

# Song Repertoire Development in Male Cowbirds (*Molothrus ater*): Its Relation to Female Assessment of Song Potency

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Two studies were conducted to investigate the relation between the male cowbird's (*Molothrus ater ater*) development of a song repertoire and the female cowbird's assessment of song potency. Male development was assayed by vocal copying and female assessment by copulatory responsiveness to song playback. The results demonstrate that males do not copy most often the particular songs that females respond to most often. Whereas rank orderings of potency were highly correlated across two independent samples of playback females, male and female rank orderings were not significantly correlated. The data highlight the potential significance of social interactions between and across the sexes for repertoire development.

Bird song is a social enterprise involving a singer and a recipient and, as such, necessitates the study of two organisms. Although the proposition that song is a social behavior is commonly accepted, most empirical work has been focused on how the behavior of the singer affects that of a listener; many fewer studies have addressed how the behavior of the listener affects that of the singer; and in even fewer have the mechanisms linking song production and song reception been investigated. New neurophysiological and behavioral evidence suggest the need for such a proximate analysis. At a neurophysiological level, the adult female canary's (*Serinus canaria*) brain appears to undergo neurogenesis, as does the male's, even though only the male sings (Nottebohm, 1984). Presumably, such neuronal development reflects the critical need for the female to evaluate and respond to new songs produced by males. At a behavioral level, the nonsinging female cowbird can socially influence a male to modify his song repertoire to suit her native preference (King & West, 1983b; West & King, 1985). In this species, the female appears to be a silent but influential partner in the epigenesis of song.

Here we explored other potential linkages in song development in cowbirds. Specifically, we investigated the male cowbird's development of his song repertoire in relation to the female's copulatory responsiveness to song. We have defined *song potency* as a song's ability to elicit copulatory postures from captive female cowbirds deprived of male companions (King & West, 1977, 1983a; West, King, Eastzer, & Staddon, 1979). A song of high potency consistently elicits

copulatory postures from females (on more than 50% of playback trials); a song of low potency infrequently does so (on less than 25% of playback trials).

Using song potency as a measure, we have documented that female cowbirds can discriminate their species and subspecies by song alone (King & West, 1977; King, West, & Eastzer, 1980; West, King, & Harrocks, 1983). In addition, we have demonstrated that females do not respond equally to the songs of all males even when the "choice" is among familiar males from the same locality. Female cowbirds can discriminate differences in songs that indicate the "right" class of male, that is, the male's subspecific or geographic identity, but, more important, they can discriminate differences that reveal the most dominant or reproductively successful male (King & West, 1983c; West et al., 1983). That the female's response to playback songs is biologically significant is indicated by data showing that playback potency predicts mate choice in captivity (Eastzer, King, & West, 1985; West, King, & Eastzer, 1981; West et al., 1983).

The sensitivity of the female cowbird to song content would perhaps be expected in a parasitic species in which information about a male's reproductive quality is more limited because nest building, territorial maintenance, defense, and parental activity do not occur. A female appears to require little to no postnatal experience with song in order to respond selectively, a capacity that may also reflect the ontogenetic implications of brood parasitism (King & West, 1983a; but see King, West, & Eastzer, in press, for populational differences in the role of postnatal experience).

Here we asked about song potency from the male's perspective. Does a male develop his repertoire on the basis of song potency, an attribute operationally defined in terms of *female* responsiveness to song? As a first step, we asked whether males, without opportunities for interaction with females, would select songs for imitation that we knew females found to be attractive. Positively correlated selectivity between males and females might seem likely given the presumed evolutionary linkages between signal perception and signal production necessary for mate identification (Doherty & Gerhardt, 1983; Hoy, 1974; Marler, 1976).

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We chose as the independent variable songs already identified as potent or not potent by previous playback to females and as the dependent variable song copying by juvenile males. We knew naive males could produce a potent, albeit structurally atypical, song without exposure to conspecifics, but did not know whether they could recognize and accurately imitate potent songs when tutored with a selection of songs (King & West, 1977). Juvenile males do copy songs from adults when tutored or housed with adults in aviaries; high levels of song sharing are also found in the field (Dufty, 1985; Eastzer, 1986). But, in these contexts, stimulation from males and females may have facilitated vocal imitation. Here we asked whether males would copy high-potency songs when no stimulation was available by interactions or observations of conspecifics.

We studied young males that had had some naturally occurring early experience with adult song. Tutoring began at the time when adults normally begin to sing again after their molt and when juveniles first begin to vocalize. The males' singing was recorded weekly not only to learn what songs males ultimately retained in their final repertoire of mature song but also to begin to identify the developmental processes guiding repertoire development. In particular, we looked for evidence of developmental overproduction and selective attrition, processes identified by Marler and Peters (1982a, 1982b) in their studies of the structural ontogeny of sparrow song.

Experiment 1

Male cowbirds typically have repertoires of three to seven song types, a song type being defined as a pattern sung repeatedly in a stereotypic fashion during the breeding season. To force males to choose among song types, we tutored them with 12 songs: 6 were high-potency (HP) songs and 6 were low-potency (LP) ones. In this experiment we correlated male copying to previously obtained estimates of song potency.

Method

*Subjects.* Five juvenile *Molothrus ater ater* males served as subjects. The males, determined to be 30–50 days old by their plumage, were captured in Orange County, North Carolina, between July 10 and August 31, 1984 and immediately placed in sound-attenuating chambers with canary (*Serinus canaria*) companions (3 cowbirds had female canary companions, and 2 had male companions). The males were maintained on a normal photoperiod for 35° latitude until late January when the rate of increase in day length was accelerated to bring them into breeding condition 4–5 weeks early. Details on housing and daily care can be found in King and West (1983a, 1983b, 1983c).

*Selection of songs for tutoring.* Twelve breeding season songs from 12 males were used (Table 1). All of the songs were originally recorded with an Otari MX5050 at 15 inches per second (ips), with Sennheiser RF condenser microphones located less than 0.3 m on axis from the singer. The unweighted signal-to-noise ratio for all of the tutor songs was at least 55 dB (SPL) measured peak to peak. The potency of the tutor songs had been assessed in two previous playback experiments which had contained 34 and 31 songs, respectively (King et al., 1980; West & King, 1985). Song potency was calculated as the mean percentage of copulatory responses as a function of the number of playback trials for each female averaged over the group. Six songs, three each of high and low potency, were chosen from each experiment.

The songs had been played back to the two groups of 10 adult *M. a. ater* females which heard the songs on 8–10 separate playback trials over a period of 6 weeks. Testing conditions were identical with those reported in Method of Experiment 2 of the present article. All females had been housed in the laboratory from early fall until the breeding season with other females in sound-attenuating chambers.

In addition to selecting songs on the basis of potency, we made an effort to select songs typifying the range of structural variation present in cowbird song. For both HP and LP song sets, three songs were from captive adult or yearling males singing common cowbird song types. The remaining three songs in each group were from males hand-reared in the laboratory which were producing song types that would be rare in nature (songs 4, 5, and 6 of the HP and LP category). Songs 4, 5, and 6 HP were from males housed with females; songs 4, 5, and 6 LP, from males housed with females of the *M. a. obscurus*

Table 1  
Comparison of Song Potency by Males and Females

Group	Song type											
	High potency						Low potency					
	1	2	3	4	5	6	1	2	3	4	5	6
Mean percent												
Females <sup>a</sup>												
Original	68	59	85	84	92	61	15	6	19	10	12	17
Experiment 2	81	55	93	67	57	71	11	47	50	21	30	44
Males <sup>b</sup>												
Experiment 1	17	13	4	35	0	0	1	5	10	0	2	0
Ranks												
Females												
Original	4	6	2	3	1	5	9	12	7	11	10	8
Experiment 2	2	6	1	4	5	3	12	8	7	11	10	9
Males												
Experiment 1	2	3	6	1	10.5	10.5	8	5	4	10.5	7	10.5

<sup>a</sup> Mean percentage of copulatory responses calculated as the percentage of copulatory responses as a function of number of trials. <sup>b</sup> Mean frequency of singing.

subspecies (but the males were singing *M. a. ater* song types) or juvenile male *M. a. ater*. All of the tutor songs were recorded from males studied in previous years, and thus none of the tutored males had had experience with the tutor songs.

**Tutoring procedure.** The males were tutored every day for 2 hr beginning August 31 and ending November 2 to coincide with the time when young cowbirds join flocks of juvenile and adult males. The results of previous research had also suggested this time period to be one in which young males would learn songs or modify development in relation to acoustic stimulation from adults (King et al., 1980). Each day at about the same time in the morning, the males were exposed to 240 repetitions of the HP and LP songs which had been randomized into 20 different orders. A song occurred every 30 s. The tutoring levels were adjusted to 83-dB impulse at 0.5 m on axis from the speaker as measured with a Brüel and Kjaer Model 2105 sound level meter.

**Recording procedure.** The males were recorded, if singing, approximately weekly in 24 sessions beginning September 22 (Session 1 for chamber 9 in Figure 1 and ending March 12, Session 24). At this time, the males had been experiencing more than 14 hr of light (breeding season level) for 2 weeks. Males were recorded to a criterion of 70–120 songs per session or from 6 to 12 hr if a male sang very little or not at all. This criterion was based on previous research showing that samples of this size capture over 95% of a male's song types (King & West, 1983b). A total of 8,629 songs (range, 1,489–2,193) were recorded for the 5 males. For 15% of the sessions in which the males sang, the minimum criterion of 70 songs could not be met. The range of singing for these sessions was 1–69. Two males did not sing consistently throughout the course of the experiment: The male in chamber 5 began singing 7 weeks later than the others, and the male in chamber 9 did not sing during the month of January (Figure 1).

**Scoring of songs.** In order to establish reference templates against which the songs could be compared, the original tutor songs were displayed on the face of an oscilloscope and measured with a zero-crossings analyzer which provides a display of frequency by time (West et al., 1979). Clear acetate was then placed over the oscilloscope, and a hand tracing was made of each of the songs. The songs of the tutored males were then displayed with the same zero-crossings display, and the acetate tracings were placed over each to determine similarity.

The majority of song classifications were made by the hand tracings. In some cases, the hand tracings were supplemented by a second set of acetate drawings. These displays were generated by scanning the tutor songs with a Brüel and Kjaer Model 2033 spectrum analyzer controlled by a Hewlett-Packard 86 computer and by plotting the scan data with a Hewlett-Packard 7470A precision plotter on clear acetate. These computer-drawn tracings provided 25-Hz frequency resolution as well as amplitude level coded by color. Any ambiguity present in the hand-drawn plots was then resolved by using the precise machine-drawn displays.

Songs were judged to be copies of a given tutor song if 75% of the song structure corresponded to the acetate template. If this test was not met, the song was divided into two phrases consisting of introductory notes and the whistle. Then the template was used to determine whether 75% of either phrase matched the reference template. When a 75% correspondence was found, the song was classed as a partial match. When a 75% match occurred for both phrases but the phrases were from different tutor songs, the song was classed as a mixed song. If no partial match could be found, the song was coded as unclassified.

In all, 8,629 songs were scored by one observer. A second observer repeated scoring on 15 sessions for a total of 1,564 songs; these sessions were selected to sample singing throughout the entire recording period. The agreement was 96.4% (range, 85%–100%) between

observers. The percentage of agreement for HP songs was 98%. Most disagreements occurred in classifying songs as unclassified, mixed, or copies of LP songs.

**Apparatus.** The tutor tapes were played back with an Otari MX5050 recorder, a Urei 537 1/3 octave equalizer, and a Crown D75 power amplifier through JBL 2105 speakers. The songs of the tutored males were recorded with a Technics 1500 recorder operating at 3 3/4 ips for 3-hr intervals. These recordings were then scanned at either 7 1/2 or 15 ips to locate vocalizations and then dubbed to an Otari MX5050 for analysis.

## Results and Discussion

High-potency song predominated in the repertoires of all 5 males, although all sang low-potency song as well (Figure 1). At the final recording session at the onset of the breeding season, the males sang an average of 81% HP and 15% LP song. The predominance of HP songs was also present throughout the experiment, with the 5 males averaging 50% (range, 37–61) high-potency and 23% (11–30) low-potency song across all sessions. High-potency songs were also sung more often in 91% (69–100) of the individual sessions. Wilcoxon matched-pairs signed-ranks tests yielded significant scores for all three comparisons ( $T = 0$ ,  $p < .03$ ).

**Song types.** All 5 males sang LP types during the winter and early spring, and although the males sang HP songs more frequently, 4 retained at least one LP song type in their final repertoire (Figure 1). The males' final repertoire size averaged 5.2 songs (range, 3–8): They copied an average of 3.6 (range, 2–5) HP songs and 1.8 (range, 1–4) LP songs. Preferences existed in the HP categories for certain song types, in particular, song 4 HP and 1 HP (Table 1). A Friedman analysis of variance on the HP choices in the final session yielded a significant effect for differences among the HP song types,  $\chi^2(5) = 14$ ,  $p < .02$ , but not among the LP types,  $\chi^2 = 6.7$ ,  $p < .30$ . Mixed songs composed of phrases from the tutor songs were infrequent except for the male in chamber 7 which consistently sang a song composed of Phrase 1 from song 4 HP and Phrase 2 from song 1 HP. One male had sung some canary-like notes, but such singing represented only a small percentage of his singing and was dropped before the end of the recording period.

**Comparison of male and female rank ordering of song types.** The 12 songs were ranked by frequency of singing with 1 representing the song with the highest mean percentage of singing (Table 1). Mixed and partial songs, a small percentage of all songs, were excluded because the original playback females had not heard them. These ranks were then correlated with the rankings of the same songs made on the basis of the original playback females' mean percentage of copulatory responses, with the 1 rank representing the song responded to most often (Table 1). The male and female responses were then correlated and yielded a Spearman correlation coefficient of .22 (*ns*).

**Song development: Changes across sessions.** Developmental changes in song production were examined for the final 10 recording sessions. The males' repertoire size decreased over the 10 sessions. By March, the males sang 1.8 (range, 0–4) fewer HP and 2.4 (1–3) fewer LP song types than

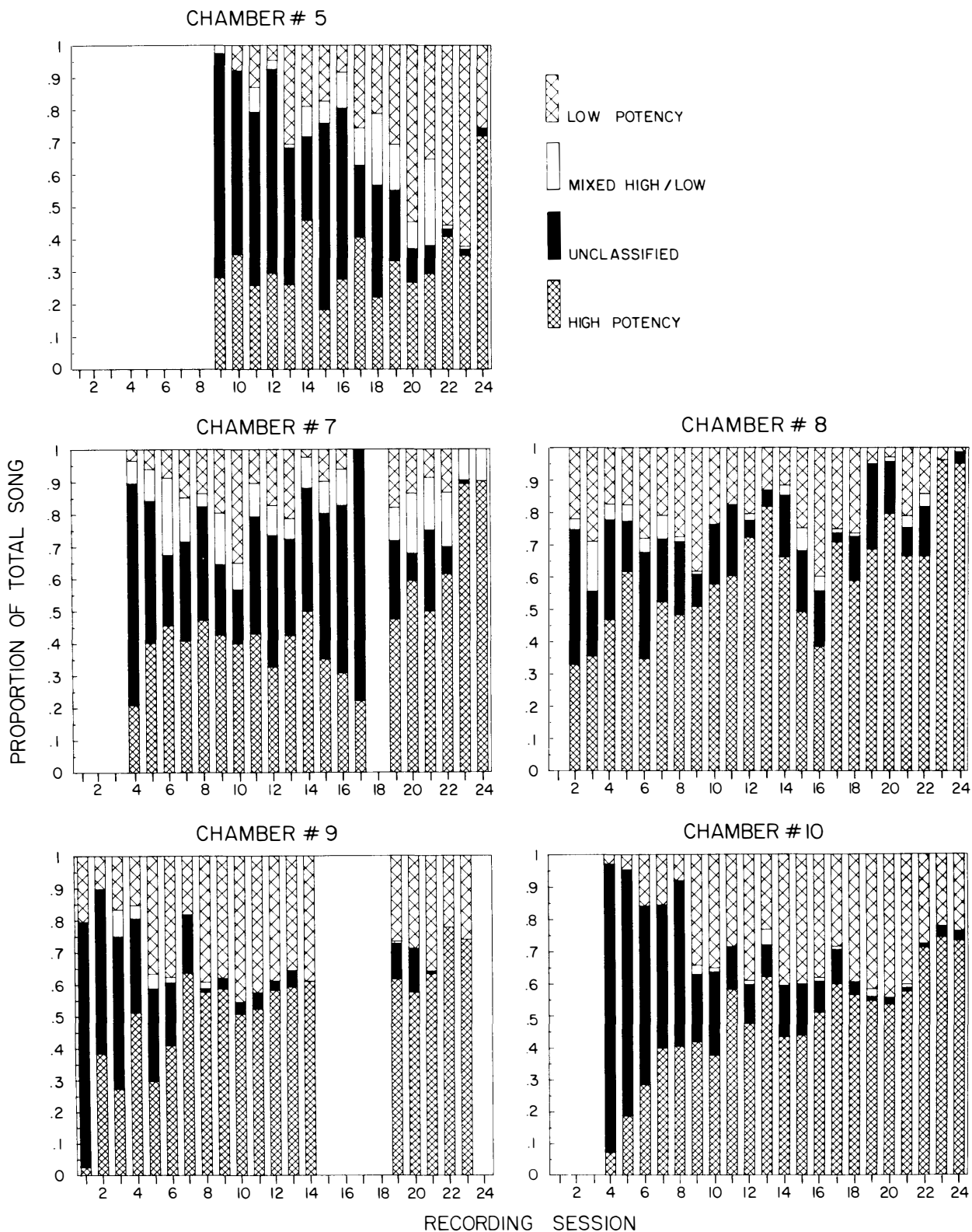


Figure 1. Proportion of all songs in each of four categories, displayed by recording session. (Sessions for which there are no bars are ones in which the males did not sing. Mixed songs that were composed of all high-potency (HP) phrases or all low-potency (LP) phrases were included in the HP and LP categories.)

they had for the 10 sessions earlier. For the songs retained, HP songs increased in frequency by 21% (6% to 56%), and LP songs decreased by 5% (-7% to 35%).

Inspection of Figure 1 reveals both similarities and differences in how the males achieved their final repertoires. The most obvious similarity is the increase in HP song production in the final three sessions relative to the previous three sessions. In addition, the males in chambers 8, 9, and 10 showed quite similar patterns of repertoire development characterized by the gradual increase in HP song and conversion of unclassified song into HP song. For these 3 males and the male in chamber 7, LP song remained a small but more constant part of their repertoires.

*Individual differences.* The males at the same time displayed considerable variability. The most unusual pattern was shown by the male in chamber 5 which began singing 2 months after the other males. After starting to sing, the total amount of his HP song varied in a narrow range, with no clear pattern of increase. By contrast, his LP song increased steadily only to fall off markedly in the final session. The males in chambers 5 and 7 also differed from the other 3 males because they sang more unclassified song and continued to do so for longer periods of time. Male 7, for example, did not begin to reduce the amount of unclassified song until late in January, peaking at 77% in the 17th recording session, a point in time when the next highest amount of unclassified song production was only 22% by Male 5. Male 7 also differed from the others in that his peak of singing LP song occurred in the 13th recording session, with a gradual decline thereafter in contrast to all the other males which maintained higher levels of LP singing until much later in the winter.

The results thus demonstrate a general concordance between male and female cowbirds at a molar level of song assessment. The males most often sang the HP set of tutor songs, which were the songs that females had originally responded to most often with copulatory postures. But in the set of HP songs, the males and females differed substantially in which songs were responded to most often, a situation producing no significant correlation between the responses of the tutored males and the original playback females. Likewise, although males and females, respectively, sang and responded less often to the LP songs, the frequency of male and female responses was statistically unrelated in the LP category.

Because of the different nature of the behaviors assayed in the male and female to obtain estimates of potency, the absolute numerical score assigned to each song is difficult to interpret. A male's being able to remember and to sing a song well enough to meet the coding criterion of a 75% match cannot be directly compared with the female's reflexive copulatory response to successive presentations of recorded songs. For this reason, we focused on the relative rank orderings of the songs. But here, too, the method of assessment of potency differed in a major way. The tutored males heard the 12 tutor songs for several months, hearing no other songs except those they may have produced themselves. In contrast, the original playback females from which the potency values were obtained had heard the tutor songs in different experiments in which songs other than those used here were played back, songs not available to the tutored males. Hence, the perceptual

series of songs differed for the males and for the females. In order to interpret this difference, a second experiment was carried out in which a new sample of females was exposed only to the 12 tutor songs. The use of new females also provided the opportunity to retest the potency of the tutor songs from the perspective of the female.

## Experiment 2

We tested the potency of the tutor songs with females captured at the same time as the tutored males of Experiment 1. We asked two questions. Would the estimates of potency agree with those obtained from the original females, and would the estimates correlate with the frequency with which the males copied the songs? We focused primarily on rank orderings of the songs because we assumed the absolute numerical level of song responsiveness would differ between the two samples of females. The females here heard only 12 songs, whereas the original groups of females had heard playback songs as part of two separate experiments in which more than 30 different songs were played back.

### Method

*Subjects.* Thirteen *M. a. ater* females served as subjects, 6 juveniles and 7 adults captured in Orange County, North Carolina. They were placed in the sound-attenuating chambers in mid-August and were housed in pairs or triads with other females during the winter. For playback tests, the females were housed alone or in pairs because no effects of social housing on the female's copulatory response have ever been found in extensive playback testing (see King & West, 1983a, 1983b; West & King, 1985). The birds were maintained on the normal photoperiod for 35° latitude.

*Procedure.* The playback songs of Experiment 1 were presented to the females with the same equipment employed in Experiment 1. Playback levels were measured with a Brüel and Kjaer Model 2209 sound pressure meter: At 0.6 m on axis, the SPL was  $83 \pm 1.5$  dB.

The females were tested in their sound-attenuating chambers. For 14 days, one song was presented per trial for seven trials a day separated by approximately 90 min. The order of the test songs varied each day but was the same for all females.

A positive response was scored if a female displayed a copulatory posture within 1 s of a song's onset. A copulatory posture was defined as follows: The female lowered and spread her wings, her neck and body were arched, and the feathers around the cloacal region separated. The onset of the display occurs approximately 400 ms after the first notes of a playback song and often lasts for 5–10 s after the song terminates.

### Results and Discussion

These females, which heard only the 12 tutor songs, responded to them much as had the original playback females: The classification of high or low potency would have been the same if the basis had been the Experiment 2 females' responses (Table 1). The major difference between the groups of females was that the females in Experiment 2 responded, as predicted, at a higher relative level to the LP songs, with three songs yielding potencies between 40% and 50%. A Spearman correlation of the rank ordering confirmed the high

level of agreement between the rankings of the two samples of females, producing a coefficient of .82 ( $p < .005$ ).

The mean percentage of copulatory responses to the HP songs was 71% (range, 32–92) in contrast to 34% (range, 0–74) to the LP songs. All 13 females responded more to HP song than to LP song, which yielded a Wilcoxon value of  $T = 0$  ( $p < .005$ ). The females also demonstrated consistency within the group with respect to their relative rankings of the 12 songs. A Friedman analysis of variance confirmed the effect,  $\chi^2(11) = 70.2$ ,  $p < .001$ .

In this experiment, the females' responses, however, were not correlated with those of the tutored males: The Spearman coefficient was .38 (*ns*). Spearman correlation coefficients were also computed between each male and the females for the HP song series to ascertain whether *any* male's copying preferences correlated with the females in the preferred singing category. The coefficients for the males in chambers 5, 7, 8, 9, and 10, respectively, were  $-.48$ ,  $.09$ ,  $.05$ ,  $-.12$ , and  $.60$ , which yielded an average correlation of  $.14$ .

Thus, the results of Experiment 2 demonstrate that the lack of concordance between the male and female rank orderings of the songs in Experiment 1 was probably not due to the different playback sets used in Experiment 1 to assay male and female responses to song potency. Whether different samples of females heard a total of 12 or 30 or more songs, they agreed with one another as to the relative potency of the songs. And, as in Experiment 1, although the females and males both responded more to the HP songs, the females in Experiment 2 did not show a significantly higher level of agreement with the males than had the females in Experiment 1 with respect to the relative potency of the individual songs within or across the HP and LP sets of songs.

### General Discussion

A female cowbird can stimulate a male cowbird to modify the acoustic nature of his song (King & West, 1983b). Moreover, the modifications made by the male are reflected in the song's potency (West & King, 1985). The present study on male song development may supply one reason for the need for social feedback from females. Previously we demonstrated that a male can develop a potent song without exposure to conspecifics (King & West, 1977; West & King, 1985), and the present study shows that a male can also recognize and copy potent songs without stimulation from conspecifics. But, although males seem naturally to orient to potent songs at a general level, they do not seem to copy selectively the particular songs females regard as more or less attractive.

From early in development, the males copied songs from the set of high-potency songs much more often than those from the low-potency set, and thus they began the process of song development with potentially appropriate signals, distinguishing between very good or very bad songs on the basis of little, if any, experience with conspecifics. But 4 of the males retained low-potency song types in their final repertoires and sang most frequently song types ranked as relatively less potent by two independent samples of females. The present study thus demonstrates that a socially naive male cowbird

does not develop a repertoire of songs of uniformly high or low potency. In that empirical evidence exists linking potency to mate choice in this species (West et al., 1981; 1983), the finding suggests that a function of social stimulation from females may be to facilitate the male's copying of particularly potent songs. In that a male sings to attract individual females in order to mate, information about which songs are *most* suited to the efficient accomplishment of that end must be assumed to be critical.

But empirical evidence also exists suggesting that a male that sings a very potent song may also attract the attention of other males which may attack and injure him. Singing a potent song may attract females but appears to offend males (West & King, 1980). In nature, this potential "approach/withdrawal" dilemma may not actually be a problem because the bioacoustics of cowbird song are such that the structural elements most important to potency degrade rapidly in the atmosphere. Thus, if a male sings when close to females, which males typically do, a male may avoid attracting the aggressive attention of other males (King, West, Eastzer, & Staddon, 1981). But the possibility remains that a male may indeed recognize a potent tutor song and elect not to sing it. His song repertoire then may contain some songs to attract females and some with which to interact when in the presence of males. Male cowbirds sing a great deal to one another at all times of year, and the functions of such singing has yet to be determined. Thus, a "mixed" repertoire in terms of song potency could accommodate the inter- and intrasexual consequences of singing.

Two of the HP songs (5 and 6) that were rarely copied were chosen for tutoring because they were structurally atypical cowbird songs, albeit very potent ones according to females. Perhaps, as the tutored males were wild-caught and had had some limited exposure to more typical adult song, their early experience biased them against the more unusual song types. We know from past research that very brief exposure to adult song influences young *M. a. ater* males' development of geographic content (King et al., 1980).

The two samples of females, however, ranked these same songs as quite potent. Males may need the additional incentive to copy such songs that normally comes from social interactions. In that songs 5 and 6 HP were atypical, they might have been more difficult to sing. It could be that the males recognized their potency but were unable to produce them and thus deleted them early in development. In other studies, we found that *M. a. ater* adult males did not copy *M. a. obscurus* song when housed alone with *M. a. obscurus* males but did copy it when housed with *M. A. obscurus* males and females (West et al., 1983). Thus, social interaction may bias males' selection of song types and reinforce rehearsal of specific and perhaps more difficult song material.

The absence of the opportunity for species-typical social interactions may also explain the lack of any original song types by the 5 males. Although the rich acoustic stimulation provided by the tutoring may have inhibited original song development, the lack of social stimulation may also have decreased the males' tendency to improvise new songs. Previous data on males housed with nonconspecifics showed that these males sang little original song whereas males with fe-

males did so (King & West, 1983c). Developing a new song appears to be a more complex task for cowbirds: They sing well-articulated copied song at least 2 months before they sing original song (King & West, 1986).

In terms of general patterns of song development, the present data suggest an ontogenetic pattern of differentiation and attrition in song content that was most clearly indicated by the reduction in number of song types produced and the correlated increase in the frequency with which the final song types were sung. Marler and Peters (1982a, 1982b) reported a similar pattern for song syllable development in sparrow species tutored in the laboratory with species-typical and atypical syllables. Thus, the present data suggest that attrition and overproduction characterize song ontogeny not only at the level of elements within a song but also at the level of the song repertoire. It remains to be seen, however, how these processes are affected in either cowbirds or sparrows when males are studied in the presence of male and female companions. In sparrows, for example, opportunities for social interactions can affect basic components of song acquisition (Baptista & Petrinovich, 1984). And in red-winged blackbirds (*Agelaius phoeniceus*), the presence of female companions appears to inhibit the male's incorporation of heterospecific song material (Marler, Mundinger, Waser, & Lutjen, 1972).

The degree of correlation between the two sets of females on the relative potency of the songs was high despite the different playback protocols and their individual histories. Eastern *M. a. ater* females possess quite stable native preferences for song which appear resistant to postnatal modification even when the birds are deprived of exposure to male song or exposed only to song from the *M. a. obscurus* subspecies (King & West, 1983c). Thus, the agreement among females may have an unlearned basis. When females are housed with an individual male and then tested for their responsiveness to his song and those of unfamiliar males also housed with females, no effects of familiarity are apparent (West & King, 1980). Such data probably do not mean that the females cannot recognize the more familiar song of their companion. Rather, because of the quite similar preferences across females, the females independently influence the males to sing similar and quite effective songs, which produces a "ceiling effect" in measuring potency.

Differences did, however, exist within both samples of females in individual rankings. These differences also argue for the importance of social interaction between the sexes. If males must attempt to court more than one female in a breeding season or across seasons, they may need a repertoire containing several potent songs to be assured of having some songs that are most attractive to individual females. Possessing several potent songs, in addition to some ineffective ones, may then be biologically advantageous. In our studies of captive colonies, the most successful males have had several potent songs in their repertoire (West et al., 1981).

In summary, the present study adds to the view that the male cowbirds' development of his song repertoire is a social as well as an acoustic process, one in which interactions with male and female conspecifics play a major role. Tutoring males with the same set of tutor songs used here but housing them in the presence of females and/or in the presence of

males, experiments now underway, should begin to specify the nature of such processes. The basic procedure used here, correlating male and female responses to songs, is also one that could be used productively in other songbirds, particularly those in which female bioassay procedures have been successful (e.g., Baker, Spitzer-Nabors, & Bradley, 1981; Searcy & Marler, 1981). In swamp sparrows, for example, male and female responses to the temporal patterning of song differ, with females responding (with copulatory postures) only to the species-typical pattern but males responding (by approaching speakers) to songs with different patterns (Searcy, Balaban, et al., 1981; Searcy, Marler, & Peters, 1981). Thus, the findings reported here on differences between males and females in song assessment may also obtain for other species (see also Williams & Nottebohm, 1985).

In addition to studying new social contexts in relation to repertoire development in cowbirds, we are continuing to attempt to understand the acoustic basis of potency from both the male's and the female's perspective. We have studied potency at two levels of analysis. First, we have explored the macrogeographic basis of potency differences between the songs of two of the cowbird subspecies, and we have explored the microgeographic basis of potency among different populations of *M. a. ater* and *M. a. obscurus* males (King et al., 1980; King et al., in press). In addition, we have looked within populations at the relative appeal of songs when geographic information is not a factor (King & West, 1983a). In the present study, we contrasted songs at this latter and perhaps most subtle level of analysis.

We have most thoroughly studied song potency at the microgeographic, or second level of, analysis (King et al., in press). Here we have shown that even when females showed a level of song discrimination such that nonoverlapping distributions of responses occurred, we could not identify the structural song elements responsible. When the playback songs were examined acoustically, no structural pattern unique to one set of songs could be found to explain the overall differences in potency. Measurement of the frequency and duration of the notes revealed overlapping distributions on almost all measures. Using fine-grained acoustic measurements of temporal features, we did discover two potential differences in the rhythm (at the millisecond level) and in the octave relations underlying the coordination of the male's two voices. These features refer to dynamic properties of songs that unfortunately cannot be seen in sonograms or zero-crossings plots and must be described in numerical statements (King et al., in press).

In the present study, the HP and LP classification rests on differences at the third level of analysis, differences in the relative appeal of songs in the playback set. Ongoing studies suggest that in addition to structural relation relating to rhythm or octave attributes, the amplitude relations between the high and low voices and the rise and fall times of the high-voice bursts are cumulatively responsible for the musical qualities that make a song more or less potent.

Our inability to articulate the nature of the acoustic differences that the birds hear has continued to sensitize us to the importance of studying the behavior of avian listeners as well as that of avian singers. But the focus is now on the nature of

the social interactions between singers and listeners that occur during, as opposed to after, the period of song development. Birds learn to sing as one means of communicating with conspecifics; the challenge now is to uncover how they communicate about singing during ontogeny.

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