EXPERIMENTS ON DEFENSES CEDAR WAXWINGS USE AGAINST COWBIRD PARASITISM

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THE defenses various North American birds employ against the parasitic Brown-headed Cowbird (*Molothrus ater*) have recently been analyzed experimentally (Rothstein 1975a, 1975b). In most experiments bird nests were artificially parasitized with imitation cowbird eggs. This approach simulates natural events relevant to host defenses as such defenses are normally restricted to responses against parasitic eggs (Hamilton and Orians 1965). These experiments generate more reliable data on host defenses than observations on naturally parasitized nests (Rothstein 1975a). The experimental results were generally clear-cut. Little intraspecific variation in response to cowbird eggs occurred and species were easily designated as either "accepters" or "rejecters" (Rothstein 1975a, 1975b). Here I present a detailed analysis of experiments on the Cedar Waxwing (*Bombycilla cedrorum*), a rejecter species whose responses to cowbird parasitism are relatively complex. I also contrast the waxwing's defenses with the simpler ones of other rejecter species and discuss reasons for the differences.

MATERIALS AND METHODS

Eggs used in experiments.—Artificial eggs were cast in plaster of paris. The dimensions averaged 21.12 × 16.32 mm as compared to real cowbird eggs, which average 21.45 × 16.42 (Bent 1958). The eggs were painted with acrylic polymer paints and shellacked. I tried to duplicate the coloration and maculation of an average cowbird egg. The preparation and properties of the artificial eggs are described elsewhere in greater detail (Rothstein 1975c). Real cowbird eggs, used as controls, were collected from Chipping Sparrow (*Spizella passerina*) and Red-eyed Vireo (*Vireo olivaceus*) nests.

Experimental procedures.—The standard procedure was to add one artificial or real cowbird egg and to remove one waxwing egg during a single visit to each experimental nest. These manipulations approximate the events at naturally parasitized nests, although female cowbirds do not usually remove host eggs and lay their eggs during the same visit (Friedmann 1963). Experiments departing from the standard procedure have been performed on other North American species. Procedures such as adding one cowbird egg and removing no host eggs yield results similar to those with the standard procedure (Rothstein 1970). Experiments were initiated up to 6 h after sunrise although natural parasitism occurs around dawn (Friedmann 1963).

Study areas.—Nearly all the nests were studied in Cheboygan and Emmet Counties, Michigan, during June to August in 1968 and 1969. One nest from Grand Manan, New Brunswick, and two from Delta, Manitoba, experimented on in 1966 and 1970

respectively, are also included. Except where noted, the New Brunswick and Manitoba nests are excluded from statistical tests.

Criteria for analyzing results.—Cowbird eggs that disappeared were counted as rejected by ejection. Damaged cowbird eggs left in the nest were also counted as rejected. Intact cowbird eggs left in nests inactive on two or more consecutive nest checks occurring on different days were counted as rejected by nest desertion. Nests that ceased to be active after losing their entire contents were assumed to have undergone predation and are not considered here. A cowbird egg was considered as accepted if left undamaged in an active nest that contained only eggs for at least 5 days after the initiation of an experiment. These guidelines define the "full term criterion." Another criterion, the "first day criterion," evaluates results on day 1, the day after an experiment was initiated. Sample sizes for the two criteria are not always the same because not all nests could be visited on day 1, and some clutches hatched or underwent predation before satisfying the requirements for full-term acceptance. Unless otherwise indicated, all statistical tests refer to applications of Fisher's exact probability test (Siegel 1956).

Determination of nest stage at the time of parasitization.—Natural parasitism usually occurs during the host's laying stage (Friedmann 1963), but I parasitized any nest that contained three or more eggs and no young when found. Thus nests were parasitized over a wide range of stages. To determine whether nest stage at the time of parasitization affects response, nests were divided into two categories, stages 1 and 2. A nest was placed in stage 1 if the egg removed from it had fresh contents lacking a macroscopically detectable embryo. If the removed egg contained an embryo the nest was placed in stage 2. Stage 1 nests were parasitized during the laying period and until 2 or 3 days after laying ceased. Stages 1 and 2 are not completely separable as at least some waxwings start incubating before their clutch is complete (Crouch 1936, Putnam 1949, Nickell 1955, pers. obs.), and some eggs removed on the last day of laying could have had detectable embryos. This source of inaccuracy does not lead to any systematic biases in the statistical tests presented below.

Some nests could not be placed in stages 1 or 2. These had clutches consisting entirely of sterile eggs or eggs with dead embryos (see Rothstein 1973) and were found after laying was over. Incubation at these nests, even before they were found, may have gone on for longer than the normal period (see Holcomb 1970). Because of uncertainties about them, data on these nests are excluded from most statistical tests. These nests were put in two groups on the basis of the degree of fouling of the contents of the egg removed from each of them. Descriptions of the egg contents were recorded shortly after the experiments and before any data analysis was undertaken. In one subsample, group I, there was no embryonic development and the contents of the removed egg had a slight odor. In the other, group II, the contents had a strong odor. Groups I and II correspond to nests parasitized after little and considerable incubation, respectively.

RESULTS OF STANDARD EXPERIMENTS

As a control for the artificial cowbird eggs, real ones were placed in six stage 1 nests. Five of the six nests (83.3%) yielded rejections as compared with 23 of 26 (88.5%) stage 1 nests parasitized with artificial cowbird eggs (Table 1). As rejection rates for real and artificial cowbird eggs are so similar, results for both are combined in statistical tests.

TABLE 1
CEDAR WAXWING RESPONSES AT EXPERIMENTAL AND CONTROL NESTS,
FULL TERM CRITERION

Procedure followed	Nest stage	Rejections				Accep- tances	Total nests
		Ejec- tion	Dam- age	Deser- tion	Total		
Michigan:							
Standard, artificial cowbird egg added and one waxwing egg removed	1	6[1]	4[2]	13	23	3	26
	2	0	1	5	6	9	15
	1 + 2	6	5	18	29	12	41
Standard, but stage not determined accurately as all eggs were infertile or had dead embryos	Grp. I	0	1[1]	3	4	1	5
	Grp. II	0	0	1	1	2	3
	I + II	0	1	4	5	3	8
Standard, but real cowbird egg used	1	4	0	1	5	1	6
Control, nests visited but no egg manipulations	1	–	–	2	2	12	14
	1 or 2	–	–	0	0	2	2
	2	–	–	1	1	3	4
	1 + 2	–	–	3	3	17	20
Manitoba: Standard	2	0	0	0	0	2	2
New Brunswick: Standard	1	0	0	1	1	0	1

[1] One nest in this group was also deserted after the cowbird egg was ejected or damaged. Desertion after damage or ejection may have occurred at other nests, too. See text.
[2] The cowbird egg in one of these nests was also ejected after being damaged.

Most Cedar Waxwings are intolerant of cowbird eggs. Rejection occurred at 69.0% or 40 of the 58 experimental nests (Table 1). Response was influenced by nest stage at the time of parasitization. Rejection occurred at 6 (40.0%) of the 15 stage 2 nests in Michigan, but at 28 (87.5%) of the 32 stage 1 nests (Table 1), a significant difference ($P < 0.005$). The differential responses at stage 1 and 2 nests are paralleled by responses at group I and II nests. Rejection occurred at 4 of 5 group I nests but at only 1 of 3 group II nests (Table 1).

Because most natural parasitism occurs during the host's laying period (Friedmann 1963), it is best to consider only nests tested during stage 1 as indicative of the responses Cedar Waxwings show to natural parasitism. Data on 32 stage 1 nests indicate 87.5% of natural parasitism is rejected, but a correction is needed. As described below, 15.6% of nests visited but not given cowbird eggs were deserted. Thus, of the 32 experimental stage 1 nests, 5 or 15.6% may have been deserted for reasons unrelated

to cowbird eggs. These five desertions should be deleted from the 28 rejections, and 28–5(100)/32–5 or 85.5% is the best figure for the frequency with which waxwings reject natural parasitism.

Table 2 presents the waxwings' responses under the first day criterion. Rejection is frequently delayed as only 47.1% (16 of 34) of the stage 1 nests in Michigan resulted in rejections by day 1, whereas rejection occurred eventually at 87.5% of such nests. Results under the first day criterion show a difference in response between stage 1 and 2 nests. As compared to the 16 of 34 stage 1 nests, only 2 of the 19 stage 2 nests yielded rejections by day 1 ($P < 0.02$). Again, this difference is reflected by group I and II nests. First day rejections occurred at 2 of 3 group I nests but at none of 4 group II nests.

Is the switch from mostly rejection during stage 1 to mostly acceptance during stage 2 abrupt or gradual? To answer this question, stage 2 nests were ranked according to the size of the embryo in the egg removed from each nest. If the switch is gradual, most stage 2 rejections should have occurred at nests where the embryos were small. If the switch is sudden, rejections should have occurred randomly throughout the ranked series. The actual sequence with nests ranked from smallest to largest embryo and with A = acceptance and R = rejection is A-A-A-A-A-R-R-A-A-R-R-A-A-R-R. As rejections were not most prevalent in nests with small embryos, it is likely that the switch is abrupt, occurring about 3 days after the last egg is laid. The tendency shown in the ranking for rejections to be more prevalent in nests with large embryos is not significant ($0.05 < P < 0.1$ with a two-tailed Mann-Whitney U-test (Siegel 1956)).

THE TYPE OF REJECTION EMPLOYED AND A CONTROL FOR NEST DESERTION

All cowbird eggs damaged in Cedar Waxwing nests were severely mutilated (Fig. 1), indicating the damage was not accidentally inflicted during egg turning. I interpret damaged artificial eggs left in the nest as unsuccessful attempts to remove eggs by spiking. Presumably, such attempts would have succeeded with real cowbird eggs. When ejecting an egg, most birds do not spike it but lift it in the mandibles (Rothstein 1975a). Both damaging a cowbird egg or ejecting it provide unambiguous evidence of rejection. In both, behavior is directed only at the cowbird egg and not at all the eggs. But nest desertion is not a reliable indicator of rejection as it affects the entire clutch, and birds desert nests for a variety of reasons, including human disturbance. Desertion of naturally parasitized nests is often equated with rejection, but I am unaware of proof that any host of any parasitic bird deserts in direct response to parasitic eggs. Friedmann (1963: 34) likewise noted the absence of proof
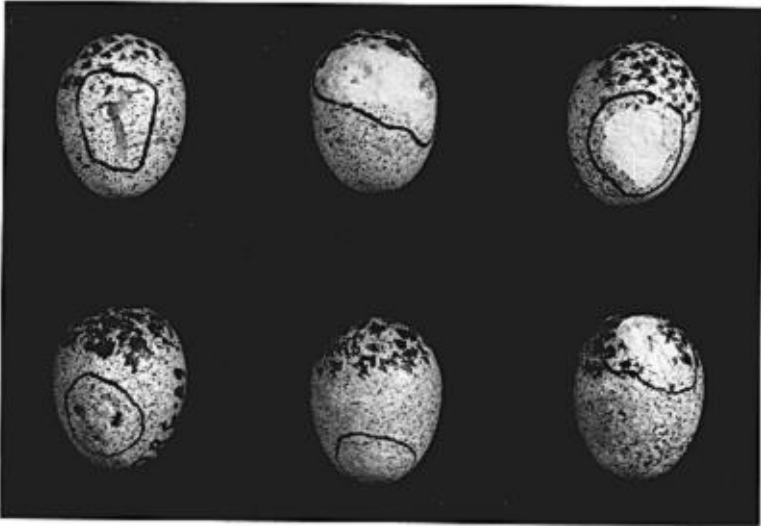
Fig. 1. Artificial cowbird eggs left in nests after being damaged by Cedar Waxwings. In each case the most severely damaged area is circled.

that parasitism leads directly to nest desertion. (See Rothstein 1975a for a more complete discussion of this problem.) As 60.0% of the rejections were by desertion it must be determined whether the desertions were caused by the cowbird eggs or by another factor.

As a control for desertion, 20 nests were visited but not parasitized. Visits to control nests were similar to those to experimental nests in both frequency and procedure. Besides the 14 desertions tabulated for experimental stage 1 nests in Michigan (Table 1), desertion subsequently occurred at one nest where the initial response was ejection. Other experimental nests may have also been abandoned, but unfortunately I often stopped checking nests after ejection occurred. Thus, a minimum of 15 of the 32 (46.8%) stage 1 nests receiving real or artificial cowbird eggs were deserted. This is significantly ($0.02 < P < 0.05$) more than the 2 of 14 (14.3%) stage 1 control nests that were deserted, and clearly the presence of a cowbird egg can cause nest desertion in the Cedar Waxwing. This is also suggested by the first day results (Table 2) for stage 1 nests. Of the 34 experimental nests, 10 (29.4%) were deserted as opposed to only 1 of the 14 (7.1%) control nests.

ADDITIONAL EVIDENCE FROM NATURALLY PARASITIZED NESTS

The Cedar Waxwing was not known to reject cowbird eggs regularly before the experiments described here. This is not surprising as it is

TABLE 2

CEDAR WAXWING RESPONSES AT EXPERIMENTAL AND CONTROL NESTS, FIRST DAY CRITERION

Procedure followed	Nest stage	Rejections				Accep- tances	Total nests
		Ejec- tion	Dam- age	Deser- tion	Total		
Michigan:							
Standard, artificial							
cowbird egg added	1	3[1]	2	9	14	13	27
and one waxwing	2	0	1	1	2	17	19
egg removed	1 + 2	3	3	10	16	30	46
Standard, but stage not determined accurately as all							
eggs were infertile	Grp. I	0	1[1]	1	2	1	3
or had dead	Grp.II	0	0	0	0	4	4
embryos	I + II	0	1	1	2	5	7
Standard, but real							
cowbird egg used	1	2	0	0	2	5	7
Control, nests visited	1	–	–	1	1	14	15
but no egg	1 or 2	–	–	0	0	2	2
manipulations	2	–	–	0	0	4	4
	1 + 2	–	–	1	1	20	21
Manitoba: Standard	2	0	0	0	0	2	2
New Brunswick:							
Standard	1	0	0	0	0	1	1

[1] One nest in this group was also deserted by day 1.

difficult to identify rejecter species by studying only natural parasitism. Cowbirds may rarely parasitize rejecters. Also, most rejections of natural parasitism may go undetected because the birds remove the cowbird egg before observers see it. Despite these difficulties rejections of natural parasitism by waxwings have been detected in the two Michigan counties where I conducted nearly all my experiments.

Table 3 lists naturally parasitized nests at which the waxwings' responses are known. These data are useful only in demonstrating rejection of natural parasitism. Quantitative interpretations of the frequency and type of rejection are not valid. Data on natural parasitism of rejecters are biased toward too many acceptances and too few ejections. These data are also biased toward too many nest desertions as hosts rejecting by desertion leave detectable evidence of parasitism, unlike those that eject. The responses are unclear at four of the 16 nests in Table 3. At my nest 4, an attempted predation could have occurred or the waxwings may have tried to eject the cowbird egg and in the process broken their own eggs. At my nest 6 and at Davis' nest 2, desertion occurred,

TABLE 3

RESPONSES OF CEDAR WAXWINGS TO NATURAL COWBIRD PARASITISM IN
NORTHERN LOWER MICHIGAN

Source of data	Contents of nest[1]	Remarks[1]	Response
Hinds 1934[2]	3 CW e + 1 CB e	Nest discovered in the morning, CB e found out of nest that afternoon.	Ejection
Davis 1942[2]	1) 2 CW e + 2 CB e	Nest found when empty, when next visited it was already deserted.	Desertion
	2) 1 CB e	Nest deserted before or right after it was found.	Desertion
Lea 1942	1) 5 CW e + 1 CB e	Deserted.	Desertion
	2) 2 CW e + 1 CB e	CB e disappeared.	Ejection
Burget 1947[2]	1) 1 CW e + 1 CB e	Nest later deserted.	Desertion
	2) 1 CW e + 1 CB e	Nest already deserted when found.	Desertion
Leich 1951[2]	3 CW e + 1 CB e	Probably accepted, but Leich's observations insufficient to be certain.	Probable acceptance
Whelan 1952[2]	4 CW y + 1 CB y	CB probably fledged (known to have survived at least until 2 or 3 days before ready to fledge).	Acceptance
Howell pers. comm.	?	Of a total of about six nests found in 1966, the one parasitized nest was the only one deserted.	Desertion
Rothstein, original observations on nests found in 1968 and 1969	1) 4 CW e + 1 CB y	CB y survived 5 to 6 days then all young (3 CW + 1 CB) died (see Table 2 in Rothstein 1976).	Acceptance
	2) 4 CW e + 1 CB e	CB e gone within 1 to 5 days after it was laid.	Ejection
	3) 4 CW e + 1 CB e	CB e gone within 1 to 5 days after it was laid.	Ejection
	4) 3 CW e + 1 CB e	Accepted at least 3 days, then nest deserted with CB e intact, one cracked CW e, and 2 CW e missing.	Attempted ejection?
	5) 4 CW e + 1 CB e	Nest deserted within 1 day after laying was completed.	Desertion
	6) 1 CB e	CB e broken and nest already deserted when found.	Desertion

[1] CW = Cedar Waxwing, CB = cowbird, e = egg, y = young. Nest contents given are those present when the nest was found if the nest was located after the clutch was completed or if the nest was visited only once. If the nest was located before the clutch was completed and visited subsequently, the contents given are those the nest eventually held.
[2] These sources are unpublished manuscripts in the files of the University of Michigan Biological Station.

but as the cowbird eggs may have been laid before the host eggs (an atypical event) these nests are better not considered with the others. At the nest Leich studied it is unknown whether sufficient nest checks were made to determine definitely if the cowbird egg was accepted. Summing up the 12 remaining nests, for which responses are reliably known, gives 6 desertions, 4 ejections, and 2 acceptances.

Some additional points on these nests are of interest. Hinds placed the cowbird egg, which was ejected (Table 3) but apparently intact, back into the nest; 3 days later he again found it missing. Lea (1942) placed a second cowbird egg into his nest number 2 after the naturally deposited one disappeared. This egg was accepted, although it did not hatch. In an unpublished 1940 manuscript (deposited at the University of Michigan Biological Station) but not in his 1942 Wilson Bulletin paper, Lea noted seeing a female cowbird approach and look into a waxwing nest. He saw no cowbird eggs in the nest, but possibly the nest was parasitized and the cowbird egg ejected before Lea saw it.

DISAPPEARANCE AND BREAKAGE OF WAXWING EGGS

One or more, but not all the waxwing eggs at once, disappeared from 19 of the 58 experimental nests in Table 1. Of these 19 cases, 17 were in Michigan, 2 in Manitoba. The disappearance of additional eggs, whose absence was not readily detected because they were replaced by newly laid eggs, almost certainly occurred (Rothstein 1970). Besides waxwing eggs that disappeared, additional ones with varying degrees of breakage were found in some experimental nests that also contained intact waxwing eggs. Broken eggs were found only in Michigan and occurred in eight nests. Two of these nests were among the 19 from which eggs disappeared.

Events at two nests are typical and worth recounting. Nest 69–473 was parasitized when it contained three eggs and was thus left with two waxwing eggs and the artificial cowbird egg. On day 1 the nest contained one heavily bruised cowbird egg glued to the nest lining by dried egg contents, one intact waxwing egg, one waxwing egg with two small slits in it, and one waxwing egg with the entire third of the egg at the pointed end missing. A waxwing was incubating. I replaced the cowbird egg with a new one. On day 2, the now abandoned nest contained only the second cowbird egg and it too was damaged. Nest 69–370 was experimentally parasitized with a real cowbird egg. Between days 2 and 4 the cowbird egg and one of the four waxwing eggs disappeared. At a few nests that I parasitized all the waxwing eggs progressively disappeared until only an undamaged cowbird egg remained in the nest. Egg disap-

pearance and breakage occurred at one of the naturally parasitized nests I studied (see nest 4, Table 3).

Disappearance and breakage of some but not all the eggs in a nest occurred with both real and artificial cowbird eggs. These phenomena occurred in 2 of 7 (28.6%) stage 1 nests in Michigan that received real cowbird eggs and in 12 of 30 (40.0%) that received artificial cowbird eggs; a difference that is not close to being statistically significant. Disappearance and breakage of some of the eggs in a nest were associated with all nest stages and types of response. Egg disappearance or breakage occurred at 8 of 20 experimental nests deserted during stages 1 and 2, so it might be suggested that some waxwings deserted in response to egg loss rather than in direct response to the cowbird egg. But seven of these nests were deserted prior to any egg disappearance or breakage. At the eighth nest one of the waxwing's eggs may have disappeared prior to desertion. Thus only one desertion might be due to egg loss. Even in the case of the eighth nest, desertion in response to the cowbird egg is more likely because at two control nests where eggs disappeared the waxwings did not desert even after losing two of their eggs.

Data on the 20 control nests confirm that missing and broken eggs are largely restricted to parasitized waxwing nests. No broken eggs were found in control nests. Eggs disappeared from two of them. As opposed to 2 of 20, egg breakage or disappearance occurred at 23 of 55 experimental nests in Michigan, a significant difference ($0.02 < P < 0.05$, $\chi^2 = 5.3$, df = 1). Because they usually remained active, control nests were visited for longer periods than experimental ones and therefore chances of noting egg disappearance and damage were greater in control nests. Thus it is clear that egg breakage and disappearance are phenomena associated with cowbird parasitism. Disappearance or breakage of some but not all the eggs in a nest is not likely to be the result of predation because predators usually take all the eggs in a nest. The probable manner in which cowbird parasitism results in missing and broken eggs is presented below.

COMPARISONS BETWEEN THE CEDAR WAXWING AND OTHER REJECTER SPECIES

The Cedar Waxwing is considerably more variable in its responses than other rejecters (Table 4). No other species showed statistically significantly different rejection rates for stage 1 and 2 nests (under either the full term or first day criteria). The waxwing had a 52.6% difference between its full term rejection rates for stage 1 and 2 nests (87.8–35.2, respectively, Table 4). Among remaining rejecters the largest comparable difference was 10.2% in the Gray Catbird (*Dumetella carolinensis*).

TABLE 4

REJECTION RATES REJECTER SPECIES SHOW TO EXPERIMENTAL COWBIRD PARASITISM[1]

	Full term			First day		
	Nest stage			Nest stage		
	1	2	1 + 2	1	2	1 + 2
Cedar Waxwing (*Bombycilla cedrorum*)						
Percent rejected	87.8	35.2	68.9	44.4	10.0	32.8
Number of nests	33	17	58[2]	36	20	63[2]
Gray Catbird (*Dumetella carolinensis*)						
Percent rejected	89.8	100	94.3	75.0	78.3	76.9
Number of nests	29	23	53[3]	28	23	52[3]
American Robin (*Turdus migratorius*)						
Percent rejected	96.5	100	97.8	60.0	50.0	57.8
Number of nests	28	17	46[3]	30	14	45[3]
Eastern Kingbird (*Tyrannus tyrannus*)						
Percent rejected	100	100	100	72.3	71.4	71.9
Number of nests	18	15	33	18	14	32
Brown Thrasher (*Toxostoma rufum*)						
Percent rejected	92.8	100	96.3	68.8	50.0	61.3
Number of nests	14	11	26[3]	16	14	31[3]
Blue Jay (*Cyanocitta cristata*)						
Percent rejected	100	100	100	77.8	60.0	75.0
Number of nests	20	4	25[3]	18	5	24[3]
Western Kingbird (*Tyrannus verticalis*)						
Percent rejected	100	100	100	100	0.0	50.0
Number of nests	1	1	2	1	1	2

[1] See Rothstein (1975a) for full details. Data grouped under the full term and first day criteria deal with the same nests. See text for reason sample sizes under the two criteria are sometimes different.

[2] Total includes nests in groups I and II (Tables 1 and 2) whose stage at the time of parasitization could not be determined.

[3] Total includes one nest whose stage at the time of parasitization is unknown.

Results for the Cedar Waxwing can be compared with those for the remaining rejecters in other ways. In its full term responses at stage 1 nests the waxwing is similar to other rejecter species (Table 4). But when the full term responses for stage 2 are considered, the waxwing shows significantly less rejection than each of the four rejecters with more than five nests (Tables 4 and 5). Under the first day criterion the waxwing shows additional differences. Even stage 1 nests had a significantly lower rejection rate than for all other rejecters combined (Table 5). Similarly at stage 2 nests the waxwing had a significantly lower first day

TABLE 5

PROBABILITIES FOR STATISTICAL COMPARISONS BETWEEN REJECTION RATES IN TABLE 4
FOR THE CEDAR WAXWING AND OTHER REJECTER SPECIES[1]

Comparisons between the waxwing and other rejecters	Gray Catbird	American Robin	Eastern Kingbird	Brown Thrasher	Blue Jay	Western Kingbird
Full term rejection rate, stage 1	NS	NS	NS	NS	NS	NS
Full term rejection rate, stage 2	< 0.01	< 0.01	< 0.01	< 0.01	NS	NS
First day rejection rate, stage 1	NS[2]	NS[2]	NS[2]	NS[2]	NS[2]	NS[2]
First day rejection rate, stage 2	< 0.01	< 0.05	< 0.01	< 0.05	NS	NS

[1] All comparisons involve two-tailed tests. NS = not significant.
[2] The waxwing has a significantly lower first day rejection rate for stage 1 when data for the other rejecter species are combined and compared against those for the waxwing in a single test ($P < 0.01$, $\chi^2 = 6.8$, df = 1). A similar test comparing the full term rejection rate for waxwing stage 1 nests against that for all other rejecters combined is not significant.

rejection rate than all four rejecters with more than five nests (Tables 4 and 5). The following patterns emerge: In its eventual response to cowbird eggs added when most naturally deposited ones are laid (stage 1), the Cedar Waxwing is like other rejecters, but it differs by accepting such cowbird eggs for longer periods before rejecting them. As for cowbird eggs added after the period when most natural parasitism occurs (stage 2), the waxwing differs both in its eventual (full term) and initial (first day) responses.

Besides these differences in speed and frequency of rejection, the waxwing's responses are unusual in other ways. Only the Cedar Waxwing showed frequent nest desertions and any rejection by damaging cowbird eggs. The waxwing employed ejection as its mode of rejection with a significantly lower frequency than every other rejecter save the Western Kingbird (*Tyrannus verticalis*), upon which only two experiments were conducted (Table 6). Disappearance or breakage of some but not all the host eggs in a nest occurred at a high frequency only in the waxwing. Compared to the 25 of 58 (43.1%) waxwing nests where egg disappearance or breakage occurred these phenomena were noted at only 5 of 190 (2.6%) nests (Table 4) of the other rejecters. The actual instances were as follows: Gray Catbird 1, American Robin (*Turdus migratorius*) 1, Brown Thrasher (*Toxostoma rufum*) 1, Blue Jay (*Cyanocitta cristata*) 2.

DISCUSSION

Except for special situations such as that described by Smith (1968), selection will always favor rejection of parasitic eggs. The most adaptive

TABLE 6

COMPARISONS BETWEEN THE TYPES OF REJECTION EMPLOYED BY REJECTER SPECIES

	Type of rejection			
Species	Ejection	Damage	Desertion	Total rejections
Cedar Waxwing	10	6	24	40
Gray Catbird	50[1]	0	0	50
American Robin	38[1]	0	7	45
Eastern Kingbird	33[1]	0	0	33
Blue Jay	23[1]	0	2	25
Brown Thrasher	25[1]	0	0	25
Western Kingbird	2	0	0	2

[1] Highly significant difference between the frequency of ejection in this species when compared to that in the Cedar Waxwing ($P < 0.001$, $\chi^2 > 20$, df = 1).

type of rejection is ejection of the parasitic egg. Ejection takes litte time and energy, has no deleterious side effects and frees a breeding attempt from parasitism. Other modes of rejection are not so adaptive (Rothstein 1975a). Thus the Cedar Waxwing's responses to cowbird parasitism are somewhat anomalous, as nest desertion and damaged cowbird eggs left in the nest were common. The waxwings' responses are unusual in other respects, too. To sum up, the Cedar Waxwing is the only rejecter whose responses to experimental parasitism have the following features: (1) frequent nest desertions, (2) any damaging of cowbird eggs, (3) frequently delayed rejection (no other rejecter had lower than 50% rejection on day 1, see Table 4), (4) a significant tendency to reject when parasitized during nest stage 1 but to accept during stage 2, and (5) frequent disappearance and breakage of host eggs after introduction of a cowbird egg. I suggest all of these peculiarities are interrelated and occur because waxwings have difficulty ejecting cowbird eggs.

Difficulty in manipulating cowbird eggs can account for the missing and broken waxwing eggs in various ways. Cowbird eggs picked up in the beak or rolled toward the nest rim could have fallen back into the nest and broken the waxwing's eggs. Waxwings may have also broken eggs when attempts to spike the cowbird egg made it strike against their own eggs. Most broken eggs would be removed, as is normally done with eggs lacking a smooth surface (Poulsen 1953), thus accounting for the missing eggs. No factor other than difficulty in ejecting cowbird eggs accounts for missing and broken waxwing eggs. Eggshell thickness in the population studied is probably slightly less than normal, but the thinning is likely to have little effect on eggshell strength (Rothstein 1972). In any event if shell thickness were the only factor, missing and broken waxwing eggs should have occurred in all nests, not just those containing cowbird eggs. It could be argued that a cowbird egg releases

rejection behavior and that waxwings do not always reject the correct egg; but such behavior would be selected against and extensive experiments (Victoria 1972, Rothstein 1975c) on other rejecter species show birds correctly distinguish between their own and parasitic eggs even when the latter outnumber their own eggs.

The waxwing is the smallest species whose rejecter status was clarified by my experiments and thus the one most likely to have trouble ejecting cowbird eggs. Roberts (1955) gives the waxwing's weight range as 30.0 to 42.5 g. By contrast, the catbird, the next smallest rejecter, has a range of 38.8 to 42.5 g. More importantly the waxwing has an unusually short bill, 9.7 to 11.7 mm versus 16.5 to 19.0 mm for the catbird, measured along the culmen (lengths from Roberts 1955). I suggested elsewhere (Rothstein 1975a) that beak length measured from the distal end of the bill along the tomia to the angle of the mouth may be more critical to a bird's ability to manipulate eggs than is culmen length. Bill lengths I measured along the tomia also show a large difference between the waxwing and the catbird, 17.6 mm versus 21.8 mm. Thus, I suggest it is no coincidence that the waxwing is the rejecter with the smallest bill and the only one in which host eggs frequently disappeared or broke.

Waxwings should be able to remove small eggs more readily than large ones. Nests experimentally parasitized with real cowbird eggs allow a test of this prediction because these eggs varied in size. The critical parameter is egg width. This is the smallest dimension and is the place where an egg will be grasped (Rothstein 1975a). The two real cowbird eggs ejected by day 1 (Table 2) had widths of 16.83 and 16.28 mm versus a range of 16.49 to 17.38 and a median of 17.35 mm for the five real cowbird eggs not ejected by day 1. This difference in egg widths, while not quite statistically significant ($P = 0.095$, Mann-Whitney U-test), is in accord with the prediction.

Additional data also strongly suggest that waxwings cannot easily eject cowbird eggs. When an egg was ejected, I searched for it beneath the nest. Usually birds carry eggs away from the nest (Rothstein 1975a), but if a species cannot easily manipulate an egg it might frequently drop it from the nest. The ejected egg was found under the nest in 2 of the 10 (20.0%) ejections by waxwings. Only 1 cowbird egg was found in the 171 (0.6%) ejections by the other six rejecter species. The difference between these two frequencies (2–8 versus 1–170) is significant at $P <$ 0.001 ($\chi^2 = 11.7$, df $= 1$).

Besides accounting for missing and broken eggs, ejection difficulties can explain the other unusual features of the Cedar Waxwing's responses to cowbird eggs. (1) Frequent nest desertion—possibly all waxwings normally try to eject cowbird eggs and rarely or never employ nest

desertion as their initial response. As discussed elsewhere, preadaptations leading to nest desertion as a direct response to a parasitic egg are unknown whereas preadaptations leading to ejection are present (Rothstein 1975a). Nest desertions may occur primarily because the birds' normal nesting behavior is upset by their unsuccessful ejection attempts. That some waxwings who deserted also tried to eject is suggested by the fact that waxwing eggs broke or disappeared at 8 of the 20 stage 1 and 2 nests that were deserted. In seven of these eight cases egg breakage or disappearance did not begin until after the birds ceased incubating. Thus some parasitized waxwings that cease incubating apparently continue to try to eject the cowbird egg. (2) Damaged cowbird eggs—I suspect waxwings initially try to lift cowbird eggs in their mandibles and spike eggs only if their initial attempts fail. Both of the ejected artificial eggs that were found were unbruised. The real cowbird egg Hinds found after it had been ejected (Table 3) was also undamaged. Other data suggest birds resort to spiking parasitic eggs only if the egg is difficult to lift in the mandibles (Rothstein 1970, 1975a). That damaged artificial eggs were left in the nest is probably an artifact of my technique. Real eggs would have been carried off. (3) Frequently delayed rejection—ejection difficulties easily account for the fact that the Cedar Waxwing shows the lowest first day rejection rate of any rejecter, even though it eventually rejects most cowbird eggs added during stage 1. (4) Differential rejection rates between nest stages 1 and 2—evidently, when they attempt to eject, waxwings may break their own eggs. Selection likely favors attempts at ejection when waxwings are parasitized during or soon after egg-laying because, on the average, the reproductive loss from accepting and hatching a cowbird egg is greater than that due to host eggs broken while trying to eject the cowbird egg. But when cowbird eggs are deposited after 2 or 3 days of incubation, there may be little advantage in rejecting them as the cowbird egg may not hatch at all, or it may hatch much later than the waxwing eggs. As the risks attendant in attempts to eject the cowbird egg still remain, the most adaptive response when parasitized during stage 2 is to leave the cowbird egg in the nest.

Some waxwings that showed acceptances of cowbird eggs probably attempted to eject, as is shown by the fact that disappearance or breakage of some but not all waxwing eggs occurred at 3 of 4 stage 1 nests and at 5 of 11 stage 2 nests tabulated as acceptances in Table 1. Quite possibly waxwings have less variation in their first response to cowbird parasitism than my results indicate. Perhaps nearly all individuals initially try to eject cowbird eggs by grasping them in their mandibles. But birds parasitized during stage 2 may rapidly cease their efforts at ejection, accounting for the high level of acceptance. Birds parasitized during stage 1 probably make

stronger and more prolonged efforts at rejection. A small number are quickly successful, resulting in first day ejections. Others are not and either eventually eject the egg or resort to spiking or nest desertion.

My interpretations of the waxwing's rejection behavior are based on the assumption that this behavior evolved in response to cowbird parasitism. This is the most reasonable assumption as rejection of foreign eggs would have no adaptive value other than in the context of brood parasitism. A related paper (Rothstein 1976) presents direct evidence that cowbird parasitism is a selective pressure on the Cedar Waxwing. Natural parasitism occurred at at least 7.5% of 334 waxwing nests located in the two Michigan counties where I conducted nearly all the experiments.

In assessing the Cedar Waxwing's antiparasite adaptations it is necessary to ask why the responses of other rejecter species are so much simpler. Apparently, selection on other rejecters has not favored differential responses to cowbird eggs during stages 1 and 2 because these species can eject without endangering their own eggs. Thus selection on other rejecters would not favor acceptance of cowbird eggs during stage 2, although two other alternatives are possible: (1) Selection may continue to favor rejection of cowbird eggs during stage 2. The incubation periods of some rejecters, such as kingbirds and the Blue Jay, are so long relative to that of the cowbird (13 or 14 to 17 days versus 11 to 12 days), that cowbird eggs laid after several days of host incubation might still hatch before the host's eggs. In these species, selection would favor retention of strong rejection behavior for at least several days after the bird completed its clutch. In addition, selection may favor rejection throughout the incubation period because a cowbird egg may lead to a greater risk of nest predation. The eggs of most birds are presumably adapted to minimize the risk of predation in the situations in which the species places its nest (Lack 1958), and differently colored eggs, such as those of the parasite, may enhance a predator's chances of locating a nest. Harrison (1968) presented a somewhat similar argument by suggesting that increased rates of nest predation caused by nonmimetic cuckoo eggs may select for egg mimicry by the cuckoo even if a host accepts nonmimetic eggs. (2) By contrast, as incubation proceeds rejection may become nearly neutral in adaptive value and selection may not maintain a high intensity of rejection. This may explain why some rejecters, other than the waxwing, show slight increases in tolerance toward certain foreign eggs as their nesting cycle progresses (Rothstein 1970).

SUMMARY

Single real or artificial Brown-headed Cowbird eggs were experimentally added to 58 Cedar Waxwing nests. Rejection occurred at 69.0% of the nests. Nests experimentally parasitized during the laying period or shortly thereafter had a significantly higher rejection rate than nests parasitized later in the cycle (87.5% versus 40.0%). Waxwings rejected by nest desertion (60.0%), ejection (25.0%), or by damaging cowbird eggs (15.0%). Control nests showed that most nest desertions were in response to the cowbird egg. Twelve naturally parasitized nests also demonstrate that rejection is the usual response. Some but not all waxwing eggs frequently disappeared or were found broken in experimentally or naturally parasitized nests. Egg breakage and disappearance were significantly rarer at control nests.

Among seven species known to reject experimental cowbird parasitism only the Cedar Waxwing shows the following: (1) frequent nest desertions, (2) any rejection by damaging cowbird eggs, (3) a higher rejection rate early in the nesting cycle than later in the cycle, (4) frequently delayed rejection throughout the nesting cycle, and (5) frequent disappearance and breakage of host eggs.

The likely reason for the waxwing's nest desertion and egg damage and for the other peculiarities of its responses is that it cannot easily eject cowbird eggs. Not only is the Cedar Waxwing the smallest rejecter species but it also has a disproportionately small beak. Waxwings trying to eject cowbird eggs may have accidentally broken and then removed some of their own eggs. Thus, waxwings trying to remove cowbird eggs apparently endanger their own eggs. If parasitized early in the cycle, when the cowbird egg is likely to hatch, selection probably favors rejection as the reproductive loss from waxwing eggs damaged during ejection attempts is less than that from the nestling cowbird. But selection may favor acceptance of cowbird eggs laid later in the cycle as such eggs will not hatch and attempting to eject them results in the loss of some of the waxwing's own eggs.

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