

THE HEAD-DOWN DISPLAY IN SHINY COWBIRDS AND ITS RELATION TO DOMINANCE BEHAVIOR¹

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Brood parasitic cowbirds (Icterinae) often give the head-down display when they approach other birds (Chapman 1928; Selander and La Rue 1961; Rothstein 1977, 1980). The display sometimes results in individuals of the same or other species preening the giver of the display. The function of the head-down is not fully understood, although some have suggested that it may appease a potential aggressor (Selander and La Rue 1961, Robertson and Norman 1976). However, experimental and naturalistic evidence now favors the opposite explanation, that the head-down display is an aggressive display which enables birds giving it to assess at close range the relative dominance of other individuals (Rothstein 1980). In addition, the donor often usurps the space occupied by the recipient of the display, while the probability that the recipient will attack may be reduced (Rothstein 1977, 1980). That some individuals preen the displaying cowbird may be a result of behavioral mimicry, as the head-down display resembles postures shown by birds engaged in body maintenance (Harrison 1965, Rothstein 1980).

The head-down display and associated allopreening have frequently been recorded for captive cowbirds (Selander and La Rue 1961; Selander 1964; Rothstein 1977, 1980), but they are less often seen in nature (Darley 1968). This study reports the occurrence of the display among free-living and captive Shiny Cowbirds (*Molothrus bonariensis*). We also report the frequency of the display, the species to which cowbirds displayed, the responses of recipients, and the contexts in which the head-down occurred. Our objective is to clarify the function of the head-down display in the Shiny Cowbird and to compare our data with similar information for the Brown-headed Cowbird (*M. ater*).

STUDY AREA AND METHODS

We collected data intermittently from 7 February 1973-25 February 1987 near La Parguera in south-

western Puerto Rico and around Ceiba, in eastern Puerto Rico. The principal study habitats were mangroves and dry coastal scrub, described in Post and Wiley (1976), Post (1981a), and Wiley (1985). We watched mixed-species groups of Shiny Cowbirds, Yellow-shouldered Blackbirds (*Agelaius xanthomus*) and Greater Antillean Grackles (*Quiscalus niger*) in the following situations: (1) Diurnal roosts located in large trees like mature red mangroves (*Rhizophora mangle*) and oxhorn bucida (*Bucida buceras*) near communal feeding areas such as monkey-chow hoppers or cattle troughs, (2) Nocturnal roost sites, most of which were located on off-shore cays, but some of which were in electric transformer stations (described in Post and Post 1984), and (3) Yellow-shouldered Blackbird breeding areas in open, usually cut-over, black mangroves (*Avicennia germinans*) and red mangroves, or in adjacent savannah-like pastures with oxhorn bucida.

As cowbirds giving the head-down often displayed repeatedly within a brief period to the same individual, we counted these cases of multiple displaying as one incident. If the displaying bird switched to another bird, it was counted as another occurrence. Multiple allopreening incidents were treated in the same fashion.

We did not estimate the number of cowbirds and other blackbirds that were in view at one time, so it is not possible to calculate a per individual rate of occurrence for the display. Instead, we estimated the contact time that cowbirds had with potential interactants. This is defined as the amount of time that one or more cowbirds were within 5 m of another individual to which they might have displayed. This enabled us to estimate the minimum rate of occurrence of the display and allows us to make crude comparisons with frequencies of occurrence that have been reported in other studies.

To obtain information on the relative dominance of the three icterine species, we monitored a feeding tray located in red mangroves at La Parguera. The feeding station was watched for 15 hr during April 1975. To gather data on the frequency of head-down among captives, on 24 July 1973 we formed a group of five Shiny Cowbirds (three males and two females) and seven Yellow-shouldered Blackbirds (three males and four females). These were housed in an outdoor aviary, 1 × 2 × 3 m. Observations were conducted during 4-8 September 1973. We were able to gather only 4 hr of data.

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RESULTS

The form of the display given by free-ranging Shiny Cowbirds did not differ from that which has been described for captives (Selander 1964). We saw 170 incidents of head-down displays given to Yellow-shouldered Blackbirds and 33 to Greater Antillean Grackles. We also observed 35 incidents of a Shiny Cowbird giving the head-down to another cowbird. In all, female cowbirds were involved in 149 of the incidents, and males in 89.

Fifty-eight of the 170 head-downs to Yellow-shouldered Blackbirds (34%) were followed by a blackbird preening a cowbird. We saw one case of a cowbird (a male) preening a blackbird. In five instances, a Greater Antillean Grackle preened a cowbird. Intraspecific head-down displays were followed by allopreening in 10 (29%) of the cases. Interspecific allopreening incidents were short: the mean length of 27 bouts in which another species preened a cowbird was 22.8 ± 20.0 (SD) sec, range 2–70 sec.

In addition to allopreening incidents among cowbirds, we recorded 21 cases of adult Yellow-shouldered Blackbirds preening each other. All these involved roosting birds that were intermittently autopreening. None of these incidents were preceded by any discernible display such as head-down. Parent Yellow-shouldered Blackbirds also preen young in the nest, and nestlings preen each other (Post 1981b).

During the 4 hr that we watched the captive group of five cowbirds and seven blackbirds, we saw 33 cases of interspecific head-down displays (8.25/hr). In 15 cases (45%), a blackbird preened a cowbird following head-down. We did not see Shiny Cowbirds give the head-down display to each other. We saw two bouts of intraspecific allopreening between Yellow-shouldered Blackbirds, but none between Shiny Cowbirds.

We saw head-down displays given by free-ranging cowbirds throughout the year. During the Yellow-shouldered Blackbird breeding season (March–September), we saw 128 display incidents. During the non-breeding period, we saw 100. In 49 hr of potential contact time between Shiny Cowbirds and Yellow-shouldered Blackbirds in the nesting areas, we recorded 0.02 displays/hr. In contrast, in 16.6 hr of potential contact time in non-nesting areas, we saw 4.0 displays/hr. As the number of cowbirds per unit area differed between breeding and non-breeding sites, we cannot test for differences in the display rates between the two situations. The display rates of birds in feeding flocks and roosting areas was similar: 4.83 displays/hr in roosts (observation time = 11.6 hr); 4.69/hr in feeding flocks (11.3 hr).

To determine the relative dominance of Shiny Cowbirds and the other icterines, we recorded the outcome of dyadic interactions such as supplants and attacks occurring at a feeding tray. We saw 119 interactions between Yellow-shouldered Blackbirds and Shiny Cowbirds, 60 of which were won by blackbirds and 59 by cowbirds. In contrast, of 35 interactions between cowbirds and Greater Antillean Grackles, only five were won by cowbirds.

DISCUSSION

Shiny Cowbirds in Puerto Rico appear to give head-down displays about as frequently as their North

American congener. Selander and La Rue (1961) stated that the display was “a regular feature” of the behavior of Brown-headed Cowbirds, but their correspondence with United States observers over about two years (October 1958–December 1960) resulted in only 24 reports of the display. Eight of these mentioned associated allopreening. Further, during 300 hr of observation of free-ranging Brown-headed Cowbirds, Darley (1968) saw a head-down display only once. In contrast, Rothstein (1977, 1980) recorded relatively high display rates for wild Brown-headed Cowbirds: about 20/hr during a 1.3-hr period in California, and 29/hr during 0.2 hr in New York. Finally, Scott and Grumstrup-Scott (1983) recorded 4.8 displays/hr during a 59-hr period in Ohio and Pennsylvania.

Geographic differences in the frequency of the display may be related to the different contexts in which they have been studied. The display may occur more often in roosts than in open places such as feeding and nesting areas. In the Brown-headed Cowbird, the largest number of displays has been recorded in diurnal mixed-species roosts (Scott and Grumstrup-Scott 1983). In general, roosts are little studied, perhaps because they are often in wooded, inaccessible sites. The frequency of head-down displays in roosts may be proximately related to bird density. Studies of captive cowbirds (Selander and La Rue 1961, Rothstein 1980, Scott and Grumstrup-Scott 1983) have demonstrated a high rate of interspecific head-down display. This may be a function of cage size, as well as the short periods that the birds had been together before the experiments were conducted (Rothstein 1980). In the wild it is likely that roosting cowbirds are found at the same densities as the captive groups. The rate that we recorded for Shiny Cowbirds in roosts (4.8/hr) is similar to the display rate of our captives (8.3/hr), as well as that reported by Selander and La Rue (1961) and Scott and Grumstrup-Scott (1983) for Brown-headed Cowbirds. A further influence on the occurrence of the display may be the presence of an appropriate interspecific stimulus. Yellow-shouldered Blackbirds may be strong releasers for Shiny Cowbirds, which are close to them in size, and which they heavily parasitize (Post and Wiley 1977). Further, Yellow-shouldered Blackbirds preen each other, which may increase the chances that they will allopreen cowbirds that give the head-down display. In turn, cowbirds that are allopreened may be reinforced when they give the head-down display. Allopreening has been rarely reported between Red-winged Blackbirds (*Agelaius phoeniceus*) and Brown-headed Cowbirds (see, however, Scott and Grumstrup-Scott 1983). Unlike Yellow-shouldered Blackbirds, Red-winged Blackbirds are not known to allopreen conspecifics.

Several authors (Rothstein 1980, Scott and Grumstrup-Scott 1983) have stated that head-down is seldom directed to common hosts. This contrasts with our finding that Shiny Cowbirds displayed most frequently to their main host in Puerto Rico, the Yellow-shouldered Blackbird. The reason that the head-down display is seldom seen given to common hosts may also be related to context. Firstly, roosts are seldom studied, and secondly, few potential host species roost with cowbirds. It is suggestive that Brown-headed Cowbirds in a four-species Ohio roost most frequently gave head-down displays to Red-winged Blackbirds

(71% of 76 incidents; Scott and Grumstrup-Scott 1983). Red-winged Blackbirds are common hosts of Brown-headed Cowbirds in some regions of western North America (Friedmann et al. 1977).

The Brown-headed Cowbird's use of the head-down display is related to the maintenance of dominance relationships (Scott and Grumstrup-Scott 1983). The head-down display may confer an ultimate advantage if it is an aggressive (dominance-related) display that allows individuals to occupy better locations in roosts, thereby improving their survival (Johnson et al. 1980, Rothstein 1980, Weatherhead and Hoysak 1984). Intraspecific dominance also has been shown to affect mating success in cowbirds (Rothstein et al. 1986) and other icterines (Robinson 1986, Post, in press).

Another factor that may select for head-down displays is establishment of interspecific dominance relationships. Behavioral dominance might facilitate integration into roosting flocks that leave the roost for nesting sites. For example, we noted an influx of Shiny Cowbirds into southwestern Puerto Rico in May, after Yellow-shouldered Blackbirds had begun nesting. The cowbirds joined mixed-species roosts, and on leaving the roosts, flew with Yellow-shouldered Blackbirds returning to nesting areas (Post and Post 1984). Selander and La Rue (1961) suggested that the head-down display may serve a similar function in allowing individuals to find feeding areas.

Compared with its interspecific occurrence, the head-down display was infrequent between conspecifics; only 15% of the displays were given to other Shiny Cowbirds. In intraspecific interactions, cowbirds may quickly learn the identity of other individuals and also be able to reliably gauge their relative position in a hierarchy by use of more subtle, but perhaps less mistakable, displays. Cowbirds may use the head-down display mainly in interspecific interactions because they are unable to accurately identify individuals of other species and also cannot correctly interpret other species' motivations (Rothstein 1980). It may be advantageous for a cowbird approaching another species to present an equivocal message, as a means of eliciting a greater array of responses.

As predicted by Rothstein's (1980) hypothesis of an aggressive function, head-down displays occur most often between cowbirds and species that are near them in size and fighting ability. Male Shiny Cowbirds weigh 96% of Yellow-shouldered Blackbirds (Post 1981). At a feeding shelf, cowbirds won 49.6% of dyadic encounters with Yellow-shouldered Blackbirds, the species to which they most commonly gave head-down displays. In contrast, cowbirds won only 14.3% of encounters with Greater Antillean Grackles, which are 50–60% larger than cowbirds. Cowbirds rarely gave head-down displays to grackles.

Selander and La Rue (1961) considered the head-down display to be an interspecific appeasement display, which would allow brood parasites to approach aggressive hosts near their nests. Our results are inconsistent with this interpretation. Interspecific head-down displays were rarely seen in Yellow-shouldered Blackbird nesting areas, and were most commonly given in roosts far away from breeding areas (see maps in Post 1981a). Further, the display was given frequently outside the breeding season of the Yellow-shouldered Blackbird.

In conclusion, our data support Rothstein's (1980) interpretation of the evolution of the display: its practitioners have increased fitness because it enables them to dominate other individuals and dominance behavior may increase survival (Fretwell 1969), as well as improve mating success (Rothstein et al. 1986). As a corollary, we suggest that by becoming dominant, cowbirds may be more easily integrated into flocks composed of potential hosts. Individual cowbirds thereby may obtain information about location of host nesting areas. However, the display does not appear to be a specific adaptation for gaining entry to host nests.

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VOCALIZATIONS OF NESTLING LEACH'S STORM-PETRELS¹

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Leach's Storm-Petrel (*Oceanodroma leucorhoa*) is a burrow-nesting seabird which breeds in colonies, often on off-shore islands. A single egg is incubated alternately by the adults for 41-42 days (Palmer 1962:232). After hatching, the chick is brooded continuously for up to five or six days (Gross 1935, Wilbur 1969). Adults forage at sea and return independently to feed the chick at intervals of about three days (Wilbur 1969, MacKinnon 1988) until the chick fledges at about 63-70 days of age (Palmer 1962:223). The vocal repertoire of adults is well-known, and consists of three main call types: the flight or chatter call, the burrow or purr call and the screech call (Hall-Craggs and Stellar 1976; Ainley 1980; Taoka et al. 1989a, 1989b).

In contrast, vocalizations of nestling Leach's Storm-Petrels have not been fully described, despite brief references by several authors (Palmer 1962:228, Hall-Craggs and Stellar 1976, Cramp and Simmons 1977:172). In this paper we describe the nestling vocal repertoire of Leach's Storm-Petrel and present sonographs of call types. Such descriptions are important for two reasons. First, in the absence of visual cues, nestling vocalizations are probably of central importance in

adult-chick interactions for nocturnal, burrow-dwelling species such as Leach's Storm-Petrel. Second, vocal behavior and vocal development of nestlings of non-oscine bird species in general is poorly known (Kroodsmma 1982).

We studied Leach's Storm-Petrels breeding on the Evelyn and Morrill Richardson Field Station property, Bon Portage Island, Nova Scotia, Canada (43°26'N 65°45'W). This 150 ha island lies 3 km off the southwest tip of Nova Scotia. MacKinnon (1988) estimated the population size of this colony at 54,000 pairs.

We made audio recordings of nestling vocalizations on 21-27 August 1988 (5 chicks), 27 July-15 August 1990 (33 chicks) and 28 July-14 October 1991 (30 chicks). Individual burrows were marked and nestlings were recorded nightly in 1988 and 1990 and every few nights until fledging or nest failure in 1991. Nestlings were aged using allometric equations developed for this population by MacKinnon (1988). Recordings were made between dusk and dawn using a Realistic 14-812 recorder and a Realistic 33-992C microphone in 1988 and 1990, and a Sony Walkman Professional recorder WM-D60 and a Sony PC-62 microphone in 1991. Three different recording methods were employed. First, we recorded spontaneous vocalizations during adult-nestling interactions. We then examined burrows in an attempt to determine the behavioral context of the call. Second, we recorded responses of nestlings to burrow disturbances by us when adults were not present. These

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