

main with the prepared skin. From this general approach, we have been able to obtain a "naked" body suitable for fluid preservation.

An initial incision is made either down the center line of the underside or along the flank from the shoulder to near the cloaca. This and all subsequent cuts must be made carefully and without excessive penetration to avoid soft tissue damage. The skin is worked off the body, and one wing and one leg are left attached to the trunk. In skin-skeletal preparations it is possible to disarticulate the limbs, which facilitates their separation from the trunk without compromising the integrity of either the skin or skeleton. This is not possible for skin-fluid preparations. For this reason, we recommend an initial side incision. Skin and feathers should not be removed from the wing and leg that are attached to the trunk.

Inevitably there is some damage of muscle around the tail when the rectrices are detached. The skull can be removed entirely, or various amounts of the anterior section can be left, if keeping the bill with the skin is deemed important. The latter involves minor soft tissue loss.

Once the skin has been removed, the body is fixed and preserved as for any fluid specimen. This provides a representation of most of the muscles in the body. Care with skinning will minimize myological loss, but some damage to dermal muscles (and those around the tail and possibly the head) cannot be avoided. The method we describe here can also be used with flat skins or pelts. If a skeleton is desired, the bones can be removed from the preserved body as they would from any fluid specimen.

Fluid specimens obtained in this way are not as satisfactory as those prepared with entire bodies, but in certain circumstances they offer advantages. We have found the technique useful with rare taxa, when both skins and fluid specimens are at a premium (Fig. 1). It has been used with specimens needed for fluid preservation, but when the plumage condition also is of particular interest. In taxa where the plumage is important for subsequent confirmation of identification, it can be used, particularly if effects of the preservative compromise salient points.

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### Evolution of Short Incubation Periods in the Parasitic Cowbirds, *Molothrus* spp.

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A short incubation period can be advantageous for a brood parasite. By hatching before host young, parasitic nestlings can dominate intrabrood hierarchies and divert parental care away from brood nest mates (Payne 1977). Friedmann (1927) argued that the 10-

day incubation period of the Brown-headed Cowbird (*Molothrus ater*) was such an adaptation; however, Nice (1953) later summarized observations on incubation periods of 62 Brown-headed Cowbird eggs in at least 8 host nests and found that none hatched in less than

11 days. Nice concluded that the Brown-headed Cowbird incubation period was not notably shorter than that of its nonparasitic relatives. Subsequent reports have supported an 11- to 13-day incubation period for this species (e.g. 11.8 days in Prairie Warbler [*Dendroica discolor*] hosts, Nolan 1978; 12.0 days in Northern Cardinal [*Cardinalis cardinalis*] hosts, D. M. Scott pers. comm.). We report 10-day incubation periods in one nest parasitized by the Brown-headed Cowbird and, using allometric analyses, we re-address the evolutionary significance of short incubation periods in *Molothrus* cowbirds in general.

Short incubation periods do not necessarily indicate adaptive acceleration of cowbird embryo development per se because incubation period is correlated positively with egg volume (Rahn and Ar 1974). Accordingly, cowbirds may have short incubation periods, not as an adaptation to parasitism but because their eggs are smaller than other birds' eggs. To determine if parasitic cowbirds have incubation periods shorter than expected by their egg size, we corrected for the effect of egg size on incubation period by allometric regression. We used incubation periods and egg volumes, from 22 species in the Icterinae (Emberizidae), that we extracted from the literature and through personal communications. *Incubation period* was defined as the time between laying of the last egg and hatching of the last nestling in clutches where all eggs hatched (Nice 1954). We defined *incubation period for parasitic eggs* as the time from commencement of full incubation by the host (usually just after laying of the penultimate egg) to hatching. Only studies where careful attention was paid to these criteria were used (Appendix). Unavoidably, our sample is biased toward north temperate species because detailed information is lacking on most tropical and south temperate species. Where possible we used egg volumes and incubation data from the same population. When these were unavailable, we calculated egg volume from Schönwetter (1983) for birds from the same subspecies. Incubation data for Brown-headed Cowbirds were obtained from two subspecies (*M. a. ater* and *M. a. artemisiae*), so we calculated a single combined mean egg volume for this species.

We also included observations on 10-day incubation periods of two Brown-headed Cowbird eggs in a single Least Flycatcher (*Empidonax minimus*) nest at Delta Marsh, Manitoba (see MacKenzie 1982 for description of study area). We located this nest on 25 June 1985 when it contained two host eggs (last checked at 2030 CDT). Next morning (0830) one cowbird and three flycatcher eggs were present, and by 27 June the nest held a completed clutch of four flycatcher and two cowbird eggs. The similar pattern and coloration of the cowbird eggs and their appearance 24 h apart suggested both were laid by the same female (Dufty 1983). When the nest was checked at 1100 on 6 July, one newly hatched cowbird nestling was present. Most of the down was dry, which in-

dicates it was an hour or two old. The second cowbird had hatched by the same time the next day. Assuming both cowbird eggs were laid around sunrise (e.g. Hann 1941) and hatched in the order laid, then only 10 days elapsed between laying and hatching. This is the first record of a 10-day incubation period in the Brown-headed Cowbird, although incubation periods this short were recently reported for Shiny (*M. bonariensis*; Wiley and Wiley 1980) and Bronzed (*M. aeneus*; Carter 1986) cowbirds.

Incubation-period and egg-volume data were log-transformed and fitted by Model I regression. Residuals from the regression line were used as a relative measure of deviation from expected incubation period. We used Model I regression because it insures residuals are independent of the control variable (Pagel and Harvey 1988). Differences in residuals between parasitic and nonparasitic icterines were compared with a one-tailed *t*-test as we predicted a priori that parasitic species should have relatively shorter incubation periods. We also treated generalist brood parasites (Brown-headed, Shiny, and Bronzed cowbirds) separately from the specialist Screaming Cowbird (*M. rufoaxillaris*). Generalist brood parasites are fostered by a variety of hosts and might be expected to evolve an incubation period that, on average, permits them to hatch before the majority of their hosts, while a specialized parasite need only hatch before its single host species.

As reported for other birds (Rahn and Ar 1974), we found a positive correlation between incubation period and egg volume in the Icterinae ( $r = 0.66$ ,  $P = 0.0016$ ,  $n = 20$ , Fig. 1). *Minimum* incubation periods of the generalist parasitic cowbirds were 1.3 days less on average than predicted by egg size, while incubation periods were 0.3 days greater on average than predicted for nonparasitic icterines ( $t = 3.47$ ,  $df = 17$ ,  $P = 0.0015$ , one-tailed *t*-test of deviations measured in log). *Mean* incubation period also was positively correlated with egg volume ( $r = 0.64$ ,  $P = 0.0018$ ,  $n = 20$ ). Mean incubation periods of the generalist brood parasites were 0.7 days less on average than expected, while nonparasitic icterines were 0.2 days greater on average than expected from egg size ( $t = 2.29$ ,  $df = 18$ ,  $P = 0.017$ , one-tailed *t*-test). Thus, even incubation periods of 11 or 12 days that are commonly found in cowbirds fall below that expected from egg size.

One criticism of using species as the taxonomic level for analyses is that artifacts that arise from phylogenetic constraint cannot be controlled (Pagel and Harvey 1988). For example, short incubation periods may have evolved only once in the icterines and subsequently been inherited by the extant brood parasites. Therefore, by counting each species separately, the number of independent evolutionary events is overestimated and the probability of a type II error is magnified. To avoid this problem, we reanalyzed our data by calculating means for each genus and using these values in the analysis. For the genus *Mol-*

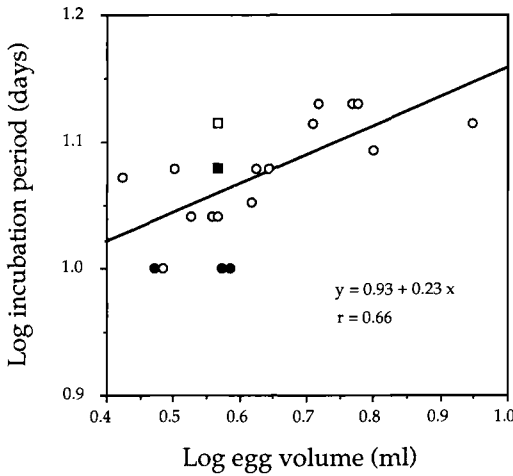


Fig. 1. Relationship between minimum incubation period and egg volume in the Icterinae. Solid circles represent the three generalist parasites (*Molothrus ater*, *M. aeneus*, *M. bonariensis*). The nonparasitic Bay-winged Cowbird (*M. badius*) and its specialist brood parasite, the Screaming Cowbird (*M. rufoaxillaris*), are represented by an open and a solid square, respectively.

*othrus*, we calculated the means for parasitic and nonparasitic species separately.

Minimum incubation period at the genus level was only weakly correlated with egg size ( $r = 0.60$ ,  $P = 0.068$ ,  $n = 9$ ), but this result was probably due to the small sample size. However, mean incubation period at the genus level was significantly correlated with egg size ( $r = 0.70$ ,  $P = 0.035$ ,  $n = 9$ ), and mean incubation periods of the parasitic cowbirds were 0.9 day less than expected, while mean incubation periods for the nonparasitic cowbirds and all other icterines were 0.1 day greater on average than expected from egg size ( $t = -1.99$ ,  $df = 8$ ,  $P = 0.04$ , one-tailed  $t$ -test). Thus, the brood parasitic cowbirds have shorter incubation periods even when possible phylogenetic constraints are controlled.

Unlike generalist brood parasites, the Screaming Cowbird has a minimum incubation period close to that expected from egg size (Fig. 1). This apparent exception actually supports our hypothesis because its only host is the nonparasitic and congeneric Bay-winged Cowbird (*M. badius*). Both species have identical egg sizes (Fraga 1983), but Screaming Cowbirds hatch approximately one day before their hosts (R. M. Fraga pers. comm.). We suggest Screaming Cowbirds evolved a shorter incubation period relative to Bay-winged Cowbirds as an adaptation to brood parasitism because it is unlikely that selection would favor the evolution of a longer incubation period in a host. The fact that all four parasitic cowbirds have

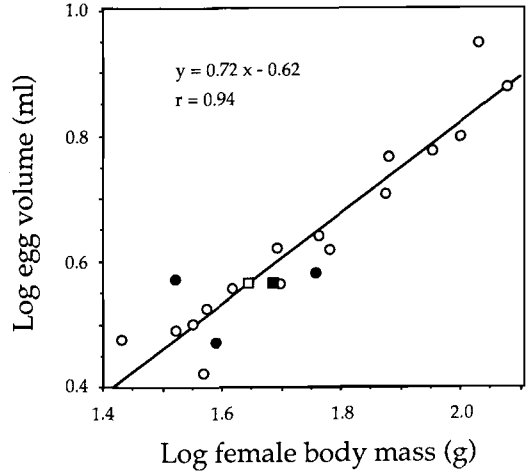


Fig. 2. Relationship between female body mass and egg volume in the Icterinae. Symbols are the same as in Fig. 1.

mean and minimum incubation periods shorter than the Bay-winged Cowbird also supports this conclusion (Fig. 1).

Next, we compared egg volume with female body mass to determine if parasitic cowbirds also shorten incubation by laying relatively smaller eggs. We obtained female body masses from Wiley and Wiley (1980), Post (1981), Fraga (1983), Dunning (1984), Robinson (1986), and Wiley (1988), and we analyzed the regression and residuals in the same manner as above. In common with other birds (Rahn et al. 1975), egg volume was highly correlated with body mass in the icterines ( $r = 0.94$ ,  $P = 0.0001$ ,  $n = 21$ ; Fig. 2) but residuals from the predicted line were not significantly different between parasitic ( $-0.014 \pm 0.037$ ,  $n = 4$ ) and nonparasitic species ( $0.003 \pm 0.010$ ,  $n = 17$ ; one-tailed  $t$ -test of deviations measured in log:  $t = -0.64$ ,  $df = 19$ ,  $P = 0.53$ ). Thus, parasitic cowbirds do not lay eggs smaller than expected from their body size.

Our observations demonstrate that some Brown-headed Cowbirds require an incubation period of only 10 days. This is shorter than reported previously for this species and shorter than expected based on egg size. Furthermore, both minimum and mean incubation periods of the generalist brood parasites were less than those found in icterines of similar egg size and less than the specialized Screaming Cowbird and the nonparasitic Bay-winged Cowbird. Such short incubation periods were not due to parasitic species laying relatively smaller eggs but due to shortened development time for a given egg size.

Payne (1977) and Davies and Brooke (1988) compared incubation periods of parasitic and nonparasitic cuckoos (Cuculidae) but did not find a significant dif-

ference between the two groups. Recently, Sibley et al. (1988) divided cuckoos into five new families. Thus, parasitic cuckoos may not be as closely related to the nonparasitic species as previously thought, and a direct comparison between the two may be complicated by taxonomic effects not related to breeding ecology (Pagel and Harvey 1988). Sibley et al. (1988) reduced the status of icterines to a tribe in the Fringillidae, so this problem does not appear to affect our analysis. Nevertheless, additional comparisons of incubation periods in these and other brood parasitic groups (e.g. ploceid finches) could provide independent tests of the hypothesis that short incubation periods evolved as an adaptation to brood parasitism, as we suggest for cowbirds.

Unlike cowbirds, cuckoo females lay eggs on alternate days. Eggs remain in the oviduct for 2 days and contain a visible embryo at laying (Liversidge 1961, Payne 1974). By initiating incubation through egg retention in the oviduct, cuckoos shorten extra-body incubation and advance hatching by a day over species that do not retain eggs. However, eggs are laid on alternate days in both parasitic and nonparasitic cuckoo species, so egg retention does not directly appear to be a strategy for brood parasitism (Payne 1977). Cowbirds normally lay daily, but to our knowledge no one has determined if embryonic development at this point exceeds that found in nonparasitic icterines. Hoffman (1929) reported that a captive Brown-headed Cowbird laid two eggs one day after capture, but whether this resulted from stress or represents a heretofore unappreciated aspect of cowbird egg-laying strategy remains unknown.

Since incubation period is correlated negatively with increasing nest attentiveness within some species (e.g. European Starling, *Sturnus vulgaris*; Ricklefs and Smeraski 1983), the incubation period of parasitic cowbirds may depend also upon host attentiveness or nest temperature. Female Least Flycatchers at Delta Marsh spent approximately 88% of the time on the nest during early incubation (Briskie and Sealy 1989a). In contrast, Davis (1959) found that Least Flycatchers in Michigan spent only 77% of the day incubating. This difference may reflect the higher productivity of arthropods at Delta Marsh, which reduces foraging costs for females and permits them to incubate more (see Briskie and Sealy 1989b). As a result, conditions for embryonic development may have been maintained longer and allowed cowbirds to hatch sooner than they would in other populations. Incubation periods of Least Flycatchers did not differ significantly between Delta Marsh ( $13.7 \pm 0.19$  days,  $n = 20$ ) and Michigan ( $13.2 \pm 0.20$  days,  $n = 5$ ;  $t = -1.38$ ,  $df = 23$ ,  $P = 0.18$ ; Walkinshaw 1966), although flycatchers at Delta also laid larger eggs than Michigan birds (Briskie and Sealy 1990), and this may have masked any difference. Cowbird eggs at Delta Marsh averaged  $2.76 \pm 0.04$  ml ( $n = 11$ ) and were similar to other *M. a. ater* (2.88 ml, no SE given; Schönwetter 1983), so

the 10-day incubation periods we observed probably were not due to cowbirds laying smaller eggs in this area.

Our analyses demonstrated that mean incubation periods of parasitic cowbirds were closer to those expected from egg size than were minimum incubation periods. This difference may result from a bias in the way incubation periods of parasitic eggs were estimated. For example, cowbird eggs laid early in the host's laying cycle may be incubated intermittently, and the incubation period (and therefore mean incubation period) will be underestimated, since incubation period is normally recorded from the laying of the host's penultimate egg. Incubation periods in nonparasitic birds are recorded using only last-laid eggs precisely to avoid this bias (Nice 1954). Alternatively, if hosts do not initiate incubation fully on the penultimate egg, cowbird incubation period will be overestimated. Ideally, incubation periods for parasitic species should be determined experimentally by placing eggs into host nests once the final host egg is laid. Both cowbird eggs we monitored were laid late in the laying cycle of the flycatcher. Because female Least Flycatchers in our population initiated full-time incubation by laying of the third egg of four (Briskie and Sealy 1989a), incubation of these two cowbird eggs likely began shortly after or as soon as they were laid, and a 10-day incubation period may represent the absolute minimum for this species.

Despite the advantage of hatching before host nestmates, hatching too early can be costly also. Kemal and Rothstein (1988) found Red-winged Blackbirds (*Agelaius phoeniceus*) regularly ejected broken eggs from their nests through day 9 of incubation. They considered this behavior adaptive because it ensured that cracked or broken eggs would not soil the nest or attract parasites. After 10 days of incubation, this behavior ceases because, in ejecting cracked eggs, a parent might inadvertently remove its own pipped eggs. Conceivably, brood parasites with incubation periods shorter than 10 days could be mistaken for damaged eggs and removed. If ejection behavior persists longer in other hosts, selection against cowbird incubation periods less than 11 days may be particularly intense and may explain why incubation periods this short are rare in parasitic cowbirds.

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APPENDIX. Egg volumes<sup>a</sup> and incubation periods<sup>b</sup> in the Icterinae. Sample sizes are in parentheses.

Species	Egg size (ml)		Incubation period (days)		
	Vol.	Source	Range	$\bar{x}$	Source
<i>Molothrus ater</i>	2.97 (222)	Schönwetter 1983	10-14	11.9 (72)	Nice 1953, Nolan 1978, this study
<i>M. aeneus</i>	3.83 (61)	Schönwetter 1983	10-12	11.0 (4)	Carter 1986
<i>M. bonariensis</i>	3.75 (225)	Schönwetter 1983	10-12	11.7 (15)	Wiley and Wiley 1980, Fraga 1978
<i>M. rufoaxillaris</i>	3.68 (255)	Fraga 1983	12	12.0 (10)	R. M. Fraga pers. comm.
<i>M. badius</i>	3.68 (226)	Fraga 1983	13-14	13.1 (7)	R. M. Fraga pers. comm.
<i>Cacicus cela</i>	5.12 (85)	Schönwetter 1983	13-14	13.4 (38)	Robinson 1986, S. K. Robinson pers. comm.
<i>X. xanthocephalus</i>	4.20 (134)	Schönwetter 1983	12-13	12.3 (71)	Fautin 1941
<i>Dolichonyx oryzivorus</i>	2.65 (100)	Schönwetter 1983	11.8-13.3	12.4 NA	Martin 1971
<i>Sturnella magna</i>	5.86 (201)	Schönwetter 1983	13.5-16	14.8 (2)	Lanyon 1957
<i>S. neglecta</i>	5.98 (206)	Schönwetter 1983	13.5-15.5	14.1 (7)	Lanyon 1957
<i>S. loyca</i>	5.20 (11)	Gochfeld 1976	13.5-14.5	13.9 (4)	Gochfeld 1976
<i>Euphagus cyanocephalus</i>	4.39 (336)	Schönwetter 1983	12-13	12.8 (5)	Williams 1952
<i>Agelaius phoeniceus</i>	3.61 (44)	Spaw & Rohwer 1987	11-14	12.1 (17)	Payne 1969
<i>A. icterocephalus</i>	3.00 (50)	Schönwetter 1983	10-11	NA (19)	Wiley and Wiley 1980
<i>A. tricolor</i>	3.68 (53)	Schönwetter 1983	11-14	11.9 (28)	Payne 1969
<i>A. xanthomus</i>	3.17 (59)	Wiley 1988	12-13	12.5 (2)	Post 1981
<i>Quiscalus mexicanus</i>	8.85 (62)	Skutch in Bent 1958	13-14	13.3 (6)	Skutch in Bent 1958
<i>Q. quiscula</i>	6.31 (159)	Schönwetter 1983	12.4-14.2	13.2 (7)	Maxwell and Putnam 1972
<i>Q. lugubris</i>	4.17 (526)	D. Lemmon pers. comm.	11.3-13.0	12.0 (13)	D. Lemmon pers. comm.
<i>Q. major</i>	7.57 (21)	Bancroft 1984	NA	13.1 NA	Bancroft 1984
<i>Icterus galbula</i>	3.10 (55)	Pank 1974	NA	11.6 (23)	Pank 1974
<i>I. parisorum</i>	3.36 (89)	N. J. Flood pers. comm.	11-15	12.8 (33)	N. J. Flood pers. comm.

<sup>a</sup> Calculated from measurements given in source using the formula:  $V = 0.498LB^2$  (Spaw and Rohwer 1987).

<sup>b</sup> NA = no information available.