THE PREENING INVITATION OR HEAD-DOWN DISPLAY OF PARASITIC COWBIRDS: I. EVIDENCE FOR INTRASPECIFIC OCCURRENCE

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Cowbirds perform a remarkable display that often results in allopreening—one individual preening another (Cullen 1963). Selander and La Rue (1961), who discovered this display in Brown-headed and Bronzed cowbirds (*Molothrus ater* and *M. aeneus*), named it the "interspecific preening invitation display" because cowbirds often were preened by members of other species when they approached these individuals and froze in a head-down position with their head feathers fluffed. This display is the only known case in which allopreening typically involves two species. Remarkably, Selander and La Rue found that cowbirds did not preen one another or members of other species. These authors also found that cowbirds were preened even by species that never engage in intraspecific allopreening. Most of Selander and La Rue's data were from captive birds, but the limited field observations they presented agreed with their data on caged individuals.

Selander and La Rue assumed that the display is an appeasement gesture because its head-down posture closely resembles classic appeasement displays of other birds. They hypothesized that the display functions in the cowbirds' parasitic breeding by reducing aggressiveness of hosts that discover cowbirds near nests. Lastly, they suggested that preening is induced by the cowbirds' fluffed feathers and serves to divert host aggression. Selander and La Rue proposed an interspecific function because intraspecific displays were too few to indicate functional value. Selander and La Rue did not prove that cowbirds perform the display near host nests, but this may have been due to the fact that there were few observations of cowbirds near host nests.

Since the display's discovery, it has been reported in all but one of the six species of cowbirds (Harrison 1963, Selander 1964, Dow 1968, Payne 1969). Harrison (1965) speculated that the display serves not only to reduce a potential host's aggression but also to "cut-off" a cowbird's tendency to flee from its host. By contrast, Friedmann (1963:29–31), suggested that the display has no functional value and that it is the result of a generalized "memory induced" reaction resulting from interactions between young cowbirds and their foster parents. None of these contributions presented strong evidence for or against the Selander-La Rue hypothesis.

As part of an overall study of parasite-host interactions, I have been investigating the behavior of captive Brown-headed Cowbirds (Rothstein 1972). My observations show that the Selander-La Rue hypothesis cannot fully explain the preening invitation display. Intraspecific as well as interspecific displays are common, and the former apparently serve a function. In this paper, I present data showing the high frequency of intraspecific displays. I also show that intraspecific displays follow strong, repeatable patterns when the identities of displayers and display recipients are analyzed. Unless qualified, "cowbird(s)" henceforth refers only to the Brown-headed Cowbird and "display(s)" only to the preening invitation behavior discovered by Selander and La Rue.

MATERIALS AND METHODS

Cowbirds were trapped during October and November, 1968, in New Haven County, Connecticut and Prince Georges County, Maryland. They were kept in three cages, each containing three males and three females. Birds captured in Connecticut were: Cage B—males W and O; Cage C—males R, P and B, female O; Cage D—males Y and V. Remaining individuals were captured in Connecticut or Maryland. Each cage contained both adult and immature males (using criteria in Selander and Giller 1960) although ages of specific males were not recorded. I was unable to age females reliably. Individuals were kept in large aviaries under natural photoperiod until placed in their cages on 7 December 1968.

Cages B and C measured 2.44 × 1.83 × 1.22 m in length, height and width, respectively. Cage D was 1.22 × 0.92 × 0.92 m. Each cage had three perches spanning its width. Cages B and C had a wire platform about 0.3 × 0.6 m and about 0.7 m high on which food and water were placed. In Cage D food and water were placed on the floor. Birds spent most of their time on the perches.

The three cages were in the same room and were visually but not acoustically isolated from one another. The room also contained additional female cowbirds as well as male and female Redwinged Blackbirds (*Agelaius phoeniceus*). The latter are henceforth referred to as "blackbird(s)." These additional birds also were visually isolated from Cages B, C and D. Photoperiod was controlled automatically. Lights

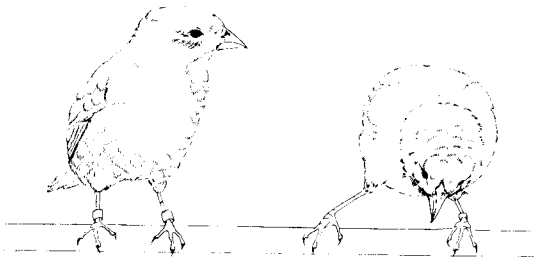

FIGURE 1. Female cowbird (left) after pecking at a displaying male cowbird. In response to the peck, the male has tilted his head away from the female while still maintaining the display.

were on during the following times: 7 Dec. 06:30–17:30; 8 Dec. 08:00–18:30; 9–25 Dec. 09:00–18:30; 26 Dec. 09:00–19:00; 27 Dec.–11 Jan. 09:00–19:30. Temperature was generally 18 to 22°C. Water and food were provided ad libitum. Food consisted solely of commercial poultry feed (Growing Mash in a "Crumbles" texture). Cowbirds adapt immediately to this food and remain healthy.

My data are from observations on birds kept in the same cage, with the same individuals for the duration of the study. Observations reported here were made while birds were not subjected to experimental manipulations and are called "steady state observations," to differentiate them from the radically different results obtained when certain manipulations are performed (Rothstein 1971). Observations were made while I sat in full view of the birds, 2–2.5 m from their cage. Cowbirds are extremely tame in captivity (pers. observ.; Selander and La Rue 1961: 492), and my presence had no detectable effect on their behavior. I recorded, via written notes, most interactions between individuals. In nearly all cases I was able to record the identity of the performer and recipient of each display. Observations were made for a fixed time period (10 or 20 min, see tables 1–6) and were started between 09:17–11:33 or 14:06–17:47.

The birds were subjected to "introduction experiments." A new individual (a male or female cowbird or blackbird) was added to a cage, left for 15 to 40 min, and removed. Results of these experiments are summarized elsewhere (Rothstein 1971). Between 12 December and 11 January I made 13 introductions each into Cages B and C and 10 into D. On days that steady state observations and introduction experiments were conducted, the former were always done first. My data fail to show that introduction experiments influenced steady state behavior.

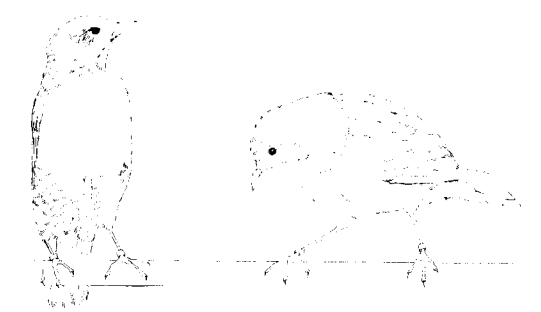

FIGURE 2. Female cowbird (left) responding to a displaying male cowbird with motions preparatory to flight or possibly with behavior intermediate between flight and a weak head-up display.

FIGURE 3. Female cowbird (right) showing no response to a displaying male cowbird.

A number of representative observation sessions were subjected to statistical analyses. Tables 1 and 2 present summaries of displays performed by birds in Cage B in early December, 1968, and early January, 1969, respectively. Tables 3–4 and 5–6 present similar data for birds in Cages C and D, respectively. Data on the December period for each cage represent the first eight observation sessions conducted after the birds were placed in their cages. In choosing data for the January period, I took the shortest run of closely spaced days that provided eight observation sessions about a month after the December sessions. Within this run a maximum of two sessions per day was included, and these sessions were always at least 4 h apart.

All statistical tests are from Siegel (1956), although tables in Computation Laboratory, Harvard University (1955) were used for applications of the binomial proportion. The binomial proportion was applied in all cases in which a test is not identified. All tests were two-tailed.

Figures were drawn from 35 mm color slides. Individuals shown in the figures were among eight cowbirds chosen at random from birds captured at the Patuxent Research Center, Laurel, Maryland in the fall of 1970. Except as subjects for photography, these individuals were not used in my studies.

RESULTS

GENERAL CHARACTERISTICS OF THE DISPLAY

Generalizations presented here are based on several hundred hours of observation on the

FIGURE 4. Female cowbird (left) displaying to a male cowbird. The extreme degree to which the female's throat is tucked against her breast is seen occasionally but occurs commonly only when a bird gives the display from an upright stance (axis of body perpendicular to the horizontal).

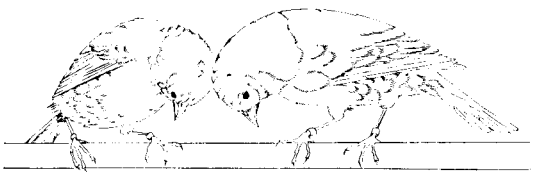

FIGURE 5. Female cowbird (left) that has responded to a displaying male cowbird by assuming the display herself, resulting in a "mutual display." Mutual displays do not always result in the bird's heads touching.

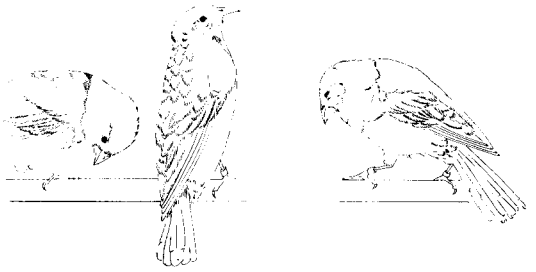

FIGURE 6. Two male cowbirds displaying simultaneously to a female cowbird.

birds in Cages B, C and D as well as on six other groups of caged cowbirds. Conditions for these six additional groups were similar to those described for B, C and D except that two groups had 3 and 15 cowbirds, and at times one to four blackbirds were present.

Selander and La Rue's (1961) detailed descriptions of postures and movements associated with the display describe adequately the displays I have seen, although cowbirds displaying to other cowbirds may fluff their head feathers less than those displaying to individuals of other species. Postures assumed during intraspecific displays in my study (figs. 1–7) and in interspecific displays in Selander and La Rue's study (1961:figs. 1A–D) are extremely similar.

Although intraspecific displays were common, cowbirds usually directed more displays to blackbirds than to cowbirds. Most responses blackbirds showed to the display were similar to those shown by cowbirds. Recipients of the display commonly pecked the displayer. When this occurred, the displayer often maintained the display and continued to be pecked but tilted its head away from the recipient (fig. 1). Recipients frequently fled from a displaying cowbird. On rare occasions, recipients did the "head-up" or "bill-tilt" display (fig. 2), a standard icterid threat behavior (see Nero 1963). Often, a recipient gave no detectable response (fig. 3). Figures 1–3 show displays initiated by male cowbirds and directed to female cowbirds. But females also initiated displays (fig. 4), and both sexes displayed to each other or to their own sex. (Data on the frequency with which each sex gave and received the display are presented below.) As described by Selander and La Rue (1961), blackbirds often preened displaying cowbirds. I never saw a cowbird preen a displaying cowbird vigorously. In a few of the several thousand intraspecific displays I observed, cowbirds gently and briefly manipulated the head feathers of a displayer with their bill. More commonly, cowbirds responded with behavior intermediate between pecking and preening. With their bill open, they softly pecked the head of a displaying cowbird. Blackbirds also showed this intermediate behavior. Cowbirds often responded to a display by assuming the display themselves. Sometimes when these "mutual displays" occurred, the heads of both cowbirds touched (fig. 5), and the birds remained nearly motionless for 5 to 10 min. Mutual displays occurred between the same or different sexes. A few times I observed three cowbirds simultaneously engaged in mutual display. Occasionally two cowbirds displayed simultaneously to a third, nondisplaying, cowbird (fig. 6). Blackbirds never gave the display to cowbirds or to other blackbirds. Selander and La Rue (1961) reported that cowbirds display to mounts of other species but made no mention of having presented mounted cowbirds to their birds. I found that cowbirds displayed readily to mounted female and male cowbirds (fig. 7).

Because the display frequently does not elicit preening even when directed to a member of another species, and because it is commonly given to cowbirds, Selander and La Rue's name, "the interspecific preening invitation display," is inappropriate. Following Darley (1968), I hereafter refer to the behavior pattern as the "head-down display." This new name describes the display in terms of its operation rather than in terms of one of several of its consequences (see Wallace 1973:4–5).

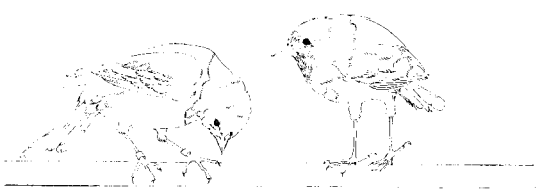

FIGURE 7. Male cowbird (left) displaying to a mounted male cowbird.

TABLE 1. Displays in Cage B during eight 20-min observation sessions between 8–13 December.[a]

Individual displaying	Total no. displays given	Recipients of displays ♂W	♂G	♂O	♀B	♀P	♀R
♂W	41	–	0	2	25	6	6
♂G	16	1	–	0	12	1	2
♂O	63	0	0	–	47	6	8
♀B	1	0	0	0	–	0	1
♀P	12	0	0	0	9	–	2
♀R	10	1	1	0	8	0	–
	Total	2	1	2	101	13	19

	Displays to ♂♂	Displays to ♀♀	Total displays
Displays by ♂ ♂	3	113	120
Displays by ♀ ♀	2	20	23
Displays by ♂ ♂ and ♀ ♀	5	133	144

[a] In this and tables 2–6, numbers of displays given sometimes deviate slightly from the sum of numbers of displays received because the identity of the displayer or recipient was not always determined. For example, W gave 41 displays but the recipient was determined in only 39 cases (39 is the sum of the displays listed under each individual in the row for W).

PARTIAL DISPLAYS

Some intraspecific head-down displays were "partial," in that displayers did not remain rigid in the head-down position. Cowbirds either froze for a moment or carried out movements characteristic of the beginning of a display, i.e. they deliberately approached another cowbird, started to lower their heads but then assumed a normal perching posture without freezing in the head-down position. Of 373 displays during the first eight observation sessions on all cages (tables 1, 3 and 5), 25.4% were incomplete. In 63.1% of the partial displays the recipient flew before the displayer froze in the head-down position.

TABLE 2. Displays in Cage B during eight 10-min observation sessions between 6–11 January.

Individual displaying	Total no. displays given	Recipients of displays ♂W	♂G	♂O	♀B	♀P	♀R
♂W	1	–	0	0	0	0	1
♂G	0	0	–	0	0	0	0
♂O	1	0	0	–	0	1	0
♀B	3	0	0	0	–	1	2
♀P	27	0	0	0	24	–	3
♀R	9	0	0	0	8	1	–
	Total	0	0	0	32	3	6

	Displays to ♂♂	Displays to ♀♀	Total displays
Displays by ♂ ♂	0	2	2
Displays by ♀ ♀	0	39	39
Displays by ♂ ♂ and ♀ ♀	0	41	41

TABLE 3. Displays in Cage C during eight 20-min observation sessions between 8–13 December.

Individual displaying	Total no. displays given	Recipients of displays ♂R	♂B	♂P	♀W	♀G	♀O
♂R	36	–	0	3	11	1	21
♂B	43	0	–	4	15	11	13
♂P	50	1	8	–	21	10	9
♀W	8	0	4	1	–	1	2
♀G	9	0	5	0	2	–	2
♀O	1	0	0	0	1	0	–
	Total	1	17	8	50	23	47

	Displays to ♂♂	Displays to ♀♀	Total displays
Displays by ♂ ♂	16	113	129
Displays by ♀ ♀	10	8	18
Displays by ♂ ♂ and ♀ ♀	26	121	147

Most partial displays probably occur because birds do not complete the display if the recipient is no longer present. In one partial display the recipient pecked at the displayer who then ceased the behavior. In the remaining 36.8% of the partial displays the recipient did not respond. In these cases it is likely that the partial displays were due to "inde-

TABLE 4. Displays in Cage C during eight observation sessions between 6–9 January.[a]

Individual displaying	Total no. displays given	Recipients of displays ♂R	♂B	♂P
♂R	29 (25)	—	2(1)	1(1)
♂B	16 (13)	4(4)	—	0(0)
♂P	4 (4)	2(2)	1(1)	—
♀W	18 (7)	6(3)	8(0)	0(0)
♀G	12 (2)	11(2)	1(0)	0(0)
♀O	6 (3)	3(2)	3(1)	0(0)
	Total	26(13)	15(3)	1(1)

Individual displaying	Recipients of displays ♀W	♀G	♀O
♂R	6(5)	12(10)	8(8)
♂B	7(6)	1(1)	4(2)
♂P	1(1)	0(0)	0(0)
♀W	—	0(0)	4(4)
♀G	0(0)	—	0(0)
♀O	0(0)	0(0)	—
Total	14(12)	13(11)	16(14)

	Displays to ♂♂	Displays to ♀♀	Total displays
Displays by ♂ ♂	10 (9)	39 (33)	49 (42)
Displays by ♀ ♀	32 (8)	4 (4)	36 (12)
Displays by ♂ ♂ and ♀ ♀	42 (17)	43 (37)	85 (54)

[a] Numbers in parentheses are display incidents. Numbers outside parentheses are total displays. Seven observation sessions were 10 min long; one was 20 min.

TABLE 5. Displays in Cage D during eight 20-min observation sessions between 8–13 December.

Individual displaying	Total no. displays given	Recipients of displays ♂Y	♂V	♂Bl	♀PO	♀R3	♀WO
♂Y	35	–	3	2	18	10	2
♂V	34	0	–	1	10	18	5
♂Bl	8	0	4	–	4	0	0
♀PO	0	0	0	0	–	0	0
♀RB	3	0	0	0	0	–	3
♀WO	1	0	0	0	0	1	–
	Total	0	7	3	33	29	10

	Displays to ♂♂	Displays to ♀♀	Total displays
Displays by ♂♂	10	68	78
Displays by ♀♀	0	4	4
Displays by ♂♂ and ♀♀	10	72	82

TABLE 6. Displays in Cage D during eight 10-min observation sessions between 6–10 January.

Individual displaying	Total no. displays given	Recipients of displays ♂Y	♂V	♂Bl	♀PO	♀RB	♀WO
♂Y	9	–	0	0	6	2	1
♂V	10	3	–	6	1	0	0
♂Bl	0	0	0	–	0	0	0
♀PO	0	0	0	0	–	0	0
♀RB	4	0	0	0	1	–	3
♀WO	1	0	0	0	0	1	–
	Total	3	0	6	8	3	4

	Displays to ♂♂	Displays to ♀♀	Total displays
Displays by ♂♂	9	10	19
Displays by ♀♀	0	5	5
Displays by ♂♂ and ♀♀	9	15	24

cisiveness" and represented intention behavior. Partial and full displays almost certainly represent the same behavior but performed under different situations or at different intensities. They are not differentiated in the remainder of this paper. Selander and La Rue (1961:480) also reported the occurrence of partial displays, but in an interspecific context.

MUTUAL DISPLAYS

Except where noted, I do not differentiate between displays given in response to a display (resulting in mutual displays) and the more numerous ones in which an individual displayed to a bird who was not displaying to it. Mutual displays can confound analyses. They inflate the number of displays because each contributes two to the total; also some individuals give most of their displays in a mutual context, i.e., they rarely display unless they are the recipient of a display. Therefore, I distinguish between "total displays" and "display incidents." The former refers to all displays, with each mutual display contributing two to the overall total; "display incidents" refers to instances in which an individual initiates a display session and disregards displays given in response to a display. The various tables tabulate the following numbers of mutual displays: tables 1 and 6, none; tables 2 and 5, one each; table 3, eight; table 4, 31. Except for the birds in Cage C in January (table 4) mutual displays were sufficiently rare so as not to bias analyses. To avoid biases, statistical tests on data in table 4 deal with display incidents. Tests for other tables deal with total displays.

FREQUENCY OF INTRASPECIFIC DISPLAYS

I recorded 523 total displays and 482 display incidents in 730 min of observation (tables 1–6). Displays did not occur at similar rates in each observation period. Total displays per observation period showed the following ranges for the eight sessions covered by each table: table 1, 4–42; table 2, 0–11; table 3, 4–32; table 4, 0–27; table 5, 0–25; table 6, 0–13. Chi-square tests determined whether displays were distributed evenly among observation sessions covered by each table. For data in tables 1, 3, 4 and 5, Chi-square values ranged from 39.0 to 81.2 (in each case $P < 0.001$ and $df = 7$). Displays recorded in table 6 were too few for a Chi-square test but analysis via the Kolmogorov-Smirnov test indicated a significant departure ($0.02 < P < 0.05$) from an even distribution. Only for data in table 2 were displays per session not significantly different from an even distribution.

One reason display occurrence was irregular was that some individuals displayed frequently during one session and rarely during other sessions. For example, male B in Cage C accounted for 28 of 32 displays during one session. B's displays in the seven other sessions covered by table 3 totaled only 15. Variation in displays per session was not correlated with time of day.

The irregular distribution of displays per session also occurred because individuals within each cage tended to perform their highest and lowest numbers of displays during the same observation periods. This tendency is shown by tests applying the Kendall coefficient of concordance to the display in-

cidents each individual initiated during each session. Because displays by males and females were so different in numbers (tables 1–6 and below), each sex was treated separately. This resulted in 12 applications of the concordancy test, one for each of the data sets on males and on females in tables 1–6. Of 12 possible applications, displays were too few to be meaningful in four cases. In the eight tests that were done, significant concordancy coefficients occurred for males in Cage B-Dec and Cage D-Dec ($0.02 < P < 0.05$, $W = 0.680$, $\chi^2_{[7]} = 14.3$, and $0.02 < P < 0.05$, $W = 0.682$, $\chi^2_{[7]} = 14.3$). Significance in two of eight tests indicates at least a weak trend for birds in a cage to respond either to some external factor or to one another (social facilitation) such that their tendency to display at a given time is similar.

PATTERNS OF INTRASPECIFIC DISPLAYS

Cage B. Between 8–13 December, 144 displays were tabulated for the six cowbirds (table 1). Each individual could display to two members of its own sex or to three members of the other sex. If displays were directed randomly without regard for the recipient's sex, male displays to males and to females should have been in the ratio 2:3. But only three displays were to males whereas 113 were to females, a significant departure ($P < 0.001$) from a 2:3 ratio. If random, female displays to males and to females should have been in the ratio 3:2. Females displayed twice to males and 20 times to females, a result significantly different ($P < 0.001$) from the expected. The tendency to display to females was characteristic of all six individuals because each directed all or nearly all of its displays to females (table 1).

If the sexes had similar tendencies to display, displays by males and females should have been in the ratio 3:2 because each male had three preferred individuals (females) to whom he could display but each female could display to only two preferred individuals. But the breakdown of 120 male and 23 female displays was a significant departure ($P < 0.001$) from the expected 3:2 result. Thus, males had a stronger tendency to display than females. Further analysis shows that within one sex, individuals displayed with different intensities. The 120 male displays were not distributed equally among males W, G and O ($P < 0.001$, $\chi^2_{[2]} = 27.4$). Bird O displayed 63 times, W, 41 times, and G, only 16 times. Similarly, the 23 female displays were not distributed equally among females B, P and R ($0.01 < P < 0.02$, $\chi^2_{[2]} = 8.95$).

Each bird showed a strong tendency to display to the same individual, female B. Considering displays directed to females by all birds, 101 of 133 were to B, a highly significant result ($P < 0.001$, $\chi^2_{[2]} = 109$). Considering males alone, 84 of 113 displays directed to females were to B, a significant departure ($P < 0.001$, $\chi^2_{[2]} = 85.8$) from displays directed randomly to all females. When considered separately, females P and R also displayed preferentially to B ($P = 0.07$ and $P < 0.01$, respectively). While displays to B accounted for most of the male displays to females, two males, W and O, also displayed to the females, P and R, in preference to males. Among displays not to female B, all 14 by O and 12 of 14 by W were to females P and R (table 1), significant departures ($P < 0.01$) in each case from random expectation.

Between 6–11 January, I noted 41 displays in Cage B (table 2). Displays by males were too few for analyses. Females still showed a significant tendency ($P < 0.001$) to display to other females. Unlike the situation in the first eight observation sessions (table 1), females displayed significantly ($P < 0.001$) more than males. Females did not display with equal frequencies ($P < 0.001$, $\chi^2_{[2]} = 24.0$). As in the earlier period, B displayed the least. Females P and R continued to show significant preferences to display to B ($P < 0.001$ and $P = 0.04$, respectively), and data for all birds combined also showed a significant tendency for displays to B ($P < 0.001$, $\chi^2_{[2]} = 37.2$).

Cages C and D. I used the same criteria and tests for analyses of data on birds in these cages (tables 3–6) as those presented in the analyses for Cage B. Results of statistical tests on data for birds in all three cages are summarized in table 7. However, the January observations of birds in Cage C include a large number of mutual displays and require some elaboration. I recorded 85 total displays in Cage C—54 display incidents and 31 mutual displays. Among mutual displays, one was initiated by a male and directed to a male, 24 by males directed to females, six by females to males, and none by females to females. Therefore, seven of 49 male displays were given in response to a display. Of 36 female displays, 24 were given in response to a display. The column for Cage C-Jan (table 4) in table 7 gives statistical tests on numbers of times birds initiated display incidents, not on total displays done by each

TABLE 7. Results of statistical tests on data in tables 1–6.[a]

Statement tested	Table 1	2	3	4	5	6
1) ♂♂ displayed preferentially to ♂♂	–	SM	–	–	–	–
2) ♂♂ displayed preferentially to ♀♀	**	SM	**	**	**	–
3) ♀♀ displayed preferentially to ♂♂	–	–	–	–	–	–
4) ♀♀ displayed preferentially to ♀♀	**	**	–	–	(*)	*
5) ♂♂ displayed more than ♀♀	**	–	**	**	**	**
6) ♀♀ displayed more than ♂♂	–	**	–	–	–	–
7) Some ♂♂ displayed more than other ♂♂	**	SM	–	**	**	**
8) Some ♀♀ displayed more than other ♀♀	**	**	**	SM	SM	SM
9) Some ♂♂ received more displays than other ♂♂	SM	SM	**	**	SM	SM
10) Some ♀♀ received more displays than other ♀♀	**	**	**	–	**	–

[a] * indicates statement confirmed at $0.02 \leq P \leq 0.05$; ** statement confirmed at $P < 0.02$; (*) statement marginally significant ($0.05 < P < 0.06$); SM sample size too small for adequate test; — statement not confirmed with statistical significance.

bird as in the other columns. In several cases dealing with data from table 4, tests done on total displays give different results from those done on display incidents and demonstrate the manner in which the latter confound analyses. For example, if one considers total displays, 32 of 36 female displays were to males. This would represent a significant ($P < 0.001$) tendency to display to males but 24 of the 32 displays females directed to males were responses to displays initiated by males. When these 24 displays are excluded, the remaining eight displays to males and four to females conform to random expectation (3:2), and females show no tendency to display to males (the result shown in table 7).

DISCUSSION

GENERALIZATIONS REGARDING INTRASPECIFIC DISPLAYS

In each cage, male displays per unit time decreased between the first and second series of observations, while the rate of female displays increased. Females accounted for a much larger proportion of the total displays in the second series of observations than in the first, e.g., female displays in Cages B, C and D were, respectively, 16.0, 12.2 and 4.9% of the total in December (tables 1, 3, 5) and 95.2, 41.7 and 20.8% in January (tables 2, 4, 6). These trends also hold when display incidents are considered.

The frequency with which individuals of the same sex displayed varied greatly. Each of tables 1–6 gives data on two groups of displays those by males and those by females, resulting in 12 data groups. In four of these 12 data groups, displays were too few (< 15) for a Chi-square test. Displays were distributed in a manner significantly different from an even distribution in seven of the remaining eight data groups (statements 7 and 8, table 7), i.e., one or more individuals did significantly more or fewer displays than other individuals of its sex and in its group. Selander and La Rue (1961) also noted much individual variation in display frequency, but this was in reference to interspecific, not intraspecfic, displays. Relative tendency to display is a characteristic that remained constant in some individuals for the time span covered. The female who displayed the least in December did likewise in January (B in tables 1–2, O in tables 3–4, and PO in tables 5–6).

Several patterns emerged when recipients of displays were considered. Significant or nearly significant trends to display to females occurred in eight of the 11 data groups large enough for statistical analysis (statements 2 and 4, table 7). In no case was there a significant tendency for displays to be directed to males (statements 1 and 3). Thus, females provided a stronger releaser for the display than males. Within the basic trend of displays directed preferentially to females, certain females received significantly more displays than others. The best example is female B (tables 1, 2). This trend was shown in four of the six data groups (statement 10). Even among the relatively few displays to males, certain males tended to be recipients more often than others as both data groups large enough for analysis showed significant trends (statement 9).

The patterns shown in table 7 dealing with the performers and recipients of displays were derived from summary analyses based on all the observations tabulated. Other significant patterns emerged when an individual's behavior over a short time period was an-

alyzed. During some observation sessions, one individual displayed to and followed another individual with such persistence that it is difficult to believe that the interactions were not manifestations of some special relationship between the birds involved and that the displays were not transmitting information. One example follows:

Cage C, 13 December, 14:28–14:48—Male B approached and displayed to female G who fled from him. B's next display was to G; she responded by immediately displaying back. B and G held the mutual display for about two min. The display ended when they began to peck at one another. Again B's next display was to G, who again responded immediately by displaying back. They held the mutual display for about seven min. Then B pecked G twice and G fled. Almost immediately after this last display, B and G were again engaged in mutual display but I could not determine who initiated the incident. After about two min of mutual display female W approached them and chased G, thus ending the mutual display. W then immediately displayed to B, but B gave no response, and W quickly ceased displaying and fled. The only other displays in which B participated occurred later in the observation session. B displayed to W who did not respond. Then B displayed to G who fled before B became set in the head-down position. Thus, five of 11 displays B directed to G between 8–13 December (table 3) occurred in one of the eight observation sessions.

Not all observation sessions contained events comparable to these but I could cite many more cases of a continuing interaction between two individuals. These results are in marked contrast to Selander and La Rue's statement (1961:478) that, "In all recorded instances of intraspecific presentation, the display was given only a single time . . . ." Because they saw so few intraspecific displays, their failure to detect patterns may have been due to small sample size.

From the data analyzed here I cannot determine reliably whether a cowbird's tendency to display is correlated with position in the social hierarchy. Females never establish a well-defined dominance hierarchy. Although male cowbirds eventually establish a rigid hierarchy (Rothstein 1972), dominance relationships were poorly defined at the time of the present study. However, the males that eventually became dominant in each cage displayed frequently during the time covered: male W in Cage B (table 1), R in Cage C (tables 3, 4) and V in Cage D (tables 5, 6). These results are only suggestive, and additional studies must be done to elucidate correlations between dominance status and tendency to display.

EVIDENCE FOR AN INTRASPECIFIC FUNCTION

My data strongly indicate that intraspecific head-down displays play some role in the social interactions of cowbirds and are not, as Selander and La Rue (1961) suggested, byproducts of a display that functions only interspecifically. Intraspecific displays were performed so often that it is highly unlikely they lack a function. While the high numbers of displays I observed is partly an artifact of captivity because confined birds are in frequent contact, it is unlikely that captivity would alter a behavior pattern so drastically that cowbirds would frequently direct to other cowbirds a display normally directed only to individuals of other species. Significantly, other cowbird displays such as the head-up and song-spread, whose intraspecific functions in nature are well established (Nero 1963), appear to function in their normal context under conditions of captivity (pers. observ.; Selander and La Rue 1961). In captivity, intraspecific head-down displays occur more frequently than some of these other displays, e.g., females rarely do head-up but frequently do head-down displays.

In addition to the high numbers of intraspecific displays, trends apparent when the performers and recipients of displays are analyzed also indicate an intraspecific role for the behavior pattern. If displays do not function intraspecifically, then displays to cowbirds might be directed randomly to any group member. By contrast, both sexes showed significant tendencies to display to females. Some individual cowbirds were recipients of displays significantly more often than other individuals of their sex. These characteristics are similar to those of displays known to function intraspecifically, e.g., male cowbirds direct most head-ups and song-spreads to other males, and often one male is the recipient of a disproportionate number of these displays (pers. observ.). The nonrandom nature of intraspecific displays is also illustrated by observations of certain individuals actively pursuing and displaying to other individuals such as described above for Cage C.

Lastly, the display communicates information to other cowbirds, and this too supports my belief that it functions intraspecifically. The display elicits from recipient cowbirds characteristic responses such as flee-

ing, pecking (fig. 1) or reciprocal display (fig. 5). Also, I suggest that behavior, such as inter- and intraspecific head-down displays, which is obviously directed toward another individual (figs. 1–7) must be transmitting information, i.e., playing a communicatory role. The communicatory role of the behavior pattern is further indicated by the fact that the display never is given unless another individual is nearby.

What the display communicates to other cowbirds was not determined from my steady state observations. Additional studies (summarized in Rothstein 1971) showed that the display is a threat gesture and is not appeasive as Selander and La Rue believed. The aggressive nature of the display may explain why most intraspecific displays are directed to females. Male cowbirds usually dominate females in captivity (pers. observ.). Both sexes are therefore more likely to direct aggressive displays to females. Given the dominant status of males, both sexes would, if the head-down display were appeasive, display preferentially to males. But such is not the case. I suggest that the cowbird's head-down display is an example of a display that posturally is nearly identical to displays by other species, e.g., the appeasement displays of corvids and many other birds, but which is motivated differently (see Selander and La Rue 1961, Harrison 1965, Lorenz 1966:128).

My findings do not negate that part of the Selander-La Rue hypothesis which suggests that cowbirds direct the display to individuals of other species when attacked near host nests. Rather, my data necessitate a broadening of the hypothesis to include also some functional role for the display in intraspecific interactions.

DISPARITIES BETWEEN STUDIES

Data presented above show that captive cowbirds perform frequent intraspecific head-down displays, at least under the conditions of my study. Darley (1968:36) also found that the display was "often given by caged birds to Cowbirds and Canaries," but he gave no quantitative data. Similarly, Dwain W. Warner (pers. comm.) observed that captive cowbirds perform frequent intraspecific displays. My findings, Darley's and Warner's contrast strongly with those of Selander and La Rue who stated (1968:478) that "In several hundred hours of observation" of cages containing cowbirds, intraspecific displays were noted "on no more than 25 occasions." The disparity between my study and Selander and La Rue's is too great to be attributed to differences in observational techniques. None of the explanations Selander and La Rue (1961) presented to account for intraspecific displays can explain the high number of such displays in my study or resolve the disparity between the studies. They believed (pp. 485, 493) that intraspecific displays often were redirected behaviors, displays directed to a cowbird when the intended recipient—an individual of another species—flew before the displayer froze in the head-down position. None of the displays reported in this paper can be explained in this manner as only cowbirds were present.

Selander and La Rue (p. 493) also suggested that intraspecific displays occurred most commonly among cowbirds that had not had contact with other species for long periods, although they presented no quantitative evidence. This could not account for the high number of intraspecific displays I observed. Because the birds in Cages B, C and D were caught in October and November, they were deprived of interspecific contact for only one to two months before the first observation periods in December. These birds performed numerous intraspecific displays in December (373 by 18 birds in 480 min or 0.0432 displays/bird/min, tables 1, 3, 5), yet in Selander and La Rue's study (1961:483) cowbirds isolated from other species for four months gave fewer intraspecific displays (17 by 35 birds in 120 min or 0.0040 displays/bird/min). If intraspecific displays increase, the longer cowbirds are isolated from other species, Selander and La Rue's birds should have performed more, not fewer, intraspecific displays. Furthermore, single female Redwinged Blackbirds were placed in Cages B, C and D for 20 min on 13, 18 and 27 December and on 9 January. Single male blackbirds were placed in Cages B and C on both 2 and 3 January for 20 min. These blackbirds received numerous displays. Thus, by the second observation period (tables 2, 4, 6) the cowbirds had had recent contact with another species, yet they still displayed frequently to one another.

A probable explanation for the small number of intraspecific displays Selander and La Rue noted is provided by my observations of birds who had been together for prolonged periods. After the cowbirds in Cages B, C and D and in other cages had been together for two to five months, the incidence of intraspecific displays between group members declined sharply (unpubl. data). Interspecific displays also decline after cowbirds have been caged with the same individual blackbirds

for prolonged periods. However, even after the decline in displays to familiar birds, cowbirds display frequently to new cowbirds or blackbirds added to their cage. Most of Selander and La Rue's observations occurred after their birds had been caged together for a month or two, and all the individuals they studied probably came from one flock (R. K. Selander, pers. comm.). Thus, it is possible that the habituation that takes place between individuals and results in a reduction of displays occurred before Selander and La Rue recorded most of their data. Significantly, many of the observations upon which Selander and La Rue based their conclusion that the display is nearly always given interspecifically occurred shortly after new individuals of other species were added to an established group of cowbirds.

Because the tendency of cowbirds to display to individuals with whom they are associated changes temporally, generalizations concerning the display must be qualified to represent only the period when birds were studied. Generalizations based on my data may have wider applicability but for the present can be applied only to cowbirds who have been together for less than two months.

INTRASPECIFIC DISPLAYS IN NATURE

Several factors make it unlikely that intraspecific displays in nature would be reported. I know of no efforts to study the display systematically in the field. The fact that some species seem to provide a stronger releaser than do cowbirds (as shown in my studies of captive blackbirds and cowbirds) may explain why all reported cases of displays in nature involved individuals of other species (Selander and La Rue 1961 and references therein, Dow 1968). Also, cowbirds in captivity display while on perches or less commonly while clinging to the wire sides of their cage. They almost never display while feeding or on the cage floor. If cowbirds in nature also display rarely while feeding or on the ground, intraspecific displays may be difficult to see because groups of cowbirds are most conspicuous while feeding on the ground. Perhaps cowbirds rarely do head-down displays on the ground (or at least while foraging on the ground) because this would reduce their visual field when they are easily seen by predators. Significantly, N. G. Smith (pers. comm.) has found that Giant Cowbirds (*Scaphidura oryzivora*) perform inter- and intraspecific displays while in the arboreal colonies of oropendolas (*Zarhynchus wagleri, Psarocolius decumanus, Gymnostinops montezuma*) and caciques (*Cacicus cela*) whose nests they parasitize (see Smith 1968). Smith's observations thus support both the Selander-La Rue hypothesis and my broader hypothesis that the display functions inter- and intraspecifically.

I have made little attempt to study the display in the field, but I have seen Brown-headed Cowbirds perform interspecific displays on about ten occasions. The recipients were House Sparrows (*Passer domesticus*), female Redwinged Blackbirds, and in one instance a Cedar Waxwing (*Bombycilla cedrorum*). These displays were given in shrubs or trees near bird feeders, never while cowbirds were on the feeders or ground, agreeing with my observations of captive birds.

On one occasion, I attempted to record all head-down displays in the vicinity of a bird feeder I maintained in Goleta, Santa Barbara County, California during late winter and spring of 1973. Much of the time 5–20 male and 1–5 female cowbirds were at the feeder or within 15 m of it. On 15 April I recorded all displays between 16:20 and 17:39. During most of this period, 10–20 male cowbirds and 5–10 House Sparrows perched on power lines above the feeder. For 30 to 50% of the time two female cowbirds also perched on the lines. The birds were unusually conspicuous; normally they perched among foliage. I noted seven displays to cowbirds and 10–15 to House Sparrows. All displays were by male cowbirds except for one directed to a House Sparrow by a female. All intraspecific displays were directed to males, and none were mutual. Three intraspecific displays were partial; in each instance the recipient cowbird pecked at the displayer before the latter froze in the head-down position. Recipients of the remaining intraspecific displays reacted by fleeing (twice), pecking (once) and giving no response (once). The last mentioned display was held for about ten sec; the others lasted less than five sec. In no instance did an intraspecific display appear to result from a redirected interspecific display. In five of the intraspecific displays only cowbirds were within 1 to 2 m of a cowbird when it displayed. Probably, at least two male cowbirds performed intraspecific displays. It was my impression that House Sparrows were stronger releasers for displays than cowbirds. House Sparrows received more displays (10–15 vs. 7) although they were outnumbered by as much as four to one by cowbirds. Nevertheless, these observations show that intraspecific displays occur in nature.

SUMMARY

Parasitic cowbirds perform a display in which they approach other birds and freeze in a bowed position. If the recipient is a bird of another species, it often preens the cowbird, even if members of its own species never preen one another. Selander and La Rue, who discovered this unique behavior pattern, found that it was nearly always directed to members of other species. They hypothesized that it is an appeasement display used by cowbirds to reduce aggressiveness of hosts. New findings show this hypothesis does not explain the display fully. Contrary to Selander and La Rue's data, captive Brown-headed Cowbirds display to each other frequently. Most responses given by birds of other species and by cowbirds to displaying cowbirds, are similar, but only the former actively preen cowbirds, and only the latter respond by doing the identical display.

There were 523 intraspecific displays in 730 min of observation of three groups of captive cowbirds, each containing three males and three females. Males displayed more than females in the week after each group was placed in its cage. A month later, male displays had decreased, but female displays had increased. Both among males and females, some individuals displayed significantly more often than other members of their sex. In most cases males and females directed significantly more displays to female than to male cowbirds. Some male and female cowbirds received displays significantly more often than other members of their sex. The high frequency with which the display was done and the nonrandom nature of the incidence with which specific cowbirds gave or received the display indicate that the display functions in intraspecific social interactions. Cowbirds do not display frequently to birds with whom they have associated for several months. The cowbirds Selander and La Rue studied may have given few intraspecific displays because these birds had been together for an extended period. Limited field observations show cowbirds in nature also display intraspecifically. Hence, Selander and La Rue's hypothesis of an interspecific function for the display must be extended to include an intraspecific function as well.

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