

## VOCALIZATIONS AND COPULATORY ATTEMPTS IN FREE-LIVING BROWN-HEADED COWBIRDS

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**Abstract.**—Audiospectrograms of vocalizations recorded during 12 copulatory attempts by male Brown-headed Cowbirds (*Molothrus ater artemesiaae*) are presented. All vocal sequences during copulatory attempts included songs, and all but one included flight whistles. In addition, a vocalization not previously described in cowbird copulatory sequences, the Kek Note, was recorded in four instances. Analysis of flight whistles indicated that they did not differ from flight whistles given in other contexts. The functional aspects of producing multiple types of vocalizations during the copulatory attempts are discussed. For example, incorporation of flight whistles during copulatory attempts may reflect conflicting tendencies to approach and to fly off during these times of heightened sexual arousal. Alternatively, flight whistles may have a direct stimulatory effect on the female's willingness to mate.

### VOCALIZACIÓN E INTENTOS DE COPULACIÓN EN INDIVIDUOS SILVESTRES DE *MOLOTHRUS ATER*

**Síntesis.**—Se presentan audioespectrogramas de las vocalizaciones de 12 individuos machos de *Molothrus ater artemesiaae* mientras intentaban copular. Todas las secuencias de vocalización, registradas mientras los individuos intentaban copular, incluyeron canciones y silbidos a vuelo (a excepción de una). Además, fue grabada en cuatro ocasiones, una vocalización previamente no descrita durante los intentos de copular (kek). El análisis de los silbidos a vuelo indica que éstos no difieren de silbidos a vuelo exhibidos en otros contextos no copulatrícez. Se discuten los aspectos funcionales de la producción de múltiples vocalizaciones durante intentos copulatrícez. Por ejemplo, la incorporación de silbidos a vuelo durante estos intentos, podría reflejar tendencias conflictivas de acercarse a la hembra o alejarse a vuelo durante períodos de gran intensidad sexual. Otra alternativa es que los silbidos a vuelo podrían tener un efecto de estímulo directo en la disposición de la hembra por aparearse.

Male Brown-headed Cowbirds (*Molothrus ater*) produce three principal types of vocalizations. One type, traditionally considered the true song, consists of a series of bubbly-sounding notes followed by a whistle, and often is accompanied by bow displays during social interactions. The second type of vocalization, the flight whistle (FW), usually consists of 2–3 notes, frequently is tonal in overall quality, but often contains rapid frequency sweeps. This vocalization is given just before or during flight, just prior to landing, and when another male approaches in flight. A third vocalization is the single syllable flight call (SS), which is functionally similar to the FW (Rothstein et al. 1988) and consists of a single, relatively pure tone whistle.

Until recently these vocalizations were thought to function in different contexts. Song is known to be used in male-male agonistic interactions and to establish dominance rank. This is based on observations of free-living and captive cowbirds (e.g., Dufty 1986, Friedmann 1929, Rothstein et al. 1986). Additionally, song is used to court females. Here again, this

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conclusion is based on observations of feral (e.g., Friedmann 1929) and captive (Rothstein et al. 1986) cowbirds, and on studies of captive cowbirds in which laboratory playbacks of song elicit copulation solicitation postures in socially-isolated females (e.g., King and West 1983).

FWs, as their name implies, have been primarily associated with flight. They appear to be used to communicate with males and females, signaling the departure, passage or arrival of a male cowbird. The third vocalization, the SS, occurs in the same context as FWs (Rothstein et al. 1988).

The distinctly different contexts in which cowbird songs and FWs are used recently has been questioned. Rothstein et al. (1988) have shown that male cowbirds respond to playbacks of FWs much as males of other species respond to songs. Interestingly, recent data (S. I. Rothstein, pers. comm.) indicate that playbacks of the local FW also will elicit copulatory postures from captive estradiol-primed females, despite earlier suggestions to the contrary (King and West 1977). FWs also exhibit geographically distinct dialects (Rothstein and Fleischer 1987), as do songs in many species. Rothstein et al. (1988) also noted that FWs are given significantly more frequently than are songs by free-living males immediately prior to copulations. Further, Dufty (1988) has shown that portions of a FW can be incorporated into a male's song, indicating that any ontogenetic barriers between the two types of vocalizations are not complete.

In this paper we present the first audiospectograms of Brown-headed Cowbird vocalizations produced during copulation attempts in free-living birds, verifying that male cowbirds emit both songs and FWs during the behavior. Further, we compare FWs given during copulation attempts with those given in other situations to determine whether production of this vocalization varies according to context.

#### METHODS

Recordings were made of an unmarked population of cowbirds (*M. a. artemisiae*) in and around Boise, Idaho from 4 May–17 June 1989. All recordings were made in the mornings, from 0630–1130 hours. A Marantz PMD221 cassette recorder and a Sennheiser ME 80 microphone (and windscreen) with a K3 power module and an SME-BA pre-amplifier were used throughout. Cowbirds were located visually, by listening for their vocalizations, and by luring them in with tape recordings of the female cowbird chatter vocalization broadcast through the Marantz. All copulatory vocalizations were recorded after using the latter technique.

Copulatory attempts were defined as instances when a male cowbird attempted to mount a female cowbird. Although we did not quantify temporal aspects of copulations, they appeared to be consistent with those described by Rothstein et al. (1988), that is, birds were together for only a few seconds before copulatory attempts occurred, and during this time males vocalized at a rapid rate (see below). No other birds were within 10 m of the male and female cowbirds. It was not possible to differentiate between successful and unsuccessful copulatory attempts, nor were the participants' pairing status known.

Audiospectrograms of tapes at half-speed were prepared using MacSpeech Lab I (GW Instruments, Inc.). These were converted to SuperPaint 2.0 (Silicon Beach Software, Inc.) files and were modified to remove vocalizations of other birds and additional extraneous background noises.

Several frequency and temporal variables were measured from the first part of the FWs (FW1; see Fig. 1A), using the MacSpeech program, in an attempt to determine whether FWs given during copulatory attempts were different from those given during solitary vocalizing. The Sweep measurement is the frequency range of the first stroke of FW1. The Minimum and Maximum Frequencies are the lowest and highest frequency values, respectively, represented on the audiospectrogram. The Length is the time from the beginning to the end of the FW1 trace. The Frequency at 0.25 s From Start is the frequency, measured at the top of the audiospectrogram trace, taken 0.25 s from the Sweep stroke. The Gap is a time measurement defined by a characteristic rapid upsweep followed by a downsweep near the end of FW1. Start Gap and End Gap refer to frequency measurements taken at the Gap's beginning and end, respectively.

#### RESULTS AND DISCUSSION

The flight whistles in the study area were of two very similar types. The Boise type (Fig. 1A) was found throughout most of the area, while the Bear Creek type (Fig. 1B) was found on the eastern fringe. These two variants differed only in their onset. Except for the Sweep measurement (see Fig. 1), there was no difference between the two FW variants in the parameters measured. Each FW consists of two components, FW1 and FW2. FW1 is largely a pure tone, with either one (Boise type) or two (Bear Creek type) initial frequency strokes; FW2 contains two notes that always occur in the same order: a shorter note rising in frequency, and a longer, tonal note with an initial frequency descent that are the same in both FW variants. The slight differences in FW2 in Figures 1A and 1B, particularly in the second note, are within the range of variation found in both FW types. We have never recorded one FW2 note without also recording the other. FW1 and FW2 are given either alone or together, however; if together, it is most common for FW1 to be followed by FW2, although the reverse often does occur.

Examples of audiospectrograms of vocalizations that accompanied copulatory attempts are shown in Figures 2-4. Flight whistles and songs both were included in 11 of the 12 attempts. The remaining attempt consisted of three songs. None of the attempts contained any single syllable flight calls (although it is possible that FW1, when given alone, serves as a SS in this population).

An additional cowbird vocalization was recorded during four of the copulatory attempts (see Figs. 2 and 3A). This call note, of short duration and broad frequency range, was referred to by Friedmann (1929:167) as "... the note given when interest in a female is aroused." We shorten

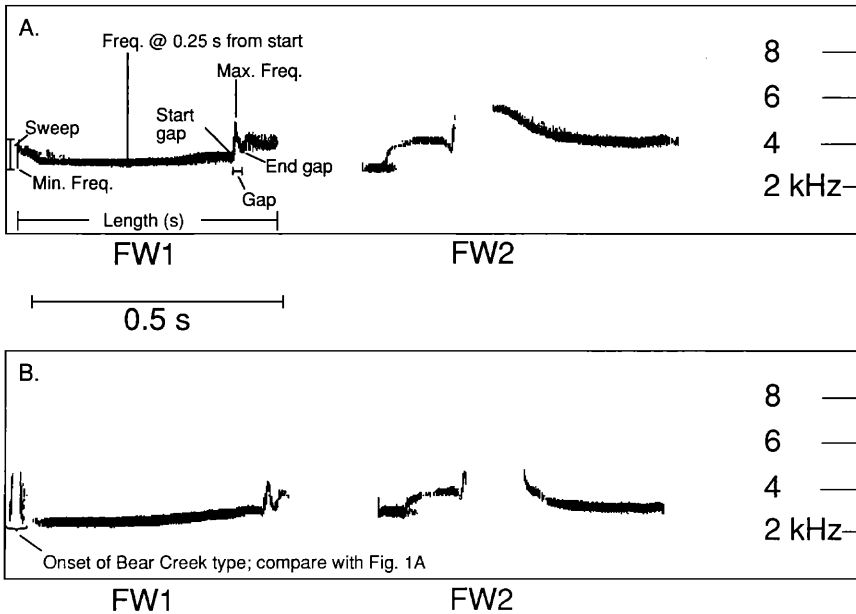


FIGURE 1. Examples of the two types of Flight Whistle (FW) encountered in the study area. A. The common Boise Type. See text for explanation of measurements taken from FW1. B. the less common Bear Creek Type. FW1 = the first component of the FW. FW2 = the second component of the FW consisting of two notes.

this description, and refer to it here simply as the Kek Note. Friedmann (1929:168) describes it as “. . . a short, clear *kek* or *tek*, quite different from the feeding note.” The latter is a *kuk* or *chuck* given while birds forage on the ground. The Kek Note can be heard during sexual chases early in the breeding season, if the birds pass close to the observer (AMD, pers. obs.); otherwise, it is rarely heard in the field, probably due to its low amplitude. Indeed, while the Feeding Note has some characteristics similar to the Kek Note, the latter has a noticeably higher-pitched quality to it, as illustrated in Figure 5; however, it is possible that these vocalizations represent the same call given under different motivational states, and their ultimate classification must await further investigation. Nonetheless, their inclusion in one-third of our recorded copulatory attempts further demonstrates the vocal richness of these events.

Vocalizations were examined from 10 different solitary males (not attracted by broadcast of female chatter) that produced at least 10 vocalizations before departing. The mean interval between vocalizations for each male was determined and averaged over the 10 males ( $\bar{x} = 11.17 \pm 4.46$  s (SD),  $n = 10$ ). This was compared with the average of the mean inter-vocalization intervals during the copulatory attempts ( $\bar{x} = 1.07 \pm 0.81$  s,  $n = 12$ ). Vocalizations during copulatory attempts occurred at a

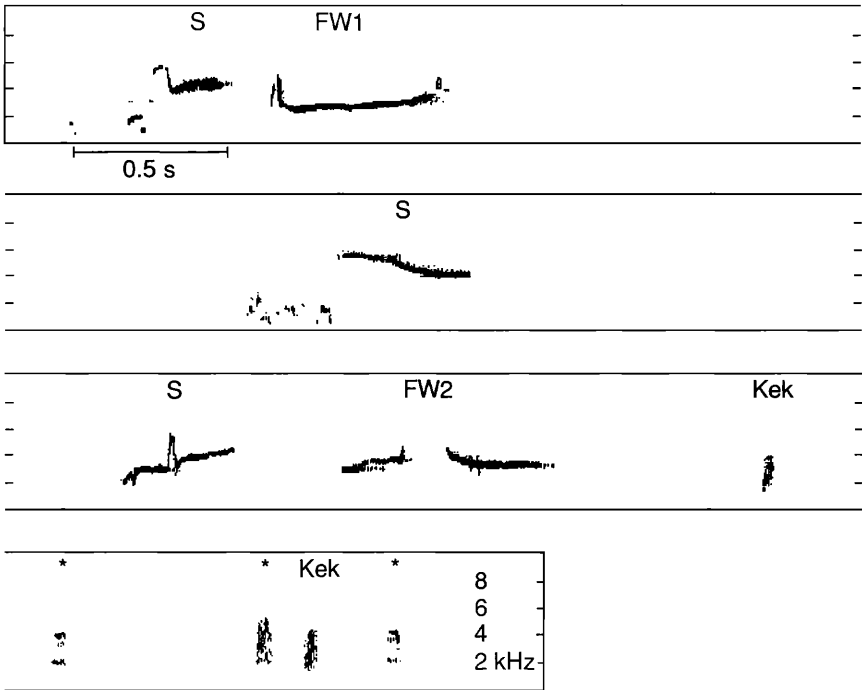


FIGURE 2. A representative wide-band audiospectrogram of vocalizations recorded during a copulatory attempt in Brown-headed Cowbirds. S = song; FW1 = first part of the Flight Whistle; FW2 = second part of the Flight Whistle; Kek = Kek Note; \* = possible cowbird vocalization, sex of vocalizing bird unknown.

significantly higher rate than those during solitary singing ( $t = 7.75$ , 20 df,  $P < 0.0005$ ).

Further, songs made up a significantly greater proportion of vocalizations during the 10 bouts of solitary singing than did FWs (FW 1 and FW2 combined) (songs:  $\bar{x} = 16.4 \pm 6.4$ , FWs:  $\bar{x} = 3.0 \pm 3.0$ ; paired  $t = 4.92$ , 9 df,  $P < 0.0005$ ). Songs and FWs were equally represented during the 12 copulatory attempts, however (songs:  $\bar{x} = 2.1 \pm 0.8$ , FWs:  $\bar{x} = 2.7 \pm 1.7$ ; paired  $t = 1.10$ , 11 df,  $P = n. s.$ ). Both FW1 and FW2 were represented equally during copulatory attempts ( $\chi^2 = 0.18$ ,  $P < 0.7$ ). FW1 was the first FW component heard in 8 of the 11 copulatory attempts that included FWs, but this difference was not significant ( $P = 0.226$ , binomial test).

Several frequency and temporal variables were measured from FW1 (Fig. 1) to determine whether FWs given during copulatory attempts were different from those given by another set of males during solitary singing. The only variables that were significantly different were Minimum Frequency (solitary singing:  $2192 \pm 189$  Hz, copulatory attempts:  $2603 \pm 222$ ;  $t = 4.80$ , 21 df,  $P < 0.005$ ) and Sweep (solitary singing:

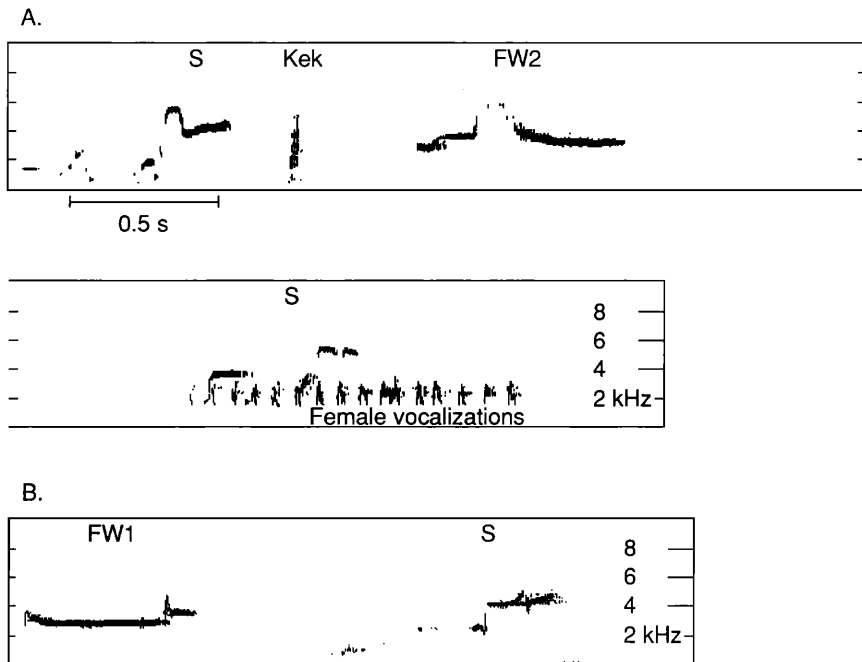


FIGURE 3. A. and B. Representative wide-band audiospectrograms of vocalizations recorded during two copulatory attempts in Brown-headed Cowbirds. Letter descriptors as in Figure 2.

1823 ± 537 Hz, copulatory attempts: 1394 ± 147;  $t = 2.56$ , 22 df,  $P < 0.01$ ). These measurements are related to each other, because both are taken from the initial frequency stroke of FW1. We believe that the differences arise from the quality of the recordings rather than from actual differences in the vocalizations. That is, only high-quality recordings from solitary males were chosen for analysis, and these tended to be better than some of the recordings made during copulatory attempts. The difference is reflected in partial loss of the initial frequency stroke from audiospectrograms of the latter group, resulting in an elevated Minimum Frequency and a shorter Sweep. Thus, despite the observed heterogeneity, we feel that there is no real difference between FWs given in the two contexts; that is, FWs given during copulatory attempts probably are acoustically identical to those produced during solitary singing.

These data confirm Rothstein et al.'s (1988) finding that flight whistles are an integral part of the copulatory behavior in Brown-headed Cowbirds, and expand upon their results to include an additional vocalization, the Kek Note. Other passerine species also include distinctly different types of vocalizations during copulatory events. Nolan (1978) noted that Prairie Warblers (*Dendroica discolor*) give Type A songs and Twitter

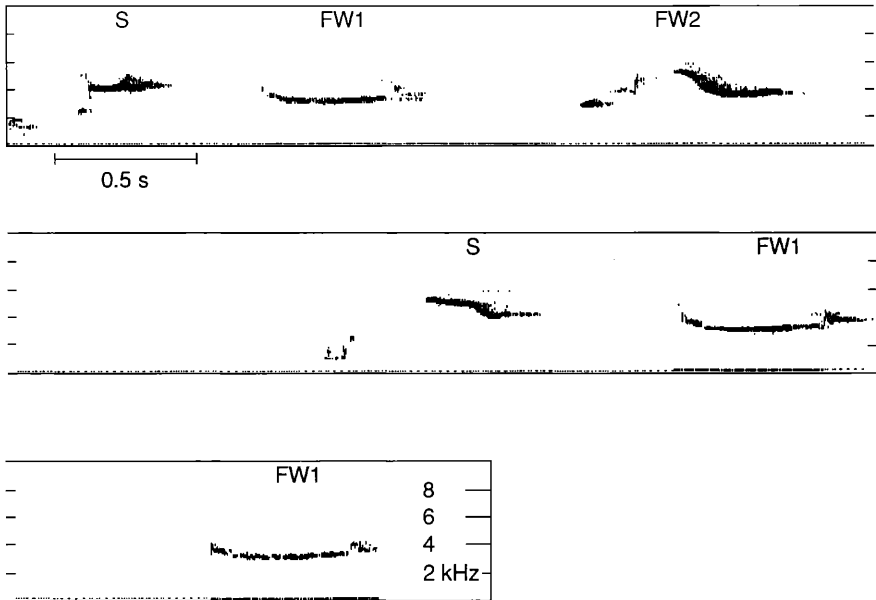


FIGURE 4. Representative wide-band audiospectrograms of vocalizations recorded during copulatory attempts in Brown-headed Cowbirds. Letter descriptors as in Figure 2.

calls, the latter characteristically given when members of a pair come into close proximity. Similarly, Armstrong (1955) and Poulsen (1958) reported that songs and calls are given just prior to and during coition in the House Wren (*Troglodytes aedon*) and the Chaffinch (*Fringilla coelebs*), respectively. Smith and Reid (1979) found that Red-winged Blackbird (*Agelaius phoeniceus*) males produce songs and precopulatory calls at a high rate prior to mating. Additional examples of species that produce multiple types of vocalizations during copulation are given by Thorpe (1961, Table 1).

Thorpe (1961) and Armstrong (1963) suggest that the inclusion of other vocalizations with courtship songs immediately prior to and during copulation may reflect the competing tendencies of the male to approach and to flee. This explanation may apply to cowbirds, for the FW, as described above, often indicates imminent flight. Unreceptive female cowbirds aggressively repel courting males that approach too closely (Darley 1968, Laskey 1950, West et al. 1981); therefore, ambivalence on the part of the male would be reasonable, and may be reflected by the incorporation of vocalizations signifying courtship and approach (i.e., song), as well as vocalizations signifying impending departure (i.e., FWs).

In addition, the use of FWs in this context may stimulate the female, and may assist her in identifying the male (Rothstein et al. 1988), thus facilitating the mating process. Further, the rapidity with which vocal-

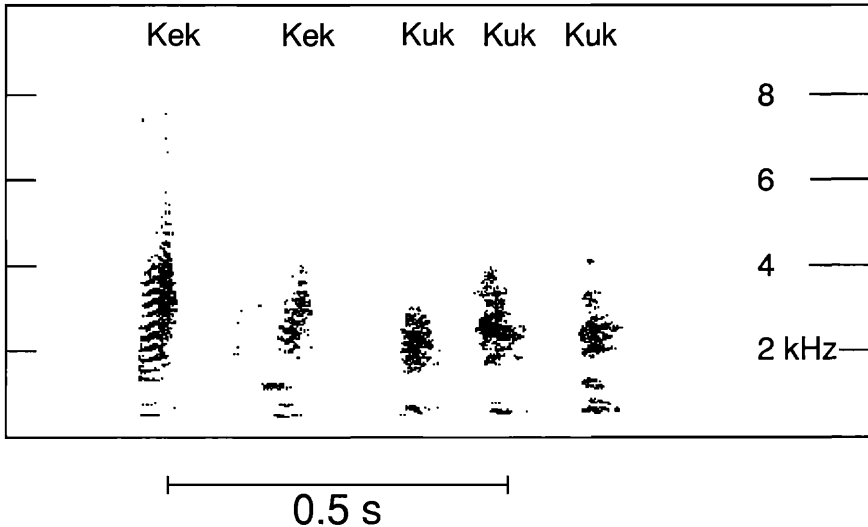


FIGURE 5. Narrow-band audiospectrograms of two Kek Notes (Kek) recorded during a copulatory attempt and three Feeding Notes (Kuk) recorded during a foraging bout.

izations are produced and the apparent immediate variation in song production (no song types were repeated within any of the 12 individual recordings, although FWs were repeated) may serve to hold the female's attention and may contribute to female choice of mate (Krebs and Kroodsma 1980). Alternatively, the male's tendency to produce myriad vocalizations (including songs, FWs, SSs and Kek Notes) at a rapid rate may simply reflect the heightened state of stimulation associated with copulation.

Our results are in general agreement with those of Rothstein et al. (1988), with a few notable exceptions. Both studies found that copulatory attempts occur shortly after the two birds come together. Additionally, both determined that FWs are produced during the vast majority of copulatory attempts (Rothstein et al. (1988): 22/25 attempts (88%); present study: 11/12 attempts (91%);  $\chi^2 = 0.05$ , 1 df,  $P > 0.8$ ).

One possible difference is that the earlier investigation noted SSs in 5/25 (20%) of the copulatory attempts, whereas none (0/12) were recorded in the present study. Although this difference is not significant ( $\chi^2 = 1.33$ , 1 df,  $P > 0.2$ ), it reflects the singular lack of SSs in our population. Indeed, this vocalization was encountered frequently by Rothstein et al. (1988), but we have yet to record it from birds in our population under any circumstances. It is possible that FW1, which has frequency and temporal characteristics similar to those of an SS (cf. Rothstein et al. 1988) and is often produced alone, doubles as an SS in our population.

Finally, Rothstein et al. (1988) found that male cowbirds sang in only 63/115 (54.8%) of the copulatory attempts during which the investigators



listened for songs, compared to 12/12 (100%) of the attempts we recorded ( $\chi^2 = 7.41$ , 1 df,  $P < 0.01$ ). Although it is possible that part of this disparity may reflect procedural differences between the two studies in noting the occurrence of a song (i.e., by ear vs. from a tape recording), we believe that a more likely explanation is that there is geographical variation in the extent of song use during copulatory attempts. Birds in our population simply may use songs in this context more often than those in the populations studied by Rothstein et al. (1988).

All three subspecies of the Brown-headed Cowbird have been shown to include FWs during mating activity. It has been observed in *M. a. artemisiae* (Rothstein et al. 1988; this study), in *M. a. obscurus* (Rothstein et al. 1988), and in captive (West et al. 1981) and one free-living (S. I. Rothstein, pers. comm.) *M. a. ater*. Given the prevalence of FWs in cowbird copulatory attempts in natural and semi-natural conditions, we agree with Rothstein et al. (1988) that systematic playbacks of FWs of the appropriate dialect must be considered in future studies of vocal interactions among cowbirds.

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