a second nest, a bluebird egg was removed and replaced with an artificial egg, which was gone the following day. A second artificial egg was added and remained in the nest, but the nest was then deserted. It is unclear from this response what occurred at this nest. Nests were never deserted after cowbird eggs were ejected, which suggests that the first experimentally added egg may have been taken by a predator rather than being ejected. No instances of natural conspecific brood parasitism were detected. Female bluebird bills measured 18.7 ± 0.1 mm (SE; n = 5).

DISCUSSION

To our knowledge, the egg ejection frequency we documented in Eastern Bluebirds is the highest of any cavity-nesting host. Mountain Bluebirds ejected 20% of nonmimetic eggs (Hébert 1999), and Redstarts rejected 44% of nonmimetic eggs (Rutila et al. 2002).

Hébert (1999) suggested that the egg rejection frequency he recorded for Mountain Bluebirds may be conservative because he added all eggs after incubation had started, which may make birds more likely to accept parasitism (Rothstein 1976). We agree that the frequency of egg rejection observed may be conservative for Mountain Bluebirds as well as Eastern Bluebirds. However, we do not believe this is due to the timing of parasitism, because we found no relationship between the timing of parasitism and rejection frequency, but rather due to the fact that these birds nest in dark cavities making it difficult to detect parasitic eggs. While we did not measure light levels, we believe this to be the case for several reasons. First, bluebirds that nested in boxes with larger entrances, which may have allowed more light to penetrate, ejected eggs at a higher frequency. Second, the pair that was parasitized twice accepted the first cowbird egg in a nest with a standard entrance hole, but rejected the cowbird egg from a second box that had vent holes drilled into it to increase light penetration. It is possible that this pair was demonstrating phenotypic plasticity, but this is unlikely because rejecters of Brown-headed Cowbird eggs always reject a second parasitism event after rejecting the first (BDP and S. Rothstein, unpubl. data). Light penetration into nests has been demonstrated to be a factor in egg rejection by Rufous Horneros (*Furnarius rufus*). These hosts apparently cannot detect Shiny Cowbird eggs based on color in their dark, domed nests, and instead reject cowbird eggs based on differences in size (Mason and Rothstein 1986). However, it is unlikely that bluebirds distinguish cowbird eggs based on dimensions because their eggs are essentially the same size, hence

they must rely on vision. Further evidence that recognition was visual, rather than based on factors such as mass, is that none of the artificial bluebird eggs were rejected, despite the fact that they weighed almost half that of real bluebird eggs (2.0 g vs. 3.6 g, respectively). Finally, all rejections occurred by egg ejection rather than by desertion, and 12 of 13 ejections occurred within 24 hr, which suggests that Eastern Bluebirds are very intolerant of parasitism (Rothstein 1982, Peer and Sealy 2004b).

The size of nest box entrance holes may also play a role in the ease of ejection. Female bluebird bills (18.7 mm) were slightly larger than the bills of the smallest known rejecter species, the Warbling Vireo (*Vireo gilvus*), which has a mean bill length of 17.6 mm (Peer and Sealy 2004a). Thus, they should have no difficulty in grasping and ejecting eggs. However, it is possible that female bluebirds can eject eggs more readily from nest boxes with larger entrances.

As predicted, bluebirds accepted conspecific eggs. This suggests that conspecific brood parasitism is not a significant factor in the evolution of egg ejection in bluebirds. Low levels of conspecific brood parasitism have been detected in Eastern Bluebirds (Gowaty and Bridges 1991, Meek et al. 1994), but the similarity among the eggs of females makes recognition of conspecific eggs difficult. Female bluebirds respond aggressively toward female bluebird models during the early portions of the nesting cycle, which may be an alternative means of preventing conspecific brood parasitism (Gowaty and Wagner 1988).

While bluebirds are one of the more common cavity-nesting hosts of the Brown-headed Cowbird (Friedmann 1963), parasitism frequencies are relatively low compared to other, open-cup nesting hosts (Ortega 1998). The typical entrance size of bluebird boxes is 4 cm and this may not be large enough to allow female cowbirds to enter. Cowbirds have been known to parasitize the cavity-like nests of Verdins (*Auriparus flaviceps*, Peer and Sealy 1999), which have openings of around 2.5 cm (Webster 1999). However, the entrance to a Verdin nest observed by Peer and Sealy (1999) had been enlarged by the female cowbird. Hoover (2003a) found that 50% of 1979 artificial nests and 41% of 115 natural cavity nests of Prothonotary Warblers were parasitized. The openings of the artificial cavities ranged from 3.2 cm to 6.4 cm and the nests with larger entrances were parasitized more often (Hoover 2003b). The highest parasitism frequency recorded for bluebirds was 16% of 27 nests; in this study, bluebird houses were made of milk cartons with large openings (5.4 cm; Woodward and Woodward 1979). Musselman (1946) found that 2.6% of 268 nests were parasitized and many of these had their lids removed, allowing cowbirds to gain entry. In contrast, Ontario nest record cards reveal a parasitism rate of 0.1% of 3167 Eastern Bluebird nests (Peck and James 1987).

Cowbird parasitism of bluebird nests may go largely undetected because many researchers utilize nest boxes and bluebirds that nest in natural cavities with larger entrances may be parasitized more frequently. Moreover, cowbird eggs may be ejected from natural cavities before researchers observe these nests (Scott 1977). Given that rejection tends to occur in members of the same taxonomic units (Peer and Sealy 2004a), it would be worthwhile to test the Western Bluebird for egg ejection behavior.

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