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# HOST-EGG REMOVAL BY BROWN-HEADED COWBIRDS: A TEST OF THE HOST INCUBATION LIMIT HYPOTHESIS

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ABSTRACT.—The incubation limit hypothesis (Davies and Brooke 1988) states that female brood parasites remove host eggs to reduce the parasitized clutch volume to a size that the host can incubate effectively, thereby ensuring that the parasite's eggs will hatch. We tested this hypothesis by adding freshly laid Brown-headed Cowbird (*Molothrus ater*) eggs to Yellow Warbler (*Dendroica petechia*) clutches and comparing hatching success in clutches from which one or no host eggs were removed (Treatments 1 and 2, respectively). Hatching success of cowbird eggs differed significantly between Treatments 1 and 2 in one of the three years of study. Warbler hatching success tended to be higher in control and in Treatment 1 clutches than in Treatment 2 clutches. Climatic conditions varied between years but did not influence cowbird hatching success. Cowbird eggs tended to hatch before warbler eggs whether or not a host egg was removed. Neither incubation period, hatching spread, nor hatching order was significantly influenced by egg removal. These results indicate that removal of a host egg is not necessary for successful hatching of cowbird eggs in Yellow Warbler clutches in all years, although it may increase hatching success in some years. *Received 15 May 1996, accepted 18 October 1996.*

FEMALES OF MANY avian brood parasites remove host eggs from nests during the breeding season. These eggs usually are those of the host, and they are removed in association with the laying of the parasite's own egg (Sealy 1992). Egg removal reduces the number of host offspring that can be raised, and numerous workers have suggested that this behavior may increase the parasite's reproductive success (Davies and Brooke 1988, Rothstein 1990). Brown-headed Cowbird (*Molothrus ater*; hereafter cowbird) eggs have been found in the nests of more than 220 host species, and cowbird young have been raised successfully by at least 140 host species (Friedmann and Kiff 1985). Female cowbirds generally remove eggs from host nests (Friedmann 1963), but the number of eggs removed and the timing of egg removal vary among host species (e.g. Mayfield 1961, Zimmerman 1963, Sealy 1992). The fact that cowbirds make additional visits to nests to remove host eggs (Scott et al. 1992, Sealy 1994) and, in doing so, increase the risk of encountering hosts, suggests that egg removal is an important cowbird strategy.

Sealy (1992) reviewed six hypotheses to explain the function of host-egg removal by female brood parasites and suggested that the incubation limit hypothesis (Davies and Brooke 1988) was the most deserving of further testing. The host incubation limit hypothesis proposes that the addition of a parasitic egg could increase clutch size above that which the host can incubate effectively (Hofslund 1957, Friedmann 1963, Post 1981, Fraga 1983, Kendra et al. 1988). Incubating females must use more energy to maintain egg temperature in large clutches (Biebach 1981, Moreno et al. 1991), but because the amount of heat energy that can be produced and transferred to the clutch is limited physiologically (Tøien 1989), egg temperatures may fall as clutch size increases (Batt and Cornwell 1972, Mertens 1977). Because most bird eggs must be maintained within a narrow range of temperatures for normal embryonic development (Webb 1987), extended cooling may reduce the hatching success of both host and parasitic eggs (Wyllie 1975, Davies and Brooke 1988). By removing a host egg, the female parasite may reduce the total clutch size to within the host's incubation limit, and possibly increase the probability that the parasite's own egg will hatch (Davies and Brooke 1988). Hofslund (1957) calculated that the addition of one cowbird egg to a Common Yellowthroat (*Geothlypis trichas*) clutch of four eggs increased the volume by 50%. Therefore, removing a host egg would appear to be especially important when cowbirds parasitize species whose eggs are smaller than cowbird eggs.

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We tested the host incubation limit hypothesis by placing live cowbird eggs into nests of a commonly parasitized host species, the Yellow Warbler (*Dendroica petechia*). We predicted that cowbird eggs would have higher hatching success in clutches from which one host egg had been removed than in clutches where no host eggs had been removed. We assumed that differences in egg size between host and cowbird eggs would not affect the amount of heat each egg received (Huggins 1941). Therefore, we predicted that warbler eggs would have higher hatching success in parasitized clutches from which a host egg had been removed than in clutches where no host eggs had been removed. We predicted this even though Yellow Warbler eggs are 33% smaller in volume (Sealy 1992), and may have different temperature tolerances, than cowbird eggs (see Groebbels and Möbert 1930, Graber 1955, Webb 1987). Inefficient transfer of heat to eggs in enlarged clutches also may prolong incubation (Smith 1989), increase hatching asynchrony (Slagsvold 1982, Moreno and Carlson 1989, Hébert and Sealy 1992), and reduce hatching success and survival of young (Hills 1980, Kendra et al. 1988, Evans 1990, Moreno et al. 1991). Therefore, we also predicted that in enlarged clutches from which no host egg was removed, eggs should have longer incubation periods and hatch more asynchronously.

In addition to the incubation limit hypothesis, four alternative (but not necessarily mutually exclusive) hypotheses could explain the function of host-egg removal by cowbirds. The nature of our study did not allow us to test the predictions of two of these hypotheses (i.e. females remove eggs to eat them [Scott et al. 1992] or to reduce competition for the cowbird nestling [Mayfield 1960, Blankespoor et al. 1982]). Moreover, we did not test whether egg removal reduces the potential for egg wear and breakage in large clutches (Lerkelund et al. 1993) because of the difficulty in distinguishing between the host removing damaged eggs or nestlings that died soon after hatching, and partial predation. We were able, however, to test the predictions of the remaining alternative hypothesis. Berger (1951) suggested that by removing a host egg early in the laying period, female cowbirds eliminate one of the host nestlings that would hatch first, thereby ensuring that the cowbird chick hatches first and gains a competitive advantage. Consequently, we examined whether cowbird eggs were more likely to hatch first in clutches where the first-laid host egg had been removed than in those where no host egg had been removed.

## METHODS

*Experimental procedures.*—In 1992, 1993, and 1995 Yellow Warbler nests were found in the forested dune ridge at Delta Marsh (50°11′N, 98°19′W) on the properties of the University of Manitoba Field Station and Portage Country Club (see MacKenzie 1982). At Delta Marsh, Yellow Warblers are common and are frequently parasitized by cowbirds (long-term average 21% of nests parasitized, Sealy 1992) and, thus, are ideal for this study. Nests found before clutch initiation were monitored daily until the first egg was laid (laying day 1 = LD1). On LD1, one of three treatment groups was assigned at random to each nest to test possible manipulation of host incubation behavior by cowbirds. Treatment 1 consisted of switching one viable cowbird egg for one warbler egg. In Treatment 2, a single cowbird egg was added, but the host egg was not removed. Yellow Warblers often bury cowbird eggs laid before LD2 (Clark and Robertson 1981) but generally not in experimentally parasitized nests (Sealy 1995). Treatment 3 (hereafter Control) was a control where cowbird eggs were neither added nor host eggs removed. Most cowbird eggs were added on the morning of LD1 (0700 to 1100 CST), although some eggs were added later in the afternoon of LD1 (1200 to 1300). Because Yellow Warblers spend little time incubating until LD 3 or 4 (Hébert and Sealy 1992, McMaster unpubl. data), eggs added in the afternoon of LD1 would have missed little (if any) incubation. Late in the season, when cowbird eggs were in short supply, some cowbird eggs were added as late as LD3. Cowbird eggs added after LD1 were used only for calculation of hatching success. Daily nest checks continued until the host finished laying.

Freshly laid cowbird eggs were obtained from naturally parasitized nests of six different species in the Delta Marsh area. Only freshly laid cowbird eggs that had been exposed to minimal incubation (i.e. were laid during early egg laying, or preferably before the host's clutch was initiated) were used in the experiment. If possible, cowbird eggs were added to Yellow Warbler clutches on the same day they were collected. If no warbler clutches were available for parasitism, eggs were kept overnight in a refrigerator at 10°C. Cool temperatures arrest embryonic development and allow the embryo to remain viable longer (Drent 1975). In 1995, additional cowbird eggs were obtained from wild females that were held in captivity for up to three nights.

The modal clutch size of Yellow Warblers at Delta Marsh is five eggs (Sealy 1992), although four-egg clutches are also common, especially later in the breeding season (Goossen and Sealy 1982). When nests were experimentally parasitized on LD1, it was impossible to know whether the female would lay four or five eggs. Therefore, to keep the number of host eggs constant, freshly laid host eggs from other nests were transferred to complete four-egg clutches to ensure that all nests had five eggs. When necessary, extra warbler eggs were added the day after the last warbler egg was laid (because we could not know whether the "last egg" was indeed the last egg until the next day). Fewer than 25% of clutches within the three treatment groups required extra warbler eggs.

All cowbird eggs were measured. In 1992, all Yellow Warbler eggs were numbered and measured once the clutch was complete. Cowbird and Yellow Warbler egg volumes were calculated using the formula:

$$V = kLB^2, \quad (1)$$

where $k = 0.515$ for cowbird eggs and $k = 0.497$ for Yellow Warbler eggs (Hoyt 1979, Mills 1987). Clutch volumes were then compared between each treatment group. Yellow Warbler eggs were not measured in 1993 or 1995.

During the incubation period in 1992, nests were checked every other day as part of another study, but in 1993 and 1995 nests were checked only once midway through the incubation period to minimize predation. Nest checks were renewed the day before the eggs were expected to begin hatching and continued daily until all eggs hatched. Cowbird and warbler eggs that remained unhatched for several days after the other eggs had hatched were removed and opened to record the stage of embryonic development. Egg contents were examined with the unaided eye for signs of an embryo. Because embryonic mortality may occur before an embryo is visible, all eggs that did not hatch were recorded as hatching failures, even when no embryo was apparent.

Incubation period was defined as the interval from the day of clutch completion to the day the first nestling hatched (see Moreno and Carlson 1989, Sanz 1996), calculated whether or not the cowbird egg hatched. This is a minimum measure of incubation period that differs from the usual measure (i.e. the time from the laying of the last egg to hatching of the last young, Nice 1954). However, our measure controls for changes in female incubation behavior (e.g. increased foraging at the expense of incubating) that could be caused by the short incubation period of the cowbird (Briskie and Sealy 1990). Hatching order was recorded as synchronous if both a warbler and cowbird nestling had hatched since the previous nest visit. If only one nestling was present, its identity was determined and hatching order was recorded accordingly. Hatching spread was the interval between the first- and last-hatched nestlings (Hébert and Sealy 1992). Only nests where the cowbird nestling and 75% or more of the Yellow Warbler nestlings hatched, and were not depredated, were used in the analysis of hatching spread. Cowbird eggs added to clutches after LD1 were not included in the calculation of either incubation period or hatching spread.

*Data analyses.*—Data were first tested for normality using the Kolmogorov-Smirnov test. Data from 4- and 5-egg clutches were examined separately when sample sizes were large enough and were combined if found to be statistically equal. Clutch volumes were compared among treatments using ANOVA. Within a clutch, individual Yellow Warbler eggs are not independent data points. Therefore, the proportion of Yellow Warbler eggs hatching successfully was calculated for each nest and compared among treatments using ANOVA with Bonferroni $t$-tests ($P < 0.05$) for multiple comparisons. Nests from which warbler eggs disappeared were not included in the analyses. Cowbird hatching success was compared among treatments using Fisher exact tests. Because incubation period, hatching spread, daily precipitation, and daily anemometer readings were not normally distributed, differences among treatments for these variables were analyzed using Kruskal-Wallis tests. When Kruskal-Wallis indicated significant differences among treatments, we conducted multiple comparisons (Student-Neuman-Keuls test).

The experiment was replicated over three breeding seasons, which introduced the possibility that annual variability in weather, prey density, etc. could influence hatching success. To ascertain if weather differed among years, the mean daily temperature deviation from the long-term average was calculated for each day of the breeding season by subtracting the mean daily ambient temperature (recorded at the Delta Marsh Meteorological Station) from the 30-year mean temperature for that day (1951–1981; Environment Canada 1988). The mean daily temperature deviations from the long-term average were added together to give a running deviation from the 30-year average temperature for each breeding season (see Myers and Pitelka 1979).

Logistic regression analysis (using the Wald statistic; Kleinbaum 1992) was used to determine if potential confounding variables influenced cowbird hatching success among years. Two models were employed, each with cowbird hatching success as the dependent variable. Data for all years were combined and analyzed using the first model (Combined Years Model), with the covariates being treatment, nest location (to control for differences among nests in exposure to prevailing north winds), the deviation of cumulative temperature from the 30-year average (during the laying, incubation, and both periods combined), and year. Data for 1992, 1993, and 1995 were analyzed separately for the second model (Individual Years Model) as above, except that the covariate year was dropped from the model.

## RESULTS

*Hatching success.*—In 1992, clutch volume differed significantly among treatments ($F = 60.58$, $P < 0.0001$; Control, $\bar{x} = 7.17$ ml, $n = 22$; Treat-

TABLE 1. Yellow Warbler hatching success (proportion [$\bar{x}$ ± SE] of warbler eggs hatched per nest) by year and treatment. Number of nests in parentheses.

| | Treatment | | | |
|---|---|---|---|---|
| Year | Control | One host egg removed, one cowbird egg added | No host egg removed, one cowbird egg added | $F$ ($P$)[a] |
| 1992 | 0.95 ± 0.04 (12) | 0.83 ± 0.04 (18) | 0.73 ± 0.06 (8) | 4.83 (0.01) |
| 1993 | 0.87 ± 0.03 (20) | 0.80 ± 0.07 (14) | 0.72 ± 0.05 (5) | 1.34 (0.27) |
| 1995 | 0.91 ± 0.04 (30) | 0.97 ± 0.02 (19) | 0.86 ± 0.07 (10) | 1.28 (0.29) |
| Total | 0.90 ± 0.02 (62) | 0.88 ± 0.03 (51) | 0.78 ± 0.04 (23) | 3.40 (0.04) |

[a] $F$-statistic comparing hatching success among the treatments within each year.

ment 1, $\bar{x}$ = 8.57 ml, $n$ = 29; Treatment 2, $\bar{x}$ = 9.91 ml, $n$ = 18). Yellow Warbler hatching success differed significantly among treatments in 1992, but not in 1993 or 1995 (Table 1). In 1992, warbler hatching success was significantly higher in control clutches than in clutches from which no warbler eggs were removed ($P < 0.05$). Warbler hatching success was higher in clutches from which one warbler egg had been removed than in clutches from which no egg had been removed in 1992, but the difference was not significant ($P > 0.05$). Although Yellow Warbler hatching success did not differ significantly among treatments in 1993, the trend was similar to that in 1992, with hatching success increasing as clutch volume decreased (Table 1). When all three years of warbler hatching data were pooled, control clutches had significantly higher hatching success ($P < 0.05$) than clutches where no host egg was removed (Table 1).

In 1992, cowbird hatching success was significantly higher in clutches where one host egg was removed than where no host eggs were removed (Table 2). However, treatment did not influence cowbird egg hatching success in 1993 or 1995, nor did a significant difference exist between treatments when the data were combined among years (Table 2).

Most cowbird eggs hatched either before or on the same day that the first warbler egg hatched (Table 3). Because hatching order did not differ among the three years ($\chi^2 = 3.59$, df = 4, $P = 0.46$), data were combined by treatment. The hatching order of parasitized clutches for the three years was not significantly influenced by treatment ($\chi^2 = 2.57$, df = 2, $P = 0.28$; see Table 3). Therefore, host-egg removal did not promote hatching of cowbird eggs before warbler eggs.

TABLE 2. Brown-headed Cowbird hatching success (% of eggs hatched) by year and treatment. Number of eggs in parentheses.

| | Treatment | | |
|---|---|---|---|
| Year | One host egg removed, one cowbird egg added | No host egg removed, one cowbird egg added | $P$[a] |
| 1992 | 75.0 (28) | 30.8 (13) | 0.014 |
| 1993 | 75.0 (20) | 75.0 (16) | 1.0 |
| 1995 | 86.4 (22) | 89.5 (19) | 1.0 |
| Total | 78.6 (70) | 68.8 (48) | 0.283 |

[a] Fisher exact test comparing hatching success between treatments within each year.

Neither treatment, year, nor treatment × year interaction significantly influenced incubation period (Table 4). Treatment did not have a significant effect on hatching spread, but both year and treatment × year covaried significantly with hatching spread (Table 5). Hatching spreads were significantly shorter in 1995 ($\bar{x}$ = 1.85, $n$ = 61) than in 1992 ($\bar{x}$ = 2.61, $n$ = 38) or 1993 ($\bar{x}$ = 2.72, $n$ = 43; Student-Neuman-Keuls test, $P < 0.05$).

*Weather.*—1995 was much warmer than either 1992 or 1993 (Fig. 1). Neither the median amount of precipitation ($H = 1.82$, df = 2, $P = 0.402$) nor wind ($H = 4.87$, df = 2, $P = 0.087$) differed significantly among years (Table 6).

*Logistic regression.*—Combined across years, only year successfully predicted cowbird hatching success (see Table 7; Wald = 7.42, df = 1, $P = 0.0064$; model $\chi^2 = 8.12$, df = 1, $P = 0.0044$; $n$ = 110). Subsequent tests blocking by year re-

TABLE 3. Hatching order (% of cases, $n$ in parentheses) of Brown-headed Cowbird and Yellow Warbler eggs in parasitized nests. Data are combined across years.

| | Species hatching first | | |
|---|---|---|---|
| Treatment | Cowbird | Warbler | Synchronous[a] |
| One warbler egg removed | 44.2 (23) | 13.5 (7) | 42.3 (22) |
| No warbler egg removed | 54.8 (17) | 3.2 (1) | 41.9 (13) |

[a] Clutches where cowbirds and warblers hatched at approximately the same time.

TABLE 4. Incubation period ($\bar{x}$ ± SE in days, $n$ in parentheses) of experimentally parasitized Yellow Warbler clutches.[a]

| Year | Treatment |  |  |
|---|---|---|---|
|  | Control | One host egg removed, one cowbird egg added | No host egg removed, one cowbird egg added |
| 1992 | 11.11 ± 0.31 (9) | 10.65 ± 0.21 (23) | 11.23 ± 0.20 (13) |
| 1993 | 10.85 ± 0.24 (13) | 11.33 ± 0.22 (14) | 10.69 ± 0.24 (15) |
| 1995 | 10.56 ± 0.10 (34) | 10.75 ± 0.14 (20) | 10.33 ± 0.16 (21) |

[a] Year comparison, $H = 2.44$, $P = 0.12$; treatment comparison, $H = 1.08$, $P = 0.343$; treatment × year interaction, $H = 1.74$, $P = 0.161$.

vealed that treatment in 1992 (Wald = 3.79, df = 1, $P = 0.051$) and cumulative temperature during the laying period in 1993 (Wald = 3.47, df = 1, $P = 0.062$) were related to cowbird hatching success. However, neither the 1992 nor 1993 model explained much variation in cowbird hatching success (model $\chi^2 = 4.006$, df = 1, $P = 0.045$, $r^2 = 0.038$, $n = 35$; model $\chi^2 = 3.82$, df = 1, $P = 0.051$, $r^2 = 0.042$, $n = 34$, respectively). No variable was a significant predictor of cowbird hatching success in 1995.

## DISCUSSION

*Variation in hatching success among years.*—The removal of a single Yellow Warbler egg at the time of experimental brood parasitism increased the hatching success of cowbird eggs in only one of three years. Yellow Warbler hatching success tended to be higher in clutches from which one host egg was removed than in clutches where no host egg was removed in two of three years, but the differences were not significant. Over the three years combined, Yellow Warbler hatching success was higher in control clutches than in clutches from which no host egg was removed, which suggests that the ability of the host to incubate all eggs effectively is compromised at large clutch sizes. Although these results are equivocal, they are consistent with the predictions of the incubation limit hypothesis.

Two previous studies have provided indirect support for the host incubation limit hypothesis (Davies and Brooke 1988; Peer and Bollinger 1997, 1998). These studies differed from ours in that (1) artificial parasitic eggs were used instead of live eggs (Davies and Brooke 1988), and (2) live eggs of a nonparasitic species (House Sparrow [*Passer domesticus*]) were used to supplement cowbird eggs placed in nests of a host species (Common Grackle [*Quiscalus quiscula*]) whose eggs are larger than those of the Brown-headed Cowbird (Peer and Bollinger 1998). These results (including our own) suggest that the addition of a parasitic egg increases the clutch to a volume that the host cannot incubate effectively, and that host-egg removal is important to ensure successful hatching of parasitic eggs. Moreover, egg removal may improve hatching success of parasitic eggs when hosts lay large eggs (Peer and Bollinger 1998) but be of lesser importance when hosts lay small eggs (this study). Perhaps due to their size, cowbird eggs in clutches with small eggs contact the host female's incubation patch continuously, which makes egg removal not as crucial for successful incubation. If true, then the hatching success of cowbird eggs may be influenced by both the size and the number of host eggs (Peer and Bollinger 1998).

The factors that resulted in variation in hatching success among years in our study are not known. Contrary to other studies (e.g. Järvinen and Väisänen 1983, Webb 1987, Siikamäki 1995), neither variation in ambient temperature among years nor nest location influenced the hatching

TABLE 5. Hatching spread ($\bar{x}$ ± SE in days, $n$ in parentheses) of experimentally parasitized Yellow Warbler clutches.[a]

| Year | Treatment |  |  |
|---|---|---|---|
|  | Control | One host egg removed, one cowbird egg added | No host egg removed, one cowbird egg added |
| 1992 | 2.4 ± 0.2 (11) | 2.7 ± 0.2 (19) | 2.6 ± 0.4 (8) |
| 1993 | 2.8 ± 0.2 (20) | 2.6 ± 0.3 (13) | 2.7 ± 0.3 (10) |
| 1995 | 1.7 ± 0.1 (31) | 1.8 ± 0.2 (18) | 2.3 ± 0.2 (12) |

[a] Year comparison, $H = 26.38$, $P = 0.0001$; treatment comparison, $H = 1.32$, $P = 0.269$; treatment × year interaction, $H = 10.12$, $P = 0.0001$.

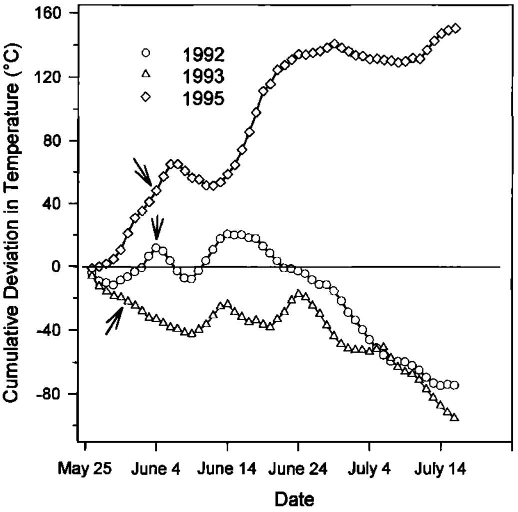

FIG. 1. The cumulative deviation in mean daily temperature from the 30-year mean temperature at Delta Marsh, Manitoba, plotted over three Yellow Warbler breeding seasons. The horizontal line at deviation = 0 represents no deviation from the 30-year mean. Lines above and below the horizontal are warmer and cooler, respectively, than the 30-year average. Arrows indicate the date the first Yellow Warbler clutch was initiated each year.

success of eggs in our study. Factors such as variation in prey abundance can influence Yellow Warbler reproductive success (Busby and Sealy 1979, Hébert 1993), but these data were not collected during our study.

Differences in the way eggs were handled during the study could have influenced cowbird hatching success. We did not conduct manipulations to demonstrate that hatching success was not affected by handling eggs, but Lerkelund et al. (1993) found that handling eggs did not reduce their hatchability. In this study, eggs were handled similarly by the same people in each year, with the exception of 1992 in which all warbler eggs also were measured. However, all cowbird eggs were measured, so in effect, handling was consistent across years for cowbird eggs.

We assumed that all unhatched eggs were capable of embryonic development, whether or not a dead cowbird embryo was visible in unhatched eggs. This introduced the potential for misinterpretation of the status of unhatched eggs. For instance, sterile eggs with no opportunity for development would have been interpreted as eggs in which embryonic mortality occurred at a very early stage of development. However, because the protocol was consistent over the three years, the frequency of such errors should have been constant. The fertility of cowbird eggs in 1992 may have been greatly reduced relative to the other years, but this appears unlikely.

Removal of host eggs by female cowbirds appears to increase the hatching success of parasitic eggs in Yellow Warbler nests in some years, and it may increase the hatching success of the remaining host eggs. Clutches where no host egg was removed, however, did not have longer incubation periods, nor did these clutches hatch more asynchronously than clutches where one host egg was removed. Therefore, removing a host egg apparently does not increase the rate of development of the remaining eggs. Hatching spread, however, did vary among years. Hébert and Sealy (1992) also found annual variation in hatching spread, which ranged from 1.4 to 2.3 days over three years. They attributed this to below-normal ambient temperatures during the laying period in one year, which resulted in shorter hatching spreads. Hatching spreads in our study, however, were significantly shorter in the warmest year (1995; $\bar{x}$ = 1.85 days) than in the coolest year (1993; $\bar{x}$ = 2.72 days).

*Hatching order.*—Contrary to Berger's hypothesis (1951), removal of the first-laid warbler egg did not increase the probability of the cowbird hatching before the host nestlings. In fact, most cowbirds hatched before or at the same

TABLE 6. Weather conditions ($\bar{x}$ ± SE, *n* in parentheses) at Delta Marsh, Manitoba, during the Yellow Warbler breeding seasons.

| Variable | Year 1992 | Year 1993 | Year 1995 |
|---|---|---|---|
| Precipitation[a] | 29 | 30 | 27 |
| Precipitation (mm/day) | 2.19 ± 0.66 (52) | 3.14 ± 0.89 (52) | 1.54 ± 0.71 (52) |
| Wind speed (km/h) | 4.5 ± 0.20 (52) | 5.4 ± 0.39 (52) | 4.2 ± 0.28 (52) |

[a] Number of days during breeding season with at least a trace of precipitation.

TABLE 7. *P*-values for explanatory variables used in the logistic regression models to explain hatching success of Brown-headed Cowbird eggs.

| Explanatory variable[a] | Combined years model | Individual years model | | |
|---|---|---|---|---|
| | | 1992 | 1993 | 1995 |
| CTEGG | 0.962 | 0.147 | 0.062 | 0.901 |
| CTINC | 0.694 | 0.439 | 0.359 | 0.845 |
| CTTOT | 0.718 | 0.937 | 0.359 | 0.788 |
| NESTLOC | 0.376 | 0.132 | 0.883 | 0.580 |
| TRT | 0.236 | 0.051 | 0.827 | 0.851 |
| YEAR | 0.006 | — | — | — |

[a] CTEGG = cumulative temperature deviation during laying period; CTINC = cumulative temperature deviation during incubation period; CTTOT = total cumulative temperature deviation during laying and incubation periods; NESTLOC = location of nest with ridge forest relative to Lake Manitoba; TRT = experimental treatment; YEAR = year of study.

time as warbler nestlings, regardless of whether a host egg was removed. Cowbird eggs probably hatched first because of their short incubation period (Briskie and Sealy 1990) and because they were added to nests early in the host laying period. Perhaps if cowbird eggs were laid later in the host laying period, they would benefit from removal of one of the first-laid host eggs.

Our results demonstrate that removal of host eggs influences cowbird hatching success in Yellow Warbler clutches, at least in some years. However, egg removal also can provide: (1) female cowbirds with an easily obtained high-energy meal (Scott et al. 1992), and (2) cowbird chicks with a reduced number of competitors during the nestling period (Mayfield 1960, Blankespoor et al. 1982). Although cowbirds lay eggs with unusually thick shells (Blankespoor et al. 1982, Spaw and Rohwer 1987, Picman 1989), egg removal also could reduce the chance of egg breakage in large clutches (Lerkelund et al. 1993). The possibility that egg removal by cowbirds serves multiple functions could be tested by examination of variation in egg removal behavior involving different host species and across several breeding seasons.

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