

BEHAVIORAL DEFENSES TO BROOD PARASITISM BY POTENTIAL HOSTS OF THE BROWN-HEADED COWBIRD

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An understanding of avian brood parasitism requires the investigation of a complicated system of co-evolutionary adaptations and interactions between host and parasite. Selection favors parasites which can best utilize their hosts while at the same time favoring hosts which best avoid parasitism. Brown-headed Cowbird (*Molothrus ater*) hosts have several behavioral adaptations for decreasing parasite success. Both nest desertion and nest reconstruction in which a cowbird egg and usually a host egg are buried involve the loss of the host's eggs and the energy required to build a new nest (Friedmann 1963). Ejection of a cowbird egg by a host, which requires accurate discrimination between parasite and host eggs, is probably an energetically preferable defense (Rothstein 1970). Yet all of these anti-parasite defenses operate after the parasite egg is laid and consequently do not prevent the loss of host eggs removed by the parasite. Rothstein (1970:133) pointed out that "the most advantageous form of host adaptation is to avoid being parasitized." One way to avoid parasitism is to guard the nest site with aggressive behavior.

Host aggression towards brood parasites has been recognized most clearly in the European Cuckoo (*Cuculus canorus*) (Rothschild and Clay 1952) and several African cuckoos (Friedmann 1948). Hosts frequently mob cuckoos and may attack when the nest is approached too closely. Edwards et al. (1949) and Smith and Hosking (1955) conducted field experiments on English songbirds using models of European Cuckoos. In general they found that the models were attacked violently by regular host species but not by birds seldom parasitized.

Antagonistic behavior towards the Brown-headed Cowbird has not been investigated previously, and only a few reports of host aggression appear in the literature. Friedmann (1963:33) stated that "On the whole, the majority of American species of passerine birds do not act as if they recognize an enemy in the cowbird." However, in an earlier work (Friedmann 1929:195) he stated "most birds are so vigilant of their nests that often a laying

cowbird must be subject to considerable attack, or at least be the witness of many intimidation displays on the part of the victim."

Selander and LaRue (1961) reviewed the literature on host aggression to cowbirds. Aggressive host-parasite interactions have been reported for the Song Sparrow (*Melospiza melodia*) by Nice (1943). She observed a few instances when Song Sparrows actually attacked a female cowbird. The American Redstart (*Setophaga ruticilla*) is also aggressive to Brown-headed Cowbirds. Female Redstarts seem to recognize the cowbird specifically and to distinguish between cowbirds and other similar species. Threat displays are directed at an intruding cowbird and violent attacks occur if the female approaches the nest (Hickey 1940, Ficken 1961). Violent encounters also have been reported for the Robin (*Turdus migratorius*; Friedmann 1929), Red-eyed Vireo (*Vireo olivaceus*; Prescott 1947), and Redwinged Blackbird (*Agelaius phoeniceus*; Sutton 1928, Selander and LaRue 1961). However, extensive studies of the Ovenbird (*Seiurus aurocapillus*) by Hann (1937) and the Yellowthroat (*Geothlypis trichas*) by Hofslund (1957) revealed no antagonistic interactions with cowbirds, even though these species are heavily parasitized (Young 1963).

Selection may also favor behavior in cowbirds which minimizes host aggressiveness. Selander and LaRue (1961) described a behavioral pattern in which a cowbird, close to an individual of another species, bows its head and ruffs its neck feathers in an "invitation to preening display." They suggested that this is an aggression-reducing posture, or at least one that redirects the other bird's aggression into less harmful displacement activities such as heteropreening (Harrison 1964).

The purpose of our study was to determine the degree to which certain Brown-headed Cowbird hosts have developed a defensive strategy that incorporates aggressive behavior. Our hypothesis is that in this instance natural selection favors hosts which can avoid parasitism and that the greater the incidence of parasitism, the greater the selective pressures

favoring the evolution of anti-parasite defenses. The intensity of selection is determined by the magnitude of the decrease in host reproductive success due to egg removal by cowbirds and competition between host and parasite nestlings (Rothstein 1970, 1975). Rothstein calls hosts that regularly eject cowbird eggs, "rejecters," and those that do not, "accepters." The ejection of cowbird eggs is an efficient anti-parasite defense that effectively reduces losses due to nestling competition. Nevertheless, it would be adaptive for rejecters to repel cowbirds from their nesting area aggressively if this behavior reduced mortality due to egg stealing by cowbirds. However, for an accepter species, aggressive defense of the nesting area is probably the best defense, and natural selection for this behavior should be greater than for rejecters because accepters suffer from both mortality factors. Therefore, one can predict that accepters will behave, in general, more aggressively towards cowbirds than rejecters; the greater the selection pressure for anti-parasite defenses, the greater will be the host's aggressiveness.

METHODS

Our study was conducted during the summers of 1972-1974, in the vicinity of Kingston, Ontario, Canada. We investigated host responses to Brown-headed Cowbirds by locating active nests of 15 potential host species, and then recording the host's responses to models of Brown-headed Cowbirds and other species positioned near the nest. The purpose of field testing was to simulate a natural encounter.

Preliminary model testing was conducted in 1972. In 1973-1974, 265 model tests were carried out. All testing was done on nests containing eggs prior to or early in incubation. Models were located 0.5 m from the test bird's nest and level with it. In a primary testing sequence each model was in place 5 min for each test, and only three models, a sparrow, a normally postured cowbird, and a bowed posture cowbird, were presented in a random sequence to each nesting pair. A 5 min rest period was allowed between each presentation. Two series of secondary tests were conducted at previously tested nests, and these are treated separately below. The behavior of each nesting pair was observed and recorded from a blind located at least 15 m from the nest and model.

In order to also test the functionality of Selander and LaRue's (1961) "invitation to preening display" in a natural environment, we presented five different types of models: (1) male cowbird in normal posture; (2) male cowbird bowed (in an invitation to preening display posture); (3) female cowbird in normal posture; (4) female cowbird bowed; (5) sparrow model. Three types of sparrow models were used: Song Sparrow, Savannah Sparrow (*Passerculus sandwichensis*), and House Sparrow (*Passer domesticus*). By presenting normally postured and bowed cowbird models we tested Selander and LaRue's hypothesis. Presentation of the sparrow model provided a basis for comparison of host responses to the cowbird models.

Birds were positioned in the various postures and freeze-dried. The models were then drilled through the long axis of the abdomen. A hardwood dowel (0.75 cm \times 10.0 cm) was glued into the body allowing the model to be positioned easily in the field using an adjustable pole clamp. Freeze-dried models are remarkably life-like, very durable, and easily prepared.

In presenting stimuli to any test individual for the purpose of observing behavioral responses, two sources of error must be considered, i.e. habituation and carry-over of aggression (or any response) from a previous stimulus. In order to determine the effect of these components on our results, we presented long series of models in variable order during the preliminary testing. Habituation became noticeable after four models had been positioned for 5 min each with no rest periods. After reducing the tests to a series of three models with 5 min between each, we detected no habituation. In order to randomize any carry-over effects, we presented the models in random order.

A nesting pair of hosts was classified and scored for aggressiveness on the basis of its behavioral response to a model during the 5 min period of observation. Neighboring birds occasionally responded during the tests, and their behavior was noted but not figured in the score for the nesting pair. All activities closer than 5 m were arbitrarily designated as "close," and those 5 m or more away were designated as "distant." The categories in order of increasing aggressiveness are as follows: (1) distant, silent observation of the model; (2) close, silent observation; (3) distant alarm calling; (4) close alarm calling; (5) fly-by investigation (a flight over the model and nest); (6) nest attentiveness (perching beside the nest, between it and the model, or sitting on the eggs before the incubation stage begins); (7) skulking or hovering near the model; (8) distraction by means of wing flapping, alarm calling, and broken wing displays; (9) attacking the model by pecking and striking with the wings; (10) dual attack (simultaneous attack by both parents).

The ratings, of course, are subjective in that the rater made a judgment as to the correspondence between the behavior and the category. However, all ratings were made by one person (RFN).

The observed behavior was classified with respect to one or more of the above categories and scored from one to four according to the duration of the response as follows: (1) response given briefly or only once; (2) response given several times or continuously for up to 1 min; (3) response given for 1 to 3 min; (4) response given for 3 to 5 min.

The relative aggressive value of the host's behavior towards a model was calculated as the sum of the products of each category number and its duration score. For example, a host which skulked and hovered around the model for 2 min, then displayed nest attentiveness by guarding the nest for 40 sec, and finally attacked the model briefly, would have a score of 42 ($7 \times 3 + 6 \times 2 + 9 \times 1$). Using this scheme, one can calculate average responses for host species and individuals and determine differences in responses. Understandably large differences exist between the behavioral repertoires of each host due to the taxonomic diversity of the species studied and their variable levels of sociality. However, it is desirable to standardize the recording of behavioral responses in broad categories to facilitate inter-specific comparisons.

Fifteen species of potential cowbird hosts were tested. They are grouped in two categories according

TABLE 1. Differences in mean aggressiveness to models of nondescript sparrows, ♀ Cowbirds in normal posture, and ♀ Cowbirds bowed, at Kingston, Ontario. Mean response calculated as described in text.

| Host species | % Incid. Parasitism ^a | Nondescript sparrow ^b | P ^c | ♀ Cowbird normal ^b | P ^c | ♀ Cowbird bowed ^b |
|---------------------|----------------------------------|----------------------------------|----------------|-------------------------------|----------------|------------------------------|
| Robin | 0.2 (2353) | 1.6 (6) | NS | 2.0 (6) | | — |
| Eastern Kingbird | 0.8 (339) | 28.6 (7) | < 0.025 | 50.4 (7) | NS | 42.0 (6) |
| Grey Catbird | 1.6 (414) | 17.8 (6) | < 0.025 | 27.0 (6) | | — |
| Redwinged Blackbird | 2.4 (2039) | 11.0 (13) | < 0.005 | 36.0 (11) | NS | 39.5 (8) |
| American Goldfinch | 3.6 (274) | 19.3 (3) | NS | 29.6 (3) | | — |
| Eastern Phoebe | 7.4 (499) | 34.6 (9) | NS | 48.1 (9) | NS | 36.6 (6) |
| Bobolink | 10.3 (58) | 42.5 (2) | NS | 56.5 (2) | NS | 37.5 (2) |
| Swamp Sparrow | 16.0 (25) | 31.0 (3) | NS | 38.0 (3) | | — |
| Traill's Flycatcher | 16.6 (72) | 46.0 (1) | NS | 95.0 (1) | NS | 103.0 (1) |
| Field Sparrow | 22.2 (117) | 32.5 (2) | NS | 46.0 (2) | | — |
| Song Sparrow | 22.5 (510) | 24.3 (6) | < 0.025 | 63.2 (11) | < 0.025 | 51.0 (7) |
| Red-eyed Vireo | 26.2 (80) | 29.5 (4) | NS | 62.7 (4) | NS | 48.3 (3) |
| Chipping Sparrow | 29.5 (713) | 29.0 (3) | NS | 39.5 (4) | NS | 35.0 (1) |
| Yellow Warbler | 29.5 (459) | 14.2 (5) | NS | 36.6 (5) | | — |
| Wood Thrush | 33.3 (54) | 20.0 (1) | NS | 40.0 (1) | | — |

^a Data from Ontario Nest Records Scheme, 1960–1972, and this study. No. of nests indicated in parentheses.

^b No. of nests tested indicated in parentheses.

^c P = probability that means in the adjacent columns are different by chance. Probabilities calculated using Wilcoxon sign-rank test for paired observations. NS = no significant difference between means.

to Rothstein's (1970) classification of host responses to artificial cowbird eggs. Traill's Flycatchers (*Empidonax traillii*), Bobolinks (*Dolichonyx oryzivorus*), and Swamp Sparrows (*Melospiza georgiana*) are assumed to be accepters because of their high incidences of parasitism. Accepters include the Traill's Flycatcher, Eastern Phoebe (*Sayornis phoebe*), Wood Thrush (*Hylocichla mustelina*), Red-eyed Vireo, Yellow Warbler (*Dendroica petechia*). Redwinged Blackbird, Bobolink, American Goldfinch (*Spinus tristis*), Field Sparrow (*Spizella pusilla*), Chipping Sparrow (*Spizella passerina*), Swamp Sparrow, and Song Sparrow. Rejecters include the Eastern Kingbird (*Tyrannus tyrannus*), Catbird (*Dumetella carolinensis*), and Robin.

The overt response of a host to a model can be regarded as the outcome of several conflicting behavioral drives, such as approach and retreat, and the size of the model could affect the host's response. Thus, the differential response of a host to cowbird and sparrow models could be due to the smaller size of the sparrow model relative to the cowbird. In order to test this hypothesis we conducted a second series of model tests at seven previously tested Song Sparrow nests by presenting female cowbird, Savannah Sparrow, and female Redwinged Blackbird models in a random order. All nests were in early incubation phase. Female Redwinged Blackbirds are slightly larger than cowbirds and therefore, if model size is a major factor contributing to response differences, then one would expect responses to the blackbird model to be greater than responses to either cowbird or sparrow models. In order to test whether host responses to models of normal posture male and female cowbirds were equal, we conducted a series of trials on 27 previously tested host nests (Yellow Warbler, Song Sparrow, Red-eyed Vireo, Eastern Phoebe, Redwinged Blackbird, and Eastern Kingbird).

RESULTS

Preliminary tests during 1972 indicated that some hosts, including Bobolinks, Redwinged Blackbirds, and Yellow Warblers, displayed

markedly aggressive behavior towards cowbird models. The results of the 1973–74 tests are listed in table 1 along with the incidence of parasitism for each species. Every species tested was more aggressive to cowbird models than to sparrow models. The differences are statistically significant for Redwinged Blackbirds, Eastern Kingbirds, Grey Catbirds and Song Sparrows, and larger sample sizes will probably add statistical significance to the responses of the remaining species. The sparrow model tests simulate an encounter between a nesting host and another harmless, cohabiting species, so the differential response to cowbird vs. sparrow models strongly suggests that some hosts have a definite discriminative ability.

In the secondary series of tests using different-sized models at Song Sparrow nests, aggressiveness toward the Redwinged Blackbird model was intermediate between the responses to the other models, with mean values of 62.9, 41.7, and 27.7 to cowbird, blackbird, and sparrow, respectively. The mean response to the cowbird is significantly greater ($P \leq 0.025$, Wilcoxon sign-rank test) than that to the other two which were not significantly different ($P \geq 0.05$). These Song Sparrow responses support the hypothesis of selective host discrimination between cowbirds and other similarly sized or smaller birds, so that model size differences seem to be a minor influence on host response.

In the secondary series of tests no statistically significant difference occurred in host responses to randomly presented male and female models ($P > 0.05$, Wilcoxon matched

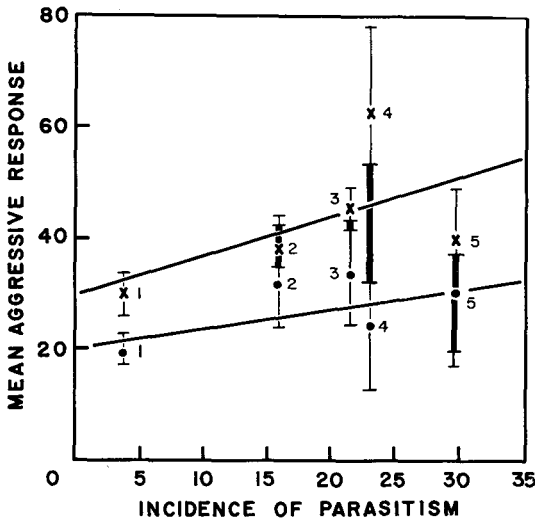


FIGURE 1. Mean aggressive responses of: (1) American Goldfinches, (2) Swamp Sparrows, (3) Field Sparrows, (4) Song Sparrows, and (5) Chipping Sparrows to normal posture female cowbird (X) and sparrow (●) models in relation to incidence of parasitism. The ranges of responses are represented by thin vertical lines, or in areas of overlap, by thicker lines.

pairs sign-rank test). However, female cowbird models were used in the primary tests because females usually search for and parasitize host nests alone (Norman and Robertson 1975).

In general, the lower level responses observed for infrequent hosts and rejecter species consisted of alarm calling and silent scrutiny of the model. Intense responses given by major host species usually included nest attention, hovering near the model, and distraction and attack displays. Redwinged Blackbirds, Eastern Kingbirds, Eastern Phoebes, Traill's Flycatchers, Song Sparrows, and Red-eyed Vireos frequently attacked the cowbird models.

A wide range of responses is indicated for the different host species. The results for the fringillids (fig. 1) illustrate the relationship between each species' aggressiveness towards

cowbirds and the frequency with which it is parasitized. A positive relation is indicated for these five species. However, although the correlations are positive ($r = 0.7$, parasitism and cowbird model; $r = 0.4$, parasitism and sparrow model; Spearman rank correlation test), they are not statistically significant for the present sample sizes. A similar positive relationship also holds for the three flycatchers tested (cf. table 1, $r = 0.4$).

Interspecific differences in response to a given model could be affected by size of the model relative to the size of the species tested, such that large hosts behave more aggressively than small ones. This relationship does not obtain in the fringillid or tyrannid responses. The five finch species are approximately equal in size, so a relatively uniform size relationship with a cowbird model exists. Host aggressiveness, however, increased with incidence of parasitism. Similarly for the three tyrannids aggression increased with increasing parasitism despite a decrease in host size from the Eastern Kingbird to the Traill's Flycatcher.

Aggressive responses by Eastern Kingbirds, Bobolinks, Eastern Phoebes, Song Sparrows, Chipping Sparrows, and Red-eyed Vireos to female cowbird models in the head bowed posture were usually intermediate between responses to normal posture cowbird models and sparrow models (table 1). Although these results are consistent with Selander and LaRue's (1961) hypothesis, only Song Sparrow responses differed significantly (table 1).

Redwinged Blackbirds reacted, on the average, more aggressively to a bowed than to a normal postured model; however, the difference is not statistically significant. The appeasement function of bowing seemed to be lacking from Redwinged Blackbirds. In fact, these birds were more aggressive to bowed male cowbird models than to male cowbird models in an aggressive bill-pointing posture. Head bowing in the cowbird bears some resemblance to the blackbird song spread display, an agonistic territorial display. Thus, it

TABLE 2. Mean intensity of attack behavior by several species in response to cowbird models in normal and bowed postures. Calculated from response categories 9 and 10 only.

| Host species | Mean attack response per trial ^a | | |
|---------------------|---|---------|---------------|
| | Normal posture | P^b | Bowed posture |
| Eastern Kingbird | 13.8 (8) | < 0.005 | 9.1 (8) |
| Eastern Phoebe | 10.3 (11) | < 0.005 | 1.8 (11) |
| Redwinged Blackbird | 15.8 (16) | < 0.05 | 11.6 (16) |
| Song Sparrow | 23.1 (8) | < 0.025 | 6.9 (8) |

^a No. of trials indicated in parentheses.

^b Probabilities calculated using Wilcoxon sign-rank test for paired data. P = probability that means in the adjacent columns are different by chance.

TABLE 3. Frequency of displacement behavior sequences per trial in response to cowbird models in normal and bowed postures. A displacement behavior sequence is defined as a discrete bout of activities such as preening.

| Host species | \bar{x} No. displacement sequences per trial ^a | | |
|---------------------|---|-----------------------|---------------|
| | Normal posture | <i>P</i> ^b | Bowed posture |
| Eastern Kingbird | 0.125 (8) | NS | 0.375 (8) |
| Eastern Phoebe | 0.375 (11) | < 0.05 | 1.125 (11) |
| Redwinged Blackbird | 0.059 (16) | < 0.025 | 0.688 (16) |
| Song Sparrow | 0.000 (8) | < 0.05 | 0.750 (8) |

^{a, b} As in footnotes, table 2.

is possible that the bowed cowbird posture is interpreted as a weak song spread display, unaccompanied by vocalization.

Table 2 lists the mean attack responses (categories 9 and 10) of four host species to normal and bowed posture cowbird models. Male and female models in both postures were used, but this should not bias the data as models of both sexes were presented in the same ratios in both postures. Also, host responses did not differ significantly according to sex of the cowbird model. Not only was overall aggressiveness to cowbirds in a head bowed posture reduced, but bowed models were less frequently and less intensely attacked than normally postured models. Selander and LaRue (1961) described cowbirds in an aviary soliciting preening by other birds with the "invitation to preen display," and often being preened. In our study we never saw allopreening of the bowed models by the test birds. However, bowed models frequently elicited bill wiping, pecking of the ground, perch, or grass stems, autopreening, and copulation attempts, all interpreted as displacement activities (table 3).

Eastern Kingbirds, Redwinged Blackbirds, and Phoebes exhibiting displacement behavior attacked bowed cowbird models less intensely than in trials when they did not exhibit such behavior (table 4). However, the differences are significant only for Redwinged Blackbirds, and the relation is reversed in Song Sparrows. Nevertheless, it seems that an aggressive drive may be redirected into displace-

ment behavior in a conflict situation; thus the posture could have an appeasement function.

Group responses by hosts to cowbird models were observed several times. In 1972 nine model trials were conducted on Bobolinks. During one experiment, the pair of Bobolinks being tested attacked the model, and another pair flew excitedly around the model and nest area giving alarm calls. Then a male Redwinged Blackbird joined in giving its alarm calls.

Redwinged Blackbirds frequently responded in groups to models positioned beside marsh nests. Usually a male from an adjacent territory would fly and hover 5–10 m above the model. Group responses did not seem to be influenced by the nesting stage of the responding neighbors, as some nests had eggs and some young. However, group responses were most frequently displayed by birds nesting at high densities in the marsh colonies. Early in the nesting season neighboring males often were excited by models, but test males were very defensive of their territories, and intruding males were driven away. Later in the nesting season males were more tolerant and paid little attention to intruding males, directing their behavior at the models. The late season group response was quite similar to Redwinged Blackbird group mobbing of aerial and terrestrial predators.

Some incidental interaction between live cowbirds and several actual and potential hosts was observed during 1973. On 25 May a female cowbird perched 3 m from an un-

TABLE 4. Intensity of attack behavior toward male and female bowed cowbird models in relation to occurrence of displacement behavior. Calculated from response categories 9 and 10 only.

| Host species | \bar{x} attack response for trials ^a | | |
|---------------------|---|-----------------------|--------------------------|
| | With displacement behavior | <i>P</i> ^b | No displacement behavior |
| Eastern Kingbird | 0.0 (3) | NS | 12.8 (5) |
| Eastern Phoebe | 1.1 (8) | NS | 4.5 (2) |
| Redwinged Blackbird | 8.1 (10) | < 0.05 | 13.8 (8) |
| Song Sparrow | 7.4 (5) | NS | 3.6 (5) |

^{a, b} As in footnotes, table 2.

parasitized Red-eyed Vireo nest. A vireo attacked the cowbird, pecked and pursued it, giving threat and alarm calls. On 26 May the nest contained a fresh cowbird egg, and a pair of cowbirds were perched 10 m from the nest. Two vireos swooped at the cowbirds, but the cowbirds seemed unconcerned and remained in the vicinity for 5 min.

Interactions between cowbirds and Northern Orioles (*Icterus galbula*) were noted on three occasions. On 25 May, a female cowbird investigated an oriole nest which contained eggs. The female oriole returned to the nest and checked the contents while the cowbird sat nearby, silently watching. Then the oriole chased the cowbird, giving alarm calls.

While watching another Northern Oriole nest on 16 June, we witnessed a male oriole attack and pursue a male cowbird for about 1 min. Before detection, the cowbird was perched about 4 m from the oriole nest. At another nest on 21 June, a female oriole vigorously and repeatedly attacked two pairs of cowbirds perched in the nest tree.

A group response by Redwinged Blackbirds in a marsh colony was observed on 22 May 1973. A male cowbird flew into the marsh and perched near the center of the colony. Immediately three male blackbirds chased it out and across a field for several hundred meters. This was the only cowbird observed entering this marsh in four weeks though cowbirds were common in the adjacent upland habitats.

No "invitation to preening" displays or other appeasement postures were observed during any of the above interactions. In every case the cowbirds flew away immediately or soon after being attacked.

DISCUSSION

It is important to view a brood parasite-host interrelationship as a dynamic system. For example, one can imagine that over a series of generations a susceptible, and hence highly parasitized, host will evolve various anti-parasite defenses. The initial level of parasitism may be determined by the innate aggressiveness of the new host, the suitability of the host's habitat for cowbirds, and the suitability of the host in terms of abundance, size, incubation period, nesting season, and the type of food it feeds its young, all of which regulate cowbird natality and fledging success (Young 1963, Mayfield 1965). The similarity of the host eggs and parasite eggs and the innate aggressiveness of the host are crucial factors in determining which defense strategy evolves.

If the host lays eggs that are distinct from cowbird eggs in size or color (e.g., a Robin egg), then rapid selection for egg discriminative ability can occur.

For hosts laying eggs of a size and color pattern similar to cowbird eggs, rejection is precluded as a defense strategy. Over a long period, selection for egg recognition can favor a differently colored egg, and thus an egg rejection defense can evolve (Fretwell 1973). However, an aggression type defense may evolve much faster. The first requirement for aggressive defense is the ability of the host to discriminate between cowbirds and other harmless cohabiting songbirds. Differential responses to cowbird and sparrow models suggest that cowbird hosts have this ability and that discrimination may increase with intensity of parasitism over the long term.

The results of our study seem to show that acceptor hosts display a level of aggressiveness proportional to the intensity to which they are parasitized. This positive relationship is especially clear within families such as the Fringillidae. The differences between families probably are related to different phylogenetic histories rather than to any effect of parasitism. Furthermore, the lower aggressiveness of rejecter species compared to confamilial accepters suggests that egg ejection is more effective than aggression, perhaps because ejecting a cowbird egg is more efficient energetically than maintaining a constant watch at the nest.

It may be argued that, in fact, the cause and effect relationship between incidence of parasitism and host aggression is the opposite of that presented. The hypothesis that more aggressive hosts are more likely to be parasitized because the cowbird uses the host behavior to find its nest can account for some of the trends in our results. According to this hypothesis, aggression is maladaptive, because reacting to cowbirds increases the chance of being parasitized. Seppa (1969) observed a European Cuckoo locating host nests in response to host alarm calling and mobbing, and a similar phenomenon was suggested by Ficken (1961) for cowbirds and the American Redstart. For the most part, however, cowbirds seem to observe nest construction or search directly for host nests (Norman and Robertson 1975). Also this hypothesis cannot account for the differences in parasitism of equally aggressive species, either within families, or between families (e.g., Eastern Phoebe and Eastern Kingbird).

Rothstein (1974) showed that egg rejection

defenses have both learned and innate components. Is aggressive defense inherited as a fully developed response, or is it learned as the result of experience with cowbirds? Indirect evidence suggests the latter. Nice (1943: 153), writing about encounters between Song Sparrows and Cowbirds, noted that "recognition of the Cowbird was something learned not innate, in the sparrows," and further, "The antagonistic actions of the sparrows to the Cowbirds seemed to depend on some conditioning of their past experience, either in early life or later."

Some of the results of our testing are consistent with the notion of a learned response. Individual hosts showing the greatest responses to cowbird models are not especially aggressive toward sparrow models; individuals showing the lowest aggression to cowbirds displayed similar responses to sparrow models. Thus it seems that experienced and inexperienced pairs of hosts may exist. Intermediate levels of response may be due to intermediate levels of experience with cowbirds (one vs. two or three seasons), and matings of experienced and inexperienced birds.

Nevertheless, it is difficult to understand the means of the learning reinforcement. Possibly, aggressiveness toward cowbirds is merely a manifestation of a general anti-predator mechanism whereby birds learn to be selectively aggressive toward any intruder at the nest site.

Although aggressive behavior may be a defense against parasitism, it does not necessarily insure safety from it. Rothschild and Clay (1952) reported that host aggression towards the European Cuckoo generally is not a successful defense. The parasite need only wait until the nest is unattended and then lay her eggs. Brown-headed Cowbird females lay their eggs at dawn when nests are unattended. Thus cowbirds still can parasitize hosts which defend their nest. Our observations of a Red-eyed Vireo attacking a female cowbird, and subsequently being parasitized strengthen this notion.

On the other hand, even if attack defenses are not effective at keeping the cowbird from eventually visiting a nest it has discovered, they can prevent cowbirds from locating nests in the first place. It is dangerous for a cowbird to search for nests in a habitat with predominantly aggressive hosts, especially if they respond as a group. Group responses by Bobolinks and Redwinged Blackbirds are an example. None of 363 nests in five blackbird marsh colonies in the Kingston area during

1972-1973 was parasitized, but 22.8% of 35 upland nests were (Robertson, unpubl. data).

Friedmann (1963) cited numerous similar cases where colonially nesting Redwinged Blackbirds were little parasitized compared to scattered upland nesters; he mentioned the indirect protection their behavior affords to other host species nesting near the colonies. The major difference between the nesting populations in these habitats is density of aggressive, territorial males. It appeared that cowbirds could not penetrate the dense colonies but were relatively free to move about the upland habitat where Redwinged Blackbirds were too widely dispersed to allow effective group mobbing. Birds nesting in aggregations benefit from increased detection of cowbirds and predators in addition to advantages of group mobbing to discourage their presence. Theoretically, a similar group response by several different species together could function with equal effect to decrease the likelihood of parasitism.

Selander and LaRue (1961) hypothesized that the "invitation to preening posture" is an appeasement posture enabling cowbirds to investigate an aggressive host's nest and also escape serious injury if attacked. Our results are consistent with this thesis in that aggressiveness towards bowed models was lower for several important hosts, and the frequency and intensity of attacks on bowed models tended to be lower.

Harrison (1964) discussed the close link between aggressive behavior, appeasement postures, and allopreening as displacement behavior in what appears to be a conflict situation. Selander and LaRue (1961) and Rothstein (1971), working with captive cowbirds, observed allopreening as a frequent response to a bowing cowbird. Although our testing with models in the field yielded no allopreening, we frequently saw other displacement activities. Displacement behavior, therefore, seems to be the common factor of these studies, and it appears that the head bowed posture can function as appeasement behavior.

Although Selander and LaRue (1961) suggested that head bowing functions interspecifically as appeasement, it is possible that this posture originated as an intra-specific communication. The notion that head bowing may serve for communication between cowbirds is strengthened by Rothstein's (1971) conclusion that the posture is aggressive, and that cowbirds use it to maintain dominance hierarchies and integrate social units. Indeed, very few "invitation to preening displays" have

been observed in nature. Selander and LaRue observed cowbirds soliciting House Sparrows, Redwinged Blackbirds, and a Scissor-tailed Flycatcher (*Muscivora forficata*). Dow (1968) observed solicitation of Cardinals (*Cardinalis cardinalis*) only once during 68 hr of observation and Darley (1968) only once in 300 hr. During our investigation, only one allopreening display (a female cowbird soliciting a House Sparrow) was witnessed. Thus we have a paradox in that an apparently advantageous and functional display seldom is used interspecifically in nature.

SUMMARY

Field experiments using cowbird models at the nests of various species were conducted. The hypothesis that potential hosts of the Brown-headed Cowbird use behavioral defenses of an intensity directly proportional to the intensity to which they are parasitized was tested. In general, the hypothesis was supported; within taxonomic families, a direct positive relationship exists between aggressive responses to cowbird models and the intensity of parasitism suffered. We reject the alternative hypothesis that host aggression is used by cowbirds in nest location, and thus that the relationship between host aggressiveness and intensity of parasitism occurs for that reason.

The hypothesis that the Brown-headed Cowbird head bowing invitation to preen posture functions as an appeasement display was tested using postured cowbird models at nests of several host species. In general, hosts were less aggressive towards cowbirds in the bowed posture than towards those in a normal posture.

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LITERATURE CITED

- DARLEY, J. A. 1968. The social organization of breeding Brown-headed Cowbirds. Ph.D. diss., Univ. Western Ontario, London, Ontario.
- DOW, D. D. 1968. Allopreening invitation display of a Brown-headed Cowbird to Cardinals under natural conditions. *Wilson Bull.* 80:494-495.
- EDWARDS, G., E. HOSKING, AND S. SMITH. 1949. Reactions of some passerine birds to a stuffed cuckoo. *Br. Birds* 42:13-19.
- FICKEN, M. S. 1961. Redstarts and cowbirds. *Kingbird* 11:83-85.
- FRETWELL, S. 1973. Why do Robins lay blue eggs? *Bird Watch* 1:1, 4.
- FRIEDMANN, H. 1929. The cowbirds, a study in the biology of social parasitism. Charles C Thomas, Springfield, Ill.
- FRIEDMANN, H. 1948. The parasitic cuckoos of Africa. *Washington Acad. Sci. Monogr.* 1:1-204.
- FRIEDMANN, H. 1963. Host relations of the parasitic cowbirds. *Smithson. Bull.* 233:1-276.
- HANN, H. W. 1937. Life history of the oven-bird in southern Michigan. *Wilson Bull.* 49:145-237.
- HARRISON, C. J. O. 1964. Allopreening as agonistic behavior. *Behavior* 24:161-209.
- HICKEY, J. J. 1940. Territorial aspects of the American Redstart. *Auk* 57:255-256.
- HOFSLUND, P. B. 1957. Cowbird parasitism of the Northern Yellow-throat. *Auk* 74:42-48.
- MAYFIELD, H. 1965. The Brown-headed Cowbird, with old and new hosts. *Living Bird* 4:13-28.
- NICE, M. M. 1943. Studies in the life history of the Song Sparrow, II. *Trans. Linn. Soc. N. Y.* 6:1-328.
- NORMAN, R. F., AND R. J. ROBERTSON. 1975. Nest searching behavior in the Brown-headed Cowbird. *Auk* 92:610-611.
- PRESCOTT, K. W. 1947. Unusual behavior of a cowbird and a Scarlet Tanager at a Red-eyed Vireo nest. *Wilson Bull.* 59:210.
- ROTHSCHILD, M., AND T. CLAY. 1952. Fleas, flukes and cuckoos: a study of bird parasites. Collins, London.
- ROTHSTEIN, S. I. 1970. An experimental investigation of the defenses of the hosts of the parasitic Brown-headed Cowbird (*Molothrus ater*). Ph.D. diss., Yale Univ., New Haven, Conn.
- ROTHSTEIN, S. I. 1971. A reanalysis of the interspecific invitation to preening display as performed by the Brown-headed Cowbird (*Molothrus ater*). *Am. Zool.* 11:89.
- ROTHSTEIN, S. I. 1974. Mechanisms of avian egg recognition: possible learned and innate factors. *Auk* 91:796-807.
- ROTHSTEIN, S. I. 1975. Evolutionary rates and host defenses against avian brood parasitism. *Am. Nat.* 109:161-176.
- SELANDER, R. K., AND C. J. LARUE, JR. 1961. Interspecific preening invitation display of parasitic cowbirds. *Auk* 78:473-504.
- SEPPA, J. 1969. The cuckoo's ability to find a nest where it can lay an egg. *Ornis Fenn.* 46:78-80.
- SMITH, S., AND E. HOSKING. 1955. *Birds fighting*. Faber and Faber Ltd., London.
- SUTTON, G. M. 1928. The birds of Pymatung Swamp and Commeaut Lake, Crawford County, Pennsylvania. *Ann. Carnegie Mus.* 18:19-239.
- YOUNG, H. 1963. Breeding success of the cowbird. *Wilson Bull.* 75:115-122.

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