SEX RATIOS, HOST-SPECIFIC REPRODUCTIVE SUCCESS, AND IMPACT OF BROWN-HEADED COWBIRDS

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ABSTRACT.—I examined Brown-headed Cowbird (*Molothrus ater*) parasitism of Red-winged Blackbird (*Agelaius phoeniceus*) and Yellow Warbler (*Dendroica petechia*) nests to determine the effects of cowbird size (male vs. female) and host size (blackbirds vs. warblers) on both host and parasite growth and reproductive success. Because the 25% adult sexual size dimorphism was not expressed in nestling cowbirds, equal hatching sex ratios remained equal at fledging with both host species. Red-winged Blackbirds were far superior hosts, primarily because they usually accepted cowbird eggs whenever they were laid. In contrast, Yellow Warblers usually accepted only those cowbird eggs laid after the warbler had laid several eggs. The cowbird lays many eggs in many nests; consequently, many eggs were poorly timed, and cowbird reproductive success in Yellow Warbler nests was much lower than in Red-winged Blackbird nests. The impact of cowbirds was far greater on Yellow Warblers than on Red-winged Blackbirds, primarily due to the poor competitive ability, and hence fledging success, of the warbler nestlings relative to the much larger cowbird nestlings. In southern Manitoba, the level of harm suffered by Yellow Warblers because of nest parasitism may be maintained at a high level because the success of cowbirds in Red-winged Blackbird nests keeps cowbirds abundant. The population dynamic relationship among these three species is very different from that reported from a study of the same three species in eastern Ontario. *Received 25 August 1988, accepted 16 January 1989.*

THE RELATIONSHIP between an avian brood parasite and its hosts is dynamic because each affects the immediate fitness of the other (May and Robinson 1985). The parasite can reduce the host's fitness directly by removal of host eggs or indirectly via competition between host and parasite nestlings, whereas the host can reduce the parasite's fitness by rejecting the parasite's egg or by inadequate parental care of the nestlings (Rothstein 1975). The population dynamics of host-parasite interactions has received relatively limited attention in the study of avian brood parasites (May and Robinson 1985), although that is likely to change with the recognition that brood parasites can threaten some hosts with extinction (e.g. Mayfield 1977, 1978; Brittingham and Temple 1983). I investigated some factors that influence the population dynamics of Brown-headed Cowbirds (*Molothrus ater*) and their hosts. Principally I considered host size, cowbird sex, and host responses to parasitism.

Brown-headed Cowbirds are obligate brood parasites that have been reported to lay eggs in the nests of 216 species (Friedmann et al. 1977). The hosts range in size from much smaller to much larger than cowbirds. This factor might be expected to make some species more suitable hosts than others, because cowbird nestlings must compete with those of the host. Cowbirds are sexually dimorphic, with adult males about 25% heavier than adult females (Ankney and Scott 1980). In Red-winged Blackbirds (*Agelaius phoeniceus*) and Great-tailed Grackles (*Quiscalus mexicanus*) (both sexually dimorphic icterids), adult dimorphism is expressed in nestlings within a few days of hatching and results in different costs to producing males and females (Fiala 1981, Fiala and Congdon 1983, Teather 1987, Teather and Weatherhead 1988). Therefore, it seems reasonable to expect sexual dimorphism to be expressed in cowbird nestlings. Size differences between male and female nestlings could affect their competitive ability and cost of rearing, both of which would interact with variation in host size to produce differences in overall success and the specific success of each sex in nests of large and small hosts.

Rothstein (1975) classified both Yellow Warblers (*Dendroica petechia*) and Red-winged Blackbirds as *accepters*, in that they nearly always accept and care for cowbird eggs laid in their nests. Adult male and female Yellow Warblers weigh 9.8 and 9.2 g, respectively, compared with 49.0 and 38.8 g for male and female cowbirds and 63.6 and 41.5 g for male and female Red-winged Blackbirds (Clench and Leberman 1978). With such a weight advantage, I expected both male and female cowbirds to be very successful in Yellow Warbler nests and also to have a strong negative impact on their host nest mates. I also expected that male cowbirds might have a slight advantage over females when raised by Red-winged Blackbirds because their size would make them more competitive. However, I did not expect the presence of cowbird nestlings in Red-winged Blackbird nests to affect the host nestlings adversely. To test these predictions, I examined sex-specific growth rates and fledging success of cowbird nestlings raised by warblers and blackbirds, and the growth rates and fledging success of warbler and blackbird nestlings raised with and without cowbirds.

If male and female cowbirds are not equally successful in all hosts' nests, there could be an advantage to female cowbirds biasing the sex ratio of eggs laid in certain hosts' nests. Although there is little evidence of deviation from a 1:1 primary sex ratio in birds (Clutton-Brock 1986), there is some evidence of nonrandom sex allocation in species confamilial with cowbirds (Howe 1976; Weatherhead 1983, 1985). Thus, one objective was to examine both hatching and fledging sex ratios of cowbirds for evidence of bias.

Methods

The study was conducted from mid-May through July in 1983 and 1984 at the Delta Marsh at the southern end of Lake Manitoba in southern Manitoba. Study sites were located in the dune-ridge forest habitat (described by MacKenzie et al. 1982) on the property of the Delta Waterfowl and Wetlands Research Station and in *Typha* marshes along roadsides on the property of the University of Manitoba Field Station and between the two field stations. This area was chosen because Red-winged Blackbirds and Yellow Warblers breed abundantly in the Delta Marsh area and are commonly parasitized by cowbirds (Robertson and Norman 1977). Yellow Warblers nested in the dune-ridge forest and Red-winged Blackbirds nested in the cattail marshes.

All study areas were checked every second day before nesting began. This continued until the completion of breeding. Most nests were found before egg laying. Nests were marked, mapped, and visited until they became inactive.

The principal objective in 1983 was to determine cowbird prehatching sex ratios to detect if females were biasing the sex ratio of eggs they laid in the nests of different host species. Prehatching sex ratios were also necessary for the interpretation of fledging sex ratios to be collected subsequently. Accordingly, all cowbird eggs that were incubated successfully were collected before hatching, preserved in formalin, and later sexed by necropsy (Weatherhead 1983, 1985). Many cowbird eggs fail to be incubated because of host responses to parasitism such as nest abandonment and egg burial (Friedmann 1963, Clark and Robertson 1981), or because the cowbird laid the egg in an inactive nest. To increase sample sizes, I attempted to salvage cowbird eggs that were not incubated for any of the above reasons. Buried eggs were uncovered, and eggs abandoned or laid in inactive nests were placed in active nests in which incubation had just begun or was imminent. For analysis these nests are considered separately from unmanipulated nests.

In 1984 I determined fledging sex ratios of cowbirds and growth rates of both cowbird and host nestlings. The general methods used were the same as in 1983, but cowbirds were not collected until close to fledging (7–9 days after hatching). Sample sizes were again increased by salvaging buried or abandoned cowbird eggs. My criteria for choosing the new host nests were proximity to the parasitized nest, no natural parasitism, and appropriate stage of incubation. I also removed one or more cowbird eggs from nests containing three or more cowbird eggs and fostered these into an appropriate host nest. I wanted salvaged eggs to mimic natural parasitism to obtain additional data on growth rates and fledging success. Hence, I adjusted host clutch sizes in foster nests to the modal size for naturally parasitized nests. For Yellow Warblers this usually required removal of one egg, as is done often by the female cowbird (Mayfield 1960, Rothstein 1975, Nolan 1978). Obviously this method meant sacrificing data on some aspects of natural host-parasite interactions (e.g. the fate of hyperparasitized nests) to increase data on growth rates and sex ratios.

I monitored the growth rate of each nestling by weighing it on each nest visit. With felt pen, I marked the feet of nestlings to identify individuals. Cowbirds could be distinguished from host nestlings by differences in appearance (e.g. skin color). I used Ricklefs' (1967) method to fit logistic growth curves for each nestling based on four or more measurements and to calculate K, the rate constant for each nestling's growth equation. The rate constants were used for statistical analysis of growth rates.

Results

I found 310 Yellow Warbler nests and 382 Red-winged Blackbird nests. Respectively, 30% and 35% of these nests were parasitized, and a total of 321 cowbird eggs were laid (Table 1). These rates of parasitism are substantially higher

TABLE 1. Summary of nesting data.

Host nests (n)	Cowbird eggs	Nests parasitized[a]	Clutch initiation[b]
	1983		
Yellow Warbler (178)	56	49 (27.5)	5 June–5 July
Red-winged Blackbird (150)	94	62 (41.3)	2 June–11 July
	1984		
Yellow Warbler (132)	51	45 (34.1)	1 June–20 June
Red-winged Blackbird (232)	96	70 (30.2)	28 May–24 June

[a] Percentage is in parentheses.
[b] These dates encompass the entire clutch initiation period.

than values previously reported from the same area (Robertson and Norman 1977), but well within the range of values found elsewhere (May and Robinson 1985).

Cowbird sex ratios.—In 1983 I determined cowbird sex ratios before hatch. Only 17 of the 56 (30.4%) eggs laid in Yellow Warbler nests survived through incubation and were fertile. An additional 4 eggs buried or deserted were salvaged and incubated in foster nests. The sex ratio (male:female) of the 21 eggs was 1.3:1 (12 ♂, 9 ♀). Of 94 cowbird eggs laid in Red-winged Blackbird nests, 41 (43.6%) survived incubation and were fertile. An additional 11 eggs were salvaged for sexing. These embryos had a sex ratio of 0.79:1 (23 ♂, 29 ♀). The sex ratios of cowbirds differed neither between the two hosts ($\chi^2 = 0.55$, $P > 0.05$) nor from unity ($\chi^2 = 0.42$ and 0.64 for Yellow Warblers and Red-winged Blackbirds, respectively; both Ps > 0.05).

In 1984 cowbird nestlings were sexed when close to fledging. Only 2 of 51 (3.9%) cowbird eggs laid in Yellow Warbler nests survived to fledging. One fledged before sexing and the other was a female. One cowbird survived almost to fledging and was sexed after being found dead in the nest. Of 25 salvaged eggs, 11 survived long enough to be sexed, although 3 were found dead in or under their foster nests. The sex ratio of the 14 "fledglings" sexed was 0.75:1 (6 ♂, 8 ♀). Of the 120 cowbird eggs laid in Red-winged Blackbird nests, 26 (21.7%) naturally reached fledgling age. I collected an additional 13 nestlings from the 25 salvaged eggs (11 live, 2 dead). From the total of 34 fledglings, the sex ratio was 0.79:1 (15 ♂, 19 ♀). Again, the cowbird sex ratios did not differ between the two hosts ($\chi^2 = 0.06$, $P > 0.05$), nor did either differ from unity ($\chi^2 = 0.29$ and 0.47 for Yellow Warblers and Red-winged Blackbirds, respectively; both Ps > 0.05).

The similarity of hatching and fledging sex ratios suggests that the sexes grew equally well in the nests of the two host species. Overall, cowbirds grew at the same rate in both hosts' nests (Fig. 1) based on mean growth rate constants ($t = 0.96$, df = 54, $P > 0.05$). Female ($t = 0.53$, df = 18, $P > 0.05$) and male cowbirds ($t = 2.04$, df = 16, $P > 0.05$) grew equally well with either host. Sample sizes for sex-specific growth rates are smaller than for combined growth rates because many cowbird nestlings were lost before fledging and were not sexed. Contrary to expectations, I found no sexual dimorphism in cowbird nestlings. Growth rates were not significantly different for males and females (mean K $\pm$ SD = 0.660 $\pm$ 0.153 and 0.619 $\pm$ 0.184, respectively; $t = 0.754$, df = 37, $P > 0.05$) nor were mean weights on day 7 (26.14 $\pm$ 3.76 g vs. 26.56 $\pm$ 4.94 g; $t = 0.216$, df = 18, $P > 0.05$).

Factors affecting cowbird success.—Cowbirds had very low per-egg fledging success for several reasons. First are the hosts' apparent responses to being parasitized. Although Rothstein (1975) classified both Yellow Warblers and Red-winged Blackbirds as accepters, some qualification is required. For example, Yellow Warblers usually respond to the appearance of the cowbird egg before or early in their own laying period by either nest desertion or by burying the egg in the nest lining. They are likely to accept the cowbird egg if it appears after several of their own eggs have been laid (Clark and Robertson 1981). My observations confirmed that pattern, in that the mean number of host eggs present when cowbird eggs were buried or nests deserted coincident with the appearance of the cowbird egg were 0.93 ($n = 27$) and 1.08 ($n = 13$), respectively, compared with 2.33 ($n = 46$) for eggs that were accepted. Although Yellow Warblers have not been reported to eject cowbird eggs from their nests, cowbird eggs disappeared from three nests that contained Yellow Warbler eggs and remained active after the

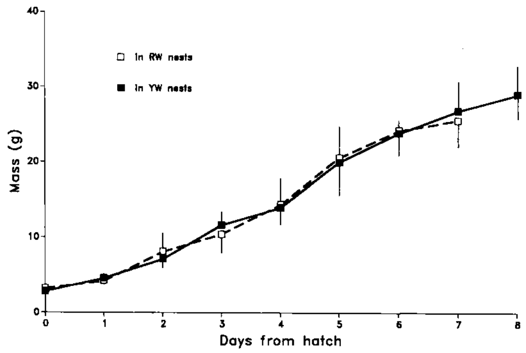

Fig. 1. Cowbird nestling mass ($\bar{x} \pm$ SD) in Yellow Warbler and Red-winged Blackbird nests. Data include all measurements for which cowbird age was known. Starting sample sizes (day 0) are 55 cowbirds in 48 Red-winged Blackbird nests, and 24 cowbirds in 24 Yellow Warbler nests.

cowbird egg disappeared (Table 2). In one case, I found the cowbird egg on the ground below the nest.

Red-winged Blackbirds were much more likely than Yellow Warblers to accept cowbird eggs (Table 1; number accepted vs. number deserted, buried, and rejected [combined], $\chi^2 = 59.06$, $P < 0.0001$). Some nests were deserted coincident with the appearance of a cowbird egg, but whether that was in response to the egg, the cowbird, or something unrelated is difficult to determine (Rothstein 1975).

In addition to the hosts' actions, the cowbirds also contributed to their own low fledging success. For example, eggs laid in inactive nests or

TABLE 2. Fate of cowbird eggs at the time of laying in Yellow Warbler and Red-winged Blackbird nests.[a]

Year	Eggs accepted	Number of failed eggs[b]					
		Desertion	Ejection	Burial	Late	Inactive	Total
		Yellow Warbler					
1983	23	10	—	16	—	2	28
1984	14	16	3	16	6	4	45
Total	37	26	3	32	6	6	73
		Red-winged Blackbird					
1983	72	15	—	1	1	3	20
1984	75	7	3	2	3	4	19
Total	147	22	3	3	4	7	39

[a] Nests preyed on before the fate of a cowbird egg could be determined are excluded.

[b] Desertion = nest abandoned coincident with cowbird egg being laid; ejection = cowbird egg(s) disappeared from a nest that remained active; burial = cowbird egg at least 50% sunk into nest lining; late = cowbird egg laid >3 days after onset of incubation; inactive = cowbird egg laid in an inactive nest.

TABLE 3. Distribution of cowbird eggs in host nests.[a]

Year	Number of cowbird eggs per nest							
	1	2	3	4	5	6	7	8
	Yellow Warbler							
1983	42	7	—	—	—	—	—	—
1984	41	2	2	—	—	—	—	—
	Red-winged Blackbird							
1983	45	12	2	—	1	1	—	1
1984	48	16	5	1	—	—	—	—

[a] Values are the number of host nests found with a particular number of cowbird eggs.

in nests where incubation was already well underway had no chance of success (Table 2). In addition, multiple parasitism of some nests was likely to result in poor cowbird success from those nests. Red-winged Blackbirds were more likely than Yellow Warblers to receive more than one cowbird egg (Table 3; Kolmogorov-Smirnov two-sample test, $P = 0.05$). Multiple parasitism in Yellow Warbler nests resulted in low cowbird success. In only two of seven nests with two cowbird eggs were the cowbird eggs accepted and incubated in 1983 and only one of those succeeded through incubation. In 1984, no nests with multiple parasitism produced cowbird fledglings. Red-winged Blackbirds accepted and incubated most cowbird eggs. In 1983 and 1984, nests with multiple parasitism had the eggs accepted in all but six cases. Even one nest with five cowbird eggs and four blackbird eggs and another with eight cowbird and five blackbird eggs were being incubated when discovered. Although the cowbird eggs had been accepted in most hyperparasitized nests, their prospects for success must have been low given the large number of eggs in those nests. Because most of these eggs were salvaged, I do not know what their fate would have been.

Between the onset of incubation and hatching, predation and infertility accounted for most of the reduction in cowbird success. All undeveloped eggs were classed as infertile although it is likely that some fertile eggs failed to develop because of improper incubation. In 1983, 16 of 33 cowbird eggs accepted naturally (i.e. excluding salvaged eggs) by Yellow Warblers were alive at the end of incubation. Five were lost to predation, one was infertile, and one was broken accidently. Of the 69 cowbird eggs accepted naturally by Red-winged Blackbirds in 1983, 41 were alive at the end of incubation, 20 were lost to predation and 8 were infertile. Pre-

TABLE 4. Host clutch size[a] distributions in parasitized and unparasitized nests in 1984.

Condition	Frequency of clutch size 1	2	3	4	5	6	Clutch size ($\bar{x}$)
Yellow Warbler							
Parasitized	0	2	5	7	4	0	3.72
Unparasitized	0	0	7	31	80	1	4.63
Red-winged Blackbird							
Parasitized	1	8	16	24	6	0	3.11
Unparasitized	0	0	13	97	29	4	4.23

[a] Clutch sizes are the number of host eggs in the nest at the end of the egg laying (i.e. after any natural egg removal has occurred).

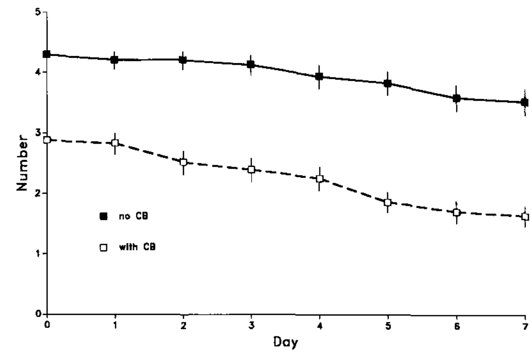

Fig. 2. Yellow Warbler nestlings ($\bar{x}$ ± SE) in parasitized (CB = cowbird) and unparasitized nests through the nestling period. Day is the age of the youngest Yellow Warbler nestling. Sample sizes for unparasitized nests range from 35 (day 0) to 29 (day 7), and for parasitized nests from 25 (day 0) to 14 (day 6). On a given day the sample size was the number of nests from the initial sample that remained active.

dation almost certainly eliminated some eggs that would have failed to hatch (e.g. a nest that initially contained eight cowbird eggs was destroyed) so the real cost of predation to cowbirds may be somewhat lower than it seems.

Of the 14 eggs accepted in Yellow Warbler nests in 1984, 4 were lost to predation and 1 was infertile by the time of hatching. Of 9 surviving nestlings, 3 were lost to predation, 3 died in the nest (probably starvation) or fell out, 1 died when the nest fell over, and 2 fledglings survived. These 2 fledglings represented only 3.9% of the original 51 eggs laid.

Of the 75 cowbird eggs accepted by Red-winged Blackbirds in 1984, 65 were not manipulated. Of these, 17 were preyed on during incubation and 5 failed to hatch. Of the 43 nestlings, 11 were preyed on, 6 disappeared, and 26 fledged. Thus, 27% of the original 96 eggs survived to fledging.

Effect of cowbirds on host success.—To assess the effect of cowbirds on their hosts, I have used both naturally parasitized nests and those involving salvaged eggs. The results must be viewed cautiously but produced much larger samples than if I had relied solely on natural parasitism. Because efforts were made to simulate natural parasitism with salvaged eggs, the results should be representative of the natural situation. All data are from 1984.

After the costs to the host associated with egg burial and nest abandonment, the cost to the hosts that accept cowbird eggs is clutch reduction. By the end of egg laying, the number of host eggs in parasitized nests averaged approximately one egg fewer than in unparasitized nests (Table 4).

To determine the effect on brood size through the nestling period, I calculated the mean number of host nestlings for each day of the nestling period, in all nests that were active each day. When, for example, five nestlings were present on day 3 and four nestlings present on day 5, I assumed that on day 4 there were four nestlings present. To avoid exaggerating brood reduction when young fledged asynchronously, young known to have fledged were still considered part of the brood until all the young had left the nest. For Yellow Warblers, the initial disparity in clutch size between parasitized

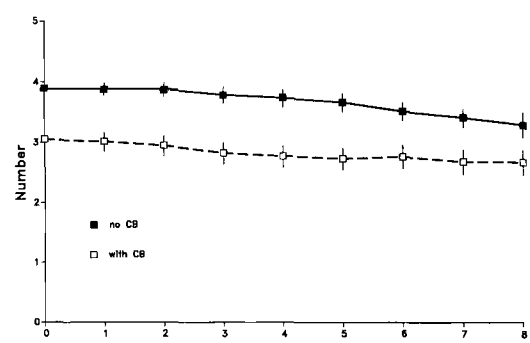

Fig. 3. Red-winged Blackbird nestlings ($\bar{x}$ ± SE) in parasitized and unparasitized nests through the nestling period. Day is the age of the youngest Red-winged Blackbird nestling. Sample sizes for unparasitized nests range from 37 (day 0) to 23 (day 8), and for parasitized nests from 41 (day 0) to 28 (day 7). On a given day the sample size was the number of nests from the initial sample that remained active.

TABLE 5. Yellow Warbler reproductive success with and without cowbirds. Sample sizes are in parentheses; fledging rate = $\bar{x} \pm$ SD.

Condition	% of nests successful[a]	Fledging rate	
		Per nest	Per successful nest
No cowbird eggs	64.0 (75)	2.28 ± 1.94 (75)	3.56 ± 1.11 (48)
Cowbird egg(s) present	46.5 (43)	0.88 ± 1.14 (43)	1.90 ± 0.91 (20)
Cowbird egg(s) hatched	56.0 (25)	0.92 ± 0.95 (25)	1.64 ± 0.63 (14)
Cowbird fledged	90.0 (10)	1.55 ± 0.93 (10)	1.89 ± 0.60 (9)

[a] A successful nest fledged at least one Yellow Warbler.

and unparasitized nests became more pronounced through the nestling period (Fig. 2; analysis of covariance, $F = 3.371$, $P = 0.067$). The presence of cowbirds in Red-winged Blackbird nests did not cause an increase in brood reduction through the nestling period (Fig. 3; analysis of covariance, $F = 0.468$, $P = 0.494$).

The data for overall reproductive success reflect some of the differences already discussed in the effect of cowbirds on Red-winged Blackbirds and Yellow Warblers. Overall, Yellow Warblers with unparasitized nests fledged significantly more young (Yellow Warblers) than those with parasitized nests (Table 5; $\chi^2 = 3.42$, $P < 0.001$). This difference reflects the high rate of nest desertion by parasitized Yellow Warblers. The difference in the number of Yellow Warbler young fledged from successful parasitized and unparasitized nests reflects the combination of both clutch and brood reduction due to cowbirds (Table 5; $t = 5.90$, $P < 0.001$).

For Red-winged Blackbirds, the success rate of parasitized and unparasitized nests did not differ (Table 6; $\chi^2 = 1.20$, $P > 0.05$). Thus, the low level of nest desertion by Red-winged Blackbirds when parasitized was insufficient to produce a difference in overall nest success between parasitized and unparasitized nests. Considering only successful nests, unparasitized nests still did not fledge significantly more Red-winged Blackbird young than those in which cowbird nestlings were present ($t = 1.78$, $P > 0.05$). These results are particularly interesting when the number of Red-winged Blackbird eggs present at the start of incubation are considered (Table 4). From a starting complement of 4.23 eggs, unparasitized nests fledged an average of 1.24 nestlings, a decline of 71%. However, parasitized nests declined from 3.11 eggs to 1.31 nestlings fledged, a decrease of only 58%. Therefore, by their greater success, parasitized nests compensated for the initial cost imposed by clutch reduction.

The higher success of parasitized nests was achieved through a combination of fewer nests lost to predation and more young fledged per egg in successful nests (Tables 4, 6). This could be just a chance phenomenon, or it may indicate that cowbirds select superior Red-winged Blackbird nests. These alternatives were tested by comparing nests with natural parasitism and those with salvaged eggs. Artificially parasitized nests were more successful than those that were parasitized naturally (50% vs. 40%), but the difference was not significant ($\chi^2 = 0.030$, $P > 0.05$). Thus, it does not appear that cowbirds select superior host nests. The overall higher success of parasitized nests is more a consequence of the nests I chose for salvaged eggs than of the nests chosen by cowbirds. Because

TABLE 6. Red-winged Blackbird reproductive success with and without cowbirds. Sample sizes are in parentheses; fledging rate = $\bar{x} \pm$ SD.

Condition	% of nests successful[a]	Fledging rate	
		Per nest	Per successful nest
No cowbird eggs	40.0 (118)	1.24 ± 1.68 (118)	3.15 ± 1.01 (46)
1 cowbird egg present	45.6 (57)	1.33 ± 1.63 (57)	2.92 ± 1.06 (24)
>1 cowbird egg present	53.8 (13)	1.23 ± 1.42 (13)	2.28 ± 1.11 (7)
Cowbird egg(s) hatched	68.3 (41)	1.83 ± 1.56 (41)	2.68 ± 1.12 (28)
Cowbird(s) fledged	86.2 (29)	2.45 ± 1.40 (29)	2.84 ± 1.07 (25)

[a] A successful nest produced at least one Red-winged Blackbird.

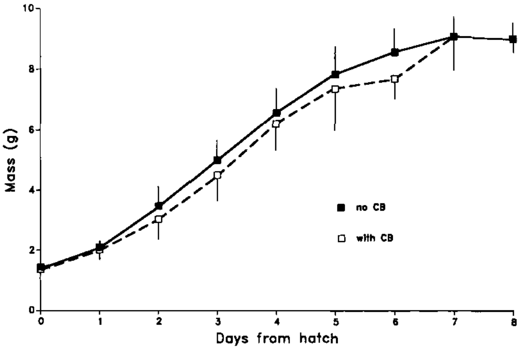

Fig. 4. Yellow Warbler nestling mass ($\bar{x} \pm$ SD) in parasitized and unparasitized nests. Parasitized nest values for each day include all measurements for nestlings where there was a cowbird present that day and the nestling age was known. Data are from 157 nestlings in 37 unparasitized nests, and from 66 nestlings in 23 parasitized nests.

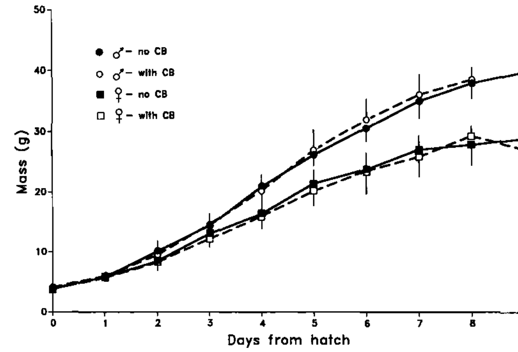

Fig. 5. Mass of male and female Red-winged Blackbird nestlings ($\bar{x} \pm$ SD) in parasitized and unparasitized nests. Parasitized nest values for each day include all measurements for nestlings where there was a cowbird present that day and the nestling age was known. Individuals that reached at least day 6 of the nesting cycle (so they could be sexed) were used (Fiala 1981: 204). Data for males are from 44 nestlings in 27 unparasitized nests, and from 40 nestlings in 32 parasitized nests. Data for females are from 46 nestlings in 27 unparasitized nests, and from 38 nestlings in 32 parasitized nests.

no attempt was made to find superior nests for salvaged eggs, this result seems most likely due to chance.

The final effect that cowbirds can have on their hosts while the young are in the nest is to depress growth rates. I found that this effect is of limited importance. Although Yellow Warbler nestlings in parasitized nests were consistently lighter than nestlings in unparasitized nests, that difference had disappeared by day 7 (Fig. 4). Growth rates did not differ significantly with or without cowbirds (mean K = 0.636 $\pm$ 0.164 and 0.667 $\pm$ 0.174, respectively; $t = 0.82$, df = 175, $P > 0.05$). It appears that the effect of competition with a cowbird in the nest is manifested principally as brood reduction. The mean Yellow Warbler nestling weight is maintained by the steady elimination of the lightest individuals.

Cowbirds did not affect growth rates of nestling Red-winged Blackbirds, even if the sexes are considered separately (Fig. 5, parasitized vs. unparasitized: female mean K = 0.544 $\pm$ 0.101 vs. 0.552 $\pm$ 0.134, $t = 0.50$, df = 80, $P > 0.05$; male mean K = 0.552 $\pm$ 0.075 vs. 0.571 $\pm$ 0.077, $t = 1.44$, df = 80, $P > 0.05$).

DISCUSSION

The very low success of cowbirds in Yellow Warbler nests and its attendant causes are similar to the results obtained by Nolan (1978) in cowbird parasitism of Prairie Warblers (*Dendroica discolor*). The likelihood of these hosts rejecting cowbird eggs through egg burial or nest desertion decreased with the number of host eggs present. Ideally for the cowbird, eggs should always be laid just before the host initiates incubation. By this criterion, many cowbird eggs are laid inappropriately, and consequently fail. There are several possible explanations. First, in spite of the long association of cowbirds with their hosts in this part of their range (Mayfield 1965), selection may have been slow to refine the behavior of cowbirds to make them more effective parasites. Second, the constraints of finding nests at the appropriate time and overcoming host aggression (Robertson and Norman 1977) may limit cowbirds to the current level of performance. Third, selection may have favored "shotgun parasitism" (Rothstein 1975) as an alternative to cowbirds timing egg laying to coincide with a handful of host nests. If eggs are inexpensive to produce and egg production is almost continuous through the breeding season (Scott and Ankney 1980), cowbirds may be more successful laying an egg almost every day, even if appropriate host nests are often unavailable. Because as few as three or four females could potentially account for the 51 cowbird eggs laid in Yellow Warbler nests in 1984 (20 days of nest initiation with a mean laying rate of 0.73 eggs/day [Scott and Ankney 1980]), the production of two fledglings does not seem as low as when considered as the percentage of eggs laid that were successful, but it is a marginal performance.

By contrast to Yellow Warblers, Red-winged Blackbirds were extremely good hosts. Cowbird eggs that appeared before any Red-winged Blackbird egg were regularly accepted and the cowbird nestlings appeared to suffer no disadvantage in competition with some of their larger nest mates. These results raise an interesting question: Given the clear superiority of Red-winged Blackbirds as hosts relative to Yellow Warblers, why were they not more heavily parasitized? Wiley (1986) proposed that large hosts may pose a serious risk of injury to a cowbird caught in the act of egg laying, which may balance the advantage of higher fledging success. Red-winged Blackbirds do respond aggressively to cowbirds (Robertson and Norman 1977). Although I did not quantify the spatial distribution of nests, my impression was that parasitism was more common in isolated Red-winged Blackbird nests. The more typical semi-colonial pattern of marsh-nesting Red-winged Blackbirds would provide the possibility of group detection and defense against cowbirds, thereby limiting cowbird opportunities for parasitism.

Another possible deterrent to greater parasitism of Red-winged Blackbirds are the cowbirds themselves. Female-female aggression (Darley 1983, Teather and Robertson 1985) may regulate female density around host nests and prevent many females from access to superior hosts. Until we are able to study in detail the movements and egg-laying activities of a community of female cowbirds, it is impossible to assess how female cowbirds behave when laying eggs.

The hypothesis that female cowbirds might bias the sex of their eggs according to the host species failed as there was no evidence of a biased sex ratio at hatching. However, even if female cowbirds had the capability of controlling the sex of the eggs they laid, there would have been no advantage to doing so. Both sexes fledged equally well from Yellow Warbler and Red-winged Blackbird nests. The reason appears to be that the sexual size dimorphism seen in adults is not expressed (at least not measurably so) prior to fledging. If both sexes cost the same to rear and are the same size, then neither should be more prone to starvation or a competitive disadvantage.

The 1:1 secondary and tertiary sex ratios I found are consistent with the reports of equal sex ratios among cowbirds caught within a few months of fledging (Hill 1976) or the following summer (Darley 1971). This supports the hypothesis that the strongly male-biased sex ratios among cowbirds > 1 yr old (Friedmann 1929, Darley 1971, Rothstein et al. 1980) must arise because of higher female than male adult mortality (Darley 1971).

Cowbirds represent a serious potential threat to the Yellow Warbler because parasitized nests are seriously affected. At the same time, however, Yellow Warblers are marginal hosts for cowbirds. Given just these two species interacting, one could imagine a stable, density-dependent host-parasite relationship. However, the presence of Red-winged Blackbirds may disrupt this stability by maintaining a large cowbird population independent of the interaction between cowbirds and Yellow Warblers. If the rate of parasitism of warblers by cowbirds increased substantially (e.g. because winter mortality reduced warbler populations), cowbirds could put the warblers at great risk. A study of the same three species in eastern Ontario produced a much different outcome (Clark and Robertson 1979). Although the cowbird-warbler interaction was similar to that in Manitoba, in Ontario Red-winged Blackbirds were not parasitized and thus did not help maintain a cowbird population to the detriment of Yellow Warblers. Moreover, the blackbirds were not neutral, because their aggressive response to cowbirds appeared to reduce parasitism of Yellow Warblers nesting in or near Red-winged Blackbird territories. Lack of overlap in breeding habitat between the warblers and blackbirds precludes this interaction in Manitoba. Given how dissimilar the interactions are between cowbirds and two of their hosts at two locations, accurate modeling of the population dynamics of Brown-headed Cowbirds and their many hosts is likely to prove most difficult.

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