

COURTSHIP DISPLAYING AND INTRASEXUAL COMPETITION IN THE BRONZED COWBIRD¹

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This note reports observations of courtship behavior in Bronzed Cowbirds (*Molothrus aeneus*) and uses these observations to test predictions regarding mate choice and intrasexual competition. Little is known of the social behavior of this obligate brood parasite, but they are thought to be promiscuous (Carter 1984). Female home ranges greatly overlap one another, and males defend localized areas of dominance analogous to exploded leks (Bradbury 1981, Carter 1984). Recent observations (Clotfelter, unpubl. data), including some of those reported here, support Carter's (1984) conclusions.

The Pin-tailed Whydah (*Vidua macroura*) of southern Africa is in many respects similar to the Bronzed Cowbird. Both are sexually dimorphic brood parasites, and males of both species perform an aerial hover display and a less-conspicuous terrestrial bow display (Friedmann 1929, Shaw 1984). The *hover* display (also called the *aerial bow* display in Bronzed Cowbirds) appears to fulfill a similar function in both species: a precopulatory male display used to solicit females at close range. Unlike male Pin-tailed Whydahs, which perform these displays primarily at dispersed call-sites (Shaw 1984, Barnard and Markus 1988), male Bronzed Cowbirds display on breeding territories and on communal feeding areas (Carter 1984; Clotfelter, pers. observ.).

Avery (1984) predicted that in lekking species of birds, sperm depletion may cause competition among females for access to dominant males. Sperm depletion has been demonstrated in several birds and mammals (e.g., Squires et al. 1979, Bakst and Cecil 1981, Synnott et al. 1981, Birkhead 1991), suggesting that this may be an important phenomenon influencing female mate choice and male copulatory behavior in these species (Birkhead and Moller 1992). The risk of sperm depletion may even cause males to withhold copulations until sperm supplies are replenished (Birkhead 1991).

In a study of the Pin-tailed Whydah, Barnard and Markus (1988) tested Avery's (1984) hypothesis. They found that males copulated infrequently, sometimes rejected soliciting females, and terminated courtship bouts more frequently than did females. Intrasexual aggression among females in the presence of courting

males was high (Barnard and Markus 1988). These observations are consistent with Birkhead's (1991) observations of the Bengalese Finch (*Lonchura striata*) and with Avery's (1984) predictions.

The current study uses behavioral observations similar to those made by Barnard and Markus (1988) to study the courtship behavior of the Bronzed Cowbird. Four predictions were made. (1) Males are more likely than females to terminate courtship bouts. (2) Females are more likely to follow males that leave first than are males to follow females. (3) Courtship bouts of greater intensity (defined below) attract greater interest from females, resulting in lower frequencies of courtship termination and higher frequencies of following. (4) Intrasexual aggression associated with courtship is greater among females than among males.

Observations were made in the Santa Ana National Wildlife Refuge, Hidalgo County, Texas, during June and July 1994. Due to the difficulties in observing male cowbirds on their breeding territories, the majority of courtship observations (72.9%) were made in recently harvested sorghum (*Sorghum vulgare*) fields adjacent to the refuge. There were no qualitative or quantitative differences between courtship displays performed in breeding areas versus those performed in feeding areas (see below). Cowbirds began to aggregate in these fields after 15:00 CST and densities peaked between 17:00–18:00 hr. This diurnal movement pattern is similar to that observed in Brown-headed Cowbirds (*Molothrus ater*; Rothstein et al. 1984).

Courtship bouts began with a male terrestrial bow display. I define a courting party as only those birds within a one meter radius of the displaying male. Courting parties were generally discrete groups of birds separated from other conspecifics. Because birds were not uniquely color-banded, I do not know precisely how many individuals are represented in the overall sample. I assume a minimum of seven males and seven females based on the maximum number of courting birds observed in close succession in the same locality. The number of hover displays was recorded, and in some cases duration was recorded. Observations of a given courting party continued until all members of the party left. An individual was thought to have followed another if they left within 10 sec of each other and flew in roughly the same compass direction ($\pm 45^\circ$). Two-tailed binomial tests and Chi-squared tests were performed according to Siegel (1956) and Snedecor and Cochran (1989). Differences were considered significant at $P < 0.05$. P -values represent results of binomial tests unless otherwise indicated.

Forty-eight courtship bouts were observed on 15 dif-

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ferent days between 13 June and 4 July 1994. At the time courtship was initiated (i.e., male began the terrestrial bow display), 46 (95.8%) of all courting parties contained one male. In the two other cases, the initiating male terminated courtship within 10 sec to chase off the second male. The *bill-tilt* display, an intrasexual antagonistic display used by both sexes in many icterid species (Orians and Christman 1968), was used in these instances to displace the second male.

Of the 48 observed courtship bouts, 44 (91.7%) of the courting parties contained only one female ($\bar{x} = 1.13 \pm 0.01$ females, range = 1–4 females). In cases where more than one female was present ($n = 4$), displays were directed to only one female (see below). If the courted female terminated the courtship bout by leaving, the other female(s) generally ($n = 3$) left as well, though in one case the male redirected his displays to the remaining female. Males ($n = 20$) and females ($n = 28$) were equally likely to terminate courtship bouts ($P = 0.312$).

Courtship bouts observed on the breeding grounds ($n = 13$) did not differ statistically from those observed on the feeding grounds ($n = 35$). Males and females were equally likely to terminate the courtship bout first ($\chi^2 = 2.55$, $df = 1$, $P > 0.10$), and the other sex was equally likely to follow the sex that left first ($\chi^2 = 0.34$, $df = 1$, $P > 0.50$).

The *terrestrial bow* display was performed as part of all courtship bouts. In all bouts in which hover displays occurred ($n = 35$), they were preceded by bow displays, and there were no cases in which only hover displays were performed. Due to difficulties in detecting the less-conspicuous bow display, its duration was not accurately recorded. As per Friedmann's (1929) description, the male erects the ruff feathers around his neck, raises his partially opened wings to head level, and turns his bill slightly downward. While maintaining this posture, he rocks from side to side and slowly circles the female (Friedmann 1929). This orientation clearly indicates the intended recipient of the males' displays.

Females continued to feed throughout males' bow displays, though 13 (27.1%) of all bouts were terminated before courtship could proceed to the hover display. Of these aborted courtship bouts, females terminated six (46.2%) and males terminated seven (53.8%; $P > 0.90$).

Immediately (< 5 sec) following the last bout of bowing, the male hovers directly above the female, approximately one meter off the ground. First hovers had a mean duration of 9.72 ± 5.34 sec (range = 2.78–21.35 sec, $n = 9$). If the female stayed through the first hover, second ($\bar{x} = 9.14 \pm 5.18$ sec, range = 1.81–16.28 sec, $n = 7$) and in some cases third ($\bar{x} = 11.66 \pm 6.07$ sec, range = 4.69–15.75 sec, $n = 3$) hover displays were performed. Of the 35 courtship bouts that went to the hover stage, 24 (68.6%) were terminated after the first hover, six (17.1%) after the second, and five (14.3%) after the third. Of these bouts, females terminated 21 (60.0%) and males terminated 14 (40.0%). Therefore, given that a hover display had been performed did not change the likelihood that males as opposed to females would terminate the courtship bout ($P = 0.312$).

There were four possible outcomes for a given court-

ship bout. If the female left first, the male either followed her ($n = 15$), or did not follow her ($n = 13$). There was no significant difference between the frequencies of these two outcomes ($P = 0.85$). Conversely, if the male left first, the female either followed him ($n = 3$) or did not follow him ($n = 17$). It was significantly more likely that females would not follow a male who left first than they were to follow him ($P = 0.0036$). Copulation was only observed once, following the first hover display, after which the male left and the female did not follow.

Chi-squared tests were used to determine if display intensity influenced which sex terminated the courtship bout and whether or not the other followed. Intensity was scored as the number of hover displays performed (0–3). Due to small sample sizes, observations of bouts with two or three hover displays were combined. Courtship intensity did not affect which sex terminated the courtship bout ($\chi^2 = 1.17$, $df = 2$, $P > 0.50$), nor did it affect the probability that the other sex would follow ($\chi^2 = 0.563$, $df = 2$, $P > 0.90$).

These observations do not support any of the initial predictions. Male and female Bronzed Cowbirds were equally likely to terminate courtship prematurely, but females were significantly more likely not to follow a male that left first than they were to follow him. There was no evidence of female intrasexual aggression, though males responded aggressively to any other males in the courting party. Females reacted passively to male courtship: courtship displays rarely interrupted the feeding of the female at whom the display was directed, and courtship intensity had no effect on the probability that a female would follow a male that left first.

A possible flaw in the interpretation of these data is the assumption that terminating courtship represents a lack of interest or motivation. The sex leaving first may in fact be soliciting the other sex, encouraging them to leave the communal feeding area for a more protected area where copulation can occur. Regardless of motivation, males and females terminated courtship with similar frequencies, suggesting that this assumption did not incorrectly bias the results.

These results are consistent with Clutton-Brock and Vincent's (1991) idea that sexual selection, and hence mate choice, are controlled by potential reproductive rates (PRRs) of males and females. Though female cowbirds have relatively high PRRs due to their extraordinary fecundity (Scott and Ankney 1983), their reproductive rate is probably lower than that of males. Hence, females are choosy (Yokel and Rothstein 1991) and show little intrasexual competition for access to males.

The intense competition observed by Barnard and Markus (1988) among female Pin-tailed Whydahs may be due to severe breeding constraints imposed by two factors. First, viduine finches are specialized brood parasites, and must synchronize courtship and egg laying with that of their host (Payne 1973). Pin-tailed Whydahs are known to parasitize seven host species, but rely primarily on the Common Waxbill (*Estrilda astrild*; Maclean 1993). During these narrow time windows, females must be assured of obtaining successful matings. To guard against the risk of male sperm depletion or sterility, they should copulate repeatedly with multiple males (Birkhead et al. 1987; Birkhead and Moller

1992). Bronzed Cowbirds, on the other hand, are generalist brood parasites known to parasitize over 80 species (Friedmann and Kiff 1985). Though the exact phenology of their breeding season is unknown, they are probably similar to the Brown-headed Cowbird, which can lay in excess of 40 eggs over a 90-day breeding season (Scott and Ankney 1983). Therefore, they are unlikely to experience the same temporal constraints that might lead to intense intrasexual competition among females.

Second, adult sex ratios in Pin-tailed Whydahs are heavily female-biased (1 male: 2.2 females; Maclean 1993). Bronzed Cowbird populations are slightly male-biased (1.4–1.6 males: 1 female; Carter 1984; Clotfelter, unpubl. data), though the operational sex ratios are probably close to unity due to delayed maturation in first-year males (Carter 1984). These differences are consistent with the observed differences in intrasexual aggression among females of the two species.

Although the differences in courtship behavior and intrasexual competition between Bronzed Cowbirds and Pin-tailed Whydahs are likely due to differences in their degrees of host specialization and operational sex ratios, they do not imply that sperm depletion poses no risk for Bronzed Cowbirds. The differences between these two species indicate only that the potential costs of mating with a depleted or sterile male are less severe for female Bronzed Cowbirds than they are for female Pin-tailed Whydahs.

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