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COWBIRD PARASITISM AND EVOLUTION OF ANTI-PARASITE STRATEGIES IN THE YELLOW WARBLER

KAREN L. CLARK AND RALEIGH J. ROBERTSON

The Yellow Warbler (*Dendroica petechia*) is frequently parasitized by the Brown-headed Cowbird (*Molothrus ater*) resulting in reduction of nest success at parasitized nests (Schrantz 1943, McGeen 1972). There are several avenues open to a Yellow Warbler once a cowbird egg has been deposited in its nest. It could accept the egg, thereby running the risk of the egg hatching and the cowbird nestlings competing with the Yellow Warbler nestlings. Alternatively, it could reject the egg. This could occur by ejection, where the cowbird egg is removed from the nest (cf. Rothstein 1975), by nest desertion, or by burial, in which the cowbird egg, along with any Yellow Warbler eggs present at the time, are covered by the addition of nesting material. The response favored by natural selection depends upon the potential for a successful nest attempt. The possibility of success varies with the amount of time and energy already invested in the nesting attempt, and the possibility of the cowbird egg hatching. The objectives of this study were to determine the frequency of occurrence of these various responses by Yellow Warblers to naturally deposited cowbird eggs and to investigate the factors eliciting each response.

METHODS

Yellow Warbler nests were located in several study areas near the Queen's University Biological Station, Chaffey's Locks, Ontario, from 1975–1977. Most nests were found during nest building. Nests for which the date of clutch initiation was unknown have not been included in this analysis unless noted. In 1975 and 1976, nests were checked every second day. In 1977, nests were checked daily during egg-laying and early incubation and then every third day until the young fledged. All references to number of Yellow Warbler eggs indicate the number present when the nest was checked. In some parasitized nests, 1 or more Yellow Warbler eggs may have been removed by cowbirds. Our measure of nest success was the number of young leaving the nest as a proportion of the number of eggs laid. All references to nest success are only to those nests not preyed upon. For nests which received more than 1 cowbird egg, only the response to the first egg is included in tables and text unless specified otherwise.

RESULTS AND DISCUSSION

Forty-one percent (45/109) of all Yellow Warbler nests were parasitized, containing 1 or more cowbird eggs (Table 1). The mean nest success of parasitized nests was 0.44 ± 0.33 compared to the mean nest success of unparasitized nests of 0.80 ± 0.16 (Mann Whitney U-test, U for large

TABLE 1

MEAN NEST SUCCESS OF PARASITIZED AND UNPARASITIZED NESTS

Nest status	No. Yellow Warbler nests	No. cowbird eggs	$\bar{x} \pm$ SD Nest success[a] (no. of nests)
Parasitized			
Buried	20[b]	28	0.78 ± 0.21 (13)
Deserted	10	12	0.0 ± 0.0 (10)
Accepted	12	16	0.53 ± 0.34 (8)
Preyed upon[c]	3	3	(0)
Total	45	59	0.44 ± 0.33 (31)
Not parasitized	64	0	0.80 ± 0.16 (35)

[a] Nest success = Yellow Warbler young to leave the nest per egg laid, including buried eggs, based only on nests (number as indicated) which were not preyed upon prior to fledging.
[b] Two nests are included which were found after clutch initiation and are not included in subsequent tables.
[c] Number of nests preyed upon before the response to the cowbird egg could be determined. They are included here to indicate the incidence of parasitism. These nests are not included in subsequent tables or in percent frequency of responses cited in text.

samples = 3.01, $P \leq 0.01$). The number of nestlings lost per nest varied greatly from 0 to some (variable) threshold number leading to termination of the nesting attempt. The reduction in nest success depended on the number of Yellow Warbler eggs removed by the cowbird, the stage of nesting when the cowbird egg was laid, and the response of the Yellow Warbler to the cowbird egg (Table 2). For 8 of 9 nests which received more than 1 cowbird egg the response to subsequent eggs was the same as for

TABLE 2

ACCEPTANCE AND REJECTION OF COWBIRD EGGS AS A FUNCTION OF THE NUMBER OF YELLOW WARBLER EGGS WHEN THE COWBIRD EGG WAS DEPOSITED

			No. nests with cowbird eggs			$\bar{x}$ (± SD) nest success[c]	
No. YW eggs[a]	No. YW nests	No. CB eggs[b]	buried	de-serted	ac-cepted	YW	CB
0	20	30	13	7	0	0.52 ± 0.42	0.0 ± 0.0
1	4	4	3	0	1	0.48 ± 0.21	0.0 ± 0.0
2	6	6	1	1	4	0.31 ± 0.52	0.17 ± 0.41
3	4	7	0	2	2	0.30 ± 0.48	0.67 ± 0.58
4	5	5	1	0	4	0.50 ± 0.25	0.20 ± 0.45
5	1	1	0	0	1	—	—

[a] Number of Yellow Warbler eggs present when the cowbird egg was laid. In some cases, a Yellow Warbler egg may have been removed by the cowbird.
[b] Total number of cowbird eggs laid, not per nest. Most nests contained only 1 cowbird egg, although some contained more than one.
[c] Nest success measured as the number of young to leave nest/eggs laid/nest, excluding nests that were preyed upon.

the first. At 1 nest the first cowbird egg was laid before any Yellow Warbler eggs, and it was buried. A second egg laid when there were 3 Yellow Warbler eggs resulted in desertion of the nest.

Acceptance of cowbird eggs.—Cowbird eggs were accepted at only 29% (12/42) of all parasitized Yellow Warbler nests (Table 1). The mean nest success of Yellow Warblers which accepted cowbird eggs was 0.53 ± 0.34 (Table 1) and where cowbird young fledged was 0.46 ± 0.33 (N = 6). Acceptance occurred most frequently at nests which had 2 or more Yellow Warbler eggs at the time the cowbird egg was laid (Tables 2, 3). These results are similar to those of Rothstein (1975) who found 100% acceptance at 16 Yellow Warbler nests which were experimentally parasitized when they contained at least 2 warbler eggs. Accepted cowbird eggs that were laid when there were 3 Yellow Warbler eggs in the nest had the highest success, although the small sample size of cowbird eggs accepted when there were 0, 1 or 5 Yellow Warbler eggs was insufficient to assess cowbird success in these nests.

The cowbird incubation period is 10–11 days (Friedmann 1963) whereas the Yellow Warbler's is 11–12 days (Schrantz 1943, this study). Yellow Warblers will initiate incubation before their clutch is complete. With a mean clutch-size of 3.6 ± 0.82 eggs for parasitized Yellow Warblers, cowbird eggs deposited on or before the day the third egg was laid hatch with or before the Yellow Warbler eggs. The chance of hatching for a cowbird egg laid when there were 3 or fewer Yellow Warbler eggs in the nest was 83% (5/6, including only nests with accepted cowbird eggs which were not preyed upon). In 3 of these 5 nests where the cowbird egg did hatch, only 1 Yellow Warbler fledged along with the cowbird. In each of the three, the cowbird hatched earlier than any of the Yellow Warblers. In the other 2 nests, in which the cowbirds hatched synchronously with or later in the day than the warblers, 3 and 4 Yellow Warblers, respectively, fledged along with the parasite's young. The time of hatching of Yellow Warbler eggs relative to cowbird eggs thus appears to be a key determinant of Yellow Warbler hatching success and nestling survival. Mayfield (1960: 173) found that Kirtland's Warbler (*Dendroica kirtlandii*) nestlings never survived when there were 2 or more older cowbird nestlings in the nest, and survival was greatly reduced when there was 1 older cowbird nestling. However, Kirtland's Warblers which hatched 2 or more days before the cowbird egg hatched were not adversely affected by the presence of the cowbird.

Another factor predicted to influence the response of the Yellow Warbler to parasitism is the timing of the event with respect to the breeding season. A delay due to egg burial or renesting could have detrimental effects associated with the timing of the nest, relative to the rest of the

TABLE 3

FREQUENCY OF OCCURRENCE OF REJECTION AND ACCEPTANCE OF COWBIRD EGGS RELATIVE TO YELLOW WARBLER NEST STAGE

No. YW eggs when CB egg was laid	No. YW nests	Frequency of response % (no.) of nests where cowbird eggs were[a]		
		buried	deserted	accepted
0, 1	24	67 (16)[b]	29 (7)[c]	4 (1)[d]
2–5	16	12 (2)[b]	19 (3)[c]	69 (11)[d]

[a] $\chi^2 = 20.02$, df = 2, $P < 0.001$—indicating that the 3 responses occurred with different frequency within host egg number groupings.

[b] $\chi^2 = 11.38$, df = 1, $P < 0.001$—indicating that the frequency of burial is different for clutches of 0–1 vs 2–5, when other responses are grouped.

[c] $\chi^2 = 0.55$, df = 1, $P > 0.05$—indicating that the frequency of desertion is similar regardless of number of host eggs when nest is parasitized.

[d] $\chi^2 = 19.07$, df = 1, $P < 0.001$—indicating that the frequency of acceptance is different for clutches of 0–1 vs 2–5, when other responses are grouped.

avian community. Asynchronous Yellow Warbler nests were subjected to higher predator pressure than nests in synchrony with the community as a whole (Clark and Robertson 1979), a difference possibly attributable to either the "swamping effect" or "selfish herd effect" on predators (Robertson 1973, Hamilton 1971). Furthermore, since a bird's initial nesting attempt is thought to be timed to take advantage of optimal conditions, delay could put the Yellow Warbler nest out of phase with the food supply (Immelmann 1971). Late in the nesting season the risk of loss associated with a delay could outweigh the potential benefits of cowbird egg rejection. Consequently, acceptance, which minimizes any delay in nesting, is expected to occur more frequently later in the breeding season.

Since response was shown to depend on the stage of the nest at the time of parasitism (Table 3) this factor should be considered when investigating seasonal changes in response. Rearranging the data into the many small categories necessary for such an analysis produced sample sizes inadequate for statistical analysis. It was evident, however, that there was a relationship between date and stage of the nest when parasitized. Defining the peak of clutch initiation as the day on which the maximum number of Yellow Warbler clutches were initiated, we found that parasitism of nests containing 0 or 1 Yellow Warbler egg(s) occurred most frequently before this peak (18 of 24 nests containing 0 or 1 Yellow Warbler egg(s) were parasitized before the peak of clutch initiation). Nests with 2 or more Yellow Warbler eggs were less frequently parasitized before the peak of clutch initiation (where 4 of 18 nests with 2 or more Yellow Warbler eggs were parasitized before the peak in clutch initiation, $\chi^2 = 11.49$, df = 1, $P < 0.01$). Because of this association between the

TABLE 4

FREQUENCY OF OCCURRENCE OF REJECTION AND ACCEPTANCE OF COWBIRD EGGS IN YELLOW WARBLER NESTS DURING THE BREEDING SEASON

Breeding season when YW nest parasitized	No. YW nests	Frequency of response % (no.) of nests where cowbird eggs were[a]		
		accepted	deserted	buried
Before peak of Yellow Warbler clutch initiation[b]	22	68 (15)[c]	23 (5)[d]	9 (2)[e]
After peak of Yellow Warbler clutch initiation	18	17 (3)[c]	28 (5)[d]	56 (5)[e]

[a] $\chi^2 = 13.06$, df = 2, $P < 0.002$—indicating that the 3 responses occurred with different frequency within season categories.

[b] Peak of clutch initiation defined as the day when the maximum number of Yellow Warbler clutches were initiated: 22 May 1975, 29 May 1976 and 26 May 1977.

[c] $\chi^2 = 10.18$, df = 2, $P < 0.002$—indicating that acceptance occurred with different frequency before vs after peak, when other responses are grouped.

[d] $\chi^2 = 0.13$, df = 1, $P > 0.05$—indicating that desertion rate was similar before and after peak.

[e] $\chi^2 = 10.61$, df = 1, $P < 0.001$—indicating that burial occurred with different frequency before vs after peak, when other responses are grouped.

number of host eggs present when the nest was parasitized and date, it is apparent that the different responses to cowbird eggs may have resulted from either nest stage or date, or a combination of both; although acceptance did occur more frequently after the peak of clutch initiation (Table 4), this is also when nests with 2 or more Yellow Warbler eggs were more frequently parasitized. Thus, it is not possible to decide which factor was more influential in determining the response. Interestingly, the only nest in which acceptance occurred when there were 0 or 1 Yellow Warbler egg(s) present was parasitized after the peak of clutch initiation.

Cowbird egg rejection by ejection.—No instances of egg ejection by the Yellow Warbler were recorded. Rothstein (1975) has shown that the Yellow Warbler beak-length-to-parasite-egg-width ratio is larger than the same ratio for some other species, suggesting that Yellow Warblers are capable of ejecting cowbird eggs. However, Rothstein (1976) also found that the Cedar Waxwing (*Bombycilla cedrorum*) has problems ejecting eggs, often incurring nest damage and/or bruising in the process. He attributed this to the small bill size of the Cedar Waxwing. Yet this species has a beak-length-to-ejected-egg-width ratio well above that of the Yellow Warbler, which has the smaller exposed culmen (9.1 mm vs 10.1 mm) of the two (Godfrey 1966). The Yellow Warbler is also smaller in body size, with a range of weight of 9.3–12.3 g (Raveling and Warner 1978) compared to the Cedar Waxwing which has a weight in the range of 30–42.5 g (Roberts

1955). If the Cedar Waxwing has problems ejecting cowbird eggs the smaller Yellow Warbler would likely have even greater difficulty in this regard.

Possibly a Yellow Warbler incapable of ejecting an intact cowbird egg might first break the egg and then remove it. However, piercing and/or breaking up an egg would likely be disadvantageous, as spilling the contents on the other eggs in the nest could make them difficult to roll during incubation (Rothstein 1975). In addition, the nest might be more vulnerable to ant infestations.

Egg rejection by burial.—Egg burial was the Yellow Warbler's most common response to a cowbird egg and occurred at 20 of 42 (48%) parasitized nests (Table 1). Burial occurred most frequently when 0 or 1 Yellow Warbler egg(s) were in the nest (Table 3). Egg burial requires a small energy expenditure on the part of the Yellow Warbler in building a new floor and increasing the sides of the nest. It also allows the bird to lay a new clutch, thus eliminating the threat of the cowbird egg hatching and a reduction in clutch-size due to the cowbird's removing a host egg. The mean clutch-size (excluding buried eggs) of Yellow Warbler nests with buried cowbird eggs (4.1 ± 0.92) was the same as at nests which were not parasitized (4.1 ± 0.55 eggs), suggesting that females were physiologically capable of producing replacement eggs to compensate for those buried. The 0.5 egg difference between the unparasitized clutch-size of mean 4.1 and the parasitized clutch-size of mean 3.6 suggests that, on average, the cowbird removes a host egg from 1 out of 2 nests it parasitizes.

The delay in nesting caused by egg burial depended upon the number of Yellow Warbler eggs that were buried along with the cowbird eggs, since these would have to be replaced in the new clutch. The mean time delay to initiation of a new clutch was 3.1 ± 1.6 days. When the cowbird egg was laid in a nest which was not complete the delay was shorter, since it could be almost entirely buried by a thick layer of lining. For each Yellow Warbler egg that was buried the delay was increased by 1 day. The energy loss from the investment in the buried eggs would also increase with each buried egg. Perhaps because of the large energy losses and extended time delays cowbird eggs were seldom buried along with more than 1 Yellow Warbler egg.

Rothstein (1975) has suggested that the Yellow Warbler's choice of nest material may be an anti-parasite adaptation. In his study, the lining of the nests was very similar to the material used in the nest frame so cowbirds may have been unable to determine when the nest was complete. The cowbird might then lay before completion, and its egg could be buried while the Yellow Warbler was finishing the nest. Mayfield (1960:156) noted that in some Kirtland's Warbler nests the cowbird eggs laid before the nest was completed were occasionally buried in the lining. The Yellow

Warbler nests in our study tended to be lined with a material distinctive from that used in the nest frame. The lining was usually a fluffy plant down, while the frame was usually coarse plant fibers. Although cowbirds may have mistaken some nests as complete when laying, other times cowbird eggs were laid when the floor of the frame was obviously incomplete. McGeen (1972) noted that the cowbird has difficulty timing its egg-laying with the nesting of the Yellow Warbler, especially when there are Song Sparrows (*Melospiza melodia*) nesting in the vicinity. Song Sparrows are a better host for the cowbird than the Yellow Warbler, and cowbird egg-laying is usually synchronized with the first nesting of the Song Sparrow, which is earlier than that of the Yellow Warbler. Synchronization of the egg-laying period by cowbirds in our study areas with that of Song Sparrows (which were common in the area) might account for the laying of cowbird eggs in unfinished Yellow Warbler nests.

The occurrence of egg burial at 5 nests where Yellow Warbler eggs were buried along with a cowbird egg indicates that egg burial was not always a result of overlap between cowbird laying and Yellow Warbler nest building. In these 5 nests, egg burial must have been a direct response to the cowbird egg.

Egg burial occurred most commonly before the peak of clutch initiation, when a delay would not place the nest greatly out of synchrony with the rest of the avian community (Table 4). An extremely late nesting Yellow Warbler would be susceptible to the disadvantages of asynchronous nesting described earlier.

Yellow Warbler nests which had a cowbird egg buried were no more susceptible to being parasitized again. Of 20 nests which had a cowbird egg buried only two were parasitized again compared to the incidence of parasitism at other nests where 25 out of 89 were parasitized ($\chi^2 = 2.87$, df $= 1$, $P > 0.10$, NS). Egg burial resulted in a mean nest success of 0.78 $\pm$ 0.21, which was not significantly different from 0.80 $\pm$ 0.16, the mean success of unparasitized nests (Table 1; Mann-Whitney U-test, U for large samples $= 0.85$, $P > 0.05$). The significantly lower nest success of acceptor nests (0.53 $\pm$ 0.34) compared to nests where cowbird eggs were buried (0.78 $\pm$ 0.21) (Mann-Whitney U-test, $U = 47$, $P < 0.05$) suggests that egg burial may be an adaptive response to cowbird parasitism.

Egg rejection by nest desertion.—Nest desertion occurred at 24% (10/42) of the parasitized nests, most commonly when 0 or 1 Yellow Warbler egg(s) were in the nest (assuming that in at least some cases, the cowbird removed a Yellow Warbler egg) (Table 2). The advantages of nest desertion were impossible to assess as the success of a second nesting attempt could not be determined without individually marked birds. Also, this estimate of desertion rate is likely conservative since deserted nests are more difficult to find. Nests deserted early involved minimal time and energy investment and the potential for successful renesting would have been high. In contrast, pairs of Yellow Warblers deserting nearly complete clutches would have incurred a delay of 6–9 days (2–4 days to build a nest and 4–5 days to lay a new clutch). The nesting season of the Yellow Warbler is sufficiently short (they are normally single brooded at this latitude) that the potential for renesting after a delay of this length is much reduced. Selection may thus favor burial over desertion early in the season because of the shorter time delay and lower energy costs. In the case of the pair which buried 1 cowbird egg but deserted after a second was laid, it may be that building a second floor and replacing the buried 3-egg clutch resulted in a delay that made desertion the best strategy.

Desertions occurred with the same frequency before and after the peak of clutch initiation. One explanation for desertion regardless of the time in the nesting season would be that in some cases the nest support structure was inadequate to allow a new floor to be built for egg burial. In fact, we observed 1 nest where the floor had been initiated over a cowbird egg, but before it was complete the nest became unstable. This nest was then deserted and a new nest was initiated less than 1 m away. Nest desertion may have also occurred late in the season as an alternative means of rejection when egg burial would have resulted in a deleterious time delay. Selection may act to favor desertion and termination of the nesting if the potential for Yellow Warbler success is low and if desertion would increase fitness in the following breeding season. High adult mortality during migration may seriously weaken evidence supporting this last hypothesis.

It is difficult to determine whether nest desertion occurred in response to a cowbird egg, human observer disturbance at nests, altered clutch-size or the discovery of the cowbird at the nest (Rothstein 1976). In this study, desertions occurred at 24% (10/42) of parasitized nests and only 3% (2/64) of unparasitized nests ($\chi^2 = 15.43$, df = 1, $P < 0.001$). Since all nests were checked in a similar fashion the majority of desertions are probably due to cowbird parasitism. Desertion at the 2 unparasitized nests occurred after a single egg had been removed each day until in 1 nest there was 1 egg left and in the other 2 eggs were left. The eggs at these nests may have been removed by either cowbirds or predators. Since there were, however, few predators which take eggs in this fashion in our study area, desertion in these cases may also have been due to cowbirds.

Cowbirds would frequently remove a host egg before laying their own so that clutch-size was not increased in parasitized nests. Yellow Warblers occasionally had clutches of 5 eggs, which were successful; the total number of eggs in a parasitized nest exceeded 5 in only 1 nest. The cowbird and 2 of the Yellow Warbler eggs in the clutch eventually hatched. Thus, an inhibition of incubation behavior by the alteration of clutch-size does not likely account for the desertion of parasitized nests.

Desertion occurred most frequently when there were no Yellow Warbler eggs in the nest. The appearance of a cowbird egg before the Yellow Warbler had initiated her own clutch, or the replacement of the first warbler egg with a cowbird egg on the day of initiation, may have been the main cause of nest desertion. Desertion may thus be an anti-parasite strategy evoked in direct response to the appearance of cowbird eggs. Alternatively, desertion may be a response to foreign objects in the nest (Rothstein 1975). Discovery of the cowbird at the nest may also have resulted in a sufficient disturbance to cause desertion in some instances. Since birds will often desert if disturbed by a predator, the presence of a cowbird might provide a similar stimulus to desert. However, Robertson and Norman (1976, 1977) showed that aggressive responses to cowbirds can reduce the incidence of parasitism, so one might expect that a fleeing response of hosts should be selected against. Also, cowbirds which harass their hosts to the extent of causing nest desertion would be selected against, since they would be lowering the number of available host nests and reducing the success of their own eggs. Thus, it seems most likely that some Yellow Warblers desert nests due to the presence of the cowbird egg per se.

In conclusion, the Yellow Warbler appears to have evolved a finely tuned anti-parasite strategy involving the rejection of cowbird eggs by either egg burial or nest desertion dependent upon the stage of the nest in which the cowbird egg is deposited and upon the timing of the nest with respect to its neighbors. This strategy reduced both the success of cowbird eggs in Yellow Warbler nests and Yellow Warbler losses due to parasitism.

SUMMARY

We recorded the responses of nesting Yellow Warblers to naturally deposited Brown-headed Cowbird eggs. The response varied, depending upon the stage of the nest when the cowbird egg was deposited, the time of the breeding season and the structure of nest support. An association between nest stage and time in the breeding season did not allow any conclusions about the relationships between either of these factors and response to the cowbird egg to be made, although both were thought to be influencing the choice of response. Acceptance of cowbird eggs resulted in significantly lower nest success for Yellow Warblers. The most frequent rejection response by the Yellow Warbler was burial of cowbird eggs. Parasitized nests in which burial occurred had success rates comparable to unparasitized nests. Egg burial was used as an anti-parasite strategy primarily when the cowbird egg was deposited early in the Yellow Warbler's laying cycle. Nest desertion was the alternative rejection response. Desertion, which released the pair from a nesting attempt in which the potential for success was low, occurred throughout the breeding season. Desertion was thought to occur when egg burial was not possible, either because of the resulting delay, or when the nest support structure would not allow burial.

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LITERATURE CITED

CLARK, K. L. AND R. J. ROBERTSON. 1979. Spatial and temporal multi-species nesting aggregations in birds as anti-parasite and anti-predator strategies. Behav. Ecol. Sociobiol. 5:359–371.

FRIEDMANN, H. 1963. Host relations of the parasitic cowbirds. Smithson. Inst. Washington, D.C.

GODFREY, W. E. 1966. The birds of Canada. Natl. Mus. Canada Bull. No. 203.

HAMILTON, W. D. 1971. Geometry for the selfish herd. J. Theoret. Biol. 31:295–311.

IMMELMANN, K. 1971. Ecological aspects of periodic reproduction. Pp. 342–489 *in* Avian biology, Vol. 1. D. S. Farner and J. R. Kings, eds. Academic Press, New York, New York.

MAYFIELD, H. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci., Bloomfield Hills, Michigan.

MCGEEN, D. S. 1972. Cowbird-host relationships. Auk 89:360–380.

RAVELING, D. G. AND D. W. WARNER. 1978. Geographic variation of Yellow Warblers killed at a TV tower. Auk 95:73–79.

ROBERTS, T. S. 1955. Manual for the identification of birds of Minnesota and neighboring states. Revised ed. Univ. Minnesota Press, Minneapolis, Minnesota.

ROBERTSON, R. J. 1973. Optimal niche space of the Red-winged Blackbird: spatial and temporal patterns of nesting activity and success. Ecology 54:1085–1093.

——— AND R. F. NORMAN. 1976. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. Condor 78:166–173.

——— AND ———. 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 55:508–518.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

———. 1976. Experiments on defences Cedar Waxwings use against cowbird parasitism. Auk 93:675–691.

SCHRANTZ, F. C. 1943. Nest life of the eastern Yellow Warbler. Auk 60:367–387.

DEPT. BIOLOGY, QUEEN'S UNIV., KINGSTON, ONTARIO K7L 3N6 CANADA. ACCEPTED 16 JULY 1980.