

MECHANISMS OF SHORT INCUBATION PERIOD IN BROOD-PARASITIC COWBIRDS

GUSTAVO H. KATTAN¹

Department of Zoology, University of Florida, Gainesville, Florida 32611, USA

ABSTRACT.—Field estimates of incubation periods of brood parasitic cowbirds (*Molothrus* spp.) indicate that they are unusually short given the sizes of their eggs. As a consequence, cowbirds usually hatch before host young, even though cowbird eggs are frequently larger. Field-estimated incubation periods, however, have an inherent uncertainty because of intermittent attendance by incubating birds, and the mechanisms for early hatching are unknown. I report incubation periods of Shiny Cowbird (*M. bonariensis*) eggs under controlled conditions in the laboratory, and test the hypothesis that cowbirds exhibit accelerated rates of embryo development, by exploring two possible mechanisms for shortening the incubation period of cowbird eggs: (1) cowbird eggs may have a low energy content, which results in a short incubation period because yolk reserves are depleted earlier; or (2) cowbird embryos may have elevated growth rates, which would be reflected in their metabolic rates. Energy content of cowbird eggs was 23.8% lower than expected from egg mass. Mean incubation period in the laboratory was 11.7 days, which is 28.8% shorter than expected from egg mass, but close to the expected from energy content. Similarly, yolk-free, dry hatchling mass was lower than expected from egg mass, but not significantly different from the expected from egg energy content. These results support the hypothesis that cowbirds shorten incubation period by reducing the energy content of the egg, although it results in a slightly smaller hatchling. The hypothesis that cowbird embryos have elevated growth rates, in contrast, was not supported because embryos did not have higher metabolic rates than expected from their size. Although the evidence presented here is correlational, there is experimental evidence that reducing yolk reserves may act as a proximate cue for early hatching in other vertebrates. Received 7 June 1993, accepted 13 November 1993.

The comparatively short time the embryo takes to hatch gives it [the Shiny Cowbird, *Molothrus bonariensis*] another and a greater advantage; for whereas the eggs of other small birds require from fourteen to sixteen days to mature, that of the cowbird hatches in eleven days and a half from the moment incubation commences [Hudson 1920:66].

BROOD PARASITISM is a reproductive strategy in which a short incubation period is at a premium. Eggs of brood parasites are abandoned in nests of host species and young parasites have to compete with foster nest mates for parental resources. One strategy used to eliminate competition in the nest is displayed by parasitic Common Cuckoos (*Cuculus canorus*). Common Cuckoo eggs usually hatch earlier than their hosts. Upon hatching, the young cuckoo ejects host eggs by pushing them over the rim of the nest with its back (Wyllie 1981). Cowbirds (*Molothrus* spp.), in contrast, do not kill nest mates,

but by hatching before host young, parasitic nestlings gain an advantage in obtaining parental resources (Payne 1977). As Hudson (1920) remarked, cowbirds usually hatch earlier than their hosts, even though cowbird eggs are frequently larger (Hamilton and Orians 1965, Payne 1977, Briskie and Sealy 1990).

Friedmann (1927) suggested that a short incubation period in Brown-headed Cowbirds (*M. ater*) represented an adaptive acceleration of embryonic development. Incubation period, however, scales allometrically to the 0.217 power of fresh egg mass (Rahn and Ar 1974). Egg mass, in turn, scales to the 0.675 power of adult female body size (Rahn et al. 1975). Thus, incubation periods in parasitic cowbirds may be short because females lay small eggs, as is the case in parasitic Common Cuckoos (Rahn et al. 1975, Payne 1977, Briskie and Sealy 1990). Briskie and Sealy (1990) addressed this problem by comparing incubation period, egg size and female size of 22 species of icterines. They found that egg size in parasitic cowbirds was not smaller than expected from female size, but they had shorter incubation periods than nonpar-

¹ Present address: Wildlife Conservation Society, Apartado 25527, Cali, Colombia.

asitic icterines. Their results suggest that short incubation periods in cowbirds reflect an acceleration of embryonic development, evolved as an adaptation for brood parasitism.

One problem faced by Briskie and Sealy (1990) was the uncertainty of incubation periods estimated in the field, because of the inherent variability associated with attendance by incubating birds, and the difficulty in knowing when incubation began. This problem had previously led Nice (1953) to question the validity of reports of 10-day incubation periods in the Brown-headed Cowbird. Briskie and Sealy (1990) defined incubation period of cowbird eggs as the time from initiation of full incubation by the host to hatching. Initiation of full incubation, however, was defined as "usually just after laying of the penultimate egg" (by the host), a definition that involves a potentially large uncertainty. Incubation periods of cowbird eggs laid early in the laying cycle may be underestimated because hosts may incubate intermittently before initiating full incubation. Alternatively, intermittent incubation throughout the nesting cycle may overestimate incubation periods. To overcome this problem, Briskie and Sealy (1990) suggested measuring incubation periods of parasitic species by placing eggs in nests after the last host egg is laid. A more precise measurement, however, can be obtained by incubating eggs under controlled conditions in the laboratory.

In this paper I present measurements of incubation periods of Shiny Cowbird (*M. bonariensis*) eggs in the laboratory and field, contrast them with those of one of its hosts, and test the hypothesis that cowbirds exhibit accelerated rates of development by examining two possible mechanisms for shortening incubation periods in avian eggs. The first mechanism is based on the assumption that there is an interval of time at the end of embryonic development during which hatching can occur. Avian embryonic growth can be represented by the equation

$$W = at^b, \quad (1)$$

where W is embryo size, t is incubation time, and a and b are constants (Fig. 1A; Ricklefs 1987). Embryonic development can be divided into two phases. During the organogenesis phase there is rapid development of new tissues to form organs, but relatively little increase in embryonic mass. Following the differentiation phase comes a phase of rapid growth (increase

in embryonic mass) and functional maturation of tissues (Freeman and Vince 1974, Balinsky 1975). Thus, it is conceivable that there is a time t_a after which maturation is complete enough to allow hatching (Fig. 1A). Embryos continue to grow after time t_a and hatch at time t_c , presumably because there is an advantage in hatching at a larger size. During the final days of embryonic development, growth continues until yolk reserves are depleted (except for small amount retained as reserve for hatchling). Depletion of yolk reserves or some unknown yolk component would signal the embryo that it is time to hatch. Thus, I hypothesized that hatching time could be controlled by altering the energy content of the egg. This hypothesis is based on the existence of a correlation between incubation period and egg energy content (tighter than correlation between incubation period and egg mass) and the observation that all avian embryos expend about the same proportion of energy stored before hatching (Vleck and Vleck 1987). Assuming that the rate of energy expenditure is constant, a reduced energy content would result in a shorter incubation period. I predicted that: (1) cowbird eggs would have an energy content lower than expected from egg mass; (2) the incubation period would be shorter than expected from egg mass, but not different from the expected from egg energy content; and (3) hatchling size (W_c) would be smaller than expected from egg mass (W_e), but would correspond to the expected from egg energy content (Fig. 1A). Expected values for these variables were derived from Vleck and Vleck's (1987) review on the energetics and metabolism of avian embryos.

An alternative hypothesis is that cowbirds could shorten incubation period by increasing embryonic growth rates (Fig. 1B). In this case, I predicted that hatchling size would not be different from that expected from egg size. I also tested this hypothesis by measuring embryonic metabolic rates, under the assumption that an increased growth rate would result in an increased rate of oxygen consumption (Vleck et al. 1980). Metabolic rates of bird embryos are usually compared using the pre-internal pipping metabolic rate ($PIP-\dot{V}_{O_2}$), defined as the metabolic rate just prior to the perforation of the internal air cell of the egg, which occurs shortly before hatching (Vleck and Vleck 1987). I predicted that cowbird embryos would have higher $PIP-\dot{V}_{O_2}$ than expected from the corre-

sponding embryo size (Fig. 1C). These two hypotheses are not mutually exclusive and both mechanisms may be operating simultaneously.

METHODS

During 1990, I collected fresh Shiny Cowbird eggs from House Wren (*Troglodytes aedon*) nests at a study area in the Cauca Valley, southwestern Colombia. I collected only cowbird eggs that were laid before the wrens started laying to ensure that the eggs had not been incubated in the field. Eggs were incubated in the laboratory at a constant temperature of 38°C and turned manually six to eight times a day. After day 10, I checked the egg every 4 h during the day and every 6 h during the night to determine hatching time. Hatching was defined as the moment in which the shell started to split (actual emergence of hatching occurred 2 to 3 h after shell split). Incubation time of cowbird eggs in the field was defined as the time between the laying of the last wren egg (which is when constant incubation by female wren usually begins) and the day of hatching. Only cowbird eggs that were laid before the last wren egg were used. Also, for determination of incubation period in the field, I only used nests in which incubation had proceeded without major interruptions.

Laboratory-incubated eggs were used for measurements of embryonic metabolic rates. Metabolic rates were measured at 38°C in a Scholander-type respirometer, using the method described in Hoar and Hickman (1983). Eggs were placed in a vial (egg chamber), together with filter paper soaked in a 10% solution of KOH (CO₂ absorbent). The compensation vial contained only the CO₂ absorbent. A V-shaped tube connected vertical tubes placed above the egg and compensation chambers. The V-tube contained a small amount of water colored with anilin. The vertical tube above the animal chamber was connected to a calibrated syringe. The egg was placed in the vial and the apparatus was immersed in a water bath. I waited 10 min for temperature in the chambers to equilibrate with water temperature.

After temperatures equilibrated, I closed stopcock valves on the vertical tubes and started a measurement of oxygen consumption. After each measurement, the manometer fluid was pushed back to its original position with the syringe and the volume of oxygen consumed was read from the syringe graduations. I made at least four consecutive measurements each time and averaged them to obtain a value of oxygen consumption. Fresh air was allowed in the chamber between readings. Oxygen volumes were converted to STPD conditions.

Additional cowbird eggs were collected for measurements of energy content. I hard boiled 10 eggs and removed the shell. Energy content of the egg was then measured by bomb calorimetry at the Industrial Analysis Laboratory of the Universidad del Valle (Cali,

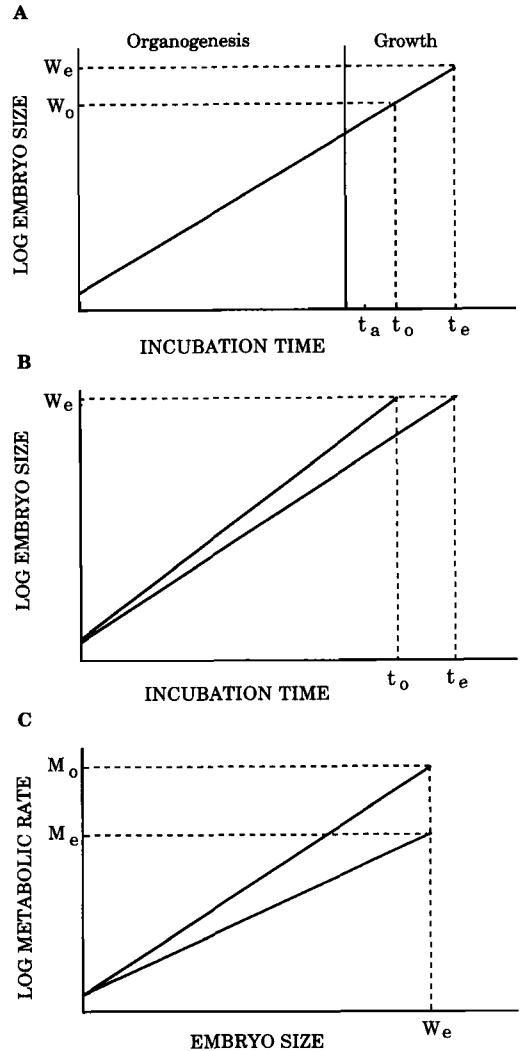


Fig. 1. Hypotheses to explain short incubation periods in cowbirds. (A) Embryo size as function of incubation time. Expected incubation time for given egg size is t_e , and hatchling size is W_e . Hypothesis that timing of hatching within period t_e-t_o determined by egg energy content. Hypothesis predicts that hatchling size (W_o) will be smaller than predicted from egg mass. (B) Alternative hypothesis is that cowbirds shorten incubation period by increasing growth rates. Hypothesis predicts hatchling size will be that expected from egg size (W_e). (C) Embryonic metabolic rate as function of embryo size. Hypothesis B predicts that metabolic rate will be higher than expected from embryo size.

Colombia). Hatchling mass was determined from laboratory-incubated eggs. I removed residual yolk from hatchlings and dried their carcasses at 70°C until a constant mass was obtained.

TABLE 1. Female size, egg size and incubation period (\pm SD, with n in parentheses) of Shiny Cowbirds and House Wrens in Cauca Valley, Colombia.

Parameter	Shiny Cowbird	House Wren
	Female size (g)	
	54.6 \pm 3.4 (47)	15.3 \pm 1.2 (16)
	Egg size (g)	
Observed	4.3 \pm 0.4 (49)	1.9 \pm 0.1 (34)
Expected ^a	5.1	2.1
	Incubation period (days)	
Observed		
Laboratory	11.7 \pm 0.5 (11)	
Field	12.0 \pm 0.8 (7)	15.3 \pm 0.8 (22)
Expected		
From egg size ^b	14.2	11.2
From energy content ^c	13.8	

^a From equation in Rahn et al. (1975) for passerines ($E = 0.34W^{0.67}$, where E is egg mass and W is female body mass).

^b From Vleck and Vleck's (1987) equation for altricial birds ($\log I = 0.97 + 0.29 \log E$, where I is incubation period and E is egg mass).

^c From Vleck and Vleck's (1987) equation for all birds ($\log I = 0.83 + 0.27 \log EC$, where I is incubation period and EC is egg energy content).

For data analyses, I compared the observed values with expected values for each parameter, derived from least-squares regressions published in Vleck and Vleck (1987). Significance of the deviations was tested by comparing values with the 95% prediction interval, calculated as described in Montgomery (1984), except for egg mass as a function of adult female body size, which was compared with the 68% confidence interval provided in Rahn et al. (1975).

RESULTS

Egg mass of Shiny Cowbirds ($\bar{x} = 4.3 \pm$ SD of 0.4 g, range 3.5–5.2 g, $n = 49$) was in the lower range of values expected from adult female body size. Egg mass expected for an average female cowbird of 54 g is 5.1 g (68% confidence interval = 4.1–6.2; Rahn et al. 1975, Table 1). The incubation period was shorter than expected from egg mass. The incubation period of Shiny Cowbird eggs under constant laboratory conditions ranged between 11.2 and 12.1 days ($\bar{x} = 11.7 \pm 0.5$ days, $n = 11$), slightly overlapping with the lower limit of the 95% prediction interval (11.8–16.9 days) derived from Vleck and Vleck's (1987) equation (predicted incubation period = 14.3 days; Table 1). The incubation period of cowbird eggs correlated significantly with egg mass (Fig. 2). Egg mass, however, explained only 44% of the variation in incubation period, suggesting that other factors are also influencing this trait.

Estimates of cowbird incubation period in the field (11 to 13 days) agreed with laboratory re-

sults, and were much shorter than the 14- to 16-day incubation periods of House Wrens (Table 1). This resulted in cowbirds hatching earlier than wrens. Cowbirds always hatched two to three days before the wrens in 15 nests in which one cowbird egg was laid before the initiation of incubation and that survived the incubation stage. The short incubation period of cowbird eggs allowed them to hatch synchronously with the wrens even when they were laid after the initiation of incubation. In eight wren nests in which a cowbird egg was laid one to four days after the last wren egg was laid, cowbirds hatched the same day or the day after the wrens.

As predicted, energy content of Shiny Cowbird eggs ($\bar{x} = 14.54 \pm 0.19$ kJ, $n = 10$) was lower than expected from mean egg mass (expected energy content = 19.05 kJ, 95% prediction interval = 16.3–22.2; Table 2). The incubation period of cowbird eggs (11.7 days) was within the limits expected from egg energy content (95% prediction interval = 11.4–16.9; Table 2). Yolk-free, dry hatchling mass of Shiny Cowbirds ($\bar{x} = 0.3091 \pm 0.04$ g, $n = 6$) was lower than the lower limit of the prediction interval expected from egg mass (expected value = 0.3786, 95% prediction interval = 0.3105–0.4613), but close to the value predicted from egg energy content (expected value = 0.2835, 95% prediction interval = 0.2371–0.3350; Table 2).

The metabolic rate of Shiny Cowbird embryos followed the typical pattern of altricial birds, with metabolic rate increasing exponentially with incubation time (Fig. 3). PIP- \dot{V}_{O_2} was cal-

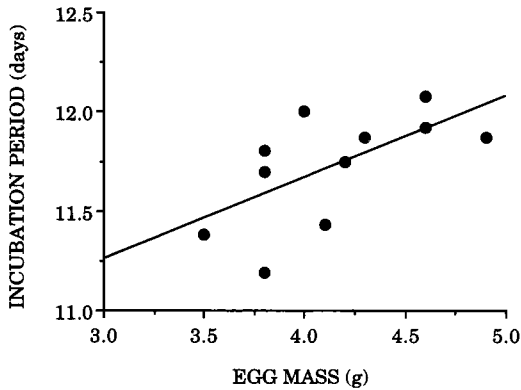


Fig. 2. Incubation period under constant laboratory conditions as function of fresh egg mass for *M. bonariensis* ($P = 0.03$, $r^2 = 0.44$, $n = 11$).

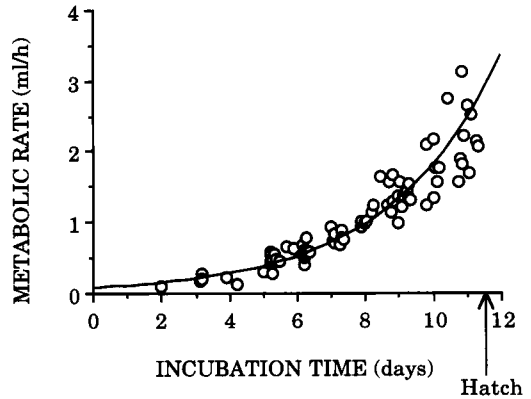


Fig. 3. Oxygen consumption (STPD) of Shiny Cowbird embryos as function of incubation time ($n = 78$ measurements on 12 eggs).

culated as the metabolic rate expected from the metabolic rate function at 90% of the mean incubation period (Fig. 3). The $PIP-\dot{V}_{O_2}$ (50.19 ml/day) was very close to the value expected from a regression of metabolic rate against energy content for altricial birds (predicted value = 47.86, 95% prediction interval = 37.9–64.4; Table 2).

DISCUSSION

Incubation of Shiny Cowbird eggs under controlled conditions in the laboratory resulted in a mean incubation period of 11.7 days. This incubation period is shorter than expected from egg size and remarkably short when compared with that of other passerines, even those smaller than cowbirds. For example, House Wrens are much smaller, but have an incubation period of 14 to 16 days (Table 1; Alvarez et al. 1984). Incubation periods of cowbird eggs under natural conditions in the field might be longer

because of intermittent attendance by the incubating bird. Estimates of cowbird incubation periods in the field, however, agree with the laboratory results (Table 1; Briskie and Sealy 1990). Incubation periods of Shiny Cowbird eggs incubated in wren nests under natural conditions varied between 11 and 13 days (Table 1). This resulted in cowbirds hatching earlier than wrens when cowbird eggs were laid before the initiation of incubation. Even when cowbird eggs were laid one to four days after the initiation of incubation, the short incubation period allowed cowbirds to hatch at around the same time as the wrens.

As predicted, I found that Shiny Cowbird eggs had an energy content lower than expected from egg mass (23.8% lower; Table 2). The incubation period was 28.8% shorter than expected from egg mass, but was closer to that predicted from energy content (Table 1). Similarly, hatchling size was smaller than predicted from egg mass

TABLE 2. Egg energy content, hatchling mass and embryonic metabolic rate (\pm SD) of Shiny Cowbirds. Expected values, as function of egg mass and egg energy content, calculated from equations in Vleck and Vleck (1987). Numbers in parentheses next to observed values are sample sizes and next to expected values are 95% prediction intervals (Montgomery 1984).

Parameter	Observed	Expected from	
		Egg mass	Energy content
Energy content (kJ)	14.54 \pm 0.19 (10)	19.05 (16.3–22.2)	
Energy used (kJ) ^a	4.45	6.95	5.28
Yolk-free, dry hatchling mass (g)	0.31 \pm 0.04 (6)	0.38 (0.31–0.46)	0.28 (0.24–0.33)
PIP- \dot{V}_{O_2} (ml/day)	50.19		47.86 (37.9–64.4)

^a Calculated as area under metabolic-rate function for $t = 0$ –11.7 (Fig. 3).

but not significantly different from that predicted from the actual energy content of cowbird eggs. These results support the hypothesis that cowbirds shorten incubation period by decreasing energy content of the egg (Fig. 1A). The alternative hypothesis that cowbird embryos have accelerated rates of development (Figs. 1B and 1C), in contrast, was not supported. Pre-internal pipping metabolic rates of Shiny Cowbird embryos were not different from the expected from a regression of $PIP-V_{O_2}$ on egg energy content in altricial birds (Table 2), suggesting that growth rates were not higher than expected based on embryonic size.

My results suggest that the mechanism by which Shiny Cowbirds shorten incubation period is a combination of laying an egg that is slightly smaller than predicted by female body size and that has a reduced energy content. Limited data available for Brown-headed Cowbirds also support this hypothesis. Reported values of egg mass and energy content are 2.9 g and 10.63 kJ, respectively (Carey et al. 1980, Vleck and Vleck 1987). The expected energy content for a 2.9 g egg is 13.1 kJ (Vleck and Vleck 1987). Brown-headed Cowbird eggs hatch in 10 to 11 days (Briskie and Sealy 1990), a period shorter than the 12.7 days expected from egg mass.

The amount of energy stored in the egg is a major factor influencing avian embryonic development (Vleck and Vleck 1987). Each egg is provided with a fixed amount of energy, which is used for growth and somatic maintenance of the embryo (except for small amount retained as residual yolk in hatchling). Energy content of the egg explains most of the interspecific variance in variables associated with embryonic development, such as incubation period, hatchling size and energetic cost of development (i.e. total energy spent during development). When these variables are regressed against egg mass, two separate lines are required to describe altricial and precocial species. This difference disappears when energy content is used as independent variable (Vleck and Vleck 1987).

The correlation between incubation period and energy content does not imply causality and the two variables may be correlated with a third, unknown variable. In a discussion of the evolution of avian altriciality, Vleck and Vleck (1987) argued that a mutation occurred that caused a shortening of the incubation period. The resulting hatchling would be smaller and

more altricial, but would have a large amount of residual yolk. At this stage, there would be selection on the female to deposit less energy in each egg. Thus, according to this interpretation, the incubation period got shorter first by an independent mechanism and then the energy density of the egg was decreased (Vleck and Vleck 1987, C. M. Vleck pers. comm.). There is experimental evidence, however, that reducing the energy content of the egg can act as a proximate cue for early hatching in other vertebrates. Sinervo (1990) manipulated energy content of eggs of the lizard *Sceloporus occidentalis* by extracting variable amounts of yolk (10–50% of total egg mass). Some eggs were sham-manipulated (poked with a syringe), but no yolk was extracted. He found that eggs with more yolk removed had shorter incubation periods than unmanipulated or sham-manipulated eggs. Eggs from which yolk was removed developed normally and hatched into viable offspring that were smaller than those from control eggs (Sinervo 1990). Sinervo (1990) also found inter-population differences in incubation time and hatchling size, among other variables, and his experimental manipulation of yolk content (i.e. energy content) demonstrated that these differences were due to differences in yolk content (reflected in egg size) among populations.

Sinervo's (1990) results lend support to the hypothesis that cowbirds could shorten incubation period by reducing the energy content of the egg. The mechanism triggering early hatching may be simply that the embryo is running out of yolk (Sinervo 1990). If there is a threshold time t_a after which hatching is possible (Fig. 1A), the amount of yolk reserve left could determine the timing of hatching. When yolk is almost depleted, the embryo would receive some signal that it is time to hatch. If more reserves are available, the embryo could continue increasing in mass. This hypothesis assumes that incubation period in altricial birds is not already minimized (i.e. that the interval t_a-t_c exists). Opposite selection for short incubation period versus large hatchling size is likely to result in the existence of this interval in which there is a balance between the two forces.

One potential problem of reducing egg energy content is that it results in a slightly smaller, more altricial hatchling. This could be a disadvantage because cowbirds have to compete with nestmates for food delivered by the foster

parents. Cowbirds, however, frequently parasitize species smaller than themselves (Friedmann and Kiff 1985). In this case, the slightly smaller hatchling size would be irrelevant, because the parasitic hatchling would still be larger than its hosts. Wren hatchlings, for example, weigh less than 2 g, as opposed to 3.2 to 4.5 g for a cowbird hatchling, and this difference increases rapidly with nestling growth (Kattan 1993). If the host species is larger than the cowbird, the latter could be at a disadvantage (e.g. Fraga 1985, Carter 1986). In this case, however, the advantage of hatching early probably outweighs the disadvantage of a slightly smaller hatchling.

This work was concerned with proximate mechanisms of short incubation period, and not with ultimate selective forces. Although my evidence is correlational, there is experimental evidence to support the idea that reducing the energy content of the egg can act as a proximate cue for early hatching (Sinervo 1990). Hatching before host young is clearly advantageous for brood parasites, but it remains unclear as to how it evolved. Incubation period has a strong taxonomic component, being shorter in nine-primaried oscines than in other passerines. I chose House Wrens as hosts because their nests were readily available, but their incubation periods may be unusually long because they are cavity nesters. Although this does not change the consequences of the difference in incubation period as regards host-parasite interaction, it prompts questions about the evolution of incubation period and egg energy content in cowbirds, compared to other passerines. What are the contributions of taxonomy and ecology to duration of incubation period and energy content of the egg in passerines? Briskie and Sealy (1990) found that, controlling for egg size, incubation periods of parasitic cowbirds were shorter than those of nonparasitic icterines. In this regard, comparative data on incubation period and egg energy content in icterines would be valuable.

A further complication is introduced by the fact that energy content of the egg may be responding to a variety of selective forces. Recent estimates of the number of eggs laid by cowbirds indicate that these are extremely fecund birds (Scott and Ankney 1983, Kattan 1993). Cowbirds lay almost continuously, without regressing the ovary and oviduct, during the en-

tire breeding season. In the North Temperate Zone, cowbirds may lay up to 40 eggs per season (Scott and Ankney 1983, Rothstein et al. 1986, Jackson and Roby 1992). My estimate of annual fecundity of Shiny Cowbirds in the Cauca Valley (Colombia), a tropical locality where cowbirds have an extended nine-month breeding season, indicates that a female may lay up to 120 eggs per year, or 9.2 times her own body mass (Kattan 1993). Life-history theory predicts a trade-off between number and quality of offspring. Increasing the number of offspring implies a decrease in the amount of energy invested in each offspring (Roff 1992). Cowbirds do not spend any energy in parental care, and probably redirect this energy into egg production. Therefore, although it is not clear whether cowbirds are energy limited, it is conceivable that the reduced energy content of cowbird eggs is a direct consequence of their extraordinary fecundity.

ACKNOWLEDGMENTS

This work is part of a doctoral dissertation submitted to the University of Florida. I thank members of my doctoral committee—L. J. Guillette, R. A. Kiltie, D. J. Levey, J. W. Fitzpatrick and S. K. Robinson—for their contribution in reducing the incubation period of ideas for this paper. Further comments by C. M. Vleck, D. Roby and S. Rothstein helped it to hatch. I thank F. Nordlie for the loan of equipment and J. Anderson for instructing me on metabolic rate measurements. Natalia Gómez provided a significant portion of the energy invested in field and laboratory work. Financial support was provided by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, the Instituto Vallecaucano de Investigaciones Científicas (INCIVA), and the Fondo de Investigaciones Científicas "Francisco José de Caldas" (COLCIENCIAS), Colombia.

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