

**AN EXPERIMENTAL INVESTIGATION OF STRATEGIES USED BY BROWN-
HEADED COWBIRDS TO OPTIMIZE PARENTAL CARE**

BY

DONALD GLEN M^cMASTER

**A thesis presented to the University of Manitoba, Department of Zoology,
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy**

Winnipeg, Manitoba

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ABSTRACT

This study tested hypotheses concerning strategies used by Brown-headed Cowbirds (*Molothrus ater*) to optimize parental care during the host's laying, incubation, and hatching periods. To test if female cowbirds remove host eggs from parasitized clutches to reduce the volume of eggs to a level the host can incubate effectively, live cowbird eggs were placed in Yellow Warbler (*Dendroica petechia*) nests. Hatching success of cowbird eggs was significantly greater in clutches from which one host egg was removed than clutches from which no host egg was removed in one of the three years of study. Removal of a host egg, therefore, is not required for successful hatching of cowbird eggs in all years, but may increase hatching success in certain years. Cowbird eggs were artificially incubated both in warbler clutches and in isolation to test whether the short incubation period of cowbird eggs is due to (1) cowbird embryos developing more rapidly than host embryos, (2) cowbird eggs gaining more heat than host eggs due to their larger size, or (3) cowbird embryos hatching in response to stimuli from host eggs. Cowbird eggs incubated in isolation took longer to hatch than either host eggs or naturally incubated cowbird eggs. Cowbird eggs incubated in warbler clutches, however, hatched at the same time as host eggs. These results suggest cowbird eggs receive more heat than smaller host eggs under natural conditions, and hatch slightly sooner in response to stimuli from host eggs. Finally, I added cowbird eggs and nestlings to warbler clutches to test whether the presence of a cowbird alters parental behaviour during the laying and hatching periods. Cowbird nestlings were brooded and fed more than warbler nestlings during the hatching period, but parental behaviour was unaltered during the laying period.

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GENERAL INTRODUCTION

Avian brood parasites exploit the parental care of other bird species, the hosts, although the amount of care received depends upon whether nestlings are altricial or precocial (Payne 1977). Parasites usually reduce host reproductive success by removing host eggs from parasitized nests (Sealy 1992), reducing the hatching success of remaining host eggs (Røskaft et al. 1990), and killing or out-competing host nestlings (e.g. Friedmann 1955, 1963; Wyllie 1981). Brown-headed Cowbirds (*Molothrus ater*, hereafter cowbirds) are generalist brood parasites known to have parasitized over 220 species (Friedmann and Kiff 1985). Much of the early research on cowbirds consisted of cataloguing the species parasitized, identifying species that successfully rear cowbirds, and the cost of rearing cowbirds to their own reproductive success (e.g. Friedmann 1929, 1963). This type of research continues to be important, especially given the conservation implications of cowbird parasitism (Brittingham and Temple 1983, Rothstein and Robinson 1994, Robinson et al. 1995). In the mid-1970's, however, Stephen I. Rothstein pioneered experimental studies of coevolution between cowbird and host species (e.g. Rothstein 1975a). Rothstein's work began a period of research investigating parasite-host interactions that focused on the responses of hosts to parasitism, including discrimination between parasitic and host eggs (e.g. Rothstein 1975b) that continues today (e.g. Sealy 1995, 1996). Hypotheses concerning cowbird behaviour and breeding biology have been more difficult to test experimentally, because unlike other passerines, cowbirds are not tied to a nest during the breeding season. Many studies, therefore, have relied on captive birds (e.g. Jackson and Roby 1992, Freeberg 1996), sacrificed birds (e.g. Scott and Ankney

1983), or field observations (e.g. Duffy and McCrystal 1992, Sealy et al. 1995) to test hypotheses. Recently, techniques using radio-telemetry and genetic markers have enabled researchers to gain an understanding of cowbird diurnal movements and mating systems, respectively (Rothstein et al. 1984, Fleischer 1985, Gibbs et al. 1997). However, few studies have experimentally tested hypotheses concerning strategies these brood parasites may use under natural conditions to optimize host parental care.

The objective of the present study was to use experimental techniques to test hypotheses concerning the impact of cowbirds on host behaviour and breeding success during the laying, incubation and hatching periods. Laying, incubation and hatching periods influence the development and growth hierarchies of most bird species (Ricklefs 1993) and, therefore, are likely to be critical periods affecting the fledging success of parasitic cowbird nestlings that are competing for food with host nestlings. For this reason, and because the scarcity of live cowbird eggs have prevented researchers on other study areas from experimentally testing such hypotheses, I chose these periods for study.

In Chapter 1, the 'host incubation limit' (Davies and Brooke 1988) and 'insurance of first hatching' (Berger 1951) hypotheses were examined. Davies and Brooke (1988) hypothesized that hosts may not be able to incubate effectively clutches enlarged by the addition of a parasitic egg, and that female brood parasites may remove host eggs from parasitized nests to ensure their own egg is incubated effectively. Berger (1951) suggested that the function of host egg removal by female cowbirds is to eliminate a host nestling that could otherwise hatch simultaneously with the cowbird, and thereby increase the probability that the cowbird chick will hatch first and gain a competitive advantage.

In Chapter 2, I tested three hypotheses about the short incubation periods of cowbird eggs. Cowbird eggs usually hatch before Yellow Warbler (*Dendroica petechia*) eggs in naturally parasitized nests. Previous researchers have proposed two possibilities for this pattern: cowbird embryos develop more rapidly than host embryos (Friedmann 1927), or the large size of the cowbird egg shields the smaller host eggs from the brood patch (Mayfield 1992), thereby lengthening their incubation period. I tested the first alternative hypothesis by artificially incubating eggs of both species to determine incubation periods under constant conditions of temperature and humidity. These data were then compared with incubation periods in natural nests to test the second alternative hypothesis. In 1996, I tested a third hypothesis that could account for the short incubation period of the cowbird. This is the possibility that cowbird embryos hatch in response to clicking, or other stimuli, from host eggs in the clutch during the last one or two days of the incubation period. To test the hypothesis I artificially incubated cowbird eggs in contact with clutches of Yellow Warbler eggs. I also tested whether there is a limit to how early cowbird nestlings can hatch relative to host nestlings (Kemal and Rothstein 1988) by adding cowbird eggs close to hatching to Red-winged Blackbird (*Agelaius phoeniceus*) clutches that were mid-way through incubation.

In Chapter 3, I tested hypotheses concerning whether cowbird nestlings manipulate adult host behaviour, and the subsequent impact of cowbird nestlings on those of the host. Warbler nests were observed during the laying period to determine whether the presence of a cowbird egg increases female nest attentiveness (Morel *in* Payne 1973:43). Warbler nest temperatures were measured to verify that females apply heat to the clutch when

attentive during the laying period, and the periodicity of nest temperatures during laying and incubation was determined. Warbler nests were observed during the hatching period to determine whether early hatching by cowbirds stimulates the host female to incubate the remaining eggs less and, thus, reduce the hatchability and retard development of host eggs (e.g. Dolan and Wright 1984, Petit 1991).

STUDY SPECIES

The Brood Parasite

The Brown-headed Cowbird is a relatively small icterine (males, 40 - 50 g; females, 36 - 45 g), whose breeding range once was limited to prairie and parkland habitats, but now breeds across much of North America (Lowther 1993). Three subspecies have been described, of which only *M. a. ater* occurs in Manitoba. The sexes are dimorphic with males having a glossy greenish-black body and brown head, while females are plain brown. Cowbirds frequently forage on the ground, often in association with large ungulates, and eat seeds and insects. Female cowbirds may supplement their diet with mollusc shells (Ankney and Scott 1980) and eggs removed from host nests (Scott et al. 1992).

Cowbirds never build their own nests. They lay their eggs in nests of other species, the hosts, which then raise the cowbird young. Over 140 host species have successfully reared cowbird young (Friedmann and Kiff 1985). The Yellow Warbler is one of the most frequently reported species parasitized by cowbirds (Friedmann 1963). Cowbirds lay their eggs shortly before sunrise (Scott 1991, Neudorf and Sealy 1994) and usually take less than one minute to lay (Sealy et al. 1995). Females appear to lay several separate clutches through the breeding season, with estimates of egg production averaging 40 eggs per season (Scott and Ankney 1980).

The Hosts

Yellow Warblers are small insectivorous passerines (approx. 10 g for both males and females) that nest at high densities at Delta Marsh, Manitoba. Female Yellow Warblers

build the nest, incubate the eggs, and brood the nestlings. Eggs are laid shortly before 0600 (CST; Sealy 1992). Incubation averages 10 - 12 days from laying to hatching of the last egg (Schrantz 1943, Bent 1953, Goossen 1978). Clutches hatch asynchronously, with approximately 1 to 2 days elapsing between the hatching of the first and last nestlings, depending on the year and clutch size (Hébert 1991). Male warblers feed the female at the nest throughout the laying and incubation periods, and feed both the female and the nestlings once hatching occurs (Biermann and Sealy 1982, Sutherland 1987). Five eggs is the modal clutch size ($\bar{x} = 4.5$ eggs) at Delta Marsh (Goossen and Sealy 1982, Sealy 1992). Yellow Warblers are frequently parasitized by cowbirds at Delta Marsh, with parasitism frequencies averaging 20% per year (Sealy 1995).

Red-winged Blackbirds are common marsh-nesting birds that also nest at high densities at Delta Marsh. Blackbird clutch sizes range from 3 to 5 eggs and incubation periods range from 11 to 14 days (Payne 1969). Female blackbirds build the nest, incubate the eggs, and brood the nestlings. Red-winged Blackbirds accept cowbird eggs (Ortega and Cruz 1988) and they are commonly parasitized where they co-occur with cowbirds (Friedmann 1963).

STUDY AREA

The study was conducted in the forested dune ridge and adjacent marsh at Delta Marsh, Manitoba, Canada (58° 11' N, 98° 19' W, see Mackenzie 1982). Insects are extremely abundant on the study area (Busby and Sealy 1979, Biermann and Sealy 1982, Mackenzie et al. 1982), which enables many species of passerine birds to nest at high densities (Goossen and Sealy 1982). However, insect abundances vary daily, seasonally, and yearly (Briskie 1986, Guinan and Sealy 1987, Pohajdak 1988, Hébert 1991). Yellow Warblers nest both in the forested dune ridge and marsh, whereas Red-winged Blackbirds nest almost exclusively in the marsh. Cowbirds are active on the study area throughout the day, with high concentrations occurring along the dune-ridge/marsh ecotone (pers. obs.). The main study site for this project stretched 3 km along the dune ridge west from the Assiniboine River Diversion to Cram Creek, spanning the properties of the University of Manitoba Field Station (Delta Marsh) and Portage Country Club. Additional work (mostly inspecting host nests for cowbird eggs) was conducted on University of Manitoba Field Station (Delta Marsh) properties east of the spillway and at Oxbow Woods, and on the properties of the Bell Estate east of the hamlet of Delta.

CHAPTER 1

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

INTRODUCTION

Females of many avian brood parasites remove eggs from nests during the breeding season. These eggs usually are those of the host, and they are removed in association with the laying of the parasite's own egg (Sealy 1992). Egg removal reduces the number of host offspring that can be raised, and numerous workers have suggested that this behaviour may increase the parasite's reproductive success (Davies and Brooke 1988, Rothstein 1990). Female Brown-headed Cowbirds generally remove eggs from host nests (Friedmann 1963), but the number of eggs removed and the timing of egg removal vary among the host species (e.g. Mayfield 1961, Zimmerman 1963, Sealy 1992). The fact that cowbirds make additional visits to host nests in order to remove host eggs (Scott et al. 1992, Sealy 1994) and, in doing so, increase the risk of encountering hosts, suggests that egg removal is an important cowbird strategy.

Sealy (1992) reviewed six hypotheses to explain the function of host-egg removal by female brood parasites and suggested that the incubation limit hypothesis (Davies and Brooke 1988) was the most deserving of further testing. The host incubation limit hypothesis proposes that the addition of a parasitic egg could increase clutch size above

that which the host can incubate effectively (Hofslund 1957, Friedmann 1963, Post 1981, Fraga 1983, Kendra et al. 1988). Incubating females must use more energy to maintain egg temperature in large clutches (Biebach 1981, Moreno et al. 1991), but because the amount of heat energy that can be produced and transferred to the clutch is limited physiologically (Tøien 1989) egg temperatures may fall as clutch size increases (Batt and Cornwell 1972, Mertens 1977). Because most bird eggs must be maintained within a narrow range of temperatures for normal embryonic development (Webb 1987), extended cooling may reduce the hatching success of both host and parasitic eggs (Wyllie 1981, Davies and Brooke 1988). Therefore, by removing a host egg the female parasite may reduce the total clutch size to within the host's incubation limit, and it may increase the probability that her own egg will hatch (Davies and Brooke 1988). Hofslund (1957) calculated that the addition of one cowbird egg to a Common Yellowthroat (*Geothlypis trichas*) clutch of 4 eggs increased the volume by 50%. Therefore, removing a host egg would appear to be especially important for cowbirds that parasitize species whose eggs are smaller than cowbird eggs.

I tested the host incubation limit hypothesis by placing live cowbird eggs into nests of the Yellow Warbler. I predicted that cowbird eggs would have higher hatching success in clutches where one host egg had been removed than in clutches where no host eggs had been removed. I assumed that differences in egg size between host and cowbird eggs would not affect the amount of heat each egg received (Huggins 1941). Therefore, I predicted that warbler eggs would have higher hatching success in parasitized clutches where a host egg had been removed, than in clutches where no host eggs had been

removed. I predicted this even though Yellow Warbler eggs are 33% smaller in volume than cowbird eggs (Sealy 1992) and may have different temperature tolerances than cowbird eggs (see Groebbels and Möbert 1930, Graber 1955, Webb 1987). Inefficient transfer of heat to eggs in enlarged clutches also may prolong incubation (Smith 1989), increase hatching asynchrony (Slagsvold 1982, Moreno and Carlson 1989, Hébert and Sealy 1992), and reduce hatching success and survival of young (Hills 1980, Kendra et al. 1988, Evans 1990, Moreno et al. 1991). Therefore, I also predicted that in enlarged clutches where no host egg was removed, eggs should have longer incubation periods and hatch more asynchronously.

In addition to the incubation limit hypothesis, four alternative (but not necessarily mutually exclusive) hypotheses could explain the function of host egg removal behaviour by cowbirds. The nature of this study did not allow me to test the predictions of two of these hypotheses (i.e. females remove eggs to eat them [Scott et al. 1992] or to reduce competition for the cowbird nestling [Mayfield 1960, Blankespoor et al. 1982]). Moreover, I did not test whether egg removal reduces the potential for egg wear and breakage in large clutches (Lerkelund et al. 1993) because of the difficulty in distinguishing between the host removing damaged eggs or nestlings that died soon after hatching, and partial predation. I was able, however, to test the predictions of the remaining alternative hypothesis. Berger (1951) suggested that by removing a host egg early in the laying period, female cowbirds eliminate one of the earliest hatching host nestlings, thereby maximizing the likelihood that the cowbird chick hatches first and gains a competitive advantage. Consequently, I examined whether cowbird eggs were more

likely to hatch first in clutches where the first-laid host egg had been removed than in those where no host egg had been removed.

METHODS

Experimental Procedures

In 1992, 1993, and 1995 Yellow Warbler nests found before clutch initiation were monitored daily until the first egg was laid (laying day 1 = LD1). On LD1, one of three treatment groups was assigned at random to each nest to test possible manipulation of host incubation behaviour by cowbirds. Treatment 1 consisted of switching one viable cowbird egg for one warbler egg. In Treatment 2, a single cowbird egg was added, but the host egg was not removed. Yellow Warblers often bury cowbird eggs laid before LD2 (Clark and Robertson 1981), but not in experimentally parasitized nests (Sealy 1995). Treatment 3 (hereafter control) was a control where cowbird eggs were neither added nor host eggs removed. Most cowbird eggs were added on the morning of LD1 (0700 to 1100), although some eggs were added later in the afternoon of LD1 (1200 to 1300). Because Yellow Warblers spend little time incubating until LD 3 or 4 (Hébert and Sealy 1992), eggs added in the afternoon of LD1 would have missed little (if any) incubation. Late in the season, when cowbird eggs were in short supply, some cowbird eggs were added as late as LD3 of the laying cycle. Cowbird eggs added after LD1 were used only for calculation of hatching success. Daily nest checks continued until the host finished laying.

Freshly laid cowbird eggs were obtained from naturally parasitized nests of 6 different species in the Delta Marsh area. Only freshly laid cowbird eggs that had been exposed to minimal incubation (i.e. were laid during early laying, or preferably before the host's clutch was initiated) were used in the experiment. If possible, cowbird eggs were

added to Yellow Warbler clutches on the same day they were collected. If no warbler clutches were available for parasitism, eggs were kept overnight in an egg crate in a refrigerator at 10°C. Cool temperatures arrest embryonic development and allow the embryo to remain viable longer (Drent 1975). In 1995, additional cowbird eggs were obtained from wild females that were held in captivity for up to 3 nights.

When warbler nests were experimentally parasitized on LD1, it was impossible to know whether the female would lay 4 or 5 eggs. Therefore, to keep the number of host eggs constant, freshly laid host eggs from other nests were transferred to complete 4-egg clutches to ensure that all nests had 5 eggs. When necessary, extra warbler eggs were added the day after the last warbler egg was laid (because I could not know whether the "last egg" was indeed the last egg until the next day). Fewer than 25% of clutches within the three treatment groups required extra warbler eggs.

All cowbird eggs were measured. In 1992, all Yellow Warbler eggs were numbered and measured once the clutch was complete. Cowbird and Yellow Warbler egg volumes (ml) were calculated using the formula (Hoyt 1979, Mills 1987):

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

where L = egg length, B = egg breadth, and $k = 0.515$ for cowbird eggs and 0.497 for Yellow Warbler eggs. Clutch volumes were then compared between each treatment group. Yellow Warbler eggs were not measured in 1993 or 1995.

During the incubation period in 1992, nests were checked every other day as part of another study, but in 1993 and 1995 nests were checked only once mid-way through the incubation period to minimize predation. Nest checks were renewed the day before the

eggs were expected to begin hatching and continued daily until all eggs hatched. Cowbird and warbler eggs that remained unhatched for several days after the other eggs had hatched were removed and opened to record the stage of embryonic development. Egg contents were examined with the unaided eye for signs of an embryo. Because embryonic mortality may occur before an embryo is visible, all eggs that did not hatch were recorded as hatching failures, even when no embryo was apparent.

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

Data Analyses

All statistical tests were performed using SPSS and followed procedures outlined in Schlotzhauer and Littell (1986) and Kleinbaum et al. (1987). Data were first tested for normality using the Kolmogorov-Smirnov *D*-test. Data for 4- and 5-egg clutches were examined separately when sample sizes were large enough and were combined if found to be statistically equal. Clutch volumes were compared among treatments using ANOVA (SPSS). Within a clutch individual Yellow Warbler eggs are not independent data points. Therefore, the proportion of Yellow Warbler eggs hatching successfully was calculated for each nest and compared between treatments using ANOVA, with Bonferroni *t*-tests ($P < 0.05$ level) for multiple comparisons. Nests from which warbler eggs disappeared were not included in the analysis. Cowbird hatching success was compared among treatments using Fisher exact tests. Because incubation period, hatching spread, daily precipitation, and daily anemometer readings were not normally distributed, differences among treatments for these variables were analyzed using Kruskal-Wallis *H*-tests. When Kruskal-Wallis indicated significant differences among treatments, I conducted multiple comparisons (Student-Neuman-Keuls test).

Logistic Regression Analysis

The experiment was replicated over 3 breeding seasons, which introduced the possibility that annual variability in weather or prey density could influence hatching success. To ascertain if weather differed between years, the mean daily temperature deviation from the long-term average was calculated for each day of each breeding season

by subtracting the mean daily ambient temperature as recorded at the University of Manitoba Field Station (Delta Marsh) Meteorological Station, from the 30-year mean temperature for that day (1951-1981, Environment Canada 1988). The mean daily temperature deviations from the long-term average were added together to give a running cumulative deviation from the 30-year average temperature for each breeding season (see Myers and Pitelka 1979).

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

RESULTS

Hatching Success

In 1992, clutch volume differed significantly among treatments ($F = 60.58$, $P < 0.0001$; Control $\bar{x} = 7.17$ ml, $n = 22$; Treatment 1 $\bar{x} = 8.57$ ml, $n = 29$; Treatment 2 $\bar{x} = 9.91$ ml, $n = 18$). Yellow Warbler hatching success differed significantly among treatments in 1992, but not in 1993 or 1995 (Table 1). In 1992, warbler hatching success was significantly higher in control clutches than in parasitized clutches where no warbler egg had been removed ($P < 0.05$). Warbler hatching success was higher in parasitized clutches from which one warbler egg had been removed than clutches from which no egg had been removed in 1992, but the difference was not significant ($P > 0.05$). Although Yellow Warbler hatching success did not differ significantly between treatments in 1993, the trend was similar to that in 1992, with hatching success increasing as clutch volume decreased (Table 1). When all three years of warbler hatching data were pooled, control clutches had significantly higher hatching success ($P < 0.05$) than parasitized clutches where no host egg was removed (Table 1).

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

Most cowbird eggs hatched either before or on the same day the first Yellow Warbler egg hatched (Table 3). Because hatching order did not differ among the 3 years

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

Year	Treatment			<i>F</i> (<i>P</i>) ^a
	Control	One host egg removed, one cowbird egg added	No host egg removed, one cowbird egg added	
1992	0.95 \pm 0.04 (12)	0.83 \pm 0.04 (18)	0.73 \pm 0.06 (8)	4.83 (0.01)
1993	0.87 \pm 0.03 (20)	0.8 \pm 0.07 (14)	0.72 \pm 0.05 (5)	1.34 (0.27)
1995	0.91 \pm 0.04 (30)	0.97 \pm 0.02 (19)	0.86 \pm 0.07 (10)	1.28 (0.29)
Total	0.90 \pm 0.02 (62)	0.88 \pm 0.03 (51)	0.78 \pm 0.04 (23)	3.40 (0.04)

^a *F*-statistic comparing hatching success among the treatments within each year.

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

Year	Treatment		<i>P</i> ^a
	One host egg removed, one cowbird egg added	No host egg removed, one cowbird egg added	
1992	75.0 (28)	30.8 (13)	0.014
1993	75.0 (20)	75.0 (16)	1.0
1995	86.4 (22)	89.5 (19)	1.0
Total	78.6 (70)	68.8 (48)	0.283

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

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

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

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

($\chi^2 = 3.59$, $df = 4$, $P = 0.46$), data were combined by treatment. The hatching order of parasitized clutches for the 3 years was not significantly influenced by treatment ($\chi^2 = 2.57$, $df = 2$, $P = 0.28$; see Table 3). Therefore, host-egg removal did not promote hatching of cowbird eggs before warbler eggs.

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

Weather

1995 was much warmer than either 1992 or 1993 ($H = 32.51$, $df = 2$, $P = 0.0001$; Student-Neuman-Keuls test, $P < 0.05$; see Figure 1). Neither the median amount of precipitation ($H = 1.82$, $df = 2$, $P = 0.4025$) nor wind ($H = 4.87$, $df = 2$, $P = 0.0874$) differed significantly among years (Table 6).

Logistic Regression

Combined across years, only year successfully predicted cowbird hatching success (see Table 7; Wald = 7.42, $df = 1$, $P = 0.0064$; Model $\chi^2 = 8.12$, $df = 1$, $P = 0.0044$; $n = 110$). Subsequent tests blocking by year revealed that treatment in 1992 (Wald = 3.79, $df = 1$, $P = 0.051$) and cumulative temperature during the laying period in 1993 (Wald = 3.47, $df = 1$, $P = 0.062$) were related to cowbird hatching success. However, neither the

FIGURE 1. The cumulative deviation in mean daily temperature (°C) from the 30-year mean temperature at Delta Marsh, Manitoba, plotted over three Yellow Warbler breeding seasons. The horizontal line represents 0 deviation from the 30-year mean. Lines above and below the horizontal are warmer and cooler, respectively than the 30-year average. Arrows indicate the date the first Yellow Warbler clutch was initiated in each year.

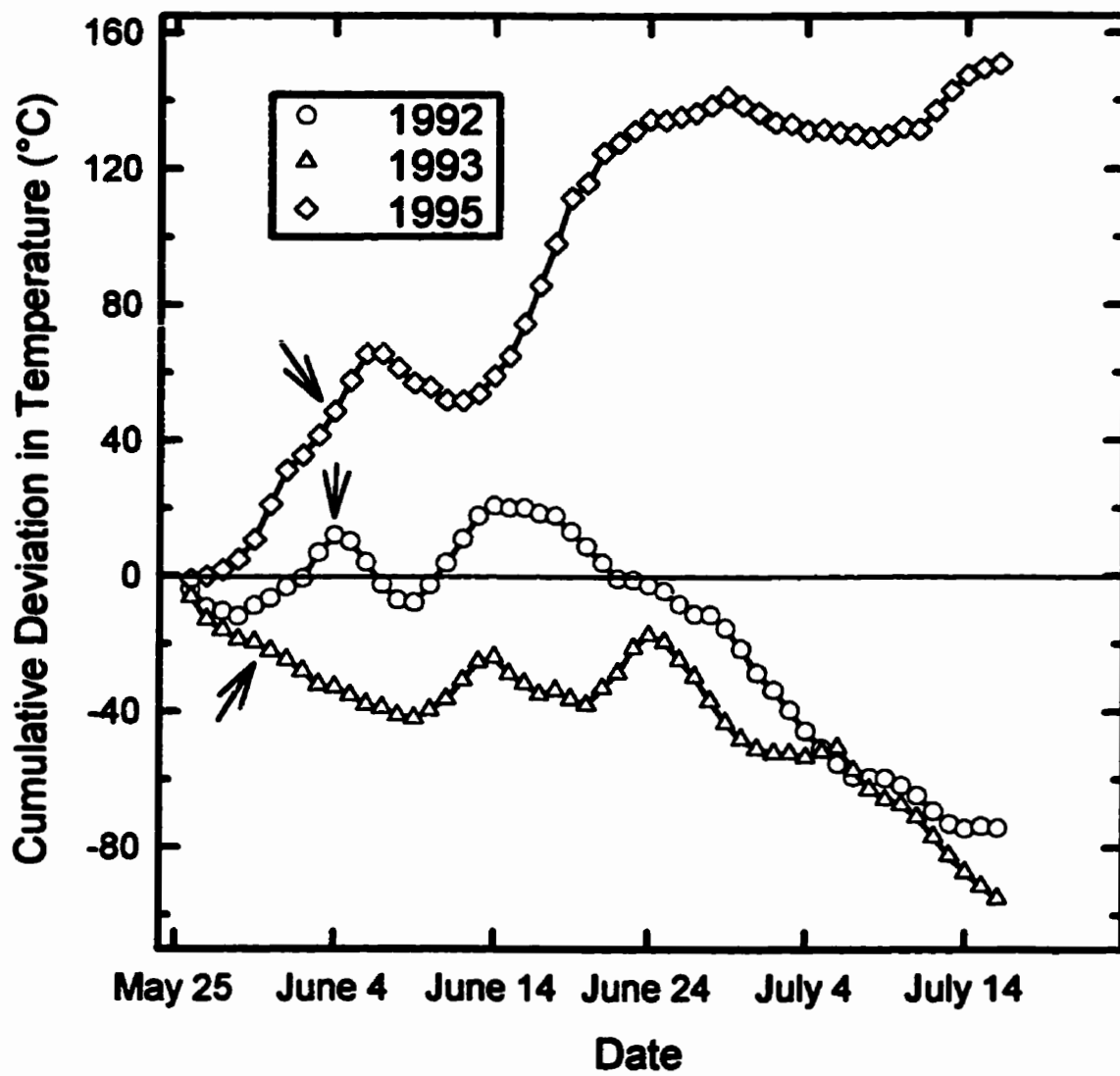


TABLE 4. Incubation period ($\bar{x} \pm SE$ in days, n in parentheses) of experimentally parasitized Yellow Warbler clutches^a.

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

^a Year comparison, $H = 2.44$, $P = 0.12$; treatment comparison, $H = 1.08$, $P = 0.343$;
treatment x year interaction, $H = 1.74$, $P = 0.161$.

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

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

^a Year comparison, $H = 26.38$, $P = 0.0001$; treatment comparison, $H = 1.32$, $P = 0.269$; treatment x year interaction, $H = 10.12$, $P = 0.0001$.

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

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

^a Number of days during the breeding season with at least a trace of precipitation.

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

Explanatory variable ^a	Combined years model	Individual years model		
		1992	1993	1995
CTEGG	0.9625	0.1468	0.0624	0.9008
CTINC	0.6940	0.439	0.3595	0.845
CTTOT	0.7176	0.9366	0.3595	0.7883
NESTLOC	0.3760	0.1322	0.8829	0.5796
TRT	0.2360	0.0513	0.8268	0.8512
YEAR	0.0064	--	--	--

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

1992 nor 1993 model explained much variation in cowbird hatching success (Model $\chi^2 = 4.006$, $df = 1$, $P = 0.045$, $r^2 = 0.038$, $n = 35$; Model $\chi^2 = 3.82$, $df = 1$, $P = 0.051$, $r^2 = 0.042$, $n = 34$, respectively). No variable was a significant predictor of cowbird hatching success in 1995.

DISCUSSION

Variation in Hatching Success Among Years

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

Two previous experimental studies have provided indirect support for the host incubation limit hypothesis (Davies and Brooke 1988; Peer and Bollinger 1997, in press). These studies differed from mine in that (1) artificial parasitic eggs were used instead of live eggs (Davies and Brooke 1988), and (2) live eggs of a nonparasitic species (House Sparrow [*Passer domesticus*]) were used to supplement cowbird eggs placed in nests of a host (Common Grackle [*Quiscalus quiscula*]) whose eggs were larger than those of the Brown-headed Cowbird (Peer and Bollinger in press). These results (including my own) suggest that the addition of a parasitic egg increases the clutch to a volume which the host cannot incubate effectively, and that host-egg removal is important to ensure successful hatching of parasitic eggs. A second experimental study using mostly House Sparrow eggs, however, did not support the incubation limit hypothesis (Wood 1995). In Wood's

(1995) study, sparrow eggs hatched at similar frequencies whether one or no host egg had been removed from clutches with large (Red-winged Blackbird) or small eggs (Chipping Sparrow, *Spizella passerina*). Therefore, egg removal may tend to improve hatching success of parasitic eggs when hosts lay very large eggs (Peer and Bollinger, in press), but be of lesser importance when hosts lay smaller eggs (Wood 1995, this study). Perhaps due to their size, cowbird eggs in clutches with small eggs contact the host female's incubation patch continuously, which makes egg removal not as crucial for successful incubation. Indeed, House Sparrow eggs had higher hatching success and shorter incubation periods in clutches with small eggs than large eggs (Wood 1995). If true, then the hatching success of cowbird eggs may be influenced by both the size and number of host eggs as predicted by the incubation efficiency hypothesis (Peer and Bollinger in press).

The factors that resulted in variation in hatching success among years in my study are not known. Contrary to other studies (e.g. Järvinen and Väisänen 1983, Webb 1987, Siikamäki 1995), neither variation in ambient temperature among years nor nest location influenced the hatching success of eggs in my study. Factors such as yearly variation in prey abundance can influence Yellow Warbler reproductive success (Busby and Sealy 1979, Hébert 1993), but these data were not collected during this study.

Differences in the way eggs were handled during the study could have influenced cowbird hatching success. I did not conduct manipulations to demonstrate that hatching success was not affected by handling eggs, but Lerkelunó et al. (1993) found handling eggs did not reduce their hatchability. In this study, eggs were handled similarly by the

same people (myself and S. G. Sealy) in each year, with the exception of 1992 in which all warbler eggs were measured. However, all cowbird eggs were always measured, so in effect, handling was consistent across years for cowbird eggs.

I assumed that all unhatched eggs were capable of embryonic development, whether or not a dead cowbird embryo was visible in unhatched eggs. This introduced the potential for misinterpretation of the status of unhatched eggs. For instance, infertile eggs with no opportunity for development would have been interpreted as eggs in which embryonic mortality occurred at a very early stage of development. However, because the protocol was consistent over the 3 years, the frequency of such errors should have been constant. Finally, the fertility of cowbird eggs in 1992 may have been greatly reduced relative to the other years.

Removal of host eggs by female cowbirds appears to increase the hatching success of parasitic eggs in Yellow Warblers nests in some years, and it may increase the hatching success of the remaining host eggs. Clutches from which no host egg was removed, however, did not have longer incubation periods, nor did these clutches hatch more asynchronously than clutches where one host egg was removed. Therefore, removing a host egg does not appear to increase the rate of development of the remaining eggs. Hatching spread, however, did vary among years. Hébert and Sealy (1992) also found annual variation in hatching spread, which ranged from 1.4 to 2.3 days over 3 years. They attributed this to below-normal ambient temperatures during the laying period in one year, which resulted in shorter hatching spreads. Hatching spreads in my study, however, were significantly shorter in the warmest year (1995, $\bar{x} = 1.85$ days) than in the coolest year

(1993, \bar{x} = 2.72 days).

Hatching Order

Contrary to Berger's hypothesis (1951), removal of the first-laid warbler egg did not increase the probability of the cowbird hatching before the host nestlings. In fact, most cowbirds hatched before or at the same time as warbler nestlings, regardless of whether a host egg was removed. Cowbird eggs probably hatched first due to a combination of their short incubation period (Briskie and Sealy 1990) and because they were added to nests early in the host laying period. Perhaps if cowbird eggs were laid later in the host laying period, they would benefit from removal of one of the first-laid host eggs.

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

CHAPTER 2

SHORT INCUBATION PERIODS OF BROWN-HEADED COWBIRD EGGS: ARE EMBRYOS STIMULATED TO HATCH EARLY?

INTRODUCTION

In most bird species short incubation periods are associated with more time for fledging, molt, and accumulation of fat reserves for migration, as well as minimizing the period of vulnerability to nest predators (Perrins 1977, Webb 1987). The incubation behaviour of parents (Ricklefs and Smeraski 1983), thermal properties of nests (Schaeffer 1980, Ricklefs and Smeraski 1983), and physical properties of eggs such as mass and shell thickness (O'Connor 1984), may all influence incubation periods. Interspecific variation in incubation period may also reflect mass-independent differences in rates of embryonic growth and development (Ricklefs 1993).

The Brown-headed Cowbird is one of several brood-parasitic cowbirds that has a short incubation period (Briskie and Sealy 1990, Kattan 1995). Young cowbirds often hatch 0.5 -1.0 days before nestlings of a variety of host species (e.g. Audubon 1831:497 *in* Nice 1953, Hann 1937, Nice 1937, Hofslund 1957, Nolan 1978). Some parasites eliminate competition for parental care (Redondo 1993) by ejecting host eggs and young, or by killing them directly (e.g. parasitic cuckoos and honeyguides, respectively; Payne 1977). The cowbird has not evolved such drastic strategies (but see Dearborn 1996), rather, cowbird nestlings compete with host nestlings for food provisioned by the foster parents, often so successfully that some or all host nestlings starve (Briskie & Sealy 1987, 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 hypotheses have been proposed to explain the short incubation periods of parasitic cowbirds: (1) cowbird embryos develop more rapidly (Friedmann 1927), (2) female cowbirds retain their eggs in the oviduct for up to 24 hours, thereby allowing the embryo to develop in the female's reproductive tract before being laid (Hoffman 1929), (3) because incubation periods increase as a function of egg mass (Vleck and Vleck 1987), female cowbirds lay small eggs relative to their body mass to shorten their incubation periods (Briskie & 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).

One hypothesis accounting for the short incubation periods of cowbirds has received support to date. Kattan (1995) found the metabolic rates of Shiny Cowbird (*M. bonariensis*) embryos were not higher than predicted on the basis of the egg's energy content, which suggests 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 (Liversidge 1961, Perrins 1967), the only observation of egg retention in cowbirds appears to have been a rare case of an egg-bound female (Nice 1954). Briskie and Sealy (1990) found that cowbird eggs conform to allometric predictions based on female body mass. Egg composition differs between species, however, and may affect the developmental characteristics of chicks (Hill 1995). Shiny Cowbird eggs have less energy content 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 with caution, 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). That is, 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 Shiny Cowbird situation does not appear to apply to the Brown-headed Cowbird because energy investment in cowbird eggs does not differ significantly from that predicted by egg mass (Ankney and Johnson 1985).

As demonstrated in Chapter 1, freshly laid cowbird eggs placed in Yellow Warbler nests on the first day of laying hatch prior to, or coincident with, the host eggs. However, the cowbird incubation periods recorded were longer than the 10-day incubation periods recorded by Briskie and Sealy (1990). As pointed out by previous researchers, incubation periods in natural nests may be influenced by variables such as egg size, female attentiveness, nest insulation, and ambient temperature that may affect egg temperature and, therefore, rate of embryonic development. To compare the incubation periods of cowbirds and Yellow Warblers in 1994 and 1995, eggs of both species were incubated artificially under constant conditions of temperature and humidity. I tested two mutually exclusive hypotheses. First, I tested the hypothesis that cowbird embryos develop more rapidly than those of a common host species by artificially incubating eggs of cowbirds and Yellow Warblers to determine incubation periods under constant conditions of temperature and humidity. This hypothesis predicts that cowbird eggs should hatch before

Yellow Warbler eggs.

Numerous researchers have suggested that cowbird eggs make better contact with the brood patch than small host eggs and, therefore, receive a disproportionate amount of heat from the incubating parent, to the detriment of the host eggs (Coues 1872, Hofslund 1957, Mayfield 1960, Friedmann 1963:118, Dolan and Wright 1984, Wiley 1985, Petit 1991). Over a half-hour recording period at a natural nest, however, a cowbird egg was not warmer on average than a smaller Chipping Sparrow egg (Huggins 1941). Given the small sample size of Huggins (1941) recordings, however, my alternative hypothesis stated that cowbird eggs hatch before small host eggs because the large size of the cowbird egg reduces the amount of heat received by host eggs, which results in longer incubation periods of host eggs. This second hypothesis predicts that owing to their smaller size, warbler eggs should hatch before cowbird eggs because all eggs receive the same amount of heat in the incubator. I also compared the incubation periods of first-hatched warbler eggs in parasitized and unparasitized Yellow Warbler nests (Chapter 1). I predicted warbler eggs in parasitized clutches would hatch later than those in control clutches.

In 1996, I extended my study to test an alternative hypothesis that explains short cowbird incubation periods. In some precocial species (particularly galliformes, but see Davies and Cooke 1983), embryos at different stages of development in the same clutch utilize clicking sounds associated with movements of cartilage of the glottis (see Vince 1966a, McCoshen and Thompson 1968) to synchronize the hatching of the clutch. Synchronization is achieved by accelerating the hatching of less-developed embryos (Vince 1966b) and retarding the hatching of the more-developed eggs (Vince 1968, Vince

and Cheng 1970). Whereas synchronous hatching is advantageous for galliform embryos, in a clutch of host embryos a cowbird embryo 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 by accelerating or retarding the development of heterospecific embryos to match their own rate of development (Pani et al. 1968). Stimuli, therefore, are capable of influencing rates of development in another species. I propose the short incubation period of the cowbird is due to the ability of the embryo to hatch in response to clicking, or other stimuli, from host eggs in the clutch during the last one or two days of the incubation period. To test the hypothesis cowbird eggs in contact with clutches of Yellow Warbler eggs were incubated artificially. I predicted that hatching order would be similar to those observed under natural conditions; that is, (1) cowbird eggs should hatch before warbler eggs and (2) cowbird eggs incubated in warbler clutches should have shorter incubation periods than cowbird eggs 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). However, 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 development at hatching. If cowbirds are stimulated by host eggs to hatch early, they may hatch at an immature stage of physical development. I tested this possibility by comparing measurements of cowbird hatchlings that had been artificially incubated in isolation with cowbirds incubated in warbler clutches. I predicted that if cowbird embryos

are stimulated to hatch early they will have shorter tarsi and wings than cowbird embryos not stimulated to hatch early.

Although it appears cowbirds should benefit by hatching as early as possible relative to host young, there may be a limit to how early cowbirds can hatch relative to host eggs. Kemal and Rothstein (1988) found that Red-winged Blackbirds ejected 83 % of artificial cowbird and blackbird eggs that simulated broken eggs (shell fragment glued to artificial egg at 45°) through Day 9 of incubation. However, only 22 % of simulated broken eggs were ejected on Day 10, the day before the blackbird clutches started to hatch. Kemal and Rothstein suggested the decline in the frequency of ejection of broken eggs at the end of the incubation period is adaptive because it ensures that parent birds do not eject their own pipped eggs. However, mistaking hatching eggs for broken eggs could be adaptive in parasitized nests if early-hatching cowbird eggs are removed. Kemal and Rothstein postulated that cowbirds hatching too early relative to host eggs may elicit parental behaviour normally directed toward removal of broken eggs, which would result in ejection of the hatching cowbird from the nest. To test whether there is a limit to how early cowbird chicks can hatch relative to host eggs, I experimentally parasitized Red-winged Blackbird nests mid-way through their incubation period with cowbird eggs that were close to hatching. I predicted the adult blackbirds would eject hatching cowbird eggs, mistaking them for broken eggs.

Therefore, the objectives of this section were to test under artificial conditions if cowbird incubation periods are shorter than Yellow Warbler incubation periods due to (1) more rapid embryonic development, (2) receiving more heat during incubation, or (3) a

mechanism eliciting hatching in response to stimuli from host eggs. Finally, I determined if cowbird nestlings suffer a penalty by hatching too early in Red-winged Blackbird nests under natural conditions.

METHODS

Experimental Procedures

In 1994, 1995, and 1996 freshly laid cowbird eggs were obtained from host nests on the study area. In 1996 cowbird eggs were also obtained from captive females held overnight in an outdoor aviary, where many laid the following morning. Yellow Warbler eggs were also obtained on the day they were laid and in all cases were either the first or second eggs of the clutch. Yellow Warblers incubate little 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 labelled and their lengths and widths were measured to the nearest 0.1 mm with dial calipers. Egg mass was recorded with an Ohaus digital scale accurate to 0.05 g in 1995 and 1996. Before being placed in the incubator, most eggs were candled to verify that no detectable embryonic development had occurred. In 1994 and 1995, eggs were placed at random 2 - 3 cm apart in the incubator. In 1996, two experimental groups of cowbird eggs were incubated. In the first group, cowbird eggs were incubated in clutches of three Yellow Warbler eggs, with all eggs in contact with each other. A clutch of three host eggs was chosen to simulate natural clutch sizes, while minimizing the number of host eggs required. Clutches were placed on a nylon mesh that covered a cardboard ring. The mass of the egg weighed the material down, which ensured the eggs contacted each other. The mesh allowed for free circulation of air around the clutch. 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 x 0.75 m plywood box insulated with 8 cm of styrofoam. The front of the incubator consisted of 2 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. To test for differences between incubators, hatching success and incubation periods were compared between incubators using logistic regression (Kleinbaum 1992) and ANOVA, respectively. Hatching success of cowbird and warbler eggs in the incubator were compared between years using χ^2 tests. Hatching success of eggs in the incubator was also compared with data from natural nests obtained in Chapter 1. Yellow Warbler hatching success in the incubator and control clutches was compared from 1992, 1993, and 1995, whereas cowbird hatching success was compared with that in two treatment groups from these years (see Chapter 1).

Eggs were turned four times daily to prevent embryonic membranes from adhering to the shells. Embryonic development was monitored during incubation by candling eggs at

3 - 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 labelled eggshell. Each egg incubated in a clutch was left in place until it hatched, at which time the nestling was removed. The incubator was checked for chicks at least every 6 hours. In all years newly hatched birds were weighed to the nearest 0.05 g and the time of their discovery recorded, while 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. The hatching event was observed directly in many instances, allowing perfect accuracy of hatching time. Nestlings were considered hatched when the shell was broken into two halves. However, if the hatching event was not observed, the hatching time was estimated to be the midpoint between the time the nestling was discovered and the time the incubator was last visited (maximum error 3 hours).

Data Analyses

All statistical tests were performed using SPSS and followed procedures outlined in Schlotzhauer and Littell (1986) and Kleinbaum et al. (1987). Data were tested for normality using Shapiro-Wilk (*W*) and Kolmogorov-Smirnov (*D*) tests. Normally distributed variables were analyzed using standard parametric techniques, whereas variables not normally distributed were analyzed using nonparametric techniques. In 1996 two clutches were deleted from the dataset because the warbler incubation periods were outliers (short incubation periods) that prevented normality. Egg volumes were calculated using Formula 1 (Chapter 1).

Eggs incubated individually.--Incubation periods were compared between years for each species using ANOVA. To control for between-year differences in egg size that could influence incubation period, egg volume was included in ANOVA models as a covariate. Cowbird and Yellow Warbler incubation periods were then compared using two sample *t*-tests for groups with unequal variance. Incubation periods of cowbird and host eggs in Yellow Warbler nests recorded in 1992 and 1993 were compared to incubation periods obtained in the incubator. 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 behaviour is not fully developed during the laying period, 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 are attentive that day as determined by afternoon watches (see Chapter 3), was added to the incubation period of each egg. All cowbird eggs had been added to host clutches on the first day of the Yellow Warbler's laying period. Incubation periods were not estimated using the (1) 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 incubation period, and the third method overestimates incubation period. Incubation periods were compared between years using the Mann-Whitney *U*-test to determine if the data could be pooled. 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 natural control clutches from 1992 and 1993, (2) the first-hatched warbler egg in natural clutches from 1992 and 1993 that had been artificially parasitized and no host egg removed, and (3) warbler eggs artificially incubated in isolation in 1994 and 1995. Yellow Warbler incubation periods were compared using the Mann-Whitney *U*-test.

Eggs incubated in clutches.—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 only data for eggs that could have been stimulated by heterospecific eggs were included in the calculation of incubation periods. 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. I tested for a relationship between cowbird and warbler incubation periods using the Pearson correlation coefficient (*P*). 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 power of the *t*-test was calculated following Cohen (1988). The incubation periods of cowbird eggs in clutches were then compared with the pooled incubation periods of cowbird eggs 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 following Cohen (1988). The incubation periods of warbler eggs in clutches were then compared

with the pooled incubation periods of warbler eggs incubated individually in 1994 and 1995 using ANOVA with egg volume as a covariate entered first into the model. Cowbird incubation periods were compared between artificial clutches and natural nests using the Mann-Whitney *U*-test.

Egg mass at the beginning of incubation was not measured in 1994, therefore, unlike Kattan (1995), I was unable to correlate incubation period with egg mass for the three years. Instead, I 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 (pers. obs.). Using the regression equation for the relationship between egg volume and mass derived from the 1995 and 1996 data, I predicted the mass of each egg and entered it into an equation predicting incubation period for birds (Vleck and Vleck 1987, $I=10^{(0.97 + 0.29 \log(W))}$, where *I* = incubation period in days, and *W* = egg mass in grams) to generate predicted incubation periods for each egg.

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.

Cost of Early Hatching

Cowbird eggs were obtained from naturally parasitized nests on the study area, incubated artificially until close to hatching, and then added to Red-winged Blackbird nests from Days 3 to 7 of incubation (\bar{x} = 5.0 days \pm 0.4 SE; Day 1 being the day after the last egg of the blackbird clutch was laid). In two nests, a model cowbird egg had already been placed in the nest as part of another study, so the real cowbird egg was simply

switched with the model egg. In the six other nests, no model cowbird egg was present, so the addition of the cowbird egg increased the clutch size by one. Nests that received cowbird eggs were visited every four to six hours throughout the day until the cowbird chick hatched. On each visit the nest contents, presence of the female blackbird, and time were recorded. Once a cowbird chick hatched its condition (e.g. warm, dry down, begging) and the presence of eggshells in the nest were recorded. The cowbird chick was then left in the nest for 2 more hours prior to removal for use in another study.

RESULTS

Eggs Incubated in Isolation

No significant difference in cowbird ($\chi^2 = 3.64$, $df = 2$, $P = 0.16229$) or warbler ($\chi^2 = 2.58$, $df = 2$, $P = 0.27524$) hatching success in the incubators was detected between years (Table 8). However, hatching success of artificially incubated eggs was significantly lower than that in natural nests for both cowbird eggs (52.3% vs. 74.6 %, respectively; $\chi^2 = 13.02$, $df = 1$, $P < 0.0001$) and warbler eggs (52.6% vs. 93.6%, respectively; $\chi^2 = 116.8$, $df = 1$, $P < 0.0001$). In 1996, neither cowbird hatching success (logistic regression Wald = 2.1042, $df = 1$, $P = 0.1469$; Model $\chi^2 = 2.451$, $df = 1$, $P = 0.1174$) nor cowbird incubation period ($F = 1.94$, $P = 0.1782$) differed significantly among the three incubators. Yellow Warbler hatching success did not differ among incubators ($\chi^2 = 1.43$, $df = 2$, $P = 0.48811$). However, Yellow Warbler incubation period differed significantly between incubators in 1996 ($F = 3.95$, $P = 0.0253$), with periods in one of the commercial incubators that averaged ca. 16 hours shorter ($\bar{x} = 16553.3 \pm 260.3$ h, $n = 18$) than in the custom-built incubator ($\bar{x} = 17609.0 \pm 212.95$ h, $n = 11$; Bonferroni t -test $P = 0.05$). However (see later), warbler incubation periods did not differ between 1994 (home-made incubator used exclusively) and 1996 (home-made and commercial incubators used) and, therefore, I pooled the 1996 data from eggs incubated in all three incubators.

Cowbird incubation period did not differ significantly between 1994 and 1995 (Table 9, model $F = 0.88$, $df = 2$, 45, $P = 0.424$; year $F = 0.27$, $df = 1$, $P = 0.608$; egg volume-covariate $F = 1.38$, $P = 0.247$). Yellow Warbler incubation period did not differ significantly between 1994 and 1995 (Table 9, model $F = 1.53$, $df = 2$, 14, $P = 0.256$; year

TABLE 8. Hatching success (% of cases, *n* in parentheses) of artificially incubated Brown-headed Cowbird and Yellow Warbler eggs.

Year	Cowbird	Warbler
1994	60.7 (61)	52.6 (19)
1995	50.0 (24)	33.3 (15)
1996 ¹	41.9 (43)	55.5 (99)
1996 ²	15.4 (13)	—

¹ Clutch

² Control

TABLE 9. Incubation period ($\bar{x} \pm SE$ in days, n in parentheses) of artificially incubated cowbird and Yellow Warbler eggs.

Year	Cowbird	Yellow Warbler
1994	12.4 \pm 0.1 (37)	11.9 \pm 0.1 (10)
1995	12.3 \pm 0.1 (11)	11.7 \pm 0.2 (5)
1994 & 1995	12.4 \pm 0.1 (48)	11.9 \pm 0.1 (15)
1996 ¹	12.0 \pm 0.2 (11)	11.8 \pm 0.1 (11)
1996 ²	11.9 (2)	—

¹ Clutch

² Control

$F = 0.164$, $df = 1$, $P = 0.224$; egg volume-covariate $F = 1.25$, $P = 0.286$). The data for both species in 1994 and 1995, therefore, were pooled. The mean Yellow Warbler incubation period was significantly shorter than the mean cowbird incubation period over 1994 and 1995 combined (Table 9, $t = -4.72$, $df = 39.56$, $P = 0.0001$). On average, Yellow Warblers in the incubator took 13.3 hours less to hatch than cowbirds.

Natural Nests

Most cowbirds hatched either before or at the same time as Yellow Warblers in natural nests (see Chapter 1). Cowbird eggs in natural nests hatched in 11.9 ± 0.1 days, 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 ($t = 2.8$, $df = 87$, $P = 0.006$).

The incubation periods of first-hatched Yellow Warbler eggs in control nests ($\bar{x} = 11.0 \pm 0.2$ days, $n = 26$) were significantly shorter than those of first-hatched warbler eggs in parasitized clutches where no host egg had been removed ($\bar{x} = 12.3 \pm 0.1$ days, $n = 41$; $U = 45.4$, $P = 0.0001$). The incubation periods of first-hatched Yellow Warbler eggs in control nests were also significantly shorter than those in the incubator ($\bar{x} = 11.8$ days ± 0.1 days, $n = 15$; $U = 33.0$, $P = 0.0001$). Warbler eggs incubated artificially hatched significantly earlier than first-hatched warbler eggs in parasitized clutches where no host egg had been removed ($U = 108.0$, $P = 0.007$).

Eggs Incubated in Clutches

Warblers hatched before cowbirds in 10 cases, while cowbirds hatched first in 3 cases. There was no significant difference in incubation periods between cowbird and warbler eggs incubated in clutches in 1996 (Table 9; $t = -0.92$, $df = 20$, $P = 0.371$). The incubation period of cowbird eggs incubated in clutches was 0.4 days shorter than those incubated in isolation, but the difference only approached significance (Table 9, Model $F = 1.71$, $df = 2$, $P = 0.19$; Main effect $F = 2.77$, $df = 1$, $P = 0.101$; Covariate $F = 0.647$, $df = 1$, $P = 0.42$). The power of the ANOVA test was only 0.509, however, so the probability of obtaining a statistically significant result was not great. The incubation period of cowbird eggs incubated in clutches, however, did not differ significantly from those in natural nests ($U = 312.0$, $P = 0.525$). Cowbird incubation period did not differ significantly with the number of warblers hatching ($F = 0.01$, $df = 1$, 9 , $P = 0.91$, $r^2 = 0.002$; $\bar{x} = 2.09 \pm 0.25$ warblers where cowbird hatched, $n = 11$), and was not significantly correlated with mean warbler incubation period (Pearson = 0.299, $P = 0.371$). Unfortunately, only 2 of 13 cowbird eggs in the 1996 control group hatched, therefore, I was unable to compare control and experimental incubation periods statistically (see Table 9). Warbler incubation periods did not differ significantly whether the eggs were incubated individually or in clutches (Table 9, Model $F = 0.158$, $df = 2$, $P = 0.854$; Main effect $F = 0.0$, $df = 1$, $P = 0.99$; Covariate $F = 0.316$, $df = 1$, $P = 0.578$).

Egg Volume and Hatchling Mass

Cowbird egg volume did not differ significantly between years (Table 10, $F =$

FIGURE 2. Cowbird incubation period (days) for three years relative to egg volume (cm³). Cowbird eggs in 1994 and 1995 were incubated in isolation, while in 1996 cowbird eggs were incubated in warbler clutches. The mass of 1994 eggs were predicted using the regression equation for the relationship between egg volume and mass derived from the 1995 and 1996 data. The diagonal line denotes incubation periods predicted from egg volumes, based on the equation: $I = 10^{(0.97 + 0.29 \times \log(W))}$, where I = incubation period in days, and W = egg mass in grams (Vleck and Vleck 1987).

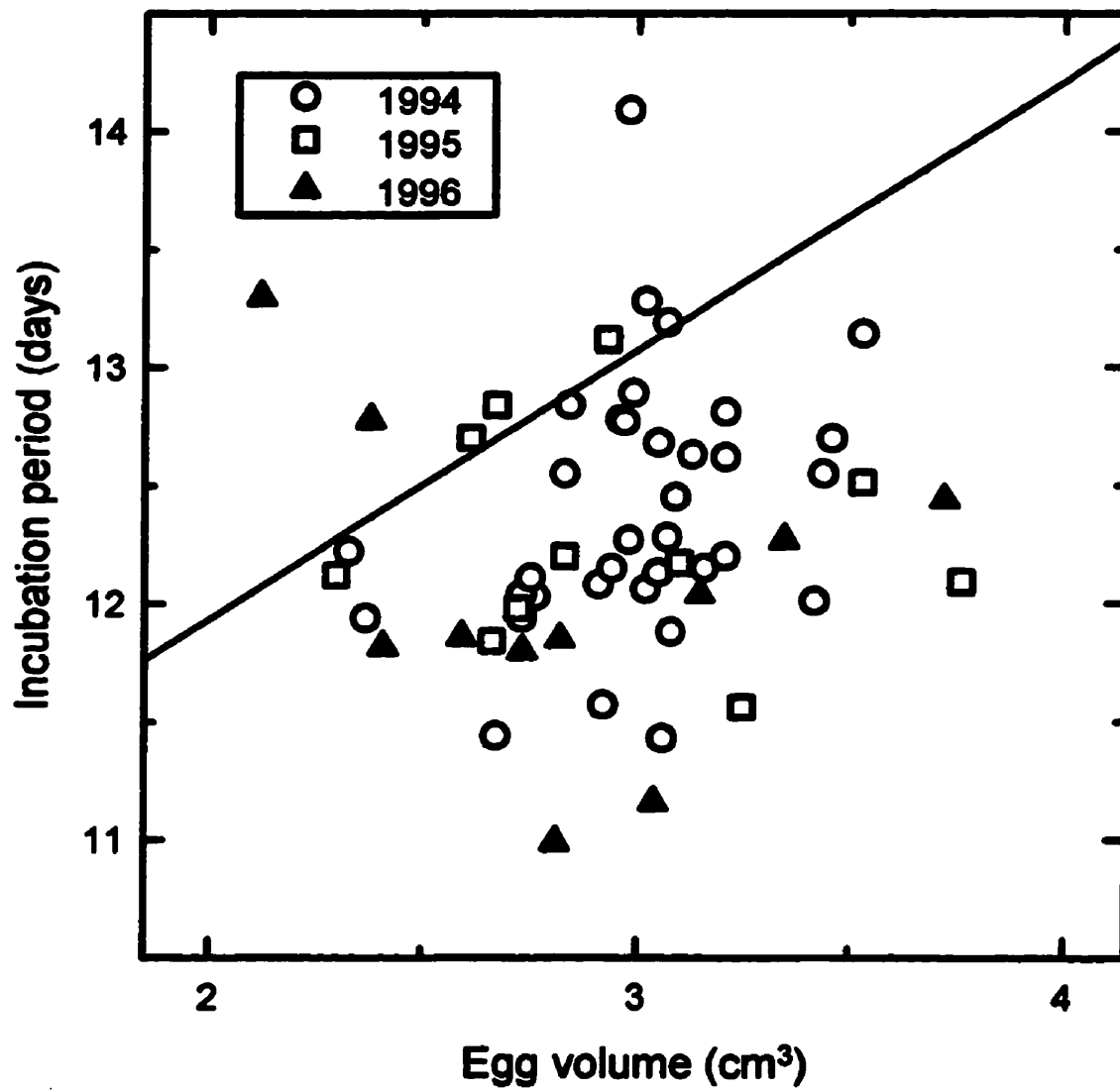


TABLE 10. Cowbird nestling measurements relative to egg volume for eggs incubated in isolation (1994, 1995 and 1996) and in clutches (1996).

Year	Tarsus length (mm)	Wing chord (mm)	Nestling mass (g)	Egg volume (ml)
1994	--	--	2.27 ± 0.04 (33)	3.0 ± 0.04 (35)
1995	7.44 ± 0.32 (10)	6.01 ± 0.41 (10)	2.12 ± 0.08 (9)	2.94 ± 0.13 (11)
1994 & 1995	7.44 ± 0.32 (10)	6.01 ± 0.41 (10)	2.24 ± 0.04 (42)	2.98 ± 0.04 (46)
1996 ¹	7.99 ± 0.24 (8)	6.8 ± 0.13 (8)	2.38 ± 0.12 (8)	2.76 ± 0.07 (11)
1996 ²	7.6 (2)	6.85 (2)	2.33 (2)	3.04 (2)

¹ Clutch

² Control

1.6053, $P = 0.2092$). Incubation periods of cowbird eggs incubated individually or in clutches were not significantly related to egg volume ($F = 1.54$, $df = 1,44$, $P = 0.22$, $r^2 = 0.034$; $F = 0.29128$, $P = 0.5963$, $r^2 = 0.0179$, respectively; see Figure 2). In Figure 2, most observed cowbird incubation periods are below those predicted from egg volume, indicating cowbird eggs have short incubation periods for their size whether or not they are in contact with host eggs.

Although the covariate egg volume explained much of the variation in hatchling mass (covariate $F = 58.3$, $df = 1$, $P = 0.000$), cowbird hatchlings weighed significantly more when incubated in clutches than when incubated in isolation (Table 10, year $F = 13.05$, $df = 1$, $P = 0.001$; model $F = 35.7$, $df = 2$, $P = 0.0001$). Cowbird hatchlings incubated individually had shorter tarsi than hatchlings incubated in clutches, a difference that approached significance (Table 10, year $F = 3.174$, $df = 1$, $P = 0.095$; egg volume $F = 3.29$, $df = 1$, $P = 0.09$; model $F = 3.23$, $df = 2$, $P = 0.068$). The difference in wing length between cowbird hatchlings incubated individually or in clutches was not significant (Table 10, year $F = 2.312$, $df = 1$, $P = 0.149$; model $F = 1.42$, $df = 2$, $P = 0.272$; egg volume $F = 0.528$, $df = 1$, $P = 0.47$).

Cost of Hatching Early

Clutch size in the eight experimental blackbird nests ranged from three to five eggs ($\bar{x} = 4.0$ eggs ± 0.3 SE). All eight cowbird eggs placed into blackbird nests hatched. The mean time interval (\pm SE) from addition of the cowbird egg to the blackbird nest to discovery of the cowbird chick was 25.5 ± 3.7 h. In all cases female blackbirds were

either flushed from the nest, or alarm-called nearby when the cowbird chick was first discovered. All cowbird chicks appeared healthy, warm, partially or completely dry, and begged when the nest was visited. In seven cases the cowbird eggshell was gone, but at one nest, half of the eggshell had capped one of the blackbird eggs. None of the blackbird clutches was reduced from its original size after the cowbird hatched. All cowbird chicks were present in the nest and appeared healthy at the second nest visit. Female blackbirds continued to incubate after removal of the cowbird, and hatched their clutches in the 6 nests that were monitored to hatching.

DISCUSSION

Artificial Incubation

Hatching success of cowbird and warbler eggs did not differ significantly among incubators or years in this study. Hatching success in the incubator, however, was significantly lower than that observed in natural nests. Passerine eggs, including cowbird eggs, have been artificially incubated by several researchers (e.g. Baldwin and Kendeigh 1932, Graber 1955, Wetherbee and Wetherbee 1961, Kattan 1995, A. Dufty pers. comm.), however, few workers have initiated incubation on fresh cowbird eggs. For studies reporting hatching success of cowbird eggs incubated artificially, success of eggs ranged from 100% ($n = 5$, Dufty pers. comm.) to 55.5% (Wetherbee and Wetherbee 1961). The temperature and humidity levels in our incubator were virtually identical to those used by all other researchers for incubating passerine eggs. Baldwin and Kendeigh (1932) suggested hatching success of passerine eggs could be maximized by mimicking the gradual onset of full incubation behaviour by female passerines. They increased incubator temperature gradually from 35.0°C to 37.8°C over the first three days of incubation, with a 0.5 hour period of cooling on each of the first four days. Despite this protocol, the maximum hatching success obtained by Baldwin and Kendeigh (1932) was only 50%. Burger and Bertram (1981) noted artificially incubated ostrich (*Struthio camelus*) eggs did not lose as much mass as naturally incubated eggs and fewer of them hatched. They suggested high humidity in the incubators could cause low hatching success by depressing the rate of diffusion of oxygen into the egg. In this study, however, cowbird and warbler eggs were weighed every other day, and all eggs lost approximately 10% of their mass

throughout incubation. Landauer (1941:7-8) noted that the hatching success of Common Cuckoo (*Cuculus canorus*) eggs that are accepted by hosts is 70% or less, and stated "It seems likely that the foster parents frequently provide incubation conditions below the optimum for cuckoo eggs, thereby reducing hatchability". Artificially incubated cowbird eggs, however, had hatching success comparable to warbler eggs. Because cowbirds are generalist brood parasites that lay eggs in nests of many species of birds, cowbird eggs should be more tolerant of variable ambient and incubation temperatures and humidity than other bird species. Therefore, the hatching success in the present study was similar to that in other studies, but the cause of reduced hatching success in all studies relative to natural incubation remains unknown.

Eggs Incubated in Isolation

In natural nests cowbird eggs hatch either before or at the same time as Yellow Warbler eggs (Chapter 1). Cowbird eggs artificially incubated in isolation, however, had significantly longer incubation periods than Yellow Warbler eggs artificially incubated in isolation ($P = 0.0001$). This finding is contrary to the hypothesis that cowbird embryos develop more rapidly than Yellow Warbler embryos, but consistent with the hypothesis that in natural nests cowbird eggs interfere with heat transfer from the brood patch to smaller host eggs. Results showing that the first warblers to hatch in natural nests have longer incubation periods in parasitized than control clutches ($P = 0.0001$) further supports the possibility that cowbird eggs reduce the amount of heat received by warbler eggs. Other studies have also 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 and longer incubation periods as host clutch size increases (Wood 1995, Peer and Bollinger in press). It appears likely, therefore, that large eggs reduce the amount of heat received by small eggs.

The fact that warbler eggs incubated naturally in control nests had significantly shorter incubation periods than warbler eggs artificially incubated in isolation ($P = 0.0001$) indicates that physical conditions in the incubator did not replicate natural conditions. However, incubation periods of warbler eggs artificially incubated in isolation were shorter than those of warbler eggs incubated naturally in parasitized nests ($P = 0.007$). Therefore, physical conditions in the incubator likely had less of an effect on warbler incubation period than did the presence of a cowbird egg in natural nests.

In this study, cowbird eggs artificially incubated in isolation had significantly longer incubation periods (0.5 days, $P = 0.006$) than cowbird eggs in natural nests. Incubation periods of cowbird eggs incubated artificially were also 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). These findings could indicate either physical conditions in the incubator were sub-optimal for cowbird development, or some other factor (such as stimuli from host eggs) was lacking in the incubator. Comparison of incubation periods of artificially incubated cowbird eggs in this study with most other artificial incubation studies is confounded by the fact that eggs either were not (Graber 1955), or may not have been fresh (Wetherbee and Wetherbee 1961). However, A.M. Dufty, Jr. (Boise State Univ., pers. comm.)

recorded an average incubation period of 12.6 days for five fresh cowbird eggs incubated artificially, which agrees closely with my results. As in this study, Kattan (1995) found artificially incubated Shiny Cowbird eggs had longer incubation periods than the minimum observed under natural conditions (Wiley and Wiley 1980). However, in contrast to this study, Shiny Cowbird eggs incubated artificially hatched earlier (11.7 days) than eggs in natural nests (12.0 days). Because the physical conditions of Kattan's (1995) incubator did not differ from those in this study, the difference in the incubation periods of artificially incubated Brown-headed and Shiny Cowbird eggs suggests the mechanism of short incubation differs between the two species.

Eggs Incubated in Clutches

The hypothesis stating that cowbird eggs hatch early in response to stimuli from host eggs predicted 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 artificially 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 hatch before or at the same time as warbler eggs (Chapter 1). However, because warbler incubation periods in parasitized nests are prolonged which likely contributes to the high incidence of cowbirds hatching first, the first prediction does not appear to be sound. Indeed, the fact that cowbird eggs do not hatch first in the incubator reinforces the possibility that cowbird eggs disrupt contact between small warbler eggs and the brood patch.

Consistent with the second prediction of the hypothesis, cowbird eggs artificially incubated in clutches tended to have shorter incubation periods than eggs incubated in isolation, a difference that approached significance ($P = 0.101$). Also, cowbird incubation periods in clutches were not significantly different from those in natural nests ($P = 0.525$), and approximated the mean of naturally incubated cowbird eggs (Briskie and Sealy 1990). Unlike cowbird eggs incubated in isolation, there was no significant difference in cowbird and warbler incubation periods when these eggs were incubated together ($P = 0.371$). Cowbird incubation period was not influenced by the number of warbler eggs that hatched ($P = 0.91$). There was no significant difference in warbler incubation periods when eggs were incubated in isolation or in clutches ($P = 0.99$). Therefore, two statistically non-significant comparisons (cowbirds incubated in clutches hatch at the same time as both cowbirds in natural nests, and artificially incubated warblers) suggest cowbird embryos incubated in contact with warbler eggs are stimulated to hatch early. The third, and potentially most persuasive comparison (cowbird incubation periods in clutches vs. those in isolation), however, only approached significance. The results from natural and artificial conditions taken together, therefore, suggest in natural nests cowbirds hatch before Yellow Warblers as a result of prolonging warbler incubation periods and hatching earlier when in contact with host eggs.

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 reported by Kattan (1995). My results suggest that for Brown-headed Cowbirds, incubation period may be a

genetically controlled trait that differs significantly between individual embryos regardless of egg size, and perhaps differs among laying females. Interestingly, the fact that the two cowbird eggs with 10-day incubation periods reported by Briskie and Sealy (1990) had similar markings, colouration and were laid on consecutive days indicates they were likely laid by the same female.

Contrary to the hypothesis that cowbirds stimulated to hatch early do so at an immature stage of physical development, the tarsus and wing length of hatchling cowbirds in clutches tended to be longer ($P = 0.095$ and 0.149 , respectively) than those of cowbirds in isolation. The significantly greater mass of cowbird hatchlings incubated in clutches than in isolation ($P = 0.001$) was likely due to the shorter time interval available for water loss from the egg. 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 eggs. Perhaps the measurements of body size were not sufficient to detect trade-offs experienced by early hatching cowbirds. Early hatching cowbirds may suffer reduced immune function, as interspecific comparisons have shown incubation period is inversely related to prevalence of blood parasites (Ricklefs 1992).

Cost of Early Hatching

Female blackbirds did not eject hatching cowbird eggs from their nests mid-way through their own incubation period. This finding is consistent with results of studies of early hatching by conspecific eggs (Emlen 1941, Holcomb 1967), and indicates that

cowbird eggs may hatch as many days earlier than blackbird eggs as their rate of development will allow, without danger of ejection by the host female. Although nests were not observed in this study to ensure the cowbird nestling was being fed, other studies have shown nestlings of both cowbirds and other species introduced into nests during incubation are usually fed by the parents, which often results in premature termination of incubation behaviour (e.g. Friedmann 1929:259, Emlen 1941, Graber 1955, Holcomb 1979). Cowbirds, however, may be at risk if they hatch too early. Nolan (1978) noted three instances of predators removing only the early-hatched cowbird nestling from Prairie Warbler (*D. discolor*) clutches, leaving the remaining host eggs intact in the nest.

In summary, the results of this study suggest cowbirds hatch first in Yellow Warbler nests due to a combination of (1) the larger cowbird egg reducing the heat warbler eggs receive from the brood patch, which results in longer warbler incubation periods, and (2) stimuli from host eggs prompting cowbirds to hatch earlier. It appears (1) is the more important factor, however, because warbler eggs hatched 1.3 days later in parasitized nests, whereas cowbird eggs artificially incubated in clutches hatched only 0.4 days earlier. Internal temperature measurements of cowbird and host eggs of different sizes would quantify differences in heat received from the brood patch. How much the cowbird hatchling will 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 could presumably outcompete the host nestlings even without an extra half-day head start. The observation by Briskie and Sealy (1990) of two cowbird eggs hatching in 10 days 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 conspecifics than host eggs. The fact that warbler eggs showed no tendency for earlier hatching when incubated in clutches suggests this trait has not been selected for in this species.

Despite the suggestive findings of this study, results also show that hatching success in the incubator is not the same as in natural nests. Therefore, the results of this study should be viewed with caution. Artificial incubation does not simulate the conditions of variation in temperature and humidity, or frequency of egg turning, found in natural nests that could influence both hatching success and incubation period (Burger and Bertram 1981). Also, Schwagmeyer et al. (1991) found effects of egg contact on hatch timing of artificially incubated altricial eggs could not be replicated under natural conditions. However, given the small numbers of cowbird eggs available, and the high predation rates on natural nests, artificial incubation remains the most feasible technique to make the first experimental tests of these hypotheses. Hypothetically, whether cowbird eggs in nature are stimulated to hatch early depends upon the stage of host embryonic development relative to that of the cowbird embryo. The alignment of cowbird and host embryonic development depends in turn upon both the incubation period of the host eggs and when the cowbird egg was laid in relation to (a) the laying of the host eggs and (b) onset of host incubation. Placing cowbird eggs in nests of different hosts throughout the laying period would determine the effect egg size has on hatching order, and further test whether cowbird eggs are stimulated to hatch early by heterospecific eggs. Certainly, the results of

this study show that cowbird nestlings can hatch much earlier than host eggs and, therefore, mechanisms for short incubation periods should be subject to selection.

CHAPTER 3

DO COWBIRDS ALTER THE BEHAVIOUR OF HOST PARENTS?

INTRODUCTION

Young brood parasites exploit their foster parents to obtain the resources necessary to attain independence. In some cases, however, young parasites could benefit by manipulating parental behaviour, perhaps to increase the rate at which the foster parents provision them relative to their nestmates, or to change the type of resources provided. Given that cowbirds parasitize many host species that range widely in body size and breeding biology, young cowbirds may have been selected to modify host parental behaviour to maximize their own benefits. Opportunities for young cowbirds to modify host behaviour exist at both the egg and nestling stages.

In many passerine species, time spent incubating increases gradually throughout the laying period, becoming fully developed late in laying or early incubation (e.g. Haftorn 1981, Mead and Morton 1985, Meijer 1990, Hébert and Sealy 1992, Magrath 1992; but see Mayfield 1992). As a result, egg temperatures during laying often are at, or near, ambient temperature, in contrast to full incubation when egg cooling stimulates females to maintain eggs close to the critical developmental temperature (e.g. Franks 1967, Mertens 1977, Davis et al. 1984, Webb 1987). The rate at which incubation increases during laying is governed largely by the clutch size the female will lay, and is instrumental in

establishing the extent of hatching asynchrony in the clutches of many species (Mead and Morton 1985, Hébert and Sealy 1992, Magrath 1992). Although females begin full incubation at the same point regardless of clutch size, females that lay smaller clutches initiate incubation earlier than females that lay large clutches (Haftorn 1981, Meijer 1990). Whereas onset of incubation behaviour during laying is controlled largely by clutch size, it appears the onset of incubation can be modified by stimuli, perhaps tactile, from the number or area of eggs contacting the brood patch (but see Meijer 1995). In some species, addition of conspecific eggs to clutches on the first day of laying increases the amount of time females spend on the nest thereafter (Blagosklonov 1977, Jones 1987, Meijer et al. 1990, Hébert and Sealy 1992; but see Moreno and Carlson 1989). Conversely, egg removal early in laying reduces the time females spend on the nest (Meijer et al. 1990). Parasitic eggs could act as a 'superstimulus' to the host, and promote increased nest attentiveness (Friedmann 1963:13, Morel *in* Payne 1973:43). If a cowbird egg elicited increased incubation, or promoted an earlier start to incubation during laying, it should gain more heat than the host eggs that are not yet laid. The cowbird embryo could, therefore, gain a developmental head start on host embryos because of its short incubation period (Briskie and Sealy 1990).

The onset of female feeding by male birds during the breeding season (hereafter female feeding) varies among the 11 orders of birds that show the behaviour (Stokes and Williams 1971). Females in 75% of passerine families are fed by the male (Andrew 1961), and the frequency of feeding increases gradually through nestbuilding and laying and becomes most intense during incubation (Krebs 1970, Davies 1977, East 1981, Nilsson

and Smith 1988). During laying and incubation, female feeding by the male augments the feeding rate of the female, decreases the frequency and length of incubation breaks, and reduces the distance traveled from the nest while foraging, all of which increase female attentiveness and reduce variability in egg temperature (Prescott 1965, Krebs 1970, Blagoskolonov 1977, Davies 1977, Lyon and Montgomerie 1985, Vleck 1985, Liffield and Slagsvold 1986, Nilsson and Smith 1988, Hobson and Sealy 1989). Female feeding may even shorten incubation periods and increase hatching success in some species (Lyon and Montgomerie 1985, Nilsson and Smith 1988). Evidence that males increase their rate of food delivery to meet increased female energy demands due to lower ambient temperatures (Nilsson and Smith 1988, Smith et al. 1989), reduced nutritional intake (Smith et al. 1989), and increased clutch size (East 1981), indicate that females 'demand' more food from their mates (Smith 1980). Male Yellow Warblers feed their mates during laying and incubation (e.g. Biermann and Sealy 1982, Sutherland 1987). If female warblers respond to the addition of a cowbird egg during laying by increasing their attentiveness, as a corollary, females may demand more feeds from the male to compensate for increased energetic output and reduced opportunities for foraging (e.g. Morton and Pereyra 1985, Westerterp and Drent 1985, Mertens 1987, Jones 1987). P. N. Hébert (Univ. Manitoba, pers. comm.) found female Yellow Warblers incubating experimentally enlarged clutches were fed significantly more often during the last three days of laying than females incubating control clutches. Blagosklonov (1977) found higher incubation feeding rates in experimentally enlarged Pied Flycatcher (*Ficedula hypoleuca*) clutches, however, in a similar study Moreno and Carlson (1989) did not.

I tested whether the increase in host clutch volume caused by the addition of a cowbird egg stimulated the laying female to increase attentiveness and, as a corollary, whether it caused the male to feed the female more frequently. I experimentally parasitized Yellow Warbler nests with real and artificial cowbird eggs, removed one host egg from some nests, and observed parental behaviour at the nest during the laying period. I predicted that females would incubate more and males would feed females more in proportion to the total volume of eggs in the clutch. Therefore, the addition of a cowbird egg without host egg removal would elicit the most intense female attentiveness and the highest male feeding frequency, followed by switching a cowbird egg with one host egg. Females at control clutches should be the least attentive and receive the fewest feeds from males.

Although some passerine species heat the eggs during the brief periods of attentiveness early in the laying period (e.g. Haftorn 1981), it was necessary to confirm that observed differences in female Yellow Warbler attentiveness among the three treatments corresponded to increased heat applied to the eggs. Also, patterns of Yellow Warbler nest attentiveness could reflect changes in ambient temperature, insolation, and energy requirements of the incubating female, among other things, and, therefore, may not be constant throughout the day. If so, observations designed to determine differences in nest attentiveness between treatment groups could be confounded by the time of day chosen for observations. Therefore, Yellow Warbler nest temperatures were recorded to determine whether diurnal cycles in attentiveness exist that could confound observations made at only one time during the day. Periodogram analysis (described in Wei 1989) was

used to ascertain whether significant periodic components existed in the nest-temperature data.

Numerous researchers have postulated that early hatching by cowbirds could affect the hatchability and development of host eggs by stimulating the host female to spend less time incubating the remaining eggs as she cares for the cowbird nestling (Nolan 1978, Mason 1980, Dolan and Wright 1984, Fraga 1985, Grzybowski et al. 1986, Petit 1991). When more mature Tricolored Blackbird (*Agelaius tricolor*) eggs added to blackbird clutches hatched, females shifted to brooding, causing embryos more than four days younger than the added eggs to die (Emlen 1941). Sealy (1989) found that single House Wren (*Troglodytes aedon*) eggs (incubation period 12-15 days) experimentally added to Yellow Warbler clutches (11-12 days) did not hatch. Sealy (1989) postulated that once the Yellow Warbler eggs had hatched the female stopped incubating to care for the nestlings, and the wren embryos died. When Shiny Cowbird (*M. bonariensis*) eggs hatch before House Wren eggs, wren eggs do not hatch or nestlings die soon after (Kattan 1996). My results show that most cowbird eggs hatch before (45%) or on the same day (41%) as the first Yellow Warbler egg (see Chapter 1). Cowbirds begin begging soon after hatching (Lorenzana 1996) and beg intensely (Briskie et al. 1994). The combination of competitive 'head starts' over their nestmates, and vigorous begging may be strategies that dramatically reduce hatching success (by almost 100 %; Walkinshaw 1961) and fledging success (by 50 % and 93 %; Klaas 1975, Rothstein 1975a, respectively) in host species that have longer incubation periods.

To test whether the presence of a cowbird nestling shifts host behaviour from

incubation to a combination of brooding and feeding the nestlings, I added cowbird nestlings hatched in an incubator to Yellow Warbler clutches one day before the warbler eggs were due to hatch. I predicted the addition of a cowbird nestling would reduce nest attentiveness by the host female, increase the frequency of incubation bouts, and that male and female warblers would make more feeding trips to nests that contained cowbird nestlings than control clutches, and males would feed females less frequently. I also predicted the cowbird nestling would cause Yellow Warbler eggs to take longer to hatch and would increase egg and nestling mortality of the host species.

METHODS

Laying Period

The same warbler nests used in Chapter 1 were observed during the laying period to quantify parental activity at nests. As in Chapter 1, therefore, one of three treatment groups was assigned at random to each warbler nest on LD1. A single cowbird egg was added to treatment clutches and either 0 or 1 warbler eggs removed. In the control group cowbird eggs were neither added nor host egg removed. Female attentiveness (s) at nests of the three groups were observed for 30 min between 1400 h and 1630 h. The female was considered attentive when she had settled deeply into the nest cup; visits to the nest by the female in which only eggs were turned were recorded, but not as attentiveness. In 1992, observations began on LD1 and ended the day after the clutch was completed (LD6), whereas in 1993 observations were made on LD1, LD3 and LD5. Observation periods at each nest began when the observer arrived at the nest and ended whether or not the female was on the nest. Effort was made to secure a vantage point at some distance from the nest or from within a blind or vehicle so the presence of the observer did not affect attentiveness. No observations were made during rain because females are generally completely attentive during rain regardless of laying day (pers. obs.). The number of times the male fed the attentive female was also recorded during the 30-min observation period.

In 1994, nest and ambient temperatures were recorded at Yellow Warbler nests from the evening of LD1 to LD3, and throughout incubation. Recordings were made at each nest using two 6-cm thermistor probes attached to a remotely located Squirrel Data Logger. A sharp piece of wire was used to make a small hole extending from the bottom

of the nest up into the nest cup. One thermistor was threaded through the bottom of the nest until the tip extended approximately 0.5 - 1 cm into the cup itself, alongside or amongst the eggs. The second thermistor was then mounted beside or under the nest, where it was shaded from sunlight. Mustad #22 Dry Fly hooks had previously been bound to each thermistor using thread. These hooks anchored the thermistor to either the nest or nearby vegetation. Squirrel Data Loggers were programmed to record the temperature of both thermistors at either 15-s, 30-s, or 60-s intervals. As the data loggers have a limited memory capacity, they were detached from the thermistors every 1 - 3 days and the data were down-loaded to a computer. Because of the remote location of the logger from the nest, it was often possible to remove the logger without flushing the incubating female. Observations were made at nests where temperatures were being recorded, to verify that declines in nest temperature were recorded when females were away from the nest.

Periodogram analysis is based on the representation of a periodic function in a time-series data set as a series of sines and cosines, derived by a process called Fourier transformation (Wei 1989). Periodogram values were calculated for each Fourier frequency in both the nest and ambient temperature data sets, each Fourier frequency corresponding to a single periodic cycle in the data set. The periodogram value, therefore, is a numerical representation of the magnitude of the periodicity present in the data at each periodic cycle. For example, a periodogram value corresponding to the Fourier frequency for 24 hours that is larger than the periodogram value for 12 hours indicates there is a stronger 24-hour periodicity in the data than 12-hour periodicity. An *F*-statistic was calculated for each periodogram value to test the significance of the corresponding

periodic cycle. If the data contained several significant periodic components, then Fisher's exact test for the maximum periodogram (T -) was calculated for each significant periodic component to determine which explained the most variation. This process was repeated for each periodogram ordinate. Fourier transformations and periodogram calculations were made using SPSS/PC+, while calculation of the F - and T - statistics were made using Quattro Pro for Windows. I then compared the periodicity of the temperature recordings between both the nest and ambient, and the laying and incubation data sets.

Nestling Period

In 1994 and 1996, single artificial cowbird eggs were added to Yellow Warbler clutches late in the laying period (treatment), whereas no cowbird egg was added to other clutches (controls). The nests were monitored through the incubation period. In 1994, the day prior to the anticipated hatching date of the first warbler eggs, the artificial cowbird egg was replaced with a cowbird nestling that had hatched in the incubator. Cowbird nestlings that hatched overnight or in the morning were immediately added to warbler clutches, whereas cowbirds that hatched in the afternoon or evening were held overnight and then added to warbler clutches. Cowbird nestlings held overnight were fed adult chironomids and larval geometrids captured on the study site. Cowbird nestlings were added to warbler nests between 0530 and 1030 h. No cowbird nestling was added to control clutches observed in 1994 and 1996. One-hour watches were conducted at nests between 1400 and 1630 h, beginning late in the incubation period, and continuing through the hatching period. Time of day does not affect the frequency at which nestlings

are fed by adult warblers (Biermann and Sealy 1982).

Observations were grouped by the presence or absence of a cowbird egg or nestling and the total number of nestlings present (including the cowbird). During the nest watches notes were made on (1) female nest attentiveness, (2) number of incubation bouts by the female, (3) number of times the male gave food to the female, who fed the food to the nestlings, (4) number of times the male fed the female at the nest, (5) number of times the male fed the nestlings directly, (6) total number of male feeding visits (categories 3, 4, and 5), (7) number of times the female fed the nestlings with food collected herself, and (8) total number of times the nestlings were fed (categories 3, 5, and 7). I also recorded the (1) incubation period of each Yellow Warbler egg in the clutch as it hatched, (2) hatching success of warbler eggs, (3) presence of dead embryos in unhatched host eggs, (4) frequency of host egg disappearance from nests, and (5) frequency of host nestling mortality up to the end of the hatching period.

Data Analyses

All statistical tests were performed using SPSS and followed procedures outlined in Schlotzhauer and Littell (1986). All data were tested for normality using Kolmogorov-Smirnov (*D*) and Shapiro-Wilks (*W*) tests. Attentiveness of female warblers laying 4-egg clutches increased throughout the laying period, whereas attentiveness of females laying 5-egg clutches increased only slightly from LD1 to LD2, before increasing rapidly on LD3. Attentiveness on LD1 did not differ between clutches, therefore the data were pooled for this day. The attentiveness of 4-egg females on each day from LD2 through clutch

completion was equal to that of 5-egg females one day later in the laying period. In order to combine attentiveness between clutches, therefore, 4-egg data on LD2, LD3, LD4, and LD5 was pooled with 5-egg data on LD3, LD4, LD5, and LD6, respectively. In subsequent tables, therefore, data for LD2 are from 5-egg females only, while data from LD3 to LD 6 are from both 4- and 5-egg females. Male feeding data were pooled between clutches using the same technique. Female attentiveness and male feeding data during the laying period were compared between clutch sizes, years, and treatments using the Kruskal-Wallis *H*-test. Multiple comparisons were made using the Mann-Whitney *U*-test. Male feeding frequency and female attentiveness for each treatment were correlated for each day of the laying period using Spearman rank correlations. During the nestling period, female attentiveness, number of incubation bouts, male-to-female feeds, male-to-nestling feeds, male-to-female-to-nestling feeds, female nestling feeds, total male feeds, and total nestling feeds were all compared between treatments using the Mann-Whitney *U*-test, after having compared the data among both clutch sizes and years using the Kruskal-Wallis *H*-test. One outlying data point was removed from the cowbird data set when one cowbird nestling was present, due to an extremely high female feeding rate (14 feeds/hr).

RESULTS

Laying Period

Female attentiveness was not normally distributed in 1992 ($D = 0.1394$, $df = 186$, $P = 0.000$) or 1993 ($D = 0.1687$, $df = 167$, $P = 0.000$). Female attentiveness differed significantly among four- and five-egg clutches in only 3 of 21 possible comparisons for the 1992 and 1993 data (see Appendix 1), therefore, the data were pooled by clutch size. Female attentiveness did not differ significantly between years in any comparisons (see Appendix 2), therefore, the data were also pooled by year. Female attentiveness did not differ significantly between clutches where a cowbird egg had been added and one or no host eggs removed, or in clutches where no cowbird egg had been added on any day of the laying period (see Table 11).

Male feeding frequency was not normally distributed in either 1992 ($D = 0.3967$, $df = 186$, $P = 0.000$) or 1993 ($D = 0.4429$, $df = 167$, $P = 0.000$). Male feeding frequency did not differ significantly among clutch sizes in 1992 or 1993 (see Appendix 1) or between years (see Appendix 2). Therefore, the data were pooled by clutch size and year. Male feeding frequency differed significantly between the three treatments only on LD2 (see Table 12). Multiple comparisons showed the frequency of male feedings on LD2 at control clutches did not differ significantly from treatment clutches where either one host egg had been removed ($U = 49.5$, $df = 1$, $P = 0.316$) or no host eggs had been removed ($U = 36.0$, $df = 1$, $P = 0.331$). Females incubating clutches with a cowbird egg where one host egg had been removed, however, received significantly more male feedings than females that incubated clutches with a cowbird egg where no host egg had been removed

TABLE 11. Female Yellow Warbler incubation attentiveness ($\bar{x} \pm SE$ seconds of incubation per 30-min observation period, n in parentheses) during the laying period, by treatment.

Laying day	Treatment			$H (P)^b$
	Control ^a	One host egg removed, one cowbird egg added ^a	No host egg removed, one cowbird egg added ^a	
1	183 ± 44 (34)	138 ± 33 (39)	199 ± 51 (39)	0.393 (0.822)
2	325 ± 125 (9)	225 ± 69 (6)	269 ± 133 (6)	0.726 (0.696)
3	793 ± 126 (22)	714 ± 110 (28)	640 ± 139 (18)	0.197 (0.906)
4	1028 ± 183 (11)	1010 ± 124 (25)	1181 ± 140 (16)	1.878 (0.391)
5	1401 ± 68 (24)	1431 ± 82 (26)	1432 ± 80 (27)	0.762 (0.683)
6	1449 ± 104 (10)	1354 ± 137 (7)	1606 ± 78 (7)	0.974 (0.615)

^a Data are combined between clutch sizes and years. Corrected for clutch size (i.e. LD2 for 4-egg clutches becomes LD3, etc).

^b Kruskal-Wallis H -statistic comparing incubation attentiveness among the treatments within each laying day. P -value is two-tailed.

TABLE 12. Male Yellow Warbler food delivery ($\bar{x} \pm SE$ feeds per 30-min observation period, n in parentheses) during the laying period by treatment.

Laying day	Treatment			$H (P)^b$
	Control ^a	One host egg removed, one cowbird egg added ^a	No host egg removed, one cowbird egg added ^a	
1	0.2 ± 0.2 (34)	0.1 ± 0.1 (39)	0.2 ± 0.1 (39)	1.239 (0.538)
2	0.9 ± 0.5 (9)	0.7 ± 0.3 (6)	0.0 ± 0.0 (6)	7.059 (0.029)
3	0.4 ± 0.3 (22)	0.9 ± 0.3 (28)	0.3 ± 0.2 (18)	3.095 (0.213)
4	0.6 ± 0.2 (11)	1.3 ± 0.5 (25)	0.4 ± 0.2 (16)	0.916 (0.633)
5	0.8 ± 0.3 (24)	1.3 ± 0.5 (26)	0.7 ± 0.3 (27)	0.593 (0.743)
6	0.3 ± 0.2 (10)	1.3 ± 1.0 (7)	1.6 ± 0.7 (7)	1.307 (0.520)

^a Data are combined between clutch sizes and years. Data are corrected for clutch size (i.e. LD2 becomes LD3 for 4-egg clutches, etc).

^b Kruskal-Wallis H -statistic comparing rate of food delivery among the treatments within each laying day. P -value is two-tailed.

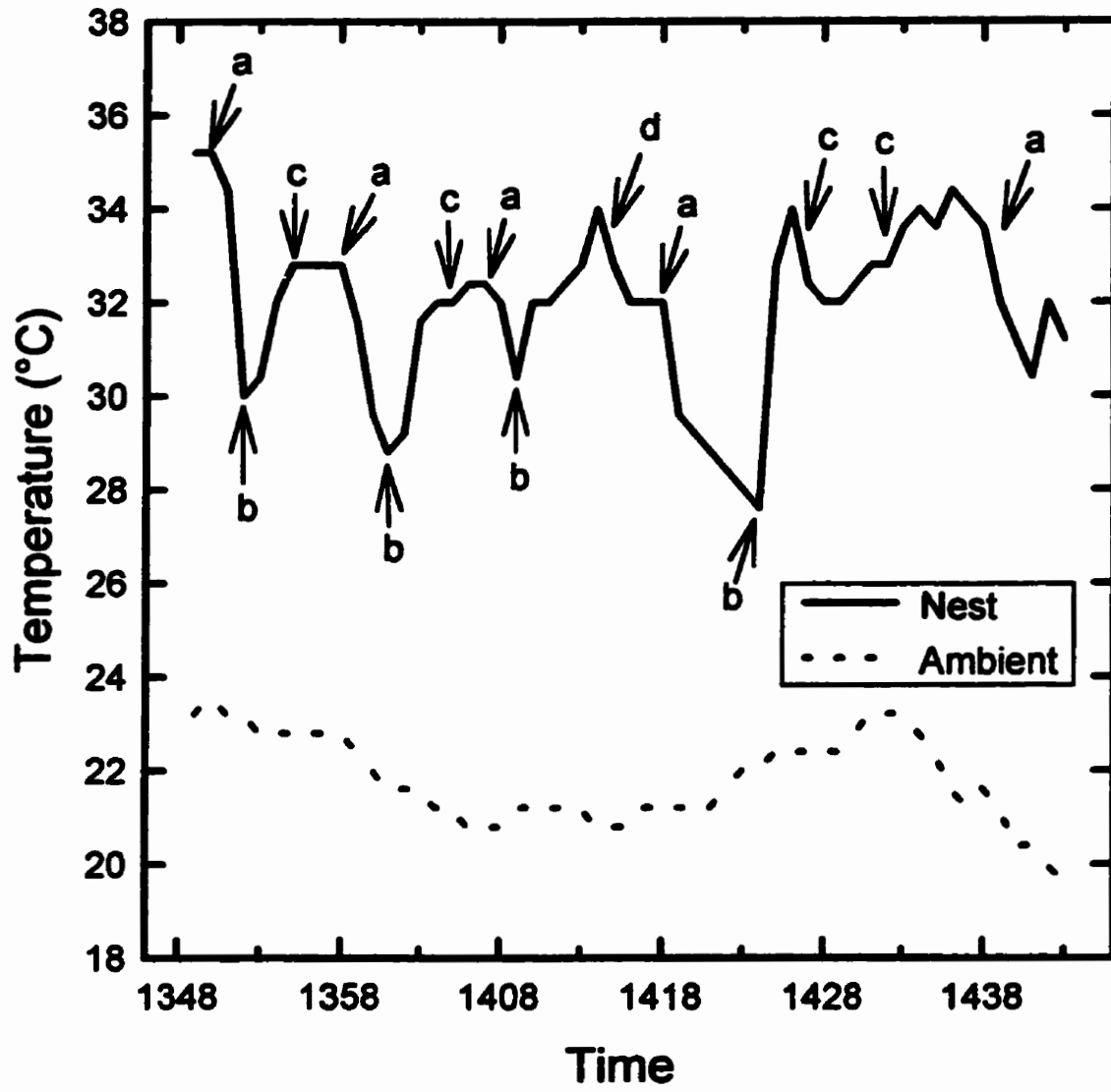
$(U = 22.5, df = 1, P = 0.023)$.

Weak positive correlations were found between mean female attentiveness and mean male feeding frequency for control clutches (day 4: Spearman rank correlation $r_s = 0.651$, $P = 0.057$), and clutches with cowbird eggs and one host egg removed (day 3: $r_s = 0.346$, $P = 0.041$), and no host eggs removed (day 1: $r_s = 0.311$, $P = 0.054$; day 3: $r_s = 0.436$, $P = 0.033$; day 5: $r_s = 0.430$, $P = 0.04$).

Nest and ambient temperatures were recorded for at least 24 hours at three nests during the laying period, and at eight nests during the incubation period. Observations at nests in concert with measurements of nest temperature showed that temperature was highly correlated with female attentiveness (see Figure 3, for example). Nest temperature was rarely above ambient temperature early in laying, but it increased relative to ambient temperature as laying progressed (Figure 4). Nest temperature always exceeded ambient temperature during incubation (Figure 5). Average nest temperatures during incubation ranged from 30 to 36°C for different nests.

Periodogram analysis identified an average of 7.33 significant cycles for nest temperatures during early laying versus an average of 9.0 significant cycles for the ambient temperature recordings taken simultaneously (see Table 13). Significant cycles in nest temperature data ranged from a minimum period of 0.83 hours to a maximum period of 21.16 hours, whereas significant cycles in ambient temperature data ranged from 1.4 to 21.1 hours (see Table 13). Most periodicity in both the nest and ambient temperature data is explained by long-period cycles, rather than short-period cycles, as indicated by the large periodogram, F -, and T -statistic values for long-period cycles (Table 13).

FIGURE 3. Ambient and nest temperatures at Yellow Warbler nest 94-G151 on the third day of incubation. Arrows and letters indicate activity at the nest noted during the one hour observation period.



- a - female left nest
- b - female onto nest
- c - male fed female at nest
- d - light rain

FIGURE 4. Ambient and nest temperatures at Yellow Warbler nest 94-S2 beginning the evening of the day on which the first egg was laid (30 May), and ending the morning the third egg was laid (1 June). Arrows indicate the approximate times the second (a) and third (b) eggs were likely to have been laid.

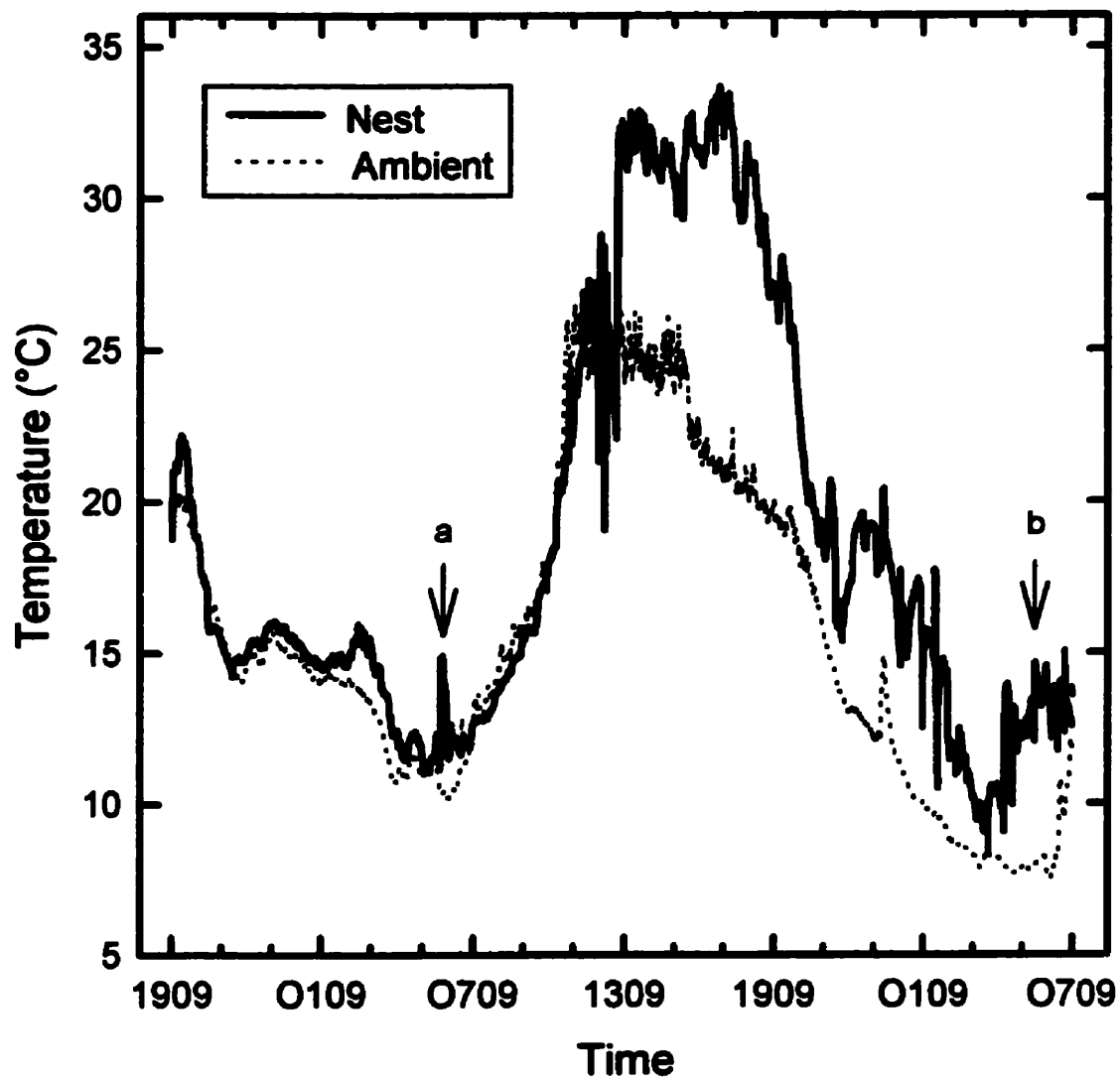


FIGURE 5. Ambient and nest temperatures at Yellow Warbler nest 94-G52 beginning the afternoon of the fourth day of incubation (6 June), and ending the afternoon of the fifth day of incubation (7 June).

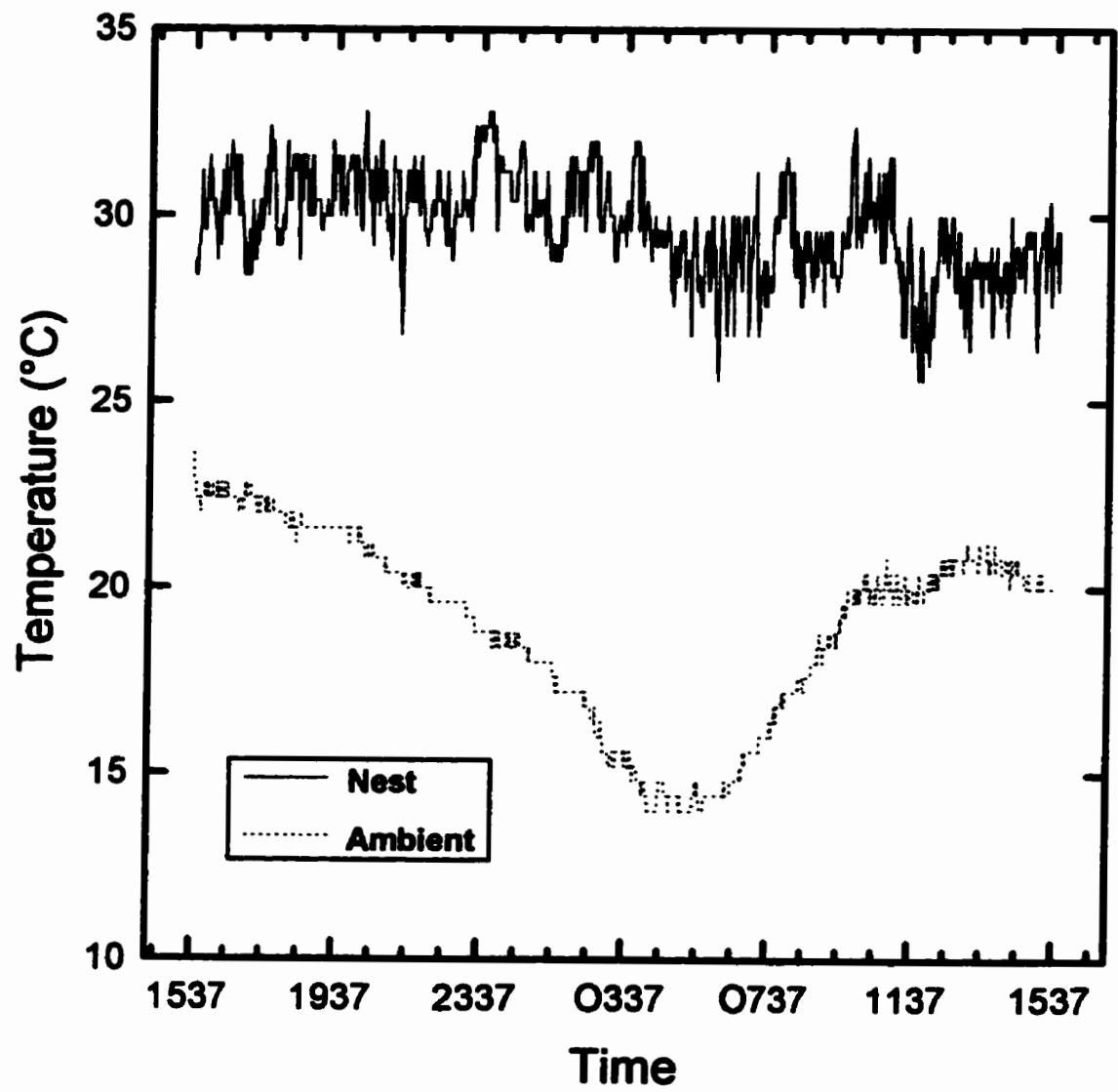


TABLE 13. Periodogram values and duration of the corresponding periodic cycles in nest and ambient temperature recordings during the Yellow Warbler laying period.

Recording	Number of significant cycles	Duration of Cycle (hours)	Periodogram		
			values ^a	<i>F</i> - ^b	<i>T</i> - ^c
Nest 1	5	21.2	71225.8	4785.7	0.788
		10.6	14979.0	252.9	0.785
		7.1	1767.1	25.3	0.431
		5.3	952.7	13.5	0.408
		3.5	301.5	4.2	0.218
Nest 2	7	21.1	53492.3	5131.0	0.798
		10.6	8329.1	180.9	0.616
		7.1	1636.8	31.9	0.315
		5.3	1277.6	24.7	0.359
		3.0	407.3	7.7	0.195
		4.2	390.7	7.4	0.179
		3.5	287.6	5.4	0.209

TABLE 13 continued

Ambient 1^d	7	21.1	39862.6	3645.4	0.732
		10.6	5701.4	150.5	0.39
		7.1	4689.1	121.2	0.527
		4.2	957.0	23.0	0.227
		5.3	912.3	21.9	0.281
		3.0	507.4	12.0	0.204
		3.5	373.6	8.8	0.217
Nest 3	10	16.7	21513.9	2255.1	0.529
		8.3	11186.3	760.5	0.586
		4.2	2837.4	150.2	0.359
		5.6	2710.1	143.0	0.535
		2.8	442.2	22.0	0.188
		3.3	425.5	21.1	0.223
		1.1	152.1	7.5	0.102
		1.4	71.3	3.5	0.053
		0.8	69.9	3.4	0.055
		1.7	63.8	3.1	0.053

TABLE 13 continued

Ambient 2^c	11	16.7	32001.9	3343.4	0.626
		8.3	11373.1	571.6	0.594
		5.6	2341.9	95.9	0.302
		4.2	2139.7	87.2	0.395
		2.8	769.9	30.5	0.235
		3.3	639.1	25.2	0.242
		2.1	539.8	21.3	0.27
		2.4	219.1	8.6	0.15
		1.9	201.2	7.8	0.162
		1.5	86.0	3.3	0.083
		1.4	84.2	3.2	0.088

^a Periodogram values indicate the amount of periodicity present in the data for each cycle of specific duration.

^b *F*- value calculated to test the significance of each periodogram value.

^c *T*- value calculated to test for the maximum periodogram.

^d Ambient temperature 1 was recorded simultaneous to recordings at Nests 1 and 2.

^e Ambient temperature 2 was recorded simultaneous to recording at Nest 3.

Relative to nest temperatures early in the laying cycle, nest temperatures during incubation showed more significant cycles ($\lambda = 31.0$ significant cycles; see Table 14), whereas the number of significant cycles in ambient temperature did not change from the laying period ($\lambda = 10.0$ significant cycles). Significant cycles in nest temperature during incubation ranged from 1.08 to 28.8 hr, whereas significant cycles in ambient temperature ranged from 6.1 to 25.8 hr. Mean periodogram values of the maximum peak of nest temperature during incubation were lower than those during laying (8407.4 vs. 48744.0, respectively; Table 14), although mean periodogram values for the maximum peak for ambient temperature during incubation were also lower than during laying (12571.7 vs. 35932.3, respectively).

Nestling Period

Comparisons by day indicated no significant differences in variables between clutch sizes for control or "parasitized" clutches (Appendix 3), or between years for control clutches (Appendix 4). Therefore, the data were pooled. Females incubating nests that contained a cowbird egg and nests that contained one cowbird nestling were more attentive than females that incubated control clutches with warbler eggs or one warbler nestling, respectively; however, the differences only approached significance (see Table 15). Conversely, females incubating nests that contained a cowbird nestling and two or more warbler nestlings were less attentive than females that incubated control nests with three or more warbler nestlings, a difference that approached significance (see Table 15). Neither the presence of a cowbird egg nor nestling significantly influenced the number of

TABLE 14. Mean (\pm SE) number of significant periodic cycles, mean maximum and minimum periodogram values, and mean length of maximum and minimum periodic cycles in nest and ambient temperatures during the incubation period.

Values are averaged among all nests at which recordings were made.

Variable	Nest temperature (<i>n</i>)	Ambient temperature (<i>n</i>)
Mean number of significant cycles	31.0 \pm 6.5 (9)	10.0 \pm 2.1 (8)
Mean max. periodogram value	8407.4 \pm 2184.5 (9)	12571.7 \pm 3909.8 (8)
Mean max. duration of significant periodic cycle (hr)	28.8 \pm 6.4 (9)	25.8 \pm 2.1 (8)
Mean min. periodogram value	49.8 \pm 9.3 (9)	565.6 \pm 457.8 (8)
Mean min. duration of significant periodic cycles (hr)	1.08 \pm 0.3 (9)	6.1 \pm 1.9 (8)

TABLE 15. Female attentiveness ($\bar{x} \pm SE$ in seconds per one-hour observation period, n in parentheses) at control and experimentally parasitized (one cowbird egg or nestling added) Yellow Warbler clutches just prior to, and during, the nestling period.

Stage	Treatment		$U (P)^b$
	Cowbird ^a	Control ^a	
Egg	3138.7 \pm 49.1 (31)	2959.6 \pm 127.6 (11)	124.0 (0.096)
One nestling	3123.2 \pm 80.5 (17)	2864.7 \pm 146.9 (10)	54.0 (0.064)
Two nestlings	2740.2 \pm 194.6 (5)	2756.5 \pm 142.7 (8)	18.0 (0.416)
Three+ nestlings	2403.1 \pm 210.9 (15)	2707.4 \pm 119.9 (26)	144.0 (0.087)

^a Data from 1994 and 1996 combined.

^b Mann-Whitney U -statistic comparing female attentiveness among treatments within each stage. P -value is one-tailed.

female incubation bouts relative to control clutches (Table 16).

The frequency of female feeding at the egg stage did not differ significantly between control clutches and those with a cowbird (Table 17). However, females brooding a single warbler nestling consumed food brought by the male significantly more often than females brooding a single cowbird nestling (Table 17). Females brooding three or more warbler nestlings ate the food brought by the male more often than females brooding a cowbird and two or more warbler nestlings, a difference that approached significance (Table 17). Female warblers fed food brought by the male to single nestlings significantly more often if the nestling was a cowbird rather than a warbler (Table 17). The rate of male-to-female-to-nestling feedings was higher when a cowbird nestling was present at larger brood sizes, but the differences were not significant (see Table 17). Female warblers brooding cowbird nestlings did not significantly increase their rate of food delivery relative to control females (Table 17). Male warblers did not significantly increase their rate of nestling feedings, or their total rate of food delivery to the nest (Table 17), if their nest contained a cowbird egg or nestling. The presence of a cowbird nestling did not significantly increase the rate of nestling feedings by the male and female warblers combined (Table 17).

Warbler nestling hatching data were not normally distributed. Comparison of hatching variables among years for each treatment indicated the data could be pooled (see Appendix 5). Yellow Warbler eggs in clutches with a cowbird nestling took longer to hatch than warbler eggs in control clutches, but the difference was significant only for the third Yellow Warbler egg (Table 18).

TABLE 16. Number of incubation bouts ($\bar{x} \pm$ SE per one-hour observation bout, n in parentheses) by the female at experimentally parasitized Yellow Warbler clutches just prior to, and during, the nestling period.

Stage	Treatment		<i>U</i> (<i>P</i>) ^b
	Cowbird ^a	Control ^a	
Egg	3.4 ± 0.3 (31)	4.3 ± 0.9 (11)	155.0 (0.336)
One nestling	5.2 ± 0.8 (17)	5.0 ± 0.7 (10)	83.5 (0.471)
Two nestlings	6.4 ± 1.3 (5)	7.5 ± 1.3 (8)	18.0 (0.416)
Three+ nestlings	5.5 ± 1.1 (15)	4.6 ± 0.4 (26)	185.0 (0.400)

^a Data for 1994 and 1996 combined.

^b Mann-Whitney *U*-statistic comparing number of female incubation bouts among treatments within each stage. *P*-value is one-tailed.

TABLE 17. Rate of food delivery ($\bar{x} \pm SE$ per 1-hr observation period, n in parentheses) at experimentally parasitized Yellow Warbler clutches prior to and during the nestling period.

Type of delivery	Stage	Treatment		$U (P)^b$
		Cowbird ^a	Control ^a	
Male-to-female	Egg	1.0 \pm 0.2 (31)	1.4 \pm 0.5 (11)	162.5 (0.41)
	One nestling	0.88 \pm 0.4 (16)	1.7 \pm 0.6 (10)	48.0 (0.049)
	Two nestlings	0.6 \pm 0.4 (5)	1.3 \pm 0.4 (8)	12.5 (0.1422)
	Three+ nestlings	0.4 \pm 0.2 (15)	1.6 \pm 0.5 (26)	143.0 (0.083)
Female-to-nestlings	One nestling	1.9 \pm 0.6 (17)	1.2 \pm 0.4 (10)	77.0 (0.356)
	Two nestlings	1.8 \pm 0.7 (5)	2.1 \pm 0.8 (8)	20.0 (0.50)
	Three+ nestlings	1.9 \pm 0.5 (15)	1.6 \pm 0.3 (26)	185.5 (0.40)
Male-to-nestlings	One nestling	1.0 \pm 0.4 (17)	1.1 \pm 0.5 (10)	81.0 (0.432)
	Two nestlings	1.6 \pm 0.5 (5)	1.3 \pm 0.6 (8)	16.0 (0.311)
	Three+ nestlings	3.3 \pm 0.7 (15)	2.8 \pm 0.5 (26)	176.0 (0.310)
Male-to-female-to nestlings	One nestling	1.9 \pm 0.4 (17)	0.5 \pm 0.3 (10)	50.0 (0.042)
	Two nestlings	2.2 \pm 1.2 (5)	1.13 \pm 0.4 (8)	16.0 (0.311)
	Three+ nestlings	1.8 \pm 0.6 (15)	1.2 \pm 0.3 (26)	177.5 (0.320)
Total male	One nestling	4.5 \pm 1.0 (17)	3.3 \pm 0.7 (10)	75.0 (0.320)

TABLE 17 continued

feeds	Two nestlings	4.4 ± 1.6 (5)	3.6 ± 1.1 (8)	17.0 (0.362)
	Three+ nestlings	5.5 ± 0.9 (15)	5.6 ± 0.7 (26)	185.0 (0.442)
Total nestling feeds	One nestling	6.5 ± 1.0 (17)	4.5 ± 0.6 (10)	72.0 (0.269)
	Two nestlings	6.2 ± 2.1 (5)	5.8 ± 0.7 (8)	17.5 (0.362)
	Three+ nestlings	7.3 ± 1.1 (15)	7.2 ± 0.6 (26)	189.0 (0.442)

^a Data for 1994 and 1996 combined.

^b Mann-Whitney *U*-statistic comparing rate of food delivery among treatments within each stage and delivery type. *P*-value is one-tailed.

TABLE 18. Yellow Warbler incubation period ($\bar{x} \pm$ SE days, n in parentheses) by treatment at experimentally parasitized clutches.

Hatching order	Treatment		<i>U</i> (<i>P</i>) ^b
	Cowbird ^a	Control ^a	
First	9.67 \pm 0.19 (24)	9.58 \pm 0.19 (26)	270.5 (0.194)
Second	10.10 \pm 0.18 (21)	10.0 \pm 0.17 (25)	232.5 (0.238)
Third	10.89 \pm 0.25 (18)	10.3 \pm 0.16 (23)	130.0 (0.015)
Fourth	11.0 \pm 0.19 (11)	10.93 \pm 0.3 (15)	73.5 (0.323)
Fifth	11.0 \pm 0.41 (4)	11.0 \pm 0.58 (3)	6.0 (0.5)

^a Data are combined between 1994 and 1996.

^b Mann-Whitney *U*-statistic comparing length of the incubation period among treatments within each stage. *P*-value is one-tailed.

The proportion of Yellow Warbler eggs that hatched successfully was significantly lower in clutches with a cowbird nestling (control: 0.96 ± 0.02 , $n = 21$; cowbird: 0.71 ± 0.07 , $n = 25$; $U = 128.5$, $df = 1$, P (one-tailed) = 0.0003). Although the number of dead warbler embryos was higher in clutches with a cowbird nestling, the difference was not significant (control: $\bar{x} = 0.19 \pm 0.09$, $n = 21$; cowbird; $\bar{x} = 0.52 \pm 0.26$, $n = 23$; $U = 209.0$, $df = 1$, P (one-tailed) = 0.115). The presence of a cowbird nestling resulted in significantly more warbler eggs disappearing (control: $\bar{x} = 0.14 \pm 0.10$, $n = 21$; cowbird: $\bar{x} = 0.54 \pm 0.16$, $n = 24$; $U = 173.5$, $df = 1$, P (two-tailed) = 0.021) and significantly more nestling warblers dying (control: $\bar{x} = 0.0 \pm 0.0$, $n = 21$; cowbird: $\bar{x} = 0.17 \pm 0.10$, $n = 24$; $U = 220.5$, $df = 1$, P (one-tailed) = 0.049).

DISCUSSION

Laying Period

The addition of a cowbird egg on the first day of laying was predicted to act as a "superstimulus" that would promote an increase in female Yellow Warbler nest attentiveness during the laying period. Contrary to predictions, the addition of a cowbird egg did not increase female nest attentiveness on any day of the laying period. The lack of stimulation of female nest attentiveness at parasitized clutches appears to contradict the results of Hébert and Sealy (1992) during the laying period, and other studies during the incubation period (Blagosklonov 1977, Morel *in* Payne 1977, Jones 1987, but see Moreno and Carlson 1989). Hébert and Sealy (1992), however, enlarged clutches on the evening of LD1 with two warbler eggs, whereas I enlarged clutches with a single cowbird egg. Cowbird eggs at Delta Marsh average 3.04 ml in volume (1993 data, $n = 130$), whereas Yellow Warbler eggs average 1.33 ml (Sealy, unpubl. data), or less than half the volume of a cowbird egg. Therefore, the onset of female attentiveness does not appear to be modified by the volume of eggs in the nest, but rather the number of eggs that contact the brood patch. Silverin and Goldsmith (1983) experimentally altered Pied Flycatcher clutch sizes and concluded that the number of eggs in a clutch does not exert a quantitative effect on prolactin levels, a hormone closely associated with incubation behaviour. Their conclusion, however, was based on a single blood sample taken from each bird on the tenth day of incubation, which left the possibility that the number of eggs could affect the onset of prolactin secretion and, hence, incubation attentiveness during the laying period.

I predicted the increase in female warbler energy expenditure during incubation and

simultaneous reduction in available foraging time, due to the increase in female nest attentiveness after addition of a cowbird egg, should result in higher frequency of female feedings at the nest by male warblers. Contrary to this prediction, and consistent with the lack of increased female nest attentiveness in this study, the frequency of male feedings was not higher in clutches containing cowbird eggs. The only difference between treatments occurred in clutches where a cowbird egg had been added on the second day of laying, and one or no warbler eggs had been removed. However, a weak positive correlation existed between female attentiveness and male feeding, which suggests that if female attentiveness increases, the frequency of male feeding should also increase, as in other studies (Nilsson and Smith 1988, Smith et al. 1989, Halupka 1994).

As noted for other passerine species (Haftorn 1981, Haftorn and Reinertsen 1985), Yellow Warbler nest temperatures gradually increased above ambient temperatures through the laying period as female attentiveness increased. Variation in nest temperature between nests was likely due to differences in the position of the thermistor relative to the incubating female within the nest. Nest temperature during early laying contained multiple significant periodic components. Significant cycles ranged in duration from just under 1 hour to 21 hours, however, maximum periodogram values were associated with long-period cycles. These results indicate most of the fluctuation in nest temperature during laying occurs over periods of slightly less than 24 hours in duration. Whereas significant temperature fluctuation occurs over several hours (about 12.5 hours), on average the magnitude of these fluctuations was quite small relative to longer-term fluctuations. The similarity in the periodic components of nest temperature in early laying, and the ambient

temperature recordings taken simultaneously, suggests that much of the fluctuation in nest temperature over a 24-hour period is due to changes in ambient temperature, rather than variation in female incubation behaviour. This observation is consistent with the observations of female Yellow Warbler nest attentiveness between 1430 and 1730 h, which demonstrates that relatively little time is spent in the nest early in the laying period.

Periodogram analysis of nest temperatures during incubation indicates a much different pattern of temperature fluctuation compared to either nest temperature during laying or ambient temperature during incubation. Although maximum periodogram values still occurred at long-period cycles (28.8 hours), numerous short-period cycles explain much of the variation in nest temperature. This pattern of periodic components reflects the rapid fluctuations in nest temperature recorded during incubation, due to rapid warming of the nest when the female begins incubating, followed by rapid cooling of nest temperature toward ambient temperature after the female leaves the nest. The rate nest temperatures cool is not an accurate indicator of egg temperature, however, because eggs lose heat much less rapidly. Because egg temperatures fall in cold weather during incubation even when the female remains on the nest (Weeden 1966, Haftorn and Reinertsen 1985, Haftorn and Reinertsen 1990), ambient temperatures are expected to influence the periodicity of egg temperatures to some extent, in addition to patterns of female attentiveness. The similarity between the periodic components of nest temperature and ambient temperature during laying over the 24-hour period indicate the low female nest attentiveness observed between 1430 and 1730 h is representative of female attentiveness patterns throughout the day during early laying.

Nestling Period

With a few notable exceptions, the presence of a cowbird nestling during the hatching period did not significantly alter parental behaviour at the nest. Consistent with predictions made for female warblers during the laying period, at the end of the incubation period females incubating clutches containing a cowbird egg tended to spend about 3 min per hr more ($P = 0.096$) on the nest than females that incubated clutches containing only warbler eggs. Contrary to predictions made for the hatching period, the presence of a single cowbird nestling tended to increase female attentiveness by 4.3 min per hr ($P = 0.064$) above that of females brooding a single warbler nestling. Consistent with predictions made for the hatching period, females at nests containing a cowbird and two or more warbler nestlings tended to be less attentive by 5.1 min per hr ($P = 0.087$) than females at control nests. The presence of a cowbird did not alter the number of incubation bouts made by female warblers at any stage. In Yellow Warblers, early hatching by cowbird eggs did not reduce female attentiveness, or prolong incubation periods of most Yellow Warbler eggs (except the third egg, $P = 0.015$), as suggested for other host species (e.g. Dolan and Wright 1984, Fraga 1985). In contrast to females of other species that must spend less time on the nest during hatching, therefore, female Yellow Warblers were able to remain on the nest throughout much of the hatching period. Unlike males of other species that begin regular feeding mid-way through hatching (e.g. Weathers and Sullivan 1989), male warblers frequently feed the female at the nest during hatching which likely enables the female to remain more attentive. Males of other warbler species also

feed both nestlings and the female during hatching (e.g. Mayfield 1992, Pitocchelli 1993, Morse 1994, Van Horn and Donovan 1994, Robinson 1995), and at a similar frequency to male Yellow Warblers in one congeneric species (Prairie Warbler Nolan 1978). Males of at least two other warbler species, however, do not deliver food to the nest during hatching (Black-throated Green Warbler *D. virens*, Morse 1993; MacGillivray's Warbler *Oporornis tolmiei*, Pitocchelli 1995) which could accelerate the negative impact of a cowbird nestling.

The presence of a cowbird nestling did not elicit significantly increased food delivery rates to the nest by the male, female, or both sexes combined, at any stage during the hatching period. However, cowbird nestlings significantly influenced the feeding behaviour of the female warbler when a male arrived at the nest with food. Observations at nests indicated that when a male warbler arrived at a nest with food, female warblers chose the fate of the food: (1) the female can leave the nest and let the male feed the nestlings, (2) the female can ignore the male and continue brooding, whereupon the male ate the food himself, (3) the female can take the food and eat it herself, and (4) the female can take the food and feed the nestling(s). In this study, decision #1 was not significantly influenced by the presence of a cowbird. Females ignored food brought by the male (decision #2) too rarely to compare values between treatment groups. However, the presence of a cowbird nestling significantly altered female warblers' choice from decision #3 to #4. Female warblers brooding one cowbird nestling fed it with food brought by the male significantly more frequently than females brooding one warbler nestling ($P = 0.042$). As a corollary, female warblers brooding one warbler nestling ate the food brought by the

male significantly more frequently than females brooding one cowbird ($P = 0.049$).

Although female warblers brooding a cowbird and one or more warbler nestlings tended to feed them with food brought by the male more frequently than control clutches, the differences were not significant ($P = 0.311$ and 0.32 , respectively). Trends for higher frequencies of male-to-female feeds at control broods with two and three or more nestlings compared to broods with cowbirds approached significance ($P = 0.142$ and 0.083 , respectively). Therefore, it appears that early in the hatching period the presence of a cowbird nestling stimulates more feedings from the female than a warbler nestling, but this difference is diminished by the end of the hatching period at larger brood sizes.

The results of this study show the presence of a cowbird stimulates changes in parental behaviour by the hosts that may benefit the cowbird. At the end of incubation, females incubating clutches containing a cowbird egg tended to be more attentive, which is consistent with Morel's observations cited by Payne (1977). Whether the cowbird egg actually receives more heat than warbler eggs can be tested only by measuring egg temperatures directly. Cowbird eggs are larger than warbler eggs, as are viduine finch eggs compared with host eggs (Morel *in* Payne 1977), and this may enable them to receive proportionately more heat from the brood patch during incubation. During hatching, cowbird nestlings tended to be brooded and fed more by the female than were warbler nestlings. Gill (1982) found one cuckoo nestling of an ejector species was brooded more than a host brood of three to four young.

How cowbird nestlings might elicit more female attentiveness is not known.

Cowbird nestlings become homeothermic later in the nestling period than do many hosts

(Neal 1973), although the brood itself may be homeothermic as early as three days after hatching (Hill and Beaver 1982). Perhaps cowbird body temperatures fall below those of warblers immediately after hatching, thereby eliciting more brooding from the female. The subsequent increase in the parasitic nestling's body temperature could enhance the nestling's begging ability (Webb 1993). In Red-winged Blackbirds, the optimal body temperature for maximizing begging response increases as nestlings mature (Choi and Bakken 1990). A combination of begging intensity and location in the nest appear to influence the likelihood a nestling will receive food from a parent (Gottlander 1987, Lamey and Mock 1991), therefore, if the parasitic nestling hatches first, as is often the case (Briskie and Sealy 1990), it will receive more food and gain an advantage over later-hatched host nestlings. Cowbird nestlings begin begging almost immediately after hatching, but not significantly earlier than nonparasitic relatives (Lorenzana 1996). Perhaps newly hatched cowbird nestlings beg more vigorously than host nestlings, as do cowbird nestlings later in the nestling period (Broughton et al. 1987, Briskie et al. 1994). Although intense nestling begging by brood parasites can increase risk of nest predation (Redondo and Castro 1992 in Redondo 1993), begging may not be an energetically costly behaviour in passerine birds (McCarty 1996). Begging exploits the host's behavioural rules for parental care because it is a reliable signal of nutritional need or physical vigor (Redondo 1993), and may mimic host nestling vocalizations (Redondo and Reyna 1988). The large mouth, bright-coloured gape, and persistent begging by cuckoo nestlings not only superstimulates feeding by foster parents, but also feeding by other neighbouring species (Payne 1977). Parasitic cuckoos at the same nutritional state as host nestlings beg

longer and call more, beg even after being fed, and have larger esophagi and gizzards and, therefore, are capable of receiving much more food than host nestlings (Redondo 1993).

The pattern of reduced differences in feeding rates between the cowbird and control groups as brood size increases is consistent with observations that parental feeding rate is affected by the mean begging behaviour of the entire brood, rather than that of a single nestling (Bengtsson and Rydén 1983). Therefore, to an adult warbler, the absolute difference in stimulation between broods of three warblers and one cowbird nestling compared to four warbler nestlings would be less than the difference in stimulation between broods of one warbler nestling and one cowbird nestling.

The fact that in this study cowbird nestlings elicited changes in female feeding behaviour contrasts with results of previous studies of food delivery to unparasitized nests. Biermann and Sealy (1982) found that male Yellow Warblers, rather than females, increased their feeding frequency to accommodate the higher nutritional demands of larger broods. In fact, male warblers fed two-day-old broods more frequently than females regardless of brood size (Biermann and Sealy 1982). Females of other species also appear unable to vary their feeding rates to compensate for increased nestling nutritive requirements (Lozano and Lemon 1996), and it is male feeding that is positively correlated with brood size (e.g. Westneat 1988). How cowbirds stimulate female feeding behaviour immediately after hatching cannot be tested from the results of this study. In addition, because parents usually feed from specific positions of the nest edge, and favor nestlings close to these positions, food may be unevenly distributed to individual nestlings within the brood (Rydén and Bengtsson 1980). The large size of a cowbird nestling relative to

warbler nestlings, in addition to its intense begging, could enable it to sequester the best feeding location in the nest. It would be instructive, therefore, to test whether cowbird nestlings receive proportionately more food than warbler nestlings as the hatching period progresses, even though the total rate of food delivery to the brood is not significantly increased relative to control broods.

Consistent with predictions, cowbird parasitism resulted in a significant negative effect on survival of young warblers. Warbler eggs in clutches with cowbird eggs experienced reduced hatching success ($P = 0.0003$), increased nestling mortality ($P = 0.049$), and more eggs disappeared just prior to or during the hatching period ($P = 0.021$). Yellow Warbler nestlings appear to be outcompeted much more easily by cowbird nestlings, than are larger nestlings of other species (Mason 1980, Fraga 1985, Weatherhead 1989). Because cowbird nestling additions did not influence warbler incubation period, and actually increased female attentiveness, it is likely that warbler hatching success was compromised during incubation, rather than in the hatching period. Also, the presence of a cowbird nestling did not increase the incidence of dead warbler embryos significantly. The greater number of warbler eggs that disappeared in parasitized clutches suggests damage during incubation or hatching (Dolan and Wright 1984), nestlings that died shortly after hatching and were removed by the parents, or partial predation.

Significantly more warbler nestlings died during the hatching period in cowbird than control nests, however, the absolute number was small. In most passerine species, parental feeding capacity is normally not exceeded when the brood is young (Bryant 1975,

Perrins and Moss 1975, Bengtsson and Rydén 1981), therefore, only exceptionally bad conditions, such as storms, lead to mortality of late-hatched chicks during the hatching period (Dence 1946, Bengtsson and Rydén 1981, Reynolds 1996). Most brood reduction in parasitized nests appears to occur later in the nestling period when the total food requirement of the entire brood is greater and parents cannot meet the demand (Weatherhead 1989). Therefore, in Yellow Warblers it appears any potential negative impact on host nestlings due to early hatching by the cowbird nestling is minimized by male feedings that allow the female to maintain attentiveness until host nestlings hatch 12 to 24 hours later. However, for host species whose eggs hatch days after the cowbird egg, and the host male does not feed the female and young soon after hatching, hatching and fledging success can be dramatically reduced (Walkinshaw 1961, Klaas 1975, Rothstein 1975a). In contrast to cowbirds, honeyguide (*Indicator sp.*) and many parasitic cuckoo nestlings eliminate competition by killing or ejecting host nestlings, despite the fact that the parasitic nestlings already hatch before host nestlings (Payne 1977). However, although parasitic viduine finches (*Vidua chalybeata*) hatch one to three days prior to host nestlings (Payne 1977), parasitism has little or no negative effect on host fledging success (Morel *in* Payne 1973).

In this study, cowbird parasitism did not alter Yellow Warbler parental behaviour during the laying period, but the presence of a cowbird nestling tended to increase female nest attentiveness, and significantly increased feeding frequency early in the hatching period. Early hatching by the cowbird nestling, therefore, reduced host reproductive success through direct competition with host nestlings, rather than indirectly by reducing

female nest attentiveness. Reduced host reproductive success was already detectable at the end of the hatching period. However, frequent feeding at the nest by male Yellow Warblers likely functions to delay most of the detrimental impact cowbird nestlings have on host nestlings until later in the nestling period. Early hatching by cowbird nestlings may reduce host reproductive success by reducing female nest attentiveness in species with longer incubation periods and less frequent feeding by the male.

GENERAL DISCUSSION

The results of this study provide some support for hypotheses stating that cowbirds employ strategies prior to the nestling period that enhance the probability of the cowbird fledging. The results of this study also indicate that the use or applicability of such strategies may be variable, dependent perhaps upon both the conditions of the current breeding season and the identity of the host species. Although evidence is indirect, this study suggests that the size of cowbird eggs negatively affects the incubation of smaller host eggs, and may be more influential in predicting the cowbirds' probability of hatching first than any behavioural strategies. Indeed, given that the Brown-headed Cowbird is now perhaps one of the most widely distributed avian species in North America, and parasitizes a wide range of hosts that vary greatly in both physical and ecological characteristics, one might expect only relatively general strategies to have evolved.

Confounding factors such as prey availability and climatic conditions make the assignment of a function to a behaviour such as host-egg removal problematic (Chapter 1). This study dealt with a single host and parasite at one locality. Patterns of cowbird parasitism between regions and landscapes have been described as complex and variable (Rothstein and Robinson 1994, Hahn and Hatfield 1995, Robinson et al. 1995), and the pattern of egg removal by female cowbirds is also variable. Sealy (1992) demonstrated that the frequency by which female cowbirds remove Yellow Warbler eggs varied within and among breeding seasons. Frequencies of egg removal from parasitized Yellow Warbler nests also vary geographically, with estimates ranging from 13% to 100% of parasitized clutches having an egg removed (Clark and Robertson 1981, DellaSala 1985,

Burgham and Picman 1989). Estimates of removal frequencies for other species vary from highs of almost 100% in parasitized nests (Mayfield 1960, Scott 1977, Nolan 1978, Weatherhead 1989) to lows near 30% (Nice 1937). Variation in host egg removal by cowbirds could indicate that removal (1) is dependent on the density of cowbirds and intensity of parasitism, (2) is highly specialized, and is used with precision only when very specific conditions are met, or (3) is generalized and may function in one or more ways simultaneously, dependent upon the host species, weather conditions, etc.

The data on cowbird incubation periods presented in Chapter 2 are consistent with the hypothesis that the presence of cowbird eggs reduces the amount of heat smaller host eggs receive from the brood patch, and suggest cowbirds may hatch earlier when stimulated by host eggs. The data are also consistent with observations that cowbirds have short incubation periods relative to the size of the egg (Briskie and Sealy 1990). Drent (1975) stated that incubation period is influenced by (1) state of development of the nestling at hatching, (2) relative proportion of reserve materials in the egg, (3) incubation temperature, and (4) ecological adjustment of growth rate. A fifth factor that modifies incubation period is behavioural stimulation (e.g. Vince 1966b). Although not tested in this study, cowbird eggs do not appear to have less energy invested per volume than expected (Ankney and Johnson 1985; but see Kattan 1995 for Shiny Cowbirds). Woodpeckers have short incubation periods because nestlings hatch at an immature stage of development relative to other altricial species (Nice 1954, Drent 1975, Yom-Tov and Ar 1993). However, no trade-off between cowbird embryonic development at hatching and incubation period was detected with the crude measurements made in this study.

Cowbird nestlings stimulated to hatch early may be less developed at hatching in terms of other variables not measured in this study, such as behaviour (but see Lorenzana 1996) or immunocompetency (Ricklefs 1993). These results suggest the rapid rate at which cowbird embryos develop is not entirely rigid, but varies in response to stimuli from other eggs. If cowbirds experience a trade-off between the costs and benefits of hatching early, the ability to hatch in response to stimuli from host eggs close to hatching would optimize the trade-off, and would be adaptive for such an extreme generalist brood parasite.

Although cowbird eggs may be stimulated to hatch earlier, they appear to hatch before Yellow Warbler eggs mostly due to the delayed hatching of warbler eggs in parasitized clutches. Other studies have also shown larger eggs are more successful than small eggs when incubated in the same clutch (Wood 1995, Peer and Bollinger in press). It would appear that smaller eggs receive less heat from the brood patch in the presence of large eggs, although evidence from a brief temperature recording showed egg size did not influence egg temperature (Huggins 1941).

The data presented in Chapter 3 show that the cowbird egg does not elicit increased parental care during laying, whereas the cowbird nestling does stimulate increased care during hatching. Early hatching by the cowbird nestling did not reduce female attentiveness, or delay the hatching of most warbler eggs. The mortality of warbler nestlings during the hatching period, therefore, was due to direct competition with the cowbird rather than reduced female attentiveness caused by the cowbird. The fact that the cowbird manipulates the behaviour of the female, rather than the male, is in contrast with previous studies of parental care in passerines. More research is required to determine

how the newly hatched cowbird manipulates female behaviour. Certainly, competition between cowbird and host nestlings of different species during the nestling period will provide a fruitful subject for research for some time to come.

In summary, cowbird nestlings sometimes benefit during the incubation period from host-egg removal behaviour by the female cowbird, which optimizes the incubation conditions of the host and ensures successful hatching of the cowbird egg. Incubation periods of cowbird eggs appear to be short, but labile, and may be influenced by stimuli from host eggs. The hatching of warbler eggs is delayed by the presence of a cowbird egg during incubation, rather than the early hatching of the cowbird nestling. It appears the hatching order is determined more by delayed hatching of warbler eggs than stimulation of cowbird eggs to hatch early. The larger cowbird egg may disrupt contact between the brood patch and the smaller warbler eggs, thus retarding host embryonic development and allowing the cowbird to hatch first. The cowbird egg does not stimulate increased parental care during the laying period, but the cowbird nestling does at least early in the hatching period. The negative impact of the cowbird nestling is already apparent at the end of the hatching period. Cowbirds appear to benefit from being larger than their hosts during the incubation and nestling stages. Because cowbirds do not have a size advantage during either the incubation or nestling stages in nests of larger hosts, it would appear cowbirds should prefer smaller hosts when they are available. Therefore, despite the findings that show cowbirds are capable of altering host parental care during the incubation and hatching periods, it appears the first and most important way cowbirds increase their chances of producing young is by parasitizing many nests and selecting the

proper host species and nest for parasitism.

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APPENDIX 1. Female Yellow Warbler incubation attentiveness ($\bar{x} \pm SE$ s per 30 minute observation period) and male Yellow Warbler frequency of food delivery ($\bar{x} \pm SE$ feeds per 30 minute observation period) compared among 4- and 5-egg clutches for each treatment, on each day of the laying period, and each year of the study to determine if the data can be pooled.

Year	Day	Treatment ^a	Female attentiveness		Male feedings	
			<i>H</i> ^b	<i>P</i>	<i>H</i> ^b	<i>P</i>
1992	1	Control	1.55	0.213	3.00	0.083
		1HER	1.49	0.222	0.04	0.845
		0HER	1.30	0.254	1.20	0.273
	2	Control	6.11	0.013	1.38	0.241
		1HER	0.32	0.570	1.06	0.303
		0HER	2.16	0.142	0.00	1.0
	3	Control	1.14	0.285	1.50	0.221
		1HER	1.93	0.165	3.35	0.067
		0HER	4.86	0.028	2.81	0.094
	4	Control	2.16	0.142	0.02	0.893
		1HER	6.75	0.009	0.27	0.605
		0HER	1.32	0.251	0.60	0.439
	5	Control	0.78	0.376	0.00	1.0
		0HER	0.34	0.558	2.62	0.105
	1993	1	Control	1.94	0.164	0.90
1HER			1.28	0.258	0.00	1.0
0HER			0.01	0.917	2.40	0.121

APPENDIX 1 continued

3	Control	0.05	0.831	1.72	0.189
	1HER	0.04	0.851	0.27	0.635
	0HER	1.67	0.196	0.01	0.909

^a 1HER = clutches where cowbird egg added and one host egg removed; 0HER = clutches where cowbird egg added and no warbler egg removed.

^b Kruskal-Wallis *H*-statistic.

APPENDIX 2. Female Yellow Warbler incubation attentiveness ($\bar{x} \pm SE$ s per 30 minute observation period) and male Yellow Warbler frequency of food delivery ($\bar{x} \pm SE$ feeds per 30 minute observation period) compared among 1992 and 1993 for each treatment, and each day of the laying period to determine if the data can be pooled. Clutch sizes are combined for this comparison.

Day	Treatment ^a	Female attentiveness		Male feedings	
		<i>H</i> ^b	<i>P</i>	<i>H</i> ^b	<i>P</i>
1	Control	1.261	0.2614	0.012	0.913
	1HER	0.510	0.475	3.149	0.076
	0HER	1.840	0.175	0.023	0.879
3	Control	0.741	0.389	1.465	0.226
	1HER	2.962	0.085	1.082	0.298
	0HER	0.032	0.858	0.016	0.890
5	Control	1.104	0.294	0.0	1.0
	1HER	0.748	0.387	0.005	0.943
	0HER	0.217	0.642	1.053	0.305

^a 1HER = clutches where cowbird egg added and one host egg removed; 0HER = clutches where cowbird egg added and no warbler egg removed.

^b Kruskal-Wallis *H*-statistic.

APPENDIX 3. Yellow Warbler parental care variables compared among clutches of 4- and 5-eggs, for both control and treatment nests at each stage of the hatching period, to determine if the data can be pooled.

Stage	Variable	Control		Cowbird	
		<i>H</i> ^a	<i>P</i>	<i>H</i> ^a	<i>P</i>
Egg	Female attentiveness	3.570	0.059	6.817	0.078
	Incubation bouts	1.304	0.254	5.988	0.050
	Male to female feeds	1.964	0.161	2.959	0.398
One nestling	Female attentiveness	0.117	0.943	1.09	0.296
	Incubation bouts	1.455	0.483	0.023	0.878
	Female to nestling feeds	2.208	0.332	2.864	0.091
	Male to female feeds	0.047	0.877	3.688	0.055
	Male to nestling feeds	3.134	0.209	1.489	0.222
	Male to female to nestling feeds	2.25	0.325	2.457	0.117
	Total male feeds	2.873	0.238	0.987	0.320
	Total nestling feeds	1.387	0.999	0.275	0.60
Two nestlings	Female attentiveness	2.083	0.149	0.6	0.439
	Incubation bouts	0.540	0.462	0.167	0.683
	Female to nestling feeds	0.089	0.766	0.0	1.0
	Male to female feeds	0.022	0.881	1.0	0.317
	Male to nestling feeds	1.916	0.166	2.4	0.121
	Male to female to nestling feeds	0.10	0.752	0.167	0.683

APPENDIX 3 continued

	Total male feeds	0.534	0.465	2.4	0.121
	Total nestling feeds	0.540	0.462	1.5	0.221
Three+	Female attentiveness	--		1.330	0.248
nestlings	Incubation bouts	--		0.333	0.564
	Female to nestling feeds	--		0.417	0.519
	Male to female feeds	--		0.0	1.0
	Male to nestling feeds	--		1.333	0.248
	Male to female to nestling feeds	--		1.5	0.223
	Total male feeds	--		1.333	0.248
	Total nestling feeds	--		0.088	0.767

• Kruskal-Wallis *H*-statistic.

APPENDIX 4. Comparison of variables quantifying Yellow Warbler parental care among 1994 and 1996 for control nests at each stage of the hatching period, to determine if the data can be pooled.

Stage	Variable	<i>H</i>^a	<i>P</i>
Egg	Female attentiveness	2.667	0.103
	Incubation bouts	2.704	0.10
	Male to female feeds	1.684	0.194
One nestling	Female attentiveness	0.062	0.794
	Incubation bouts	0.157	0.692
	Female to nestling feeds	0.666	0.414
	Male to female feeds	0.020	0.889
	Male to nestling feeds	0.078	0.780
	Male to female to nestling feeds	0.938	0.333
	Total male feeds	0.867	0.352
	Total nestling feeds	0.074	0.786
Two nestlings	Female attentiveness	0.429	0.513
	Incubation bouts	1.778	0.182
	Female to nestling feeds	1.266	0.261
	Male to female feeds	0.821	0.365
	Male to nestling feeds	0.487	0.486
	Male to female to nestling feeds	0.514	0.473
	Total male feeds	1.220	0.270

APPENDIX 4 continued

	Total nestling feeds	0.0	1.0
Three+nestlings	Female attentiveness	0.593	0.441
	Incubation bouts	0.0	1.0
	Female to nestling feeds	1.990	0.1457
	Male to female feeds	0.003	0.958
	Male to nestling feeds	0.293	0.588
	Male to female to nestling feeds	0.171	0.679
	Total male feeds	0.009	0.923
	Total nestling feeds	0.601	0.438

^a Kruskal-Wallis *H*-statistic.

APPENDIX 5. Comparison of hatching variables of Yellow Warblers among years for each treatment, to determine if the data can be pooled.

Variable	Control		Cowbird	
	<i>H^a</i>	<i>P</i>	<i>H^a</i>	<i>P</i>
Incubation period of first warbler	0.466	0.495	0.261	0.609
Incubation period of second warbler	0.150	0.699	0.046	0.831
Incubation period of third warbler	1.123	0.289	1.01	0.315
Incubation period of fourth warbler	0.345	0.557	--	--
Incubation period of fifth warbler	1.50	0.221	--	--
Hatching success	1.178	0.278	0.377	0.539
Embryo mortality	1.779	0.182	0.256	0.613
Nestling mortality	0.0	1.0	0.468	0.494
Eggs disappeared	0.656	0.418	0.159	0.089

^a Kruskal-Wallis *H*-statistic.