

WHY DO BROWN-HEADED COWBIRDS PERFORM THE HEAD-DOWN DISPLAY?

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ABSTRACT.—Four hypotheses for the function of the head-down display performed by Brown-headed Cowbirds were tested with observational data from free-ranging and captive cowbirds. Free-ranging cowbirds performed 284 interspecific and four intraspecific displays during 59.2 daylight hours while roosting in mixed-species flocks adjacent to feeding areas. The most common recipients of displays, female Red-winged Blackbirds and House Sparrows, preened cowbirds during 25 displays. Cowbirds that had just been preened displayed more often than those that had not recently been preened. Captive cowbirds displayed intraspecifically 475 times during 13.3 h, and dominant captive birds displayed more often than their subordinates. The following hypothesis was proposed to explain the display's function: the head-down display of Brown-headed Cowbirds is an appeasing agonistic behavior, the displayer is most often dominant to the recipient, and subsequent displaying is stimulated by interspecific preening. The display may function in: (a) obtaining food, (b) minimizing roosting energetics, and/or (c) establishing flock order. Received 26 November 1979, resubmitted 5 January 1982, accepted 30 August 1982.

BROWN-HEADED COWBIRDS (*Molothrus ater*) perform an unusual head-down display (Darley 1968) during which they direct the backs of their heads and necks toward other birds (Selander and La Rue 1961). The head-down display, also called the preening invitation display (Selander and La Rue 1961), is performed both intra- and interspecifically (Selander and La Rue 1961; Stevenson 1969; Rothstein 1977, 1980; Scott 1977). Interspecific displays may include, in addition to the above posture, the preening of the displaying cowbird's feathers by the display recipient (Selander and La Rue 1961, Scott 1977). Several other species of cowbirds perform a display similar, but not identical, to that of the Brown-headed Cowbird (Selander 1964). Hereafter "display" will refer to the head-down display and "cowbird" will refer to the Brown-headed Cowbird.

The function of the head-down display has been explained by a number of authors in sometimes contrasting ways. The purpose of this study, therefore, was to summarize expla-

nations of the display in the form of four hypotheses and to evaluate those hypotheses using data from free-ranging and captive cowbirds.

Hypothesis 1.—The display is an adaptation for brood parasitism, which functions in reducing host species' aggressive tendencies toward a cowbird so that the cowbird can remain on the host's territory and/or approach the host's nest with less opposition (Selander and La Rue 1961).

Hypothesis 2.—"The display is an aggressively motivated gesture that cowbirds use in a variety of contexts to assess the fighting potential of other birds, . . . to establish dominance," or to integrate social units (Rothstein 1980).

Hypothesis 3.—The display is an example of behavioral mimicry. Cowbirds deceive display recipients: the recipient interprets the display as appeasing, while the cowbird's intent is to threaten (Rothstein 1980).

Hypothesis 4.—The display is rare in nature, and, because there is a lack of recorded observations, the display has little "biological significance" (Dow 1968).

STUDY AREA AND METHODS

Free-ranging cowbirds.—The first field study was conducted near Bowling Green, Ohio, from 6 March

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until 28 April 1976. The site, a rectangular strip of land of approximately 3 ha, was bisected by a paved road and adjacent to the east bank of the Portage River (North Branch) in Wood County. Observations were recorded from a car parked 10–25 m from the river. That portion of the study site west of the road and adjacent to the river was a flood plain dominated by deciduous trees, while the portion east of the road was a cultivated field consisting of corn stubble.

The second field study was conducted in State College, Pennsylvania, from 6 January until 12 January 1981. The site included a row of forsythia bushes (*Forsythia* sp.) approximately 8 m × 18 m × 2 m. A gravel road curved around the bushes and passed within 2 m of their north end. Observations were recorded from a car parked 10–20 m from the bushes. The area surrounding the bushes was mowed grass to the east and cultivated fields of corn stubble to the west.

Behavioral interactions were observed with the aid of 7–15 × 35-mm binoculars during 59.2 h of observation between 0800 and 1830.

Captive cowbirds.—A total of 45 cowbirds (24 AHY males, 8 HY males, and 13 females) was maintained in captivity during the winter and spring of 1976. HY males (males that hatched during 1975) were distinguished from AHY males (males that hatched before 1975) by an incomplete post-juvenile molt of the humeral tract (Baird 1958, Selander and Giller 1960). All 45 birds were caught in northwestern Ohio during the late summer and fall of 1975 with modified crow traps.

Captive birds were separated by sex, housed in 1.84 m × 2.63 m × 2.31 m holding cages in a barn near Bowling Green, and exposed to the natural photoperiod via windows. The observation cage, of the same size as the holding cages, had one window and five perches. Food (50–50% mixture of cracked corn and chick starter) and water were constantly available.

Canvas covered the north wall of the observation cage, providing visual but not auditory isolation of the study group from the other captive birds in the barn. Observations were made from an opening in a burlap enclosed walkway so that the study group as well as the rest of the birds in the barn could not see the observer.

Captive cowbirds were observed in four different groups of six birds each: females, HY males, AHY males, and mixed groups (two females, two HY males, and two AHY males). Females could not be separated confidently by age and therefore were not divided into age groups. Each group type was observed for a 5-day period during 11 January–22 February and during 26 March–30 April. Observations were recorded between 0805 and 1838.

All study groups were treated identically. Birds in each group were banded with U.S. Fish and Wildlife Service bands and unique colored leg bands, then

allowed to habituate to the observation cage for 5 days. Observations began on the sixth day.

The entire group was observed for 20 min, and a record was kept of the total supplants, retreats, and head-down displays for 5 days; the group was then removed and the succeeding group placed in the cage to begin its habituation period. The order of group observation was randomized.

Description of behaviors.—“Supplanting” is an agonistic behavior that occurs when one bird displaces another (Darley 1968: 20–21). Variation in supplanting can arise from the speed of approach and the sequence or amplitude of behaviors.

“Retreating” includes “any pattern, walking, hopping, or flying, used by a submissive bird to leave” (Darley 1968: 21). When a two-bird interaction resulted in one bird displacing the other, there was always at least one supplant and one retreat.

The head-down display was first described by Selander and La Rue (1961). While displaying, the cowbird’s “head is bowed” so that “the bill is directed vertically downward or in toward the cowbird’s body.” The orientation of the cowbird’s body to the recipient can either be directly toward or at an angle away from the recipient. Commonly, the cowbird will display as it approaches the recipient, ceasing its approach when it is about 2 cm away from the recipient. Occasionally, the cowbird’s approach continues until it touches the recipient bird’s breast with the top of its head. Like supplanting and retreating, head-down displays varied in duration, amplitude, and speed of the displayer’s approach.

Data analysis.—Captive birds were ranked by social status based on their supplant and retreat records (Scott 1977). The bird that supplanted its group members most often and retreated least was ranked as the alpha bird.

Displays by free-ranging birds were compared by sex, recipient species, and supplants. Displays by captive birds were compared by social status. In Tables 2 and 3 we analyzed “display incidents” as defined by Rothstein (1977: 17).

Statistical analyses followed methods presented by Zar (1974). Sample sizes greater than or equal to 10 and less than or equal to 25 were analyzed using a binomial distribution. Samples greater than 25 were evaluated using a two-tailed χ^2 test corrected for continuity. A sample size of less than 10 was considered too small for meaningful statistical analysis.

RESULTS

Free-ranging cowbirds.—None of the recipients of displays by free-ranging cowbirds responded by displaying in return to the initiator. Recipients responded either by retreating, pecking at the displayer, supplanting the displayer, or seeming to ignore the displayer. None of the recipients preened conspecifics.

TABLE 1. Head-down displays performed by free-ranging Brown-headed Cowbirds in northwestern Ohio and central Pennsylvania.

Sex of displaying cowbird	Recipient species	Number of displays	Number of displays where recipient preened cowbird	Supplants by	
				Cowbird	Recipient
A. Ohio observations (54 h during 33 visits, 0820–1830, 6 March–28 April 1976)					
FEMALE	♀ House Sparrow	6		5	1
	♂ House Sparrow	2		2	
	♀ Red-winged Blackbird	54	12	21	4
	♀ Rusty Blackbird	2		1	
	♀ Brown-headed Cowbird	1			1
MALE	♂ House Sparrow	1		1	
	♀ Red-winged Blackbird	10		6	
OHIO TOTAL	4 species	76	12	36	6
B. Pennsylvania observations (5.2 h during 5 visits, 1125–1610, 6 January–12 January 1981)					
FEMALE	♀ House Sparrow	23	2	12	
	♂ House Sparrow	30		9	2
MALE	♀ House Sparrow	52		37	4
	♂ House Sparrow	104	11	74	1
	♀ Brown-headed Cowbird	2		1	
	♂ Brown-headed Cowbird	1			
PENNSYLVANIA TOTAL	2 species	212	13	133	7
GRAND TOTAL	4 species	288	25	169	13

Free-ranging cowbirds performed 288 head-down displays during 38 visits to the study sites that totalled 59.2 h of observation (Table 1). Cowbirds presented displays to four species: female Red-winged Blackbirds (*Agelaius phoeniceus*), a female Rusty Blackbird (*Euphagus carolinus*), male and female House Sparrows (*Passer domesticus*), and male and female cowbirds (Table 1).

All but two recorded displays were observed while cowbirds were roosting during daylight hours in trees or shrubs in mixed-species flocks adjacent to the feeding areas of corn stubble or stockyard. The remaining two displays were performed by cowbirds in Pennsylvania while on snow-covered ground.

Some displays were seen in rapid succession, separated by about 1–5 s. The birds performing these successive displays quickly followed and repeatedly displayed toward the recipient if the recipient remained in place or hopped or flew a short distance away (≤ 1 m). If the recipient bird flew a longer distance away, the cowbird either displayed toward another bird or stopped displaying altogether. As a result of these successive displays, the head-down

display appeared to be more clumped than evenly spread out in time. If display rate is considered, based upon the number of minutes that cowbirds were present, a display was observed every 42.6 min in Ohio and every 1.5 min in Pennsylvania.

Female cowbirds in Ohio displayed more often than males (65 times vs. 11 times, $P \leq 0.001$; Table 1), though maximum estimates of males ($n = 338$) and females ($n = 333$) observed were nearly equal. Male cowbirds displayed more often than females in Pennsylvania (159 times vs. 53 times, $P \leq 0.01$; Table 1); maximum estimates of males ($n = 125$) and females ($n = 46$) showed that males predominated.

Eighty-six percent of female cowbird displays and 91% of male cowbird displays in Ohio were directed toward female Red-winged Blackbirds ($P \leq 0.001$ in both cases; Table 1). Other passerines such as male Red-wings, European Starlings (*Sturnus vulgaris*), Common Grackles (*Quiscalus quiscula*), Northern Cardinals (*Cardinalis cardinalis*), and Song Sparrows (*Melospiza melodia*) were commonly observed at the Ohio site and appeared to be available

TABLE 2. Head-down displays performed by captive cowbirds during 1976. Each group was observed for five 20-min periods. Matrices are arranged with the alpha bird in the top left corner and progressively subordinate birds to the right and below the alpha bird. Because no displays were observed in the group of six AHY ♂ (16 April–20 April), no matrix is included for that group. Recipients are listed horizontally, displayers vertically.

6 AHY ♂ (16 Feb–20 Feb); mutual displays = 14								6 HY ♂ (23 Jan–27 Jan); mutual displays = 23							
C	C	A	E	B	D	F	Σ	D	D	B	E	A	C	F	Σ
A	—	2	0	1	4	4	11	B	—	0	0	0	0	0	0
E	0	—	0	0	0	0	0	E	3	—	0	0	17	5	25
B	0	0	—	0	0	14	14	A	0	1	—	3	0	0	4
D	0	0	0	—	0	0	0	C	0	0	0	—	0	2	2
F	0	0	0	0	—	16	16	F	0	0	0	0	—	0	0
Σ	2	0	0	0	6	—	8	Σ	0	0	0	0	0	—	0
							Σ = 49								Σ = 31
5 ♀ (11 Jan–15 Jan); mutual displays = 3								2 AHY ♂, 2 HY ♂, 2 ♀ (4 Feb–8 Feb); mutual displays = 83							
E	E	C	A	D	B	Σ	HY♂	HY♂	AHY♂	AHY♂	♀	♀			
C	—	0	2	0	0	2	H	H	G	H	G	G	F	Σ	
A	0	—	1	0	1	2	G	—	1	0	0	0	4	5	
D	0	1	—	1	0	2	H	0	—	0	0	3	16	19	
B	0	0	0	—	0	0	G	0	0	—	9	0	37	46	
Σ	0	0	0	0	—	0	F	0	0	0	—	0	1	1	
							Σ	0	0	0	0	—	13	13	
							Σ = 6		0	2	6	0	0	—	8
															Σ = 92
6 HY ♂ (6 Apr–10 Apr); mutual displays = 7								6 ♀ (26 Apr–30 Apr); mutual displays = 48							
D	D	H	G	B	C	F	Σ	G	G	E	C	D	A	B	Σ
H	—	0	0	2	6	1	9	E	—	0	12	0	0	0	12
G	0	—	0	0	0	0	0	C	0	—	11	0	2	0	13
B	0	0	—	0	0	2	2	D	1	7	—	1	1	1	11
C	0	0	0	—	0	0	0	A	0	2	0	—	1	2	5
F	3	0	0	0	—	0	3	B	5	0	3	10	—	6	24
Σ	0	0	0	0	0	—	0	Σ	1	1	1	3	14	—	20
							Σ = 14								Σ = 85
2 AHY ♂, 2 HY ♂, 2 ♀ (4 Feb–8 Feb); mutual displays = 7															
AHY♂	AHY♂	HY♂	HY♂	AHY♂	♀	♀									
N	N	F	C	O	C	E	Σ								
F	—	0	0	0	0	0	0								
C	0	—	0	0	4	0	4								
O	0	0	—	0	0	1	1								
C	0	0	0	—	0	0	0								
E	0	0	0	0	—	7	7								
	0	0	0	0	1	—	1								
							Σ = 13								

in time and space for cowbirds to display toward if they had chosen to do so.

In Pennsylvania, where only cowbirds and House Sparrows were observed, House Sparrows were recipients of 209 of 212 displays (Table 1). Male and female House Sparrows were present in approximately a 1:1 ratio. House Sparrows outnumbered cowbirds during all

days of observation; estimates of the number of birds present per visit varied from 18 to more than 150 for House Sparrows and from 5 to 75 for cowbirds. Male cowbirds displayed more often toward male House Sparrows ($P \leq 0.001$) than toward female House Sparrows (Table 1).

Female Red-wings in Ohio and male and female House Sparrows in Pennsylvania were the

TABLE 3. Summary of two-tailed χ^2 analysis of head-down displays performed by dominant versus subordinate captive cowbirds.

Group type, age, and sex of displaying cowbird	Dominance position of birds that performed display most often ^a		Total
	Jan-Feb	March-	
	observ- ation period	April observ- ation period	
Segregated AHY ♂♂	—	—	—
Segregated HY ♂♂	top	top	top
Segregated ♂♂	top	top	top
Segregated ♀♀	sm ^b	—	—
Segregated ♂♂ + ♀♀	top	—	top
Mixed ♂♂ + ♀♀	top	—	top
Total	top	—	top

^a Top denotes that the top three birds (top two for females Jan-Feb segregated group) in the dominance hierarchy performed the display more often ($P \leq 0.05$) than subordinates.

^b Sample size was <10 and therefore not tested.

only birds observed responding to the head-down display by preening the feathers of the displaying cowbird. These birds preened male and female cowbirds on the cowbirds' capital tracts and/or the backs of their necks during 25 of 288 displays (9%; Table 1).

Preening seemed to be a strong stimulus for subsequent displaying at both sites, as a cowbird that had been preened seemed more quickly and more persistently to pursue and display toward the bird that had preened it. In Pennsylvania, we tested this prediction by recording displays performed by birds that had just been preened versus those birds that had not been preened but that had displayed within the previous 5 min. The birds that had been preened displayed far more often than those that had not been preened ($P \leq 0.001$); two birds that had just been preened displayed 29 times during the 3.5 min that we could follow them, while three birds that had not been preened displayed 33 times during 15.5 min.

Displaying cowbirds in both Ohio and Pennsylvania supplanted recipients more often ($P \leq 0.001$) than they retreated from recipients (Table 1). Following a supplant, displaying cowbirds were often observed to continue their approach toward the recipient, which had moved a short distance away. Frequently, this sequence of behaviors was repeated, resulting in a series of supplants by the displayer. When

recipients supplanted a displaying cowbird, it was done most often by pecking. Eight of 17 pecks by recipients toward displaying females were associated with the retreat of the displaying female.

Captive cowbirds.—A total of 475 intraspecific displays by captive birds was recorded during 13.3 h of observation (Table 2). Head-down displays were observed in all groups during both observation periods except AHY males from 16 April until 20 April; they were not observed performing any displays.

Captive cowbirds, in all groups and during both observation periods, exhibited a peck dominance hierarchy, and females were subordinate to males (see Scott 1977: 25–26 for dominance data). Using the term dominant to refer to the top three birds in the dominance hierarchy (top two for females Jan-Feb segregated flock) and subordinate to refer to the bottom three birds in the hierarchy, we found that when there were differences in display frequencies, dominant birds always performed the display more often ($P \leq 0.05$) than subordinates (Table 3). Differences in favor of dominant birds were observed more often during the first observation period than during the second.

DISCUSSION

Hypothesis 1.—Our study, as well as other evidence, supports the appeasement portion of hypothesis 1. We observed recipients preening free-ranging cowbirds during 25 of 288 displays (Table 1). Interspecific preening was not observed in any other context. Similarly, it was not uncommon for captive birds to contact each other during a mutual display. Thus, displaying birds, both free-ranging and captive, were able to get close enough to recipients to make physical contact for periods of time up to 2 min, something that was not observed in any other context.

Similarly, Stevenson (1969) concluded after observing 2,530 displays by captive cowbirds that the display allows birds to approach recipients more closely than if they were not displaying. Results from our study support Stevenson's conclusion.

In addition, Selander and La Rue's (1961) study showed that during interspecific displays, recipients most often initially responded by pecking at the displaying cowbirds but, af-

ter additional exposure to the display, gradually began to peck less and preen more. Allo-preening was considered less aggressive than pecking. Robertson and Norman (1976) in their field study with mounted birds also showed that the display appeases; potential hosts were less aggressive to mounts in the display posture than mounts in the "normal" posture. Finally, Lowther and Rothstein (1980) suggested that displays performed by cowbirds less than 1.5 months of age may function in appeasement.

We found no evidence during our field observations that the display and brood parasitism are directly associated. The possibility that it is infrequently performed in that context, however, cannot be ruled out by this study. Displays performed by free-ranging birds and observed during this study were directed toward species that are uncommon hosts of the cowbird (Friedmann 1929, Hicks 1934, Scott unpubl. data). Friedmann (1963) and Rothstein (1980) also state that the display is seldom directed toward common hosts.

Observations and conclusions by other authors similarly fail to support the parasitism component of hypothesis 1. Mayfield (1961) and Friedmann (1963) state that at the time when female cowbirds lay their eggs, small passerines are not apt to be present at their nests. Hence, female cowbirds in the process of egg laying would not commonly interact with potential hosts. Hann (1937, 1941), Mayfield (1961), and Norman and Robertson (1975) observed female cowbirds "inspecting" potential host nests before cowbird egg laying took place. No cowbird behavior was reported that could be interpreted as a head-down display. Though Prescott (1947) observed an instance when a female cowbird approached a Red-eyed Vireo (*Vireo olivaceus*) sitting on its nest and Hann (1937) observed the same with Ovenbirds (*Seiurus aurocapillus*), the cowbirds supplanted the vireo and Ovenbirds without performing a behavior that could be interpreted as a head-down display. In fact, the cowbird observed by Prescott supplanted the vireo with a "distinct pecking motion."

Frequency of the display does not appear to be influenced by hormone production in males (Selander and La Rue 1961). Assuming that the display is directly involved in brood parasitism, one could predict that the frequency of the display would increase during the breeding

season concomitantly with increasing hormone production. Selander and La Rue (1961), however, did not observe variation in the rate at which their captive male cowbirds displayed during mid-April following bilateral castration in January.

Displays performed by other species of cowbirds suggest that the display may not have evolved in a direct relationship with brood parasitism. Selander (1964) suggests that the Bay-winged Cowbird's (*Molothrus badius*) "preening invitation display" is an evolutionary precursor to the head-down display of the more evolutionarily specialized Brown-headed Cowbird. The Bay-winged Cowbird is not a brood parasite (Friedmann 1929). Hence, the display may have evolved before the habit of brood parasitism.

Hypothesis 2.—Two aspects of hypothesis 2 were supported by this study. Patterns of displaying were observed that support the display's involvement in integrating social units (Rothstein 1977). For example, birds in the top half of the dominance hierarchy displayed more often than birds in the bottom half ($P \leq 0.05$; Table 3). In addition, when differences in display rates existed in comparisons between segregated groups and the corresponding age or sex class of mixed groups, birds displayed more often ($P \leq 0.01$) when both sexes were present than when just one sex was present (Table 2). The only exception to this trend was that females in the segregated flock during March-April displayed more often than females in the mixed flock. It also appeared from the study of captive birds that a displayor may be assessing the agonistic tendencies of the recipient, especially when cowbirds first interact with an unfamiliar individual (Rothstein 1980). This appeared to be true following the introduction of House Sparrows and additional cowbirds to the observation cage (Scott unpubl. data).

We do not agree with that portion of hypothesis 2 that describes the display as a threat. Rothstein concluded "that the display's true message is threat" (Rothstein 1980: 157), because dominant captive birds display more often than their subordinates and because some displaying captive birds alternately displayed and pecked. We take issue with this conclusion for two reasons. First, it was not disproven that dominants may display toward subordinates in order to appease them. That dominant birds display most often to subordinates does not

clearly indicate that the display is aggressive. Dominant birds, free-ranging or captive, may display most often toward subordinates in order to get and stay close to subordinates, not to threaten them. For example, among captive birds dominant males may display toward subordinate females in order to stay close to them. We, as well as Stevenson (1969), interpret no clear intent by displaying cowbirds to displace recipients. On the contrary, based on the frequent observation that displaying free-ranging and captive cowbirds persistently pursued fleeing recipients, it seemed to us that displaying cowbirds "wanted" recipients to remain in close proximity. We discussed under hypothesis 1 additional reasons why the display is appeasing. Second, the conclusion that pecking and displaying have the same meaning for cowbirds simply because their performances are closely associated in time is not necessarily valid.

Rothstein's (1980) results show that the display is performed by captive birds in a situation of conflict. Observations during this study agree. Such a context may explain why some cowbirds alternately displayed and pecked. Because we interpreted the display to be non-aggressive, appeasing, and performed in a situation of conflict, we prefer to refer to it as a complex agonistic behavior, i.e. "any behavior associated with conflict or fighting between two individuals," (Scott 1956: 214-215) rather than as an aggressive behavior.

Rothstein (1977, 1980) defined the situation of conflict as the violation of another bird's individual distance. The only thing that we thought could be threatening about the display was the displayer's close proximity to the recipient, not the displayer's posture or movements.

Rothstein's (1980) experiments also show that the display is most often performed by birds that are dominant to recipients. Observations during this study support that conclusion.

Our results show that among captive birds males were dominant to females (Table 2) and that females, across observation periods and while in mixed groups, responded to 66 displaying males by displaying in return 58 times. If cowbirds display in order to dominate other birds and the display is a threat, we would not expect that a subordinate female, who seldom threatens males with recognized cowbird threat behaviors (Scott 1977), would commonly return

the head-down display of a dominant male as was observed in our study. Furthermore, it is not clear why such a complicated threat behavior would be selected for when other threats, like bill pointing or pecking, would seem to displace and dominate a subordinate recipient more quickly than would a head-down display.

Rothstein (1980) explains mutual displays, like those above, as a "test of wills" or, alternatively, as mutual threats by individuals of similar social status. Although mutual displays could be mutual threats by birds of similar status, in this study subordinate females and dominant males commonly displayed mutually. Our observations, therefore, show that the prediction that mutually displaying birds are of similar social status frequently is not true.

Hypothesis 3.—The display cannot be behavioral mimicry, because there is no model for cowbirds to mimic. Suggesting that the display is an example of behavioral mimicry implies that there is selective pressure on cowbirds to mimic intraspecific behaviors of recipient species. No field-verified model behavior was proposed with the mimicry theory, nor have we seen during hundreds of hours in the field a behavior performed intraspecifically by recipient species that might be interpreted as a model for the display. Furthermore, the mimicry theory does not explain what specific selective advantage(s) a displayer gains by mimicking the behavior of another species.

As an alternative to the behavioral mimicry theory, we propose a simpler, more straightforward explanation: both displayer and recipient interpret the display as appeasement. Even if additional investigation substantiates the more complex deception/aggression hypothesis (Rothstein 1980) and it is shown that "receivers do not respond to the true message being sent" (Rothstein 1980: 173), the display should not be labeled as behavioral mimicry. Not all forms of deception constitute mimicry.

Hypothesis 4.—Hypothesis 4 is refuted by our observations of free-ranging cowbirds. We observed the display 288 times during 59.2 h of field observation (Table 1). Furthermore, the widespread occurrence of the display is supported by the geographical variation in its sightings. We have observed the display in Connecticut, Maryland (unpubl. data), Ohio, and Pennsylvania. Lowther and Rothstein (1980) reported it in Kansas; Rothstein (1980)

saw it in California, Connecticut, and New York; Dow (1968) observed it in Tennessee; and Darley (1968) saw it in Ontario. Selander and La Rue (1961) have sightings from Texas, Rhode Island, New York, Oklahoma, and Florida.

If more observations were undertaken of cowbirds as the birds roost during the day in mixed-species flocks adjacent to feeding areas, it would become apparent that the display is performed often by free-ranging cowbirds. Rothstein (1977, 1980) previously reported cowbirds displaying in this context; observations during this study support the context and provide additional details.

Incorporating those aspects of hypotheses 1-4 that were not rejected, we propose a consolidated hypothesis for the function of the head-down display as follows:

The head-down display is an appeasing, agonistic behavior that reduces agonistic behaviors of the recipient toward the displaying cowbird. The display is generally dominant to the recipient, and preening is a stimulus for subsequent displaying by the preened cowbird. The display functions in: (a) obtaining food, (b) minimizing roosting energetics, and/or (c) establishing flock order.

For the display recipient, preening could be a "conflict behavior performed" toward cowbirds who have violated the recipient's individual distance (Rothstein 1971, 1980). For cowbirds, preening appears to be important to the display's appeasement function. Pennsylvania cowbirds that had just been preened displayed more often than those that had not been preened ($P \leq 0.001$). Moreover, cowbirds may display toward female Red-wings or House Sparrows most often, because the probability of being preened is greatest with those birds. Field observations during this study suggest that preening is a positive response to the display that might signal that the agonistic tendencies of the recipient have been reduced. In this way, the display may be assessing agonistic tendencies, as Rothstein (1980) has proposed.

The hypothesized display functions are speculative. Although we will discuss them separately, they are not necessarily mutually exclusive and may or may not operate in concert.

Selander and La Rue (1961) were the first to

speculate briefly about the feeding and roosting functions of the head-down display. Joining a foraging group may be advantageous for a cowbird in obtaining food (Ricklefs 1973: 226). The head-down display may facilitate a cowbird's joining a foraging group by appeasing flock members or by helping to assess agonistic tendencies of flock members. In addition, the display may help a cowbird position itself in roosting trees where overnight energy expenditure for thermoregulation would be minimized. Lustick and Kelty (1979) have shown that location in roosting trees affects thermoregulation by Starlings and blackbirds. In a study of a winter roost in Texas (Johnson et al. 1980), researchers found that cowbird mortality was positively associated with freezing temperatures and "depletion of winter food supplies." Because feeding and roosting are often flock activities for cowbirds (pers. obs.), the display may placate other bird species with whom cowbirds flock, thereby facilitating the cowbirds' inclusion in the flock.

Rothstein (1980) suggested the flock-order function for the head-down display. It has long been known that disorganization of bird flocks can result in negative effects on individuals within the flock (Guhl and Alee 1944). Social disorganization could occur, especially when cowbirds are first captured and placed in a cage with unfamiliar individuals, because the birds are unnaturally overcrowded in their cage (Emlen 1950). Rothstein (1977) has stated that for captive cowbirds the number of intra- and interspecific displays decreased rapidly after birds had been maintained in intact groups for 2-5 months. Perhaps the display is observed less often among birds that have been together for a long time because social order has been established and group agonistic interactions have, therefore, become less frequent. In this captive setting, an appeasement display could benefit a dominant bird by reducing agonistic behaviors from conspecifics and allowing more time for behaviors that are more productive than fighting (like feeding), by allowing males to remain close to females, or by providing cowbirds with an assessment of the agonistic tendencies of other flock members (Rothstein 1980).

The flock-order function of the display for free-ranging birds may operate as follows. Free-ranging cowbirds might display most often interspecifically toward species with whom they flock because interspecific flocking is impor-

tant to their survival (e.g. for food gathering, roosting-site location, or predator avoidance) and the head-down display reduces the disorganizing effects of a cowbird joining a mixed-species flock. Because interspecific relationships are more fragile and more easily broken off than intraspecific ones (Scott 1975), the display may have evolved into a behavior that fosters important interspecific relationships.

To the best of our knowledge it is not known whether or not particular free-ranging cowbirds display most often or whether or not those birds are intraspecifically dominant, a trend that has been observed among captive cowbirds (Table 3). If this trend were verified for free-ranging cowbirds, our hypothesis would predict that dominant, free-ranging birds display most often because the display allows them to remain close to birds with which they flock, which in turn leads them to feeding or roosting sites, helps in avoiding predators, and/or provides assessment of the agonistic tendencies of flock members.

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