COWBIRD PARASITISM ON THE GRAY CATBIRD AT LONDON, ONTARIO

D. M. SCOTT

ABSTRACT.—Parasitism by the Brown-headed Cowbird on the Gray Catbird, the Red-eyed Vireo, the Yellow Warbler, the Cardinal, and the Song Sparrow was studied at London, Ontario, in 1969 to test the hypothesis that no difference exists between the amounts of parasitism on catbirds and on other hosts known to be commonly parasitized. The incidence of observed parasitism on 16 catbird nests was 44%, and 85% on 27 nests of the other hosts. The frequency distribution of the numbers of cowbird eggs per parasitized catbird nest was significantly different from that on the other hosts. I concluded that the actual amount of parasitism was probably less for catbirds than for the other hosts. Egg loss attributable to removal by cowbirds was significantly less from all catbird nests than from all Cardinal nests. This suggests that cowbirds parasitize catbirds less than Cardinals or that cowbirds remove fewer eggs from catbird nests. Parasitized catbird nests lost relatively fewer eggs than parasitized Cardinal nests if cowbird eggs lost from Cardinal nests are included. Early in the laying phase catbirds seemed more attentive to their nests than were Cardinals. The differences between the effects of cowbirds on catbirds and on the other hosts were attributed to more effective guarding of their nest by catbirds, which reduces the opportunities for a female cowbird to make preliminary inspection visits, to lay, and to remove host eggs. The number of cowbird eggs in catbird nests was about 9% of the estimated number laid in the nests of all hosts studied. Parasitism on catbirds and other hosts that eject eggs may be an important cause of cowbird egg mortality.—*Department of Zoology, University of Western Ontario, London, Ontario, Canada N6A 5B7.* Accepted 12 May 1975.

THE recorded incidence of parasitism by the Brown-headed Cowbird (*Molothrus ater*) on the Gray Catbird (*Dumetella carolinensis*) is very low. Nickell (1958) reported an incidence of 0.3% in about 3000 Gray Catbird nests. As this species usually ejects cowbird eggs from its nests (Rothstein 1971) the low observed incidence of parasitism seems attributable, as Berger (1951) suggested, to an observational bias, namely that cowbird eggs are ejected before an observer finds the nest. In 1963 and 1964 my former students, N. K. Taylor and J. A. Darley, studied catbirds on the campus of the University of Western Ontario, London, Ontario (Darley et al. 1971). They made daily visits, usually before mid-morning, to catbird nests, most of which were found before or early in the laying phase; 10 of 88 (11.4%) nests contained at least one cowbird egg. This incidence of observed parasitism, although much higher than that previously recorded, was still much lower than that I noted locally for Cardinals (*Cardinalis cardinalis*) (Scott 1963) and for some other hosts (this paper). My experience has been that some catbirds tolerate cowbird eggs laid early in the catbird laying phase and that ejection does not always occur soon after the cowbird egg is laid. This observation and the low incidence of parasitism noted by Taylor and Darley, despite their regular and often early visits in the laying phase, suggested that ejection of cowbird eggs before discovery might not be the sole reason for the low recorded incidence of parasitism. Possibly cowbirds do not parasitize catbirds as often as other hosts. Accordingly in 1969 I tested the hypothesis that the amount of parasitism on catbirds is not different from that on hosts known to be parasitized commonly.

METHODS

I chose for a study tract a narrow strip of second-growth shrubby woodland, about 900 m long and varying in width to a maximum of about 50 m, bordered on one side by the open lawns of the University of

Western Ontario campus and on the other by the Thames River. This tract was roughly that shown by Fig. 3, territories 36–46, in Darley et al. (1971). Here nested, I knew from previous experience, a substantial number of four commonly parasitized hosts: Song Sparrow (*Melospiza melodia*), Cardinal, Yellow Warbler (*Dendroica petechia*), and Red-eyed Vireo (*Vireo olivaceus*). For these species I had collected on the campus considerable information on cowbird parasitism in the preceding decade; this information served as a basis for determining if parasitism observed in 1969 occurred at a normal level.

I trapped and color-banded in the study area 10 male Song Sparrows and at least one member of each of nine pairs of Gray Catbirds. I determined the sex by the criteria listed in Darley et al. (1971). These represented most of the pairs of these species nesting within the study area. The pairs of the other species referred to above—four pairs of Yellow Warblers, three of Red-eyed Vireos and three of Cardinals—could be identified throughout the season because of the discontinuous distribution of their territories.

Other potential host-species in the study tract were: several pairs each of American Robins (*Turdus migratorius*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Common Grackles (*Quiscalus quiscula*); three pairs of Brown Thrashers (*Toxostoma rufum*); two pairs each of Warbling Vireos (*Vireo gilvus*) and Northern Orioles (*Icterus galbula*).

Observations on nests began on 16 May, when catbirds were first noted nest building, and ended on 27 June. As my goal was to determine the actual proportion of catbird nests that were parasitized, it was essential that I visit nests before a catbird ejected a cowbird egg but not before a cowbird had laid in a nest. Thus I ran the risk of visiting a nest too early, that is before a cowbird had laid in it. Consequently, my field assistant, Susan Geil, or I attempted to visit certain catbird nests twice in the early morning. Both Hann (1941) and Mayfield (1960: 165–171) agree that cowbirds lay within the half-hour before 0500. As London lies at about the same latitude as the places where Hann and Mayfield worked, cowbirds here should lay at about the same time. Accordingly we began our visits at about 0445 and visited each nest in the following 20 min. We then retraced our steps to make a second visit to ensure that at least one visit occurred after the time of cowbird laying. Thus most visits to catbird nests fell between 0430 and 0545.

There is little evidence that cowbirds lay after 0545. Friedmann (1929: 185) reported a cowbird laying at 0730 on 19 May (presumably standard time), but neither in the present study nor in an earlier intensive study of parasitism on Cardinals (Scott 1963) did I find any unequivocal evidence of laying after 0545. The following personal observations indicate, in agreement with Hann and Mayfield, that cowbirds normally lay well before 0545. On two occasions, 18 May at 0456 and 25 May at 0453, I saw cowbirds laying. On 19 May at 0502 I found a slightly warm cowbird egg in an otherwise empty Yellow Warbler nest. On four occasions I found that a cowbird egg had been laid in the period between two morning visits: 17 May 0445–0510 (egg cool); 25 May 0441–0503 (egg cool); 1 June 0400–0500; 4 June 0425–0545. In my study of Cardinals, my earliest visits to nests were typically between 0530 and 0700. Frequently a cowbird egg that had not been there on the previous day was now present. Possibly these eggs had been laid on the previous day after 0530–0700, but I have made several visits to the same Cardinal nests on the same day and never found evidence of cowbirds laying in the late morning or afternoon. Hence the following records of visits to Cardinal nests also estimate the latest possible time of laying in the morning by cowbirds: 8 May 1900 to 9 May 0545, 16 May 1500 to 17 May 0515, 28 May 1115 to 29 May 0500, 29 May 1300 to 30 May 0500, 8 June 1600 to 9 June 0545 (2 eggs). Thus it seems unlikely that we missed cowbird eggs because our visits were too early.

In 1963 and 1964 27 pairs of campus catbirds whose complete nesting histories were known averaged 2.3 nests per pair before 27 June. Therefore I expected about 15–20 nests from the pairs in the study tract in 1969. However in 1969 the first six pairs suffered no nest loss by the end of periods ranging from 8 to 15 days. To ensure the expected sample size I destroyed these first nests, and I destroyed replacement nests at my second visit on day 5 or on day 6. Between 16 May and 26 June I found 20 catbird nests; of these 2 were never completed, 1 was too high to be examined, and 1 had eggs being incubated when found. The remaining 16 nests were found before incubation started: 13 at least 2 days before the first catbird egg was laid, 1 on the day before the first egg, 1 on the day of the first egg, and the last on the second day of egg-laying. All but one were kept under daily observation at least until the 5th day after the beginning of laying. The exception was a nest found 2 days before observations ended.

The nests of the four other species considered were found at various stages before hatching.

As my Cardinal studies showed that cowbirds usually lay in a nest before incubation begins, the twice-morning visits to catbird nests were made only until day 5 when one could be certain that the clutch was complete and that incubation had begun; thereafter only one visit was made and that early in the morning. My assistant and I made the twice-daily visits on about 85% of the days when they should have been made. About two-thirds of the first visits were made between 0430 and 0500, about 70% of the remainder were made between 0500 and 0530, and 50% of the second visits were made between 0500 and

0600. We visited each nest, with one exception, at least once daily. At each visit we usually recorded the presence or absence of the birds. Nests of other hosts were visited at least once daily.

Each catbird egg was marked at one end by one or more dots of black ink to determine if any eggs were lost later. Cowbird eggs in catbird nests were removed when found to reduce the chance of desertion. Cowbird eggs in other nests were marked.

A daily search was made below each catbird nest over an area about 2 m in diameter for cowbird eggs ejected by catbirds and catbird eggs that might have been removed from the nest by cowbirds. Female cowbirds frequently remove a host egg (Hann 1941).

Unless otherwise specified, I used 2×2 G tests with Yates' correction and 1 df for all statistical tests (Sokal and Rohlf 1969: 591).

RESULTS

Parasitism on catbirds and other hosts.—Table 1 presents the observed parasitism in two ways: first the percentage of parasitized nests for each species, which gives equal weight to a parasitized nest whether it was parasitized only once or more frequently. Second the numbers of nests that contained one, two, or more cowbird eggs are given. This method has the advantage of showing more accurately the actual number of successful laying visits made by a cowbird or cowbirds to a nest.

By either criterion catbirds were apparently parasitized less often than other hosts. Cowbird eggs were found in 3 of 8 first catbird nests noted on the study tract and 4 of 8 replacement nests. Thus nothing indicates that my destruction of nests affected the percentage incidence of parasitism. In total, 44% (7 of 16) of catbird nests and 85% (23 of 27) of nests of the other hosts combined were parasitized; the difference is significant (7:9 vs. 23:4, $G = 6.256 > \chi^2_{0.025} = 5.024$).

The frequency distribution of the numbers of cowbird eggs in known parasitized catbird nests is strikingly different from the summed frequency distributions for the parasitized nests of other hosts. Six parasitized catbird nests each contained one cowbird egg; the 7th contained 3 (1 laid one morning and 2 on another morning). Only 5 parasitized nests of other hosts contained 1 cowbird egg but 18 contained more than 1. These proportions are significantlv different (6:1 vs. 5:18; $P = 0.009$, Fisher's exact test, Sokal and Rohlf 1969: 595).

The preceding analyses are probably biased as some cowbird eggs in catbird nests may have been ejected before my visits. I found nine cowbird eggs in catbird nests and these nests lost three host eggs, likely to cowbirds. Two apparently unparasitized nests each lost an egg (in one case the female catbird possibly failed to lay on one day). Assuming that I missed no cowbird eggs in the known parasitized catbird nests and applying the ratio of 3 host eggs lost for 9 cowbird eggs found in those nests to the 2 apparently unparasitized nests that lost an egg, I estimate that I may have missed no more than about 6 cowbird eggs (3:9 as 2:6). On the other hand I did not find a cowbird egg below any catbird nest. I found 69 cowbird eggs in 27 nests of the other hosts. If parasitism in catbird nests was equal then the 16 catbird nests observed should have had about $(16 \times 69)/27 = 41$ cowbird eggs laid in them. That would mean that I failed to find about 32 cowbird eggs. I think this is unlikely because of my early visits and my searches below nests. Accordingly I conclude that the actual amount of parasitism on catbirds in 1969 was probably significantly less than that on the other hosts.

The amount of parasitism on hosts other than catbirds was higher in 1969 than in other years, but the data from the two periods are not strictly comparable. In 1969 daily visits were made to each host nest, while in earlier years fewer visits were made

TABLE 1

INCIDENCE OF COWBIRD PARASITISM ON THE CATBIRD AND FOUR OTHER HOSTS[1]

Species	No. of nests in 1969 containing different no. of cowbird eggs								% nests parasitized		Mean no. cowbird eggs per parasitized nest	
	0	1	2	3	4	5	6	7	1969	1960–68	1969	1960–68
Catbird	9	6	0	1	0	0	0	0	44	11 (88)[2]	1.3	1.1
Song Sparrow	1	2	4	0	3	1	0	0	91	91 (22)	2.7	1.7
Cardinal	0	3	0	0	0	0	0	0	100	81 (85)	1.0	1.8
Yellow Warbler	3	0	1	2	3	0	0	1	70	65 (14)	3.9	2.7
Red-eyed Vireo	0	0	0	1	1	1	0	0	100	100 (3)	4.0	4.3

[1] At London, Ontario between 17 May and 27 June 1969 and in May and June 1960–68.
[2] No. of nests.

and all cowbird eggs were not necessarily found. Accordingly I do not believe that the amount of parasitism in 1969 was abnormally high.

Between 17 May and 27 June I found 78 cowbird eggs. I found all catbird, Cardinal, and Yellow Warbler nests, but not all nests of Song Sparrows and Red-eyed Vireos. I estimate that about 20 cowbird eggs were laid in the unfound nests of the last two species. Thus at least about 9% of all cowbird eggs laid in the nests of the five species studied were in catbird nests. As I do not know the number of cowbird eggs laid in the nests of the other potential hosts listed earlier, I cannot estimate accurately the proportion of cowbird eggs laid in catbird nests when all hosts are considered.

Rate of egg loss.—My records of daily visits to catbird and Cardinal nests in which each egg was marked on the day it was laid show that one egg, rarely two, often disappeared without the nest being deserted. Cowbirds cause losses from parasitized nests as they are known to remove eggs; predators probably account for some losses. The relative effects of predators and cowbirds have not been directly determined, but can be estimated for Cardinals by comparing the egg-loss rates in parasitized and unparasitized Cardinal nests. If cowbirds cause most of the losses from parasitized nests, then rates of egg loss should indicate indirectly the amount of cowbird parasitism on species such as the catbird that eject cowbird eggs. Accordingly I determined the proportions of catbird and Cardinal nests that lost at least one egg, without the nest being deserted, in the 5 days following laying of the first host egg. I chose this period because my records showed that most such losses occurred then. I used only nests that were visited daily and that with the few exceptions listed below had been visited the day before the first host egg was laid. I also used 13 catbird and 6 Cardinal nests that had one egg when found because the ultimate clutch size appeared normal (4 for catbirds, 3 for Cardinals) and because the interval between the first observed egg and destruction of the preceding nest of those pairs was not greater than 6 days, which is the usual interval between nest loss and the first egg in replacement nests of catbirds and Cardinals (Scott MS). Thus in these nests the first observed egg was probably the first host egg laid in that nest.

A nest that lost eggs without desertion was counted as having a loss. One that survived to the morning of day 6 without egg loss was scored as a no-loss. All eggs disappeared from some nests, that had not previously lost an egg, before the end of the 5-day observation period. As some might have eventually lost an egg if they had survived longer, I prorated these nests to the loss and no-loss categories on the basis of the sum of the daily probabilities of them losing an egg in the remainder of the

TABLE 2

RATES OF HOST EGG LOSS[1] FROM CATBIRD AND CARDINAL NESTS IN FIRST 5 DAYS OF NESTING SEQUENCE

Category	Nests with	
	Loss	No loss
Unparasitized Cardinals (11 April–19 August)	4	28
Once-parasitized Cardinals (16 April–18 July)	22 (25)	8 (5)
All parasitized Cardinals (15 May–9 July)	34 (38)	11 (7)
All Cardinals (15 May–9 July)	36 (40)	18 (14)
All catbirds (13 May–9 July)	27	53
Parasitized catbirds (13 May–9 July)	9	9

[1] Nests that lost either Cardinal or cowbird eggs are in parentheses.

5-day period. I calculated the daily probabilities of loss from the nests that survived for particular numbers of days. Thus in the loss column in Table 2 I added two nests to the all catbird category, one to the parasitized catbird category, and none to the Cardinal categories.

Table 2 presents the proportions of nests that lost at least one egg for six categories of Cardinal and catbird nests. To obtain a reasonably sized sample of nests I used all records of unparasitized Cardinal nests between April and mid-August. Likewise I used all records of once-parasitized Cardinals between mid-April and mid-July. Otherwise the time span of the samples of Cardinal nests corresponded closely to the local catbird breeding season (Darley et al. 1971). Most catbird data are from 1963, 1964, and 1969; I added two parasitized catbird nests from other years; Cardinal data are from 1955–61.

Cowbird eggs frequently disappeared from Cardinal nests; 33% of the 45 parasitized nests in Table 2 lost at least one cowbird egg. Possibly some Cardinals eject cowbird eggs but there is no evidence of this. Indeed all available evidence indicates that they do not. Ejection by Cardinals has never been reported and Rothstein (1971) failed to demonstrate it experimentally with a sample of seven Cardinal nests. Mayfield (1960: 164) and Mengel and Jenkinson (1970) suspected that a cowbird has difficulty discriminating between a host and a cowbird egg when the patterns are similar and the cowbird egg is smaller or similar in size. A Cardinal egg is conspicuously larger than a cowbird egg but otherwise similar in appearance. As cowbirds are known to remove eggs and Cardinals are not, I think that cowbirds remove most, if not all, of the cowbird eggs that disappear from Cardinal nests. Nevertheless I have treated Cardinal nests that lost only Cardinal eggs separately from those that lost either Cardinal or cowbird eggs.

Only 4 of 32 unparasitized Cardinal nests lost eggs, a rate significantly less than that for all parasitized Cardinal nests (4:28 vs. 34:11; $G = 29.588 > \chi^2_{0.005} = 7.879$). Thus I conclude that cowbirds remove most of the Cardinal eggs lost from parasitized Cardinal nests. As catbirds and Cardinals nest here in the same habitat and have similar nest sites, catbird losses to predators are unlikely to be greater than for Cardinals. As the effect of predators seems small, the rate of egg loss from catbird nests should indicate the amount of cowbird activity at catbird nests. The sample of catbird nests had significantly fewer egg losses than the sample of all Cardinal nests (27:53 vs. 36:18; $G = 12.914 > \chi^2_{0.005} = 7.879$). From this analysis I

TABLE 3

COMPARISON OF ATTENTIVENESS OF CATBIRDS AND CARDINALS AT THE NEST[1]

	0400–0459	0500–0559	0600–0759		Remainder of day	
	Catbird	Catbird	Catbird	Cardinal	Catbird	Cardinal
Day −1	0.33 (6)	0.25 (4)	—	0.12 (17)	0.33 (3)	0.10 (10)
Day 1[2]	0.14 (7)	0.20 (5)	0.80 (5)	0.48 (31)	0.50 (4)	0.35 (17)
2	0.36 (11)	0.62 (13)	1.00 (5)	0.52 (33)	1.00 (7)	0.40 (20)
3	0.38 (8)	1.00 (9)	1.00 (3)	0.68 (25)	1.00 (7)	1.00 (17)
4, 5	0.87 (15)	0.90 (19)	0.89 (9)	0.83 (30)	0.83 (12)	0.85 (23)

[1] Attentiveness is expressed as proportion of occasions that a bird was present at the nest at different times of day. Number of records are in parentheses.
[2] Day when first host egg was laid.

infer that cowbird activity was less at catbird nests than at Cardinal nests. This could mean that cowbirds laid less in catbird nests or removed fewer eggs or both.

To determine if cowbirds remove relatively fewer eggs from catbird nests, I compared the rates of egg loss from parasitized catbird nests and once-parasitized Cardinal nests. The two samples are not quite comparable: the catbird sample was slightly more heavily parasitized (23 cowbird eggs in 18 nests) than the Cardinal sample (30 cowbird eggs in 30 nests). Furthermore the catbird sample may have contained some undetected parasitism. Thus if egg-loss rates were the same for each species, greater losses from catbird nests would be expected. This was not the case; considering host eggs only, fewer catbird nests lost eggs but the difference is not significant (9:9 vs. 22:8; $G = 1.736 < \chi^2_{0.1} = 2.706$). If losses of cowbird eggs are included the difference is significant (9:9 vs. 25:5; $G = 4.466 > \chi^2_{0.05} = 3.841$). The evidence is inconclusive but it suggests that cowbirds remove fewer eggs from catbird nests than from Cardinal nests. The difference in egg-loss rate in parasitized nests seems insufficient to account for the large difference in egg-loss rate observed in the comparison between all catbird and all Cardinal nests. Therefore the analysis of data on egg removal supports my earlier inference that catbirds are not parasitized as much as other hosts.

I propose that some interaction between catbirds and cowbirds reduces the likelihood of a catbird nest being parasitized and may also reduce the chance of a cowbird removing an egg. I now offer some fragmentary data indicating that catbirds usually remain closer to their nests than Cardinals do in the early part of the nesting sequence when parasitism and egg loss to cowbirds usually occur.

Attentiveness of catbirds and Cardinals.—Variation in attentiveness could result in differences in the real incidence of parasitism and the rate of loss of eggs. When I began fieldwork in 1969 I had the impression, based on 15 years of field experience with catbirds and Cardinals, that catbirds were more attentive to their nest and perhaps defended it more aggressively. Accordingly in 1969 I recorded the presence of catbirds at the nest to compare with data collected earlier in my studies on Cardinals. The data for each species (Table 3) were collected between 15 May and 27 June and probably contain many biases. Many factors influence the probability of a bird being present at the nest at a particular hour early in the nesting sequence, e.g. interspecific and intraspecific variation, and seasonal changes in the laying time. Variations in clutch size will affect the onset of incubation and hence the degree of attentiveness on particular days. My data are insufficient to allow analysis of the contribution of these variables and so, because of the potential biases, I present

statistical analyses with reservation. Also it could be argued that I failed to detect Cardinals at their nest because they scold less vigorously than catbirds.

Catbirds were present at their nests between 14% and 33% of the time up until the first egg was laid (day 1). Thereafter attentiveness was higher at all periods. After the third egg catbirds were present between 83% and 100% of the time. Relevant to the incidence of parasitism was the low attentiveness in the hour preceding sunrise (ca. 0500) on days −1 to 3, when in 1969 all cowbird eggs found in catbird nests were laid.

One or both catbirds were seen on 105 visits: the female alone, either on the nest or close by 67 times; the female and male together on 25 occasions; the male alone 4 times; and on 9 visits the sex was undetermined. The female was on the nest 45 times; the male was seen only twice at these times.

Cardinals appeared equally as attentive as catbirds after the last egg was laid (day 3 for almost all Cardinals, day 3 or 4 for catbirds), but they seemed less attentive earlier. Sums of the values after 0800 for days −1, 1, and 2 in Table 3 show Cardinals present 15 times on 47 visits, catbirds 10 times on 14 visits (15:32 vs. 10:4; $G = 5.386 > \chi^2_{0.025} = 5.024$). Similarly the proportions of times present on days 1, 2, and 3 at 0600–0759 are also significantly different between the two species (12:1 for catbirds vs. 49:40 for Cardinals; $G = 5.904 > \chi^2_{0.025} = 5.024$). Unlike female catbirds that, when present at the nest, were often just nearby, female Cardinals were almost always on the nest. Male Cardinals, unlike male catbirds, were not seen at nest with the female, although occasionally the male sang nearby when the female was on the nest.

In conclusion I suggest that catbirds are more attentive than Cardinals to their nest in the early part of the nesting sequence, when cowbirds are most likely to be laying or removing a host egg.

DISCUSSION

I have demonstrated two aspects by which cowbird parasitism on catbirds apparently differs from that on other hosts, particularly the Cardinal: (1) catbirds were parasitized less frequently than other hosts, (2) egg removal, presumably by cowbirds, was less in parasitized catbirds than in parasitized Cardinals. Several explanations, not necessarily mutually exclusive, may account for these differences.

Cowbirds may not find catbird nests as readily as those of other hosts. Catbirds normally nest in darker places than do most other hosts. Yet I found their nests easily and it seems highly unlikely that cowbirds would experience difficulty in finding them, although the darkness of the nest site may deter cowbirds from entering the nest bush. In any case, the high level of attentiveness of catbirds to the nest site may act in at least two ways to reduce the opportunity for a cowbird to use a particular nest.

The attentiveness of catbirds to their nest may prevent cowbirds from visiting it, either for preliminary inspection or for laying. Female cowbirds watch and visit nests while they are being built (Friedmann 1929: 187; Hann 1937: 207). The persistence with which a cowbird tries to visit a nest and the length of time spent on these visits suggest that the visits may be important in some sense other than locating a nest and determining its contents.

Two examples may be instructive. On 10 April 1960 I saw a female Cardinal starting to build in a small honeysuckle; on 13 April the Cardinal was in the

bush close to the nest when a female cowbird flew low into the bush. The cowbird climbed slowly towards the nest but the Cardinal chased her out. The same cowbird returned almost immediately and was again driven out by the Cardinal. The account of the second example is paraphrased from the field notes of my former student-assistant, A. L. A. Middleton. On 27 May 1960 he saw a female Cardinal starting a nest in a bale of fence wire inside and near the entrance of an open-ended lean-to attached to a large shed. The next day the female Cardinal made frequent trips with nesting material. On one occasion a female cowbird appeared while the Cardinals were absent, landed on the ground, walked into the shed, and climbed to the nest and studied it. After about a minute she emerged and flew to the edge of the roof of the lean-to where she remained for about 25 min. During this time the Cardinals returned, whereupon the cowbird squatted on the roof. As the Cardinals entered the shed, she looked over the edge, apparently watching the Cardinals. Again the next morning a female cowbird appeared from the lean-to and sat on the roof for 10 min. Each nest was subsequently parasitized.

These observations suggest that prelaying visits are a critical part of the behavior of a breeding female cowbird. Hann (1937: 209) suggested that "ovulation may be stimulated by the sight of nest-building" and I have some suggestive, although inconclusive, evidence based on egg-laying by captive cowbirds in canary nests that this is true. If the number and duration of prelaying visits is important, then any behavior of the host limiting the opportunities for prelaying visits would reduce the amount of parasitism. Catbirds were seen at the nest as or more frequently than Cardinals during those periods for which I have data for both species. Unfortunately I lack data on Cardinals for early morning, but they are probably less attentive then than catbirds.

Some authors have commented upon the attentiveness of catbirds and particularly upon the role of the male in guarding the nest when the female is absent (Skutch 1953: 9; Zimmerman 1963). Catbird territories are small here, averaging about 0.32 ha (Darley et al. 1971), about one-fifth the size of local Cardinal territories. Thus even if a catbird is not actually at the nest site, in most territories catbirds are likely to be within 50 m of their nest and thus usually able to see a cowbird approaching it. Cardinals on the other hand are likely to be farther away simply because their territories are much larger and they often forage far from the nest. I submit then that one cause of the relatively low incidence of parasitism in catbirds results from the inability of some cowbirds to visit catbird nests either before or for laying.

I have only one example of catbirds repelling a female cowbird at laying time. On 23 May 1969 at 0450 both catbirds were near their nest. A female cowbird flew into the nest bush and approached to within less than 1 m of the nest. A catbird then chased her for about 20 m. The cowbird flew in a wide circle, returned to the nest bush, and approached the nest to within about $^1/_3$ m. Both catbirds chased the cowbird, diving at her over a distance of about 30 m, and drove her away. I checked the nest; there were still two catbird eggs and no cowbird eggs. Judged from the time and behavior, this cowbird was probably ready to lay in the nest and was thwarted by the presence and aggressiveness of the catbirds. Other hosts may have small territories and thus be close to their nest most of the time, but most hosts are smaller than cowbirds and many are incapable of defending their nest effectively against cowbirds. I have twice seen a cowbird lay in a nest, once that of a Song Sparrow and

once a Yellow Warbler, despite the presence, alarm, and agitation of the host pair. Hann (1937: 202) reported a similar incident with an Ovenbird (*Seiurus aurocapillus*).

I can offer little or no evidence for other reasonable explanations. Cowbirds may discriminate between catbirds and other species. Very little evidence of host specialization in cowbirds exists apart from that submitted by McGeen and McGeen (1968), but clearly selection must operate strongly against cowbirds that parasitize catbirds disproportionately. The basis for discrimination, if it exists, is unknown. Although most cowbirds presumably select a host nest before eggs are present, they usually lay when there is at least one host egg. Perhaps cowbirds discriminate between the dark blue-green egg of catbirds and the speckled egg of most other hosts as Fretwell (1973) implied, but this seems unlikely because cowbirds lay almost instantaneously (within a minute) when it is often still quite dark and recognition of eggs under those conditions might be difficult. Furthermore cowbirds commonly parasitize Wood Thrushes (*Hylocichla mustelina*), which also lay blue-green unspotted eggs, although paler than catbird eggs (Bent 1949: 107; Friedmann 1963: 73).

If guarding the nest prevents high levels of parasitism then it should also reduce the opportunities for a cowbird to remove an egg. Mengel and Jenkinson (1970) commented on the marked attentiveness of a female catbird whose nest was twice parasitized but lost no eggs. My data suggest that cowbirds remove relatively few catbird eggs but this rests on the unprovable assumption that Cardinals never eject cowbird eggs.

Parasitism may diminish the productivity of a host pair in two ways. First a young cowbird frequently grows at the expense of the host young. Mayfield (1960: 176) estimated that in parasitized nests of Kirtland's Warblers (*Dendroica kirtlandii*) 59% of warblers hatched did not fledge because cowbird nestlings were present. Second, because of egg removal, even if a cowbird egg does not hatch the potential output of fledglings by the parasitized host will still be less than that of a pair that was not parasitized. Catbirds have defenses that may reduce both effects of parasitism. Their guarding behavior could restrict access to a nest resulting either in a reduction in parasitism or, if that fails, then in a reduction of loss of catbird eggs. Finally the catbird's ejection of cowbird eggs removes the threat of competition to its own young. This behavior may also moderate the effect of a loss of its own egg because the reduction of the clutch size may increase the survival rate of the fledglings.

The habit of egg ejection may have evolved in relation to parasitism (Fretwell 1973, Rothstein 1974). It would be informative to compare the behavior of catbirds in an area without cowbirds with that in one where cowbirds are present. If ejection of cowbird eggs has evolved in relation to parasitism and is not simply a response to a foreign object in the nest, then the response should be absent in a place where catbirds and cowbirds are not sympatric, unless their allopatry is of recent origin.

The habit of guarding the nest likely evolved as a mechanism of defense against small predators (in this context egg removal by female cowbirds is simply predation); possibly it evolved directly in relation to cowbirds. It remains to be shown that catbirds suffer less loss to predators than do other species in the same habitat.

I do not know how representative my results are of cowbird and catbird interactions throughout the mutual range of these species. In general my values of parasitism on several species are much higher than those recorded by others (Young

1963), but I do not know whether this reflects differences in the abundance of cowbirds or differences in the methods of collecting the data. My destruction of some catbird nests probably made more catbird nests available for parasitism than would normally have occurred in 1969. Thus the proportion of cowbird eggs laid in catbird nests may have been abnormally high. Regardless, it is clear that a substantial number of cowbird eggs are laid in catbird nests. Therefore it seems important that workers on the population dynamics of cowbirds should pay more attention to those species that are not considered to be common hosts. Rothstein (1971) showed experimentally that several common species, Eastern Kingbird (*Tyrannus tyrannus*), Blue Jay (*Cyanocitta cristata*), Brown Thrasher, and American Robin, almost invariably ejected cowbird eggs, as do Common Grackles according to Fretwell (1973). These species and others are probably parasitized much more than the literature indicates and because they are abundant must represent an important source of mortality on cowbird eggs.

ACKNOWLEDGMENTS

I thank Susan Geil for her invaluable field assistance. I greatly appreciate valuable discussions with C. D. Ankney. The National Research Council of Canada provided financial support.

LITERATURE CITED

BENT, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. Natl. Mus. Bull. No. 196.

BERGER, A. J. 1951. The cowbird and certain host species in Michigan. Wilson Bull. 63: 26–34.

DARLEY, J. A., D. M. SCOTT, & N. K. TAYLOR. 1971. Territorial fidelity of catbirds. Canadian J. Zool. 49: 1465–1478.

FRETWELL, S. 1973. Why do robins lay blue eggs? The Bird Watch 1 (No. 1): 1, 4.

FRIEDMANN, H. 1929. The cowbirds/A study in the biology of social parasitism. Springfield, Illinois, Charles C. Thomas Co.

———. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. No. 233.

HANN, H. W. 1937. Life history of the Oven-bird in southern Michigan. Wilson Bull. 49: 145–237.

———. 1941. The cowbird at the nest. Wilson Bull. 53: 211–221.

MCGEEN, D. S., & J. J. MCGEEN. 1968. The cowbirds of Otter Lake. Wilson Bull. 80: 84–93.

MAYFIELD, H. 1960. The Kirtland's Warbler. Bull. Cranbrook Inst. Sci. 40.

MENGEL, R. M., & M. A. JENKINSON. 1970. Parasitism by the Brown-headed Cowbird on a Brown Thrasher and a catbird. Wilson Bull. 82: 74–78.

NICKELL, W. P. 1958. Brown-headed Cowbird fledged in nest of catbird. Wilson Bull. 70: 286–287.

ROTHSTEIN, S. I. 1971. Observation and experiment in the analysis of interactions between brood parasites and their hosts. Amer. Naturalist 105: 71–74.

———. 1974. Mechanisms of avian egg recognition: possible learned and innate factors. Auk 91: 796–807.

SCOTT, D. M. 1963. Changes in the reproductive activity of the Brown-headed Cowbird within the breeding season. Wilson Bull. 75: 123–129.

SKUTCH, A. F. 1953. How the male bird discovers the nestlings. Ibis 95: 1–37, 505–542.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman and Co.

YOUNG, H. 1963. Breeding success of the cowbird. Wilson Bull. 75: 115–122.

ZIMMERMAN, J. L. 1963. A nesting study of the catbird in southern Michigan. Jack-Pine Warbler 41: 142–160.