

Vocalizations of Juvenile Cowbirds (*Molothrus ater ater*) Evoke Copulatory Responses from Females

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The functional attributes of the vocalizations produced by young male cowbirds during their first fall and winter, termed "vocal precursors," were tested by playing the sounds back to female cowbirds. Five classes of vocalizations were tested: subsong, plastic, formatted, and stereotyped song, and songs of nonconspecifics. Females responded selectively to the four classes of cowbird vocalizations. Stereotyped songs evoked the most responding but the key eliciting element was the inclusion of note clusters, which first occurred in plastic song. The data suggest that juvenile cowbirds possess vocalizations capable of evoking biologically relevant responses from companions early in development.

Vocal precursors to adult song, typically called subsong and plastic song, occur in many songbirds but have been studied thoroughly in few species. The most extensive studies have focused on the structural organization of the sound and the nature of the ontogenetic mechanisms underlying transitions in vocal maturation (Marler & Peters, 1982a,b). Functional properties of precursors have typically not been studied.

Experimental tests of the functional properties of the adult songs developed by acoustically naive songbirds, songs often resembling vocal precursors in their impoverished species-specific detail, have typically been found to be inferior to

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the songs of normally reared individuals in evoking behavioral responses from males or females (Spitler-Nabors & Baker, 1987; Searcy, Marler, & Peters, 1985; Searcy & Marler, 1987). Thus, the primitive precursors to stereotyped song, subsong and plastic song, would seem capable of communicating little beyond the singer's youthful status.

The vocal productions of young cowbirds are also quite rudimentary and variable, but two lines of evidence suggested that vocal precursors might be communicative. First, although the songs of acoustically naive cowbirds were found to be atypical compared to the songs of normally reared males, the songs proved to be superior releasers of the female cowbird's copulatory posture (King & West, 1977). The songs of acoustically naive males were twice as effective as those of normally reared males. The songs of naive males contained the acoustic elements critical to the song's reproductive function, perhaps even emphasizing those attributes. Thus, male cowbirds do not seem to need to hear other males sing to develop effective courtship signals. Given these data, we asked when in ontogeny do these evocative properties appear?

Longitudinal studies of the vocal ontogeny of acoustically deprived eastern cowbirds housed with social companions suggested that evocative properties were present early in song ontogeny. By 175 (± 10) days of age (December), only 1 month after males had begun to vocalize routinely, acoustic differences occurred among males housed with different social companions (King & West, 1983a; King & West, 1988). The stereotyped songs of the males also differed leading to reliably different vocal phenotypes when the males reached sexual maturity (West & King, 1985). These findings suggest that the vocal precursors were sufficiently stimulating to evoke differential behavior from listeners.

Taken together, the findings led to the present interest in exploring the communicative properties of vocal precursors. What is the minimum level of acoustic information necessary to evoke copulatory responding by females? We chose this measure to make the findings comparable to previous studies in which we measured the functional properties of adult songs by assessing their effectiveness in eliciting copulatory responses from captive females deprived of male companions during the breeding season.

The classes of vocal precursors were selected on the basis of detailed analyses of the vocal behavior of males reared under various conditions in the laboratory and on the basis of a field study of the vocal behavior of free-living males (King & West, 1988). These studies demonstrated that, like many other songbirds, the singing of eastern brown-headed cowbirds changes in predictable ways during the male's first year.

The earliest vocalizations, subsong, are characterized by their variable structure and timing, low amplitude, and inclusion of vocal elements that are not identifiable to the human ear as "cowbird-like." Within a month or two after the onset of subsong, subsongs co-occur with and ultimately are replaced by variable or plastic songs, songs containing low- and high-frequency notes and whistles characteristic of cowbirds. The vocalizations are poorly articulated, variably ordered, and range widely in duration from 200 msec to 4–5 sec. Finally, the purely variable renditions wane and vocalizations possessing definite timing and syntactic ordering appear. These formatted songs last between 800 and 1200 sec but are variable in the song content included. The achievement of stable song content, along with excellent articulation and high amplitude, mark the

achievement of stereotyped song. These songs possess such structural and temporal fidelity that repeated renditions may vary by no more than ± 1 msec in timing and with a frequency correspondence within 5% of an octave.

Thus, four stages of song ontogeny emerge: subsong, plastic song, formatted song, and stereotyped song. Plastic song is further subdivided into two categories to distinguish precursors composed of "notes" and those containing "note clusters" (Fig. 1). A note is defined as a tone burst produced by either the high or low voice ranging in duration between 5 and 100 msec. A note clusters is an arrangement of at least four or more notes with a total duration of 150 to 200 msec. The notes within a cluster are produced by both voices, usually in alternation, and are characterized by ascending frequency for each voice (King & West, 1983b). The peak amplitude of each note within a cluster usually occurs within 5 msec after the onset of each of the notes in the cluster.

The categories describing transitions in vocal ontogeny used here for the cowbird also appear to obtain for other songbirds, especially the several species of sparrows studied intensively by Marler and Peters (1982 a,b). So too, the developmental timetable marking transitions is similar (King & West, in 1988). Thus, the classes of precursors tested have identifiable counterparts in other songbirds.

For the present experiment, we obtained vocalizations for playback from wild-caught males housed in the laboratory with females and tape-tutored for three months with 12 different adult songs varying greatly in structure and in their effectiveness as releasers of the female's copulatory posture. Male cowbirds generally possess repertoires of three to seven songs and thus the tutoring regime presented more songs than could be copied, hopefully providing a stimulating acoustic and social environment. We provided acoustic and social experience to make the results more comparable to the natural setting for young males where stimulation from both sexes is present. Vocalizations were recorded at 175 (December) and 330 (May) days of age. The playback test consisted of three phases in order to evaluate the relative impact of transitions in vocal structure on song potency. The songs of other species were included in the first phase to determine when and what kind of precursors possess species-specificity.

Methods

Subjects

Eight *M.a. ater* males served as sources of playback songs. The birds were caught at our aviaries in July when under 50 days of age as judged by their plumage. They were immediately placed in sound-attenuating chambers with adult *M.a. ater* females, captured from the same site in the previous year. The birds were maintained on a normal photoperiod for 36 degrees latitude and fed a modified version of the Bronx Zoo diet for omnivorous birds and given vitamin-enriched water daily.

Ten females participated in the playback experiment. All were wild-caught adults captured the previous year at the same site as the males. They were housed in pairs or triads throughout the winter in sound-attenuating chambers. During the playback period, females were housed in pairs. No effects of social housing have been found in previous playback tests (King & West, 1983).

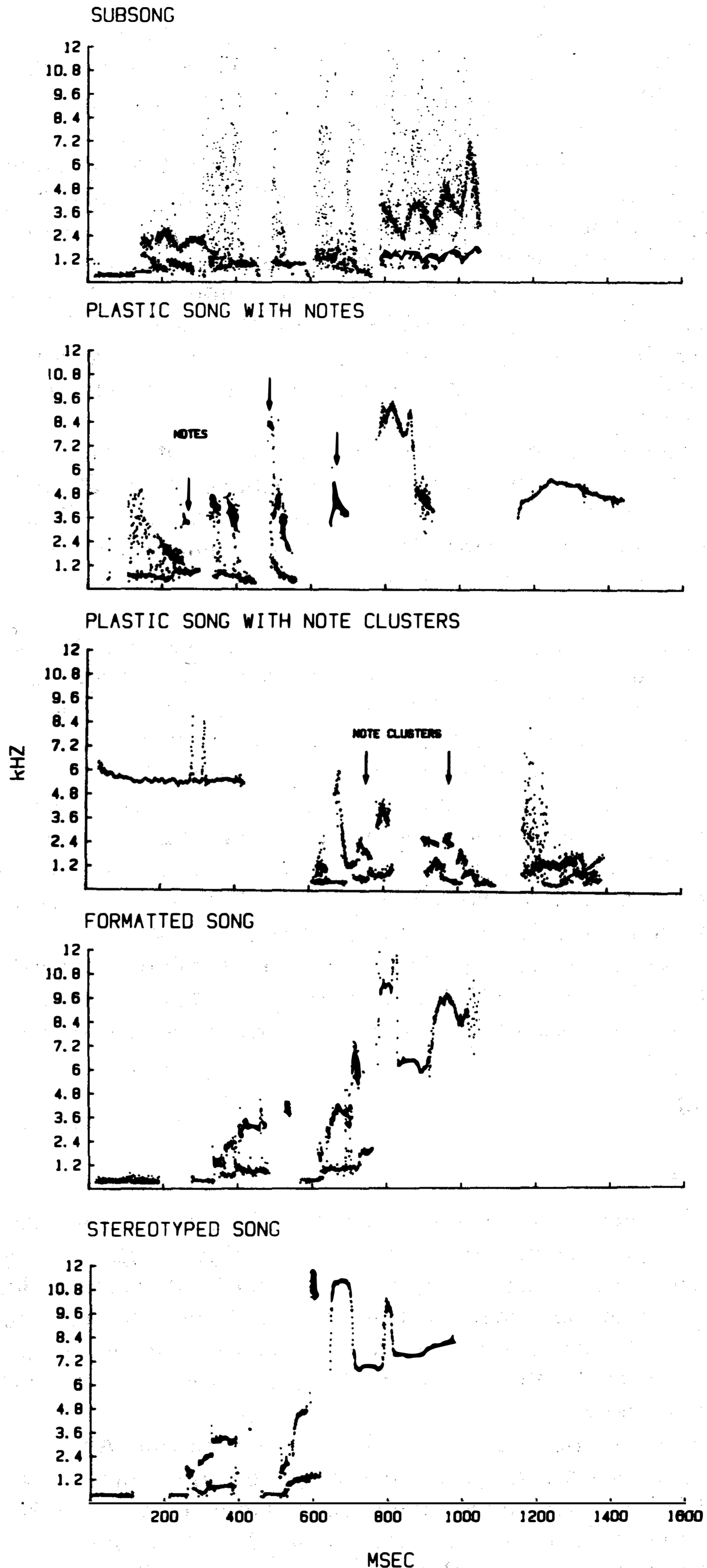


Fig. 1. Zero-crossings-analyzer displays of the classes of vocal precursors (see Staddon, McGeorge, Bruce, & Klein, 1978 for a description of the zero-crossings technique). On the ordinate is frequency and on the abscissa is time. The stereotyped song shown is the final version of the formatted song displayed. Examples of notes and note clusters are marked with arrows.

Apparatus

Songs were recorded monthly with a Nagra IVS at 19.05 or 38.1 cps using Sennhesider RF directional condenser microphones. See King and West (1977) for details of the construction of the sound-attenuating chambers.

Procedures

Exposure to adult song. The males were tutored for three months beginning September 1. Each day, 240 repetitions of 12 different adult songs in 10 different orders were presented. The songs were recorded from 12 different males. The exposure lasted 2 hr with a song occurring every 30 sec. The playback levels were adjusted to 83 dB impulse at .5 m on axis using a B&K 2209 sound pressure meter.

Recording procedures. The males were recorded once a month beginning at 140 days of age for a minimum of 32 min of singing. Recordings were made in stereo to maximize the chance of obtaining high-quality recordings. For a song to be chosen for playback, a male had to sing into the microphone as $<.15$ m on axis. Such a criterion was necessary to capture the sound as females normally hear it because males sing at very close distances to females when they are about to copulate with them (King, West, Eastzer, & Staddon, 1981).

Playback songs. In the first phase, 18 songs were played. Five were subsongs obtained from two males; five were plastic songs with notes obtained from five males, five were plastic songs with note clusters from five males. Three songs were from other species. Of these three, the first was from a male canary (*Serinus canaria*), the second from an orchard oriole (*Icterus spurius*), and the third from a western meadowlark (*Sturnella neglecta neglecta*). The canary was recorded in our laboratory, the other two recordings were taken from "Songs of Eastern Birds" recorded by D. J. Borror in Dover catalog #22378-7.

In the second phase, 10 songs were played, the five plastic songs with note clusters from the first phase and five exemplars of formatted songs from five males. In the third phase, the two "best" plastic songs with note clusters from Phase Two were played back, the three best "formatted" songs, and five stereotyped songs developed from the five formatted songs in Phase Two. All precursors were recorded in the first week of December when the males were 175 days old and receiving 10.7 hr of light. The stereotyped songs were recorded in early May when the males were 330 days old and receiving 14 hr of light.

Playback songs within each category were selected on the basis of their recording quality and a duration limit of 2000 msec for plastic song. The unweighted peak-to-peak mean signal-to-noise ratios for the song categories were as follows: 43.5 dB (SD = 14.7) for other species; 47.1 dB (SD = 2.9) for subsong; 44.1 dB (SD = 5.3) for plastic song with notes; 45.5 dB (SD = 2.7) for plastic song with note clusters; 50.5 dB (SD = 3.8) for formatted song; and 55.6 dB (SD = 1.4) for stereotyped song. The songs were played through a Urei 537 equalizer, Crown D-75 amplifier and JBL 2105 speakers which were located in each chamber. Playback levels were measured with a Bruel & Kjaer 2209 sound pressure meter. For all songs, the sound pressure level (SPL) was 82 ± 1.5 dB, impulse setting, measured .6 m on axis from the speaker. This was the maximum distance a female could be from the playback speaker and thus represents the minimum playback level.

Playback tests

The females were tested in their sound-attenuating chambers. Six playbacks occurred each day, separated in time by a minimum of 90 min., for a 6-week period. Only one song was presented on each playback trial. The order of the songs varied daily but was the same for all females. Each female heard each song on five to seven playback trials. The playback tests began in May when the female were judged to be in breeding condition as indicated by egg-laying. Each of the three phases took approximately 2 weeks to complete falling within the 8 to 10 weeks in which females are in reproductive condition (Dufty & Wingfield, 1986). A positive response was recorded for a female if she adopted a copulatory posture within 1 sec of a song's onset. To be scored as a copulatory response, a lowering and spreading of the wings, an arched neck and body, and separation of the feathers around the cloacal area had to be present.

Results

Phase One

The females responded significantly more to all classes of cowbird precursors than to nonconspecific songs (Table 1). Two females responded infrequently to the songs of the canary, but both also responded as often or more often to cowbird subsong. Among the classes of cowbird precursors, plastic songs with note clusters were significantly more effective than the other two categories, eliciting the most responding from all females.

Agreement among the females as to the relative ranking of the songs was tested by a Friedman analysis of variance yielding a significant value, $\chi^2 = 17.1$, $p < .001$. Differences between categories were tested with the Wilcoxon test for matched pairs with corrected probability levels of multiple pairwise contrasts (Marascuilo & McSweeney, 1977). The songs of other species were significantly less effective than subsongs ($T = 0$, $p < .01$), subsongs were reliably less potent

TABLE 1. Number of Playback Presentations to Each Female (N), Mean Percentage, and Standard Deviation of Copulatory Responses to Vocal Precursors and Stereotyped Song.

N		Playback Songs		
<i>Phase One</i>				
126	Subsong 11% ± 9	Plastic with Notes 22 ± 15	Plastic with Note Clusters 68 ± 14	Other Species 2% ± 3
<i>Phase Two</i>				
70			Plastic with Note Clusters 39% ± 24	Formatted 42% ± 16
<i>Phase Three</i>				
70		Plastic with Note Clusters 31% ± 27	Formatted 28% ± 33	Stereotyped 59% ± 26

than plastic songs with note clusters ($T = 0, p < .01$) but not significantly different from plastic song with notes ($T = 5, n.s.$), which were, in turn, less potent than plastic song with note clusters ($T = 0, p < .01$).

Phase Two. The females did not differentiate between plastic song with note clusters and formatted song ($T = 18, n.s.$).

Phase Three. Stereotyped songs were significantly more potent than plastic song with note clusters or formatted song but the latter two categories did not differ from one another. The Friedman test for agreement across categories was significant, $Xr = 7.8, p < 0.02$. The Wilcoxon values for differences between categories were as follows: $T = 13$ (n.s.) for plastic song with note clusters versus formatted song and $T = 2$ ($p < .01$) for formatted song versus stereotyped song.

Comparison of relative potency across phase. Two of the plastic songs with note clusters were played back in all three phases affording an opportunity to test the females' responsiveness when hearing the same song in contrast to different levels of song stereotypy. The two songs averaged 90% (range 75–100) in Phase One, 71% (range 33–100) in Phase Two, and 29% (range 0–81) in Phase Three. The Friedman value for the three-way comparison was $Xr^2 = 13.6$ ($p < .001$). Phase 1 songs were significantly more potent than Phase 2 songs ($T = 3, p < .01$) which in turn were significantly more potent than Phase 3 songs ($T = 0, p < .01$).

Discussion

Eastern female cowbirds responded selectively to primitive precursors to cowbird song suggesting that males possess species-recognizable signals early in ontogeny. Embedded within the considerable amount of variable and inarticulate vocal material produced by young males appears to be key acoustic elements that can be "read" accurately by conspecific females. The most critical element may be the note cluster, which produced a threefold increase in responding in Phase One. This element, combined with the shape of the associated amplitude envelopes of the notes, imparts to cowbird song its distinctive "liquid" sound. The precise quality of that sound was also found to be used by females to discriminate among stereotyped songs that were "superficially" quite similar in terms of frequency and temporal qualities (King, West, & Eastzer, 1986).

The attainment of characteristic cowbird syntax and timing marking the structural transition from plastic to formatted song did not produce a qualitative change in female responsiveness: plastic songs with note clusters were as effective as formatted songs in Phase Two, even though the former had lower signal-to-noise ratios. The finding is noteworthy for two reasons. First, the auditory differences between plastic and formatted song are striking to the human ear, providing another example of the need to be cautious when basing conclusions about ontogenetic mechanisms on structural analyses. Second, the findings suggests that the ultimately extraneous acoustic elements marking plastic song may not have a negative effect on a song's potency as long as the note cluster is present.

In evaluating the present data, the assumption cannot be made that reproductively active females perceive song in the same way as do reproductively inactive females during the fall and winter. But the data show that the information for species-specificity is available soon after the onset of song development and can be used by females to identify males as cowbirds. The subsongs tested here were not the earliest possible renditions produced by young males. Subsongs occur

during the fall and are composed of even more primitive structure. Whether these sounds are also species-recognizable remains to be tested. We chose to begin with the vocalizations that mark the point at which males begin to vocalize routinely, using predictable singing as the onset of song ontogeny.

Our previous studies indicated that males are sensitive to different social contexts as early as December (King & West, 1988). Males produced different numbers and kinds of notes if housed with females from their local population as opposed to females from a different subspecies (*M.a. obscurus*). The present results add to those findings by showing that males' early attempts at song are sufficiently provocative to elicit different responses from listeners, at least those in breeding condition. Thus, the accumulating evidence suggests that the acoustic changes that mark transitions in song ontogeny may be facilitated by the male's ability to attend and act on differential feedback from females.

Females display a rich variety of behavioral responses to vocal overtures of males during the fall and winter. Females routinely ignore, approach, threaten, and react using head, beak, wing, and body movements. Although males may be affected by all such behavior, one particular pattern of wing strokes displayed by females to certain songs during the winter and early spring seems especially influential. Songs recorded in early March that had elicited wing strokes were found to elicit significantly more copulatory responses from females in breeding condition than March songs not followed by wing strokes (West & King, 1988, West & King, in press). The results suggest that females may normally react to certain vocalizations with behaviors functionally related to later reproductive behavior: precursors to song appear to elicit precursors to copulatory postures. Thus, the need now arises to study transitions in female, as well as male, communicative capacities.

The appearance of potentially functional song elements so early in development might be expected in cowbirds because of their brood parasitic habit. Because young cowbirds may miss opportunities for the kinds of learning afforded to non-parasitic species, they may have evolved vocal programs that rely less on imitation and more on self-stimulation and social learning (Gottlieb, 1973). Because the vocal precursors of nonparasitic species have not been functionally evaluated, such a conclusion may be premature. Moreover, tests of the functional properties of the adult songs of acoustically naive males in song sparrows (*Melospiza melodia*) indicate that both males and females discriminate between such songs and those of deafened males implicating self-stimulation in the song development of other species as well (Searcy & Marler, 1987).

The present data, along with the earlier findings of the superior potency of the songs of naive singers, should not be taken to mean that other forms of learning are not a vital part of vocal ontogeny. In studies of naive adult song, we demonstrated that males reared in social isolation produced songs that placed them at a competitive disadvantage because the naive songs elicited aggression from males (West & King, 1980). Because males must interact with males to establish dominance relationships prior to courtship, the changes in vocal behavior that result from social and vocal exchanges with males must also be considered to explain song development.

Dufty (1986) has shown that song is critical to the establishment of male dominance in the late winter and early spring. Thus, some of the acoustic modifications occurring during song ontogeny are undoubtedly responses to social and

auditory intrasexual experience. These sources of influence warrant further study to create a comprehensive view of song development.

The data from Phases Two and Three also indicate the potential importance of postnatal experience to song ontogeny. In Phase Two, the five plastic songs of highest potency in Phase One were less potent when heard in comparison to the structurally more detailed formatted songs. In Phase Three, exposure to stereotyped song reduced responding to plastic song. The same pattern emerged for the two songs played back in all three phases: They were responded to less and less when in competition with more articulate songs.

It is unlikely that these differences reflected systematic fluctuations in reproductive state because egg-laying rates remained stable. If reproductive state was to have had any effect, it would have been to decrease the probability of eliciting responses in the first phase when females first came into breeding condition. The data suggest no such effect in that plastic song with note clusters elicited more responses in phase one than phase two.

But the data do indicate that song potency is a relational attribute (King & West, 1983b). Females listen to a finite set of songs from a limited group of males: the same male's song may thus fare better or worse in terms of potency depending on the other songs available to females. The relative nature of song potency suggests that the function of the ontogenetic progression to stereotyped song may be to embed key communicative elements in as stimulating and acoustically clear a configuration as possible. The vocal precursors played back naturally differed in signal-to-noise ratios with the more stereotyped songs being sung louder. Thus, even though the earliest vocalizations of the males can identify them as cowbirds, males may continue to modify their song to maximize their chances of developing repertoires containing the best songs with which to compete with other males during courtship.

That effective songs are essential to successful courtship has been demonstrated in a series of studies of mate choice under captive conditions (West, King, & Eastzer, 1981; West, King, & Harrocks, 1983; Eastzer, King, & West, 1985). The results of the three studies represent, to date, some of the clearest evidence in birds of the role of song in mate choice (Searcy & Andersson, 1986). It is not enough for a male to be able to signal that he is "a" cowbird: he must communicate that he is "the best" cowbird available. The present experiment suggests that young cowbirds are outfitted with an abundance of appropriate vocal material from which to fashion a repertoire suited to the dual adult obligations of competition and courtship.

Notes

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