

AN EXPERIMENTAL AND TELEONOMIC INVESTIGATION OF AVIAN BROOD PARASITISM

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The term "teleonomy" has been suggested by Williams (1966:258) to describe the scientific study of adaptations. Williams indicated that relatively few evolutionary studies deal primarily with teleonomy despite the fact that adaptation is the most basic feature of evolution and of all biology. Avian brood parasitism, the phenomenon in which certain birds, the parasites, deposit their eggs in the nests of other birds, their hosts, is especially well suited to teleonomic studies since it provides a system in which the presence or absence of relatively obvious adaptations can be examined in two interacting genetic lineages. Parasitism is typically detrimental to the host's reproductive efforts and selection favors defenses that reduce the impact of the parasite. These host defenses are in turn damaging to the parasite's reproductive efforts and selection favors counter-adaptations by the parasite.

Adaptations for and against brood parasitism have relatively high selective values. In other forms of parasitism, selection favors a benign effect (Croll 1966:8) because an individual parasite is dependent upon its host for its immediate survival and continuing reproductive output. However, brood parasites depend on their hosts only for their immediate reproductive output and the maximum possible harm to the host (zero reproductive output for the host) usually increases the individual parasite's reproductive output. In the absence of host young, a parasite's offspring is assured a maximum amount of food. To suggest that selection adjusts brood parasitism so that it inflicts as little harm to the host as possible necessitates strong teleological or group selection processes because when a brood parasite inflicts maximum harm to the host, any detriment to the parasite, such as scarcity of a host species, occurs in future breeding seasons and is dissipated over all members of the parasitic population that utilize the host species. In many instances brood parasitism is maximally harmful. Some cuckoo and honeyguide nestlings are known to kill all of the host's own young (Friedmann 1955, 1968). Cowbird (*Molothrus*) nestlings often

cause the death of all of the host's own young through competition for food (Friedmann 1963). In certain cases, brood parasites seem to have extirpated or caused declines of local host populations (Schiermann *in* Southern 1954:221, Bond *in* Friedmann 1971:250, Mayfield 1961a). Thus, the adaptive value of host defenses is clearly very great.

Adaptations for and against brood parasitism usually occur when eggs are in the nest. Host defenses occurring at other stages of the nesting cycle would seem to be evolved with greater difficulty. Avoiding parasitism would be the best defense, but a mechanism for achieving it is not easily available. Refusing to feed the parasitic nestlings would remove some of the deleterious effects of being parasitized, but as Hamilton and Orians (1965) pointed out, the adaptive value of a positive response to nestlings begging for food is apparently so great that host adaptations based on insufficient care of the parasitic nestlings are largely precluded. Lack's (1968:327) listing of parasites whose nestlings mimic the host's young suggests that some hosts have evolved adaptations which operate during the nestling stage. But other selective pressures also act on parasitic nestlings (e.g., to make them cryptic) and these may sometimes be responsible for parasitic nestling mimicry.

The most common host adaptation is believed to be the rejection of foreign eggs. The most common counter-adaptation by parasites seems to be mimicry of the host's eggs. Although egg-related adaptations have received much discussion (Baker 1942, Southern 1954, Friedmann 1964, 1968, Payne 1967, Smith 1968, Rothstein 1971, and others), large-scale experimental studies of host adaptations are lacking. Especially critical is the scarcity of conclusive evidence for the basic assumption that some hosts reject foreign eggs. The experiments of Swynnerton (1916, 1918) and Rensch (1924, 1925) were among the first to demonstrate rejection but were too few to allow quantitative analyses. The present study examines adaptations in the actual and potential hosts of the Brown-headed Cowbird (*Molothrus ater*), the only brood parasite

widespread in North America. My intent is to determine whether any generalizations can be drawn regarding the nature and origin of these adaptations and possibly of adaptations in general. This paper reports the results of experiments on 640 nests of 43 species. Mayfield (1965) conducted the only previous teleonomic study of cowbird hosts but analyzed only one factor relevant to the evolution of host defenses.

ADVANTAGES OF AN EXPERIMENTAL APPROACH

My experiments imitated natural cowbird parasitism by placing artificial and, occasionally, real cowbird eggs into bird nests. Others (Friedmann 1929, 1963, Howell 1942, Nice 1941, 1944, Nuttall *in* Chamberlain 1891, Berger 1951, Nickell 1958, Wilson *in* Brewer 1840:158, Lea 1942, Holcomb 1968, Potter 1939) have performed similar egg manipulations on North American birds, but in each case only one to several experiments were done and the total number of nests studied by all experimenters probably did not exceed 25–50. In studying host responses to cowbird eggs, experiments have four critical advantages over observation of naturally parasitized nests. (1) In the study of naturally parasitized nests, vital data remain unknown if the hosts eject a cowbird egg before the observer has seen the egg, and if the hosts have deserted due to parasitism. (Abandoned nests are less likely to be found than are active nests.) Observations of natural parasitism may inflate the apparent frequency of acceptance and in this study, responses to naturally deposited cowbird eggs are not incorporated into formal analyses. (2) All nests found, not only those naturally parasitized, can be utilized in cowbird research. (3) The responses of species whose nests are rarely or never found to contain cowbird eggs can be determined. It is important to determine if a species is rarely parasitized or if its members remove cowbird eggs so rapidly that observers rarely see them. Research with artificial cowbird parasitism can thus yield insights to frequencies of natural parasitism. (4) By varying the experimental design, many factors thought to be important to a species' responses can be investigated.

MATERIALS AND METHODS

The artificial cowbird eggs used in the experiments are similar in size and pattern to typical real cowbird eggs (fig. 1). The latter average 21.45×16.42 mm in length and breadth (Bent 1958) whereas the former average 21.12×16.32 mm. The eggs were

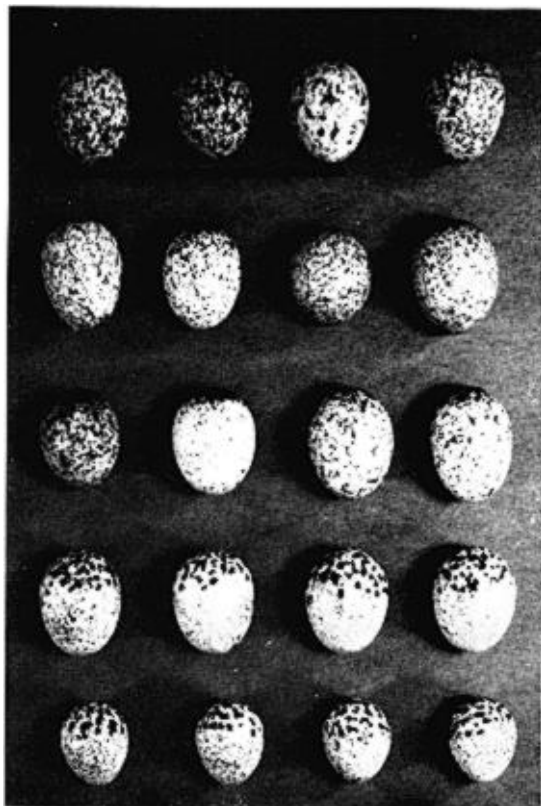


FIGURE 1. Brown-headed Cowbird eggs and two sizes of artificial eggs painted with the standard cowbird coloration and pattern. The three top rows are real eggs, the two bottom rows are artificial ones. The eggs in the top row above the black line were laid in captivity, almost certainly by the same female. Eggs in the fourth row are standard-sized artificial cowbird eggs. Eggs in the fifth row are the undersized cowbird eggs referred to in table 6.

cast in plaster of Paris and painted with acrylic polymer paints and shellac. They were 10–15% heavier than real eggs of similar volume, but it is unlikely that birds respond to eggs that are denser than normal. Unusually dense eggs would be evolutionarily unique since the specific gravity of eggs varies very little (Bergtold 1929). Poulsen (1953) concluded that egg density was unimportant to the egg-related behavior of non-passerines. Artificial cowbird eggs are not quite as smooth as real ones and do not conduct heat as well as real ones. However, my controls showed that the differences between the artificial and the real cowbird eggs did not cause the former to be rejected. I have described in detail elsewhere (Rothstein 1970) the artificial eggs and my techniques for producing them.

To mimic natural parasitism, I tried to follow the procedures employed by cowbirds. Although there is much variation, naturally parasitized nests most commonly receive one cowbird egg and lose one host egg, which is removed by the cowbird (Friedmann 1963). Egg-laying by cowbirds has been described by Friedmann (1929), Hann (1941), Norris (1947), Mayfield (1960, 1961b), and Prescott (1965). Cowbirds lay around dawn and generally remove host eggs either the day before or from several hours after to a day

TABLE 1. Results of experimental introductions of artificial and real cowbird eggs.

Species	Rejections			Acceptances	Total nests	% Rejections	95% confidence intervals on % rejection
	E ^a	B ^a	D ^a				
<i>Rejecters</i>							
Gray Catbird (<i>Dumetella carolinensis</i>)	50			3	53	94.3	84-99
American Robin (<i>Turdus migratorius</i>)	38		7	1	46	97.8	90-99
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	33			0	33	100.0	86-100
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	10	4	15	4	33	87.8	78-96
Blue Jay (<i>Cyanocitta cristata</i>)	23		2	0	25	100.0	86-100
Brown Thrasher (<i>Toxostoma rufum</i>)	25			1	26	96.3	80-99
Western Kingbird (<i>Tyrannus verticalis</i>)	2			0	2	—	16-100
Northern Oriole (<i>Icterus galbula</i>)	1			0	1	—	—
<i>Accepters</i>							
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	2	1		89	92	3.3	1-8
Common Grackle (<i>Quiscalus quiscula</i>)	5		3	62	70	11.4	6-25
Eastern Phoebe (<i>Sayornis phoebe</i>)		2	1 ^b	47	50	6.0	1-16
Chipping Sparrow (<i>Spizella passerina</i>)			3	16	19	15.8	4-41
Yellow Warbler (<i>Dendroica petechia</i>)				16	16	0.0	0-22
Mourning Dove (<i>Zenaidra macroura</i>)	1		4	11	16	31.2	11-59
Barn Swallow (<i>Hirundo rustica</i>)	1			12	13	7.7	< 1-36
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	2		3	7	12	41.7	15-72
American Goldfinch (<i>Spinus tristis</i>)		1	1	8	10	20.0	3-56
Song Sparrow (<i>Melospiza melodia</i>)	1			8	9	11.1	< 1-48
Cardinal (<i>Cardinalis cardinalis</i>)	1			6	7	14.3	< 1-58
Wood Thrush (<i>Hylocichla mustelina</i>)				6	6	0.0	0-46
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)				4	4	0.0	0-60
Mockingbird (<i>Mimus polyglottos</i>)	1			3	4	25.0	1-81
Vesper Sparrow (<i>Poocetes gramineus</i>)				3	3	0.0	0-71
Eastern Meadowlark (<i>Sturnella magna</i>)			1	2	3	33.3	1-91
Red-eyed Vireo (<i>Vireo olivaceus</i>)	1			2	3	33.3	1-91
Prairie Warbler (<i>Dendroica discolor</i>)				2	2	0.0	0-84
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)				2	2	—	—
Rough-winged Swallow (<i>Stelgidopteryx ruficollis</i>)				2	2	—	—
Starling (<i>Sturnus vulgaris</i>)				2	2	—	—
House Finch (<i>Carpodacus mexicanus</i>)				2	2	—	—
Yellow-headed Blackbird (<i>Xanthocephalus xanthocephalus</i>)				2	2	—	—

Experiments on the following species yielded no rejections and one acceptance for each: Yellow-billed Cuckoo (*Coccyzus americanus*), Least Flycatcher (*Empidonax minimus*), House Wren (*Troglodytes aedon*), House Sparrow (*Passer domesticus*), Hermit Thrush (*Catharus guttatus*), Veery (*Catharus fuscescens*), Common Yellowthroat (*Geothlypis trichas*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Field Sparrow (*Spizella pusilla*), Dark-eyed Junco (*Junco hyemalis*), Indigo Bunting (*Passerina cyanea*), Purple Finch (*Carpodacus purpureus*).

Controls for the rejecter species were as follows: Real cowbird eggs were used in some experiments (Robin—1, Catbird—1, E. Kingbird—5, Cedar Waxwing—6, Blue Jay—4, Brown Thrasher—4). All of these cowbird eggs were ejected except for 2 placed in Cedar Waxwing nests, one of which was deserted and the other accepted. Since results for real cowbird eggs do not differ from those for artificial cowbird eggs, they are included in the data tabulated above. Other controls are described in the text.

^a Rejection nearly always occurred by ejection of cowbird egg (E), bruising of cowbird egg (B), or nest desertion (D).

^b Rejection at this nest was by egg burial.

after their own egg is laid. My standard procedure was to add one cowbird egg to a nest and to remove one "host" egg at the same time, doing so up to seven hours after sunrise. I saw no evidence that these departures from the events at naturally parasitized nests influenced host response. In some experiments, no host eggs were removed. All species tested responded similarly, whether or not a host egg was removed, and experiments of both types are included in the results.

I attempted to parasitize nests during the host's laying period. Most naturally-deposited cowbird eggs are added at this time (Friedmann 1929); cowbird eggs laid outside of the host's laying period have reduced chances of success (Norris 1947, McGeen 1971). I also parasitized nests found during the incubation stage to determine whether nest stage at the time of parasitization affects host response. Only the Cedar Waxwing (*Bombycilla cedrorum*) showed vari-

ation in response that was dependent on nest stage. Over 90% of the experiments were conducted in Connecticut, Michigan, Maryland, and Manitoba. The remainder were done in Nebraska, Illinois, New York, New Brunswick, and Saskatchewan. Experiments reported here were conducted from 1966 to 1971.

After nests were parasitized, I visited them to determine the host's response. I considered eggs as rejected if they were ejected, were damaged but left in the nest, if the nest was deserted, or if the eggs were buried with nest material. Few ejections were observed but they were assumed to have occurred if the cowbird egg was missing and the host's eggs were still present. Nests were considered to be deserted if they retained their contents but lacked evidence of activity (warm eggs and/or presence of the hosts) on at least two consecutive visits on different days. Eggs were assumed to be damaged by birds

intending to spike them if they had bruises penetrating through the shellac and paint to the underlying plaster. Rejection nearly always occurred within five days of deposition of the cowbird egg; undamaged cowbird eggs remaining in active nests for at least five days during the host's egg stage were considered to have been accepted.

CONTROLS FOR THE ARTIFICIAL EGGS

Controls were of three types. (1) Real cowbird eggs were used in experiments if a species was found to reject artificial ones. In all cases the birds responded to the real and the artificial cowbird eggs in similar fashion (table 1, bottom). (2) Artificial eggs similar to the host's own eggs were employed with two species which rejected artificial cowbird eggs. Artificial or real cowbird eggs were rejected at 50 of 53 Gray Catbird (*Dumetella carolinensis*) nests whereas artificial catbird eggs were accepted at five nests. The difference between the rejection rates for these two egg types (50-3 versus 0-5) is significant at $P < 0.005$ Fisher Exact Probability Test (Bailey 1959). Artificial cowbird eggs were rejected at 44 of 45 American Robin (*Turdus migratorius*) nests. Artificial eggs, with robin coloration but equal in size to the artificial cowbird eggs were accepted at 6 of 7 robin nests. The difference between the rejection rates for these two egg types (44-1 versus 1-6) is significant at $P < 0.005$. (3) The real eggs of a third species were placed in the nests of some species which rejected real and artificial cowbird eggs, e.g. all but one of the catbird eggs, in three nests, were replaced with real Red-winged Blackbird (*Agelaius phoeniceus*) eggs. All the red-wing eggs were ejected while the catbird eggs remained in the nests. All but one of the Blue Jay (*Cyanocitta cristata*) eggs in one nest were replaced with real robin eggs. The latter disappeared while the jay egg remained in the nest. These and similar manipulations are presented elsewhere in greater detail (Rothstein 1975b). These experiments, in which birds rejected eggs other than those of the cowbird, show that rejection behavior is not specific to cowbird eggs but is released by any foreign egg which is sufficiently nonmimetic.

RESULTS

Table 1 presents the results of experiments that were intended to duplicate natural parasitism. I found no geographical variation in a species' response to the experiments, so results from all regions were combined. Cedar Waxwing nests parasitized after more than three days of incubation showed a statistically significantly lower rejection rate than nests parasitized earlier (35% versus 88% rejection). Table 1 presents the results only for waxwing nests parasitized before the fourth day of incubation. This includes the period when natural parasitism usually occurs.

The species studied fall into two groups, those in which at least 88% of the pairs reject cowbird eggs and those in which the rejection rate is no more than 42%. These species will be referred to as rejecters and accepters, respectively. This grouping is apparently natural because no arbitrary division is necessary.

Prior to these experiments, only two North American birds, the Gray Catbird and the American Robin, were known regularly to reject cowbird eggs (see Friedmann 1963). Despite the abundance of other rejecters and their widespread sympatry with cowbirds, naturally deposited cowbird eggs are rarely found in the nests of rejecters (see Friedmann 1963). Some of the few cases of natural parasitism of rejecter species have had outcomes similar to those in my experiments. Savage (*in* Friedmann 1963:49) noted an Eastern Kingbird (*Tyrannus tyrannus*) nest from which a cowbird egg disappeared. I have described (Rothstein 1970, *in press b*) 12 cases of natural parasitism on the Cedar Waxwing, resulting in 4 ejections, 6 desertions, and 2 acceptances. Four cases are known in which naturally-deposited cowbird eggs disappeared from Brown Thrasher (*Toxostoma rufum*) nests (Nickell 1955, Taylor and Goertz 1965, Mengel and Jenkinson 1970, Herskowitz unpubl. data). Mengel and Jenkinson believed that the two cowbird eggs in the nest they studied were removed mistakenly by the cowbird, but their observations do not preclude the possibility that the thrashers removed one or both of the cowbird eggs. Warren (*in* Friedmann 1963:132) reported three cases in which broken cowbird eggs were found directly beneath Northern Oriole (*Icterus galbula*) nests, and Smith (1972) witnessed an oriole ejecting a cowbird egg from a nest. These observations and one of my experiments (table 1) lead me tentatively to consider this oriole a rejecter. I know of no cases of natural parasitism of the two remaining rejecters, Blue Jay and Western Kingbird (*Tyrannus verticalis*) that resulted in observed rejection.

Except for the Cedar Waxwing, I have not tabulated the few cases of acceptance of natural parasitism by rejecters. These cases have limited significance since in rejecters there is a strong bias toward observing excessive acceptance. The validity of experimental parasitism is not reduced because some rejecters may "seem" to accept natural cowbird parasitism at significantly higher rates than experimental parasitism. Unless a nest is watched almost continuously, one is likely to observe parasitism of rejecters only in those few cases where the birds accept the cowbird egg.

TYPES OF REJECTION BEHAVIOR

Ejection is the most adaptive type of rejection. It requires little time and energy, and frees the host's reproductive efforts from parasitism. Nest desertion is far less efficient since the

birds lose the time and energy invested in their nest and clutch. Furthermore, nest desertion may not free a host from parasitism because a second attempt at nesting may also be parasitized. Lastly, nest desertion is less adaptive because the second breeding attempt may occur when environmental conditions are no longer optimal for reproduction. Immelmann (1971) and others have argued that the initial breeding attempt is scheduled so as to take advantage of optimal conditions. Nest desertion might have an advantage over ejection in that adult cowbirds generally remove a host egg and ejection does not recoup this loss, whereas nest desertion can, because a bird that renests can lay a full-sized clutch. However, this potential advantage may often be nil since replacement clutches are smaller than initial ones in many species (Klomp 1970). Egg burial, in which the hosts build a new nest floor over the cowbird egg and then lay a replacement clutch in the same nest, is also thought to be a form of rejection. It is only slightly more efficient than nest desertion because only part of a new nest must be built. Piercing the shell of the parasitic egg and leaving the egg in the nest would result in the failure of the parasitic egg to hatch, but a damaged egg is liable to break or leak egg contents. The sticky egg contents could cause the host's own eggs to become glued to the nest lining and to one another. Once eggs are "glued" in this manner they have little chance of hatching since egg turning is difficult and, if attempted, could result in breakage of the host's eggs.

Because of the comparatively high adaptive value of ejection one might predict that rejection would occur most frequently by ejection. This prediction is borne out since 197 (80%) of the 245 rejections (table 1) were by ejection. Under natural cowbird parasitism, nest desertion and egg burial seem far more prevalent than ejection (see Friedmann 1963:34), but the bias against detecting ejection may explain this anomaly. A bird deserting a nest containing a cowbird egg leaves the evidence of parasitism behind, but in the case of ejection there may be no indication of parasitism at all. Furthermore, birds usually carry the ejected egg away from their nest, thereby reducing the likelihood that evidence of parasitism will be detected. Egg recognition experiments on other continents also show that ejection is by far the most common form of rejection (see Rensch 1924, Swynnerton 1918, Ali 1931, Promptov and Lukin *in* Dement'ev et al. 1966:497).

FEATURES OF EJECTION BEHAVIOR

The actual process of ejection has been observed at four nests: three of the Brown Thrasher and one of the Gray Catbird. In all 11 ejections that were observed (more than one ejection was observed at two of the four nests), the bird took the artificial egg in its beak and dropped it at least 5 m from the nest. These observations indicate that ejected eggs are normally carried in the beak and rarely tossed over the side of the nest. When an egg was ejected, a search was usually made in a circle 3–6 m around the nest. These searches yielded the missing egg in less than 3% of the ejections reported in table 1 and in other experiments using a variety of experimental eggs. On three occasions, ejected eggs were accidentally found approximately 11, 14, and 32 m from the nests in which they were deposited. Ejected eggs that were found were generally unbruised or had a few shallow peck marks. None of them showed any signs of having been pecked hard, substantiating the generalization that ejected eggs are picked up in the bill and not spiked. Before some birds ejected eggs, I watched them peck weakly into the nest, although I was never certain that the pecks were directed at the foreign egg. The few eggs rejected by bruising (table 1) were probably due to atypical birds which unsuccessfully attempted to spike the plaster egg.

The few observations of ejection in the literature (summarized in Rothstein 1970) indicate that the above features of ejection behavior are common to most species that remove foreign eggs. In some cases, however, eggs were definitely spiked and/or simply dropped over the side of the nest. Spiking may have occurred in instances in which the birds tried to remove eggs too large to be held in the bill.

THE PROBABLE EVOLUTIONARY ORIGIN OF EJECTION BEHAVIOR

Egg ejection resembles nest sanitation behavior, i.e., the removal of fecal sacs and eggshells, as was noted by Swynnerton (1918). In nest sanitation, objects are usually lifted in the beak and carried from the nest (Blair 1941, Nethersole-Thompson and Nethersole-Thompson 1941). Dropping eggs, eggshells, or fecal sacs directly beneath the nest would be selected against because it can reveal the nest's location to a predator. This may explain why birds with relatively predator-free nests drop these objects directly from the nest (e.g., the oropendolas and caciques studied by Smith 1968). Nest sanitation, which is nearly

universal among passerines, may have been a preadaptation from which egg ejection evolved. The motor patterns involved in nest sanitation, which are likely to be largely innate, may be virtually identical to those employed in egg ejection. All that is needed for these behaviors to become an antiparasite adaptation is for the motor pattern to be released early in the egg stage of the breeding cycle (instead of at the beginning of the nestling stage and later) and to be released in response to a foreign egg instead of in response to a releaser lacking the characteristics of intact eggs (fecal sacs and eggshells).

THE QUESTIONABLE SIGNIFICANCE OF NEST DESERTION AND EGG BURIAL

In contrast to egg ejection and damage, nest desertion and egg burial are neither as adaptive nor as easily evolved. There is nothing in the behavioral repertoire of a bird that would lead from the sight of a foreign egg in its nest to nest desertion or egg burial, and I doubt whether these behaviors are in fact antiparasite adaptations. Egg ejection is almost certainly an antiparasite adaptation because it has no adaptive value other than in the context of brood parasitism. This interpretation of ejection, besides being the simplest, is supported by several lines of direct evidence (Rothstein 1970). By contrast, birds deserting their nest in apparent response to cowbird eggs may actually be deserting because (1) a human observer visited their nest, (2) the cowbird has so altered the total clutch size that the combined egg mass is too small or too large to release normal incubation behavior, or (3) the cowbird may have been discovered at the host's nest. It is well known that some birds abandon their nest merely because of visits by humans. Cowbirds sometimes remove so many host eggs or add so many of their own eggs that the combined clutch is beyond the range normally occurring in that host species. The hosts may desert not because there are cowbird eggs but simply because there are too few or too many eggs. Holcomb (1970) showed that the Red-winged Blackbird, an acceptor species, will not incubate clutches consisting of especially large or small artificial blackbird eggs. Desertion in response to discovering a cowbird at the nest may be similar to desertion in response to a human observer. The hosts may be responding to the cowbird with a generalized response released by any potential predator rather than a specific response to the cowbird. Controlled experiments must be performed to

show that nest desertion is a response to the cowbird egg as such. Such tests with the Cedar Waxwing, the only rejecter species that frequently deserts its nest (table 1), show that the presence of a cowbird egg increases the likelihood of desertion. But even for the waxwing, I have evidence that birds which desert their nests try to eject the cowbird eggs but are unsuccessful (Rothstein in press, b).

Cowbird eggs that are deposited before any host eggs appear are sometimes said to have an especially high likelihood of being rejected by nest desertion (Norris 1947, Friedmann 1963, McGeen 1971). The usual interpretation is that the nest is abandoned because the cowbird egg is deposited when no host eggs are present and birds have a weak bond to their nest at this stage. But cowbirds select host nests before eggs are present (Hann 1941). Perhaps cowbirds sometimes commit themselves to nests that are active but deposit their eggs after the nest has been abandoned for reasons unrelated to parasitism (a common occurrence). In my own experience as a parasite mimic, I have visited nests that I intended to parasitize and that I expected to contain eggs, only to find them empty and no longer active. In addition, there is the simpler possibility that cowbirds sometimes deposit eggs in nests which were, in the cowbird's experience, never active. Even if the appearance of a cowbird egg before any host eggs are present is shown to increase the likelihood of nest desertion, it must be proved that the desertion is truly antiparasitic behavior and not just a generalized response released by any object appearing in the nest before the host's own eggs. Holcomb (1970) found that 4 of 8 red-wings either ejected eggs or abandoned nests when artificial red-wing eggs were placed in their nests before the egg-laying stage. The interpretation of such responses is difficult and caution must be exercised before concluding that deserted nests with cowbird eggs represent rejection behavior.

Egg burial too, is sometimes explainable as a generalized behavior rather than as a specific response to cowbird parasitism. The only case of egg burial in my experiments occurred at an Eastern Phoebe (*Sayornis phoebe*) nest during unusually stormy weather, and may have represented clutch desertion in response to severe weather rather than rejection of the cowbird egg. Other phoebes in the area showed the effects of the severe weather by abandoning young for extended periods. The nest in question was reparasitized when a sec-

TABLE 2. Statistical comparisons between responses of rejecter and accepter species.

Acceptor species	R-A ^a	Rejecter species (R-A ^a)						
		Gray Catbird (50-3)	American Robin (46-1)	Eastern Kingbird (33-0)	Blue Jay (25-0)	Brown Thrasher (24-1)	Cedar Waxwing (29-4)	Western Kingbird (2-0)
Red-winged Blackbird	3-89						0.001	0.01
Common Grackle	8-62						0.001	0.04
Eastern Phoebe	3-47						0.001	0.02
Chipping Sparrow	3-16						0.001	—
Yellow Warbler	0-16	The probabilities for the 60 comparisons in this block are all < 0.0002					0.001	0.02
Barn Swallow	1-12						0.001	0.06
Song Sparrow	1-8						0.001	—
American Goldfinch	2-8						0.001	—
Cardinal	1-6						0.001	—
Wood Thrush	0-6						0.001	—
Rose-breasted Grosbeak	0-4						0.001	—
Mourning Dove	5-11						0.001	—
Black-billed Cuckoo	5-7	0.001	0.001	0.001	0.001	0.001	0.01	—
Vesper Sparrow	0-3	0.005	0.005	0.005	0.005	0.005	0.005	—
Mockingbird	1-3	0.02	0.02	0.02	0.02	0.02	0.04	—
Eastern Meadowlark	1-2	0.03	0.03	0.02	0.02	0.05	—	—
Red-eyed Vireo	1-2	0.03	0.03	0.02	0.02	0.05	—	—
Prairie Warbler, Rufous-sided Towhee, Rough-winged Swallow, Starling, House Finch, Yellow-headed Blackbird	0-2	0.02	0.02	0.01	0.01	0.02	0.055	—

Note: This table contains the results of analyses of 161 2×2 contingency tables (7 rejecter species multiplied by 23 acceptor species). Figures given at the intersections for species pairs range from slightly larger to much larger than the actual probability for that particular comparison. All comparisons were tested with two-tailed applications of the Fisher Exact Probability Test using either the computational methods of Bailey (1959) or when possible the tables in Siegel (1956) or Owen (1962).

^a R = Rejections, A = Acceptances.

ond clutch was laid on the new floor, and the second cowbird egg was accepted. Although I have no proof that the same individuals were responsible for both clutches, it is unlikely that both birds tending the second clutch were new.

Egg burial at naturally parasitized nests usually involves only the cowbird egg and may happen when female cowbirds lay their eggs before the hosts complete nest building. e.g. before it was experimented on one of the Yellow Warbler (*Dendroica petechia*) nests listed in table 1 contained a naturally-deposited cowbird egg and no warbler eggs. This cowbird egg was buried, but an artificial cowbird egg that I added on the day the warbler laid its third egg was accepted. In the few cases where host eggs are also buried, the explanation may be that a cowbird egg laid in a nest shortly before nest completion may release the same behavior as any foreign object and be buried. The burial process, especially for a small host, may delay nest completion so that nest construction and egg laying, which normally occur consecutively, now occur simultaneously. Convincing evidence that egg burial is a direct response to a cowbird egg could be provided by observations of natural parasitism if cowbird eggs are buried when laid after one or more host

eggs are laid and if unparasitized clutches, coincident in space and time, are not buried. However, I am unaware of such observations. Controlled experiments could also determine that egg burial is a specific response to cowbird eggs. Eastern Phoebes occasionally bury naturally-deposited cowbird eggs laid before any of their own eggs (Friedmann 1963), but in controlled experiments in which I added eggs to active phoebe nests that were empty but judged to be completed, phoebes did not bury cowbird eggs any more frequently than they did artificial phoebe eggs (Rothstein 1970). Just as cowbirds may do, I apparently was mistaken in judging nests to be completed, and some eggs of both types were partially buried. Possibly some hosts use nesting materials that make it difficult for cowbirds to determine when a nest is nearly completed and this, rather than a direct response to cowbird eggs, may represent an actual antiparasite adaptation. It may be no coincidence that the Yellow Warbler, the species most noted for burying cowbird eggs (Friedmann 1963), often builds an unusual nest with similar material used for both the nest frame and the nest lining (pers. observ.).

In sum, only egg ejection and bruising are clearly rejection or antiparasite adaptations. Other putative types of rejection may not be

direct responses to cowbird eggs and because of lack of definitive evidence should not be interpreted as antiparasite adaptations.

COMPARISONS BETWEEN REJECTER AND ACCEPTER SPECIES

Table 2 compares the results for all rejecter species (two or more experiments each) with those for all accepter species (two or more experiments each). These comparisons result in 161 2×2 contingency tables (7 rejecters times 23 accepters), any of which can be reconstructed from the data given in table 2. Most (144) of these comparisons result in probabilities of < 0.05 . Deleting the only rejecter species with a small sample, the Western Kingbird, there are 138 comparisons between rejecters and accepters, nearly all of which (135) are significant at $P < 0.05$. Rejecter and accepter species clearly form two distinct groups.

Do species within the rejecter and accepter groups have features in common which have, respectively, increased or decreased the likelihood that rejection behavior would have evolved by the present time? Another significant question concerns the ease with which rejecter and accepter species can be separated. The small degree of intraspecific variation in response to cowbird eggs was an unexpected finding that may have considerable evolutionary significance (see Rothstein 1975a).

These two questions are especially clear-cut for queries of an evolutionary nature because (1) adaptations generally cannot be identified as easily as can rejection behavior (i.e., it is not always clear which of various character states imparts the highest fitness), and (2) it is not always easy to distinguish between alternative character states (i.e., character states often intergrade and are neither clearly present nor absent). On the other hand, rejection behavior is an all-or-none phenomenon with only two distinct character states, presence or absence, the former being more adaptive than the latter.

FACTORS IMPORTANT TO EVOLUTION OF REJECTION BEHAVIOR

Primary factors in evolution relate to the adaptive value an attribute would afford to the members of a species. The presence or absence of adaptive value for an attribute determines whether or not a species is likely ever to evolve the attribute. The amount of adaptive value, if any, also relates to the likelihood of the attribute's having evolved by the present time. Secondary evolutionary factors deal only with the likelihood of a trait's

having evolved by the present, and relate not to adaptive value but to such matters as the possession of suitable preadaptations and the length of time available for development of the adaptation.

Intensity of parasitism. The adaptive value of rejection behavior, a primary factor, can be measured on a scale of zero to one, ranging from no adaptive advantage (parasitism causes no reproductive loss) to maximum adaptive advantage (only individuals with rejection behavior contribute to the next generation). Adaptive value can be quantified roughly as: $(R - A)P/R$ where R is the mean number of offspring produced per parasitized nest by individuals with rejection behavior, A the mean number of offspring produced per parasitized nest by individuals with acceptance behavior, and P the probability that an individual will be parasitized during a given breeding attempt. If either $R = A$ or $P = 0$, the adaptive value of rejection behavior is at the absolute minimum (zero). If $A = 0$ and $P = 1.0$, the adaptive value is maximal (one). Adaptive value as estimated here corresponds to the selection coefficient normally used in population genetics to quantify the relative adaptive value of alternative character states. I have discussed quantification of the adaptive value of rejection behavior more fully elsewhere (Rothstein 1975a).

In species that are rarely or never parasitized (zero or very low P), rejection behavior is unlikely to evolve because its selective advantage will be small or nil. Rejection behavior may be elicited by several genes and very small selective advantages may not suffice to coadapt the necessary gene complexes. This would be especially true when rejection behavior is incipient or if the genes involved are strongly pleiotropic. Even if rejection is determined by only a single nonpleiotropic gene, strong selection pressures may be necessary to avoid its loss by genetic drift when it is still rare.

Hypothesis: Accepters should be subjected to little or no parasitism and rejecters to occasional to heavy parasitism. Acceptor species vary greatly in the frequency with which they are parasitized. Friedmann's (1963) records and my own data reveal that nine of the accepter species in table 2 experience virtually no parasitism. These species are the Common Grackle (*Quiscalus quiscula*) Barn Swallow (*Hirundo rustica*), Mourning Dove (*Zenaida macroura*), Black-billed Cuckoo (*Coccyzus erythrophthalmus*), Rough-winged Swallow (*Stelgidopteryx rufi-*

TABLE 3. Acceptor species listed according to rate of parasitism and degree of harm caused by parasitism.

Parasitized least intensely	1. American Goldfinch 2. Vesper Sparrow 3. Eastern Meadowlark 4. Rose-breasted Grosbeak, Red-winged Blackbird 5. Wood Thrush 6. Cardinal, Prairie Warbler 7. Yellow Warbler, Eastern Phoebe, Chipping Sparrow
Parasitized most intensely	8. Song Sparrow, Red-eyed Vireo, Rufous-sided Towhee
Harmed the least	1. Red-winged Blackbird 2. Eastern Meadowlark 3. Wood Thrush, Cardinal, Rufous-sided Towhee, Rose-breasted Grosbeak 4. Song Sparrow, Vesper Sparrow, Red-eyed Vireo 5. American Goldfinch 6. Yellow Warbler, Chipping Sparrow
Harmed the most	7. Prairie Warbler, Eastern Phoebe

collis), Starling (*Sturnus vulgaris*), House Finch (*Carpodacus mexicanus*), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), and Mockingbird (*Mimus polyglottos*). Table 3 lists the remaining 14 acceptor species in the order of the intensity with which they appear to be parasitized, ranging in rate from about 5% at level one to about 25–75% at level eight. Statistical analyses using Kendall's rank correlation coefficient show no significant association between percent rejection and intensity of parasitism in the 14 acceptors listed in table 3.

Unfortunately, data on cowbird parasitism are often presented in a nonquantitative fashion, and accurate intensities of parasitism are not available for most species. Field studies of brood parasitism should report the number of nests parasitized and the total number of nests surveyed, even if no parasitism was observed. Such data are more significant than reports stressing parasitism of unusual hosts.

Because the rejecter species remove cowbird eggs, it is difficult to determine how frequently they are parasitized. However, there is no evidence that they are not parasitized frequently today or were not in the past. Indeed, there is evidence that at least some of the rejecters are parasitized more frequently than some acceptors. In Connecticut, for example, I noted parasitism on the catbird, a rejecter, more frequently than on the Red-winged Blackbird, an acceptor. In Michigan, I found the Cedar Waxwing, another rejecter, to be parasitized more frequently than the Eastern Phoebe. Furthermore, for each case of parasitism that I detected in rejecters, many more may have gone undiscovered. It seems to be poor reproductive strategy for cowbirds to parasitize rejecters, but these species are so diverse that it may be difficult to evolve an

innate avoidance of all rejecters. Overall, the most adaptive strategy for cowbirds may be to parasitize all nests they find, because if they attempted to avoid rejecter species, they might also bypass some acceptors. Possibly cowbirds learn which species are good hosts and rejecters are parasitized primarily by naive females. Mayfield (1961b) and others (summarized by Friedmann 1963) have noted that female cowbirds occasionally visit host nests after egg laying. At some of these nests the female cowbirds remove host eggs but in some or all cases the primary purpose may be to determine the success of the cowbird egg. Elsewhere I discuss possible reproductive behavior of cowbirds in greater detail (Rothstein, in press a).

In sum, only 9 of the 23 acceptors in table 2 are subjected to little or no parasitism. I find no strong relationship between intensity of parasitism and response to parasitism because acceptor species vary so greatly in intensity of parasitism.

Harm to the host. Rejection behavior would be of no adaptive value if a host and its young suffered no deleterious effects from parasitism. Unless it can be shown that parasitism helps a host's total lifetime reproductive efforts, it is reasonable to assume that it is harmful because any individual who devotes time and energy to the offspring of an unrelated individual will be selected against. In nearly all cases of brood parasitism, the harmful effects of being parasitized are evident. The host fledges fewer and/or inferior young than unparasitized individuals. The deleterious effects are not easily observed in hosts which are larger than the cowbird, but even here, hosts devote time to the parasitic hatchling that they could have spent attending to their own offspring. The quality of

their young may thus suffer, although this may be detectable only by reduced postfledging survival. Furthermore, the relationship $(R - A)P/R$ does not account for the fact that caring for young may place a burden on an adult's safety (Lack 1968:300). Even if $R = A$, and even if host young raised with and without cowbirds are equal in quality, parasitism may reduce the lifetime reproductive output of a host because the extra effort devoted to caring for the parasite may reduce the parent's chances of postbreeding survival.

Hypothesis: Cowbird parasitism is harmful to rejecter species (or would be if they accepted cowbird eggs) but of little harm or even beneficial to accepter species. There is no evidence that being parasitized by the Brown-headed Cowbird benefits the individuals of any species. To the contrary, voluminous reports show that cowbird parasitism reduces the reproductive output of the host although most of this literature does not allow a quantification of how much loss is due to cowbird parasitism. Even in the only known case in which a brood parasite aids its host (Smith 1968), the situation is beneficial only under certain circumstances; when it is not beneficial, the hosts reject nonmimetic parasitic eggs.

Cowbirds lower host reproductive output by egg stealing, reduced egg hatchability, and reduced nestling success. Adult cowbirds usually remove one host egg. Reduced hatchability occurs mostly in small hosts who cannot provide sufficient heat for incubation if parasitized with two or more cowbird eggs. In such cases, the cowbird eggs usually have a higher rate of hatching success than the host's eggs, presumably because they are larger and make more contact with the brood patch of the incubating bird (Hofslund 1957, Mayfield 1960, Friedmann 1963:22, 118).

The chief source of reproductive loss is reduced nestling success. Nestling cowbirds often outdo the host's young in competing for food. This is especially true for small hosts but occurs even among some larger ones. Cowbirds often cause the host's young to receive too little food by requiring more food and begging for it more vigorously than their smaller nest-mates. Friedmann (1963) showed that small hosts are harmed more than larger ones. He also suggested that the relative growth rates of host and parasite are important factors, slow-growing hosts being harmed most because of the nestling cowbird's rapid development. Nestling competition also involves the relative incubation periods of

host and parasite eggs. Cowbird eggs hatch in 11–12 days, the shortest incubation period among passerines although attained by a few other species as well (Nice 1953). Thus, with most hosts, cowbirds possess the advantages of hatching first and being stronger, larger, and more developed. This "headstart" may more than compensate for size disadvantages of cowbirds in the nests of large hosts.

The advantages in nestling competition that cowbirds derive from their hosts' early hatching are well known, but the fact that early hatching may regularly preclude nestling competition altogether in some species is not. Emlen's (1941) experiments on Tricolored Blackbirds (*Agelaius tricolor*) suggest that songbirds cease incubation if a nestling appears prematurely in their nest. Similarly, Friedmann (1929:259) placed "very young cowbirds" in the nest of a robin (a rejecter species) and found that the robins ceased incubation of their own eggs and began to feed the cowbirds. Thus if cowbird eggs were to hatch too early before the completion of development of the host's eggs, the latter would not even hatch. This occurs naturally in some hosts that have long incubation periods. Walkinshaw (1961) described nine nests of three species of *Empidonax* at which naturally-deposited cowbird eggs hatched. At each of the nests, only a cowbird fledged, and in all but possibly one of the nests the host eggs did not even hatch. *Empidonax* incubation periods are usually 14 days, with a range of 12–15. Klass (1970) and I (Rothstein 1970, 1975a) found a similar situation in the Eastern Phoebe which has a 15–16 day incubation period. If a cowbird egg hatches, there is virtually no chance of any phoebe young fledging successfully; in many cases the phoebe eggs do not even hatch.

The eight species that are known or thought to be rejecters have incubation periods ranging from 12–14 days for the robin to 17–18 days for the Blue Jay (using data in Bent 1942, 1946, 1948, 1949, 1950, 1958). Despite their relatively large size, rejecters might have less reproductive success if they accepted the cowbird because the host eggs would hatch 1–7 days after the cowbird eggs, if at all. The reproductive loss might be even greater than in relatively small hosts such as warblers (Parulidae), which have shorter incubation periods. By contrast, Friedmann (1963:61) suggested that cowbird eggs might pose little threat to birds as large as the Blue Jay because they would not hatch in the presence of the larger eggs.

The larger eggs might prevent the host's brood patch from making contact with the cowbird egg. Using average egg measurements from Bent (1946, 1958), I calculated that Blue Jay eggs are 4.02 mm wider than cowbird eggs. However, cowbird eggs have hatched in nests of robins (whose eggs average 3.58 mm wider than cowbird eggs; Nice 1944), Eastern Meadowlarks (*Sturnella magna*, av. 3.93 mm wider; Trautman 1940), and Brown Thrashers (av. 2.98 mm wider; Moore 1947, Nickell 1955, Taylor and Goertz 1965). Hence, it seems likely that the large eggs of rejecters would not forestall hatching of cowbird eggs.

The degree of harm caused by accepting cowbird eggs varies among the 14 accepters that are parasitized to any extent (table 3). This list represents comparable degrees of harm at each level but the increment in the degree of harm from one level to the next is not necessarily consistent. In the red-wing (level one), cowbirds have no advantage of early hatching because red-wing eggs also hatch in 12 days or less; red-wings are also a little larger than cowbirds. Meadowlarks (level two) have a decided advantage of size but are at a hatching disadvantage. The four species at level three have a slight size advantage but all are at a hatching disadvantage. The species at level four have the same hatching disadvantages as those at level three but also have small size disadvantages. The American Goldfinch (*Spinus tristis*) at level five is at a hatching disadvantage and at an extreme size disadvantage. Nestling cowbirds may often die before they can harm goldfinches because this host may be one of the few whose nestling food (seeds) is too specialized to sustain cowbirds. The two species at level seven are at a great size disadvantage but their short incubation periods are a partial saving factor. Of the two species at level eight, the phoebe is at an enormous hatching disadvantage, and the Prairie Warbler (*Dendroica discolor*), while at less of a hatching disadvantage, is the smallest host in table 3.

The degree of harm caused by cowbird parasitism obviously varies greatly among the rejecter and accepter species; except for a few especially well-studied species (Rothstein 1975a), attempts to quantify it more firmly than is done in table 3 would be difficult. Statistical analyses using Kendall's rank correlation coefficient fail to find a significant association between percent rejection and the probable reproductive loss caused by the cowbird. One can say that cowbird parasitism

inflicts harm or would inflict harm in all species in table 2. The hypothesis that accepter species should be harmed minimally or not at all is not upheld. It cannot be said that parasitism would in general be more deleterious to the rejecters than to the accepters. While rejecters would suffer more from the cowbird's hatching advantage, this would probably be made up by the fact that the cowbird is smaller than nearly all the rejecters but larger than, or about the same size as, most of the accepters.

Historic duration of exposure to cowbird parasitism. Rejection has no adaptive value until a species is parasitized. There is reason to believe that various species or at least populations of some species have been exposed to cowbird parasitism for different lengths of time and thus have had different periods when rejection could evolve. Mayfield (1965), elaborating on arguments first presented by Friedmann (1929), stressed that the cowbird is a bird of short grasslands and that primeval North America provided large areas of this habitat only in the Great Plains. He showed that with the opening up of the eastern forest by European immigrants, cowbirds were able to spread eastward. Cowbirds probably were not found in New York State earlier than two to three hundred years ago, but today are common residents there.

Because of the cowbird's recent range extension, Mayfield suggested that species which tend to accept cowbird parasitism and those which tend to reject it would separate geographically, with the former more prevalent in eastern North America and the latter more prevalent in the central part of the continent. He compared the host defenses of birds of the grasslands, the grassland edge, and the eastern forest. Historical data suggest that birds in these areas have been exposed to parasitism for progressively shorter periods of time. As his measure of the defenses that a host has evolved, Mayfield used the frequency of parasitism of the host and what he denoted as the "tolerance" of the host. Tolerance was defined as the ratio of cowbirds fledged to the number of cowbird eggs laid. However, tolerance is not an accurate measure of the antiparasite adaptations of a species because it lumps together all sources of failure, not just those accruing from actions specifically directed against the cowbird. Under Mayfield's measure of tolerance, for example, two hosts may accept cowbird eggs at equal rates but will be said to have different tolerance levels to cowbird parasitism if one species

suffers a higher rate of nest predation. Frequency of parasitism, Mayfield's other measure of antiparasite adaptations, is not an accurate criterion for determining the state of a host's defenses since many complicating factors, such as ecological overlap enter into this consideration.

Although Mayfield's analysis was too insensitive to reveal host adaptations, his initial hypothesis is valuable. I will attempt to test Mayfield's hypothesis by considering the ranges and preferred habitats of the species I studied. Just as the cowbird has changed its range, some host species may have also changed their ranges and even their habitat preferences. It may be difficult to distinguish hosts that were allopatric with cowbirds from those that were sympatric with them during pre-Columbian times. Furthermore, it is likely that birds of woodlands and grassland edges were distributed throughout much of the Great Plains, which were more extensively forested than is generally realized (Wells 1970). It is probable that birds classed today as species of the grassland edge or even of the forest occupied some of the Great Plains before Europeans came to North America. These factors suggest that Mayfield's hypothesis will be difficult to test. Perhaps, it is very critical in special cases. Species with extremely restricted ranges that appear never to have been in contact with the Great Plains should be expected to accept cowbird eggs. Birds that have only recently been exposed to cowbird parasitism, such as those on Newfoundland (L. M. Tuck, pers. comm.), may be more tolerant of cowbird eggs than comparable avifaunas from the mainland of North America.

Hypothesis: The breeding ranges of acceptor species should generally not include the Great Plains, whereas the ranges of rejecters should encompass this region. Acceptor species should generally breed in forested habitat while rejecters should breed in grasslands. The rejecters and 20 of the accepters breed across all or some of the Great Plains (for ranges, see Robbins et al. 1966). Even the ranges of the three remaining accepters, the Wood Thrush (*Hylocichla mustelina*), Prairie Warbler, and House Finch penetrate to the plains at least slightly. Acceptor and rejecter species thus are not easily separable geographically. Only among accepters are any species whose range but marginally overlaps the Great Plains, although this may be sampling error.

Few of the accepters or rejecters are restricted to either grasslands or forests. Under

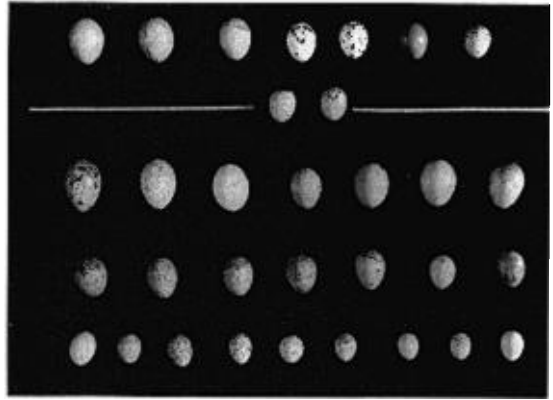


FIGURE 2. Eggs of all species on which two or more experiments were conducted. Eggs of the rejecters are above the white line, those of accepters below the line. Between the first and second rows are a real cowbird egg (left) and an artificial one.

The species names along with the ground color of their eggs are as follows (species whose eggs might be confused with cowbird eggs are indicated thusly*): first row—American Robin (blue), Blue Jay (gray), Brown Thrasher* (white), Eastern Kingbird (white), Western Kingbird (white), Gray Catbird (dark blue), Cedar Waxwing (light blue); second row—Common Grackle (light gray), Eastern Meadowlark (white), Mourning Dove (white), Wood Thrush (blue), Black-billed Cuckoo (blue), Starling (light blue), Yellow-headed Blackbird (light gray); third row—Mockingbird (light gray), Rose-breasted Grosbeak* (light blue), Red-eyed Vireo (white), Vesper Sparrow* (light gray); fourth row—Eastern Phoebe (white), Chipping Sparrow (blue), Song Sparrow* (light gray), Barn Swallow* (white), House Finch (light blue), Yellow Warbler (white), American Goldfinch (light blue), Prairie Warbler (white), Rough-winged Swallow (white).

primeval conditions, probably very few species bred in those parts of the Great Plains that were completely treeless. Contrary to predictions, two such species, the Eastern Meadowlark and the Vesper Sparrow (*Poocetes gramineus*), are accepters. Another grassland species, the Dickcissel (*Spiza americana*), is also likely to prove to be an accepter because nesting studies on this species (Zimmerman 1966) have included many naturally parasitized nests with no trace of rejection behavior. Although rejecters occur throughout the plains, none of them inhabits areas that are largely or totally treeless. Except for the Red-eyed Vireo (*Vireo olivaceus*) and the Wood Thrush, none of the rejecters or accepters is limited to breeding in wooded areas and even these two species often breed among dispersed trees in park-like settings. Nearly all the rejecters and accepters breed primarily in ecotonal areas and are clearly not separable by breeding habitat. That only two of the species studied are usually restricted to forests is not a problem in testing Mayfield's hypothesis since the data show that most species not restricted to forests accept cowbird eggs. Therefore, total acceptance by all forest species would not make them strongly distinct from birds of open

TABLE 4. The relation between host size, weight of introduced eggs, and ejection (egg volume used as indicator of host size and egg weight).

Species	Egg size, mm (LW ² cc)		Ratio*
Part A. Comparison of artificial cowbird eggs with eggs of species which normally do not eject cowbird eggs.			
<i>Spinus tristis</i>	16.2 × 12.2 ^a (2.39)		0.37
<i>Dendroica petechia</i>	16.6 × 12.6 ^a (2.64)		0.41
<i>Spizella passerina</i>	17.9 × 12.9 ^a (2.93)		0.45
<i>Hirundo rustica</i>	18.8 × 13.5 ^a (3.43)		0.53
<i>Sayornis phoebe</i>	19.0 × 14.7 ^a (4.12)		0.64
<i>Poocetes gramineus</i>	20.7 × 15.2 ^a (4.79)		0.74
<i>Melospiza melodia</i>	20.4 × 15.6 ^a (4.97)		0.77
Part B. Comparison of ejected eggs with eggs of ejecting species.			
		<i>Type and size (mm) of ejected egg</i>	
<i>Sayornis phoebe</i>	19.0 × 14.7 ^a (4.12)	Artificial egg, size no. 6, 28.3 × 20.7 (13.95) (original)	0.30
<i>Prinia inornata</i>	15.8 × 11.7 ^b (2.16)	<i>Otocompsa emeria</i> , 22.3 × 16.1 ^b (5.80), (Ali 1931)	0.37
<i>Apalis thoracica</i>	16.8 × 12.3 ^c (2.50)	<i>Sitagra ocellaria</i> , 23 × 15.5 ^c (5.53), (Swynnerton 1918)	0.45
<i>Dumetella carolinensis</i>	23.3 × 17.5 ^a (7.15)	Artificial egg, size no. 6, 28.3 × 20.7 (13.95), (Rothstein 1970)	0.51
<i>Molothrus ater</i>	21.5 × 16.4 ^a (5.80)	<i>Turdus migratorius</i> , 28.1 × 20.0 ^a (11.20), (Blincoe 1935, Morton pers. comm.**) <i>Toxostoma rufum</i> , 26.9 × 19.8 ^d (10.60), (Mengel and Jenkinson 1970)	0.52 0.55
<i>Hippolais icterina</i>	18.1 × 13.4 ^e (3.25)	<i>Emberiza citrinella</i> , 21.6 × 16.3 ^e (5.74), (Rensch 1925)	0.57

* Ratios are LW² of host's egg : LW² of artificial cowbird egg (Part A) or ejected egg (Part B). The artificial eggs averaged 21.2 × 16.3 mm; the value of LW² for these eggs was increased 15% because they were as much as 15% heavier than real eggs. Hence, LW² for the artificial eggs was calculated as 21.2 × 16.3² × 1.15 = 6.48.

** Eugene S. Morton placed an American Robin nest with eggs at a bird feeder. Upon arriving at the feeder, a female cowbird speared a robin egg in her beak and flew away with it.

Sources of egg measurements: (The figures given are averages for the species involved.) ^aBent 1942, 1948, 1953, 1958, 1968, ^bAli 1953, ^cPriest 1933-1936, ^dMengel and Jenkinson 1970, ^eNiethammer 1937.

country which, presumably, have had longer exposure to cowbird parasitism.

Mayfield's hypothesis does not separate clearly rejecter and accepter species although it helps to explain the status of two accepters (Red-eyed Vireo and Wood Thrush). Perhaps the strongest support for Mayfield's hypothesis comes from the wood warblers, many of which are forest species that may have had little or no sympatry with cowbirds in primeval times. Many nesting studies have demonstrated considerable natural parasitism on parulids yet failed to detect any definite rejection behavior (i.e., ejection).

Appearance of the host's egg. If a cowbird egg matches that of the host, antiparasite adaptations based on egg recognition are precluded. Alternatively, rejection might evolve most easily in those hosts whose eggs are most unlike cowbird eggs. Such hosts would require the least development of discriminatory skills. It is reasonable to assume that the species studied perceive the various features of eggs with a degree of peripheral filtering similar to that in humans (see Pumphrey 1948, Sturkie 1965).

Hypothesis: Rejecter species should have eggs easily distinguishable from those of the cowbird whereas accepter species should have cowbird-like eggs. This hypothesis has numerous exceptions (see fig. 2). In my judgment, only one rejecter and six accepters have eggs that could be confused with cowbird eggs. These species are listed in the legend for figure 2. All three species in which the similarity is greatest [Song Sparrow (*Melospiza melodia*), Cardinal (*Cardinalis cardinalis*), and Rufous-sided Towhee] are accepters. But even in these species the differences between real or artificial cowbird eggs and the host eggs were nearly always sufficient for me to differentiate easily between them; presumably the birds also possess this ability. My experiments on catbirds, robins, and Eastern Kingbirds have shown that these species eject some types of eggs intermediate between cowbird eggs and their own (Rothstein 1970). If the accepters with cowbird-like eggs exercised equal discriminatory powers they probably would have been able to detect the artificial cowbird eggs. Thus, egg appearance does not separate accepter

TABLE 5. The relation between bill size, egg width, and ejection.

Species	Beak (tomial) length mm*		Beak length : egg width
Part A. Comparison of beak length in species which normally do not eject cowbird eggs to width of artificial cowbird eggs (16.3 mm).			
<i>Spizella passerina</i>	10.1		0.62
<i>Spinus tristis</i>	10.2		0.63
<i>Melospiza melodia</i>	12.4		0.76
<i>Poocetes gramineus</i>	12.9		0.79
<i>Dendroica petechia</i>	13.6		0.83
<i>Hirundo rustica</i>	14.4		0.88
<i>Sayornis phoebe</i>	18.5		1.14
Part B. Comparison of beak length to width of ejected egg.			
		<i>Type and size (mm) of ejected egg</i>	
<i>Serinus sharpei</i>	10.5	<i>Pycnonotus layardi</i> , 23.5 × 17 ^a , (Swynnerton 1918)	0.62
<i>Emberiza citrinella</i>	11.9	<i>Cuculus canorus</i> , 22.2 × 16.5 ^b (Muller in Meiklejohn 1917)	0.66
<i>Molothrus ater</i>	15.1	<i>Turdus migratorius</i> , 28.1 × 20.0 ^c (Blincoe 1935, Morton pers. comm.**)	0.75
<i>Molothrus ater</i>	15.1	<i>Toxostoma rufum</i> , 26.9 × 19.8 ^d (Mengel and Jenkinson 1970)	0.76
<i>Carduelis cannabina</i>	10.1	Its own egg, 17.7 × 13.3 ^e (Rensch 1924)	0.76
<i>Parus caeruleus</i>	9.2	Its own egg, 15.4 × 11.9 ^f (Dagley 1929)	0.77
<i>Prinia inornata</i>	13.7	<i>Otocompsa emeria</i> , 22.3 × 16.1 ^g (Ali 1931)	0.85
<i>Sayornis phoebe</i>	18.5	Artificial egg, size No. 6, 28.3 × 20.7 (Original)	0.89
<i>Hippolais icterina</i>	15.4	<i>Emberiza citrinella</i> , 21.1 × 16.3 ^h (Rensch 1925)	0.95
<i>Bombycilla cedrorum</i>	17.6	Artificial cowbird egg, 21.1 × 16.3 (This study, table 1)	1.08

* Measured from the commissural point to the tip of the upper mandible. Where possible, two males and two females were measured for each species, except in the case of *Molothrus ater*, which has marked sexual dimorphism in bill size. (Both *M. ater* ejections of *Turdus migratorius* eggs were done by females and it is assumed that a female also removed the *Toxostoma rufum* egg.) All measurements were taken from specimens in the Peabody Museum of Yale University.

** See table 4 for details.

Sources of egg measurements: (The figures given are averages for the species involved.) ^aPriest 1933-1936, ^bBaker 1942, ^cBent 1949, ^dMengel and Jenkinson 1970, ^eNiethammer 1937, ^fWitherby et al. 1943, ^gAli 1953.

and rejecter species; at the most, evidence suggests that a few accepters have difficulty in detecting cowbird eggs.

Ability to eject cowbird eggs. Since ejection is the most adaptive type of rejection behavior and the type most easily evolved from preadaptations common to most birds, it is likely that the evolution of rejection behavior will be retarded without the ability to eject cowbird eggs.

Hypothesis: Acceptor species should generally be physically incapable of ejecting cowbird eggs, whereas rejecters should have this ability. The rejecter species are, by definition, capable of ejecting cowbird eggs and thus conform to the hypothesis. But are the accepters too small to lift cowbird eggs? Using egg size as an indicator of body size, it can be seen from figure 2 that the first 12 of the 23 accepters are at least as large as the

rejecters. However, some accepters are much smaller than the smallest rejecter, the Cedar Waxwing. Can these especially small accepters eject cowbird eggs? By determining the sizes of eggs that other birds are known to have ejected and comparing them to the smallest accepters (listed in part A of tables 4 and 5), the capabilities of these latter species can be estimated.

Addressing the question of whether some accepters lack the strength to lift cowbird eggs, I compared host size (table 4). Since body weights were unavailable for some species, I used egg volume as an indicator of body size. Egg volume is also a good substitute for relative egg weight since the specific gravity of eggs is similar among all birds (Bergtold 1929). Table 4 lists ratios of a "host's" egg volume to the volume of the egg it either usually does not eject (part A) or has been known

TABLE 6. Responses of selected accepter species to undersized cowbird eggs measuring 17.3×13.6 mm.

Species	Rejections			Acceptances	Total nests	Beak length : Egg width
	E ^a	B ^a	D ^a			
Red-winged Blackbird	2	1		22	25	—
Common Grackle	1		4	13	18	—
Eastern Phoebe				11	11	1.36
Chipping Sparrow				6	6	0.74

The nests used in these experiments are different from those used in the experiments in table 1. Ratios were not determined for the Red-winged Blackbird and Common Grackle because these species are as large or larger than some of the rejecters.

^a E = ejection, B = bruising, D = nest desertion.

to eject (part B). Since only relative sizes are important here, only the length times the width squared (LW^2) has been computed for each egg. I increased the value of LW^2 for the artificial cowbird egg by 15% because these eggs are as much as 15% heavier than real eggs of the same dimensions. Comparing the ratios for the species in part A with those for the species in part B gives a rough idea of the ejection capabilities (as relates to egg weight) of the former species. Since the ratios in part B are as small as those in part A or smaller, it is unlikely that a cowbird egg is too heavy for the species in part A to eject.

Ejection is probably limited by the dimensions of the eggs. Egg-shaped objects are difficult for birds to handle with their beaks. The critical factors for ejection are the host's beak and the smallest dimension of the foreign egg; the most important dimension of the beak in this regard is probably the length of the tomlia.

Table 5 lists the ratio of tomial length to the width of the egg that birds either accept (part A) or are known to have ejected (part B). Six of the nine ratios in part B are in the range of 0.62–0.80, which suggests strongly that the birds in part A with ratios of more than 0.7 can eject cowbird eggs. Hence, the last five species in part A should be able to remove cowbird eggs from their nests. In one of my experiments, a phoebe removed an egg much larger than a cowbird egg. Even the two smallest accepters, *Spizella passerina* and *Spinus tristis*, may be capable of ejecting cowbird eggs. Their ratios of 0.62 and 0.63, respectively, equal the smallest ratio in part B, 0.62 for *Serinus sharpei*. Possibly, in these extreme cases where the ratio of beak length-to-egg width is small, the egg is usually speared on the beak rather than carried in it.

I conducted a series of experiments to determine if inability to eject cowbird eggs is responsible for the behavior of the accepters. Four of the accepters were parasitized with miniature cowbird eggs (fig. 1 and table 6). In nearly all cases these eggs were accepted,

although as the ratios in table 6 show, these species are capable of ejecting such small eggs.

In summary, I cannot distinguish clearly between the ejection abilities of accepters and rejecters. Some accepters are fairly small and probably cannot manipulate cowbird eggs as easily as the rejecters, but my analyses indicate that all or nearly all accepters can eject cowbird eggs.

Population size of the host. As with any inherited trait the appearance of incipient rejection behavior requires the occurrence of special genetic events in one or more individuals. The probability of such individuals appearing is proportional to the size of their population. Host species whose total population is small and those in which the parasitized segment of the total population is small may go for longer periods of time than hosts with large populations before features (incipient, genetically determined rejection behavior) appear which selection can act upon.

Hypothesis: Populations exposed to parasitism in accepter species should be so small that their gene pools are depauperate, whereas rejecter species should have larger and presumably more diverse gene pools exposed to parasitism. Most of the species I studied are abundant and widespread. Some species may have relatively little genetic variability but I am unaware of any evidence that such is the case in any North American bird species.

Possibly the population of the Kirtland's Warbler is small enough to forestall effectively the evolution of rejection. This species is harmed greatly by cowbird parasitism. Mayfield (1960, 1961a) attributed its apparent lack of antiparasite adaptations to the fact that it has been exposed only recently to cowbirds. However, its small population, currently about 400 individuals (Mayfield 1973) and possibly as high as 20,000 shortly after it was first parasitized (Mayfield 1960, 1961), may also be a factor since a species with such a small gene pool is unlikely to develop new adaptations rapidly.

Some accepters, which today have nearly all of their widespread populations exposed to cowbird parasitism, may have had only small populations exposed to parasitism before the habitats of North America were altered radically. Eastern Phoebes may have been rare before they were provided with structures that satisfy their specialized nesting needs. Wood Thrushes and Prairie Warblers may have had only slight overlap with cowbirds in primeval times. While the Red-eyed Vireo may have had considerable geographical overlap with the cowbird, the number of individuals exposed to cowbirds may have been relatively small in this arboreal species. It may have been only within the last century that these accepters have had large gene pools exposed to parasitism. But for none of these species is it likely that the gene pool was as small as that of the Kirtland's Warbler.

Characteristics of the host's nest sanitation. I have suggested that ejection evolved from nest sanitation behavior. Thus, species which lack nest sanitation or manifest it only weakly might not evolve ejection as easily as other species.

Hypothesis: Rejecter and accepter species should, respectively, show intense and weak nest sanitation behavior. I am unaware of comparative studies of nest sanitation in North American birds. Nearly all birds practice nest sanitation in similar ways. Experimental studies examining the responses of accepter and rejecter species to foreign objects that occasionally fall into bird nests (small twigs, leaves, fruit) might be valuable, although any heightened degree of nest sanitation in rejecters may be a by-product of their ejection behavior rather than a pre-adaptation.

In the lack of comprehensive data on nest sanitation, it is worth discussing only those few species which are clearly aberrant. The Black-billed Cuckoo, an accepter, often does not remove egg shells after its young have hatched. This could result in difficulty in its evolving ejection behavior, but since cuckoos are almost never parasitized by cowbirds, rejection behavior would have little adaptive value. Unlike other birds, cardueline finches do not carry fecal sacs from their nests although they may occasionally drape them over the sides of the nest (pers. observ.). Of the three cardueline accepters—House Finch, Purple Finch (*Carpodacus purpureus*), and American Goldfinch—only the latter species is a frequent host although all are parasitized

somewhat and would benefit from ejection behavior. Perhaps the evolution of rejection behavior has been retarded in these species because of a lack of a highly developed pre-adaptation. Countering this is the fact that these species remove egg shells and that other workers have shown that carduelines elsewhere practice ejection behavior [*Serinus sharpei* in Africa (Swynnerton 1918) and *Carduelis cannabina* in Europe (Rensch 1924)]. Thus the consideration of nest sanitation fails to produce any strong generalizations regarding accepters and rejecters.

Egg-robbing. Species accustomed to robbing eggs from the nests of other birds might evolve ejection with relative ease since they already possess the motor skills needed to manipulate eggs. However, this factor cannot be of general importance since most species do not engage in egg-robbing.

Hypothesis: Egg-robbing species should be more prevalent among the rejecters than among the accepters. Of the species studied, only the Blue Jay is well known as an egg-robber and it is a rejecter. Grackles and Black-billed Cuckoos, among the few accepters that showed any ejection, are also egg robbers (Bent 1940, 1958). The catbird, a rejecter, is known occasionally to steal eggs (Pearson 1936, p. 178, Part III). Thus, in a few species, egg-robbing behavior, possibly combined with the motor patterns of nest sanitation, may have enhanced the evolution of rejection.

It might be argued that ejection in the Blue Jay is not an antiparasite adaptation but simply a result of the species' egg-eating propensity. It seems likely, though, that selection would have perfected a shut-off mechanism for egg-robbing at a bird's own nest to ensure against self-destruction of its own eggs. Furthermore, virtually all the Blue Jays I studied ejected cowbird eggs (table 1), indicating that ejection itself has been favored by selection and is not merely a by-product of some other attribute such as egg-robbing. If the latter were true, the jays' responses should have been more varied.

Taxonomic affiliation of the host. Certain taxa may have characteristics that enhance or retard the evolution of ejection behavior. For example, the unusual nest sanitation of the carduelines may hinder them from evolving ejection. Some taxa may have relatively little genetic variability. Unknown characteristics may be critical in certain taxa.

Hypothesis: Rejecter and accepter species should sort out along taxonomic lines,

either rejection or acceptance being characteristic of all or most of the members of a taxon. A larger number and diversity of species must be experimented upon before this hypothesis can be tested rigorously. No clear pattern emerges at the familial level with the species studied thus far.

The species in table 1 with two or more records are distributed among 12 families, seven of which are represented by two or more species. Of the seven families, four contain accepters and rejecters: Mimidae—Gray Catbird and Brown Thrasher (rejecters) versus Mockingbird (accepter); Turdidae—Robin versus Wood Thrush; Tyrannidae—Eastern and Western Kingbirds versus Eastern Phoebe; Icteridae—Northern Oriole (only one experiment has been done but this species' status as a rejecter is documented in literature sources cited previously) versus Red-winged Blackbird, Common Grackle, Eastern Meadowlark, and Yellow-headed Blackbird.

The three remaining families with two or more species studied contain only accepters: Hirundinidae—two species, Parulidae—two species, Fringillidae—eight species. Swallows are almost never parasitized, so their status as accepters is to be expected. By contrast, parulids and fringillids are frequent cowbird hosts and the lack of rejection in the species I studied suggests that certain characteristics of these birds make the evolution of rejection difficult. However, rejecters are known among fringillids from other continents (the carduelines cited above). I know of no experimentally demonstrated rejection in parulids, so it may be especially difficult for this family to evolve rejection behavior. More importantly, most wood warblers are forest birds and probably had little contact with cowbirds in the past. Thus, taxonomic affinities yield no generalization regarding accepter and rejecter species.

Other host defenses. This study is primarily directed towards one type of adaptation—rejection of the parasitic egg. Other adaptations are possible, although they are probably not evolved as easily. There is a reduced probability that hosts will evolve rejection behavior if they are protected effectively by some other adaptation.

Hypothesis: Acceptor species should possess host defenses other than rejection behavior that protect them from cowbird parasitism. My experiments would not have revealed host adaptations that function by reducing the likelihood of being parasitized. However, many accepters do not avoid all

parasitism since heavy natural parasitism is often observed. Even if such species possessed adaptations that reduce the incidence of parasitism, rejection of cowbird eggs would still be of obvious value.

Another type of adaptation my experiments would not have uncovered is desertion in response to nest visits by cowbirds, as opposed to desertion in response to cowbird eggs. More often than not, cowbirds deposit their eggs in the host's absence, but cowbirds make other visits to the nest (Mayfield 1961b). At some visits, hosts might detect the cowbird and respond by deserting. I know of no host which definitely deserts in response to visits by cowbirds. Evidence for this would be difficult to gather from nature but could be accumulated experimentally by placing live or mounted cowbird and control birds near active nests. Similar experiments with mounted Common Cuckoos (*Cuculus canorus*) placed near a limited number of nests of European birds supported the common belief that these birds recognize cuckoos as special enemies (Smith and Hosking 1955, Promptov and Lukin in Dement'ev et al. 1966: 496–497).

Evidence concerning whether or not North American birds recognize cowbirds as special enemies is anecdotal and contradictory (Friedmann 1963: 33). However, there is suggestive evidence that a few species evolved nest desertion in response to nest visits by cowbirds. Cardinals, Yellow-breasted Chats (*Icteria virens*), Painted Buntings (*Passerina ciris*), and Field Sparrows (*Spizella pusilla*) all "frequently" desert their nests when parasitized (Friedmann 1963: 35). Until experimentally confirmed, this contention is open to doubt. Nevertheless, it may be no coincidence that these species, the only ones Friedmann listed as frequently deserting when parasitized, have eggs similar to those of the cowbird. This is especially true for the Cardinal and the chat. These species may not easily distinguish cowbird eggs from their own, and adaptations based on egg recognition may be difficult to evolve. Nest desertion, if parasitism is indicated by cowbird visits to the nest, may be the most feasible option. Thus, except for the Cardinal, none of the accepter species I studied seems to possess any adaptation that would reduce the need for rejection behavior. Even in the case of the Cardinal though, rejection accomplished by highly developed egg discrimination would be adaptive since it is more efficient than nest desertion and most Cardinals do not

desert when naturally parasitized (pers. observ.).

DISCUSSION

Accepters and rejecters present a confusing array of species. None of the factors thought to be important in the evolution of host defenses clearly separates the two groups although certain factors may have special importance to particular species. I presume that rejection behavior has evolved only in species where it has been of adaptive value. The puzzle, however, is why rejection behavior has not evolved in all species in which it would be adaptive. The development of a valuable adaptation that requires no gross changes in morphology, ecology, and behavior is a reasonable expectation.

Two factors are of prime importance—the intensity of parasitism and the degree of harm caused by the parasitism. I assume that any species would be harmed by parasitism, so the most critical factor is whether or not a species is parasitized. Some accepters are not parasitized, so their lack of rejection is to be expected, but most are parasitized to some degree. Some of these species may possess an attribute that has retarded the evolution of rejection behavior. For example, the Wood Thrush may be a recent host of the cowbird and the American Goldfinch may lack a suitable preadaptation because of its unusual nest sanitation. However, except for the problem of cowbird-like eggs in the Cardinal, Rufous-sided Towhee, and Song Sparrow, I find none of these arguments convincing.

Since consideration of the accepter species does not yield any generalizations, it might be more valuable to assess those features of the rejecters that seem to have favored the evolution of rejection behavior. I suggest six such factors: (1) eggs unlike those of the cowbird; (2) long history of sympatry with the cowbird; (3) large population size; (4) pronounced nest sanitation; (5) large beaks, allowing ejection with relative ease; and (6) large, easily-found nests. In the rejecters, all of these factors favor the evolution of rejection behavior. But, except for the last two, all are also favorable in most of the parasitized accepters.

Thus, bill size and easily-found nests may be especially important. While all the accepters are probably capable of ejecting cowbird eggs, it is likely that the smaller ones are not able to do so as easily as the rejecters. Ease of ejection, not simply the ability to

eject, may be critical. I assume that a genetic change which results in incipient ejection behavior can appear in an individual of any species. As the expression of this change, individuals exert effort to eject cowbird eggs. In the case of a large-billed bird, the amount of effort may be sufficient to remove the cowbird egg and such a bird will then be selected for. By contrast, in a small-billed species, a genetic change resulting in a similar amount of effort to remove cowbird eggs may not ordinarily suffice to remove the cowbird egg. Unlike the large-billed bird, the small-billed one would not have a selective advantage over conspecifics even though it possessed a comparable genetic trait. Thus, selection for rejection in small-billed species may occur only after an unusually adept individual with the new genetic material appears or after the appearance of perhaps a rarer genetic change programming considerable effort in removing cowbird eggs.

Nest concealment is related to intensity of parasitism. Species with large and/or poorly concealed nests may be parasitized heavily because cowbirds can find their nests with relative ease. Nice (1937) found the incidence of cowbird parasitism of the Song Sparrow to be lowest on those nests she judged to have "excellent" concealment. In general, the nests of rejecters are found more easily than the nests of accepters. My nest-searching efforts may be analogous to those of cowbirds, either currently or when they began to parasitize North American birds. I initially searched for nests at random and experimented on all nests I found. I generally found more nests of rejecter species than of accepters. This is partially shown by the sample sizes in table 1. Often, I was aware of unfound nests of accepters because the birds were in my study areas. Possibly cowbirds also find the nests of rejecters more easily than those of most accepters. This would result in heavier parasitism on rejecters than on accepters (or did in the past). Sometimes I formed search images for the nests of species with relatively easily found nests; this probably increased my parasitization of such species and took pressure off the species with better concealed nests. If this occurs in cowbirds, it would also result in high rates of parasitism on rejecters. Stephen Fretwell (pers. comm.) has suggested that cowbirds should prefer large hosts over small ones since the former are better able to defend their nests against predators and are more likely to be able to provide adequate food for nestling cowbirds. Since the rates of

parasitism on the relatively large rejecters may have been (or still are) especially high, the adaptive value of rejection behavior could have been greater in rejecters than in accepters. Consequently, once suitable genetic material appeared in rejecters it would be selected for more rapidly than in accepters, would be less likely to be lost by drift when still present at a low rate, and would be co-adapted more rapidly into a cohesive unit if multigenic.

However, even the consideration of large bill size and easily-found nests does not explain the lack of rejection in all accepters. Grackles and mockingbirds have easily-found nests, yet experience virtually no natural parasitism; they do not support my contention that easily-found nests lead to high rates of parasitism. Red-winged Blackbirds and Eastern Phoebes have easily-found nests, often experience intense parasitism, and have large bills, yet accept cowbird eggs. I suggest that chance may be responsible for the acceptance of nest parasites by some species (e.g. red-wing and phoebe). Rejection must be molded initially from new genetic material that alters a phenotype in some adaptive way. Accepters may lack rejection largely because the necessary genetic material upon which selection can act has not yet appeared due to random processes. Presumably, suitable genetic material has appeared randomly in the rejecter species while they have been exposed to parasitism.

The presence or absence of rejection behavior (i.e., ejection) has been analyzed largely in the context of its role as an antiparasite adaptation. Consideration of factors dealing with interactions between cowbirds and their hosts has failed to generate strong generalizations. This is what one would expect if ejections were not an antiparasite adaptation but due to some other facet of a species' biology. However, ejection is interpreted most reasonably as an evolved response to cowbird parasitism. The stimulus that triggers ejection behavior—a foreign egg in the nest—cannot occur outside the context of brood parasitism.

If the evolution of ejection requires no large changes in a species' biology (and this seems to be the case), then it might take place easily. However, ejection is an all-or-none trait; if it were multigenic, selection could not begin to favor the genes that code for it until all the necessary genes were present in one individual. Such individuals would be very rare since they

would be the product of more than one improbable genetic event. By contrast, most multigenic characters do not have such a threshold or all-or-none nature and can evolve much more easily. In the case of multigenic traits that are expressed along a continuum, selection can favor individuals who have only some of the genes of the total complex because they may realize some of the increased adaptiveness of individuals who possess all the genes of the complex. Thus if ejection is multigenic, it may be difficult to evolve, in spite of its apparent simplicity. If ejection is multigenic in all species, then accepters and rejecters have had to face the same evolutionary bottleneck. This would not be the case if ejection can be determined by a single gene in rejecter species but requires more than one gene in accepters. But there is no *a priori* reason to expect such genetic differences and the fact that species in the same families, presumably with similar genetic systems, can be accepters or rejecters argues against the view that the potential genetic determinants of ejection have basic differences in rejecter and acceptor species.

Certain parasitic birds (e.g. honeyguides, viduine finches, and some cuckoos) possess highly specialized adaptations such as egg or nestling mimicry or unusual behaviors that result in the death of the host's own young. Since the cowbird lacks comparable adaptations, it has often been cited as a relatively recently evolved parasite. The data presented here which indicate that most North American birds lack antiparasite adaptations also suggest that the host-parasite interactions of the Brown-headed Cowbird are not of great vintage. This situation can be compared to that in European birds which are exposed to parasitism by the Common Cuckoo. Rensch's (1924, 1925) experiments on egg recognition in European birds, while too few to allow any firm quantitative comparisons, suggest that antiparasite adaptations occur more commonly in European than in North American birds since most of the species he tested rejected nonmimetic eggs. Although my experimental techniques differed from Rensch's, we both tested the basic question of whether birds accept nonmimetic eggs placed in their nests; comparisons between our studies are thus meaningful.

SUMMARY

This study is the first systematic attempt to investigate experimentally the presence or absence of antiparasite adaptations in a large

number of actual and potential host species of a parasitic bird. Experiments were conducted by adding artificial Brown-headed Cowbird eggs to 640 nests of 43 species of North American passerine and other small birds. Within each species studied, all individuals tended to either accept or reject cowbird eggs, and the species are easily separable into "accepters" and "rejecters." Of the species with sufficient data, 23 are accepters and 7 are rejecters. Previously, only two North American species were known to reject cowbird eggs frequently. In the absence of experimental data it is not surprising that the true status of the other rejecters has gone undetected since there may be much unseen natural cowbird parasitism with rejecters removing cowbird eggs before observers determine that parasitism has occurred.

Most (80%) rejections were by removal (i.e., ejection) of the cowbird egg. This agrees with time and energy considerations which show that ejection is more adaptive than other possible types of rejection such as nest desertion or egg burial. Ejection is also the most easily evolved type of rejection. Ejection is similar to nest sanitation behavior, which is found in nearly all birds, and it is likely that ejection has evolved from the motor patterns employed in nest sanitation. There are no widespread behavior patterns in birds that could easily have served as pre-adaptations for other types of rejection. Nest desertion and egg burial in apparent response to cowbird eggs usually may be manifestations of behaviors unrelated to host adaptations and may not be evolved antiparasite adaptations.

The central evolutionary questions arising from the results of the experiments are why certain species are accepters and others are rejecters, whether any causal explanations can be found that separate these two groups, and whether investigation of this system gives insight into the nature and evolution of adaptations in general. An assessment of factors thought to be important to the evolution of host defenses fails to generate any strong statements. For example, most or all accepters and rejecters have eggs easily distinguishable from cowbird eggs, long histories of sympatry with the cowbird, and the physical capability to eject cowbird eggs. Rejecters and accepters do not separate taxonomically, since at least four families (Tyrannidae, Mimidae, Turdidae, Icteridae) contain both accepter and rejecter species. The most critical factors may have been nest concealment and bill size.

Easily found nests may have resulted in relatively high rates of parasitism on rejecters, and large bills may have enabled rejecters to evolve rejection more easily than many accepters. Even these factors do not separate clearly all rejecters and accepters. The greatest puzzle is the absence of rejection in many species where it would seem to be of adaptive value. Chance may play an important role in the evolution of rejection behavior, the random occurrence of new genetic types which could lead to rejection behavior being critical.

The results of this study indicate that most North American birds lack host defenses, and support the belief that the host-parasite system of the Brown-headed Cowbird is not a highly evolved interaction.

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