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Egg Removal by Brown-Headed Cowbirds: A Field Test of the Host Incubation Efficiency Hypothesis

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Egg Removal by Brown-headed Cowbirds: A Field Test of the Host Incubation Efficiency Hypothesis

(TITLE)

BY

Douglas R. Wood

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Egg Removal by Brown-headed Cowbirds: A Field Test of the Host Incubation Efficiency Hypothesis

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Abstract. Obligate brood parasites, like the Brown-headed Cowbird (Molothrus ater), lay their eggs in the nests of host species, usually to the detriment of the host's reproductive effort. In addition, Brown-headed Cowbirds often remove one or more host eggs near the time of parasitism. Although several hypotheses exist, the adaptive significance of egg removal has not been clearly established. Peer and Bollinger (in press) proposed the host incubation efficiency hypothesis which states that the number and size of host eggs influences the incubation efficiency of a parasitic egg. Thus, host egg removal by cowbirds should increase the parasitic egg's chance of hatching in a host's nest or reduce its incubation length, especially if the host eggs are larger. They tested this hypothesis using a large host, the Common Grackle (Quiscalus quiscula), and found that cowbird eggs had a greater chance of hatching and a shorter incubation length in smaller clutches. Thus, for cowbirds parasitizing larger host species, egg removal was adaptive.

However, Brown-headed Cowbirds currently parasitize species noticeably smaller than grackles. Therefore, I tested the host incubation efficiency hypothesis to determine whether egg removal confers an advantage in hatching efficiency and incubation length for medium and small host species. Red-winged Blackbirds (Agelaius phoenicus) and Chipping Sparrows (Spizella passerina) served as host species. Either a House Sparrow or a Brown-headed Cowbird egg was placed in each host

nest. In some nests, a host egg was removed as well (addition/removal nests), whereas in others no host egg was removed (addition nests). Overall, the addition/removal treatment did not decrease incubation length or increase the incubation efficiency of parasitic eggs compared to the addition treatment. However, in addition/removal nests of Red-winged Blackbirds, parasitic eggs were more likely to hatch and have a shorter incubation length in smaller clutches. In addition nests, parasitic eggs hatched sooner in smaller clutches, although hatching efficiency was not dependent upon clutch size.

Parasitic eggs always hatched successfully in Chipping Sparrow nests and host eggs were often inefficiently incubated. The addition/removal treatment did not increase hatching efficiency or shorten incubation length for parasitic eggs compared to the addition treatment. Clutch size did not affect hatching efficiency or incubation length in either treatment. Overall, parasitic eggs hatched earlier and were less likely to be inefficiently incubated in Chipping Sparrow nests compared to Red-winged Blackbird nests.

These results provide support for the incubation efficiency hypothesis of host egg removal by Brown-headed Cowbirds. Although Red-winged Blackbird nests with smaller clutches had shorter incubation lengths and increased hatching efficiency for parasitic eggs, the addition/removal treatment did not significantly decrease the incubation

length of parasitic eggs. Secondly, although parasitic eggs in Chipping Sparrow nests had shorter incubation periods than Red-winged Blackbird nests and caused the inefficient incubation of host eggs, addition/removal and addition treatments did not differ.

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Introduction

Obligate brood parasitism represents a rare reproductive strategy practiced by only 1% of all bird species (Payne 1977). Brood parasites provide no parental care other than laying their eggs in host nests. Host species incubate and feed the parasitic nestlings, often at the expense of their own offspring (Friedmann 1963, Payne 1977, Rothstein 1990).

The Brown-headed Cowbird (Molothrus ater) is North America's only widespread, obligate brood parasite. This species has parasitized over 200 species of North American birds (Friedmann and Kiff 1985). In conjunction with forest fragmentation, Brown-headed Cowbirds have negatively impacted numerous North American passerine species (Payne 1977, Clark and Robertson 1981, Brittingham and Temple 1983, Finch 1983, Marvil and Cruz 1989).

Cowbirds utilize a variety of strategies and adaptations to successfully parasitize their hosts. One of the most poorly understood behaviors 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 (Smith 1981, Blankespoor et al. 1982, Earely 1991, Sealy 1992). 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 (Blankespoor 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 host clutches. In support of this hypothesis, Lerkelund et al. (1993) reported higher rates of unhatched eggs in enlarged clutches of the Fieldfare (Turdus pilaris). In addition, Moreno et al. (1991) found reduced hatching success in enlarged clutches of the Collared Flycatcher (Ficedula albicollis). Similarly, Peer and Bollinger (in press) found parasitic eggs were more likely to hatch in smaller clutches of the Common Grackle (Quiscalus quiscula). Thus, egg removal may increase the probability of a parasitic egg hatching in a host nest by reducing its clutch size.

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 affects 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 these 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. 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.

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, Peer and Bollinger (in press) found parasitic eggs not only had a greater chance of hatching in experimentally reduced grackle clutches, but they also had shorter incubation lengths than parasitic eggs in larger grackle clutches. Furthermore, the hatching differential between host and parasitic egg was greater in smaller clutches, possibly allowing the parasitic nestling to gain an early growth advantage over the larger grackle nestlings.

Rothstein (1975) reported most rejecter species of cowbirds eggs are larger host species, indicating an evolutionary response to prevent brood parasitism. Bronzed Cowbirds (Molothrus aeneus) and Shiny Cowbirds (Molothrus 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). Since cowbird eggs in these in nests would have more contact with the host's brood patch, egg removal may not confer an added advantage in relation to incubation efficiency. In some smaller hosts, cowbirds do not remove eggs as often as in larger hosts. Sealy (1992) reported Brown-headed Cowbirds removed a Yellow Warbler host egg from only one in three nests. Similarly, Petit (1991) found Brown-headed Cowbirds removed a Prothonotary Warbler (Protonotaria citrea) host egg 66% of the time. Conversely, cowbirds may remove host eggs more frequently in larger species (Elliott 1978, Blankespoor et al. 1982, and Roskaft et al. 1990).

In this study, I tested the incubation efficiency hypothesis in two host species of different size. One, the Red-winged Blackbird (Agelaius phoenicus), is noticeably larger than the cowbird. The other, the Chipping Sparrow (Spizella passerina) is much smaller. The objectives of this study were to determine: 1) how egg removal affects incubation efficiency of both parasitic and host eggs in host species of different sizes; 2) how egg removal affects incubation efficiency in relation to clutch size; 3) if egg removal affects incubation lengths of parasitic eggs between clutch sizes and treatments; and 4) the effect of egg removal on clutch size of host species.

Methods

Study Sites

Research was conducted at six sites in Coles 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 (Typha spp. and Salix spp.). Chipping Sparrow nests were located in three small Christmas tree farms. Scotch Pines (Pinus sylvestris) under 3 m in height comprised the majority of trees at these sites.

I 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).

I recorded when host eggs were laid and if any experimental manipulation was performed. During hatching, I 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

I performed two experimental manipulations concurrently with

Red-winged Blackbird and Chipping Sparrow clutches. The manipulations simulated strategies employed by Brown-headed Cowbird females (Payne 1977, Smith 1981, Sealy 1992). 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. I alternated between these two treatments as nests were found to achieve approximately equal sample sizes. I also tracked the progress of control nests in which no egg additions occurred.

Experimental manipulations tested whether host egg removal by a parasite: 1) decreased the incubation length of the parasitic egg, 2) increased the chance of the parasitic egg hatching in relation to clutch size, 3) adversely affected the hatching success of the host's eggs (i.e. inefficient incubation) and 4) had any effect on incubation length in the host.

Since Brown-headed Cowbirds parasitize hosts close to sunrise (Scott 1991), all clutch manipulations were performed between 0600 and 1200 CST. I manipulated clutches at the one or two egg stage to mimic cowbird strategies as closely as possible (Payne 1977). However, in early Chipping Sparrow clutches, manipulation at the one egg stage may have caused premature clutch completion at the three egg stage (although see Beuch 1982). I delayed clutch manipulation until two or three host eggs were laid in later Chipping Sparrow nests. Greater clutch size variation

was attained after the change in treatment.

Parasitic Eggs

Since I could not obtain large numbers of freshly-laid Brown-headed Cowbird eggs, I used House Sparrow (Passer domesticus) eggs in our manipulations. House Sparrow eggs resemble cowbird eggs in size and maculation (Rothstein 1977, Peer and Bollinger, in press). Brown-headed Cowbirds and House Sparrows also have similar incubation lengths of 10-13 days (Murphy 1978, Briskie and Sealy 1990, Anderson 1994).

House Sparrow eggs used in this study averaged 21.93 mm (SD = 1.01) x 15.65 mm (SD = 0.84) (N = 113). These eggs were collected from nests on the campus of Eastern Illinois University, Charleston, Illinois. House Sparrow eggs were collected daily and transported within several hours to study sites.

Brown-headed Cowbird eggs were collected whenever possible in the field. Brown-headed Cowbird eggs were removed from naturally parasitized nests of various species such as House Finches (Carpodacus mexicanus) (N = 1), Song Sparrows (Melospiza melodia) (N = 2), Red-winged Blackbirds (N = 2) and Chipping Sparrows (Spizella passerina) (N = 6) and transplanted to Red-winged Blackbird and Chipping Sparrow nests. Cowbird eggs averaged 20.16 mm (SD = 0.24) x 16.08 mm (SD = 0.20) (N = 11). Hereafter, the term "parasitic egg" refers collectively to both

House Sparrow and Brown-headed Cowbird eggs.

Outcomes

Nests were checked daily until hatching, abandonment, or nest destruction by predators. Post-hatching outcomes were not monitored in this study. 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.

Nests were considered abandoned if the eggs were not incubated on three consecutive nest checks after clutch completion (Graham 1988). A nest was classified as depredated if the eggs were suddenly absent or broken shells were found in the nest. The destruction of nests by indirect factors (cattail growth, wind damage, muskrats [Ondatra zibethicus] chewing down the vegetation supporting the nests) were also monitored.

Since most data were measured in discrete units (i.e., whole days), nonparametric tests were performed. I used one-tailed Mann-Whitney U-tests for most statistical analysis of incubation data. However, I used Wilcoxon tests to compare incubation differences within individual clutches. Chi-square tests were used to analyze incubation efficiency. In all tests, $P < 0.05$ was used to denote statistical significance.

Results

Nest Outcomes

Red-winged Blackbird Nests

From 20 April to 15 June, I monitored a total of 230 nests of the Red-winged Blackbird. Seventy six percent of the nests survived to the hatching stage (101 experimental and 74 control nests). Predation eliminated 12% of all nests (Table 1). Eighteen nests were destroyed by indirect factors such as wind/storm damage, cattail growth, muskrats, and Marsh Wrens (Cistothorus palustris). Abandonment accounted for the loss of 5 experimental and 4 control nests (Table 1).

Chipping Sparrow Nests

From 8 June to July 24, I monitored a total of 40 Chipping Sparrow nests. Seventy percent of the nests (28) reached the hatching stage (Table 1). Raccoons (Procyon lotor) and avian predators eliminated 20% of all nests. Experimental nests were abandoned on 4 instances and no control nests were abandoned. No nests were destroyed by indirect factors (Table 1).

Clutch Size

Red-winged Blackbird Nests

Experimental Red-winged Blackbird nests were divided into either addition or addition/removal treatments. The mean clutch size of addition nests was 4.5 (SD = 0.91, N = 48) and ranged from 3-5 eggs per clutch, including the parasitic egg (Table 2). Addition/removal nest clutch size averaged 3.8 eggs (SD = 0.52, N = 53) and ranged from 2-5 eggs per

clutch (Table 2). Mean clutch size for control nests was 3.6 (SD = 0.58, N = 74) with a range of 2-5 eggs per clutch (Table 2).

Experimental and control clutch sizes were significantly different (ANOVA, $F = 29.18$, $df = 2$, $P < 0.01$). The mean clutch size of addition nests was significantly greater than control (Student Newman-Keuls' Multiple-Range test, $P < 0.01$) and addition/removal nests (Student Newman-Kuels' Multiple-Range test, $P < 0.01$). No difference existed between mean clutch sizes of addition/removal and control nests (Student Newman-Kuels' Multiple Range test, $P > 0.05$).

Chipping Sparrow Nests

The mean clutch size in Chipping Sparrow addition nests was 4.2 (SD = 0.79, N = 10) ranging from 3-5 eggs per clutch, compared to addition/removal nest clutch size of 3.9 (SD = 0.67, N = 12) with a range of 3-5 (Table 2). Control nest clutch size averaged 4.2 (SD = 0.75, N = 6) with a range of 3-5 eggs (Table 2). Experimental and control clutch sizes were not significantly different (ANOVA, $F = 0.48$, $df = 2$, $P > 0.05$).

Egg Outcomes

Red-winged Blackbird Nests

In 48 addition nests, parasitic eggs hatched first in 11 nests, in 12 nests the host egg hatched first, in 7 nests the parasitic egg and a Red-winged Blackbird egg hatched simultaneously, in 16 nests the parasitic egg was inefficiently incubated, and in 2 nests the parasitic egg was

infertile (Table 3). In 53 addition/removal nests, House Sparrow eggs hatched first in 10 nests, a host egg hatched first in 17 nests, and a parasitic egg and a host egg hatched simultaneously in 4 clutches (Table 3). The parasitic egg was inefficiently incubated in 21 nests and in one nest the parasitic egg was infertile (Table 3).

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) ($X^2 = 0.326$, df = 1, $P > 0.50$). In addition/removal nests considered separately, parasitic eggs were somewhat more likely to be inefficiently incubated in clutches of ≥ 4 (46%, 19 of 41) than in clutches of ≤ 3 (18%, 2 of 11) ($X^2 = 2.86$, df = 1, $P < 0.10$). In addition nests, the percentage of inefficiently incubated parasitic eggs was not significantly different between clutches of ≤ 4 (38 %, 8 of 21) and clutches of 5 (32 %, 8 of 25) ($X^2 = 0.187$, df = 1, $P > 0.50$).

Chipping Sparrow Nests

Parasitic eggs were highly successful in Chipping Sparrow nests. In 10 addition nests, the parasitic egg hatched first in all 10 clutches (Table 3). Eight Chipping Sparrow eggs were inefficiently incubated (Table 4). The parasitic eggs hatched first in 12 of 12 addition/removal nests as well (Table 3). One infertile and 6 inefficiently incubated host eggs were recorded for these nests (Table 4). In 6 control Chipping

Sparrow nests, hatching success of host eggs was 100% (25 of 25 eggs) (Table 4).

Overall, the proportion of host eggs that were inefficiently incubated did not differ significantly in addition nests (25%, 8 of 32) and addition/removal nests (18%, 6 of 34) ($X^2 = 0.533$, df = 1, $P > 0.40$). By clutch size, no significant difference existed between inefficiently incubated host eggs in addition/removal clutches of 3 (17%, 1 of 6) and ≥ 4 (18%, 5 of 28) ($X^2 = 0.005$, df = 1, $P > 0.90$). In addition nests, Chipping Sparrow host eggs were more prone to inefficient incubation in clutches of 5 (44%, 7 of 16) than those in clutches of ≤ 4 (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) ($X^2 = 12.01$, df = 1, $P < 0.01$).

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 d, SD = 1.11, N= 31) and addition nests (11.0 d, SD = 1.09, N = 30) (Mann-Whitney U-test, U = 587.5, N = 64, $P > 0.50$). 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 (Wilcoxon test, T = 215, z = 0.043, $P > 0.05$). In addition nests, parasitic eggs hatched sooner than the mean incubation length of host eggs in the same clutch (Wilcoxon test, T = 108.5, z = 2.14, $P < 0.05$).

In addition/removal nests (Figure 1), the incubation length of all hatching parasitic eggs in clutch sizes of ≤ 3 (10.3 d, SD = 0.87, N = 9) was shorter than in clutch sizes of 4 (11.5 d, SD = 1.06, N = 21) (Kruskal-Wallis test, $X^2 = 22.71$, $P < 0.001$). In addition nests, incubation lengths for parasitic eggs in clutches of 3 (10.5 d, SD = 0.71, N = 2) were significantly shorter than those in clutches of 4 (11.1 d, SD = 0.79, N = 11) (Kruskal-Wallis test: $X^2 = 12.02$, $P < 0.05$) and 5 (11.1 d, SD = 1.34, N = 17) (Kruskal-Wallis test: $X^2 = 19.28$, $P < 0.05$) (Figure 1). The incubation length of a parasitic egg in an addition clutch size of 4 was not significantly shorter than clutches of 5 (Kruskal-Wallis test: $X^2 = 1.642$, $P > 0.05$).

<u>Chipping Sparrow Nests</u>

In experimental Chipping Sparrow clutches (Figure 2), the incubation length of parasitic eggs in addition/removal nests (10.4 d, SD = 0.51, N = 12) was virtually identical to parasitic eggs in addition nests (10.4 d, SD = 0.52, N = 10) (Mann-Whitney U-test, U = 75.5, N = 24, $P > 0.50$). Clutch size did not affect the incubation length of parasitic eggs in

addition/removal nests (Kruskal-Wallis test, $X^2 = 1.41$, $N = 12$, $P > 0.05$) or addition nests (Kruskal Wallis test, $X^2 = 1.86$, $N = 10$, $P > 0.05$).

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

Red-winged Blackbird vs. Chipping Sparrow Nests

The incubation length of all parasitic eggs in Red-winged Blackbird clutches (11.1 d, SD = 1.09, N = 61) was significantly longer than in Chipping Sparrow nests (10.4 d, SD = 0.50, N = 22) (Mann-Whitney U-test, $U = 399.5$, $N = 83$, $P < 0.05$). Incubation lengths for parasitic eggs were significantly longer in both Red-winged Blackbird addition/removal (Mann-Whitney U-test: $U = 102.5$, $N = 43$, $P < 0.05$) and addition clutches (Mann-Whitney U-test: $U = 96$, $N = 40$, $P < 0.05$) than parasitic eggs in Chipping Sparrow clutches.

Brown-headed Cowbird vs. House Sparrow Eggs

Between Red-winged Blackbird and Chipping Sparrow

experimental nests, Brown-headed Cowbird eggs hatched significantly sooner than House Sparrow eggs (Mann-Whitney U-test: $U = 4938$, $N = 144$, $P < 0.001$). In addition nests, Brown-headed Cowbird eggs had shorter incubation lengths than House Sparrow eggs (Mann-Whitney U-test: $U = 1022.5$, $N = 66$, $P < 0.001$). Brown-headed Cowbird eggs hatched significantly sooner than House Sparrow eggs in addition/removal nests (Mann-Whitney U-test: $U = 1466$, $N = 78$, $P < 0.001$).

In Chipping Sparrow experimental nests, Brown-headed Cowbird and House Sparrow eggs showed no significant difference in incubation length (Mann-Whitney U-test: $U = 118$, $N = 22$, $P > 0.05$). In Chipping Sparrow addition nests, the incubation length of House Sparrow and Brown-headed Cowbird eggs was not significantly different (Mann-Whitney U-test: $U = 17.5$, $N = 10$, $P > 0.05$). Similarly, Brown-headed Cowbird and House Sparrow incubation lengths did not differ significantly in addition/removal nests (Mann-Whitney U-test: $U = 40$, $N = 10$, $P > 0.05$). Brown-headed Cowbird eggs hatched significantly sooner than the mean incubation length of Chipping Sparrow eggs in addition/removal (Wilcoxon test: $T = 0$, $z = 1.643$, $N = 4$, $P < 0.05$) and addition clutches (Wilcoxon test: $T = 0$, $z = 1.887$, $N = 5$, $P < 0.05$).

Discussion

The incubation efficiency hypothesis predicts cowbirds remove host eggs to increase the likelihood of hatching with a decreased

incubation length in larger host species. Although some support exists for this hypothesis in large host species (Peer and Bollinger in press), my data indicate little support for this hypothesis in small and medium-sized hosts.

Egg removal did create smaller clutches in Red-winged Blackbird nests, but had no apparent effect on clutch size in Chipping Sparrow nests. In the smallest Red-winged Blackbird clutches, parasitic eggs were more likely to be efficiently incubated and had a shorter incubation length than parasitic eggs in larger clutches. However, host egg removal (i.e. the addition/removal treatment) did not result in increased hatching efficiency or decreased incubation length of parasitic eggs.

In Chipping Sparrow nests, parasitic eggs were extremely successful, regardless of treatment or clutch size. Furthermore, the presence of parasitic eggs adversely affected host eggs, resulting in decreased hatching success of Chipping Sparrow eggs. However, removal of host eggs did not significantly reduce the incubation length of parasitic eggs or significantly increase their hatching success.

Parasitic Eggs

In a large host species, the Common Grackle, Peer and Bollinger (in press) reported a mean incubation length of 13.4 days for House Sparrow eggs. I report an incubation length of 11.1 and 10.5 days for all House Sparrow eggs in Red-winged Blackbird and Chipping Sparrow nests, respectively. Although my incubation lengths are shorter compared

to Peer and Bollinger (in press), they are comparable to typical incubation lengths (10-12.2 d) reported for House Sparrows in their own nests (Sappington 1977, Murphy 1978, Anderson 1994).

Brown-headed Cowbirds are known to have an incubation length of 10-13 days (Nice 1953, Friedmann 1963, Rothstein 1975, Briskie and Sealy 1990). Hofslund (1957) recorded a mean incubation length of 11.6 days for cowbird eggs. Petit (1991) found cowbird eggs hatched after 11-12 days in Prothonotary Warbler nests. Similarly, Peer and Bollinger (in press) reported an incubation length of 12.1 days for cowbird eggs in Common Grackle nests. Average incubation lengths for cowbird eggs in all Red-winged Blackbird and Chipping Sparrow nests were 10.5 and 10.3 days, respectively.

Although Brown-headed Cowbird eggs had shorter incubation lengths compared to House Sparrow eggs, House Sparrow eggs showed a similar trend in incubation length when compared to clutch size. Peer and Bollinger (in press) found the same trend for House Sparrow and Brown-headed Cowbird eggs in the nests of Common Grackles. Thus, House Sparrow eggs appear to be an adequate substitute for Brown-headed Cowbird eggs in incubation studies.

Host Incubation Efficiency Hypothesis

Davies and Brooke (1988) proposed that brood parasites, like cuckoos (Cuculus canorus), remove eggs to prevent the total clutch size

from exceeding the host female's ability to incubate an enlarged clutch. They found a greater number of Reed Warbler (Acrocephalus scirpaceus) eggs were inefficiently incubated in nests when a parasitic egg model was added, but no host eggs removed, compared to nests when one or more host eggs were removed. Thus, enlarged clutches may reduce the incubation efficiency of parasitic eggs in some instances.

Several studies have used artificial or natural parasitic eggs to determine the effects of host size on parasitic eggs. Peer and Bollinger (in press) tested the host incubation efficiency hypothesis in a large host species and found some support. Using House Sparrow and Brown-headed Cowbird eggs in nests of Common Grackles, they reported parasitic eggs in clutches of $\leq$ 3 had a shorter incubation length (12.9 d) than clutches of 4 (13.6 d) or $\geq$ 5 (13.9 d). Furthermore, parasitic eggs in smaller clutches were inefficiently incubated only 6% of the time, compared to 20% in larger clutches.

Several authors have shown that enlarged clutches experienced decreased hatching success and increased incubation length. Moreno et al. (1991) reported decreased hatching success in enlarged clutches of the Collared Flycatcher (Ficedula albicollis), although incubation length was not increased. In the Fieldfare (Turdus pilaris), Lerkelund et al. (1993) found an 8% reduction in relative hatching success in experimentally enlarged clutches. Furthermore, they reported eggs in larger clutches

were often damaged due to handling (e.g. turning the eggs) and lack of space in the nest. Wicklund (1985) also found enlarged clutches in the Fieldfare had decreased hatching success. Thus, by reducing clutch size through egg removal, damage to the parasitic egg may be reduced.

However, other studies with experimentally enlarged clutches found no difference in the frequency of hatching success. Baltz and Thompson (1988) found that House Wrens (Troglodytes aedon) successfully incubated enlarged clutches, although incubation length increased by 0.6 d compared to control clutches. Similarly, Smith (1989) experimentally enlarged clutches of Blue Tits (Parus caeruleus) and reported no difference in hatching success compared to control clutches. Again, enlarged clutches required an average of 11.6 h (or 4%) more incubation time than control clutches (Smith 1989). Moreno and Carlson (1989) also reported increased incubation length in experimentally enlarged clutches of Pied Flycatchers (Ficedula hypoleuca). Since enlarged clutches experience reduced hatching success or increased incubation length, egg removal by cowbirds may serve to reduce clutch size and hence increase its egg's chances of hatching sooner, especially in larger host species.

The impact of egg removal on medium/large-sized host species often results in decreased clutch size, allowing cowbird eggs to hatch sooner than host eggs. Zimmerman (1983) reported significantly smaller

numbers of host eggs (2.4 eggs) in parasitized Dickcissel (Spiza americana) nests than unparasitized nests (4.0 eggs). In parasitized Red-winged Blackbird nests, the number of host eggs/nest was significantly smaller than in unparasitized clutches (3.1 eggs versus 4.2 eggs) (Weatherhead 1989). I report a mean control clutch size of 3.6 eggs compared to 3.5 and 2.8 host eggs/nest respectively for addition and addition/removal treatments. Furthermore, parasitic eggs in smaller clutches had shorter incubation lengths than in larger clutches.

The negative effects of cowbird parasitism on smaller host species has been well documented (Hofslund 1957, Mayfield 1960, Rothstein 1975, Wolf 1987, Sedgwick and Knopf 1988, Marvil and Cruz 1989, Weatherhead 1989, Petit 1991, and Sealy 1992). Egg removal may have two important effects on smaller host species: reduced clutch size and decreased hatching success of host eggs. Marvil and Cruz (1989), for example, reported significantly smaller numbers of host eggs in parasitized Solitary Vireo (Vireo solitarius) nests (parasitized = 2.2; unparasitized = 3.7), as well as significantly lower host hatching success. In the Dark-eyed Junco (Junco hyemalis), Wolf (1987) also found parasitized clutches (3.0 eggs) were significantly smaller than unparasitized nests (3.3 eggs). Petit (1991) found reduced host clutch sizes in early and late parasitized Prothonotary Warbler nests. In addition, 27% of parasitized nests had unhatched host eggs compared to only 10.7% of unparasitized nests.

Parasitized Yellow Warbler nests had a host clutch size of only 3.7 eggs versus 4.6 eggs in unparasitized clutches (Weatherhead 1989, but see Burgham and Picman 1989).

I found no significant reduction in clutch size due to egg removal in Chipping Sparrow nests, but 21% of host eggs were inefficiently incubated. Similarly, Hofslund (1957) reported 15% of host eggs in the Common Yellowthroat (Geothlypis trichas) were inefficiently incubated. He speculated that the presence of the larger Brown-headed Cowbird eggs caused the inefficient incubation of smaller Common Yellowthroat eggs in the same nest.

Thus, removal of host eggs in smaller host species may serve to reduce the overall clutch size and decrease host hatching success. The larger cowbird egg causes the inefficient incubation of the smaller host eggs due to heat shielding, much as cowbird eggs have reduced contact with the brood patch of a larger host (Wiley 1985). The removal of host eggs may reduce nestling competition and allow the cowbird nestling to receive more parental care (Scott 1977, Blankespoor et al. 1982, Zimmerman 1983, and Wolf 1987).

The pattern of incubation length decreasing in relation to host size provides some support for the incubation efficiency hypothesis. Larger hosts lay clutches with larger eggs, i.e. with greater volume, thus the smaller parasitic egg would receive less heat, resulting in increased

incubation length or inefficient incubation. 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 incubation length or hatching success, the removal of smaller host eggs, may serve to reduce nestling competition.

Incubation Efficiency in Other Cowbird Species

Shiny Cowbirds (Molothrus bonariensis) parasitize a wide variety of hosts, including the Greater Antillean Grackle (Quiscalus niger), which is larger than the Shiny Cowbird. Wiley (1985) found that hatching success of Shiny Cowbird eggs was lower in Greater Antillean Grackle nests than in smaller host species. Wiley (1985) suggested the inefficient incubation of parasitic eggs was probably due to heat shielding by the larger host eggs, which decreased direct contact with the female's brood patch.

However, some cowbirds are able to hatch efficiently in the nests of larger hosts. In an uncommon, but large host species for Brown-headed Cowbirds, the Yellow-headed Blackbird (Xanthocephalus xanthocephalus), Ortega and Cruz (1991) reported 47% of cowbird eggs were effectively incubated by host females, while only 17% of eggs were inviable (e.g. infertile or inefficiently incubated), with 36% of parasitic eggs lost to predators.

Host Egg Removal

The adaptive significance of host egg removal by Brown-headed Cowbirds has yet to be determined. 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, since the female's brood patch cannot cover all the eggs efficiently (Klomp 1970). This results in the host female leaving the nest to increase her nutritional intake in response to artificially increased incubation requirements (Biebach 1984, Hafthorn and Reinertsen 1985). The absence of the female from the nest can lead to increased predation or reduction in fledgling success (Zimmerman 1983).

I found little direct support for the incubation efficiency hypothesis in a medium and small host species, with the exception of reduced clutches in Red-winged Blackbirds. 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 large host species(e.g. the Common Grackle-see Peer and Bollinger, in press), this strategy appears to have little adaptive value in relation to medium and small host species.

However, cowbirds do remove eggs from the nests of many

small and medium-sized hosts. The host deception hypothesis is not a likely explanation since many species accept cowbird eggs equally well regardless of whether or not one their own eggs has been removed (Rothstein 1975, Rothstein 1986). However, removal of too many host eggs may cause abandonment or risk of injury to the female cowbird. Cowbirds have been observed removing and eating host eggs, although approximately 40% of all removed host eggs were not eaten (Scott et al. 1992).

The host incubation limit hypothesis suggests that removal of host eggs increases hatching success and has received some support (Davies and Brooke 1988). If parasitic and host eggs are of approximately equal size, this hypothesis seems appropriate. If host egg sizes are larger, the incubation efficiency hypothesis appears to offer a clear explanation of host egg removal (Peer and Bollinger, in press). Neither of these hypotheses explain why cowbirds remove eggs from the nests of smaller host species.

The removal of host eggs may reduce the number of potential nestlings with which the nestling cowbird would compete for resources (Blankespoor et al. 1982). The elimination of one or more host eggs by the cowbird female would clearly increase the chance of her own nestling monopolizing parental care, especially since cowbird nestlings do not evict their nestmates.

Brown-headed Cowbirds have undergone a dramatic expansion of their breeding range in the last several hundred years (Mayfield 1965, Brittingham and Temple 1983, May and Robinson 1985). Many new host species have been parasitized by Brown-headed Cowbirds in that period. Although host egg removal may have been a necessity in the past, cowbirds may be removing host eggs without any present adaptive value.

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TABLE 1. Outcomes for all Red-winged Blackbird and Chipping Sparrow nests. Number in parantheses indicates percentage of total nests.

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

TABLE 2. Mean overall clutch size (including parasitic egg) and number of nests per clutch size for experimental and control Red-winged Blackbird and Chipping Sparrow nests.

Nest type	n	mean clutch size	Clutch size (with parasitic egg) 2	3	4	5
Red-winged Blackbird						
-experimental						
+1	48	4.5	0	4	18	26
+1/-1	53	3.8	1	10	40	2
-control	74	3.6	2	24	46	2
Chipping Sparrow						
-experimental						
+1	10	4.2	0	2	4	4
+1/-1	12	3.9	0	3	7	2
-control	6	4.2	0	1	3	2

TABLE 3. The hatching success of parasitic eggs in experimental nests of Red-winged Blackbird and Chipping Sparrow nests was divided into five categories: 1) parasitic egg hatched first (parasitic 1st), 2) the host egg (s) hatched first, but the House Sparrow egg did hatch (host 1st), 3) a House Sparrow egg and the first Red-winged Blackbird egg hatched simultaneously (simult.), 4) parasitic egg was inefficiently incubated, and 5) parasitic egg was infertile (infertile).

Species	n	parasitic 1st	host 1st	simult.	ineff. incub.	infertile
Red-winged Blackbird						
+1*	48	11	12[a]	7	16	2
+1/-1#	53	10	17[b]	4	21	1
Chipping Sparrow						
+1*	10	10	0	0	0	0
+1/-1#	12	12	0	0	0	0

* Indicates addition nest experimental group

\# Indicates addition/removal experimental group

[a] Host Red-winged Blackbird eggs also hatched first in 16 nests but the House Sparrow eggs were inefficiently incubated and 2 nests when the House Sparrow eggs were infertile.

[b] Host Red-winged Blackbird eggs also hatched first in 21 nests but the House Sparrow eggs were inefficiently incubated and 1 nest when the House Sparrow egg was infertile.

TABLE 4. Host egg outcomes were classified in three categories: hatched, inefficiently incubated or infertile for Red-winged Blackbird and Chipping Sparrow clutches. The total number of eggs are listed for each category.

Species	n	hatch	inefficient incubation	infertile
Red-winged Blackbird				
-experimental				
+1	166	165	0	1
+1/-1	150	146	4	0
-control	269	260	9	0
Chipping Sparrow				
-experimental				
+1	32	24	8	0
+1/-1	35	28	6	1
-control	25	25	0	0

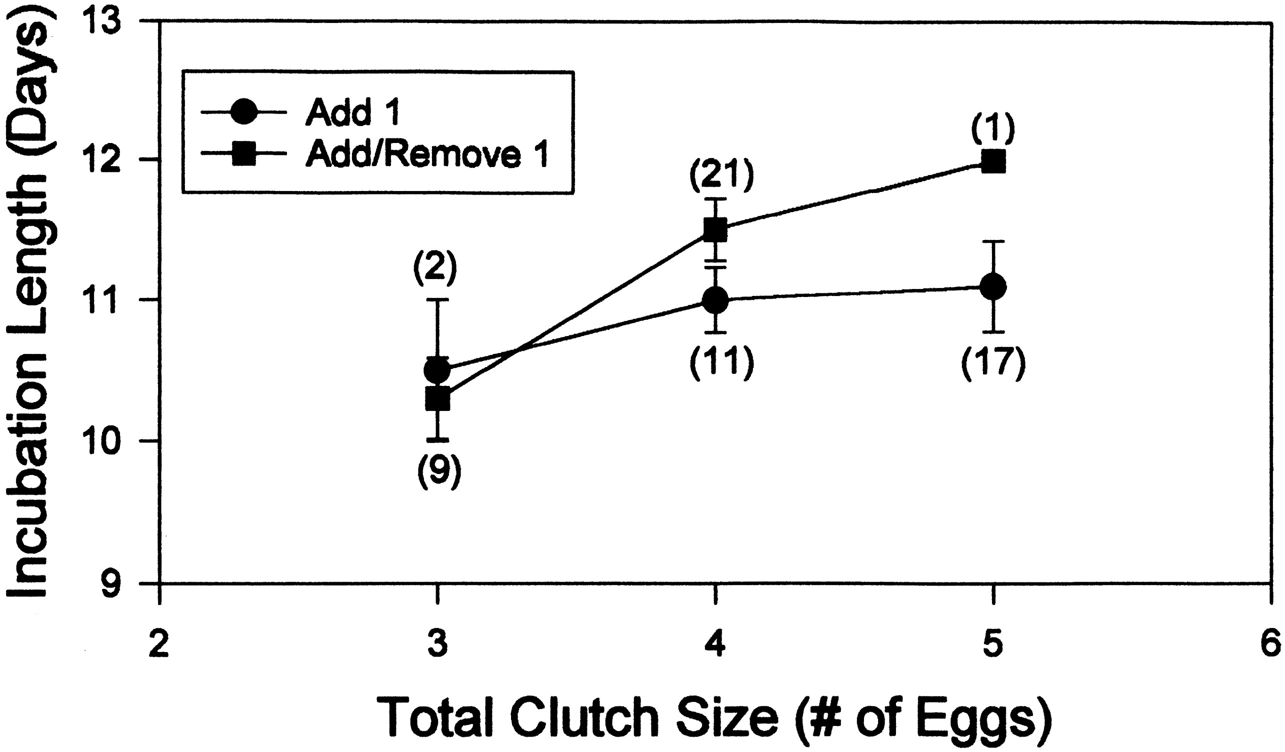

Figure 1. Parasitic egg incubation length in addition/removal and addition Red-winged Blackbird nests. Numbers in parantheses represent sample sizes; standard error bars included.

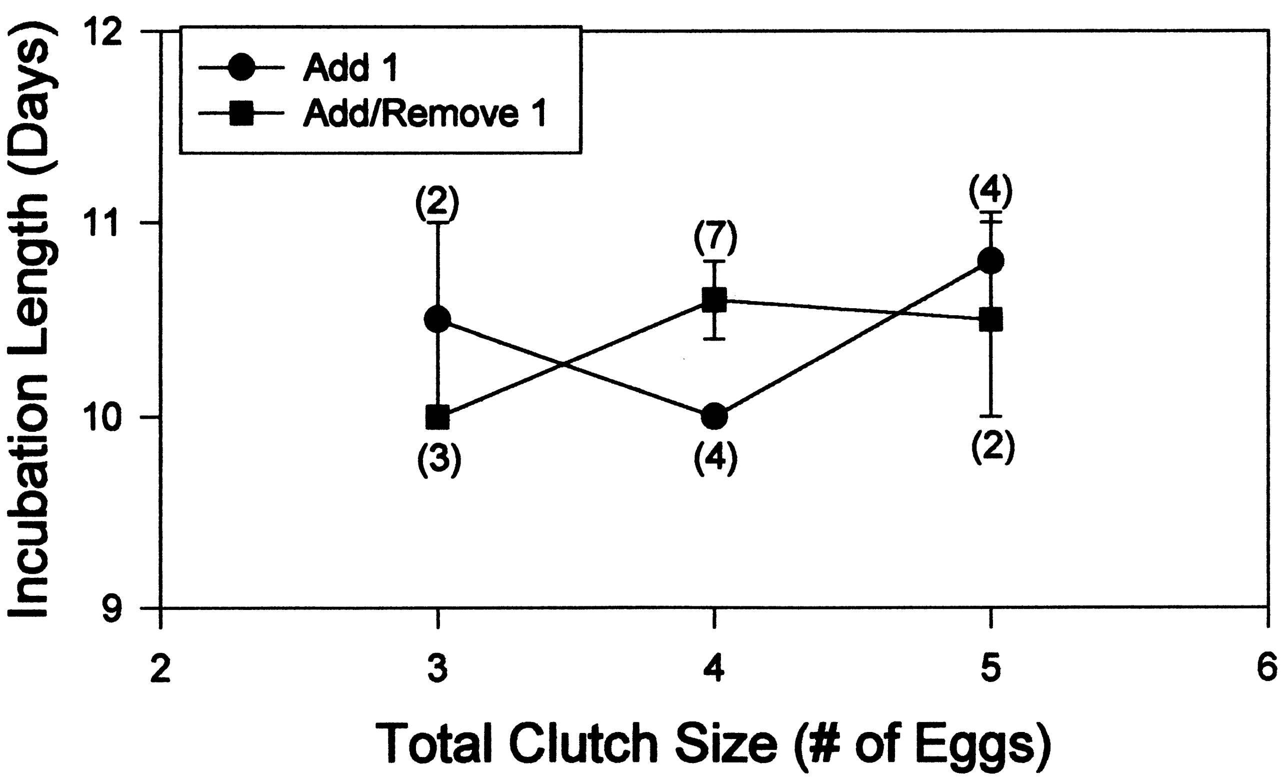

Figure 2. Parasitic egg incubation length in addition/removal and addition Chipping Sparrow nests. Numbers in parantheses represent sample sizes; standard error bars included.