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EGG REMOVAL BY BROWN-HEADED COWBIRDS: A FIELD TEST OF THE HOST INCUBATION EFFICIENCY HYPOTHESIS[1]

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Abstract. Brown-headed Cowbirds (*Molothrus ater*) often remove host eggs, usually to the detriment of the host's reproductive success. We tested the hypothesis that host egg size and number influence the incubation efficiency of a parasitic egg. A single House Sparrow (*Passer domesticus*) or Brown-headed Cowbird egg was placed in each host nest (addition), and in some nests a host egg was removed as well (addition/removal). Hatching success and incubation length were measured to determine whether host-egg removal conferred an advantage in incubation efficiency compared to simple addition of a parasitic egg. Red-winged Blackbirds (*Agelaius phoeniceus*) and Chipping Sparrows (*Spizella passerina*) served as medium-sized and small-sized host species, respectively. In Red-winged Blackbird nests, host-egg removal produced smaller clutches, and parasitic eggs had shorter incubation lengths in smaller clutches. However, the parasitic egg's incubation length and probability of hatching did not differ between the addition and addition/removal treatments. Parasitic eggs in Chipping Sparrow nests had shorter incubation periods than in blackbird nests and frequently caused the inefficient incubation of host eggs. Egg removal again did not reduce incubation lengths or increase hatchability of parasitic eggs. Thus, we found little support for the incubation efficiency hypothesis to explain host-egg removal by Brown-headed Cowbirds.

Key words: Brown-headed Cowbirds, Molothrus ater, *brood parasitism, egg removal, Red-winged Blackbirds, Chipping Sparrows, incubation efficiency.*

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*) is North America's only widespread, obligate brood parasite. This species parasitizes over 200 species of North American birds (Friedmann and Kiff 1985). One poorly understood behavior associated with cowbird parasitism is the removal of host eggs. Cowbird females often remove one or more host eggs after they have laid their own egg in a host clutch. Various hypotheses have been proposed to explain the adaptive significance of egg removal including host deception (Moksnes and Røskaft 1987), increased nutritional intake (Scott et al. 1992), decreased nestling competition (Blakespoor et al. 1982), increased hatching efficiency (Davies and Brooke 1988), and increased incubation efficiency of the parasitic egg (Peer and Bollinger, in press).

Davies and Brooke (1988) proposed the host incubation limit hypothesis, which states that egg removal may increase the probability that a parasitic egg will hatch in larger clutches. In support of this hypothesis, Lerkelund et al. (1993) reported higher rates of unhatched eggs in enlarged clutches of the Fieldfare (*Turdus pilaris*), and Moreno et al. (1991) found reduced hatching success in enlarged clutches of the Collared Flycatcher (*Ficedula albicollis*). Thus, egg removal may increase the probability of a parasitic egg hatching in a host nest by keeping the clutch size constant.

In addition to supporting the host incubation limit hypothesis, Peer and Bollinger (in press) proposed the incubation efficiency hypothesis, which states that host egg size and number affect

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the incubation efficiency of a parasitic egg. If a cowbird parasitizes a species with larger eggs, the cowbird egg may have little contact with the host female's brood patch and may be subject to heat shielding by the larger host eggs. Therefore, a parasitic egg may have a decreased chance of hatching and possibly an increased incubation length in such nests.

Egg removal by a female cowbird may compensate for her own smaller egg by increasing its contact with the host's brood patch and increasing its chances of hatching (Wiley 1985). For smaller host species, the larger cowbird egg may have a negative impact on the host eggs due to heat shielding. Therefore, egg removal would probably not improve the incubation efficiency of the cowbird's eggs, since they already enjoy a size advantage over smaller host eggs.

In this study, we tested the host incubation efficiency hypothesis with two host species. One, the Red-winged Blackbird (*Agelaius phoeniceus*), is noticeably larger than the cowbird. The other, the Chipping Sparrow (*Spizella passerina*) is much smaller. We predicted that the addition/removal of host eggs should increase the hatching efficiency and decrease the incubation length of parasitic eggs in larger hosts compared to parasitic eggs in addition treatments, whereas there would be no such differences in nests of smaller hosts.

METHODS

STUDY SITES

Research was conducted at six sites in Coles, Cumberland, and Douglas Counties, Illinois from 10 April to 28 July 1994. Red-winged Blackbird nests were located in one large cattail marsh (*Typha* spp.) and around the periphery of two ponds in emergent vegetation, primarily cattail and willows. Chipping Sparrow nests were located in three small Christmas tree farms.

We searched for nests every 1–2 days throughout the field season or opportunistically during nest checks. Nests were marked with flagging tape 3–5 m north of the nest, and a compass bearing and distance were recorded to a reference marker near the nest (Martin and Guepel 1993).

During hatching, we recorded hatching dates of individual eggs, incubation lengths, and the presence of any unhatched eggs. Unhatched eggs were broken to analyze their contents. Eggs were classified as inefficiently incubated if a partially developed embryo was detectable with the unaided eye (Peer and Bollinger, in press). If no embryo was detected, the egg was classified as infertile.

CLUTCH MANIPULATIONS

We performed two experimental manipulations concurrently with Red-winged Blackbird and Chipping Sparrow clutches. Addition nests received one parasitic egg, increasing the existing clutch size by one egg. Addition/removal nests received one parasitic egg, but one host egg was simultaneously removed from the clutch, therefore clutch size remained the same. We also tracked the progress of control nests in which no egg additions or removals occurred.

PARASITIC EGGS

Because we could not obtain large numbers of freshly-laid Brown-headed Cowbird eggs, we used House Sparrow (*Passer domesticus*) eggs in most of our manipulations. House Sparrow eggs resemble cowbird eggs in size, maculation and 10–13 day incubation length (Peer and Bollinger, in press). House Sparrow eggs used in this study averaged ($\pm$ SD) 21.93 $\pm$ 1.01 mm $\times$ 15.65 $\pm$ 0.84 mm (n = 113). House Sparrow eggs were collected daily from nests on the campus of Eastern Illinois University and transported within several hours to study sites.

Whenever possible, Brown-headed Cowbird eggs were removed from naturally parasitized nests of various species and transplanted to experimental nests. Cowbird eggs averaged 20.16 $\pm$ 0.24 mm $\times$ 16.08 $\pm$ 0.20 mm (n = 11). Hereafter, the term "parasitic egg" refers collectively to both House Sparrow and Brown-headed Cowbird eggs.

Incubation length was measured from the day the penultimate egg was laid until each egg hatched. All incubation lengths were recorded to the nearest day. We used two-tailed Mann-Whitney U-tests (MWU) for most statistical analyses of incubation data, and chi-square tests were used to analyze hatching efficiency. Wilcoxon matched-pairs signed-rank tests (T) were used to compare incubation differences within individual clutches. In all tests, $P < 0.05$ was used to denote statistical significance. Values presented are means $\pm$ SD.

RESULTS

CLUTCH SIZE

Red-winged Blackbird nests. We monitored a total of 230 Red-winged Blackbird nests from 10 April to 15 June (Table 1). The mean clutch size of addition nests was 4.5 ± 0.91 (n = 48) and ranged from 3–5 eggs/clutch, including the parasitic egg. Addition/removal nest clutch size averaged 3.8 ± 0.52 eggs (n = 53) and ranged from 2–5 eggs/clutch. Mean clutch size for control nests was 3.6 ± 0.58 (n = 74) with a range of 2–5 eggs.

Experimental and control clutch sizes were significantly different (ANOVA, $F_{2,172}$ = 29.2, $P < 0.01$). The mean clutch size of addition nests was significantly greater than control (Student Newman-Keuls' test, $P < 0.01$) and addition/removal nests ($P < 0.01$). Mean clutch sizes of addition/removal and control nests did not differ ($P > 0.05$).

Chipping Sparrow nests. A total of 40 Chipping Sparrow nests were monitored from 8 June to 24 July (Table 1). The mean clutch size in Chipping Sparrow addition nests was 4.2 ± 0.79 (n = 10, range 3–5 eggs/clutch), compared to addition/removal nest clutch size of 3.9 ± 0.67 (n = 12, range 3–5 eggs/clutch). Mean clutch size for control nests was 4.2 ± 0.31 eggs (n = 6). Experimental and control clutch sizes did not differ ($F_{2,25}$ = 0.5, $P > 0.05$).

HATCHING EFFICIENCY

Red-winged Blackbirds. The percentage of inefficiently incubated parasitic eggs was not significantly lower in addition/removal nests (40%, 21 of 52) than in addition nests (35%, 16 of 46) (χ^2_1 = 0.3, $P > 0.50$). In addition/removal nests considered separately, parasitic eggs tended to be inefficiently incubated in clutches of ≥ 4 eggs (46%, 9 of 41) than in clutches of ≤ 3 eggs (18%, 2 of 11), although this difference was not significant (χ^2_1 = 2.9, $P < 0.10$). In addition nests, the percentages of inefficiently incubated parasitic eggs did not differ between clutches of ≤ 4 eggs (38%, 8 of 21) and clutches of 5 eggs (32%, 8 of 25) (χ^2_1 = 0.2, $P > 0.50$).

Chipping Sparrows. Parasitic eggs (Table 2) were highly successful in Chipping Sparrow nests, often to the detriment of the smaller host eggs (Table 3). Overall, the proportion of host eggs that were inefficiently incubated did not differ significantly in addition nests (25%, 8 of 32) compared to addition/removal nests (18%, 6 of 34) (χ^2_1 = 0.5, $P > 0.5$). There was no significant difference between inefficiently incubated host eggs in addition/removal clutches of 3 (17%, 1 of 6) and ≥ 4 eggs (18%, 5 of 28) (χ^2_1 = 0.0). In addition nests, Chipping Sparrow host eggs were more prone to inefficient incubation in clutches of 5 eggs (44%, 7 of 16) than in clutches of ≤ 4 eggs (17%, 1 of 16) (Fisher Exact test, $P < 0.02$).

Finally, the percentage of inefficiently incubated parasitic eggs in Red-winged Blackbird nests (38%, 37 of 98) was significantly higher than in Chipping Sparrow nests (0%, 0 of 22) (χ^2_1 = 12.0, $P < 0.001$).

TABLE 1. Outcomes for all Red-winged Blackbird and Chipping Sparrow nests. Numbers in parentheses indicate percentage of total nests.

Outcomes	Red-winged Blackbird n	Red-winged Blackbird %	Chipping Sparrow n	Chipping Sparrow %
Total # of nests	230		40	
Hatched	175	(76)	28	(70)
Predation (avian)	19	(8)	6	(15)
Predation (other)	9	(4)	2	(5)
Abandoned				
experimental	5	(2)	4	(10)
control	4	(2)	0	(0)
Destroyed	18	(8)	0	(0)

INCUBATION LENGTH

Red-winged Blackbird nests. The incubation lengths of all hatching parasitic eggs, regardless of hatching order, did not differ between addition/removal (11.2 ± 1.11 days, n = 31) and addition nests (11.0 ± 1.09 days, n = 30) (MWU, z = 1.02, $P > 0.05$). In addition/removal nests, the incubation length of all hatching parasitic eggs was not significantly shorter than the mean incubation length of host eggs in the same clutch (T = 214, z = 0.04, $P > 0.05$). In addition nests, parasitic eggs hatched sooner than the mean incubation length of host eggs in the same clutch (T = 108.5, z = 2.14, $P < 0.05$).

In addition/removal nests (Fig. 1), the incubation length of all hatching parasitic eggs in clutch sizes of ≤ 3 (10.3 ± 0.87 days, n = 9) was shorter than in clutch sizes of 4 (11.5 ± 1.06 days, n = 21) (MWU, z = 2.71, $P < 0.01$) In addition nests, incubation lengths for parasitic eggs in clutches of 3 (10.5 ± 0.71 days, n = 2) were significantly shorter than those in clutches

TABLE 2. Parasitic egg outcomes (%) in experimental nests were divided into five categories: (1) parasitic egg hatched first, (2) host egg hatched first, but the parasitic egg did hatch, (3) parasitic and a host egg hatched simultaneously, (4) parasitic egg was inefficiently incubated, and (5) parasitic egg was infertile.

Species	n	Parasitic 1st	Host 1st	Simultaneous	Inefficient incubation	Infertile
Red-winged Blackbird						
Add	48	23	25	15	33	4
Add/Remove	53	21	35	8	44	2
Chipping Sparrow						
Add	10	100	0	0	0	0
Add/Remove	12	100	0	0	0	0

of 4 (11.1 ± 0.79 days, n = 11) (MWU = 94, $P < 0.05$) and 5 eggs (11.1 ± 1.34 days, n = 17) (MWU = 101.5, $P < 0.05$) (Fig. 1). The incubation length of parasitic eggs in addition clutches of 4 was not significantly shorter than in clutches of 5 (MWU, $z = 0.24$, $n = 28$, $P > 0.05$).

Chipping Sparrow nests. In Chipping Sparrow clutches (Fig. 1), the incubation length of parasitic eggs in addition/removal nests (10.4 ± 0.51 days, n = 12) was virtually identical to parasitic eggs in addition nests (10.4 ± 0.52 days, n = 10) (MWU = 52.5, $P > 0.50$). Clutch size did not affect the incubation length of parasitic eggs in addition/removal nests (KW test, $\chi^2_2 = 1.4$, $n = 12$, $P > 0.05$) or addition nests (KW test, $\chi^2_2 = 1.9$, $n = 10$, $P > 0.05$).

When compared to mean incubation length of Chipping Sparrow eggs in addition/removal clutches (12.1 ± 0.65 days, n = 28), parasitic eggs hatched significantly earlier (10.4 ± 0.51 days, n = 12) (Wilcoxon $T = 0$, $z = 2.75$, $n = 40$, $P < 0.01$). Parasitic eggs in addition clutches (10.4 ± 0.52 days, n = 10) also hatched significantly sooner than the mean incubation length of host Chipping Sparrow eggs (12.4 ± 0.62 days, n = 24) (Wilcoxon $T = 0$, $z = 3.02$, $n = 34$, $P < 0.01$).

Red-winged Blackbird vs. Chipping Sparrow nests. The incubation length of all parasitic eggs in Red-winged Blackbird clutches (11.1 ± 1.09 days, n = 61) was significantly longer than in Chipping Sparrow nests (10.4 ± 0.50 days, n = 22) (MWU, $z = 2.24$, $P < 0.05$). Incubation lengths for parasitic eggs were significantly longer in both Red-winged Blackbird addition/removal (MWU, $z = 2.03$, $n = 43$, $P < 0.05$) and addition clutches (MWU, $z = 1.84$, $n = 40$, $P < 0.05$) than parasitic eggs in Chipping Sparrow clutches.

TABLE 3. Host egg outcomes were classified into three categories for experimental clutches: hatched, inefficiently incubated, and infertile. Percentage of eggs is listed for each category.

Species	n	Hatched	Inefficiently incubated	Infertile
Red-winged Blackbird				
experimental				
Add	166	99	0	1
Add/Remove	150	97	3	0
control	269	97	3	0
Chipping Sparrow				
experimental				
Add	32	75	25	0
Add/Remove	35	80	17	3
control	25	100	0	0

DISCUSSION

We found little direct support for the incubation efficiency hypothesis in a medium and small host species. Although Red-winged Blackbirds are a medium-sized host species, their eggs are still larger than Brown-headed Cowbird or House Sparrow eggs. Therefore, egg removal should have conveyed an advantage in relation to incubation efficiency. Although egg removal appears to be a necessity when parasitizing a very large host species (e.g., the Common Grackle, Peer and Bollinger, in press), this strategy appears to have little adaptive value in relation to medium and small hosts.

Several studies have used artificial or natural parasitic eggs to determine the effects of host egg size on parasitic eggs. Davies and Brooke (1988) found that brood parasites, like the Common Cuckoo (*Cuculus canorus*), may remove eggs to prevent the total clutch size from ex-

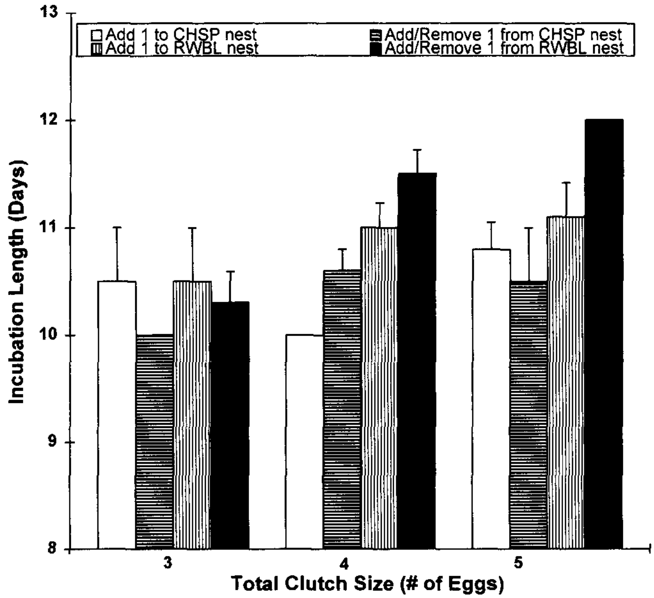

FIGURE 1. Mean (± SE) parasitic egg incubation length in addition/removal and addition Chipping Sparrow (CHSP) and Red-winged Blackbird (RWBL) nests.

ceeding the host female's ability to incubate an enlarged clutch. Thus, enlarged clutches may reduce the incubation efficiency of parasitic eggs in some instances. If parasitic and host eggs are of approximately equal size, the host incubation limit hypothesis seems appropriate. Peer and Bollinger (in press) tested the host incubation efficiency hypothesis in a large host species and found that egg removal increased hatching efficiency and decreased incubation length of parasitic eggs. If host egg sizes are larger, the host incubation efficiency hypothesis appears to offer a sufficient explanation of host egg removal. Neither of these hypotheses explains why cowbirds remove eggs from the nests of smaller host species.

Thus, the adaptive significance of host-egg removal by Brown-headed Cowbirds has yet to be clearly delineated. The lack of egg removal creates several problems. If a cowbird does not remove one or more host eggs, the increased clutch may take longer to incubate, because the female's brood patch cannot cover all the eggs sufficiently (Klomp 1970). Thus, a host female may leave the nest to increase her nutritional intake in response to increased incubation requirements (Biebach 1984, Haftorn and Reinertsen 1985). The absence of the female from the nest can lead to increased predation or reduction in fledgling success (Zimmerman 1983).

The effects of enlarged clutches, where no egg removal occurs, are well known. Several authors have shown that enlarged clutches experience decreased hatching success and increased incubation length (Wicklund 1985, Moreno et al. 1991, Lerkelund et al. 1993). Other studies with experimentally enlarged clutches found no difference in hatching success, but clutch enlargement may have increased incubation length of eggs in the clutch (Baltz and Thompson 1988, Moreno and Carlson 1989, Smith 1989). Furthermore, egg removal from medium-sized hosts often results in decreased clutch size only if more eggs are removed than replaced by the parasite, allowing cowbird eggs to hatch sooner than host eggs (Zimmerman 1983, Weatherhead 1989). Therefore, egg removal by female cowbirds may serve to reduce clutch size and hence increase its egg's chances of hatching sooner, especially in larger host species.

EVOLUTION OF EGG REMOVAL BEHAVIOR

Rothstein (1975) suggested that Brown-headed Cowbirds may have initially parasitized larger host species. The strategy of egg removal may have allowed cowbirds to increase their chances of successfully parasitizing a larger host species. In a large host species, the Common Grackle (*Quiscalus quiscula*), Peer and Bollinger (in press) found that parasitic eggs not only had a greater chance of hatching in experimentally reduced clutches, but they also had shorter incubation lengths than parasitic eggs in larger clutches. Furthermore, the hatching differential between host and parasitic egg was greater in smaller (fewer egg) clutches, possibly allowing the parasitic nestling to gain an early growth advantage over the larger grackle nestlings.

Rothstein (1975) reported that most rejecter species of cowbird eggs are larger host species, indicating an evolutionary response to prevent brood parasitism. Bronzed Cowbirds (*M. aeneus*) and Shiny Cowbirds (*M. bonariensis*) frequently parasitize larger host species and are rejected more frequently by larger host species than by smaller host species (Carter 1986, Mason 1986). After larger hosts began rejecting cowbird eggs, selection may have favored parasitizing smaller host species (Rothstein 1990). In some smaller hosts, cowbirds may not remove eggs as often as in larger hosts (Elliot 1978, Petit 1991, Sealy 1992).

The negative effects of brood parasitism on smaller host species have been well documented (Mayfield 1960, Marvil and Cruz 1989, Sealy 1992). Egg removal may reduce host clutch size and decrease hatching success of host eggs (Wolf 1987, Marvil and Cruz 1989, Petit 1991).

Incubation length decreases in small hosts, which provides some support for the incubation efficiency hypothesis. Larger hosts lay larger eggs, so that the smaller parasitic egg may receive less heat, possibly resulting in inefficient incubation or increased incubation length. Conversely, as host size decreases the parasitic egg would equal and then surpass host eggs in size, thereby reducing host hatching success. Although no advantage may be gained in terms of parasitic-egg incubation length or hatching success, the removal of smaller host eggs may serve to reduce nestling competition.

In small host species, cowbirds may remove host eggs to reduce nestling competition and allow the cowbird nestling to receive more parental care (Scott 1977, Zimmerman 1983). Because egg removal does not appear to have an effect on incubation length or hatching efficiency in small hosts, further research into the post-hatching implications of egg removal seem appropriate. Analysis of nestling growth rates, fledging times, and survival rates of cowbird and host nestlings in hosts of different size might provide further insight into the evolution of egg removal behavior by cowbirds.

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