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INTERSPECIFIC PREENING INVITATION DISPLAY OF PARASITIC COWBIRDS

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BROOD parasitism holds special interest for the student of behavior, since adoption of this highly specialized way of life, which has evolved independently in five avian families (Miller, 1946), involves not only the loss of nesting and parental behavior but also the development of a complex of new patterns of behavior adapting the parasite to the host. Specialization for parasitism is most marked in the European Cuckoo (*Cuculus canorus*) and related forms of the subfamily Cuculinae (Chance, 1940) and perhaps least so in the cowbirds (Icteridae) of the New World, which have very closely related, nonparasitic relatives and have had a comparatively short evolutionary history as parasites (Friedmann, 1929, 1955). A considerable volume of information on cowbirds has been provided by the pioneer work of Friedmann (1929) and later studies by Nice (1943), Hann (1941), Norris (1947), Laskey (1950), Mayfield (1960, 1961a and b), and others, but we are still far short of an adequate understanding of the biology of these birds. In particular, the complex behavioral interactions occurring between parasite and host, both at the time of egg laying by the cowbird and during the course of development of the cowbird in the care of the foster parents, are essentially unknown.

Early in the course of studies on the behavior of the Brown-headed Cowbird (*Molothrus ater*), beginning in February 1959, we noted that captive cowbirds persistently approached individuals of certain other species of birds and invited heteropreening of the head and neck by adopting a special head-bowed posture (Figure 1). Surprisingly enough, repeated presentation of this display was often effective in inducing other species to preen the cowbirds' plumage. Subsequently, we obtained a number of field records of this behavior in Brown-headed Cowbirds, and a similar display was seen in captive Red-eyed Cowbirds (*Tangavius aeneus*). It would seem, therefore, that heteropreening invitation is a regular, although hitherto unstudied, part of the behavioral

repertoire of these parasitic icterids. The behavior is all the more unusual in that cowbirds only infrequently direct the invitational display to members of their own species and do not themselves indulge in social heteropreening.

The present report deals almost entirely with preening invitation in the Brown-headed Cowbird, and, unless otherwise indicated, the term "cowbird" refers to that species. It is our hope that this paper will stimulate other workers to observe and report further instances of the use of this display by cowbirds in the field, since the significance of this behavior can be judged only when an abundance of field records is available.

DISCOVERY OF THE DISPLAY

The display was first seen on 27 February 1959, while we were observing a group of 22 Brown-headed Cowbirds in a large, outdoor aviary. A male cowbird approached a female cowbird and displayed, at which point the female flew. Later in the day, a male directed display to another male resting on a perch; and, as the displaying bird approached, the resting bird pecked it away.

When this behavior was first observed, we suspected that it represented an intraspecific display in some way associated with courtship or pair formation. However, this supposition proved to be erroneous, and the normal use of the display became apparent when other species of birds were placed in the aviary with the cowbirds. On 3 March, a few minutes after a meadowlark (*Sturnella*) was introduced, several cowbirds approached it and displayed. At first the meadowlark simply retreated to a new position, often flying to another perch, at the approach of the cowbirds; but, later the same day, we noted that the meadowlark was less prone to flee and now often remained in a fixed position, pecking at the cowbirds as they displayed. Next day, the meadowlark sometimes responded to the display by preening the cowbirds rather than fleeing from them. And for a period of two weeks during which the meadowlark was confined with the cowbirds, preening became the usual response of the meadowlark to any cowbird in display. As a consequence, the meadowlark was "victimized" to the extent that it spent several hours each day in this activity.

In late March, several female Red-winged Blackbirds (*Agelaius phoeniceus*) were placed in the aviary, where they remained through the summer and fall. A day or two after their introduction, they were seen to preen displaying cowbirds, and this behavior was noted hundreds of times in the following months.

DESCRIPTION OF THE DISPLAY

We have used the term "display" for this behavior since it involves distinctive postures and movements having obvious communication function, inducing, normally, flight, attack, or heteropreening in the individual to which it is directed, hereafter called the recipient. In display (Figures 1A, 1B, and 1D), the head is bowed to a point at which the bill is directed either vertically downward or in toward the cowbird's body. The feathers of the head and nape are conspicuously ruffed, but other body plumage is generally slightly compressed or sleeked. The wings and tail are held in normal resting position, and the cowbird is often slightly crouched.

Assumption of the head-bowed posture is accompanied or shortly followed by a movement of the cowbird toward the recipient. This may be a sidling motion along a perch or a direct head-on approach. Usually the cowbird halts when its head is about one inch from the recipient, but the approach may continue until the top of the cowbird's head is actually placed against the breast of the recipient (Figure 1A). Orientation of the cowbird's body with respect to the recipient's position varies: frequently the body is oriented along a perch as frontal

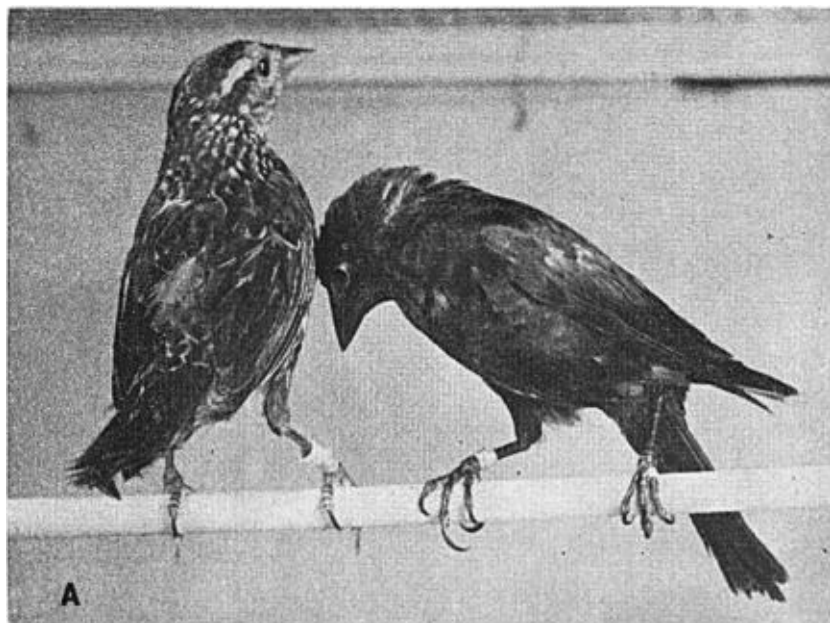


Figure 1A. Male cowbird gives preening invitation to female Red-winged Blackbird.

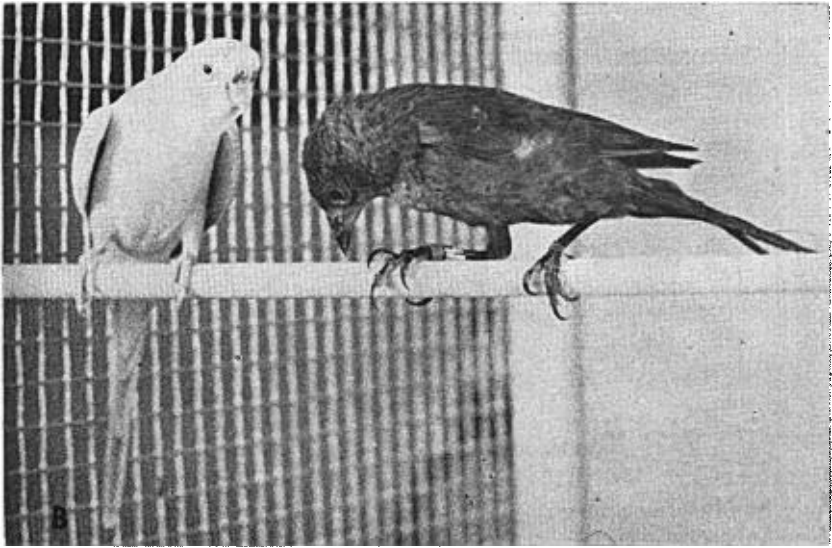


Figure 1B. Female cowbird invites preening from a Shell Parakeet.

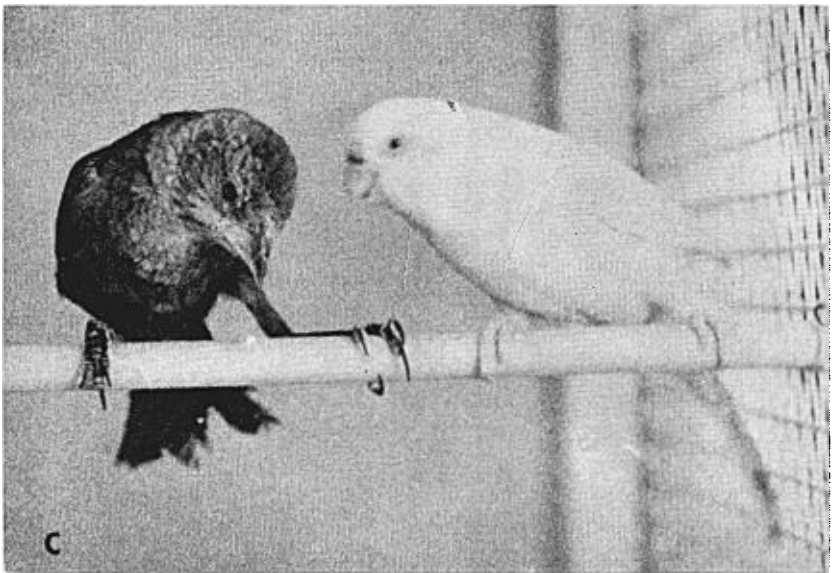


Figure 1C. Displaying female cowbird dodges peck by Shell Parakeet.

presentation of the head is made (Figure 1B), but cowbirds also posture with the body at an angle, often about 45° , to the recipient. Or the cowbird may perch side-by-side with the recipient, bowing the head and cocking it toward the recipient. Oblique presentations are most likely to be used when the recipient is in the habit of pecking at the displaying cowbird; this permits the cowbird to dodge the blows by turning rapidly away (Figure 1C).

Regardless of the orientation of the displaying cowbird's body, the cowbird postures in a position in which the occipital region of the head is directed toward the head of the recipient. While presenting the fluffed feathers of the head, the cowbird maintains a rigid pose, avoiding rapid or sudden movement; and it avoids direct visual fixation of the recipient. In the displaying cowbird, the eyes have a characteristic "glassy" appearance. The display is not accompanied by vocalizations.

Display is given on perches, on the ground, or while both the recipient and the cowbird cling to the wire sides of an aviary or cage. If heteropreening is induced, the cowbird maintains the bowed posture and continues to avoid sudden movement, although it may make slight changes in position of the head, as if to encourage the responding recipient to preen particular regions.

THE DISPLAY IN CAPTIVE BIRDS

All our observations of the preening invitation display in cowbirds confined to aviaries and cages have involved adult and first-year indi-

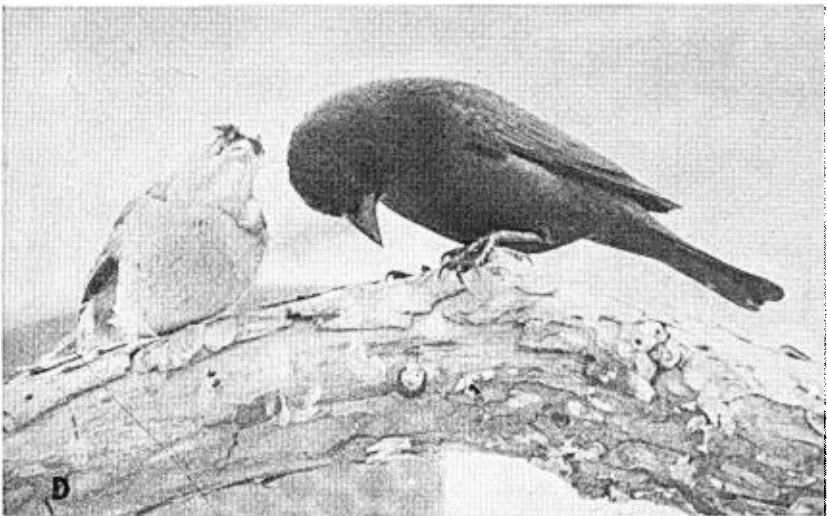


Figure 1D. Male cowbird displays to dummy White-crowned Sparrow.

viduals captured in the spring in the Austin region, Texas. We have not yet had an opportunity to study this behavior in juveniles or in immature individuals less than six months old; but James Baird (pers. comm.) has observed the display in a two-month-old juvenile female held in a cage with a female Red-winged Blackbird.

INTRASPECIFIC PRESENTATION

As we have indicated previously, a cowbird only occasionally directs the display to another member of its own species. In several hundred hours of observation of several groups of cowbirds confined to aviaries and cages in the absence of individuals of other species, we have noted intraspecific presentation of the display on no more than 25 occasions. Our records indicate that it is most likely to occur among cowbirds that have been deprived of contact with other species for long periods. Also, the frequency of intraspecific presentation usually rises for a brief period following the introduction of an individual of another species.

In all recorded instances of intraspecific presentation, the display was given only a single time and invariably resulted in withdrawal or

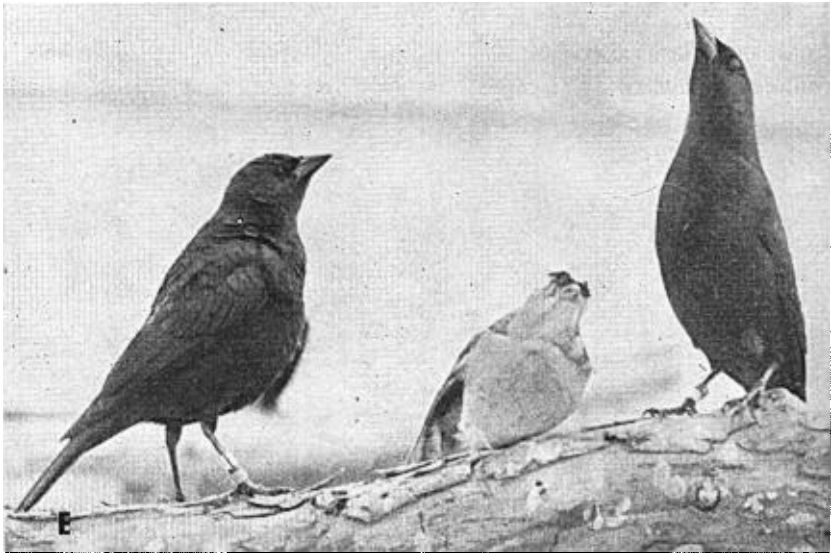


Figure 1E. Agonistic behavior of two male cowbirds, each intent on soliciting preening from dummy White-crowned Sparrow. The bird on the left is beginning ruff-out display as the other bird gives head-up display; both displays have threat function.



Figure 1F. Male cowbird at height of ruff-out display to dummy White-crowned Sparrow.

attack on the part of the recipient cowbird. Most frequently the recipient cowbird pecked at the displaying cowbird as it approached, and this brought an end to the episode. In no instance did intra-specific presentation of the display lead to heteropreening.

INTERSPECIFIC PRESENTATION

Response of the recipient. Individuals of other species placed in an aviary or cage containing cowbirds initially respond to the approach and display of the latter either by pecking or fleeing. The reaction of female Red-winged Blackbirds is typical of the latter type of response. As the recipient blackbird retreats a step or two, the cowbird quickly follows and again displays at close range; and this behavior may occur repeatedly along a perch. If the recipient flies, the cowbird may follow at once, or it may remain momentarily in display before flying after the retreating recipient, to display at the new position. If the recipient makes no overt response to the displaying cowbird, the latter moves forward a half inch or so, adjusting its position to bring the head more precisely into direct view of the recipient; and soon the cowbird's head may come to rest against the recipient's breast (Figure

1A). Usually this contact induces the blackbird to retreat or to peck at the cowbird.

The usual initial response of the domestic Shell Parakeet (*Melopsittacus undulatus*) when placed in a cage with a cowbird is to peck and bite as the latter approaches. In response, the displaying cowbird dodges by rapidly turning or leaning away from the blow (Figure 1C). Unless the recipient actually moves forward in attack, the cowbird usually keeps its head bowed as it dodges and quickly returns to its former position, with its head about one inch from the recipient.

It is remarkable that cowbirds persist in their attempts to induce preening even in the face of repeated hostile responses on the part of the recipient, especially if the latter is a small species and merely pecks instead of moving forward in attack. To illustrate this point, we have summarized in Figure 2 the results of a test conducted on 13 June 1959, in which a pale-blue adult parakeet and a female cowbird were placed in an observation cage measuring 60 x 60 x 120 cm (2 x 2 x 4 feet). Neither individual had previously had any direct contact

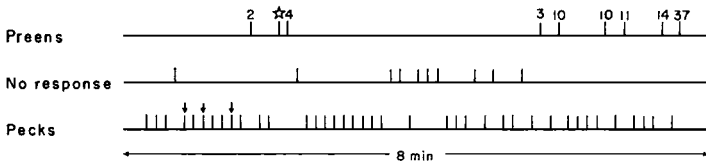


Figure 2. Responses of Shell Parakeet to preening invitation displays of female Brown-headed Cowbird; numbers indicate duration of preening episodes in seconds. ↓ Parakeet strikes cowbird. ☆ Starts to preen, then pecks.

with the other species, although both had been housed for several days in separate cages in the same room. In an eight-minute period, during which the behavior was filmed, the cowbird displayed 58 times and made four intention movements to display. The latter consisted of brief nodding movements of the head given at distances from seven to 15 cm from the parakeet. Two of them occurred in the first 30 seconds of the period, before a full display was given, and the other two occurred just after the cowbird had dodged particularly vigorous pecks by the parakeet. To the displays of the cowbird, the parakeet

responded 39 times by pecking at the cowbird's head. Following the fifth, seventh, and tenth presentations of the display, the parakeet actually struck the cowbird on the head and managed to pull out a feather before the cowbird escaped. Thereafter, the cowbird seemed better able to judge the intentions of the recipient and succeeded in avoiding all other pecks. The parakeet's response to the fifteenth presentation was highly ambivalent; it began to preen the cowbird, then pecked, striking the cowbird's head. About midway through the test period, there was an increase in the frequency with which the parakeet made no overt response to the cowbird's display; and, finally, a number of preening episodes followed. It will be noted (Figure 2) that these gradually lengthened, with the parakeet continuously preening the cowbird for 37 seconds at the end of the period. In the course of this episode, the parakeet twice attempted to "bill" with the cowbird, but the latter refused, moving its bill aside.

During the test period, the parakeet, which was accustomed to small quarters, perched more or less calmly; but the cowbird, which had not previously been confined to a small cage, was obviously distressed. Other disturbing factors included our presence at one end of the cage, four photoflood lamps directed on the cage, and the sound of a movie camera. Between displays, the cowbird flew about attempting to escape, and presentations in the first few minutes of the period were very brief. In anthropomorphic terms, the cowbird's displays suggested the performance of a "nervous" habit, for they were directed in an "offhand" fashion whenever the cowbird happened to find itself near the parakeet. In this situation it was particularly clear that the causal basis of this behavior involved something other than a simple "need" for preening of the feathers.

That the parakeet was induced to preen the cowbird soon after they were placed in the cage should be considered in light of the fact that heteropreening is a normal part of parakeet social behavior. In subsequent tests involving the same individual parakeet but other cowbirds, the parakeet showed even less readiness to peck on first encounter with a cowbird. About an hour after the first test, another female cowbird was placed in the cage. It at once assumed the invitational posture, and the parakeet responded by preening the head and neck of the cowbird for a period of 35 seconds; and several similar episodes followed. In a third test a few days later, the parakeet preened a cowbird's plumage for a period of four minutes and 45 seconds, with only two brief interruptions occurring as the cowbird adjusted its position on the perch. This was the longest preening episode recorded in our study.

Occasionally the recipient bird may respond to the cowbird's display by mounting and attempting copulation. Griffin (1959) watched a male House Sparrow (*Passer domesticus*) attempt to copulate with a male cowbird as the latter was, according to our interpretation of Griffin's notes, giving preening invitation display. He notes that the cowbird "had its head bowed with the lower mandible touching the breast feathers and the wings slightly raised at the shoulder." The position of the wings, as described by Griffin, is not typical and suggests the presence of some behavioral tendency not noted in our birds, but other aspects of the cowbird's behavior were typical; it followed the sparrow about and nudged it when no response to the display was forthcoming. Griffin reports that the sparrow mounted the cowbird four times and that the episode continued for from five to eight minutes; heteropreening was not observed.

A second record of this type is supplied by Teale (pers. comm.), who saw a male House Sparrow mount a male cowbird four times on 4 January 1954. Teale's notes do not indicate whether or not the cowbird evoked this behavior by giving preening invitation display, but it is probable that this was the case. In addition, Behrendt (1960) reports that House Sparrows that are preening displaying cowbirds sometimes climb on their backs.

That male House Sparrows sometimes respond to displaying cowbirds by attempting copulation is not surprising, since, as previously noted by Eisenmann (footnote to Griffin, 1959), the display posture bears some resemblance to that of a sexually receptive female. In particular, the rigidity of the pose probably serves as a potent stimulus releasing copulatory behavior. Many birds, including both House Sparrows and Brown-headed Cowbirds, can be induced to mount lifeless dummies (Allen, 1934; Howell and Bartholomew, 1954; Selander and Giller, 1961; Thompson, 1960), and, in fact, as noted beyond, captive male cowbirds occasionally responded in this way to dummies of other species presented in attempts to induce preening invitation display.

Variation in frequency of presentation. In testing the reactions of cowbirds to dummies of other species (see below), we detected a decrease in readiness to display in late summer during the annual molt. This variation we are inclined to regard as a reflection of the reduced general activity level characteristic of molting birds rather than an effect of changing levels of sex hormone production, for cowbirds with active gonads in April and May exhibited no greater readiness to display than did sexually inactive birds in December and January. Moreover, bilateral castration of males does not affect their readiness to display,

as indicated by a test conducted on 14 April 1960, in which a female Red-winged Blackbird was placed in a small aviary containing seven normal males, ten castrated males, nine normal females, and nine ovariectomized females. The castrations and ovariectomies had been performed in January 1960, and the cowbirds had been deprived of close contact with individuals of other species for a period of four months. In two 30-minute periods, the number of displays given by the cowbirds was recorded. Distinctively colored bands permitted recognition of the normal and castrated males; but, as the females were not color banded, no distinction was made between the two groups. The results of the first test period and a second period following the first by two hours, during which the blackbird remained with the cowbirds, are shown in Table 1. In the first 30-minute period, castrated and normal males gave equal numbers of displays, an average of 2.7 for

TABLE 1
NUMBER OF DISPLAYS DIRECTED TO A FEMALE RED-WINGED BLACKBIRD IN
TWO 30-MINUTE PERIODS

| | No. of cowbirds | First period | | Second period | |
|--------------------------------------|--------------------|--------------------|----------------------------------|--------------------|----------------------------------|
| | | No. of displays | Mean no. displays per bird | No. of displays | Mean no. displays per bird |
| Castrated males | 10 | 27 | 2.7 | 52 | 5.2 |
| Normal males | 7 | 19 | 2.7 | 14 | 2.0 |
| Total, all males | 17 | 46 | 2.70 | 66 | 3.88 |
| Ovariectomized and normal females | 18 | 64 | 3.5 | 55 | 3.0 |
| Total, all birds | 35 | 110 | 3.14 | 121 | 3.46 |

each individual. The 18 females gave a total of 64 displays, or an average of 3.5 per individual. In the second test period, the numbers of displays given by females and normal males decreased slightly, but the mean number given by castrated males increased to 5.2, largely as a result of the efforts of one especially persistent individual that alone displayed 25 times. Preening was not performed by the blackbird, which made repeated attempts to escape from the unfamiliar aviary and rarely spent more than a few seconds in any one position.

Eight intraspecific presentations of the display were noted in the first test period, and nine were seen in the second, whereas no displays were given in the hour preceding the first test.

There appears to be no marked sexual difference in readiness to display, although we suspect that females are slightly more persistent in their efforts to approach other species.

A considerable degree of individual variation in frequency of display was noted. This is shown by a test made on 4 April 1960, when a female Red-winged Blackbird was placed in a small aviary containing five male and five female cowbirds that were color banded for individual recognition. The cowbirds had not been in contact with other species for three weeks. The blackbird had been housed with another group of cowbirds for a one-year period and had developed the habit of preening in response to the display.

The response of the cowbirds to the blackbird was immediate; in a one-hour period, the 10 cowbirds gave a total of 265 displays (Table 2). Of the males, *Green* gave 93 displays, whereas *Red* gave only 2. This

TABLE 2
INDIVIDUAL VARIATION IN NUMBER OF DISPLAYS DIRECTED TO A FEMALE
RED-WINGED BLACKBIRD IN A ONE-HOUR PERIOD

| <i>Males</i> ¹ | <i>No. of displays</i> | <i>Females</i> | <i>No. of displays</i> |
|--------------------------------------|------------------------|----------------|------------------------|
| Red | 2 | Red | 3 |
| Orange | 17 | Orange | 23 |
| Green | 93 | Green | 1 |
| Pink | 3 | Pink | 60 |
| Purple | 5 | Blue | 58 |
| Totals ² | 120 | | 145 |
| Average number of displays per bird: | 24.0 | | 29.0 |

¹ Males arranged in order of position in dominance hierarchy, Red being the alpha individual.

² Difference between sexes not significant at 95 per cent level of confidence.

trial supported previous observations that had suggested that the alpha male in a dominance hierarchy of males is less prone to display than are birds midway in the hierarchy, and that birds low in the order also display relatively infrequently. In females, there was also notable individual variation in frequency of display, but we are unable to correlate this variation with position in the female dominance hierarchy, which was not determined and, in any event, is poorly defined in cowbirds.

The data in Table 2 again demonstrate the persistence with which

cowbirds display to blackbirds. As in the test conducted on 14 April, the blackbird almost invariably flew at the approach of the cowbirds and was greatly disturbed by the unfamiliar surroundings. As the blackbird flew from perch to perch and to the wire sides of the aviary, one or more cowbirds followed, displaying whenever she remained perched for a moment.

In the course of the one-hour observation period, we recorded several agonistic interactions between cowbirds and between the blackbird and cowbirds as follows:

"*Green* male pecked away two female cowbirds which were displaying simultaneously to the blackbird, then he went into display; when no response from the blackbird was forthcoming, he butted her breast with his bowed head; this induced the blackbird to fly.

"*Orange* male, displaying to the blackbird, is displaced with a peck by *Pink* male, who then displays.

"*Green* male pushes aside a female to get near the blackbird. He displays for 15 seconds then pecks the blackbird once.

"Toward the end of the hour, *Green* male displays twice, then catches hold of the blackbird's tail with his bill; she flies and he chases her back and forth across the aviary; when she comes to rest on a perch, he displays twice again.

"*Blue* female, after displaying 19 times to the blackbird, pecks, then bites at the blackbird's tail; the blackbird flies and she follows, displaying four more times.

"*Blue* female displays, then bites the wing feathers of the blackbird and holds on; the blackbird flies and she follows, displays, and is pecked on the head by the blackbird. Eight seconds later, *Blue* female grasps the blackbird's tail with her bill and a fight ensues in which the blackbird dominates after repulsing *Blue* female with a hard peck to the head. A few seconds later, the blackbird pecks *Orange* female as she approaches and displays. *Blue* female again approaches, displays twice, pecks at the blackbird's wing, displays eight more times, and then catches hold of the blackbird's tail; the blackbird flies and *Blue* female follows, again pecking and biting at the tail of the blackbird.

"*Orange* male is pecked on the head as he displays; he retreats four inches, starts to display again but stops as the blackbird gives a peck intention movement; *Orange* male straightens up and flies away."

The effect of an individual of another species in increasing the frequency of intraspecific presentation is illustrated by the following episode: "*Green* male moves toward the blackbird and begins to display. The blackbird immediately flies and *Green* male turns to display to *Pink* female for two seconds; then he flies after the blackbird and again displays."

As a general rule, cowbirds do not behave aggressively toward the recipient until they have presented the display a number of times and have failed to induce preening. In the hour observation period, *Green* male, displaying a total of 93 times, pecked or otherwise attacked the blackbird three times, and *Blue* female, displaying 58 times, attacked

the blackbird seven times; all aggressive behavior occurred in the second half of the period. Other cowbirds did not behave aggressively toward the blackbird. Similarly, when presented with a dummy bird, cowbirds typically display a number of times, then behave aggressively toward it (see below).

THE VARIETY OF SPECIES ELICITING DISPLAY

We have had opportunity to observe the reactions of captive cowbirds to a small number of species of birds confined with them in aviaries for periods ranging from a few weeks to several months or introduced for brief test periods. In addition, we have attempted to test the reactions of cowbirds to a variety of species by wiring museum study skins cross-wise to perches (Figure 1D). Unfortunately, these dummies proved to be much less effective than living birds in evoking the display, and our efforts to apply this technique were hindered further by seasonal variation in responsiveness on the part of the cowbirds, to which we have already referred. In April, strong responses were given to a number of dummies, but, in July and August, even those dummies to which cowbirds had been most responsive in April sometimes failed to induce the display and were at best effective in stimulating displays in only one or two individuals of a large group. Despite this change in responsiveness of cowbirds to dummies, the level of response to live birds remained relatively constant. In a 10-minute test on 6 July 1960, a female dummy Red-winged Blackbird failed to evoke the display in seven cowbirds that had been deprived of contact with other species for a period of six weeks. Yet when a live female blackbird was substituted for the dummy immediately following the test period, all seven cowbirds at once responded, delivering a total of 160 displays in a 30-minute period.

Observations on the reactions of captive cowbirds to other species are summarized in Table 3. Since little effort was made to control many of the factors that could affect readiness of cowbirds to display, the results of our crude tests probably have little significance other than indicating that cowbirds will respond to a wide variety of species and suggesting the existence of some variation in the effectiveness of different species in evoking the display. We will reserve comment on the possible significance of this variation for the Discussion section of this paper.

In addition to the records shown in Table 3, we have an interesting report from James Baird on the behavior of a captive female cowbird that was held in a cage in a room with a small group of tropical finches:

the latter were confined to a separate cage on the wall above the cowbird's quarters. Baird notes that "the cowbird spent a great deal of time at the end of the perch closest to the finches and would remain in a 'head bow' position for long periods (10-15 minutes). This was so regular that . . . she spent an hour or more each day in this position."

Aggression and copulation in response to dummies. After displaying to a dummy bird, both male and female cowbirds sometimes pecked at the dummy (usually at the cotton "eye") or made an outright attack, employing both feet and bill. Their behavior was thus similar to that seen in cowbirds following display to nonresponsive live birds. In addition, male cowbirds occasionally mounted the dummies in attempts to copulate or showed ambivalence between tendencies to copulate and to attack. For example, on 17 June 1959, a male displayed to a dummy Robin (*Turdus migratorius*) for 37 seconds, then pecked at the Robin's head, mounted, and attempted copulation. Dismounting, the male again displayed briefly, pecked at the dummy, mounted, and vigorously attacked the dummy from above. Later the same day, this male also attempted copulation with a dummy Brown Thrasher (*Toxostoma rufum*) and followed this attempt with an attack.

A dummy female House Sparrow also elicited ambivalent behavior in a male cowbird, which displayed, stepped up on the back of the dummy, and pecked at the head. A dummy female Red-winged Blackbird was also mounted by a male cowbird; after the copulation attempt, the cowbird dismounted and attacked the dummy's head, pulling cotton from the "eye."

Considering the wealth of evidence supporting the thesis that an aggressive tendency underlies the courtship and mating behavior of birds and other vertebrates (Morris, 1956; Tinbergen, 1954), overt expression of this tendency by cowbirds responding sexually to dummies is neither unusual nor unexpected. Among icterids, attack following or during copulation attempts has been noted on many occasions when Great-tailed Grackles (*Cassidix mexicanus*) or Brown-headed Cowbirds are responding to dummy females of their own species (Selander, MS), and similar behavior has been reported in the Brewer's Blackbird, *Euphagus cyanocephalus* (Howell and Bartholomew, 1954), and other species.

An unusual response of male cowbirds to dummies of other species is the performance of the ruff-out display (Figure 1F), which is normally used both as a hostile display in territorial interactions with other males and in courtship of females (Selander and La Rue, MS). This display consists of a more or less "standard" icterid ruff-out (see

TABLE 3
RESPONSES OF CAPTIVE BROWN-HEADED COWBIRDS TO LIVE INDIVIDUALS
AND DUMMIES OF OTHER SPECIES

| <i>Species</i> | <i>No. of individuals</i> | <i>Response</i> |
|--|---------------------------|--|
| I. Live individuals confined to aviary with cowbirds for periods of two or more weeks. | | |
| ♂ ♂ Red-winged Blackbird (<i>Agelaius phoeniceus</i>) | 2 | Moderate numbers of displays evoked; preening rarely induced. |
| ♀ ♀ Red-winged Blackbird | 3 | Frequent display evoked; preening became habitual. |
| Meadowlark (<i>Sturnella</i> sp.) | 1 | Frequent display evoked; preening became habitual. |
| ♀ ♀ Red-eyed Cowbird (<i>Tangavivus aeneus</i>) | 3 | Displays infrequent; no preening. |
| ♂ ♂, ♀ ♀ Great-tailed Grackle (<i>Cassidix mexicanus</i>) | 20 | Two brief displays to ♀ ♀ noted; none given to ♂ ♂; no preening. |
| ♂ Common Grackle (<i>Quiscalus quiscula</i>) | 1 | Negative (no displays or preening). |
| (Feral) Rock Dove (<i>Columba livia</i>) | 4 | Negative |
| ♂ ♂, ♀ ♀ House Sparrow (<i>Passer domesticus</i>) | 4 | Displays fairly frequent; preening induced. |
| II. Live individuals confined to aviary with cowbirds for periods of from 10 minutes to one hour. ¹ | | |
| ♂, ♀ Inca Dove (<i>Scardafella inca</i>) | 2 | Numerous displays followed by attack in which doves were injured; no preening. |
| ♂ Cockatiel (<i>Leptolophus hollandicus</i>) | 1 | Many displays; no preening; Cockatiel very aggressive and cowbirds unable to approach closely. |
| ♂, ♀ Shell Parakeet (blue variety) (<i>Melopsittacus undulatus</i>) | 3 | Frequent display evoked; extensive preening induced. |
| Mourning Dove (<i>Zenaidura macroura</i>) | 1 | Negative |
| ♂ Domestic Canary (yellow) (<i>Serinus canaria</i>) | 1 | ♂ cowbird displayed through wire separating adjacent cages; no opportunity for preening. |

TABLE 3—Continued

| <i>Species</i> | <i>Response</i> |
|---|---|
| III. Dummies (study skins) wired to perch of aviary for 5- to 10-minute periods. ² | |
| 1. Loggerhead Shrike (<i>Lanius ludovicianus</i>) | 1 display |
| 2. White-crowned Sparrow (<i>Zonotrichia leucophrys</i>) | 11 displays |
| 3. Starling (<i>Sturnus vulgaris</i>) | Negative ³ |
| 4. Chimney Swift (<i>Chaetura pelagica</i>) | Negative |
| 5. Brown Thrasher (<i>Toxostoma rufum</i>) | 1 display ⁴ |
| 6. Killdeer (<i>Charadrius vociferus</i>) | Negative |
| 7. Meadowlark (<i>Sturnella</i> sp.) | 5 displays |
| 8. Cedar Waxwing (<i>Bombycilla cedrorum</i>) | 4 displays |
| 9. Blue Jay (<i>Cyanocitta cristata</i>) | Negative |
| 10. Robin (<i>Turdus migratorius</i>) | 2 displays and a copulation attempt and attack |
| 11. Screech Owl (<i>Otus asio</i>) | Negative |
| 12. Yellow-breasted Chat (<i>Icteria virens</i>) | Positive ⁵ |
| 13. ♂ Cardinal (<i>Richmondia cardinalis</i>) | Positive |
| 14. ♂ Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>) | Positive |
| 15. ♂ Hooded Oriole (<i>Icterus cucullatus</i>) | Negative; two cowbirds approached but seemed too apprehensive to display. |
| 16. Eastern Kingbird (<i>Tyrannus tyrannus</i>) | Positive |
| 17. ♂ Painted Bunting (<i>Passerina ciris</i>) | Positive |
| 18. ♂ Prevost Cacique (<i>Amblycercus holosericeus</i>) | Negative |
| 19. ♂ Myrtle Warbler (<i>Dendroica coronata</i>) | Positive |
| 20. ♂ Ladder-backed Woodpecker (<i>Dendrocopos scalaris</i>) | Negative |
| 21. ♀ Red-winged Blackbird (<i>Agelaius phoeniceus</i>) | Positive |

¹ In addition to the species listed, captive cowbirds were seen to display to Evening Grosbeaks (*Hesperiphona vespertina*) and lovebirds (*Agapornis* sp.) in tests conducted at the Laboratory of Ornithology, Cornell University, in October 1960.

² The dummy Loggerhead Shrike was presented to a group of 10 cowbirds for 10 minutes and remained in the aviary an additional 60 minutes while dummies of species 2 through 7 were presented in successive 10-minute periods on 8 April 1960. At the end of the series of tests, a live Cockatiel was placed in the aviary and induced 13 displays in a 10-minute period.

Dummies of species 12 through 21 were presented to a group of seven cowbirds in successive 5-minute periods on 5 July 1960.

³ Negative response also obtained in previous test in 1959.

⁴ Evoked copulation attempt and attack in previous test in 1959.

⁵ Indicates one or more displays evoked.

Williams, 1952) followed by bill wiping, the two separate activities often but not invariably being "welded" in a single, continuous series of movements. Midway in the display, the cowbird's bill is pointed down as the bow to bill wipe begins. High-speed photographs show that the bird is momentarily in a posture suggesting that of the preening invitation display, but that the body feathers are fluffed and the wings and tail are spread.

THE DISPLAY IN NONCAPTIVE BIRDS

We have shown that preening invitation display is seen repeatedly in aviaries in which cowbirds and other species are closely confined together; and we have indicated that the frequency with which the display is given by captive birds is directly related to the length of time that they have been deprived of contact with other species. In the field, the display undoubtedly is given less frequently, but our own casual observations and those of several correspondents indicate that it is a regular feature of the behavior of noncaptive individuals. Following are summaries of all field observations of preening invitation that have come to our attention; these are arranged under the species to which the displays were directed. It should be noted that we have no field records of intraspecific presentation of the display.

HOUSE SPARROW

Austin, Texas, 29 April 1959. As La Rue watched three House Sparrows and two male cowbirds perched on the screened roof of an outdoor aviary, one cowbird briefly directed display to a female sparrow, which did not respond. *1 July 1959.* La Rue saw a male cowbird pursue a female sparrow along the branch of a willow tree, moving close and displaying whenever the sparrow stopped; heteropreening was not elicited. *28 November 1959.* Selander saw two males and two females displaying to House Sparrows in mixed flocks at a stockyard. One male displayed to six individuals in turn, going from one to another in rapid succession. The intensity of the display varied from simply perching with bowed head near a sparrow to full horizontal presentation of the head and nape. The sparrows generally hopped, walked, or flew away as the cowbirds approached or assumed the bowed posture; preening was not seen.

Norman Bird Sanctuary, Middletown, Rhode Island, 20 December 1958. The following notes were supplied by James Baird (pers. comm., 4 November 1959). "I was watching a small cowbird flock (20-30) in the backyard. They had finished feeding and were sitting quietly, preening, in the dogwoods . . . or walking about rather aimlessly beneath or near the bushes. With the cowbirds were a number of House Sparrows and White-crowned Sparrows [*Zonotrichia leucophrys*]. My attention was . . . drawn to a female cowbird which had finished preening and started sidling up the branch toward a male House Sparrow which was sitting a foot away. As she approached the sparrow, she pointed her bill toward the ground, thus presenting the back of her head to the sparrow. The

wings were held at rest. . . . The sparrow hopped to the ground and the cowbird immediately followed, running after the retreating male and all the while keeping her head pointed downward. Finally, the sparrow hopped on her back and pecked the back of her head for a short time and then hopped off. The cowbird followed again and the sparrow flew off."

Baird notes that he witnessed cowbirds giving the display to House Sparrows on several other occasions in the winter of 1958-1959.

Weinberg Wildlife Refuge, New York (date not indicated). Ilse Behrendt (1960), watching House Sparrows and a group of 14 cowbirds, including three males and a number of females and "young birds," in bushes near a feeding station, saw "one of the male cowbirds settle down on a branch right under a female . . . sparrow, bending his head and taking a kind of crouching position. Right away the female . . . sparrow . . . [probed] with her bill deep into his head-feathers and worked down all the way to his bill, cleaning and scratching all the spots the bird could not reach himself.

"Sometimes it seemed that it hurt him, for he would suddenly throw up his head and the . . . sparrow would fly away. But the cowbird went after her, taking a branch right under her . . . waiting. And she started to work on him again, over and over.

"I saw four different cowbirds being [preened] . . . by four female . . . sparrows. They worked delicately and gracefully. Sometimes they would climb on the cowbirds' back[s], but then they would slide down and always end up by working from a little higher branch." This behavior was observed for "nearly fifteen minutes."

Stillwater, Oklahoma, 26 October 1958. Griffin's observations (1959) of a male cowbird displaying for a period of from five to eight minutes to a male House Sparrow, which responded by attempting to copulate, have already been discussed.

SCISSOR-TAILED FLYCATCHER (*Muscivora forficata*)

Austin, Texas, April 1959. Donald R. Giller saw a male cowbird display to an individual of this species. The flycatcher flew from its nest on a telephone pole to another pole across a highway where two male and one female cowbirds were perched. As the flycatcher landed on the pole, one of the male cowbirds began a display that continued for about 10 seconds. The episode ended as the cowbird pecked at the flycatcher, which then flew back to its nest.

RED-WINGED BLACKBIRD

Eugene Eisenmann (pers. comm., 22 March 1960) informs us that several people have mentioned to him their observations of Brown-headed Cowbirds being preened by Red-winged Blackbirds; and a full account of observations was supplied by Edwin Way Teale (pers. comm., 24 September 1959).

Baldwin, Long Island, New York, 21 March 1959. At 0630, a female blackbird was seen preening a female cowbird as they perched among canes. As the cowbird held the invitational pose, the blackbird, which was perched slightly above, preened the cowbird's nape. Teale notes that the blackbird "ran its bill horizontally back and forth. . . . At other times it moved it vertically, lifting the neck feathers as it advanced. Again it seemed to work in spots here and there.

Our impression was that it was getting something. At intervals it would stop, withdraw its bill and seem to swallow." This performance, which was in progress when observations began, continued for 10 minutes, terminating as the blackbird suddenly flew to the ground to feed on scattered seed. The cowbird followed and displayed three times again; but the blackbird made no response and the cowbird soon stopped displaying.

At 1630 the same day, a female blackbird (possibly the same individual that was watched in the morning) was seen preening the neck, "shoulders," and face of a male cowbird. "At times the cowbird was pressed close with its head seemingly against the breast of the redwing. The redwing moved about, jumping to other canes in the rose tangle, but always the cowbird followed, coming up a little below and nudging with its head which was bent down, arching its back, [and] getting as close to the redwing as possible." The male cowbird was later joined by a female cowbird and both displayed together to the blackbird. "At times the two cowbirds were pressing against the redwing," one on each side. Once a third cowbird, a female, approached the trio but did not display. Still later, a lone female cowbird displayed to the blackbird and was preened for a few seconds.

Kissimmee, Florida, 13 December 1960. Selander saw a male displaying repeatedly to a first-year male blackbird that backed up along a wire at each approach of the cowbird. Nearby, a female cowbird displayed to a female red-wing. Observations were interrupted when a passing car caused the birds to fly.

THE DISPLAY IN OTHER SPECIES OF COWBIRDS

In the summer of 1959, two captive Red-eyed Cowbirds were occasionally seen to respond to a female Red-winged Blackbird by giving preening invitation displays that were closely similar to those of the Brown-headed Cowbird. Heteropreening was occasionally induced, but usually the Red-eyed Cowbirds displayed for only a few seconds at any one time and were not preened. This we attributed to fright on the part of the cowbirds induced by our presence at the aviary, for, unlike the Brown-headed Cowbird, the Red-eyed Cowbird is difficult to accustom to captivity and remains wary and restless even after weeks of confinement. It is noteworthy that the Red-eyed Cowbirds invariably displayed in a more or less oblique position, which, in the other species of cowbird, is the characteristic position of individuals that have demonstrated a relatively strong tendency to flee as a result of having been attacked by the recipient.

Possibly a similar interspecific preening invitation display is employed by the parasitic Giant Cowbird (*Psomocolax oryzivorus*), which is, according to Friedmann (1929), closely related to *Tangavius*. Chapman (1928) reports seeing a female Giant Cowbird twice bow her head and present the fluffed feathers of the nape to a female Wagler Oropendola (*Zarhynchus wagleri*) at the latter's nest.

DISCUSSION

The foregoing observations raise a host of questions concerning the motivation, ontogeny, function, and possible adaptive significance of heteropreening invitation behavior in relation to brood parasitism of cowbirds. Final answers to these questions must await further informa-

tion not only on the use of the display under natural field conditions but also on other aspects of the host-parasite relationship. We are also handicapped in our attempt to interpret this behavior by the paucity of available information on the biological significance of intraspecific heteropreening in birds in general. At present we can do little more than offer tentative answers to some of the major questions posed by our findings.

If cowbirds themselves practiced social heteropreening, their solicitation of preening from other species would be less surprising; but, as noted previously, intraspecific heteropreening has not been observed in Brown-headed Cowbirds, and Friedmann (1929) does not mention its occurrence in other cowbird species. It is also clear that the preening invitation display itself is not regular intraspecific behavior that is only occasionally directed to individuals of other species. On the contrary, intraspecific display has not been observed in wild birds; and, working with captive birds, we have found that it is infrequent and may be expected only after cowbirds have been deprived of contact with other species for long periods or following the introduction of an individual of another species, when the cowbirds' "drive" to display apparently increases to a level at which stimuli provided by members of their own species become sufficient to elicit the behavior. Often it is clear that the display is in fact released by the other species and merely redirected to another cowbird.

Among other icterids, social heteropreening appears to be uncommon. Our observations have demonstrated its absence in grackles of the genera *Cassidix* and *Holoquiscalus*, and it is not reported in comprehensive studies of the behavior of the meadowlarks (Lanyon, 1957), Red-winged Blackbird (Nero, 1956), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*; Nero, MS), and Brewer's Blackbird (Williams, 1952). To the best of our knowledge, the only icterid in which heteropreening is recorded is the Wagler Oropendola, studied by Chapman (1928), who on four occasions saw a female working her bill through the neck feathers of a male as the latter postured with bowed head and half-open bill.

Since "individual distance" (Hediger, 1950) is absent or weakly expressed in many species of birds that have social heteropreening ceremonies, we have considered the possibility that intraspecific heteropreening in cowbirds is somehow precluded by their rigid maintenance of spacing of individuals at distances no less than five inches. Violation of this critical interval invariably leads to rapid adjustment of position, effected by hostile display or pecking, on the part of one or both of the

individuals involved. (As a result, two adult cowbirds come into direct physical contact only while fighting and during copulation; and the latter activity is preceded by mutual mating displays functioning in part to adjust the behavioral tendencies of the participants in such a way that individual distance can temporarily be violated without the induction of overt aggressive behavior.) Following this line of argument, we might speculate that young cowbirds initially approach and direct their displays to other cowbirds when they assemble in flocks in the fall, but that aggressive responses stemming from violation of individual distance result in the young cowbirds becoming conditioned to avoid close approach to others of their species. But arguing against this explanation is the fact that cowbirds persist in approaching Red-winged Blackbirds and other species in the face of continuing hostile responses resulting from the cowbirds' violation of the individual distance maintained by the recipient. And since displaying cowbirds are successful in reducing the aggressive and/or escape tendencies of individuals of other species and are able to induce heteropreening by species that, like cowbirds, do not practice social grooming (for example, Red-winged Blackbirds and meadowlarks), it is difficult to believe that, other factors being equal, persistent display could not evoke the same response in members of their own species. Therefore, it seems necessary to introduce, as a supporting hypothesis, the suggestion that cowbirds, as recipients, are on the sensory side unusually resistant to stimuli provided by a displaying cowbird, or that another cowbird simply does not normally provide the stimuli releasing the display behavior. In either case, the result would be a restriction of use of the display to inter-specific interactions.

It is interesting to note that a socially subordinate cowbird that "wishes" to remain in the vicinity of a superior of its own species does not adopt the head-bowed posture; instead it assumes a "sick-bird" attitude, crouching with the body feathers fluffed. This type of submissive display is common to many passerines.

We have previously noted variation in the effectiveness of different species in evoking the preening invitation display (Table 3). In our tests, species of large size were ineffective, no response being given to male Great-tailed Grackles or to the Common Grackle, Rock Dove, and Mourning Dove. But individuals of moderate size, notably female Great-tailed Grackles and the Cockatiel, were effective. And here it is noteworthy that cowbirds do not parasitize species larger than the Mourning Dove (Friedmann, 1929).

Our cowbirds seemed relatively reluctant to display to black or

dark-brown individuals, but otherwise color and pattern of the potential recipient apparently has minor if any significance. We note that cowbirds responded less frequently to male than to female Red-winged Blackbirds, and they displayed rarely to Red-eyed Cowbirds and not at all to the Prevost Cacique, Chimney Swift, and Starling, all of which are black. This may indicate that our captive cowbirds had been conditioned to avoid black individuals as a consequence of previous experience with males of their own species. But it is possible that black is a relatively ineffective releaser (if not an actual inhibitor) quite apart from any conditioning effect. Experiments with individual cowbirds raised in visual isolation from other birds may be required to settle this problem. At present we can only note that the failure of cowbirds to display to the Blue Jay and their relatively weak response to the Loggerhead Shrike perhaps provide some support for the idea that the response is influenced by previous experience. Both species are notoriously aggressive toward other species, and Friedmann (1929) suggests that the absolute freedom from "molothrine annoyance" enjoyed by the shrikes is due to the hawklike habits of these birds. Both shrikes and jays occur commonly in the Austin region, where our cowbirds were trapped.

The whole problem of the influence of previous experience on this behavior is indeed complex. In the Austin region, cowbirds are associated in winter flocks with Red-winged Blackbirds, and they also have frequent contact with meadowlarks and House Sparrows at stockyards and about farms. It is, therefore, perhaps significant that these species were particularly effective in evoking preening invitation display in our cowbirds; but strong response was also given to two exotic species, the Shell Parakeet and the Cockatiel, with which the cowbirds had not had previous experience in the field.

HETEROPREENING IN OTHER SPECIES

Preening invitation postures similar to those of parasitic cowbirds occur in a number of bird species, where, however, they normally function to induce heteropreening by conspecific individuals rather than those of other species. In some species, heteropreening may have no function apart from feather maintenance or the control of ectoparasites; the adaptiveness of this cooperative behavior is apparent since the feathers that are most frequently preened are those that the individual cannot itself reach with its bill. In other species, however, heteropreening ceremonies unquestionably have further significance on a sexual or other social level. Similarly, in mammals, social grooming serves a biologi-

cal function in removing parasites and the like, but at least in the higher primates it is generally agreed that social grooming takes on added significance as a "social service" (Sahlins, 1959).

A display similar to that of cowbirds is reported by Lorenz (1938, 1952) in the Jackdaw (*Corvus monedula*), in which it has an appeasement function. He notes (1952) that "if one jackdaw wants to show submission to another, he squats back on his hocks, turns away his head, at the same time drawing in his bill to make the nape of his neck bulge, and, leaning towards his superior, seems to invite him to peck at the fatal spot." This behavior illustrates what Lorenz (1952) regarded as "the essence of all the gestures of submission by which a bird or animal of a social species can appeal to the inhibitions of its superior. . . . The supplicant always offers to his adversary the most vulnerable part of his body. . . . In most birds, this area is the base of the skull." This interpretation now seems questionable in light of recent analyses by Tinbergen and Moynihan (1952), which suggest that the bowing and head-turning displays to which Lorenz refers have appeasement function (*i.e.*, reduce the attack and/or escape tendencies of other individuals; see Moynihan, 1955) not in the presentation of a vulnerable part of the body *per se* but as the opposite of threat movements, an idea previously expressed in Darwin's principle (1872) of antithesis (see discussions by Marler, 1956, 1959). Representative of this class of display are head-flagging movements of gulls (Tinbergen and Moynihan, 1952), and, perhaps also, the bowing of Red-winged Parakeets (*Psephotus haematonotus*) reported by England (1945).

The effectiveness of these displays in reducing the probability of attack lies in the fact that they minimize stimuli for attack by the recipient (Marler, 1957). A similar end may be achieved by presenting stimuli for responses that are incompatible with attack, that is, by diverting the "attention" of the recipient to a nonhostile activity (the "deceptive" displays of Moynihan, 1955). Finally, as noted by Marler (1957 and *pers. comm.*), reduction of the aggressive tendency of another individual may be achieved by presenting stimuli that are especially evolved for the inhibition of attack.

Returning to Lorenz's description of the Jackdaw display, it seems possible that the head is presented as an invitation to preen rather than to peck. Social heteropreening is common among Jackdaws, and, even if presentation of the fluffed feathers of the nape and head to an antagonist did not actually induce heteropreening, the resemblance of the display to that used to invite "friendly" social heteropreening might have a "soothing" effect, as suggested by Moynihan (1955) in refer-

ence to a comparable display of the Spice Finch (*Lonchura punctulata*). Observations on captive Jackdaws by Marler (pers. comm.) have recently confirmed our interpretation, for he notes that the display does in fact often elicit heteropreening.

Goodwin (1959, 1960) has recently published some interesting notes on heteropreening in estrildines of the genus *Amandava*. In three species studied, the Avadavat (*A. amandava*), the Golden-breasted Waxbill (*A. subflava*), and the Blue-breasted Waxbill (*A. angolensis*), mutual heteropreening is common; and, in agonistic situations, the subordinate of any two birds is likely to offer its head as an appeasing response to actual or threatened aggression. Goodwin has advanced the thesis that heteropreening "involves sublimated . . . aggression on the part of the preener and submission on the part of the preenee," and he notes that individuals will only permit heteropreening from individuals that are regarded as superiors or equals. Surprisingly enough, "weaker" birds, especially when apparently "feeling depressed or socially insecure through having been defeated in a fight," will approach "stronger" individuals of their own or of other species of *Amandava* and deliberately offer the head for preening. In the solicitation of other species, the behavior of these estrildines resembles that of cowbirds, but it would be premature to conclude that the similarity extends to motivational factors or that the functional significance of the behavior is the same in these two different groups of birds.

In the highly gregarious Bronze Mannakin (*Lonchura cucullata*), social heteropreening of the head feathers occurs both in pair members and in nonreproductive individuals in flocks (Morris, 1957). A bird invites preening by moving close to another individual and tilting the head as the two birds perch side-by-side. Similar behavior is recorded (Moynihan and Hall, 1954) for the Spice Finch, in which "a bird wanting to be preened tries to incite its immediate neighbor(s) to do so by raising the feathers of the whole head and neck equally, and turning the nape or chin towards the other bird(s)." It is noteworthy that neither species of *Lonchura* maintains individual distance; frequently individuals come into close bodily contact, clumping together on perches to rest or sleep and to clean one another.

Analogous behavior is reported in the Groove-billed Ani (*Crotophaga sulcirostris*) by Skutch (1959), who notes that "while one stretches up its neck its neighbor carefully bills and nibbles at the feathers, possibly searching for insect pests; and when the first has finished its kind office to the second, the latter reciprocates the favor." Again it is noteworthy that anis are social birds showing no individual distance.

In several species of wrens of the genus *Campylorhynchus*, heteropreening ceremonies are a regular feature of the behavior of pair members and presumably function in pair-bond reinforcement (Selandier, 1956). When pair members meet after periods of separate foraging or other activity, the female holds a rigid pose as the male carefully preens her head and neck. Preening by the male is interpreted as a ritualized "substitute" for pecking, which actually occurs in one species, *C. brunneicapillus*, in the absence of the heteropreening ceremony.

Among psittacines, heteropreening ceremonies initiated by head-bowed invitational displays are widespread and frequently seem to have appeasement function. We have recently observed heteropreening in captive Cockatiels, Shell Parakeets, and African Grey Parrots (*Psittacus erithacus*); and Dilger (1961) describes this behavior in lovebirds (*Agapornis*). In Cockatiels, a mutual preening and billing ceremony precedes copulation of mated pairs. In a manner suggestive of a cat soliciting head scratching from a human, hand-raised African Grey Parrots will invite "preening" from humans by bowing the head and fluffing the feathers of the head and neck. Analogous behavior is reported in captive Bateleur Eagles (*Terathopius ecaudatus*), which greet humans by bowing the head and inviting scratching (Moreau, 1945).

THE COWBIRD'S DISPLAY AS AN ADAPTATION FOR PARASITISM

We come finally to a consideration of the possible adaptive significance of preening invitation display as manifested by parasitic cowbirds. Perhaps the simplest interpretation is that the behavior represents an exploitation of other species for skin and feather care, with the benefit to the cowbird being limited to the preening that is obtained. But there is no reason to believe that the cowbirds have unusual requirements for preening of the feathers of the head region; nor are they subject to unusually heavy infestations of lice or other ectoparasites (Friedmann, 1929). Moreover, if we assume that cowbirds have special needs for feather and skin care, it is perhaps surprising that the problem of obtaining preening has not been solved by evolution of intraspecific heteropreening ceremonies. Considering all aspects of the problem, we wish to suggest that, while the occasional heteropreening obtained by cowbirds may be beneficial from the standpoint of feather and skin maintenance and may serve to reinforce the cowbirds' tendency to display to individuals of other species, the prime adaptive significance of the behavior is in the effect it has in reducing the hostile

tendencies of individuals of other species that are potential hosts for the cowbirds' brood parasitism.

In the cowbird's display, appeasing elements tending to minimize stimuli for attack include the lack of movement, the careful avoidance of direct visual fixation of the recipient, and the partial or complete concealment of the bill (a major aggressive weapon) by bowing the head. (In contrast, a highly aggressive cowbird that is about to attack moves rapidly, visually fixates the opponent, and adopts a posture in which the bill is directed forward.) At the same time, according to our interpretation, the presentation of the fluffed feathers of the head may be "designed" further to reduce the probability of attack by diverting the recipient's "attention" to the act of preening.

The fact that cowbirds actively seek out and approach recipients may at first sight seem inconsistent with the thesis that the behavior reduces the likelihood of attack; but, as suggested by Marler (pers. comm.), this may actually facilitate the process of appeasement if the cowbird approaches quickly and confidently before the recipient becomes aggressive.

The potential advantages of an interspecific appeasement display are apparent, for it is well known that female cowbirds are attacked by their hosts when they are discovered at the nests; and the furtive behavior of a female cowbird approaching a nest that she intends to examine or in which she will deposit an egg in itself suggests that the female is exposed to the danger of discovery and attack by host individuals (Mayfield, 1960). According to Friedmann (1929) "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 victims." As an example of the reaction of hosts to the female cowbird at the nest, we may cite Friedmann's observation of a Robin (*Turdus migratorius*) that "began yelling its distress call" and drove her off the nest. Another Robin (the mate), two Catbirds (*Dumetella carolinensis*), three Yellow Warblers (*Dendroica petechia*), and one Blackpoll Warbler (*Dendroica striata*) joined in the chase of the female cowbird, "each screaming its loudest." Another example is provided by Prescott's record (1947) of attacks by a Scarlet Tanager (*Piranga olivacea*) and two Red-eyed Vireos (*Vireo olivaceus*) on a female cowbird at a nest of the vireos.

Largely as a result of research by Hann (1941), it is known that the female cowbird not only visits the host's nest to lay but also spends a considerable amount of time in the vicinity of nests, waiting for the appropriate time to deposit her eggs. She watches nest building by

potential hosts for extended periods and makes regular trips of inspection to nests in the absence of the owners (Mayfield, 1961a). In the forenoon of the day before she lays, on the day of laying, or, rarely, on the following day, she usually visits the nest and removes one of the host's eggs; and she may visit a nest in which she has deposited an egg even after incubation has begun (Mayfield, 1961a). Male cowbirds presumably do not visit the nests of hosts, but they do spend time in the territories of host species and are also subject to hostile responses by the hosts. For example, we have seen Red-winged Blackbirds chasing both male and female cowbirds from their territories on several occasions; and hostility of blackbirds to cowbirds is also reported by Sutton (1928).

Hostile responses of Song Sparrows (*Melospiza melodia*) to cowbirds have been described by Nice (1943), who notes that the sparrows habitually react to the presence of adult cowbirds in their territories with vigorous warning notes and threat postures; and, as a female cowbird approaches the nest, the sparrows frequently attack. The following are representative of Nice's field notes on cowbird-Song Sparrow interactions:

Mar. 30. A female Cowbird spends about 10 minutes in 1M's territory. 1M and K2 [a pair] *tchunk* [warning note] continually, following her closely in trees, on burdocks and on the ground. K2 [female] seems more zealous than 1M. 4M and K3 [a second pair occupying an adjacent territory] are also *tchunking*. 1M flies as though to drive off 4M; returns within a meter of Cowbird with tail spread. K2 utters *zee* [threat note]. . . . Apr. 3. Male Cowbird comes within a few centimeters of 1M and K2 feeding on the hillside; one of the pair pecks him in the breast; he leaves.

Nice also reports that a presumed first-year Song Sparrow on its territory in the spring was "greatly disturbed" over the courting activities of cowbirds early in the season before nesting had begun.

In American Redstarts (*Setophaga ruticilla*) on their territories, Hickey (1940) found that "males were silent in the presence of female cowbirds, but females reacted with sharp hisses, a rapid snapping of the bill and much spreading of the tail."

Additional records of hostile responses by potential hosts to female cowbirds in the vicinity of nests are given by Leathers (1956) and Mayfield (1960).

Apparently not all host species respond aggressively to cowbirds, for Hann (1937) determined that Oven-birds (*Seiurus aurocapillus*) are heavily parasitized but "do not recognize the Cowbirds at sight as enemies," and he observed (1941) one Oven-bird flee from the nest as a female cowbird approached.

In advancing our speculative interpretation, we are not unduly discouraged by the fact that we have no observations of cowbirds actually using the display to appease hostile host individuals in the vicinity of nests, for few observers have studied the behavior of the cowbird. Moreover, brief presentations of the preening invitation display, especially where heteropreening is not induced, may easily be overlooked or confused with other behavior patterns of the cowbird by an observer not familiar with the display.

Since the effectiveness of display in inducing preening increases with repeated exposure of the recipient to it, the cowbirds' persistent use of the display in the nonbreeding season may be adaptive in conditioning potential hosts to respond in a "friendly" manner, thus increasing the likelihood that the display will be effective in forestalling attack in the breeding season when the cowbirds are in the territories of the host species. Additionally, by using the display in winter flocks, the cowbirds may gain some advantage over individuals of other species in potentially agonistic situations involving food or roosting sites.

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SUMMARY

Brown-headed Cowbirds (*Molothrus ater*) approach individuals of other species of birds and solicit heteropreening by giving a special head-bowed display. Through persistent presentation of the display, heteropreening may be induced from a variety of species, including meadowlarks, Red-winged Blackbirds, and other forms that do not engage in intraspecific heteropreening. Intraspecific presentation of the preening invitation display is uncommon among cowbirds and does not result in the induction of heteropreening.

In captivity, the readiness of cowbirds to display is increased by depriving them of opportunity for close contact with individuals of other species. There is no marked seasonal variation in frequency with which the display is given, and bilateral castration of males does not affect their readiness to display. Preliminary tests with live birds and dummies of other species suggest that cowbirds will not display to species larger than a Mourning Dove and are relatively reluctant to display to birds that are black in color.

A similar preening invitation display was seen in captive Red-eyed Cowbirds (*Tangavius aeneus*).

Avian appeasement displays are discussed, and it is suggested that the interspecific display of parasitic cowbirds is an adaptation for parasitism, functioning to decrease the probability of attack by individuals of host species by decreasing their aggressive tendencies.

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