The Auk 115(4):843–850, 1998

TEMPERATURE, EGG MASS, AND INCUBATION TIME: A COMPARISON OF BROWN-HEADED COWBIRDS AND RED-WINGED BLACKBIRDS

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ABSTRACT.—Eggs of the parasitic Brown-headed Cowbird (*Molothrus ater*) often hatch before those of its hosts. I artificially incubated the eggs of the cowbird and the taxonomically related but nonparasitic Red-winged Blackbird (*Agelaius phoeniceus*) to determine if cowbird eggs have unique adaptations. To determine if cowbirds have a wider tolerance of acceptable incubation temperatures, the eggs from both species were incubated at 35, 38, and 40°C. Neither species' eggs hatched at 35 or 40°C, whereas 24 out of 42 cowbird eggs and 19 out of 36 redwing eggs hatched at 38°C. When corrected for differences in mass, cowbird and redwing eggs hatched 10 and 15%, sooner than expected, respectively, suggesting that cowbirds do not have an accelerated rate of embryonic development. Cowbirds may be adapted to lay smaller eggs that generally hatch sooner. Using values obtained from allometric equations that relate body mass and egg mass, cowbird and redwing eggs were 25 and 4% smaller, respectively, than expected. For cowbirds, there was no correlation between egg mass and length of incubation period, whereas there was a positive (but not significant) correlation for redwings. Additional cowbird eggs were incubated at 36 and 39°C to determine the effect on the length of the incubation period. The incubation periods of individual cowbird eggs ranged from 10.49 to 14.04 days at 39 and 36°C, respectively, whereas eggs incubated at 38°C had a mean incubation period of 11.61 days ($n = 24$), suggesting that cowbirds can tolerate some variation in incubation temperature and indicating a strong temperature effect. I found evidence that internal egg temperature varies with clutch composition. This may partially explain the variation in cowbird incubation periods and why cowbird eggs often hatch before host eggs. *Received 2 July 1997, accepted 20 November 1997.*

THE BROWN-HEADED COWBIRD (*Molothrus ater*) is a well-studied brood parasite that possesses a variety of adaptations for parasitism including parasitizing nests when hosts are least likely to be present (Scott 1991), rapid laying of eggs (Sealy et al. 1995), and producing eggs with unusually thick shells that resist damage (Blankespoor et al. 1982, Spaw and Rohwer 1987). Brown-headed Cowbirds (hereafter "cowbird") parasitize many different species (Friedmann and Kiff 1985) that have different incubation temperatures (Huggins 1941, Rahn and Ar 1974, Webb 1987), a variable that strongly affects egg hatchability (Drent 1973, White and Kinney 1974). As a result, it has been suggested that brood parasites such as cowbirds and parasitic cuckoos have flexible incubation temperature requirements (Groebbels and Möbert 1930, Graber 1955).

Relatively short incubation periods of some brood parasites have been suggested to be an adaptation to parasitism (O'Connor 1984). By hatching before host eggs, parasites would likely be better competitors for food. Friedmann (1927) first suggested that cowbirds have evolved an accelerated rate of embryonic growth and an unusually short incubation period (10 days), whereas Hoffman (1929) suggested that cowbirds lay partially developed eggs, as do some cuckoos (Perrins 1967, Vernon 1970). Studying the Shiny Cowbird (*Molothrus bonariensis*), Kattan (1995) found a relationship between an egg's incubation period and energy content.

Nice (1953), however, found that cowbird eggs ($n = 62$) took at least 11 days to hatch, and she concluded that the cowbird's incubation period was similar to that of some nonparasitic icterids. Other reports of cowbird incubation periods range from 10 to 14 days, with means ranging from 11.6 to 11.9 days (Norris 1947, Briskie and Sealy 1990, Scott and Lemon 1996). Because higher temperatures generally increase the rate of embryonic development (Ro-

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manoff 1960, O'Connor 1984), variation in incubation periods may result from different incubation temperatures.

A strong positive allometric relationship usually exists between egg mass and incubation period (Rahn and Ar 1974) and between egg mass and female body mass (Rahn et al. 1975). Species that lay relatively small eggs, such as some parasitic cuckoos (Lack 1968), may experience a reduced incubation period. Similarly, within species, relatively small eggs also may hatch sooner than larger ones (Landauer 1967, Parsons 1972, Drent 1975; but see MacCluskie et al. 1997). Species-specific incubation periods often are correlated with taxonomic group (Lack 1968). Icterids (i.e. "blackbirds") collectively lay relatively small eggs (Weatherhead and Teather 1994). Briskie and Sealy (1990), however, did not find a smaller egg mass for parasitic (n = 4) compared with nonparasitic (n = 17) icterids.

Using eggs of the related nonparasitic Red-winged Blackbird (*Agelaius phoeniceus*), I predicted that artificially incubated cowbird eggs would tolerate a wider range of temperatures than Red-winged Blackbird (hereafter "redwing") eggs. Next, I tested the hypotheses that cowbird eggs hatch sooner than predicted from egg mass and/or lay smaller eggs than predicted. I predicted that artificially incubated cowbird eggs would hatch sooner than those of redwings, after correcting for egg mass differences. To test whether cowbirds laid smaller eggs than predicted from female body mass, I compared the expected egg masses of both species with the actual mass of collected eggs. Finally, I suggest an explanation for the variation in the lengths of reported cowbird incubation periods and earlier hatching compared with many host eggs.

STUDY AREA AND METHODS

I collected fresh redwing and cowbird eggs at The Morton Arboretum in northeastern Illinois during the 1995 to 1997 nesting seasons. Cowbird eggs were collected from a variety of host species' nests. I monitored nests daily, and collected eggs before 1000 CST on the day they were laid and only from nests where incubation had not yet started. To prevent nest abandonment after egg removal, I replaced redwing eggs with marked eggs removed from other redwing nests. Cowbird eggs were replaced with plaster of Paris eggs that were painted to resemble cowbird eggs. All eggs were weighed (± 0.01 g) on a Mettler balance (Model AE 100).

TABLE 1. Observed and expected egg mass and incubation period of Brown-headed Cowbird and Red-winged Blackbird eggs incubated at 38.0°C. Observed values are $\bar{x}$ ± SD, with n in parentheses.

	Egg mass (g)	Incubation period (days)
	Brown-headed Cowbird	
Observed	3.04 ± 0.28 (65)	11.61 ± 0.24 (24)
Expected	4.05 ± 0.09[a]	12.88[b]
	Red-winged Blackbird	
Observed	4.09 ± 0.42 (52)	12.09 ± 0.40 (19)
Expected	4.24 ± 0.09[a]	14.17[b]

[a] From Rahn et al. (1975) for passerines: $E = 0.34W^{0.677}$, where E is expected egg mass and W is female body mass.

[b] From Vleck and Vleck (1987) for altricial birds: $\log I = 0.97 + 0.29(\log E)$, where I is incubation period and E is egg mass.

In 1995, I assessed the effects of incubation temperature on hatchability. I placed a random sample of eggs of both species into TX7 incubators (Lyon Electric Company) with temperatures of 35.0, 38.0, and 40.0°C and 64% relative humidity. All eggs were turned automatically every hour. Of these, only eggs incubated at 38°C hatched. Therefore, in 1996 I incubated eggs at 38°C and 64% relative humidity, to determine the mean length of each species' incubation period at this temperature. To determine the effects that slightly different temperatures have on the length of the incubation period, I incubated 5 and 11 cowbird eggs at 36.0 and 39.0°C, respectively. After 10 days of incubation, all eggs were checked approximately every 4 h for pipping. Once pipping was observed, eggs were checked more often. Hatching was defined as the moment a chick forced the cap off the shell and fully extended its neck, and was measured to the nearest 15 minutes. I used linear regression analysis to determine if egg mass and incubation period were correlated.

For other analyses, I compared observed and expected values obtained from regressions of each parameter. Expected incubation periods and associated 95% confidence intervals based on egg mass were obtained from Vleck and Vleck (1987):

$$\log I = 0.97 + 0.29(\log E), \quad (1)$$

where I is incubation period in days and E is egg mass in g (Table 1). The mean incubation period of an egg was defined as the interval between placement in an incubator and hatching. The mean length of each species' incubation period was determined at 38°C. For each species, deviations of mean egg mass from an expected value based on female body mass and 68% confidence intervals were obtained from Rahn et al. (1975). The expected egg mass (g) for a

TABLE 2. Hatching success of Brown-headed Cowbird and Red-winged Blackbird eggs incubated at different temperatures and 64% relative humidity.

	Temperature (°C)		
	35.0	38.0	40.0
Brown-headed Cowbird			
No. of eggs incubated	11	42	16
No. of eggs hatched (%)	0 (0)	24 (57)	0 (0)
Red-winged Blackbird			
No. of eggs incubated	15	36	20
No. of eggs hatched (%)	0 (0)	19 (53)	0 (0)

species of known average body mass (g) can be estimated from:

$$\text{egg mass} = a(\text{female body mass})^b, \qquad (2)$$

where a and b are constants for each taxonomic group (Rahn et al. 1975). Values for female cowbird and redwing body masses, 38.8 and 41.5 g, respectively, were obtained from Dunning (1993). Values of the constants (a = 0.340, b = 0.677) were obtained from Rahn et al. (1975) for passerines. I used the z-statistic to determine if individual cowbird eggs incubated at 36 or 39°C had incubation periods similar to the mean incubation period of eggs incubated at 38°C. For each species, the deviations of egg masses and incubation periods from predicted values were calculated as the proportion of the observed values to expected values.

To obtain the incubation temperature of eggs in unparasitized nests and experimentally parasitized nests, I replaced an incubating Zebra Finch (*Taeniopygia guttata*) egg with a fresh cowbird egg. Although the Zebra Finch is not a naturally occurring host of the cowbird, its body mass (ca. 12 g) is similar to that of frequently parasitized species, including Field Sparrows (*Spizella pusilla*) and Chipping Sparrows (*S. passerina*; Dunning 1993). Finch eggs are much smaller than cowbird eggs, weighing approximately 1.1 g (Williams 1996), whereas cowbird eggs are nearly three times heavier (Table 1; see Lowther 1993). To measure egg temperatures, a thermistor (YSI model 42SC telethermometer with 400 series probe) was placed 1 mm beneath the upper surface of a finch egg, i.e. approximately at the location of the blastoderm, as described by Haftorn (1978). No embryonic development took place in eggs that had a thermistor inserted, whereas others developed naturally. The temperature measurements were unlikely to be influenced by embryonic heat production, which generally is too low to be significant in small passerines (Kendeigh 1963:898). The movement of the egg with the inserted thermistor was restricted due to an attached wire probe. The remaining eggs were free to move during egg turning by the attending adult. Cowbird eggs are much larger and heavier

TABLE 3. Incubation period for Brown-headed Cowbird eggs incubated at 36.0 and 39.0°C. Only 2 of 5 eggs and 5 of 11 eggs hatched at 36.0 and 39.0°C, respectively.

Egg number	Incubation (days)	z[a]	P
36.0°C			
672A	14.04	10.39	<0.001
672B	13.96	10.04	<0.001
39.0°C			
573A	11.04	−2.43	<0.05
573B	11.25	−1.54	>0.05
574A	11.11	−2.18	<0.05
5111A	10.79	−3.50	<0.001
6111A	10.49	−4.79	<0.001

[a] All z-values obtained by comparing an egg's incubation period at a given temperature with the mean value obtained from eggs incubated at 38.0°C ($\bar{x}$ = 11.61 days, n = 24).

than Zebra Finch eggs, and they tended to rest at the bottom of the nest. Care was taken to place the egg with the inserted thermistor at the level in the nest at which it would naturally rest when not attached to a thermistor. Egg temperature was recorded continuously by a Linear Instrument electronic data logger. The mean egg temperature was determined by averaging egg temperature recorded every 6 min at a constant ambient air temperature of 22.0°C. A total of 331 and 427 observations (i.e. 6-min intervals) was recorded from: (1) a finch egg in a clutch of three other finch eggs, and (2) a finch egg in a clutch of two others and a cowbird egg, respectively. Because both sexes of Zebra Finches will incubate simultaneously, the male was removed.

RESULTS

Temperature tolerance.—No eggs hatched at 35 or 40°C, whereas 24 out of 42 (57%) and 19 out of 36 (53%) cowbird and redwing eggs, respectively, hatched at 38°C (Table 2). Subsequent candling revealed that most embryos began growth at 35°C but soon died, whereas those at 40°C survived approximately seven days.

Temperature and cowbird incubation period.—Two out of five cowbird eggs hatched at 36°C, whereas 5 out of 11 hatched at 39°C. Both eggs hatched at 36°C had significantly longer incubation periods compared with the mean of 24 eggs at 38°C, whereas each of five eggs at 39°C had shorter incubation periods (Table 3).

Egg mass.—Total observed mean egg masses for both cowbirds and redwings were lower than predicted from female body mass (Table 1). Cowbird and redwing egg masses ranged

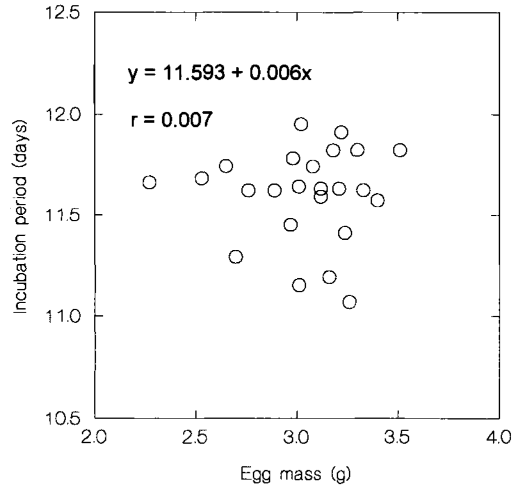

FIG. 1. Relationship between Brown-headed Cowbird egg mass and incubation period ($P = 0.974$, $n = 24$) at 38.0°C and 64% relative humidity.

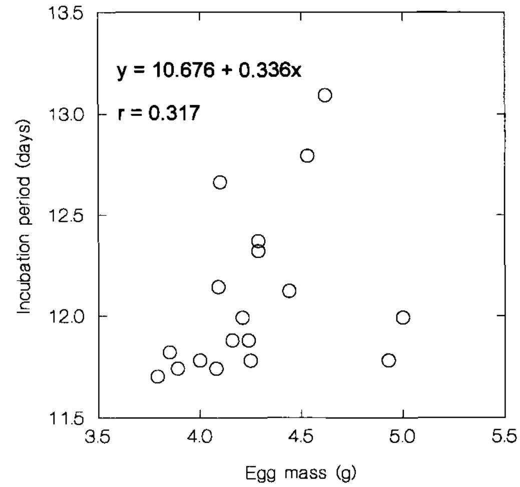

FIG. 2. Relationship between Red-winged Blackbird egg mass and incubation period ($P = 0.185$, $n = 19$) at 38.0°C and 64% relative humidity.

from 2.27 to 3.66 g ($\bar{x} = 3.04$ g) and 3.40 to 5.00 g ($\bar{x} = 4.09$ g), respectively. The expected egg mass for a passerine the mass of a female cowbird or redwing is 4.05 g (68% confidence interval 3.38 to 4.94 g; Rahn et al. 1975) and 4.24 g (68% confidence interval 3.47 to 5.16 g; Rahn et al. 1975), respectively. The ratio of observed to predicted egg mass was 0.75 for cowbirds and 0.96 for redwings.

The mean incubation period was shorter than predicted from egg mass for hatched cowbird and redwing eggs incubated at 38°C (Table 1). The incubation periods for cowbird and redwing eggs incubated at 38°C ranged from 11.08 to 11.96 days ($\bar{x} = 11.61 \pm$ SD of 0.24 days, $n = 24$) and 11.71 to 13.10 days ($\bar{x} = 12.09 \pm 0.40$ days, $n = 19$), respectively. The mean incubation period was below the lower limit of the 95% prediction interval derived from Vleck and Vleck's (1987) equation for cowbirds (12.05 to 13.77 days; predicted incubation period = 12.88 days) and redwings (12.90 to 15.28 days; predicted incubation period = 14.17 days; Table 1). For cowbird eggs, there was no correlation between egg mass and length of the incubation period (Fig. 1). For redwings, there was a positive, but not significant, correlation between egg mass and length of the incubation period (Fig. 2). The addition of a cowbird egg to the nest significantly reduced the internal temperature of the Zebra Finch egg (Table 4).

DISCUSSION

To support the hypothesis that an attribute is a specialization for parasitism, one must demonstrate that the attribute is unique to parasites. My evidence suggests that cowbirds and redwings have similar incubation temperature requirements, and that cowbirds do not have a uniquely accelerated rate of embryonic development. However, cowbird eggs were smaller than expected, which is consistent with the hypothesis that cowbirds lay small eggs that hatch sooner.

Temperature tolerance.—Given the effects of temperature on physiological and developmental processes, species may be constrained in their ability to hatch under different incubation temperatures (Dawson 1984:Table 1, Webb 1987), even if such an attribute is favorable. In

TABLE 4. Egg temperature (°C; $\bar{x} \pm$ SD) in Zebra Finch nest with and without a Brown-headed Cowbird egg. Ambient air temperature was constant at 22°C.

Nest contents	Egg recorded	Egg temperature[a]	n[b]
4 finch eggs	Finch	37.3 ± 0.74	331
3 finch eggs, 1 cowbird egg	Finch	36.8 ± 0.78	427

[a] Difference in temperatures significant (Mann-Whitney U-test, $P < 0.001$).
[b] Observation recorded every 6 min.

my experiment, failure to hatch suggests that neither species is tolerant of continuous incubation at 35 or 40°C. Cowbird eggs hatched at 36, 38, and 39°C, confirming they are able to withstand some variation in incubation temperature. For both species, 38°C may not be the optimal incubation temperature. Hatching success that I measured did not exceed 57%, whereas that of naturally incubated eggs of both species, and of avian eggs in general (not lost to total nest failure), has been found to be ≥88% and 90%, respectively (Southern 1958, Koenig 1982, Beletsky 1996:212). Other factors (e.g. lack of temperature variation) also may be responsible for the relatively low hatching success that I measured.

Incubation period.—The mean incubation period of cowbirds was 1.27 days (10%) shorter than expected based on egg mass. It is interesting to speculate that the cowbird's short incubation period is an adaptation for parasitism. However, the nonparasitic redwing had an even shorter incubation period than predicted by egg mass, hatching 2.08 days (15%) sooner. These results differ from expected values based on Briskie and Sealy (1990), who found that the mean incubation periods of host-generalist parasitic and nonparasitic icterids averaged 0.7 days shorter and 0.2 days longer, respectively, than expected from egg mass. It is unlikely that the shorter incubation periods that I observed resulted from earlier hatching of artificially incubated eggs. The incubation period for artificially incubated redwing eggs was the same as that used by Briskie and Sealy (1990) and similar to that found by others for naturally incubated eggs (Case and Hewitt 1963, Payne 1969, Strehl and White 1986). Why redwings have an apparently accelerated rate of embryonic development is unclear, but it could be due to intense sibling competion favoring earlier hatching.

Egg mass.—The mean cowbird egg mass in my study was much smaller (25%) than expected, whereas redwing eggs were only slightly smaller (4%). Huxley (1927) found that the eggs of 436 oscine species with a mean body mass of 37.92 g (i.e. similar to that of cowbirds and redwings) averaged 9% of adult body mass. Cowbird and redwing egg masses were 7.84 and 9.86% of female body masses, respectively, suggesting that cowbirds lay relatively small eggs. Small eggs may enable cowbirds to effectively parasitize small species. Cowbirds usually parasitize species smaller than themselves (Robinson et al. 1995, Scott and Lemon 1996, but see Peer and Bollinger 1998), and in captivity they have been shown to preferentially parasitize nests with eggs smaller than their own (King 1973, 1979). Alternatively, smaller eggs may enable cowbirds to lay more eggs or eggs that hatch sooner. A variety of other factors, including degree of sexual size dimorphism, are also correlated with a species' mean egg mass (Weatherhead and Teather 1994), making it difficult to draw general conclusions from two species. In an extensive study, Briskie and Sealy (1990) found that egg volumes for parasitic icterids (including the Brown-headed Cowbird) were not smaller than those of nonparasitic icterids, suggesting that parasitic icterids do not lay smaller eggs than many nonparasitic icterids. Brown-headed Cowbirds, however, may lay unusually small eggs for a parasitic icterid, or redwings may lay unusually large eggs for a nonparasitic icterid.

Although egg mass generally varies allometrically with body mass, substantial intraspecific variation exists within this general relationship (Gill 1990). In my study, egg mass of individual cowbird eggs was not correlated with length of the incubation period, indicating that small cowbird eggs do not hatch sooner. In redwings, egg mass was positively (but not significantly) correlated with length of the incubation period.

Incubation temperature.—The reported variation in the length of cowbird incubation periods may result from different mean incubation temperatures. Briskie and Sealy (1990) considered the possibility that the 10-day incubation periods they observed may have resulted from higher incubation temperatures from an unusually attentive host. In my experiment, cowbird incubation periods ranged from 10.49 to 14.04 days at 39 and 36°C, respectively. Cowbird eggs incubated at 36°C took up to 34% longer to hatch than eggs incubated at 39°C, indicating a strong temperature effect.

The ostensible paradox of cowbird eggs hatching in less time than host eggs, even when the cowbird eggs are larger (Hamilton and Orians 1965, Payne 1977, Briskie and Sealy 1990, McMaster and Sealy 1997), may be explained if they receive sufficient heat for incubation while interfering with incubation of host eggs. Egg temperatures vary widely within a nest depending, in part, on the amount of contact with the attending bird's incubation patch (Baldwin and Kendeigh 1932, Drent 1973). The addition of an egg to a clutch may decrease the efficiency of incubation because the energy costs of incubation increase by 6 to 7% for each additional egg (Haftorn and Reinertsen 1985, McMaster and Sealy 1997). Similarly, the replacement of a host's egg with a relatively larger egg, such as a cowbird's, may decrease the incubation efficiency of the host's eggs (Friedmann 1929, Huggins 1941, Hofslund 1957, Zimmerman 1983, Wiley 1985, Petit 1991, Sealy 1992, McMaster and Sealy 1997, Peer and Bollinger 1998) and result in extended incubation periods and reduced hatchability. Sayler (1996) found that Canvasback (*Aythya valisineria*) eggs in nests parasitized by Redheads (*A. americana*) often had longer incubation periods and hatched asynchronously as a result of less effective incubation due to the addition of parasitic eggs (but see McMaster and Sealy 1997). Although a larger sample size is needed to eliminate alternative explanations that may have been responsible for the observed temperature reduction (e.g. the use of a thermistor that inhibited egg movement), evidence from my experiment is consistent with the hypothesis that replacement of a host egg with a larger cowbird egg reduces the incubation temperature of host eggs. This, in turn, may result in a longer incubation period and lower hatchability of host eggs. Conversely, cowbird eggs that are relatively small compared with host eggs may receive less heat and experience longer incubation periods. As a result, host-egg size and clutch composition may affect the length of a cowbird egg's incubation period, which may help explain variation in reported cowbird incubation periods under natural conditions.

ACKNOWLEDGMENTS

I am grateful to Mary V. Ashley, Peter E. Lowther, D. Glen McMaster, William Moskoff, and Scott K. Robinson for their comments and suggestions in manuscript preparation. Additionally, I thank The Morton Arboretum for allowing me access to their site, and David E. Springer, whose assistance helped make this study possible. This work was supported in part by a grant from the National Science Foundation (IBN-9601201).

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Associate Editor: M. E. Murphy