COWBIRD PARASITISM OF THE CEDAR WAXWING AND ITS EVOLUTIONARY IMPLICATIONS

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INVESTIGATIONS of defenses North American bird species express against Brown-headed Cowbird (*Molothrus ater*) parasitism demonstrated that each species can be designated as either a rejecter or an accepter (Rothstein 1975a, 1975b). In six rejecter species, 88 to 100% (mean = 96.0%) of the individuals reject artificial or real cowbird eggs experimentally placed in their nests. By contrast, 12 accepter species tend to show close to 100% acceptance, as zero to 42% (mean = 13.5%) of the individuals reject. No species showed between 43 and 87% rejection (Rothstein 1975b). The Cedar Waxwing (*Bombycilla cedrorum*) is a rejecter species (Rothstein 1976), but its responses to cowbird eggs are relatively complex. Other rejecter species showed close to 100% rejection throughout their egg laying and incubation periods. But in the waxwing, rejection occurred significantly more frequently if a cowbird egg was added during egg-laying and the first 3 days of the incubation period than if it was added later during incubation. Most natural parasitism occurs during a host's laying period (Friedmann 1929), and the experiments therefore demonstrated that waxwings are most likely to reject cowbird eggs during the period when natural parasitism is most likely to occur.

In interpreting the significance of the waxwing's behavior toward cowbird eggs I assumed that such behavior evolved in response to cowbird parasitism. Here I present data showing that cowbird parasitism is indeed a selective pressure on the waxwing and that it is meaningful to interpret responses to experimental parasitism as behavior evolved in defense against natural parasitism. The selective value of a host defense is determined by the frequency with which the host is parasitized and by the amount of reproductive loss caused by the parasitism when it occurs at a nest (see Rothstein 1975b for a general model). The following sections discuss the frequency of parasitism and the probable degree of reproductive loss caused by the parasitism. Lastly, I discuss the implications that parasitism of the waxwing has for considerations of the "strategies" cowbirds may use in choosing host species.

FREQUENCY OF COWBIRD PARASITISM

Even if cowbird parasitism of the Cedar Waxwing occurred only in the past, waxwings might still express some rejection of cowbird eggs experimentally placed in their nests. A species that evolves rejection of parasitic eggs may retain this behavior even after it ceases to be a host because in the absence of parasitism its rejection may be nearly neutral in selective value. This near neutrality might occur because rejection behavior does not seem to involve changes in the other behavior patterns of a species or in any aspects of the species' morphology or physiology. Therefore the evolution of rejection behavior appears to occur at no cost to other adaptations. More importantly, if a rejecter species were no longer parasitized its rejection behavior could be manifested only under experimental conditions. Thus any deleterious side effects associated with the act of rejection would not occur naturally and therefore could not be selected against. Obviously the past interactions between the cowbird and the Cedar Waxwing are impossible to ascertain. Unfortunately even the level of the present interaction is difficult to study because of the waxwing's rejection behavior. Data on frequency of observed parasitism give only a minimum figure for the actual rate of parasitism because many cowbird eggs may be ejected by waxwings before seen by investigators. Despite this problem, data on natural parasitism are valuable so long as their inherent difficulties and biases are known.

Friedmann (1963, 1966) regarded Cedar Waxwings as infrequent hosts, having found records of only 22 cases of parasitism. The total number of nests from which Friedmann's figure of 22 was drawn is unknown so the frequency with which parasitized nests are observed cannot be determined. (Even this figure would not equal the actual frequency of parasitism.) Data on frequency exist for specific regions. Terrill (1961) found cowbird eggs in four of 329 nests in southern Quebec. Putnam (1949) noted no parasitism in 65 nests in northern Ohio.

Nests I subjected to experimental cowbird parasitism also provided data on natural parasitism. The presence of experimental cowbird eggs should not have altered the likelihood of the nests being naturally parasitized, because cowbirds choose the nests they parasitize before host eggs are present (Hann 1941) and apparently ignore the presence of cowbird eggs when laying their own egg (Mayfield 1965). Nearly all (96%) the nests I experimented on were located in Cheboygan and Emmet Counties, Michigan (Rothstein 1976a), and my tabulations of natural parasitism are restricted to these two counties. Besides nests I studied, I have accumulated data on nests found by others working in Cheboygan and Emmet Counties; nearly all these data are from unpublished manuscripts filed at the University of Michigan Biological Station. To avoid biases I have included only studies that gave data for all the nests found. I have excluded 44 nests never seen to contain more than two waxwing eggs and that were visited only once. The clutches of such nests were

TABLE 1

FREQUENCY OF OBSERVED COWBIRD PARASITISM OF THE CEDAR WAXWING IN NORTHERN LOWER MICHIGAN

Source of data	Years nests were found	Nests lacking observed parasitism	Nests with observed parasitism	Total nests	Percent with observed parasitism
S. I. Rothstein	1968, 1969	102	6	108	5.6
F. L. Hinds[1]	1933, 1934, 1935, 1936, 1937, 1938	96	7	103	6.8
17 other workers[1]	1924, and 14 years between 1939–67	111	12	123	9.8
Total of 3 groups		309	25	334	7.5

[1] Data from unpublished manuscripts in the University of Michigan Biological Station files, except for those on 18 nests received from J. Howell (pers. comm.)

probably not complete, and they could have received a cowbird egg after the single nest visit.

Table 1 gives frequencies of observed parasitism. Three groups of data are differentiated, based on nests found in my field studies, found by Hinds or by 17 other workers. Cowbird eggs or young were seen in 25 or 7.5% of 334 nests. Probably few or none of these 25 parasitized nests were included by Friedmann (1966), so they can be added to the 22 instances he was aware of to give a total of nearly 50 known cases of parasitism.

Obviously the data in Table 1 have limited value. What is needed is to approximate the actual frequency of parasitism. Such an approximation is possible if samples are large and observers report responses of all waxwings known to be parasitized. Data on experimental nests demonstrated that during egg-laying and shortly thereafter waxwings show seven rejections for each acceptance. There were 28 rejections vs. four acceptances (see stage 1 nests in Table 1 in Rothstein 1976). Because every acceptance of natural parasitism within a sample should be seen, the number of acceptances, Na, can be extrapolated to give the total number of nests parasitized via use of the expression $7\ Na + Na$. Acceptance occurred at one of the six naturally parasitized nests that I studied. Thus, $Na = 1$ and since $7\ Na + Na = 8$, there were two additional parasitized nests that I did not see for a total of eight cases among 108 nests or a frequency of parasitism of 7.3%. This demonstrates a feasible method, but possibly these specific results, based solely on my own sample, are too low because of sampling error in the frequency with which I found naturally deposited cowbird eggs that were accepted. Sampling error is possible because 7.3% is lower than the combined

8.4% frequency with which Hinds and the 17 other workers simply observed parasitized nests (Table 1). This extrapolation technique will prove more accurate as additional parasitized nests are found and to make its application feasible, it is hoped that future workers on any rejecter species (see Rothstein 1975a) will report the number of all nests found and the response at every nest known to be parasitized. Extrapolation is impossible for the nests found by Hinds and the 17 other workers (Table 1) because in many cases they did not indicate whether the cowbird parasitism was accepted or rejected.

Another approximation to the actual rate of parasitism is possible. Investigators are least likely to see natural cowbird parasitism of rejecter species if nests are found after the host's laying period. As nearly all cowbird eggs will have been ejected prior to the nests' discoveries, in rejecters consideration of only nests found during laying is more desirable than consideration of all nests. I found 38 of my waxwing nests during egg-laying. Of these 38, three or 7.9%, were naturally parasitized; but this is still a minimum frequency for the rate of actual parasitism. This kind of approximation is impossible for nests in Table 1 reported by others because almost none of the individuals indicated whether nests were found during laying.

CONSEQUENCES OF NATURAL COWBIRD PARASITISM OF THE CEDAR WAXWING

Even if only 7 to 8% of the nests are parasitized, the cowbird is potentially a strong selective force on the Cedar Waxwing. But how detrimental is the parasitism if the cowbird egg is accepted? Few observations bear on this question, but breeding parameters of the cowbird and waxwing indicate the deleterious effects of accepting cowbird eggs are great indeed. In intrabrood competition, cowbirds have both an initial size advantage at hatching as well as the advantage of hatching first. Neonatal cowbirds are larger than neonatal waxwings as indicated by egg sizes. Cowbird eggs average 3.1 cc in volume as opposed to 2.8 cc for the waxwing, or 10.7% larger using egg dimensions in Bent (1950, 1958) and a standard formula for egg volume in Romanoff and Romanoff (1949). Cowbird eggs require 11 to 12 days of incubation (Nice 1953) whereas waxwing eggs require 12.5 days (Putnam 1949). Quantification of the hatching advantage is complicated because waxwings begin incubating before their clutch of three to five is completed (Crouch 1936, Putnam 1949, Nickell 1955, pers. obs.). But cowbird eggs laid during a waxwing's laying period will always hatch before at least some of the host eggs. Available data demonstrate a range in the disparities between ages of cowbirds and waxwings in the same nest. Nickell (1955) found

TABLE 2

WEIGHTS (g) OF NESTLING CEDAR WAXWINGS AND A COWBIRD IN A NATURALLY PARASITIZED NEST

Date	Time	Cowbird	Cedar Waxwing-1	Cedar Waxwing-2	Cedar Waxwing-3	Cedar Waxwing-4
25 July	1705	Nestling, weight not taken[1]	Egg	Egg	Egg	Egg
26 July	0922	5.6	2.0	Egg	Egg	Egg
27 July	1105	9.6	3.2	2.4	Egg	Hatched, but dead in nest[2]
28 July	1603	13.5	Weight not taken	Weight not taken	Hatched, weight not taken	–
29 July	1640	13.8	6.0	6.3	2.8	–
30 July	1644	13.2	8.8	8.3	3.2	–
31 July	1639	10.3[3]	Disappeared	5.9[3]	2.8[3]	–

[1] Appearance of nestling indicated it hatched on 25 or 24 July.

[2] The dead nestling was removed by the investigator.

[3] These young were found dead on this visit. The cowbird was on the ground beneath the nest, waxwings 2 and 3 were in the nest.

a nest with two cowbirds and two waxwings and estimated that one cowbird was 6 to 7 days older than the waxwings, the other 1 to 2 days younger. I studied one waxwing nest in which a cowbird egg hatched. The cowbird ranged from about 1 day older than the oldest waxwing to about 3 days older than the youngest one (Table 2).

Even in the absence of a hatching or size advantage, cowbirds would usually outcompete waxwing nestlings. The latter fledge after 15.5 to 15.9 days (Lea 1942, Putnam 1949) whereas cowbirds require only 8.7 days (Norris 1947). At early ages, general behavior is presumably more highly developed in cowbirds than in waxwings.

Because of the advantages it would have from its early hatching, its large size and its rapid development, a nestling cowbird must often cause the death or reduce the viability of at least some of the waxwing's young. The two waxwing young seen by Nickell (1955) in a parasitized nest is a low number, as this species has a mean clutch size of 4.3 (based on data in Putnam 1949). Possibly one or more waxwing nestlings died and were removed before Nickell inspected the nest. Probable reproductive loss attributable to a cowbird nestling occurred in the only parasitized nest I studied at which acceptance occurred. The cowbird was consistently heavier than the waxwings until the time of the unexplained death of the entire brood (Table 2). The daily weight gains for waxwing nestlings 1, 2, and 3 were much below normal. Waxwing nestlings gain about 3.1 g per day for the first 10 days (Putnam 1949: 170). Conditions for all nestlings apparently began to deteriorate after 28 July; but, as the cowbird showed good weight gains until then, it is likely that feeding conditions were initially good. Therefore the low weight gain (1.2 g) waxwing 1 showed from 26 to 27 July was probably due to competition with the cowbird. Furthermore the death of waxwing 4 might not have occurred if the nest had not contained a cowbird nestling much larger than the waxwings.

Cowbirds hatching in waxwing nests may occasionally fail to fledge because waxwings feed their young on a largely frugivorous diet after the young are about 3 days old (Putnam 1949), and cowbirds are probably adapted to develop on insects, the more usual passerine nestling food. Young (1963) saw single nestling cowbirds in three waxwing nests. In each case the cowbird died but some host young fledged. Even if they survived for only the first 3 days when they were fed insects, cowbirds would probably cause some reduction in the waxwing's reproductive output and cases are known in which cowbirds have almost certainly fledged successfully from waxwing nests (Friedmann 1963, Table 3 in Rothstein 1976a).

If a cowbird nestling is present, the waxwing's frugivorous diet may indirectly cause the death of its own young. The cowbird may continue to beg even after it has been given large quantities of fruit because fruit does not provide adequate nourishment (see Morton 1973: 18–19). In response to a cowbird's continuous begging, adult waxwings may provide it with most of the food they bring, the end result being that all the nestlings starve. This may have happened at the nest described in Table 2 as the nest contained what appeared to be mashed blue-colored berries. This material could have been food that passed through the cowbird with little digestion. Also, it may be no coincidence that the cowbird showed good weight gains for the first 3 days (until 28 July) but not thereafter and that it is after the third day that waxwings usually begin to feed their young on fruit.

REPRODUCTIVE STRATEGY OF THE COWBIRD

Cowbird eggs laid in Cedar Waxwing nests have little chance of success. Close to 90% are rejected (Rothstein 1976a); some of the few accepted may fail because of the waxwing's fruit feeding. Why then does the cowbird parasitize such an obviously poor host? This question would have less evolutionary importance if the waxwing were a rare species. Selective pressures against cowbirds parasitizing a rare species that is a poor host are low, as such parasitization, unless done by a few host-specific female cowbirds, represents only a small proportion of each cowbird's total reproductive effort. But the Cedar Waxwing is the most abundant bird in Cheboygan and Emmet Counties (Nelson 1956), and especially so in the nonforested habitats used by the cowbird. Even if only 7 to 8% is taken as the incidence of parasitism on waxwings (it is probably higher), a significant proportion of the cowbird's reproductive effort is wasted.

This problem can be explored further by comparison with the Chipping Sparrow (*Spizella passerina*), which is a good host. It accepts cowbird eggs (Rothstein 1975a) and provides suitable care for cowbird nestlings (pers. obs.; Friedmann 1963: 162–163). The Chipping Sparrow was the second most plentiful breeding bird in my study areas. I searched for nests of all species and, in 1968 and 1969, found 118 waxwing and 83 Chipping Sparrow nests; 35 cowbird eggs were distributed among 30 or 36.2% of the sparrow nests. This is opposed to the minimum of eight waxwing nests that were probably parasitized. Thus, cowbirds wasted at least one egg on Cedar Waxwings for each 4.4 eggs placed advantageously in Chipping Sparrow nests. Maladaptive host choices are not limited to the Cedar Waxwing. In 1974 and 1975 I detected 3 cases of parasitism among 34 Northern Oriole (*Icterus galbula*) nests studied near Shandon, California. Experiments on 18 oriole nests in the same area showed total rejection of cowbird eggs (Rothstein 1977), and no accepter species in the area showed as high a rate of parasitism as did the oriole. In a similar vein, Scott (1976) found that another rejecter species, the Gray Catbird (*Dumetella carolinensis*) experienced at least a 44% incidence of parasitism among 16 nests near London, Ontario. By repeatedly visiting catbird nests around dawn, the time when cowbirds usually lay, Scott was able to see many cowbird eggs before catbirds ejected them. By contrast, Nickell (1958) and Terrill (1961), who also worked in areas where cowbirds were plentiful but who did not systematically check nests at dawn, saw cowbird eggs in only 0.3% and 0.6% of the approximately 3000 and 163 nests, respectively, that they studied.

It could be argued that parasitism of rejecters is actually adaptive. Conceivably the energetic cost of laying an egg is so small for a cowbird that selection favors parasitizing a rejecter nest once it is found because even the slight chance of success is worth the minimal cost of forming the egg; but this hypothesis seems most unlikely. Egg production is in fact costly in energetic terms (Payne 1973). The explanation of why cowbirds parasitize rejecters must be sought in the context of the ways in which a maladaptive phenomenon could occur.

That some of the cowbird's eggs are placed in highly unsuitable nests cannot be explained by suggesting that the cowbird can afford to waste eggs because it, like most parasites, has a high fecundity. Payne (1965) found that cowbirds in the region I worked in do not lay an excessive number of eggs; but more importantly natural selection, regardless of fecundity, always favors an optimal reproductive strategy. Clearly the cowbird's reproductive strategy is not optimal. Eggs are wasted because they are laid in nests in which they have almost no chance of success. The apparently simple adaptation of not parasitizing rejecter species would allow the cowbird to optimize its reproduction. Evidently, though, the genetic determinants needed for an optimal strategy have not yet appeared and have thus not been subjected to selection, or the genetic determinants of an optimal strategy would be so complex that such a strategy is not feasible. I believe that the cowbird's inefficient system of host choice exists largely because the suitable genetic determinants for complete optimality are simply not achievable.

The cowbird's probable status as a comparatively recently evolved parasite (Friedmann 1963) cannot totally explain what appears to be its poor system of host choice. A related species, the Giant Cowbird (*Scaphidura oryzivora*), has evolved some remarkably intricate adaptations for parasitism (Smith 1968); but the large size of the Giant Cowbird limits suitable hosts to the few passerines that are similarly sized, whereas the smaller Brown-headed Cowbird can parasitize many species. Therefore adaptations related to host choice by the Brown-headed Cowbird must deal with numerous species, and I suggest that North American rejecter species are such a diverse group that it may be impossible for selection to program cowbirds so that they innately avoid parasitizing rejecters but still parasitize all suitable hosts. The current optimum strategy possible for the cowbird may be to parasitize all nests found, as at present most North American species are accepters (Rothstein 1975a). The reproductive loss occurring through the parasitization of rejecter species may be less than what would occur if cowbirds innately avoided all species with the features of the rejecters because this latter system might result in the avoidance of many suitable hosts whose appearance or other features are similar to those of some rejecters. Thus the cowbird appears to be confronted with the evolutionary choice of being a generalist or a specialist and, given the current preponderance of accepter species, the former is more adaptive. This model infers that the Brown-headed Cowbird practices the most adaptive system of host choice possible within the overall limitations of its innate behavioral capabilities, although such a system is not the best one humans could conceive. As more North American species evolve into rejecters the cowbird's strategy is likely to change, as it may become feasible for selection to develop a mechanism whereby the few hosts that remain suitable are chosen innately. Alternatively, as more accepter species become rejecters, the cowbird may evolve egg mimicry and thereby successfully parasitize rejecter species.

Parasitization of rejecter species could be interpreted as due totally to an evolutionary lag rather than to the factors presented above. A species such as the Cedar Waxwing may have only recently evolved into a rejecter and the cowbird may have not yet developed a suitable evolutionary response—namely avoidance of the species. But while cowbirds may have easily evolved innate avoidance of the first few hosts that evolved into rejecters, it seems that as more and more rejecter species appeared the cowbird's system of innate host choice became overloaded and avoidance of new rejecters became difficult or impossible to evolve. Therefore I suggest that an evolutionary lag cannot explain parasitization of rejecters.

Additional features can be added to the model of cowbird reproductive strategy I have proposed. While cowbirds may have few or no innate host preferences they could develop preferences through learning. Cowbirds make repeated visits to parasitized nests (Mayfield 1961). During many visits cowbirds remove host eggs, but the visits may also have the purpose of informing the female cowbird as to the success her offspring is having with a particular species. Because species show little intraspecific variation in their responses to cowbird eggs (Rothstein 1975a, 1975b), a naive female cowbird would only need to parasitize a small number of nests of a species to learn its suitability as a host. This hypothesis accounts for the cowbird's proprietory interest in parasitized nests as a functional trait with adaptive value, not only as the result of a vestigial nesting drive as Mayfield (1961) suggested.

Possibly cowbirds innately prefer a small number of highly suitable host species, such as the Song Sparrow (*Melospiza melodia*) and Red-eyed Vireo (*Vireo olivaceus*) and innately avoid a small number of totally unsuitable ones, such as the Mourning Dove (*Zenaida macroura*) and the cuckoos (*Coccyzus* spp.), but still exhibit no strong preferences among remaining small and moderate sized birds. Alternatively, selection may program cowbirds genetically so that they prefer to parasitize species having certain general features shown by many good hosts but by some poor ones as well. Egg size, for example, is an important factor relating to host quality, and King (1973) found it is the primary determinant captive female cowbirds use in choosing nests in which they lay eggs. It is also possible that female cowbirds, through learning, develop weak preferences for the species that reared them but have no preferences among other species.

Lastly the anomalies of cowbird host choice may be partly explained by physiological constraints on egg-laying. Most cowbird eggs are laid in clutches of two to seven eggs (Nice 1949, Payne 1965, McGeen and McGeen 1968). Payne noted a mean of 3.1, although single eggs are occasionally laid. Because cowbirds choose host nests several days in advance (Hann 1941), laying in clutches requires them to schedule a number of host nests ready for parasitization on consecutive days. This would not seem to be an easy task, especially if only good hosts are chosen. I suggest that laying single eggs at irregular intervals in response to each host nest that becomes ready for parasitization would be more efficient, but cannot easily evolve because of certain physiological restraints forcing cowbirds to lay eggs in series. It may be that cowbirds employ adaptive choices (possibly by imprinting on their foster parents) in placing the first one or two eggs of a clutch but end up dispersing the remaining eggs among a diversity of hosts, some of which are unsuitable like the waxwing. Physiological restraints forcing cowbirds to lay in clutches could also result in the excessive number of nests known to be multiply parasitized (see Preston 1948, Mayfield 1965) because cowbirds may often lay the later eggs of a clutch in the same nest that received the first egg and stimulated the onset of laying. This speculation agrees with Preston's (1948) interpretation of the distribution of numbers of cowbird eggs in host nests because his analysis suggested that cowbirds distribute their eggs among a selected group of nests (but see Mayfield (1965) for an alternative interpretation of the distribution of cowbird eggs).

An alternative to the models of cowbird host choice presented above would be for cowbirds to imprint on the host species that reared them and to parasitize no other species. Although there is no experimental proof (see Lack 1963), host imprinting is believed to occur in the Common Cuckoo (*Cuculus canorus*). Host imprinting by the Brown-headed Cowbird is highly unlikely because most female cowbirds do not appear to be host specific (Friedmann 1963; McGeen and McGeen 1968). Most cases supporting host specificity may be based on unusual habitat situations where most of the available nests were of a single species. Furthermore, if cowbirds did imprint on the host that reared them it is difficult to see how there could be enough cowbirds raised by such a poor host as the waxwing to account for the minimum rate of 7.5% parasitism on this host. (The six parasitized nests I found were sufficiently dispersed to indicate that they were victimized by at least five individuals.)

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SUMMARY

Experiments showed that most Cedar Waxwings reject cowbird eggs placed in their nest during that part of the nesting cycle when cowbirds typically parasitize nests. It is reasonable to interpret the waxwing's rejection behavior as an antiparasite adaptation that evolved in response to brood parasitism because evidence presented here shows that cowbird parasitism is a selective pressure on the Cedar Waxwing. Natural parasitism was detected at 7.5% of 334 nests. Parasitism is probably greater than 7.5%, as many cowbird eggs may be ejected before being seen. If accepted, a cowbird egg is likely to reduce the waxwing's reproductive output. Cowbirds hatch sooner, are larger at hatching, and develop more quickly than waxwings and hence would normally outcompete the latter.

Most cowbird eggs laid in waxwing nests are rejected and others may fail because of the waxwing's frugivorous diet. Even if only 7.5% of the waxwing nests are parasitized, a considerable proportion of the cowbird's reproductive effort is wasted. Despite this inefficiency selection may still have produced the most adaptive breeding strategy possible within the confines of the cowbird's innate abilities. Several models are presented to explain the ways in which cowbirds choose host species. Each model accounts for the fact that the cowbird's breeding strategy is not optimal.

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