

Presence of Female Cowbirds (*Molothrus ater ater*) Affects Vocal Imitation and Improvisation in Males

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In this article we report that imitation and improvisation of tutor songs by eastern male cowbirds (*Molothrus ater ater*) differs when they are housed with conspecific females as opposed to nonconspecifics. When males, tutored with 12 different song types, were individually housed with females, they developed repertoires composed primarily of improvised and original song types, whereas the repertoires of males housed with canaries were composed entirely of copies of the tutor songs. Song preferences of the female companions for individual tutor songs were unaffected by social housing. The potency of the males' repertoires, as tested by playback to females, appeared to be related to the song responsiveness of their female companions. The results add further evidence that suggests that male cowbirds configure their song repertoire by attending to social signals from companions.

In this experiment we asked three questions. First, do male cowbirds (*Molothrus ater ater*) housed with females show different patterns of vocal imitation than males housed with canaries? Second, is the males' imitative behavior related to differences in song responsiveness of females? Third, are females' song preferences affected by the vocal behavior of the males?

Different forms of social stimulation have different effects on vocal development in songbirds (Pepperberg, 1985; Petrinovich, 1988). White-crowned sparrows (*Zonotrichia leucophrys*), for example, can learn heterospecific songs after 50 days of age when exposed to live male tutors but not when exposed to tape recordings (Baptista & Petrinovich, 1984; Petrinovich, 1985). So too, red-winged blackbirds (*Agelaius phoeniceus*) copy less heterospecific song when in the presence of female, as opposed to male, conspecifics (Marler, Mundinger, Waser, & Lutjen, 1972). Thus, social stimulation, as well as acoustic stimulation, appears to mediate vocal learning, although how these sources of stimulation are integrated remains to be specified.

Because female cowbirds do not sing, they provide an opportunity to study the effects of social stimulation in the absence of species-typical song stimulation. Several lines of evidence suggest that females exert discernible effects on males' vocal ontogeny. First, although juvenile eastern males learned nonnative song variants when housed with males from a second cowbird subspecies, *M. a. obscurus*, adult eastern males copied nonnative variants only when housed with males and females of the second subspecies (West, King, & Harrocks, 1983). Second, hand-reared, acoustically naive eastern males developed different repertoires when individ-

ually housed with females of their own or the *M. a. obscurus* subspecies. The structural differences in the males' songs involved acoustic elements used by females to discriminate between songs of the two subspecies (King & West, 1983b, 1983c; West & King, 1985). Third, the subsongs and plastic songs of yearling males displayed different characteristics when eastern males were housed with *M. a. ater* rather than *M. a. obscurus* females, which suggests that the females' presence had effects early in ontogeny (King & West, 1988b).

Thus, vocal development in cowbirds involves improvisation as well as imitation. Some other songbirds also display similar capacities, but in the case of cowbirds, males appear to be able to modify song content on the basis of social, as opposed to auditory, stimulation. Whether other songbirds can use social stimulation alone is not known. During ontogeny male cowbirds appear to learn about song function by attending to the behavior of females and by listening to themselves and other males. In this study we probed for evidence of female influence at a new level of analysis. In past work we had exploited the different subspecific preferences of females to acquire evidence of female influence. But in nature, if females affect males, it is presumably at the microgeographic level of acoustic differences among the songs of local males. Thus, the aim of this investigation was to study the effect of the presence of local females on the repertoire development of males from the same population.

A previous experiment with eastern cowbirds established that juvenile males copy songs presented by tutoring (West & King, 1986). In that experiment we housed 5 wild-caught juvenile males individually with pairs of canaries and tutored them with 12 different songs. We investigated males showed selectivity in their copying and if their selectivity was correlated with female preferences for the songs. Female preferences was assessed by measuring the potency of each of the 12 songs in two playback tests. In those tests the songs were played back to captive females deprived of males companions: We measured the percentage of trials on which each song elicited a copulatory posture. Six of the songs were of high potency (evoking responses on 50% or more of all

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playback trials), and 6 were low-potency songs (which evoked responses on 25% or fewer trials).

Twelve songs were used to force selectivity because male cowbirds' song repertoires range between three and seven song types. The results indicated that males copied more of the high-potency songs but did not copy the particular songs the playback females had responded to most often. Males displayed little intrasexual concordance: The 5 males' choices of tutor songs were not positively correlated with each other, whereas the females' responses to the same songs were highly correlated. None of the males developed any original (non-copied) song types. In nature and in captive colonies, males often share as much as 50% of their song types with other males, but most usually sing unique songs as well (Dufty, 1985).

In this study we asked if males would behave differently when housed with female conspecifics. Thus, we repeated the same procedures of West and King (1986) but used a new set of males housed individually with local females. Moreover, we selected females whose individual preferences for the tutor songs had been established by playback in the previous breeding season in order to look for specific relations between the behavior of individual males and females.

The prior playback testing of the females provided two potentially important pieces of information. First, we could ask if males differentially copied songs in relation to the specific rankings of those songs by their female companions. Although the females as a group had shown a high level of agreement with respect to potency, individual differences in song preferences were present. Second, we could look for relations between male production and differences in absolute female responsiveness to song.

It is important to state at the outset that differences in absolute responsiveness are an index of differences among females during the breeding season. How such differences map onto behavioral differences in female behavior at other times of the year is not known. Our aim was to see if males housed with different females but exposed to the same acoustic stimulation would show differences in their behavior that could be related to female responsiveness. If so, investigation of possible behavioral precursors to playback responsiveness in females would be warranted.

We examined the males' repertoires from several perspectives. First, we measured how much of their singing derived from the 12 tutor songs and which tutor songs were selected. Second, we measured the potency of their songs to the females with which they were housed. Finally, we played back the males' songs to a new set of females with whom they had had no contact in order to obtain an independent estimate of song potency. In addition, we probed for evidence of female modifiability by retesting the companion females' preferences for the tutor songs in the subsequent breeding season.

Method

Subjects

Eight male eastern cowbirds (*Molothrus ater ater*), determined by their plumage to be between 30 and 50 days of age, served as subjects.

They were captured in Orange County, North Carolina, during July and August. Each was immediately placed in a sound-attenuating chamber with 1 adult female cowbird. The birds were maintained on the normal photoperiod for 34° latitude. Details on housing and daily care may be found in West and King (1986).

Eight adult *M. a. ater* females served as companions. All had been wild-caught as yearlings in 1984 at the same site as the males. Their responsiveness to the tutor songs had been determined in the next year, 1985. The females differed among themselves in terms of the absolute number of times they responded to song. Thus, although the females' rankings of the songs from high to low potency were highly correlated, the range in the mean percentage of responses from high to low varied. Thus, one female's range extended from 100% to 50%, and another female's responses ranged from 43% to 0%. For this experiment we chose females with different levels of absolute playback responsiveness. Two females exhibited mean levels of responsiveness to the 12 tutor songs above 75%, 3 had levels between 50 and 65%, and 3 had levels below 30%. (Despite these absolute differences the females' relative rankings yielding significant differences in potency among the 12 songs as tested by a Friedman two-way analysis of variance, $\chi^2(11) = 51.5, p < .001$).

Before the females were housed with the males for this experiment, they had been housed with other females in pairs or triads. For the retest of the tutor songs in 1986, the males were removed, and each female was housed alone.

In the following year, 1987, 12 wild-caught *M. a. ater* females served as playback subjects (hereinafter referred to as the 1987 cohorts). They were collected by the procedures outlined earlier and housed in groups of 3 or 4 throughout the fall and winter and housed singly or in pairs during playback tests. For playback the 12 females were divided between eight chambers, 4 in pairs and 4 alone. No effects of social housing on the female's copulatory response have ever been found in extensive playback testing (see King & West, 1983a, 1983c; West & King, 1985).

Selection of Songs for Tutoring

The 12 songs used in West and King (1986) served as the tutor songs: Six were high-potency and 6, low-potency songs as previously described. Further details on how potency was initially established can be found in West and King (1986). The unweighted signal to noise ratio for all of the tutor songs was at least 55 dB measured peak to peak.

Tutoring Procedure

Tutoring commenced on September 1 and ended November 30. Previous research indicated this time period to be one in which the young male learns or modifies developing songs (King, West, & Eastzer, 1980; King & West, 1988b). Each morning the males were exposed to 240 repetitions of the 12 songs. The songs had been randomized into 20 different orders with songs occurring at 30-s intervals. The tutoring levels were adjusted to 83dB impulse at 0.5 m on axis from the speaker as measured with a Bruel and Kjaer 2105 sound-level meter.

Recording Procedure

The males were recorded in early December at 150 days of age and in early May at 300 days of age to a criterion of 32 min of singing. In the first session a total of 2,050 vocalizations were recorded ranging from 187 to 386 with an average of 216 for each male. In the May session 646 songs were recorded with a mean of 80 songs and a range

of 41 to 139. Previous research has shown that a sample of 41–85 songs yields a probability of 99% of having obtained all of a male's song types (King & West, 1983b).

Scoring of Songs

To establish reference templates against which the songs could be analyzed, a zero-crossings-analyzer was used to generate a Frequency \times Time display that was then stored in digital memory and transferred to a Hewlett Packard 86B computer. Each song was then plotted on clear acetate with a Hewlett Packard 7470 plotter with scaling identical to the zero-crossings display generated in real time on a Tektronix 5113 oscilloscope. Thus, transparencies, which exact duplicates of the oscilloscope display, were made of each tutor song.

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 in two phrases consisting of introductory notes and a whistle. Then the template was used to determine whether 75% of either phrase matched the reference template. If 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 classified as a mixed song. Both partial and mixed categories were considered as improvised songs. Unclassified songs were those containing variable or primitive structures that failed to meet the 75% test.

To analyze song content further, we measured the number of different note clusters represented in the final repertoires of the 8 males. The first half of a cowbird song consists of one or two note clusters: A *note cluster* is defined as a group of at least four low and high voice notes, usually sung in alternation and characterized by ascending frequency. Acetate plots were made of each note cluster; a criterion of a 100% match was required for two clusters to be considered the same. The same individual note cluster often appears in different song types of a given male accompanied by a different note cluster or different whistle.

Playback Apparatus

The tutor tapes were played back with an Otari MX5050 recorder, a Urei 537 $\frac{1}{2}$ -octave equalizer, and Crown D75 power amplifier through JBL 2105 speakers. The songs of the tutored males were recorded with a Nagra IVS operating at 19.05 cm/s.

Playback Procedure

The playback tests carried out in 1986 and 1987 followed the same general procedures of West and King (1986). All females were tested in their sound-attenuating chambers. In the tests one song was presented per trial for six trials a day separated by approximately 90 min. Each song was played back a minimum of five times to each female. In 1986, the playback series included the 12 tutor songs, played back to all females in different orders each day, and the final songs developed by the companion males, which were played back only to their companion females. Thus, each day a female heard two of the high-potency tutor songs, two low-potency songs, and two songs from her male's repertoire. The four tutor songs were the same for all females. In 1987, the playback series consisted of the 36 song types developed by the 8 companion males. The females heard the songs in varying orders, but each song was presented an equal number of times at different times of day.

A positive response to song was scored if a female displayed a copulatory posture within 1 s of the song's onset. A copulatory posture had to include all of the following components: The female had to

lower and spread her wings, to arch her neck and body, and to separate the feathers around the cloacal region.

Results

Content of Males' Repertoires

Early song. Figure 1 displays the mean percentage of singing in each category for the males from this experiment, as well as summarized data for the 5 males from West and King (1986). In the first recording session (150 days of age), 80% of the males' vocalizations fell into the unclassified category. Only 9% of the males' vocalizations were copies of high-potency tutor songs, produced by 7 of the 8 males. The 8th male sang a low-potency song that accounted for 1% of his singing. Improvised songs were produced by all males and averaged 4% of their singing (range, .005%–15%). Fragments of high-potency songs accounted for 75% of the tutor song material contained within the improvised songs. An average of 7% (range, 1%–19%) of the December vocalizations could be matched to final song types of the 8 males; all were original song types.

The males housed with canaries differed. At the same time of year and at the same age, only 26% of the males' vocalizations could not be typed. The males with canaries averaged 49% high-potency songs (range, 28%–60%), 22% low potency (range, 10%–42%), 3% improvised songs (sung by 2 males), and no original songs. The ranges for the two groups of males in the two experiments did not overlap with respect to the frequency of production of copied and original song.

Final songs. The 8 males developed a total of 36 song types; mean repertoire size was 4.5 (range, 2–7). Of the 36 song types, 5 were copies of high-potency tutor songs produced by 3 males, 22 were original types collectively produced by 7 males, and 9 were improvised song types produced by 5 males. The tutor song material contained in the improvised types derived entirely from the class of high-potency songs.

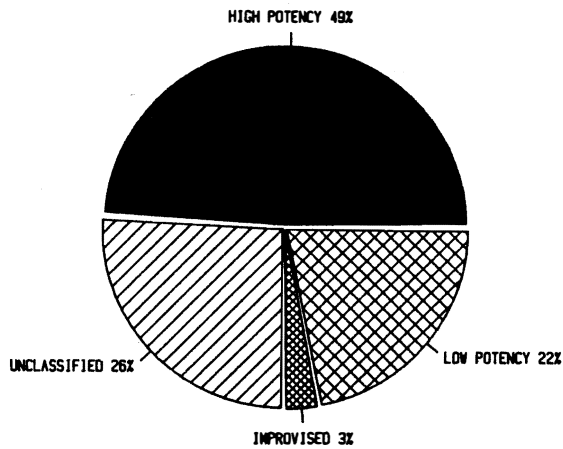
In the final session, original song accounted for 54% of all singing (7 males; range, 39%–82%); improvised song averaged 26% (5 males; range, 18%–100%); and high-potency copied song accounted for 20% (3 males; range, 40%–61%). In contrast, the 5 males housed with canaries had averaged 97% copied song in the final session (range, 90%–100%) and 3% mixed or unclassified song. High-potency songs predominated, but low potency songs were produced by 4 of the males accounting for 15% of all copied song. No original song was produced. Thus, nonoverlapping ranges also existed between the two groups in the final session.

Song Potency

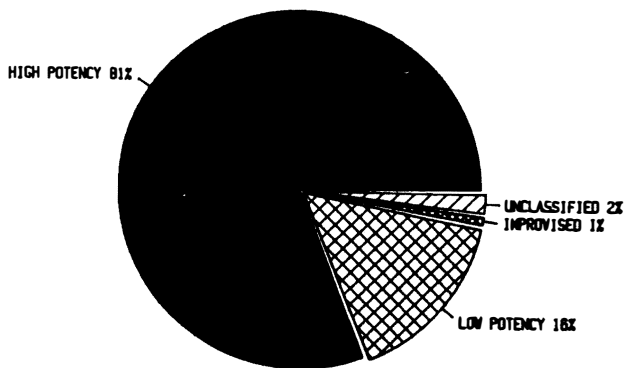
Table 1 provides data on relations between male song production and female responsiveness. The potency of the songs in each male's repertoire were averaged to yield a single score for each male's repertoire. The mean potency of the males' repertoires was 52% (range, 12%–97%) when played back to the male's companion and averaged 60% (range, 42%–79%) to the 1987 cohorts. A Mann-Whitney *U* test

TUTORED MALES WITH CANARIES

REPERTOIRES AT 150 DAYS

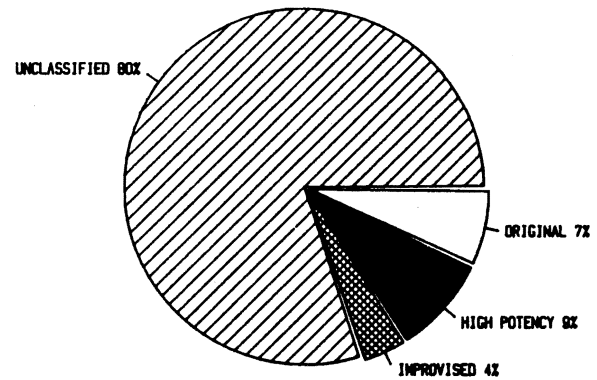


FINAL REPERTOIRES



TUTORED MALES WITH FEMALES

REPERTOIRES AT 150 DAYS



FINAL REPERTOIRES

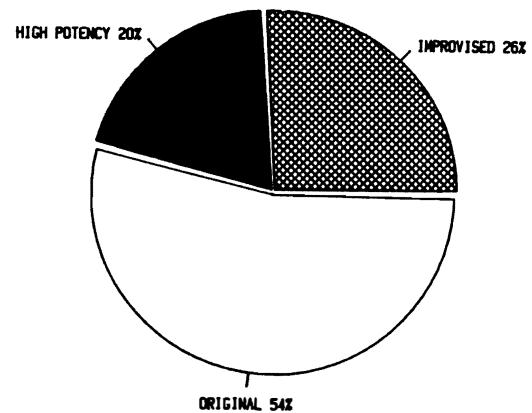


Figure 1. Content of males' repertoires at 150 and 300 days of age. (See text for definitions of categories. Data from West & King, 1986, and the present experiment are presented for comparison. All scores are mean percentages for each group.)

indicated no significant differences between the responses of the 1986 and 1987 females ($U = 26$, ns). Repertoire potency was positively correlated across the two playback tests; the Spearman rank-order correlation was $.69$, $p < .05$.

Because the two groups of females heard the males' songs as part of different playback protocols, a second index of potency was used: The relative ranking of the songs of each male with respect to the other songs heard by the playback female (1986) or cohorts (1987), an index termed *relative repertoire potency*. Thus in 1986, each of the male's songs was ranked along with his female's responses to the retest playback of the 12 tutor songs. In 1987, each male's songs were ranked

relative to each female's ranking of 36 songs and then averaged for the group. Relative repertoire potency of the males' songs was positively correlated across the two playback tests; the correlation between 1986 and 1987 was $.74$, $p < .05$.

Interrelations between relative repertoire potency and three measures of song content, amount of original song, number of song types, and number of different note clusters, were assessed. No relation was found between relative potency and amount of original song in either year, $r = .50$, ns , in 1986, and $r = .24$, ns , in 1987. Both number of song types and number of different note clusters were negatively correlated with relative potency. In 1986, the correlation between rela-

Table
Functional Attributes of the Males' Songs

Measure	Male companions ^a							
	LB	2R	OW	DG	PG	YB	RB	2O
Female responsiveness ^b	80%	68%	61%	54%	52%	34%	27%	26%
Mean potency ^c								
Own female	70%	67%	97%	40%	46%	44%	40%	12%
1987 cohort	51%	72%	79%	63%	62%	60%	42%	49%
No. of song types	4	2	4	3	4	5	7	6
No. note clusters	5	2	4	2	7	9	9	9

^a Males are arranged in descending order of the averaged playback responsiveness of their female companion to the 12 tutor across the two years. ^b Averaged playback responsiveness to the 12 tutor songs across the two years. ^c Mean % of responses to each song type divided by the number of song types of each male.

tive repertoire potency and number of song types was $-.64$, $p < .05$, and in 1987, the correlation was $-.73$, $p < .05$. For the number of different note clusters, the correlation with relative repertoire potency was $-.29$, *ns*, in 1986, and in 1987, the correlation was $-.82$, $p < .01$.

Retest of Playback Responsiveness to Tutor Songs

The female companions' responsiveness to the 12 tutor songs in 1986 differed little from that in 1985; the mean percentage of responses on retest was 52% (range, 39%–77%) in contrast to 51% (range, 16%–83%) the previous year. The mean percentage of responses to the songs of their male companions was 52% (range, 12%–97%). The 8 females' rankings indicated significant differences in potency among the songs; a Friedman analysis of ranks for the 12 songs was significant, $\chi_r^2(11) = 47$, $p < .001$. Moreover, the specific rankings correlated with those obtained in 1985 that yielded a Spearman rank-order coefficient of .86, $p < .01$, between the 2 years.

Each female's averaged responding to the 12 tutor songs in 1985 and 1986 was used to order the females in terms of playback responsiveness: The female who responded most was assigned a rank of 1 and so on. (These scores are listed in Table 1.) This ordering was used as a correlate with measures of the males' vocal behavior. Playback responsiveness was not significantly correlated with amount of original song, $r = .42$, $p > .05$, but both number of song types and number of note clusters were negatively correlated with playback responsiveness: $r = -.70$, $p < .05$ for song types, and $r = -.66$, $p < .05$ for note clusters.

Because only 5 of the 36 song types were faithful copies of tutor songs and were produced by only 3 males, comparisons between male copying and female preferences could be assessed on only a limited basis. The five copied songs represented two high-potency tutor songs (termed 3HP and 4HP in West & King, 1986). Two males had two copied types, and 1 male had one. All 3 males had copied song 4HP, and 2 had copied song 3HP. These songs were ranked first, 3HP, and fourth, 4HP, by the 8 females in both playback tests. Song 3HP was the most preferred song for 1 of the 2 females whose males sang it, and it was the second most preferred for the

2nd female. Song 4HP ranked fifth, sixth, and ninth for the 3 females whose males copied the song type.

Discussion

The results indicate that eastern male cowbirds reacted quite differently to songs presented by tutor tape when in the presence of conspecific females as opposed to canaries. When males were with canaries, they focused almost entirely on the tutor songs. They showed minimal improvisation and no original singing. In contrast, males with female conspecifics incorporated few of the tutor songs, instead inventing or improvising the major proportion of their song types. The data therefore suggest that the presence of conspecific females affected microgeographic song production in much the same way that it affected macrogeographic features (King & West, 1983b). Previously, we had shown differences in song copying when eastern males were tutored with one *M. a. ater* song and individually housed with canaries or *M. a. obscurus* females. The males with canaries retained significantly more copied song, and conversely, the males with *M. a. obscurus* females produces more original song.

The explanation for both findings is most likely related to the different forms of stimulation provided by the different social companions. Although the canaries provided abundant vocal and social stimulation, none was of species-typical relevance. Incidental observations of the males with canaries suggested that the groups formed cohesive interspecific social units involving counter-singing, group feeding, and perching. In other words, the male cowbirds attended to the presence of their canary companions but not in relation to the tutor songs. Males with female companions also engaged in frequent social interactions but with a different outcome.

Ongoing analyses of videotaped interactions of the males and females studied here suggest that the females may have used visual signals to communicate about vocal overtures. One of the more striking visual displays used by females during the winter was a wing stroke—a rapid flicking of one or both wings that occurs during a male's song. Songs recorded in March that elicited wing strokes were found to be significantly more potent than songs sung in the same singing bout but unaccompanied by wind stroking by the female. Moreover, individual females differed in the frequency of wing stroking: the females that wing-displayed most often were the ones that ranked highest in playback responsiveness (King & West, 1988a).

Thus, the correlational relations reported in this article between female responsiveness and male song production imply that males and females are communicating about song long before courtship begins. The data also show that the effect of the female's behavior can be traced to the level of individual differences. But the small sample size of 8 male-female pairs means that the reported relations between number of song types, number of note clusters, and absolute female responsiveness must be interpreted cautiously. Further experiments are warranted. But the data are encouraging in terms of providing an empirical means of linking the behaviors of singers and listeners. If features of male song production can be predicted a priori on the basis of characteristics of the

listener, a strong case can be made for viewing song epigenesis as a social phenomenon.

Retests of the responsiveness of the female companions and comparisons to the 1987 cohorts replicate previous data that showed the eastern females' preferences for particular songs appear generally unaffected by social experience with males or females (King & West, 1983a, 1983c). Such stability in responsiveness would seem a necessary condition if females are to have an influence on a male's vocal behavior.

Cowbirds are one of the first species in which the role of nonvocal female stimulation has been investigated in detail. But investigations in a diversity of songbirds and other avian taxa reveals the multiple ways in which social stimulation can affect vocal behavior (see Pepperberg, 1985, and Petrinovich, 1988, for extensive reviews). One of the more immediate conceptual needs is for a taxonomy of the kinds and degrees of social influence identified. Social influence ranges from the effects of song stimulation presented by tape recording to the effects of live, interacting tutors, which may be the student's father, sibling, mother, neighbor, consort, or rival (Baptista & Petrinovich, 1984, 1986; Eales, 1985, 1987; Marler, Dufty, & Pickert, 1986; Marler et al., 1972; Payne, 1981, 1982; Pepperberg, 1985; Price, 1979; Todt, 1975; Todt, Hultsch, & Heike, 1979).

It is not clear at present how any of these forms of social stimulation produce the effects obtained. It is particularly important to know how visual or social (i.e., nonvocal) stimulation affect song development because cross-modal perception and nonimitative learning are forms of learning that go beyond traditional definitions of vocal learning in songbirds (Kroodsma, 1982). An obvious conclusion of our study is that researchers need to expand the measures of vocal development. What males and females see, as well as what they hear, must become serious topics of inquiry.

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