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Dual Signaling during Mating in Brown-headed Cowbirds (*Molothrus ater*, Family Emberizidae/Icterinae)

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Abstract

Male brown-headed cowbirds (*Molothrus ater*) vocalize to females during pair formation, a period usually lasting several days. Males also vocalize to females in the seconds immediately prior to females' adopting copulatory postures. The two major classes of male vocalizations occurring during courtship and copulation are songs and flight whistles. Observations across the species' North American range suggest that the function of these two courtship vocalizations may differ geographically. Aviary observations of eastern and midwestern populations suggested, furthermore, that the precise timing of song and whistle used during copulation sequences differs, with flight whistles occurring most often after a copulatory posture but before the male mounts and the pair copulates. Such timing of the two signals suggested different proximate functions. Here, we report three experiments that addressed the communicative properties of the two signals in two midwestern populations. First, we tested females of the two populations in two playback experiments to determine copulatory responsiveness and discrimination of the two signals. We asked whether females of the two populations gave more copulatory responses to the playbacks of songs and flight whistles of males of their own population than to those of males of the other population, and whether females responded differently to songs than to whistles. In the third experiment, we observed courtship interactions among males and females from one population in a large aviary to assess the use of flight whistles in relation to courtship success. Females of both populations responded more frequently to playbacks of songs than to playbacks of flight whistles and showed reliably more responsiveness to local song variants. Thus, information in male song can be used by females to discriminate the local population. The aviary data revealed that the rate of flight whistling correlated strongly with male courtship success. Thus, the vocal antecedents to mating in midwestern cowbirds include close-range signaling to females followed by longer range signaling, perhaps to other males and to females other than the mate. Acoustic and behavioral differences between these two signals in diverse parts of the cowbirds' range suggest that the function of 'species-typical' signals such as songs or whistles may not be fixed, a conclusion in keeping with the growing evidence of vocal and social malleability in these brood parasitic birds.

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Introduction

We studied variations in the use of two vocal signals during courtship in cowbirds. Although the brood parasitic habit of cowbirds would not appear compatible with behavioral plasticity, there is now extensive information documenting the effects of social and acoustic experience on species identification, vocal learning, cultural preferences for mates, and courtship skills (FREEBERG et al. 1995; FREEBERG 1996; KING et al. 1996;

WEST et al. 1996). There are also extensive data on geographic variation in the details of the aforementioned patterns of behavioral development, with some populations showing greater malleability than others (KING & WEST 1990; O'LOGHLEN & ROTHSTEIN 1993). Some of the intraspecific differences appear to be variation on a central theme (e.g. all male cowbirds use vocalizations during courtship, but the acoustic details of those vocalizations vary). Other differences between populations, however, suggest a second type of diversity, a categorical variation — that is, a shift in function from one acoustically distinct vocal signal to another. In the present study, we used playback and observational techniques to learn more about the proximate dynamics of the two major vocalizations used by male cowbirds during courtship (songs and flight whistles).

We tested two midwestern populations: one from southwestern South Dakota (*Molothrus ater artemisiae*) and one from southern Indiana (*M. a. ater*). We examined these populations of cowbirds because of the relative paucity of information about midwestern and Great Plains populations relative to east and west-coast populations (but see FRIEDMANN 1929; ELLIOT 1980; DUFTY & MCCHRYSAL 1992; DUFTY & PUGH 1994).

Assessment of potential mates by female cowbirds may rely more heavily on vocal signals than is the case in nonparasitic songbirds (see also PAYNE & PAYNE 1977, 1997; PAYNE 1985 for an example with another brood parasitic species, Village Indigobirds, *Vidua chalybeata*). Unlike brood parasitic species, assessment of resources such as nest sites or territories can be used in addition to vocalizations in nonparasitic species (WEST & KING 1987; YOKEL & ROTHSTEIN 1991; O'LOGHLEN & ROTHSTEIN 1995). In previous studies with captive populations, we documented many parameters of males' songs important to the elicitation of copulatory postures in females (the female behavior immediately preceding copulation). These parameters range from the specific acoustic features of the signal to the social status or courtship competencies of the males vocalizing to the female (WEST et al. 1981, 1996; KING & WEST 1990; FREEBERG et al. 1995). Here, we expanded our focus to include the male cowbird's flight whistle. We did so for two reasons. First, several studies of cowbirds from far western populations suggest that whistles may replace songs as proximate elicitors of female copulatory postures (ROTHSTEIN et al. 1988; O'LOGHLEN & ROTHSTEIN 1993). Second, observations of male and female cowbirds in our aviaries indicated that songs and whistles often occur in close proximity to one another during mating, suggesting the need to look at the specific timing of the two signals in relation to female assessment.

Three steps, reported here as experiments 1, 2, and 3, were undertaken to study the acoustic and functional properties of these signals. In experiment 1, we used playback procedures to establish female responsiveness to local signals in the South Dakota and Indiana populations, that is, whether population-specific acoustic information exists in songs of males from South Dakota and Indiana, and whether this information could be used by females of the two populations as potential cues in their mating decisions. For the playback study, we used the relative numbers of copulatory postures given in response to playbacks of vocalizations as an assay of female preferences. This methodology has been experimentally validated for captive populations (WEST et al. 1981). Experiment 2 was designed to address the relative effectiveness of songs and flight whistles as elicitors of copulatory behavior by females and to test whether population-specific acoustic information in flight whistles by themselves (i.e. with no other acoustic information from males

available) could be used by females as potential cues in their mating decisions. In some parts of the cowbirds' range, especially in the far western USA, females show strong copulatory responsiveness to flight whistles of males, while in eastern parts of the range, female responsiveness appears to be restricted more to songs of males (ROTHSTEIN et al. 1986; KING & WEST 1990; DUFTY & MCCRYSTAL 1992; O'LOGHLEN & ROTHSTEIN 1995). Compared with eastern populations, flight whistles in the far west are acoustically more complex, can be categorized into dialects, and often are not fully developed until a male's second breeding season (ROTHSTEIN et al. 1988; O'LOGHLEN & ROTHSTEIN 1993; O'LOGHLEN 1995). These three characteristics suggest more selective pressures on flight whistles as reliable mating cues. We also noted that males from the South Dakota population appeared to use flight whistles more often than the cowbirds we studied in Indiana and North Carolina. Thus, we played back songs and flight whistles of South Dakota and Indiana males to South Dakota and Indiana females, respectively, to assess differential copulatory responding to the two signals.

Experiment 3 consisted of analyses of the courtship behavior of South Dakota males and females in large outdoor–indoor aviaries. We documented the relationship between rates of flight whistles by males and their courtship success. We assessed this relationship because earlier observations of a North Carolina population had suggested that dominant males give more flight whistles than subordinate males, especially in the moments just prior to copulation (M. J. WEST unpublished data). These data suggested that flight whistles may advertise a male's social status to other individuals (ROTHSTEIN & FLEISCHER 1987; ROTHSTEIN et al. 1988).

Experiment 1: Playback Tests of Songs of South Dakota and Indiana Males to South Dakota and Indiana Females

Here, we tested the playback responsiveness and selectivity of South Dakota and Indiana females to songs from males of both populations. We focused on responsiveness because we had found that other populations differed in this parameter. Some populations responded on more playback trials than others, even when the songs being played were similar (such as local songs of each population). For example, *M. a. ater* females from North Carolina responded, on average, to 51% of local North Carolina songs whereas *M. a. obscurus* females from Texas responded to 36% of local Texas songs (KING et al. 1980; KING & WEST 1990). These differences appeared to map onto differences in the social behavior of females from the respective populations: North Carolina females were much more likely to depart after a male had directed one song to them whereas females from Texas often did not depart until several songs had been sung. Males also could sing in closer proximity to Texas females than to North Carolina females. Thus, the *M. a. obscurus* females appeared to have a different threshold for responsiveness to song (KING & WEST 1984); these findings indicate that the assessment (and rejection) of a courting male may occur more rapidly in some populations than in others. Earlier tests of first-year South Dakota *M. a. artemisiae* females also suggested lower responsiveness, as measured by playback, compared with Indiana or North Carolina populations (FREEBERG et al. 1995; WEST et al. 1996). Thus, in the first experiment, we sought to establish whether there were intraspecific differences in responsiveness between the *M. a. ater* Indiana population and the *M. a. artemisiae* South Dakota population.

Next, we wished to examine differences in perceptual selectivity between the two populations. Although it is routine for investigators to look for and to find differences in the acoustic characteristics of males' songs (differences termed dialects or geographic variants), it is less common for investigators to look for differences in song perception among females. But, these differences (an appropriate parallel term might be dia-cepts) exist. Tests from a range of geographic locations indicate that female cowbirds do not share species-wide patterns of song discrimination. Indeed, each new population we have studied appears to differ on key perceptual parameters (see KING & WEST 1990 for a summary). Within the eastern subspecies, *M. a. ater* females differ in their degree

of selectivity and modifiability. For example, *M. a. ater* females from an eastern population (North Carolina) responded equally to local and distant Oklahoma *M. a. ater* variants whereas *M. a. ater* females from the Oklahoma population responded reliably more to songs from their local population and much less to songs from the North Carolina population (KING et al. 1986). Moreover, whereas attempts to modify North Carolina females' preferences failed, the same procedures revealed modifiability in Oklahoma females (KING & WEST 1987), suggesting the Oklahoma females' finer discrimination of songs may rely on learning. Finally, in a population in Austin, Texas, in the border zone between two of the three subspecies (*M. a. ater* and *M. a. obscurus*), females failed to show any local preferences, and responded as much to songs from North Carolina or Oklahoma as they did to local songs (A. P. KING unpublished data). Differences in perceptual selectivity within a population also have neural correlates: in a study of North Carolina females, volume of song-related nucleus IMAN (lateral portion of the magnocellular nucleus of the anterior neostriatum) was strongly and positively correlated with females' playback discrimination of local songs (CLEAL et al. 1996; HAMILTON et al. 1997). Absolute responsiveness was not correlated with IMAN, suggesting these two properties are under different control. The neural data indicate that although females do not sing, they use song-related nuclei in their perception and assessment of male songs, a finding that provides another incentive to look carefully at intraspecific variation in selectivity and responsiveness.

Methods

Playback subjects

Eleven South Dakota females (from Fall River and Custer Counties, SD) and 11 Indiana females (from Monroe County, IN) served as playback subjects. All females had been collected between May and mid-Aug. from the same sites as males whose songs were played back. The South Dakota females were between two and 4 yr of age at the time of playback testing. The Indiana females were yearlings entering their first breeding season. Five of the 11 South Dakota females had served as playback subjects when they themselves were yearlings (1992) and the same five had served as companions for juvenile South Dakota males prior to the 1992 playback test. The remaining six South Dakota females had been housed with South Dakota males and females in aviaries for 1–2 yr. Playback females were placed (separated by population) in two indoor flight cages (1.8 × 2.4 × 1.8 m) next to one another from Jul. 1992 until May 1993. The three windows in the room were open when the temperature was above 15°C. The females could hear adult South Dakota and Indiana males in the outside aviaries 30 m away, as well as wild Indiana cowbirds that congregated daily at a feeding area adjacent to the room housing the females. Canaries (*Serinus canaria*) and zebra finches (*Taeniopygia guttata*) occupied other cages in the room.

In early May 1993, all females were transferred to sound-attenuating chambers (1.2 m³) for playback testing (WEST & KING 1986). Eight of the Indiana females were tested in pairs and three alone. Ten of the South Dakota females were tested in pairs and one alone. No effects of social or solitary housing have been found on female responsiveness, selectivity, or concordance in previous studies (KING & WEST 1983a; KING & WEST 1983b), nor were any effects found in the present study.

Playback procedure

Beginning on 10 May 1993, we played six vocalizations daily to the females, with one vocalization per trial and each trial separated in time by 90 min, beginning around 07.00 h. The females heard the vocalizations in varying orders each day and each vocalization was presented an equal number of times at different times of day. We played back each vocalization eight times to each female over the course of the experiment. We scored a positive response if a female adopted a copulatory posture (if she arched her neck and back and separated the feathers around the cloacal area) within 1 s from onset of the sound. Observer agreement, scored five times during the experiment by three different observers, was 100% on the presence or absence of a copulatory response. The second observer could not hear the playback of the song.

We played back songs using an Otari MX5050 recorder, a Urei 537 1/3-octave equalizer, and a Crown D75 power amplifier through JBL 2105 speakers located in each chamber. The Urei equalizer was adjusted by playing white noise through the playback system and recording speaker output with a Bruel & Kjaer 2033 spectrum analyzer. The SPL was 85 ± 2 dB adjusted with a B&K 2209 sound pressure meter, set to A weighting, impulse reading.

Selection and Recording of Songs

The songs played back in Experiment 1 were obtained from eight adult Indiana males captured at the laboratory in Monroe County, IN, in Apr. 1993, and from six South Dakota adult males captured in Fall River and Custer Counties, SD, in Jul. 1991 or May 1992. The males lived in large indoor-outdoor aviaries (each aviary $1.3 \times 9.1 \times 3.4$ m) with conspecific males and females from their respective collection sites. We placed 4–6 Sennheiser RF condenser microphones in locations within the aviaries to maximize our chances of obtaining recordings from males vocalizing less than 0.3 m on axis of the microphones. The vocalizations of the South Dakota males were recorded with a Nagra IVS recorder at 38.1 cm/s in May 1992. The vocalizations of the Indiana males were recorded with a Sony TCD-D10 PRO II DAT recorder in May 1993. We recorded an average of 136 vocalizations (range, 68–267) for the South Dakota males and an average of 127 vocalizations (range, 100–176) from the Indiana males. Sixteen vocalizations, eight from each population, were played to the females. One song from each male was used, with the exception of one South Dakota male from whom we used three songs to create the equal sample sizes. Particular vocalizations were chosen for playback on the basis of acoustic quality and to sample the range of different song types in the two populations. For inclusion, the unweighted signal-to-noise ratio measured peak-to-peak had to be 53 ± 2 dB measured between 300 and 12 000 Hz (see Fig. 1).

Data analyses

We used the Wilcoxon–Mann–Whitney signed ranks test and Kendall's coefficient of concordance to test for differences between groups of females (SIEGEL 1956; SIEGEL & CASTELLAN 1988).

Experiment 2: Playback Tests of Songs and Whistles to South Dakota and Indiana Females

We studied both songs and flight whistles in the second playback set to get a comparative measure of their functional properties and to learn whether whistles, like songs, carried geographic information to be used by females to discriminate local populations. We carried out tests of flight whistles with other eastern and southern populations, finding very low rates of response to flight whistles, with values in the same range as responses to nonconspecific signals (WEST & KING 1989). The populations we studied, however, whistled less than either the Indiana or South Dakota populations. Moreover, in those studies, we played back all songs and whistles in a male's repertoire in the same playback set, interspersing songs and flight whistles by playback trial. O'LOGHLEN & ROTHSTEIN (1995) reported playback discrimination of local and foreign flight whistles in California cowbirds under conditions in which females heard only flight whistles. To test flight whistles alone, but to compare them with songs as well, the playback procedure of experiment 2 differed from that of experiment 1 in several respects. In Phase I, females heard local and distant flight whistles; in Phase II, they heard local and distant songs; in Phase III, they heard flight whistles again; and in Phase IV, they heard only songs. We also included heterospecific songs and whistles as controls to rule out effects of familiarity.

Methods

Playback subjects

Ten South Dakota females and 10 Indiana females served as playback subjects in experiment 2. All females had been collected from the same sites as previous females, between the month of May and mid-Aug. The South Dakota females were between 4 and 6 yr old at the time of playback testing, and the Indiana females between 2 and 3 yr old.

Four of the 10 South Dakota females had served as subjects in Experiment 1. These females had resided in aviaries with South Dakota conspecifics during several breeding seasons. The remaining six females had been housed with South Dakota males and females in aviaries, including breeding seasons. The Indiana females had been used for playback in May and Jun. 1994 and had resided in aviaries with Indiana males at other times.

In Sep. 1994, the Indiana and South Dakota females were housed (separated by population) in two outdoor flight cages ($3.2 \times 3.2 \times 9.1$ m) until Feb. 1995, when they were moved into the indoor flight cages described earlier. All the females could hear adult South Dakota and Indiana males in the outside aviaries and hear wild

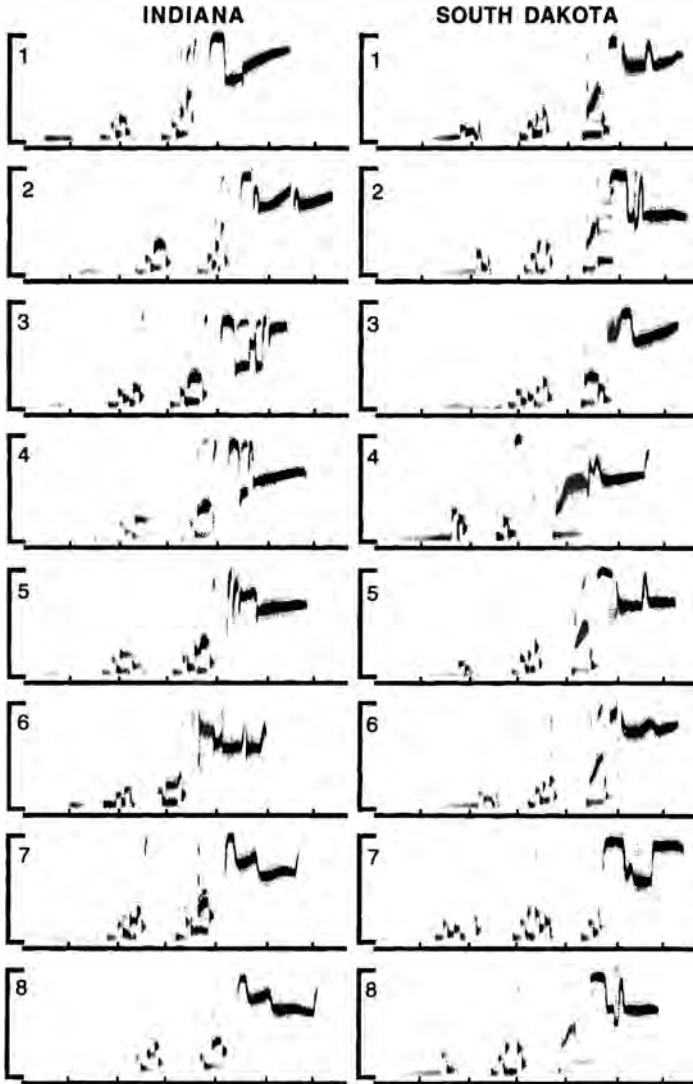


Fig. 1: Wide-band (300 Hz) spectrograms of Indiana and South Dakota cowbird songs were generated by the program SIGNALYZE produced by InfoSignal Inc. by Eric KELLER. The frequency range (y axis) is 0–12 kHz and time (x axis) is expressed in 200 ms units

Indiana males beginning in Mar. In addition, a vocalizing Indiana male was housed in an adjacent cage in the same room from Feb. until Mar. 9, 1995, as part of a separate experiment. During playback testing, all 10 of the Indiana females were tested in pairs. Eight of the South Dakota females were tested in pairs and two alone.

Recording and selection of flight whistles and songs

The flight whistles of South Dakota and Indiana males were recorded either during a breeding season or immediately prior to a breeding season: 6 May to 30 Jun. 1992, 25 Apr. to 17 Jun. 1994, and 6–9 May 1995. All

flight whistles were recorded with a Sony TCD-D10 PRO II DAT recorder and Sennheiser RF-condenser microphones in large indoor-outdoor aviaries. Flight whistles with the highest signal-to-noise ratio (between 50 and 56 dB) measured peak-to-peak between 300 and 12 000 Hz were used as playback stimuli. Typically, these were recorded at a distance of 0.3–0.5 m from a vocalizing male, and occasionally as much as 1.0 m from a vocalizing male. Four flight whistles from four different males from each population were played in Phase I and two new flight whistles from two new males from each population were added to the Phase I flight whistle set in the Phase III (see Fig. 2).

For three South Dakota and Indiana whistles, the same males' songs had been played in Experiment 1 and were tested again. Recordings from a larger set of males were used to identify local flight whistle variants. The Indiana flight whistle set was based upon the best recordings of 117 recorded flight whistles from 18 different males, and the South Dakota flight whistle set was based upon the best recordings of 205 recorded flight whistles from 27 different males.

In addition to recording quality, flight whistles were chosen to sample as widely as possible the flight whistle variation by population. The three primary South Dakota flight whistles, and combinations of these three flight whistles, are the only flight whistles ever recorded (or heard by T. M. FREEBERG) from captive vocalizing males that had been caught in South Dakota as adults. Flight whistle 3 appears to be the introductory vocalization of flight whistle 1 in Fig. 2. Note also that although flight whistles 2 and 4 have two syllables, the simplicity of their acoustic structure indicates that they may be more appropriately considered single-syllable flight calls (ROTHSTEIN et al. 1986, 1988). However, these vocalizations were included in the playback because they are used very frequently by South Dakota males during courtship of females. The two primary Indiana flight whistles (note that one whistle appears to be the introductory vocalization to the other) are given by the majority of wild and

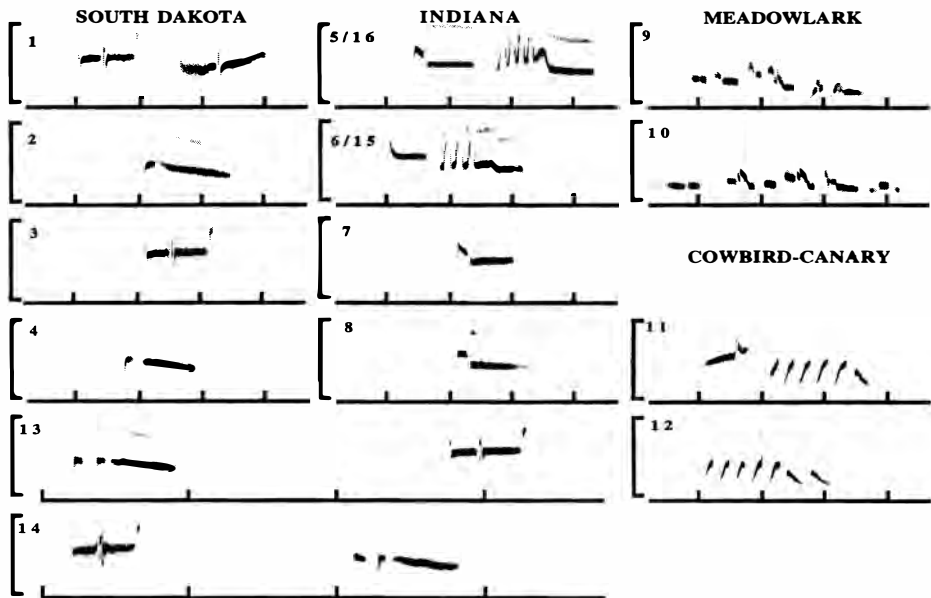


Fig. 2: Wide-band spectrograms of Indiana and South Dakota flight whistles. The frequency range (y axis) is 0–12 kHz and time (x axis) is expressed in 400 ms increments for vocalizations 1–12 and 800 ms units for vocalizations 13 and 14. Whistles 13 and 14 were added in Phase III. The two additional Indiana whistles are not shown because they were structurally highly similar to those portrayed here but produced by new males

captive Indiana males. A third and relatively rare flight whistle has been heard by T.M.F. in both wild and captive Indiana males, but we were not able to record it for testing.

Four whistle-like vocalizations were used as control playbacks. Two of these were vocalizations produced by male cowbirds, and two were vocalizations produced by a western meadowlark (*Sturnella neglecta*). Two canary-like whistles were recorded from two different South Dakota male cowbirds that had been housed with canaries (*Serinus canaria*) as juveniles. These two canary-like whistles were chosen from a set of 27 canary-like whistles, recorded between 25 Apr. and 8 May, 1994. These vocalizations were recorded using the same equipment and criteria as for the flight whistles. Two meadowlark songs were recorded from a vocalizing male in Custer County, SD, at a distance of ≈ 10 m on 30 Apr., 1992. These vocalizations were recorded with a Sony TCD-D10 PRO DAT recorder and a Sennheiser electret microphone. For Phases II and IV, we chose six songs from six different Indiana males and six different South Dakota males from the playback recordings used in experiment 1, to sample the variation of songs in the two populations but to reduce the size of the playback set.

Two playback sets were assembled: the flight whistle set and the song set. We used the same procedures as previously described for Experiment 1 for daily presentation. The flight whistle set was played back first for 7 d (Phase I), followed by the song set for 12 d (Phase II), the whistle set again for 7 d, with four new whistles (Phase III), and the song set again for 2 d (Phase IV). We had originally planned to play back whistles and songs for equal numbers of days in a row but the initial patterns of responding caused us to shorten the Phase I to II interval. Given the constraints of the number of playback days needed to document differences in responsiveness to whistles vs. songs, we used the Phase IV song set only to test whether females were still responding to conspecific sounds. Each of the 12 songs of Phase IV was only played back once, whereas in Phase II (the first song set), each song was played back six times. Thus, in Phase IV, we were not able to test for geographic differences as it only lasted 2 days.

Data analyses

We used the sign test, the Wilcoxon–Mann–Whitney signed ranks test, Friedman analyses of variance, and Fisher exact-test to test for differences between groups of females for responses to songs or to whistles (SIEGEL & CASTELLAN 1988).

Experiment 3: Correlations between Flight Whistle Rates and Courtship Success

Questions about the actual timing of songs and whistles in relation to mating led us first to re-examine records of copulatory activity from several populations (see Methods below for procedures). Did males whistle more before copulatory postures occurred or after? Observations of cowbirds from North Carolina and Indiana populations (*M. a. ater*) and from a South Dakota population (*M. a. artemisiae*) suggested differences in when the two signals were produced during copulations with females (Fig. 3; M. J. WEST unpublished data). In these three populations, songs were far more likely to precede a copulatory response, with both flight whistles and songs as the second most frequent occurrence to precede a copulatory response. Following the copulatory posture and during mounting, however, whistles were the most frequent vocalization to occur, ranging between 33% in North Carolina (out of $n = 72$ observed copulations) and 40% and 41%, respectively, for Indiana ($n = 71$ copulations) and South Dakota ($n = 44$ copulations) males. Our observations suggested that the South Dakota males seemed to use more songs and whistles in general during mounting and to be more variable in the vocalizations they used than did North Carolina and Indiana males (Fig. 3). But, in all three populations, whistles occurred most often after elicitation of a copulatory posture but before actual mounting.

Observations of North Carolina males also were suggestive of a relationship between flight whistles, male dominance, and copulatory success: 50% of the copulations with whistles after a copulatory posture were by the dominant males, as judged by displacements from perches during fall and winter months and by overall copulatory success (M. J. WEST unpublished data). Moreover, over 70% of all whistles anywhere in a copulatory sequence came from the successful males. In contrast, the least successful males produced no whistles at any point in copulations with females. The most successful males' whistle variants also differed from those used by the lower ranking males, making their use even more distinctive. Although the direction of effects is not clear between successful mating and whistling, the data are suggestive of a possible function for whistling while mating: signaling social status to other individuals.

The data also suggest that whistles may be produced more often in copulation sequences involving South Dakota cowbirds than North Carolina and Indiana cowbirds. Work with wild west-coast populations of cowbirds

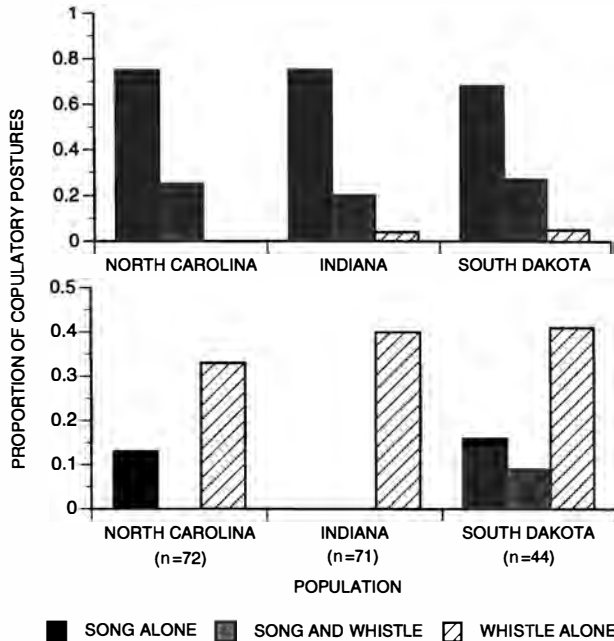


Fig. 3: Breakdown of use of songs and whistles before (top) or during (bottom) copulatory events for three populations: North Carolina, Indiana (both *Molothrus ater ater* populations) and South Dakota (*Molothrus ater artemisae*). The data for the three populations are from birds housed in large aviaries during the breeding season, all had been wild caught (see respective Methods). The North Carolina birds ($n = 6$ males) were collected and observed in Orange Co., NC, and the Indiana ($n = 13$ males) and South Dakota birds ($n = 15$ males) at the sites described in the text. Methods for observing and scoring copulations were the same as those described for experiment 3

also indicates that flight whistles are the most frequently used vocalization during copulations (ROTHSTEIN et al. 1988). ROTHSTEIN et al. (1988) and YOKEL (1986) reported that 45% of 115 copulations observed in the wild in California were unaccompanied by song (in the previous 5 s) whereas only 12% were unaccompanied by flight whistles. In Idaho, DUFTY & MCCHRYSAL (1992) observed and recorded 12 copulatory attempts in wild cowbirds: all vocal sequences included songs, and 11 of the 12 included flight whistles.

To learn more about the functional properties of whistles, we examined flight whistle rates of South Dakota males in relation to courtship success during the breeding season. The birds for which we report data here were subjects in other studies assessing mating patterns of South Dakota cowbirds from different social backgrounds (for details see FREEBERG 1996, 1997); however, whistle data were not analysed as part of those studies.

Methods

Subjects

Subjects were 16 males that were studied during their first breeding season (1994), 14 of which were studied again during their second breeding season (1995: two of the males had died over the previous winter), and 13 new males that were studied during their first breeding season (1996). All of these males had been caught in South Dakota as juveniles and had been housed in captivity in Bloomington, IN, with adult male and female cowbirds from the South Dakota population. The courtship behavior and pairing patterns of these males were

tested in a large aviary containing other South Dakota males of the same age that had been housed with Indiana adults and with South Dakota females previously housed either with South Dakota or Indiana adults (FREEBERG 1996). Only data from the South Dakota males housed with South Dakota adults are reported here.

Breeding season data collection

During the breeding seasons, the courtship interactions and pairing patterns of these males were observed. Each morning, between \approx 06.00 and 10.30 hours, data on each male were collected in two 10-min focal samples. Males were sampled individually with methodologies that had been successfully used in earlier studies (EASTZER et al. 1985; FREEBERG et al. 1995; WEST et al. 1996). Here we report data on average numbers of flight whistles of males per morning's observations. We included both flight whistles that were undirected, when no other birds were within 1 m, and those that were directed to females, when vocalized within 0.5 m of a female with the male's body or body movements oriented towards the female (WEST et al. 1981; ROTHSTEIN et al. 1986; DUFTY & MCCRYSTAL 1992).

Courtship success of males was based upon a hierarchy of criteria associated with stable mating pairs in cowbirds (EASTZER et al. 1985; YOKEL 1986; FREEBERG 1996). Males were ranked on courtship success by the following:

1. Number of pairings with different females obtained over the breeding season (for descriptions of pairing measures, see FREEBERG 1996).
2. Number of different females with which the male copulated. Note that males were determined to have paired with females if they copulated with them. The number of different females with which the male copulated therefore was always less than or equal to the number of different females with which the male paired.
3. The Consortship Persistence Level (CPL) of the males, which is defined as the number of consort days with females obtained by a given male divided by the number of days that male was in the testing aviary during the breeding season (EASTZER et al. 1985). Thus, a male that consistently courted females each day he was in the testing aviary would have a CPL of 100% (or greater if he courted more than one female on some days), while a male that courted females on only half the day he was in the multiple choice aviary would have a CPL of 50%.
4. If males could not be ranked according to pairings, copulations, or CPL (if they had scores of zero for all these measures or had tied for all these measures), we scored them in terms of the average numbers of songs they directed to females per 20-min of a morning's focal observations. The use of these four criteria together permitted the ranking of each of the males with no ties.

Data analyses

We predicted that if flight whistles played an important role in the overall courtship success of males, those that were more successful at obtaining pairings and matings and at courting females would produce flight whistles at rates different from males that were relatively unsuccessful at courting, mating, and pairing with females. Spearman rank order correlation coefficients (SIEGEL & CASTELLAN 1988) were obtained by comparing the courtship success rankings of males with their rankings for average numbers of flight whistles produced per 20-min focal observation. Each statistical test performed was two-tailed.

Results and Discussion

Experiment 1

Both populations of females responded reliably more often to songs of males from their local areas. The South Dakota females responded to a mean of 63% (range 33–98) of the South Dakota males' songs compared with 38% (range 15–98) of the Indiana males' songs (Wilcoxon–Mann–Whitney signed ranks test, $T = 1$, $p < 0.01$). One South Dakota female responded to almost every song playback, regardless of population (98%) and one South Dakota female responded essentially equally (48% to South Dakota vs. 50% to Indiana). The remaining nine responded more to South Dakota than to Indiana songs,

with an average 30% difference in favor of South Dakota males. We inspected the data for differences between the females that had been housed in their first year with juvenile South Dakota males compared with the six females living in aviaries: the mean responsiveness to South Dakota song was 64% for both groups (ranges 33–88 and 48–98, respectively).

The Indiana females responded to 59% (range, 25–82) of the Indiana songs as opposed to 47% of the South Dakota songs (range 22–63), a significant difference (Wilcoxon–Mann–Whitney signed ranks test, $T = 3$, $p < 0.02$). Two females never responded to songs and thus we based the results on responses by the other nine females. One female responded essentially equally to the two playback sets (50% vs. 52%) and a second responded more to South Dakota song (37% vs. 25%). For the remaining seven, the average difference in responsiveness was 18% in favor of Indiana males.

We looked within groups of females at the level of concordance in song preferences, using Kendall's coefficient of concordance. Kendall's coefficient measures the level of agreement across females in their preferences for the vocalizations of males. For both groups of females, responses to local songs yielded significant levels of concordance (South Dakota females to South Dakota song $W = 0.48$, $p < 0.01$; Indiana females to Indiana song $W = 0.32$, $p < 0.01$). We found no significant levels of concordance to nonlocal songs or in overall responsiveness to local songs (63% vs. 59% for South Dakota and Indiana, respectively).

South Dakota and Indiana females showed reliably higher levels of copulatory responsiveness to local, rather than nonlocal, songs. Thus, both populations' pattern of selectivity resembled the other midwestern population we studied (Oklahoma), and differed from eastern populations where no discrimination of local vs. distant *M. a. ater* song was found (KING & WEST 1990). Moreover, the females displayed concordant responses to local songs, but not to distant songs, indicating a shared perception of specific features of local as opposed to nonlocal variants. We also found high concordance in Oklahoma but not in first-year females, as was found here for the Indiana females. Absolute responsiveness did not differ by population.

Experiment 2

Responsiveness to whistles was very low in both groups, far lower than to songs (Fig. 3). No female in either group responded more to flight whistles than to songs (sign test for both populations of females: $p < 0.001$). The Indiana females responded, on average, to 10% of the flight whistles in Phase I (range 0–20) and to 5% (range 0–26) in Phase III. In the flight whistle playback tests, there were no significant differences in responsiveness to local, distant or heterospecific sounds ($r^2 = 5.8$, ns for Phase I; $r^2 = 0.4$, ns for Phase III). The Indiana females responded more frequently in Phase II, responding to an average of 53% (range 0–92) of all songs, and responded more to Indiana than to South Dakota variants (Wilcoxon–Mann–Whitney signed ranks test, $T = 3.5$, $p < 0.06$). Two of the Indiana females responded equally to the songs of South Dakota and Indiana males, and a third female never responded. Of the seven remaining females, five responded more to the songs of Indiana males than to those of South Dakota males.

The South Dakota females responded to an average of 7% (range 0–60) of the flight

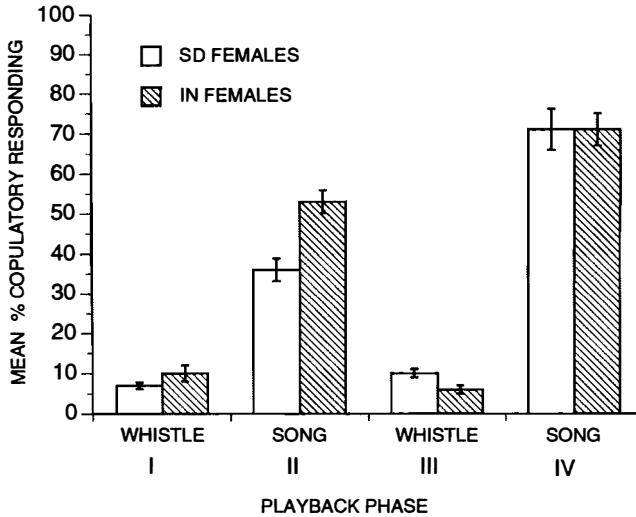


Fig. 4: Mean percentage of copulatory responses of Indiana (IN) and South Dakota (SD) females to flight whistles and songs during Phases I–IV. See text for differences in responsiveness within populations

whistles in Phase I and to 10% (range 0–41) in Phase III. The females showed no geographic preferences for any whistle variants, responding essentially equally to Indiana, South Dakota, and heterospecific/atypical whistles ($r^2 = 0.2$ for Phase III). The South Dakota females responded more often in Phase II, averaging 36% (range, 0–92), and responded reliably more often to the South Dakota prototypes (Wilcoxon–Mann–Whitney signed ranks test, $T = 0$, $p < 0.01$). One of the South Dakota females responded equally to the songs of South Dakota and Indiana males, and a second female never responded. All eight of the remaining females responded more to the songs of South Dakota males than to those of Indiana males. Responsiveness to songs in Phase IV for both groups averaged 71% (range for Indiana, 50–100; range for South Dakota, 42–100%).

The contrast in responsiveness to whistles and songs was also reflected in the number of females responding. Far fewer responded to whistles. In Phase I, five Indiana females (50%) and eight South Dakota females (80%) never responded to any whistle, whereas in Phase II, only one Indiana female (10%) and two South Dakota females (20%) did not respond to songs (Fisher exact-test for Indiana females, $p < 0.07$; Fisher exact-test for South Dakota females, $p < 0.05$). In Phase III, five Indiana females (50%) and six South Dakota females (60%) never responded, whereas in Phase IV, all females responded on at least 1 d to songs (Fisher exact-test for Indiana females, $p < 0.05$; Fisher exact-test for South Dakota females, $p < 0.01$).

To summarize, we found substantial levels of copulatory response to songs of local males in two midwestern populations of cowbirds, but we found negligible responding to flight whistles. In fact, the frequency of copulatory responses to flight whistles was as low as the frequency of responses to the controls (heterospecific vocalizations). We found no

local vs. distant whistle discrimination. These data are consistent with results from previous tests of local and distant flight whistles and songs in populations from the eastern and southern range (WEST & KING 1989). Thus, South Dakota and Indiana females, if provided only with flight whistles as breeding season acoustic stimuli, show no populational preferences for those vocalizations.

In addition to finding evidence of females' responsiveness to flight whistles, O'LOGHLEN & ROTHSTEIN (1993, 1995) have considerable evidence to indicate that young males must learn flight whistles and that such learning may not be completed until after a male's first breeding season. Some evidence also exists suggesting that young females may not hear or learn local flight whistles until after their first breeding season (BURNELL & ROTHSTEIN 1994). Such learning by females might explain why O'LOGHLEN & ROTHSTEIN (1995) found strong discrimination of local vs. foreign whistles in one California population, but not in the other.

Could the low responsiveness to flight whistles by the two midwestern populations of females reflect lack of opportunities to learn local variants? The possibility seems unlikely. First, all females tested had heard both South Dakota and Indiana songs and whistles in several contexts over considerable lengths of time; they had not been deprived of opportunities to hear the relevant sounds. Second, if preferences for flight whistles are learned when females are on prospective breeding grounds, one might have expected both groups to respond more to Indiana whistles, as they would have heard more of these from wild males and from the Indiana male housed with them for part of the winter. Third, the experimental design afforded females an opportunity to be exposed to all whistle variants first. If learning and priming were necessary for discrimination by females, we should have seen an increase in responsiveness in Phase III relative to Phase I: we did not.

To conclude, female copulatory responsiveness in playback chambers was not stimulated by whistles; indeed, whistles were equivalent to nonconspecific sounds, suggesting that this vocalization may have another function. Male cowbirds in our aviaries (and in the field) often use whistles in close proximity to songs just prior to copulating. Given the males can elicit copulatory postures with songs, why do they whistle? Moreover, whistles are long distance signals, capable of alerting other males to ongoing activity. Why risk alerting rivals? Experiment 3 begins to address these questions.

Experiment 3

The number of pairings obtained by males in 1994 ranged from none to two, as did the number of different females with which the males copulated. The mean CPL of these males was 66.1% ($n = 7$, range 42.9–100). The average CPL of males that did not pair with females was 11.9% ($n = 9$, range 0–36.4).

The number of pairings obtained by these same males in 1995 ranged from none to three, and the number of different females with which the males copulated ranged from none to two. The average CPL of the 2 males that paired with 3 females was 81.3% (range 62.5–100), while the average CPL of males pairing with one or two females was 69.9% ($n = 6$, range 50–100). The average CPL of males that did not pair was 6.1% ($n = 6$, range 0–20). The courtship success rankings for the males were not correlated across the two years (Spearman rank order correlation coefficient, $r_s = 0.38$, ns). The 1996 males obtained

from none to four pairings, and the number of different females copulated with ranged from none to three. The average CPL of males pairing with three or four females was 73.5% ($n = 4$, range 58.1–88.9). The average CPL for males pairing with one or two females was 30.8% ($n = 5$, range 10–46.2). The average CPL of males that did not pair was 5.7% ($n = 4$, range 0–8.3).

In all three breeding seasons, there were significant positive correlations between courtship success and flight whistle rate for South Dakota males. Thus, males with higher courtship success were those that produced more flight whistles during morning courtship. For the first-year males tested in 1994, the r_s was $+0.671$ ($n = 16$, $p < 0.01$). For the same males tested in their second year in 1995, the r_s was $+0.60$ ($n = 14$, $p < 0.05$). For the first-year males tested in 1996, the r_s was $+0.830$ ($n = 13$, $p < 0.01$).

While it is not possible from this experiment to determine causation, these results indicate that the rates at which males produce flight whistles are predictive (to us as observers and perhaps to female and male cowbirds in the male's immediate social environment) of their courtship competencies. Flight whistles in South Dakota males may indicate the overall quality of males to potential female mates. In addition, or conversely, flight whistles may advertise to other males the dominance status of the signaler (ROTHSTEIN & FLEISCHER 1987). Alternatively, males that are of high quality may also have a higher level of general arousal during the breeding season, and may simply produce more flight whistles as a byproduct of their arousal. Finally, we found strong positive correlations in two of the years between courtship success and singing rate from South Dakota males (1994 $r_s = +0.741$, $n = 16$, $p < 0.001$; 1995 $r_s = +0.758$, $n = 14$, $p < 0.005$; 1996 $r_s = +0.549$, $n = 13$, $0.05 < p < 0.1$). In other words, males that produced a greater average number of songs per morning, whether directed to females, to males, or undirected, had greater courtship success during the breeding season than males that produced a lower average number of songs. Thus, the strong positive correlations between courtship success and flight whistle rates in South Dakota males may be a by-product of overall vocal rate, and flight whistles themselves may play a more specialized role in a male's abilities to court and to copulate with a mate. Clearly, more work is needed to address the extent to which flight whistle rate may be indicative of or perhaps causal to a male's courtship status.

Flight whistles have multiple functions, including courtship. DUFTY & MCCRYSTAL (1992) speculated that the use of the two classes of vocalizations immediately prior to copulation may be a reflection of the male's state of heightened arousal. We also see such changes in arousal in males in our aviaries. Indeed, a critical acoustic cue for human observers that a copulation is about to occur is the rapid change in the tempo with which the male vocalizes: his excitement is present in his voice, regardless of the vocalizations emitted. Why would more dominant or more reproductively successful males use dual signaling during copulations more often than other males? The possible explanation is that the whistle, as a long-range signal, may communicate to males and females other than the mate the status of the male, which may serve to decrease the potential for other males to interrupt the copulation with aggressive behaviors. Aggression among male cowbirds can lead to severe injury. In contrast, the parts of the male's song most likely to elicit female copulatory postures are lower in frequency and amplitude and degrade rapidly in the atmosphere such that a song recorded at 3 m or 10 m is far less effective in playback tests than a song recorded at 0.3 m (KING et al. 1981). Higher-ranking males may be more

inclined to use both signals because they are less likely to provoke attacks by subordinate males and may benefit from advertising their presence and status. Thus, use of two different vocal signals may relate to the two components of sexual selection: mate choice and male–male interaction.

General Discussion

To summarize, the results of the first experiment tell us that captive, midwestern female cowbirds can discriminate local vs. distant males on the basis of song alone. The results of the second experiment reveal that male flight whistles do not stimulate copulatory responsiveness. The third experiment reveals, however, that use of the flight whistle is a frequent occurrence during the breeding season and during courtship and copulatory interactions, especially among more successful males. Taken as a whole, these data indicate that the two major vocalizations of male cowbirds from midwestern populations have different functions during the breeding season. Thus, these data indicate that generalizations about how female cowbirds respond to mating signals and how males use such signals must be made with caution.

Both midwestern groups responded significantly more to local vs. distant song, a characteristic they thus share with an earlier-studied *M. a. ater* population in Oklahoma, but not with the population of *M. a. ater* in North Carolina (KING & WEST 1990). Reproductive outcomes of crosses between Indiana and South Dakota cowbirds suggested that such local discrimination is advantageous. Although crosses between the two populations led to some viable offspring, laying rate and egg viabilities decreased relative to reproductive outcomes of Indiana–Indiana or South Dakota–South Dakota matings (T. M. FREEBERG unpublished data).

Both groups also responded frequently to song, as we had seen in North Carolina and Oklahoma populations. The responsiveness of other populations of *M. a. artemisiae* females to song has not been established and is needed to calibrate their responsiveness to whistles. In a previous study, we found lower responsiveness to song in first-year South Dakota females than in the present test, suggesting the need for researchers to focus more on developmental assessments of perceptual characteristics (FREEBERG et al. 1995). Attention to responsiveness is also called for because our previous studies of the southern subspecies, *M. a. obscurus*, whose range extends westward into California, suggest that some populations of these females are far less responsive to song or whistles. Attempts to hybridize North Carolina *M. a. ater* and Texas *M. a. obscurus* were also far less successful than the South Dakota–Indiana hybridization studies mentioned above: there were decreases in success at all stages from egg viability onwards, with only one female (out of 18 nestlings) surviving to 1 yr (KING & WEST 1990). Thus, perceptual differences in females' assessment of males seem to correlate, broadly speaking, with larger reproductive variables. For example, in what may be a natural 'hybrid' area (the border zone between *M. a. ater* and *M. a. obscurus* in Texas), females showed no local selectivity for song or whistles, although they were very responsive to song (A. P. KING unpublished data; WEST & KING 1989). Perhaps, under these circumstances, other vocal or visual cues are weighted more heavily by females.

The results of Experiment 2 indicated that in the midwest, males' whistles did not stimulate copulatory responsiveness and thus could not provide a basis for populational

discrimination. The level of responding was equivalent to heterospecific sounds. However, the aviary observations of experiment 3 revealed the limits of playback tests to reveal the actual dynamics of courtship, because flight whistles occurred frequently in close temporal relationship to the act of copulation. Moreover, more successful males used flight whistles more often. Use of multiple contexts has revealed other differences in vocal use and in courtship interactions in cowbirds (FREEBERG et al. 1995; WEST et al. 1997).

The data from the three experiments described here suggest that songs by males are the primary vocal signal that elicit copulatory postures in South Dakota and Indiana females, while flight whistles are the primary vocal signal produced by males following a copulatory posture of a female and prior to or during mounting. Further playback tests to both females and males would help to elucidate the function of flight whistles during courtship. For example, pairing different flight whistles with the same songs in playbacks to females may indicate that some flight whistles cause longer duration copulation solicitation displays in females than others. This would suggest a role for flight whistles in maintaining copulatory solicitations in females, increasing the likelihood of the male obtaining a mating with the female. Playbacks of flight whistles of dominant or successful males to males in aviaries (or in the wild) may elicit different behavioral responses during the breeding season than flight whistles of subordinate or unsuccessful males (see also DUFTY & PUGH 1994). Finally, to address the question of geographic variation in the function of the two vocal signals, playbacks of songs alone and in the same playback sets as flight whistles must be carried out to females of the California populations studied by O'LOGHLEN & ROTHSTEIN (1995). To date, ROTHSTEIN and colleagues have exposed females only to playbacks of flight whistles and so the functional properties of songs are not known in these populations. We also need to expand our studies to focus more on copulatory behavior in wild birds in the midwestern populations described here, such as the work of ROTHSTEIN et al. (1988) in California. When this additional information has been obtained we will know whether the differences found between these west coast females and other populations of females result from inherent populational differences.

How might these data contribute to understanding the apparent shift in salience of songs and whistles in the far west? Cowbirds from California populations appear to spend less time with their mates owing to the habitat separation of areas in which to feed and areas in which females can find nests (ROTHSTEIN et al. 1980, 1984). Other studies have also suggested habitat constraints on patterns of monogamy or promiscuity in the midwest (ELLIOT 1980). Thus, habitat differences are potentially associated with changes in parasitism patterns, as well as exclusivity of mating within social pairs. Dual signaling may have different consequences when males are faced with many nearby rivals in areas of dense populations, as in the midwest (the sex ratio is skewed 1.5:1 toward males). In populations with habitats combining extensive travel in the diurnal pattern and social monogamy, there may be selection for increased use of long-range signals to facilitate individual recognition of males by other males, females, or both, at greater distances (YOKEL 1986).

When vocalizations vary structurally, as in dialects, they are still presumed to possess the same species-specific function, albeit by means of altered acoustic morphology. Few studies have examined cases where the same signal appears to have a different function within the same species, as might be the case with the two vocal signals studied here in cowbirds, songs and flight whistles. Although the data from the present study are only an

initial step in the study of this question, they suggest the possibility that biological shifts in vocal function accompanied the cowbird's geographically diverse radiation throughout North America (ROTHSTEIN et al. 1988). To understand these shifts also requires attention to geographic variation in female responsiveness and discrimination, as signal use and signal reception are clearly coupled (KING & WEST 1983a).

Studies in a wide variety of taxa have now documented intraspecific variation related to diverse and variable ecological demands (LOTT 1991). The last decade has produced a wealth of evidence documenting intraspecific differences in the use, ontogeny, and structure of avian songs in general (KROODSMA 1988). Such diversity has led to new questions about the definitions or functions of avian signals (KROODSMA & BYERS 1991; SPECTOR 1994). The present data support the need for such re-examination of songs and flight whistles in cowbirds.

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