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ALLOPREENING BY BROWN-HEADED COWBIRDS

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Brown-headed Cowbirds (*Molothrus ater*) perform an allopreening invitation display, called the "head-down" display, in which a bird holds its body horizontally, tips its bill downward, and holds its head within about 5 cm of the recipient (Fig. 1). In effect, the cowbird offers its head and neck region to another bird for preening.

When a cowbird directs this display toward birds of certain other species, especially in captivity, the recipient often preens the displaying cowbird (Selander and LaRue, Auk 78:473, 1961; Rothstein, Condor 79:113, 1977, Behaviour 75:148, 1980). On the other hand, cowbirds have "almost never" (Rothstein 1977) been seen to allopreen when other cowbirds perform the head-down display to them. This seeming paradox has made it hard to understand the origin and function of the head-down display.

Here I report that allopreening was common in a group of captive Brown-headed Cowbirds at the (Gainesville) Florida Field Station of the Denver Wildlife Research Center, U.S. Fish and Wildlife Service. These cowbirds, 22 males and 6 females, were captured in February 1981 within 16 km of Gainesville. They were kept in an outdoor cage 1.2 m × 1.2 m × 1.8 m long, with three 1.2-m perches. They were given unlimited Purina poultry food and water.

From 17 November 1981 to 1 March 1982, when they were released, I saw allopreening by these birds every time I watched them for more than about 10 min, which was about three times a week. On 29 November 1981 I watched them continuously from 09:30 to 11:30, while I stood in the open at a distance of about 5 m. During this 2-h period I saw cowbirds preen other cowbirds 34 times. The following details pertain to that period.

In every case the bird that was preened started the action by approaching another cowbird and performing the head-down display. Preening movements ranged from prolonged manipulation of the feathers to outright jabs at the body, but they usually consisted of one of two basic types. In one type, the preener gently and repeatedly nipped and poked at the very ends of the feathers with the extreme tip of its bill, without touching the skin. This type was characteristic of shorter bouts of preening (1–19 s, $\bar{x} = 4$ s, $n = 10$). The second type of preening consisted of thrusting the partly-opened bill among the feathers of the head or nape and running it through the plumage, like a plow through a thicket of palmettos (Fig. 1). When preening in this way, preeners always moved their bills against the direction in which the feathers grew. Each such sweep through the plumage covered 1 to 2 cm and took about 1 s to perform. I never saw a preener move its bill down the shafts of individual feathers. Occasionally the preener seemed to make fine nibbling movements as it moved its bill through the plumage. This second type of preening was characteristic of longer preening bouts (1–30 s, $\bar{x} =$ 10 s, $n = 22$). In two bouts, the preener used the first type for about 5 s and then the second type for about 15 s.

Preeners concentrated on the crown and upper nape. In three bouts, the preener occasionally plucked gently at the feathers of the back, and in one bout each, at those of the flank and the base of the bill. While being preened, birds held still in the head-down posture.

Most of the bouts ended when the preener flew or walked away from the bird it had been preening. Five bouts ended when a third cowbird drove away the bird who was being preened in order to perform the head-down display to the preener. One bout ended in mutual pecking, with each bird trying to drive the other off the perch; they both fell off simultaneously.

There were at least 3 preeners among these 28 cowbirds: I once saw two males preening simultaneously (not mutually), and I twice saw a female preen a male. I did not see any females being preened.

Harrison (Behaviour 24:162, 1965) reviewed the strong evidence that allopreening is a ritualized form of attack, that it is usually a means of exerting dominance, and that allopreening-invitation displays are usually an expression of subordination. While the cowbirds' allopreening movements seem related to those used when striking another bird, the roles of cowbirds who are doing or receiving the preening are the opposite of those usually seen in other species of birds. Rothstein (1980) showed that the head-down display is used by dominant individuals, and my observations indicate that allopreening by cowbirds is not an expression of dominance, because the preeners were, in effect, usually supplanted by the birds they preened.

Rothstein (1977) saw "a few" perfunctory bouts of allopreening in response to "several thousand" head-down displays, and Stevenson (Agonistic behavior in the cowbird *Molothrus ater*, Ph.D. diss., Kansas State Univ., Manhattan, 1968) saw allopreening 54 times in response to a total of 2,530 head-down displays (0.02 times per display). Head-down displays were so common among the Gainesville cowbirds that I could not count all of them, but the number of displays that resulted in allopreening was certainly a small fraction of all those given, perhaps about one-tenth. Stevenson (1968) saw allopreening 54 times among 36 birds in 28 h (0.05 times per bird per h), while I saw allopreening 34 times among 28 birds in 2 h (0.6 times per bird per h).

The captive Gainesville cowbirds may have allopreened so often because they were so crowded. Stevenson (1968) and Rothstein (1977) kept only six cowbirds in each of their cages, which ranged in size from about one-half to about four times the volume of the one at the Gainesville lab. Crowding may prevent alternatives, such as escape, to the more extreme forms of agonistic behavior.

Familiarity among the individual birds may also have contributed in some way to their willingness to allopreen; by November 1981 these cowbirds had been together in their small cage for almost a year. In mid-March of 1982 I placed in another 1.2 m × 1.2 m × 1.8 m cage 22 male and 6 female cowbirds that had been caught in the same place as the original birds. Between mid-March and mid-May 1982 I watched these birds for about 3 h and never saw any allopreening. The difference in the season may also have contributed to this difference in behavior.

If allopreening is not an artifact of captivity, its occur-

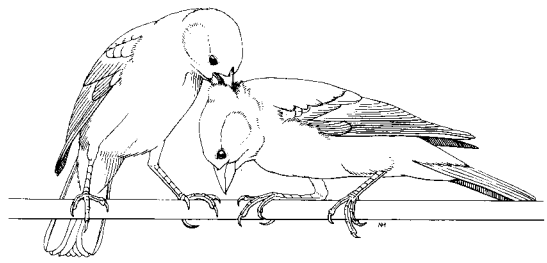

FIGURE 1. Allopreening of the second type (see text).

rence among cowbirds suggests that the interspecific head-down display arose in the intraspecific allopreening context, similar to that in other species of allopreening birds, and was then used in interspecific contexts.

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POSSIBLE "DECEPTIVE" USE OF SONG BY FEMALE BLACK-HEADED GROSBEAKS

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Among the species of birds in which females are known to sing is the Black-headed Grosbeak (*Pheucticus melanocephalus*; Weston 1947, Van Tyne and Berger 1976). In this species, such singing seems to function in maintaining family-groups after the young fledge (Ritchison 1983). Further, spectrographic analysis of 267 female songs and 521 male songs has shown that the songs of males and females differ in many respects, e.g., syllable morphology, song length, syllable duration, and intersyllable duration. Such differences allow Black-headed Grosbeaks to recognize the sex of an individual by its song (Ritchison 1980). These differences, however, apparently are not due to the inability of females to produce male-like songs. During a two-year study that I conducted, on two occasions females departed from their normal singing patterns and uttered remarkably male-like songs (Fig. 1). The situations in which the two female grosbeaks uttered these male-like songs were similar, i.e., their mates were long overdue at the nests and had failed to respond to repeated "chip" calls (the calls usually given when a pair of grosbeaks exchanged places on the nest).

One possible explanation for these male-like songs is that they simply represent one of the many vocalizations in the vocal repertoire of the female Black-headed Grosbeak. Such songs may serve to inform a male that the female has left the nest, and the eggs or young are in jeopardy if he does not return. Such an explanation seems unlikely, however, because it supposes individual recognition and my observations indicate that females sang these male-like songs so infrequently that their mates might not have had the opportunity to learn to recognize them.

Alternatively, the infrequent use of male-like songs by female grosbeaks suggests that the females may have been attempting to deceive their mates. There appear to be at least two requirements for successful deceit: the deceit must be relatively rare, so that on average a responder is paid for reacting as it does, and the responder must at least sometimes be unable to distinguish between fakes and the real thing (Dawkins and Krebs 1978). My observations of the grosbeaks suggest that these requirements appear to be satisfied, i.e., females rarely utter male-like songs and the songs appear similar enough to the songs of males that males would be unable to tell them apart. I hypothesize that upon hearing these male-like songs a female's mate would react as though another male were intruding. He would return to the nest to confront the intruder and, not finding any, would presumably remain to assume his incubation or brooding duties.

Such an observation has been reported by Morton et al. (1978) in a study of the Eastern Bluebird (*Sialia sialis*). These authors noted that at least five incubating or brooding females sang when frightened from their nests by an approaching investigator (and when the females' mates were absent). These were the only instances in which female bluebirds sang and, further, these songs were apparently identical to those given by male bluebirds in territorial advertising and defense. Upon hearing these female songs, males quickly returned to the nest, presumably primed to attack an intruding "male," but redirected their aggression toward the investigators. Morton et al. (1978:

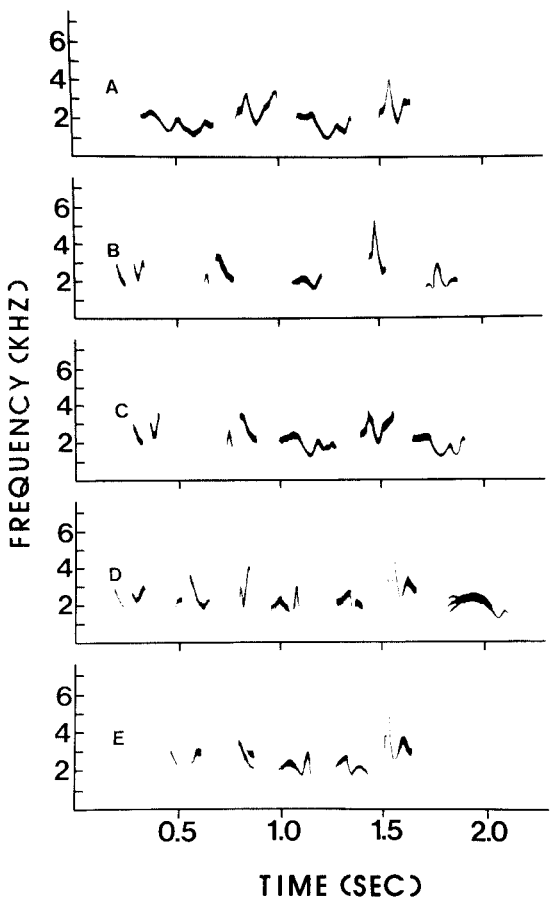

FIGURE 1. "Deceptive" songs used by female Black-headed Grosbeaks: (A) typical song of Female 1, (B) typical song of Male 1, (C) "deceptive" song uttered by Female 1, (D) typical song of Male 2, (E) "deceptive" song uttered by Female 2.