

SHORT INCUBATION PERIODS OF BROWN-HEADED COWBIRDS: HOW DO COWBIRD EGGS HATCH BEFORE YELLOW WARBLER EGGS?¹

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Abstract. Brown-headed Cowbird (*Molothrus ater*) eggs in natural nests hatch either before or at the same time as Yellow Warbler (*Dendroica petechia*) eggs despite being almost twice the size. Cowbird eggs may hatch before Yellow Warbler eggs because they (1) prolong the incubation of host eggs, (2) have more rapid embryonic development, or (3) hatch in response to stimuli from host eggs. We tested these hypotheses by comparing the incubation periods of cowbird eggs incubated in natural nests, incubated artificially in isolation from other eggs, and incubated artificially in clutches of Yellow Warbler eggs. Cowbird eggs incubated artificially in isolation from other eggs took significantly longer to hatch than either artificially incubated warbler eggs or naturally incubated cowbird eggs. The ratio of incubation period to egg volume was less for cowbirds than warblers, which indicates that cowbird embryos develop more rapidly relative to their size. The presence of a cowbird egg in natural nests significantly prolonged the incubation period of warbler eggs. Therefore, cowbird eggs appear to disrupt the incubation of smaller host eggs. Finally, the incubation periods of cowbird eggs incubated artificially in contact with warbler eggs were shorter, but not significantly so, than cowbird eggs incubated in isolation from other eggs. These results suggest that in addition to rapid embryonic development, cowbirds hatch before many hosts by disrupting incubation of smaller eggs and, possibly hatching early in response to stimuli from host eggs.

Key words: brood parasitism, Brown-headed Cowbird, *Dendroica petechia*, embryonic communication, incubation period, *Molothrus ater*, Yellow Warbler.

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*) is one of several brood-parasitic cowbird species that has a short incubation period relative to its egg mass (Briskie and Sealy 1990, Kattan 1995). Young cowbirds often hatch before nestlings of a variety of host species (McMaster and Sealy 1997). Some parasites eliminate competition for parental care (Redondo 1993) by ejecting host eggs and young, or by killing them directly (Payne 1977). Cowbirds rarely employ such drastic strategies (Dearborn 1996); instead, cowbird nestlings compete with host nestlings for food provisioned by the foster parents, often so successfully that some or all host nestlings starve (Weatherhead 1989). Hatching before host nestlings may enable cowbirds to gain competitive "head starts" (Mayfield 1992) that are important for the growth and development of the cowbird.

Four explanations have been proposed to explain the short incubation periods of parasitic cowbirds: (1) cowbird embryos develop more rapidly than host embryos (Friedmann 1927), (2) female cowbirds retain their eggs in the oviduct for up to 24 hours, which allows embryos to develop in their reproductive tracts before being laid (Hoffman 1929), (3) incubation periods increase as a function of egg mass (Vleck and Vleck 1987), hence, female cowbirds lay small eggs relative to their body mass to shorten the incubation period (Briskie and Sealy 1990), and (4) female cowbirds invest less energy per egg than predicted by allometry, which forces the embryo to hatch earlier when it runs out of yolk reserves (Kattan 1995).

Kattan (1995) found that the metabolic rates of Shiny Cowbird (*M. bonariensis*) embryos were not higher than predicted on the basis of an egg's energy content. This suggests that Shiny Cowbird embryos do not develop more rapidly than embryos of other species. Although retention of eggs in the oviduct by some cuckoo species may shorten incubation periods (Perrins 1967), the only observation of egg retention in

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cowbirds (Hoffman 1929) appears to have been a rare case of an egg-bound female (Nice 1954). Briskie and Sealy (1990) found that Brown-headed Cowbird eggs conform to allometric predictions based upon female body mass. Egg composition differs between species and may affect the developmental characteristics of chicks (Hill 1995). Shiny Cowbird eggs contain less energy than predicted by their mass (Kattan 1995), which is consistent with the hypothesis that cowbird embryos are forced to hatch early when they run out of energy. Kattan's results (1995) should be viewed cautiously, however, as energy investment per unit egg mass is expected to be lower in species with short incubation periods because embryonic maintenance functions are fueled for shorter periods (Ricklefs 1993). Therefore, the low energy content of Shiny Cowbird eggs may be due to the short incubation period, rather than the cause of the short incubation period. In any case, the situation in Shiny Cowbirds does not parallel that of the Brown-headed Cowbird because energy investment in eggs of Brown-headed Cowbirds does not differ significantly from that predicted by egg mass (Ankney and Johnson 1985).

We initially tested two nonmutually exclusive hypotheses concerning cowbird incubation periods: first, that naturally incubated cowbird eggs hinder the incubation of small host eggs (Mayfield 1960, Dolan and Wright 1984), possibly by reducing the amount of heat host eggs receive, and thus extending the incubation period of host eggs. We tested this hypothesis by comparing incubation periods among cowbird and Yellow Warbler (*Dendroica petechia*) eggs incubated artificially and in unmanipulated nests. This hypothesis predicts that (1) because incubation periods increase with egg mass across species (Vleck and Vleck 1987) and Yellow Warbler eggs are approximately half the size of cowbird eggs (Sealy 1992), warbler eggs should hatch before cowbird eggs when artificially incubated at identical temperatures, and (2) incubation periods of warbler eggs would be longer in parasitized than unparasitized Yellow Warbler nests. Secondly, we tested the hypothesis that cowbird embryos develop relatively faster for their size than Yellow Warbler embryos. This hypothesis predicts that the ratio of incubation period to egg volume would be smaller for artificially incubated cowbird eggs than Yellow Warbler eggs.

We also tested a third hypothesis for short

cowbird incubation periods. All avian embryos tested to date, including five passerine species, make clicking noises associated with movements of cartilage of the glottis beginning when the embryo's bill ruptures the inner shell membrane and connects the respiratory system with the gaseous medium for the first time (McCoshen and Thompson 1968). In some precocial species embryos at different stages of development in the same clutch use clicking sounds to synchronize hatching of the clutch (Vince 1966). Synchronization is achieved by accelerating the hatching of less-developed embryos (Vince 1966) and retarding the hatching of more-developed eggs (Vince 1968). Parasitic Snow Goose (*Chen caerulescens*) eggs laid in conspecific nests early in incubation hatch synchronously with the rest of the clutch (Davies and Cooke 1983). Whereas synchronous hatching is advantageous for precocial embryos, a cowbird embryo in a clutch of host embryos would benefit by hatching first and securing a competitive advantage (Mayfield 1992). When two species of quail eggs are incubated together, the embryos of one species control the timing of hatching of the other species by accelerating or retarding the hatching of embryos to match their own stage of development (Pani et al. 1968). Embryonic stimuli, therefore, influence the timing of hatching in other species. We propose the short incubation period of the cowbird is facilitated by the ability of the embryo to hatch shortly after it detects clicking, or other stimuli, from the host's eggs during the final one or two days prior to hatching. This mechanism proposes that cowbird embryos hatch at an immature stage of development, rather than accelerating their rate of development in response to clicking. To test the hypothesis, cowbird eggs were incubated artificially in contact with clutches of Yellow Warbler eggs. We predicted that (1) cowbird eggs should hatch before warbler eggs as they do under natural conditions (McMaster and Sealy 1997) and (2) cowbird eggs incubated in warbler clutches should have shorter incubation periods than cowbird eggs artificially incubated in isolation.

When the embryos of some species are stimulated to hatch early, the chicks are less developed at hatching and are more likely to die within the first month of life (Cannon et al. 1986). Yet when embryos of other species are stimulated to hatch early they apparently pay few (Vince and Chinn 1971) or no costs (Griere et

al. 1973) in terms of their developmental status at hatching. Our hypothesis predicts cowbird embryos stimulated to hatch early will do so at an immature stage of physical development relative to cowbirds with longer incubation periods. We recorded the length of hatchling cowbird tarsi and wings, and predicted both measurements would be shorter for cowbirds incubated in clutches than cowbirds incubated in isolation. Thus, our objectives were to test under natural and artificial conditions whether cowbirds hatch before Yellow Warblers because cowbirds (1) prolong the incubation of warbler eggs, (2) develop more rapidly, or (3) hatch earlier in response to stimuli from host eggs.

METHODS

From 1992 to 1996, freshly laid cowbird eggs were obtained from host nests at Delta Marsh (50°11'N, 98°19'W) on the properties of the University of Manitoba Field Station, Delta Waterfowl and Wetlands Research Station, and Portage Country Club (see MacKenzie 1982 for description of study area). In 1996 cowbird eggs also were obtained from captive females held overnight in an outdoor aviary. In 1995 and 1996, Yellow Warbler eggs were obtained from natural nests on the day they were laid, and in all cases were either the first or second eggs of the clutch. Yellow Warblers do not incubate much early in laying (Hébert and Sealy 1992), therefore, eggs collected at this time had undergone little or no development. Eggs were relocated to the University Field Station where they were labeled, and length and width were measured to the nearest 0.1 mm with dial calipers. Cowbird and warbler egg volumes were calculated using the formula (Mills 1987):

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

where $k = 0.515$ for cowbird eggs and 0.497 for Yellow Warbler eggs, $L =$ egg length, and $B =$ egg breadth. Egg mass was recorded in 1995 and 1996 with a digital scale accurate to 0.05 g.

NATURAL NESTS

In 1992 and 1993, freshly laid cowbird eggs were added to Yellow Warbler nests on the day the first warbler egg was laid (see McMaster and Sealy 1997). For this analysis we only used data from experimentally parasitized nests where no warbler egg was removed. Other natural warbler nests were left unparasitized to serve as controls.

Nests were visited daily beginning the day before hatching was expected to start to record incubation periods. Cowbird and warbler incubation periods were estimated by measuring the interval from the time the egg was introduced to the nest to the time the egg hatched. Because Yellow Warbler incubation behavior is not fully developed during the laying period (Hébert and Sealy 1992), days during this period were not counted as full incubation days. Rather, a proportion of each day during the laying period, equal to the proportion of time female warblers were attentive that day as determined by afternoon watches (McMaster 1997), was added to the incubation period of each egg. Incubation periods were not estimated using (1) the interval from host clutch completion to hatching, (2) interval from the laying of the penultimate host egg to hatching, or (3) interval from the time of introduction of the cowbird egg to the nest to hatching, because the first two methods underestimate, and the third method overestimates, incubation period in species that gradually initiate incubation over the laying period.

ARTIFICIAL INCUBATION

Before being placed in the incubator, most cowbird and warbler eggs were candled to verify that no detectable embryonic development had occurred. In 1994 and 1995, cowbird and warbler eggs were placed in random positions, 2–3 cm apart in the incubator. In 1996, two experimental groups of cowbird eggs were incubated. In the first group, each cowbird egg was incubated in clutches of three warbler eggs, with all four eggs in contact with each other. Although warblers usually lay four- or five-egg clutches at Delta Marsh (Goossen and Sealy 1982), clutches of three warbler eggs were used to simulate natural clutches to minimize the number of host eggs required for the experiment. Clutches of one cowbird and three warbler eggs are found in natural nests, because female cowbirds often remove host eggs from parasitized clutches (Sealy 1992). Artificially incubated clutches were placed on a nylon mesh that covered a cardboard ring. The mass of the eggs weighed down the material, which ensured the eggs contacted each other. The mesh allowed for free circulation of air around the eggs. The second group of cowbird eggs in 1996 provided a control group in which cowbird eggs were incubated in isolation, as in 1994 and 1995.

In 1994 a custom-built incubator was used. It consisted of a 0.75×0.75 m plywood box insulated with 8 cm of styrofoam. The front of the incubator consisted of two clear plastic panels between which a styrofoam sheet could be lifted to view the contents without opening the incubator. A small door on the side allowed the eggs to be turned manually without the temperature inside dropping substantially. A YSI temperature controller maintained the air temperature at $37.5 \pm 0.1^\circ\text{C}$. A large pan filled with water maintained relative humidity at 50–60%. Three electric fans located at different levels of the incubator continuously circulated air inside the incubator without blowing directly on the eggs. In 1995 two commercial hatchery incubators were used in addition to the custom-built incubator. Unlike the custom-built incubator, temperatures in these incubators fell more rapidly while eggs were being turned. We measured temperature and humidity in the three incubators to ensure identical conditions.

Eggs were turned four times daily to prevent embryonic membranes from adhering to the shells. Embryonic development was monitored during incubation by candling and weighing eggs at 3- to 4-day intervals. Once eggs incubated in isolation neared hatching, a cardboard ring was placed around each egg to ensure the newly hatched chick could be identified by the presence of its labeled eggshell. Each egg incubated in a clutch was left in place until it hatched, then the nestling was removed. The incubator was checked for chicks at least every 6 hr. The hatching event was observed directly in many instances, which allowed hatching time to be determined precisely. Nestlings were considered hatched when the shell broke into two pieces. In cases where the hatching event was not observed ($n = 32$), hatching time was estimated as the midpoint between the time the nestling was discovered and the time the incubator was last visited (maximum error, 3 hr). In all years, newly hatched birds were weighed to the nearest 0.05 g and the time of their discovery recorded. Tarsus and wing length (from the wrist to the tip of the wing) were measured with dial calipers to the nearest 0.01 mm only in 1995 and 1996.

To compare cowbird and warbler incubation periods, only data from clutches in which the cowbird and at least one Yellow Warbler hatched were used. This criterion ensured that incubation periods were calculated using only

cowbird eggs that could have been stimulated by warbler eggs. If more than one warbler egg hatched in a nest, the mean incubation period for warbler eggs in that clutch was calculated for comparison with the cowbird incubation period. Because egg mass was not measured at the beginning of incubation in 1994, unlike Kattan (1995), we could not correlate incubation period with egg mass for the three years. Instead, we substituted egg volume for egg mass, and examined the relationship between egg volume and incubation period using linear regression. Cowbird egg volume and mass are tightly correlated (McMaster, unpubl. data). Using the regression equation for the relationship between egg volume and mass derived from the 1995 and 1996 data, we predicted the mass of each egg and entered it into an equation that predicts incubation period for birds (Vleck and Vleck 1987):

$$I = 10^{[0.97 + 0.29 \log(W)]} \quad (2)$$

where I = incubation period, and W = egg mass. Only data for cowbird and warbler eggs incubated in isolation were used to calculate the mean ratio of incubation period to egg volume.

STATISTICAL ANALYSES

Data were tested for normality using Shapiro-Wilk (W) and Kolmogorov-Smirnov (D) tests, and then analyzed using standard parametric or nonparametric tests, where appropriate.

Eggs incubated in isolation. Hatching success between the incubators and natural nests was compared using a χ^2 test. Cowbird and Yellow Warbler incubation periods were compared using two-sample t -tests for groups with unequal variance. Cowbird incubation periods were compared between the incubator and natural nests using a two-tailed t -test for groups with equal variance. Yellow Warbler incubation periods were compared between (1) the first-hatched warbler egg in control clutches (1992 and 1993), (2) the first-hatched warbler egg in natural clutches (1992 and 1993) that had been artificially parasitized and no host egg removed, and (3) warbler eggs artificially incubated in isolation (1994 and 1995). We used Mann-Whitney U -tests for all three comparisons.

Eggs incubated in clutches. In 1996 two clutches were deleted from the dataset because the warbler incubation periods were outliers (short incubation periods) that prevented normality. We tested for a relationship between

TABLE 1. Incubation period ($\bar{x} \pm SE$ in days, n in parentheses) of artificially incubated cowbird and Yellow Warbler eggs.

Treatment	Cowbird	Yellow Warbler
Isolation	12.4 \pm 0.1 (48)	11.9 \pm 0.1 (15)
Clutch	12.0 \pm 0.2 (11)	11.8 \pm 0.1 (11)

cowbird and warbler incubation periods using the Pearson correlation coefficient (r). The relationship between cowbird incubation period and number of warbler eggs hatching in the clutch was examined using linear regression. The incubation periods of cowbird and warbler eggs incubated together in clutches in 1996 were compared using a two-tailed t -test for samples with equal variance. The incubation periods of cowbird eggs in clutches (or warbler eggs) were then compared with the pooled incubation periods of cowbird eggs (or warbler eggs, respectively) incubated individually in 1994 and 1995 using ANOVA, with egg volume as a covariate entered first into the model. The power of the ANOVA test was calculated for cowbird eggs. Cowbird incubation periods in artificial clutches and natural nests were compared using the Mann-Whitney U -test. Body mass, tarsus and wing length of cowbird hatchlings were compared between years using ANOVA with egg volume entered first into the model as a covariate.

Data were tested for differences among years and incubators, and pooled where possible. Egg volume was included in all applicable ANOVA tests as a covariate, but was deleted from the final model unless significant. Results of these tests are available from the authors. All results are reported as mean \pm SE. We used $P < 0.05$ as our level of accepted significance.

RESULTS

EGGS INCUBATED IN ISOLATION

Hatching success of artificially incubated eggs was significantly lower than that in natural nests for both cowbird eggs (52.3% vs. 74.6%, re-

spectively; $\chi^2_1 = 13.0$, $P < 0.001$) and warbler eggs (52.6% vs. 93.6%, respectively; $\chi^2_1 = 116.8$, $P < 0.001$). In the incubator, the mean Yellow Warbler incubation period was significantly shorter than the mean cowbird incubation period (Table 1; $t_{39.6} = -4.72$, $P < 0.001$). On average, artificially incubated Yellow Warbler eggs took 0.5 days less to hatch than cowbird eggs. Nevertheless, cowbird embryos incubated in isolation took significantly less time to hatch relative to their egg volume than did warbler embryos (Table 2; $t_{64.9} = -33.7$, $P < 0.001$).

NATURAL NESTS

Cowbird eggs in natural nests hatched in 11.9 \pm 0.1 days ($n = 41$), or about 0.5 days sooner than cowbird eggs artificially incubated in isolation. Cowbird incubation periods in natural nests were significantly shorter than those incubated artificially in isolation ($t_{87} = 2.8$, $P < 0.01$). The incubation period of first-hatched Yellow Warbler eggs in natural control nests ($\bar{x} = 11.0 \pm 0.2$ days, $n = 26$) was significantly shorter than that of first-hatched warbler eggs in parasitized clutches ($\bar{x} = 12.3 \pm 0.1$ days, $n = 41$; $z = -5.8$, $P < 0.001$). The incubation period of first-hatched Yellow Warbler eggs in natural control nests also was significantly shorter than those of warbler eggs artificially incubated in isolation (Table 1; $z = -4.7$, $P < 0.001$). Warbler eggs artificially incubated in isolation hatched significantly earlier than first-hatched warbler eggs in parasitized clutches ($z = -2.7$, $P < 0.01$).

EGGS INCUBATED IN CLUTCHES

Warblers hatched before cowbirds in 10 cases; cowbirds hatched first in 3 cases. There was no

TABLE 2. Mean (\pm SE) egg volume and ratio of incubation period to egg volume for artificially incubated Brown-headed Cowbird and Yellow Warbler eggs. Sample sizes in parentheses.

Species	Egg volume (ml)	Incubation period/egg volume (days ml ⁻¹)
Brown-headed Cowbird	2.83 \pm 0.05 (69)	4.22 \pm 0.07 (57)
Yellow Warbler	1.37 \pm 0.01 (99)	8.82 \pm 0.12 (38)

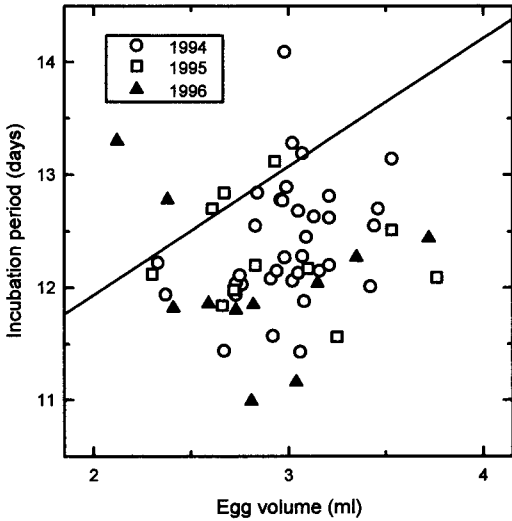


FIGURE 1. Cowbird incubation period (days) for three years relative to egg volume (ml). Cowbird eggs in 1994 and 1995 were incubated in isolation, whereas in 1996 cowbird eggs were incubated in warbler clutches. The mass of 1994 eggs was predicted using the regression equation for the relationship between egg volume and mass derived from the 1995 and 1996 data. The mass of each egg was then entered into Vleck and Vleck's (1987) equation (see equation 2 in text) to predict the incubation period. The predicted incubation periods were then plotted as the diagonal line against egg volume.

significant difference in incubation periods of cowbird and warbler eggs incubated in clutches in 1996 (Table 1; $t_{20} = -0.92$, $P > 0.3$). The incubation period of cowbird eggs in clutches was 0.4 days shorter than those incubated in isolation, but the difference only approached significance (Table 1; $F_{1,58} = 2.77$, $P = 0.10$). The power of the ANOVA test was only 0.51, however, so the probability of obtaining a statistically significant result was small. The incubation period of cowbird eggs incubated in clutches did not differ significantly from those in natural nests ($U = 312.0$, $P > 0.5$). Unfortunately, only

2 of 13 cowbird eggs in the 1996 control group hatched, therefore, we could not compare control and experimental incubation periods statistically. Cowbird incubation period did not differ significantly with the number of warblers hatching ($F_{1,9} = 0.01$, $P > 0.9$, $r^2 = 0.002$; $\bar{x} = 2.09 \pm 0.25$ warblers where cowbird hatched, $n = 11$), and was not significantly correlated with mean warbler incubation period ($r = 0.3$, $P > 0.3$). Warbler incubation periods did not differ significantly whether the eggs were incubated individually or in clutches (Table 1, $F_{1,25} = 0.0$, $P > 0.9$).

Incubation periods of cowbird eggs incubated individually or in clutches were not significantly related to egg volume ($F_{1,44} = 1.5$, $P > 0.2$, $r^2 = 0.03$; $F_{1,10} = 0.3$, $P > 0.5$, $r^2 = 0.02$, respectively; see Fig. 1). In Figure 1, most observed cowbird incubation periods are below the predicted line, which indicates cowbird eggs have short incubation periods for their size regardless of whether they are in contact with host eggs.

HATCHLING SIZE

Although the covariate, egg volume, explained much of the variation in hatchling mass (covariate $F_{1,48} = 58.3$, $P < 0.001$), cowbird hatchlings weighed significantly more when incubated in clutches than when incubated in isolation (Table 3; clutch $F_{1,48} = 13.1$, $P < 0.001$; model $F_{2,47} = 35.7$, $P < 0.001$). Although cowbird hatchlings incubated in clutches had longer tarsi than hatchlings incubated in isolation, the difference only approached significance (Table 3; clutch $F_{1,16} = 3.2$, $P > 0.09$; egg volume $F_{1,16} = 3.29$, $P = 0.09$; model $F_{2,15} = 3.2$, $P > 0.06$). The difference in wing length between cowbird hatchlings incubated individually or in clutches was not significant (Table 3; $F_{2,15} = 1.4$, $P > 0.25$).

DISCUSSION

Our results indicate that cowbird embryos hatch prior to Yellow Warbler embryos because (1)

TABLE 3. Cowbird nestling measurements ($\bar{x} \pm SE$) relative to egg volume for eggs incubated in isolation (1994 and 1995) and in clutches (1996). Sample sizes in parentheses.

Condition	Tarsus length (mm)	Wing chord (mm)	Nestling mass (g)	Egg volume (ml)
Isolation	7.44 ± 0.32 (10)	6.01 ± 0.41 (10)	2.24 ± 0.04 (42)	2.98 ± 0.04 (46)
Clutches	7.99 ± 0.24 (8)	6.8 ± 0.13 (8)	2.38 ± 0.12 (8)	2.76 ± 0.07 (11)

their rate of development is faster than that of warbler embryos relative to egg volume and (2) they prolong incubation periods of warbler eggs. Our results suggest that cowbird eggs may be stimulated to hatch earlier when in contact with warbler eggs.

EGGS INCUBATED IN ISOLATION

In the incubator, cowbird eggs incubated in isolation had significantly longer incubation periods than Yellow Warbler eggs, but their rate of development relative to egg volume was faster than that of warbler embryos. This result supports the contention that interspecific variation in incubation period reflects mass-independent differences in rates of embryonic growth and development (Ricklefs 1993).

The first warblers that hatch in natural nests have longer incubation periods in parasitized than unparasitized clutches, suggesting that cowbird eggs disrupt incubation of warbler eggs, probably by reducing the amount of heat warblers receive (Braden et al. 1997). The finding that cowbird eggs did not hatch before warbler eggs in the incubator further supports this possibility. Other studies have documented longer host incubation periods in the presence of a larger parasitic egg (Dolan and Wright 1984, Wood 1995). Conversely, cowbird eggs in clutches of larger host eggs suffer reduced hatching success or longer incubation periods as host clutch size increases (Wood and Bollinger 1997, Peer and Bollinger, in press), perhaps due to decreased contact with the brood patch. Cowbirds in Northern Cardinal (*Cardinalis cardinalis*) clutches (eggs 50% larger than cowbird eggs) still hatched in 11.9 days (Scott and Lemon 1996), perhaps because the modal cardinal clutch size was only three eggs. Therefore, cowbirds parasitizing larger hosts may risk prolonged incubation periods, even though larger hosts are usually considered preferable to small hosts due to increased feeding rates and reduced predation risk (Fretwell, in Rothstein 1975). To demonstrate that smaller eggs experience reduced incubation temperatures, egg temperatures of both small and large eggs must be measured simultaneously in the same nest. Huggins (1941) recorded temperatures of both a cowbird egg and one of several smaller Chipping Sparrow (*Spizella passerina*) eggs in a naturally parasitized nest, albeit for less than one half-hour, but found that whichever egg was in the center

of the clutch was warmer. In the laboratory, the temperature of a Zebra Finch (*Taeniopygia guttata*) egg fell by 0.5°C when a larger cowbird egg was in the clutch (B. M. Strausberger, unpubl. data).

In our study, cowbird eggs artificially incubated in isolation hatched 12 hr later than cowbird eggs in natural nests. Incubation periods of cowbird eggs incubated artificially also were 0.5 days longer than the mean cowbird incubation period reported under natural conditions (Briskie and Sealy 1990), but 2.5 days longer than the shortest incubation periods reported by Briskie and Sealy (1990). Comparison of incubation periods of artificially incubated cowbird eggs in our study with most other studies of incubation under laboratory conditions is confounded by the fact that eggs were not fresh (Graber 1955) or may not have been fresh (Wetherbee and Wetherbee 1961). A. M. Dufty Jr. (unpubl. data) recorded an average incubation period of 12.6 days for five fresh cowbird eggs incubated artificially, which agrees closely with our results. As in our study, Kattan (1995) found artificially incubated Shiny Cowbird eggs had longer incubation periods than the minimum observed under natural conditions (Wiley and Wiley 1980). In contrast to our study, Shiny Cowbird eggs incubated artificially hatched earlier (11.7 days) than eggs in natural nests (12.0 days).

EGGS INCUBATED IN CLUTCHES

Predictions of the hypothesis that cowbird eggs hatch early in response to stimuli from host eggs were that (1) cowbird eggs artificially incubated in warbler clutches should hatch before warbler eggs and (2) cowbird eggs artificially incubated in warbler clutches should have shorter incubation periods than cowbird eggs incubated in isolation. Contrary to the first prediction, most cowbird eggs incubated artificially in clutches hatched after warbler eggs (77% of cases), whereas in natural nests cowbirds hatched either before or at the same time as first-hatched warbler eggs (McMaster and Sealy 1997). However, because warbler incubation periods in parasitized nests apparently are prolonged by the presence of the cowbird egg, which likely contributes to the high frequency of cowbirds hatching first, the first prediction seems unrealistic.

Two statistically nonsignificant comparisons suggest cowbird embryos incubated in contact with warbler eggs were stimulated to hatch ear-

ly. Consistent with predictions, the incubation period of cowbird eggs incubated in clutches did not differ significantly from both cowbirds in natural nests and warblers artificially incubated in isolation. The third, and potentially most persuasive comparison, revealed that cowbird eggs artificially incubated in clutches tended to have shorter incubation periods than eggs incubated in isolation, but the difference only approached significance ($P = 0.10$). Because the power of the test was low, larger sample sizes may have yielded a significant result. Although communication among embryos has been suggested to possibly control the duration of the incubation period in other altricial species (Schwagmeyer et al. 1991, Viñuela 1997), effects of egg contact on hatch timing of artificially incubated eggs were not replicated under natural conditions (Schwagmeyer et al. 1991).

How much the cowbird hatchling would benefit from a half-day reduction in incubation period due to stimulation from host eggs is questionable. As most host species with incubation periods as short as those of cowbirds are small anyway, cowbirds presumably could outcompete the host nestlings even without an extra half-day head start. In those larger hosts with short incubation periods, a half-day head start appears insufficient for cowbird nestlings to overcome their size disadvantage (Scott and Lemon 1996, Peer and Bollinger 1997). The observation of two cowbird eggs hatching in 10 days recorded by Briskie and Sealy (1990) is intriguing, because both cowbird eggs were in the same nest. To a cowbird nestling in a brood of a small host species, another cowbird is likely a greater threat than the host nestlings. Perhaps under natural conditions cowbird eggs can be stimulated to hatch earlier by conspecific eggs than host eggs. The fact that warbler eggs showed no tendency to hatch earlier when incubated in clutches suggests this trait has not been selected for in Yellow Warblers (see Viñuela 1997). Indeed, stimulation of early hatching by embryonic communication appears more likely to be found in altricial species such as Cliff Swallows (*Hirundo pyrrhonota*), where intraspecific parasitism is frequent and parasitic eggs have short incubation periods (Brown 1984). Comparison of incubation periods of cowbird eggs placed in host nests at various times throughout the laying period would further test whether cowbird eggs are stimulated by heterospecific eggs to hatch early.

Contrary to the hypothesis that cowbirds stimulated to hatch early do so at an immature stage of physical development, the tarsi and wings of hatchling cowbirds in clutches tended to be longer than those of cowbirds incubated in isolation. The significantly greater mass of cowbird hatchlings incubated in clutches than in isolation may have been due to the shorter time available for the egg to lose water. Could cowbird embryos be stimulated to grow more rapidly and hatch earlier? Intuitively, there should be a cost to the cowbird for hatching early that is exceeded only by the benefit the cowbird receives by hatching before the host's eggs. In the absence of a trade-off between incubation period and development, cowbird embryos should be expected to always hatch as early as possible, unless limited by parental behavior (Kemal and Rothstein 1988). Perhaps our measurements of body size were insufficient to detect trade-offs experienced by early hatching cowbirds. Early-hatching cowbirds may suffer reduced immune function; interspecific comparisons have shown incubation period is inversely related to prevalence of blood parasites (Ricklefs 1992). Documentation of when host embryos begin clicking relative to hatching would aid in the evaluation of whether cowbirds use this behavior as a cue.

The absence of a relationship between the incubation period of artificially incubated cowbird eggs and egg volume in this study is contrary to the significant correlation between cowbird incubation period and egg mass for Shiny Cowbirds (Kattan 1995). Our results suggest that for Brown-headed Cowbirds, incubation period may be genetically controlled and differs significantly between individual embryos regardless of egg size, and perhaps differs among laying females. Other studies also have found that variation between females or within the laying order of the clutch influenced incubation periods more so than did egg volume (MacCluskie et al. 1997, Viñuela 1997). This variance may reflect differences in female incubation behavior (Ricklefs and Smeraski 1983), rather than differences in genetically coded embryonic growth rates. Interestingly, the two cowbird eggs with 10-day incubation periods reported by Briskie and Sealy (1990) had similar markings and coloration and were laid on consecutive days, which indicates they were likely laid by the same female (Dufty 1983).

Despite the suggestive findings of our study,

results also showed that hatching success in the incubator was lower than in natural nests. Because all eggs were freshly laid and handled carefully to avoid damage during transport to the laboratory, low hatching success was likely due to differences between artificial and natural incubation. Artificial incubation did not simulate the temperature gradients that exist between the top and bottom of eggs (Turner 1991), the variation in temperature and humidity, and frequency of turning experienced by naturally incubated eggs (Baldwin and Kendeigh 1932, Burger and Bertram 1981). In other studies reporting hatching success of freshly laid cowbird eggs incubated artificially, success ranged from 100% ($n = 5$, A. M. Dufty Jr. unpubl. data) to 55.5% ($n = 17$, Wetherbee and Wetherbee 1961).

In summary, the results of this study demonstrate cowbirds hatch first in Yellow Warbler nests due to a combination of (1) faster rate of embryonic growth relative to egg volume and (2) the larger cowbird egg prolongs warbler incubation periods, likely by reducing the amount of heat warbler eggs receive from the brood patch. Our results also suggest stimuli from warbler eggs may elicit earlier hatching by cowbirds. It appears that disruption of host incubation is more important than stimulation of early hatching in determining whether cowbirds hatch before warblers, because warbler eggs hatched 1.3 days later in parasitized nests, whereas cowbird eggs artificially incubated in clutches hatched only 0.4 days earlier.

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