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# DO BROWN-HEADED COWBIRD HATCHLINGS ALTER ADULT YELLOW WARBLER BEHAVIOR DURING THE HATCHING PERIOD?

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Abstract.—Early hatching and intense begging by nestling Brown-headed Cowbirds (*Molothrus ater*) have been hypothesized to reduce host incubation attentiveness, thereby extending the incubation periods of host eggs and ultimately increasing the competitive advantage of the cowbird chick. We tested this hypothesis by adding newly hatched cowbirds to Yellow Warbler (*Dendroica petechia*) clutches one day prior to their predicted hatch date, and observing whether the presence of the cowbird nestling brought about changes in parental behavior during the hatching period. The presence of a cowbird nestling did not significantly alter female nest attentiveness relative to control clutches. The presence of a cowbird nestling did not significantly increase the rate at which either the female or male Yellow Warbler delivered food to the nest. Female Yellow Warblers tended to feed food delivered to the nest by the male to a cowbird nestling more frequently than to a warbler nestling, but the difference only approached significance. The presence of a cowbird nestling resulted in significantly longer Yellow Warbler incubation periods for only the third egg to hatch in the clutch. Host clutches with a cowbird nestling experienced decreased hatching success and increased frequency of egg disappearance, but the difference in nestling mortality only approached significance. Our data indicate minimal alteration of host behavior by the cowbird nestling during the hatching period. Although the detrimental effect of the cowbird nestling is measurable by the end of the hatching period, its full effect, especially for small hosts, does not manifest itself until later in the nestling and fledgling periods.

## AFECTAN LOS PICHONES DE TORDO PARDO LA CONDUCTA DE *DENDROICA PETECHIA* DURANTE EL PERIODO DE INCUBACIÓN

Sinopsis.—El nacimiento temprano y la fuerte conducta de pedir alimento por parte de los pichones del tordo pardo (*Molothrus ater*) han sido implicados en reducir la atención de los adultos a la incubación del resto de la camada, extendiendo de esta manera el periodo de eclosionamiento e incrementando entonces las ventajas competitivas de los pichones de tordo. Pusimos a prueba la hipótesis indicada introduciendo en nidos del cerrojillo *Dendroica petechia* recién nacidos del tordo pardo un dia antes de la fecha de eclosionamiento. Se observó entonces la conducta de los adultos para determinar cambios en la conducta parental durante el periodo de eclosionamiento. La presencia del tordo no afecto significativamente la conducta del cerrojillo hembra con respecto a la atención al nido durante el eclosionamiento de su camada. La presencia del tordo tampoco afecto significativamente la tasa de acarreo de comida al nido por parte de la pareja. No obstante, la hembra del cerrojillo tendió a alimentar con mayor frecuencia al tordo que a uno de sus hijos con la comida que traía al nido el macho. Pero la diferencia tan solo se acercó al grado de significancia. La presencia del pichón de tordo en el nido tan solo resultó en un incremento significativo en el periodo de eclosionamiento del tercer huevo de la camada. La camada de los cerrojillos con un pichón de tordo experimentó un decrecimiento en el éxito de eclosionamiento e incrementó la frecuencia en la desaparición de huevos. Sin embargo, la diferencia en la mortalidad de pichones solo se acercó al grado de significancia. Los datos obtenidos indican una alteración mínima en la conducta del huesped ante la presencia de un parásito en su nido durante el periodo de eclosionamiento. Aunque el efecto detrimental del pichón de tordo en el nido puede ser determinado al final del periodo de incubación, su efecto neto,

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especialmente para huespedes pequeños, no se manifiesta hasta tarde en el periodo de crianza de los pichones y la fase de volantones.

Brown-headed Cowbirds (*Molothrus ater*) have relatively short incubation periods and frequently hatch before host young (Briskie and Sealy 1990, McMaster and Sealy 1997). Cowbirds begin begging soon after hatching (Lorenzana 1996) and beg vigorously (Briskie et al. 1994). Several studies have shown that early hatching of young in either con- or heterospecific clutches results in lower hatching success of the remaining eggs (Tricolored Blackbird [*Agelaius tricolor*] in conspecific nests, Emlen 1941; Yellow Warbler eggs with a single House Wren [*Troglodytes aedon*], Sealy 1989; Shiny Cowbirds [*M. bonariensis*] in House Wren nests, Kattan 1996). Researchers have postulated that early hatching by parasitic cowbirds could divert the host female's attention away from incubating the remaining eggs as she begins to forage for the cowbird nestling, thereby reducing the hatching success, or slowing the development of host eggs (Nolan 1978, Dolan and Wright 1984, Petit 1991). The combination of competitive head starts over their nestmates, and vigorous begging by nestling cowbirds may be strategies that dramatically reduce hatching success (by almost 100%; Walkinshaw 1961) and fledging success (by 50% and 93%; Klaas 1975, Rothstein 1975, respectively) in host species with longer incubation periods.

To test whether the presence of a cowbird hatchling induces the host to shift prematurely from incubation to a combination of brooding and hatchling feeding, we added cowbird nestlings hatched in an incubator to Yellow Warbler clutches one day before the warbler eggs were expected to hatch. Most cowbird eggs hatch before or on the same day that the first Yellow Warbler egg hatches (McMaster and Sealy 1997). We predicted that in the presence of a cowbird nestling Yellow Warbler eggs would take longer to hatch or be less likely to hatch. We predicted that during the hatching period the addition of a cowbird nestling would reduce cumulative nest attentiveness by the host female, increase the frequency of incubation bouts, increase the rate of food delivery to the nest by both male and female warblers, and stimulate male warblers to feed the nestling rather than the brooding female. Yellow Warbler nestlings were also predicted to experience increased mortality up until all eggs had hatched in the presence of a cowbird nestling.

## METHODS

In 1994 and 1996, we searched for Yellow Warbler nests in the forested dune ridge at Delta Marsh, Manitoba, Canada (58°11′N, 98°19′W, see Mackenzie 1982). Single artificial plaster 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. One day prior to the anticipated hatching date of the first warbler eggs, the artificial cowbird egg in experimental nests was replaced with a cowbird nestling that had hatched in an incubator housed at the University of Manitoba Field Station, Delta Marsh (see McMaster and Sealy 1998 for details). Cowbird nestlings that hatched overnight or before 1000 h (CST) 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 geometrid larvae captured on the study site. Cowbird nestlings were added to warbler nests between 0530 and 1030 h.

One-hour watches were conducted at both control and cowbird 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 we recorded (1) female nest attentiveness (seconds female was in the nest covering the eggs), (2) number of incubation bouts by the female, (3) number of times the male gave food to the female, who in turn fed 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 (sum of 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). We also recorded the (1) incubation period of each Yellow Warbler egg in the clutch as it hatched, (2) hatching success of warbler eggs, (3) frequency of host egg disappearance from nests, and (4) frequency of host nestling mortality up to the end of the hatching period. The incubation period of Yellow Warbler eggs was defined as the period from clutch completion to hatching, and was measured by visiting nests twice daily at 12-h intervals.

*Data analyses.*—All comparisons were made using nonparametric tests as the data could not be transformed to normal distributions. Five eggs is the modal clutch size at Delta Marsh; however, four-egg clutches are also common (Sealy 1992). We compared data for all variables among both clutch sizes and years of the study using the Kruskal-Wallis *H*-test. Because neither comparison yielded significant differences for any variable, the data were pooled. During the hatching period, categories 1–8 were compared between treatments using the Mann-Whitney *U*-test. One outlying data point was removed from the experimental data set due to an extremely high female feeding rate (14 feeds/h versus average range of 1.2–2.1 feeds/h). Comparison of hatching variables between treatments was also made using the Mann-Whitney *U*-test. All values are presented as means ±SE, and all *P*-values are two-tailed.

## RESULTS

Yellow Warbler eggs in clutches with a cowbird nestling tended to have longer incubation periods than warbler eggs in control clutches, but the difference was significant only for the third Yellow Warbler egg (Table 1).

TABLE 1. Incubation period (x̄ ± SE days, *n* in parentheses) for control and experimentally parasitized Yellow Warbler clutches.

| Hatching order | Treatment | | |
|---|---|---|---|
| | Cowbird[a] | Control[a] | *U* (*P*)[b] |
| First | 9.67 ± 0.19 (24) | 9.58 ± 0.19 (26) | 270.5 (0.388) |
| Second | 10.10 ± 0.18 (21) | 10.0 ± 0.17 (25) | 232.5 (0.476) |
| Third | 10.89 ± 0.25 (18) | 10.3 ± 0.16 (23) | 130.0 (0.03) |
| Fourth | 11.0 ± 0.19 (11) | 10.93 ± 0.3 (15) | 73.5 (0.646) |
| Fifth | 11.0 ± 0.41 (4) | 11.0 ± 0.58 (3) | 6.0 (1.0) |

[a] Data are combined between 1994 and 1996.

[b] Mann-Whitney *U*-statistic comparing length of the incubation period among treatments within each stage.

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, $P = 0.0005$). The presence of a cowbird nestling resulted in the disappearance of significantly more warbler eggs (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, $P = 0.042$), but the difference in nestling warbler mortality only approached significance (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, $P = 0.097$).

The presence of a cowbird egg or nestling did not significantly alter female attentiveness relative to control clutches (Table 2). Neither the presence of a cowbird egg nor cowbird nestling significantly influenced the number of incubation bouts relative to control clutches (Table 3).

The rate of male food delivery to the female at the egg stage did not differ significantly between control clutches and those with a cowbird egg (Table 4). Although females brooding a single warbler nestling tended to

TABLE 2. Female attentiveness (x̄ ± SE seconds per 1-h observation period, *n* in parentheses) at control and experimentally parasitized Yellow Warbler clutches (one cowbird egg or nestling added) just prior to, and during, the hatching period.

| | Treatment | | |
|---|---|---|---|
| Stage[a] | Cowbird[b] | Control[b] | *U* (*P*)[c] |
| Egg | 3138.7 ± 49.1 (31) | 2959.6 ± 127.6 (11) | 124.0 (0.192) |
| One nestling | 3123.2 ± 80.5 (17) | 2864.7 ± 146.9 (10) | 54.0 (0.128) |
| Two nestlings | 2740.2 ± 194.6 (5) | 2756.5 ± 142.7 (8) | 18.0 (0.832) |
| Three+ nestlings | 2403.1 ± 210.9 (15) | 2707.4 ± 119.9 (26) | 144.0 (0.174) |

[a] Refers to the total number of cowbird and Yellow Warbler nestlings present in the nest (i.e., one cowbird nestling is present at the one nestling stage, and one cowbird nestling and one Yellow Warbler nestling are present at the two nestling stage).

[b] Data from 1994 and 1996 combined.

[c] Mann-Whitney *U*-statistic comparing female attentiveness among treatments within each stage.

TABLE 3. Number of incubation bouts (x̄ ± SE per 1-h observation bout, *n* in parentheses) by female Yellow Warblers at control and experimentally parasitized clutches just prior to, and during, the hatching period.

| Stage | Treatment | | |
|---|---|---|---|
| | Cowbird[a] | Control[a] | *U* (*P*)[b] |
| Egg | 3.4 ± 0.3 (31) | 4.3 ± 0.9 (11) | 155.0 (0.672) |
| One nestling | 5.2 ± 0.8 (17) | 5.0 ± 0.7 (10) | 83.5 (0.942) |
| Two nestlings | 6.4 ± 1.3 (5) | 7.5 ± 1.3 (8) | 18.0 (0.832) |
| Three+ nestlings | 5.5 ± 1.1 (15) | 4.6 ± 0.4 (26) | 185.0 (0.800) |

[a] Data for 1994 and 1996 combined.

[b] Mann-Whitney *U*-statistic comparing number of female incubation bouts among treatments within each stage.

consume food brought by the male significantly more often than females brooding a single cowbird nestling, the difference only approached significance (Table 4). Conversely, female warblers tended to feed food brought by the male to single nestlings more often if the nestling was a cowbird rather than a warbler, but this difference also only approached significance (Table 4). The rate of male-to-female-to-nestling feedings did

TABLE 4. Rate of food delivery (x̄ ± SE visits per 1-h observation bout, *n* in parentheses) to control and experimentally parasitized Yellow Warbler clutches prior to and during the hatching period.

| Type of delivery | Stage | Treatment | | |
|---|---|---|---|---|
| | | Cowbird[a] | Control[a] | *U* (*P*)[b] |
| Male-to-female | Egg | 1.0 ± 0.2 (31) | 1.4 ± 0.5 (11) | 162.5 (0.82) |
| | One nestling | 0.88 ± 0.4 (16) | 1.7 ± 0.6 (10) | 48.0 (0.098) |
| | Two nestlings | 0.6 ± 0.4 (5) | 1.3 ± 0.4 (8) | 12.5 (0.284) |
| | Three+ nestlings | 0.4 ± 0.2 (15) | 1.6 ± 0.5 (26) | 143.0 (0.166) |
| Male-to-female-to nestlings | One nestling | 1.9 ± 0.4 (17) | 0.5 ± 0.3 (10) | 50.0 (0.084) |
| | Two nestlings | 2.2 ± 1.2 (5) | 1.1 ± 0.4 (8) | 16.0 (0.622) |
| | Three+ nestlings | 1.8 ± 0.6 (15) | 1.2 ± 0.3 (26) | 177.5 (0.640) |
| Female-to-nestlings | One nestling | 1.9 ± 0.6 (17) | 1.2 ± 0.4 (10) | 77.0 (0.712) |
| | Two nestlings | 1.8 ± 0.7 (5) | 2.1 ± 0.8 (8) | 20.0 (1.00) |
| | Three+ nestlings | 1.9 ± 0.5 (15) | 1.6 ± 0.3 (26) | 185.5 (0.80) |
| Male-to-nestlings | One nestling | 1.0 ± 0.4 (17) | 1.1 ± 0.5 (10) | 81.0 (0.864) |
| | Two nestlings | 1.6 ± 0.5 (5) | 1.3 ± 0.6 (8) | 16.0 (0.622) |
| | Three+ nestlings | 3.3 ± 0.7 (15) | 2.8 ± 0.5 (26) | 176.0 (0.620) |
| Total male feeds | One nestling | 4.5 ± 1.0 (17) | 3.3 ± 0.7 (10) | 75.0 (0.640) |
| | Two nestlings | 4.4 ± 1.6 (5) | 3.6 ± 1.1 (8) | 17.0 (0.714) |
| | Three+ nestlings | 5.5 ± 0.9 (15) | 5.6 ± 0.7 (26) | 185.0 (0.884) |
| Total nestling feeds | One nestling | 6.5 ± 1.0 (17) | 4.5 ± 0.6 (10) | 72.0 (0.538) |
| | Two nestlings | 6.2 ± 2.1 (5) | 5.8 ± 0.7 (8) | 17.5 (0.714) |
| | Three+ nestlings | 7.3 ± 1.1 (15) | 7.2 ± 0.6 (26) | 189.0 (0.884) |

[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.

not differ significantly between cowbird and control nests at larger brood sizes (Table 4). Female warblers brooding cowbird nestlings did not deliver food to the nest at significantly higher rates than control females (Table 4). Neither the rate of nestling feeding, nor the total rate of food delivery to the nest by male warblers increased significantly in the presence of a cowbird egg or nestling (Table 4). The rate of nestling feedings by male and female warblers combined did not increase significantly in the presence of a cowbird nestling at any brood size (Table 4).

## DISCUSSION

The presence of a cowbird nestling during the hatching period did not significantly alter Yellow Warbler incubation attentiveness or the rate of food delivery to the nest. The presence of a cowbird did not alter the number of incubation bouts of female warblers at any stage of the hatching period. In Yellow Warblers, therefore, early hatching by cowbird eggs did not reduce female attentiveness, or prolong incubation periods of all but the third Yellow Warbler egg, as suggested for other host species (e.g., Dolan and Wright 1984, Fraga 1985). Female Yellow Warblers may remain more attentive during the hatching period than females of other species because male Yellow Warblers frequently feed the female at the nest (see also Mayfield 1992, Pitocchelli 1993, Morse 1994, Van Horn and Donovan 1994, Robinson 1995), unlike males of some other species that begin regular feeding mid-way through hatching (Weathers and Sullivan 1989, Morse 1993, Pitocchelli 1995). Delayed onset of male food delivery to the nest after hatching could accelerate the negative impact of a cowbird nestling if the female is forced to leave the nest to forage.

The presence of a cowbird nestling did not influence food delivery rates to the nest by the male, female, or both sexes combined, at any stage during the hatching period. While females tended to feed a single cowbird with food brought by the male, whereas females with a single warbler nestling tended to eat food brought by the male, these nonsignificant differences disappeared completely with the hatching of the second egg. Therefore, it appears that any increased feeding rate stimulated by the cowbird nestling disappeared with increasing brood size. Female Yellow Warblers appear not to vary their feeding rates to compensate for increased nestling nutritive requirements (Biermann and Sealy 1982, Lozano and Lemon 1996), rather, male Yellow Warblers increase their feeding frequency to accommodate the higher nutritional demands of larger broods (Biermann and Sealy 1982; see also Westneat 1988). In fact, male warblers fed 2-day-old broods more frequently than females regardless of brood size (Biermann and Sealy 1982).

Consistent with predictions, cowbird parasitism resulted in a significant negative effect on survival of young warblers (see also Weatherhead 1989). Warbler clutches with cowbirds experienced reduced hatching success, increased disappearance of eggs just prior to or during the hatching period, and a tendency for increased nestling mortality. Because artificial cowbird eggs were present in clutches throughout incubation, however, it is difficult to differentiate between effects due to the cowbird egg and those due to the cowbird nestling. As in a previous study (McMaster and Sealy 1997), the presence of a cowbird egg significantly reduced warbler hatching success. Although real cowbird eggs also prolong incubation period of warbler eggs (McMaster and Sealy 1998), artificial cowbird eggs did not have the same effect on warbler incubation period in this study, perhaps because artificial eggs are easier to heat (McMaster, pers. obs.). Given that cowbird nestlings did not significantly reduce female warbler attentiveness during hatching, cowbird nestlings appear to have little or no effect on either hatching success or incubation period in this host species. The greater number of warbler eggs that disappeared from experimentally 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.

Yellow Warbler nestlings may be outcompeted by cowbird nestlings much more easily than are larger nestlings of other species (e.g., Mason 1980, Fraga 1985, Weatherhead 1989). Although cowbird nestlings tended to reduce the survival of Yellow Warbler nestlings during the hatching period, the difference was not significant and the absolute number of dead nestlings 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).

In summary, the presence of a cowbird nestling resulted in minimal changes of adult Yellow Warbler behavior during the hatching period. The presence of the artificial cowbird egg, rather than the cowbird nestling, likely reduced host hatching success. Frequent food delivery to the nest by male Yellow Warblers possibly delays most of the cowbird nestling's impact on host nestlings until later in the nestling and fledgling periods. For host species with incubation periods that are days longer than those of the cowbird, and with delayed initiation of food delivery to the nest by the male after hatching, early hatching by cowbird nestlings may impact host reproductive success more severely.

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