

## Social Experience Affects the Process and Outcome of Vocal Ontogeny in Two Populations of Cowbirds (*Molothrus ater*)

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Longitudinal vocal records of 26 juvenile male cowbirds from 2 populations (*Molothrus ater* and *Molothrus ater artemisiae*) were analyzed to look for susceptibility to social influence from either female cowbirds or heterospecifics. Within each population, 1 group of males was individually housed with female conspecifics, and the other with pairs of canaries (*Serinus canaria*). Evidence was found for female influence in both populations. *M. a. artemisiae* males showed more vulnerability to heterospecific influence and developed song more slowly than did *M. a. ater* males. Greater vocal production was correlated with faster acquisition of song, especially for the males housed with female conspecifics. In that female cowbirds do not sing, these data indicate the inadequacy of mechanisms based on imitation to explain vocal ontogeny. The data also reinforce the need to consider the intraspecific impact of social and ecological parameters on vocal learning.

The nature and the timing of vocal learning vary across populations of brown-headed cowbirds, as has been documented in laboratory and field studies (King & West, 1990; O'Loughlen & Rothstein, 1993; Rothstein, Yokel, & Fleischer, 1986). No single pattern describes vocal ontogeny, either for songs (the focus of the present study) or for flight whistles (the vocalization studied in western populations [Dufty & McChrystal, 1992; Dufty & Pugh, 1994; O'Loughlen, 1995; O'Loughlen & Rothstein, 1993; Rothstein et al., 1986; Rothstein, Yokel, & Fleischer, 1988]). Here, we looked at possible differences in susceptibility to social influences, in particular, the possible role of female conspecifics or heterospecifics in shaping song learning.

Studies of hand-reared eastern *Molothrus ater ater* cowbirds first identified the need to consider social influence. When young males were housed solely with females from one of two different cowbird populations, they developed vocalizations with population-specific features, although they could not have heard these sounds as female cowbirds do not sing (King & West, 1988; West & King, 1988). Thus, song learning in cowbirds cannot solely be explained by vocal imitation. The males did not imitate the females' behavior but modified the content of their vocal repertoires in response to social cues. This is not to say that males do not play an important role as vocal and social tutors, but

they do so as complementary, not sole, sources of influence (West & King, 1980, 1986b).

The effects of female conspecifics on songs of young cowbirds would seem to constitute evidence for *action-based* learning, that is, the shaping of vocal repertoires through social reinforcement (Adret, 1993; Marler, 1991; Marler & Nelson, 1993). There is, however, an important difference. As articulated by Marler, the actions of companions influence vocal material "already present in the individual's plastic-song repertoire, having been acquired, improvised, or invented earlier" (Marler, 1990, p. 111). However, in the case of the cowbirds, the females' presence also affected the contents of the males' plastic-song repertoires. From as early as vocalizations could be recorded, when the males were less than 150 days of age, reliable differences occurred in the most primitive vocalizations of the males housed with females from different populations. Thus, the very building blocks of songs, the notes themselves, were altered by female stimulation. The presence of species- and population-typical song structures also did not depend on any prior stage of *memory-based* acquisition from vocal tutors, as the males had never heard adult models. Instead, the data suggested that social influence is systemic to the process of vocal growth (King & West, 1988).

Although the previous study (King & West, 1988) had been designed to probe female influence in the most detail possible, it included 3 males housed individually with heterospecifics, 2 males with canaries (*Serinus canaria*), and 1 with a starling (*Sturnus vulgaris*) to rule out general social stimulation as the mechanism underlying the female's effect. Each showed some evidence of heterospecific influence during ontogeny; that is, they copied elements of their companions' vocalizations but deleted these variants before crystallization. We did not attempt, however, to probe the course of heterospecific influence because our major interest was documenting when stimulation from female cowbirds began to exert an effect.

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The aim of the present study was to test the generality of female influence by studying other populations of two of the three subspecies of cowbirds. In addition, we chose to follow the course of possible heterospecific influence more closely to see if we could see evidence of systemic influence from an atypical social source. We used canaries as heterospecific companions for two reasons. First, we knew that the species would interact socially with cowbirds under captive conditions (West & King, 1986b). Second, cowbirds have no natural contact with the species, thereby ruling out that any signs of heterospecific influence could be explained by early experience in the wild that might have triggered innate mechanisms such as "pre-active and latent song templates" (Marler & Nelson, 1992, p. 422), constructs invoked to explain vocal origins, especially *selective* models of vocal ontogeny, and a recent elaboration of action-based learning (Marler & Nelson, 1992).

We selected an *M. a. ater* population from Indiana (IN) to extend our knowledge of the eastern subspecies. The IN population represented an older and more central population within the subspecies' range (Potter & Whitehurst, 1981; Thompson, 1994). In addition, we chose a second subspecies, *M. a. artemisiae*, collected in South Dakota (SD), to see if social mediation of vocal development could be extended beyond the *M. a. ater* subspecies. In neither case did we use hand-reared, acoustically naive birds. In both cases, males were collected when between 50 and 100 days of age and housed either with pairs of females (hereinafter female-housed [FH] birds) or pairs of male and female canaries (canary-housed [CH] males).

Some measures of social outcome for these males were already established before the present analyses of vocal origins: We had learned that social housing had demonstrable effects on the males' mate recognition and vocal use during courtship in the first and second breeding seasons (Freeberg, King, & West, 1995; West, King, & Freeberg, 1996, in press). We found striking differences between SD and IN males in their interactions with heterospecifics. The CH males from the SD *M. a. artemisiae* population failed to demonstrate a preference for female cowbirds over canaries when tested in three contexts during the breeding season, directing significant amounts of vocal and social behavior to unfamiliar canaries even when unmated female cowbirds were available and actually soliciting males with copulatory postures (Freeberg et al., 1995). In contrast, the parallel study of IN *M. a. ater* males housed with canaries revealed much less evidence of heterospecific influence. Although these males were no more successful at courting female conspecifics than their SD counterparts, they directed much less social or vocal behavior toward canaries than did the SD males (West et al., 1996). Thus, the SD population displayed an openness at the species level with respect to mate recognition that was less evident in the IN population.

Differences between the two groups of FH males were less obvious. Both groups directed vocalizations to female conspecifics when other males were not present, but both showed inferior courtship in comparison to more normally reared SD or IN adult males. A functional measure of vocal outcome revealed another similarity: We played the males'

vocalizations to females from the males' respective populations, using the number of copulatory postures elicited in response as the measure of song potency. The songs of FH males from both populations were more effective than those of CH males. Indeed, the FH males' songs were as effective as those of normally reared males, a similarity we had also found in eastern *M. a. ater* (King, West, & Eastzer, 1980). Thus, the FH males' songs had been shaped into potentially more effective courtship signals than those of CH males.

The objectives of the present study were to trace, during development, evidence of female influence on song production in both populations and to look for differential signs of attention to heterospecific stimulation between SD and IN males. The greater degree of interest by the SD males in canaries suggested that the two populations might possess different mechanisms of species identification (e.g., some process analogous to visual imprinting) unrelated to vocal acquisition. The SD-CH males, for example, may have learned their vocalizations along essentially the same time course as the SD-FH males, with similarly timed shifts toward stereotyped production. They may only have diverged with respect to the class of birds to whom they preferred to direct their vocalizations, on the basis of visually acquired preferences.

If, however, SD males were generally more malleable than IN males, signs of heterospecific influence might have occurred in vocal structures as well, as we had found for female influence. Such differences in malleability may have arisen due to ecological conditions. Adequate information about ecological differences between SD and IN cowbirds does not exist, but basic aspects of their natural history suggest that juvenile SD males hear less adult song in their hatching summer and probably return later to breeding sites than do IN cowbirds (Friedmann, 1929; Lowther, 1993). Such conditions might have led to temporal shifts in the timing of vocal production so that the young SD males remain modifiable longer to allow them to profit from hearing adult males and interacting with females late into the spring when adults return to breeding grounds—a developmental shift consistent with findings in some sparrows and wrens (Kroodsma & Pickert, 1980; Nelson, Marler, & Palleroni, 1995).

We concentrated our acoustic analysis on features of cowbird song known to produce different levels of copulatory responsiveness in female cowbirds from several other populations (King, West, Eastzer, & Staddon, 1981). For example, in earlier playback tests dissecting the potency of vocal precursors to crystallized breeding season song, *M. a. ater* female cowbirds displayed increases in the frequency of copulatory responding when they heard plastic song with identifiable clusters of notes (see the Method section for definitions) as opposed to plastic song without note clusters. The females also showed a second increase in responsiveness once the order of notes and whistles within a song became stereotyped from rendition to rendition, an event coinciding with a better signal-to-noise ratio (King et al., 1981; West & King, 1988). Thus, we chose to focus on plastic song and stereotyped song as our major comparative measures (although we scored intermediate changes as well).

## Method

### Subjects

*Juvenile males: SD.* Ten juvenile SD male cowbirds, determined by plumage and date of capture to be between 35–70 days of age, served as subjects. They were collected in August 1991 in Fall River and Custer Counties in SD and were returned to the laboratory where they were divided into two experimental groups of 5 birds. The FH males were housed individually with pairs of juvenile female cowbirds collected from the same site. The CH males were housed with pairs of adult male and female canaries from our resident colony.

*Juvenile males: IN.* Sixteen IN juvenile male cowbirds, determined by plumage and date of capture to be between 25 and 60 days of age, served as CH and FH subjects. The CH males ( $n = 9$ ) were collected in July 1992, and the FH males ( $n = 7$ ) in July 1993—all in Monroe County at the laboratory. The CH males were housed individually with pairs of adult male and female canaries. The FH males were housed with pairs of juvenile IN female cowbirds collected from the same site.

All birds resided in sound-attenuating chambers (West & King, 1986b) from the time of collection until the following May. After that point, they were housed in aviaries for observation of other behaviors reported elsewhere (Freeberg et al., 1995; West et al., 1996). All were fed a modified version of the Bronx Zoo diet for omnivorous birds and were maintained on natural light cycles while in the sound-attenuating chambers.

### Recording Schedules and Procedures

The SD and IN males were recorded between the following dates in nine sessions (labeled 1 to 9 in text and figures): December 6–15 (males approximately 175 days of age), December 28–January 3, January 17–27, February 9–17, February 28–March 3, March 11–15, March 29–April 2, April 12–13, and April 28–May 10 (males approximately 325 days of age). The vocalizations of the SD males (December 1991–May 1992) were recorded with Technics RS 1500 recorders at 9.53 cps. The vocalizations of the IN males (CH males: December 1992 to May 1993; FH males: December 1993–May 1994) were recorded with Panasonic SV-3700 DAT recorders. Vocalizations of all the males were recorded by using Sennheiser RF-Condenser microphones. All recordings were made between 0715 and 1400 hr. Males were recorded in 2-hr blocks, after which time the tapes were scanned to determine whether males had vocalized for at least 30 min, with no more than 3 min of silence between any two vocalizations. We attempted to obtain at least 200 vocalizations/male per session by using this method. Recording was terminated for a given session if a male failed to reach the criterion of vocalizing for 30 min after 8 to 14 hr of recording in that session. The mean number of recording hours per male was 32 (Range, 27–34) across the nine sessions.

The vocalizations of the 26 males across the nine sessions were analyzed by using a zero-crossings-analyzer that generated a Frequency  $\times$  Time display on the face of an Tektronix 5113 oscilloscope (West, King, Eastzer, & Staddon, 1979). Where necessary to compare two or more signals, the signals were stored in a digital memory that allowed multiple signals to be viewed simultaneously on the face of a second oscilloscope. The vocalizations were placed into categories reflecting the structural shifts found during the ontogeny of song in this species, as shown in Figure 1 (King & West, 1988; West & King, 1988, Figure 1). The definitions were as follows.

*Plastic song.* Vocalizations in this category possess low- and

high-frequency notes and whistles characteristic of the species, but the elements are poorly articulated and variably ordered across renditions. The vocalizations last from 100 ms to 4–5 s.

*Plastic song with note clusters.* Highly variable vocal sequences, as in plastic song, but ones always containing at least one note cluster. A note cluster consists of at least four notes, with two of low and two of high frequency. The low notes are produced by one voice and high notes with the other—usually in alternation (e.g., low followed by high, or vice versa) and characterized by ascending or descending frequency.

*Formatted song.* Vocalizations possessing definite timing and with syntactic ordering to the elements such that the note clusters occur before the whistle. The songs last between 500 and 1,200 ms, with variable content across renditions in terms of the specific elements used. These songs start with low-frequency tone bursts (notes) grouped into note clusters and terminate with a high-frequency whistle. (*Note:* We report the frequency of formatted song in Figure 3, but we did not test for group differences on this measure because its decline is correlated with the increase in stereotyped song.)

*Stereotyped song.* These vocalizations possess a fixed number and order of elements across renditions, with the vocalization lasting approximately 1 s. Some shifting of frequency or time does occur but affects entire phrases rather than individual notes. We included crystallized songs in this category. They occurred only in Session 9 for all males in the study. *Crystallized songs* are defined by even greater uniformity in terms of the precise timing and frequency of the elements such that new repetitions represent virtually identical copies of one another. We also included songs composed only of note clusters in this category if they met the criteria for highly consistent patterning from rendition to rendition (i.e., the same note clusters were produced in the same order and with the same duration).

*Canary-like sounds.* These were defined as repeated-modulated notes between 700 and 6000 Hz. The repetition rate of the notes was typically slower than when sung by canaries. The notes were structurally similar to canary songs or calls.

*Other elements.* Several other vocalizations were categorized that are not typically defined as part of song ontogeny (see Duffy & Pugh, 1994; Rothstein et al., 1988) or occurred so rarely that we combined the records after scoring. We defined *subsong* as highly variable, unstructured sounds of generally low amplitude containing elements not recognizable to the human as cowbird like. Subsong contains no discrete high notes or high-frequency whistles and is marked by the presence of broadband noise. We defined *whistles* as vocalizations composed of one or two high-frequency (greater than 2.5 but less than 13 kHz) tones lasting between 200 and 1,000 ms. *Rattles* were defined as sequences of broadband frequency-modulated syllables. The durations of individual syllables ranged from 20–45 ms, with a bandwidth between 700–10000 Hz. The total duration of a series of syllables ranged from 100 to 1,000 ms. The vocalization is often termed *chatter* and is usually associated only with female cowbirds (Burnell & Rothstein, 1994; Friedmann, 1929). *Interphrase units* were vocalizations composed solely of a high-frequency note (greater than 6 kHz) with a duration of 15–75 ms. As with formatted song, we did not test for differences in this category across groups because it represented a small proportion of each male's repertoire and we had no predictions about the elements contained within it.

*Observer reliability.* Two observers scored the vocalizations according to the categories defined above. We calculated observer agreement on the basis of the records of 5 birds in five sessions (2 from Session 1, 2 from Session 7, and 1 from Session 8) involving 1,443 vocalizations. We tabulated the percentages of vocalizations

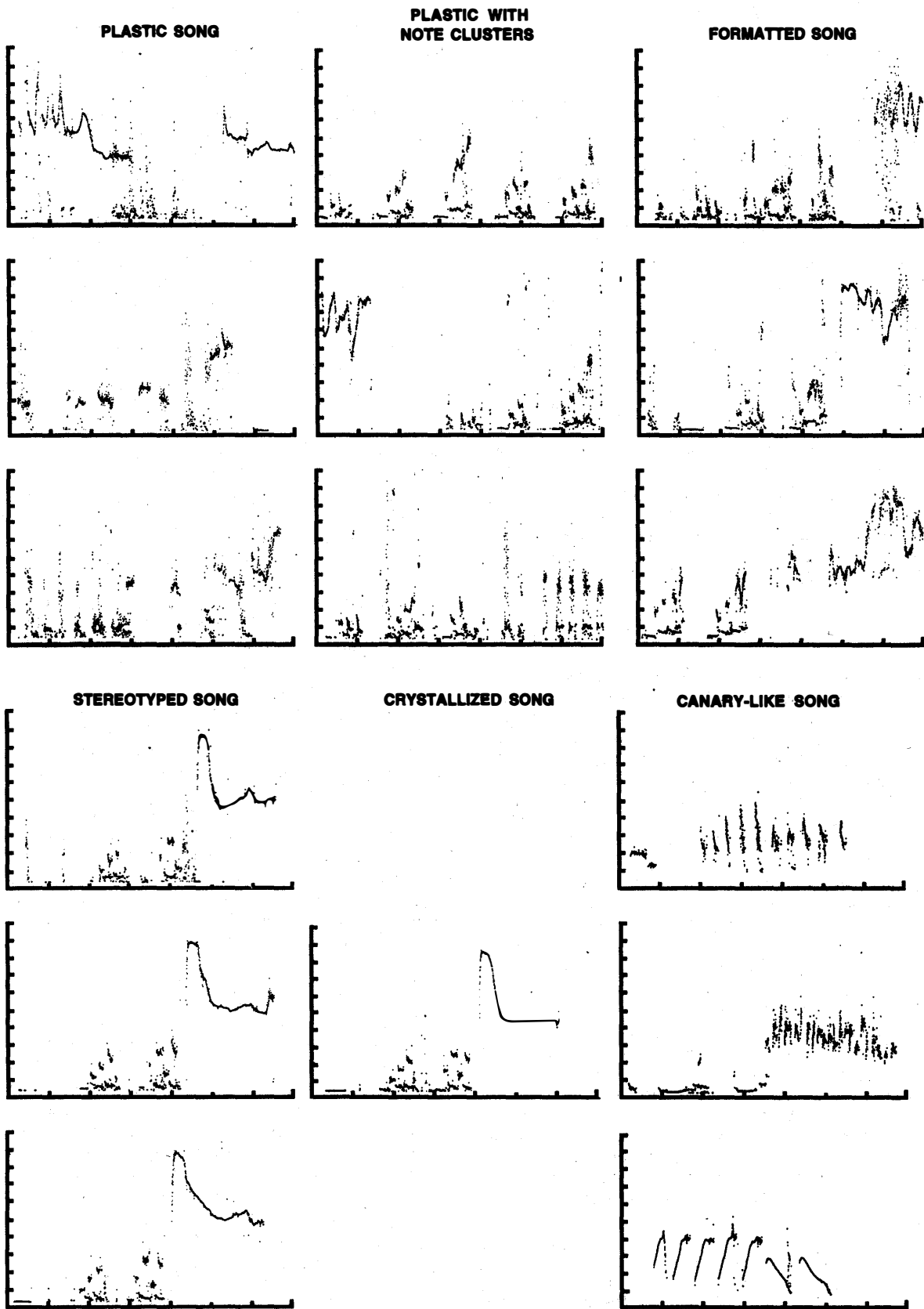


Figure 1. Examples of vocal categories used to score song production.

placed into the same category by the two observers for each of the sessions: The mean percentage of agreement was 87% (Range, 84–93). In cases of disagreement, the original scorer's data were used. Although we report stereotyped song and other elements as combined categories, the smaller units (e.g., stereotyped song vs. crystallized song or rattles vs. whistles) making up the categories were used to calculate the most conservative estimate of observer agreement.

**Statistical analyses.** We used nonparametric tests for all analyses, using Kruskal–Wallis analyses of variance (ANOVAs) for tests across the four groups and Mann–Whitney tests for four comparisons between groups. We did not test all possible differences between groups (six) as we had no predictions about SD-FH males versus IN-CH males or SD-CH males versus IN-FH males. We did not test for some possible statistical differences between the SD males for Sessions 1–5 because too few birds vocalized. Where appropriate, we used sequential Bonferroni adjustments with Mann–Whitney tests to control for multiple tests (Rice, 1989). Probability values were two-tailed.

## Results

We analyzed a total of 44,962 vocalizations from the four groups of males across the nine sessions ( $N = 26$ ). The averages for the four groups were as follows: SD-CH males,  $M = 1,342$  (Range, 1,086–1,894); SD-FH males,  $M = 1,750$  (Range, 1,517–1,986); IN-CH males,  $M = 1,834$  (Range, 1,372–2,337); and IN-FH males,  $M = 1,856$  (Range, 1,548–2,136). No reliable group differences occurred in the number of hours each male was recorded, Kruskal–Wallis ANOVA,  $H(3) = 5.6, p > .20$ .

The vocal development of the males differed by housing condition and by subspecies population (Table 1; Figures 2 and 3). The most obvious difference was in the temporal pace of vocal ontogeny with both groups of SD males beginning to vocalize later and producing fewer vocalizations per hour, especially in the first five recording sessions (Figure 2). The 10 SD males did not all vocalize in the same session until Session 6. More SD-FH males vocalized in Sessions 1–5 than SD-CH males, with a median of 4 SD-FH

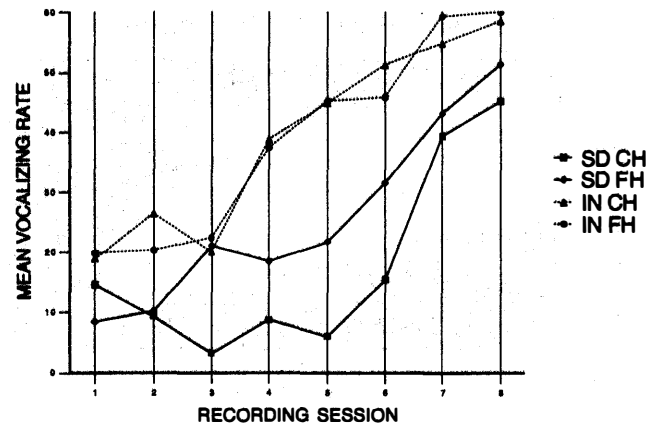


Figure 2. Mean rate of vocalizing by the four groups of males across Sessions 1–8. All 26 males sang so frequently in Session 9 that rate differences were not calculated. The rate for each male for each session was calculated by dividing the number of minutes of vocalizing by the number of hours of recording. SD = South Dakota; CH = canary housed; FH = female housed; IN = Indiana.

birds singing in Sessions 1–5 (Range, 3–4) compared with a median of 2 SD-CH males (Range, 1–4). The 16 IN males vocalized in almost every session: One male failed to sing in Sessions 1–2 (IN-FH). A Kruskal–Wallis ANOVA across all sessions indicated significant differences in vocal rate among the four groups,  $H(3) = 15.5, p < .01$ . Comparisons between groups yielded significant differences for the following comparisons: SD-CH vocalized less than IN-CH males, computed value of Mann–Whitney  $U = 1, p < .002$ , and SD-FH vocalized less than IN-FH males,  $U = 2, p < .01$ , both significant with Bonferroni adjustment  $\alpha = .01$  and  $\alpha = .012$ , respectively.

### Canary-Like Vocalizations

The SD-CH males incorporated significantly more canarylike vocalizations than did the IN-CH males, producing

Table 1  
Median Differences and Range in Amount (Sessions 6–9) and Timing (Sessions 1–9)

Song	South Dakota males		Indiana males	
	Canary housed	Female housed	Canary housed	Female housed
Plastic song (%)	24	8	2	3
Range	9–56	3–22	0–20	0–14
No. of sessions to <10% plastic song	8	7	5	2
Range	7–9	4–7	1–7	1–8
Note cluster song (%)	13	28	14	11
Range	5–33	7–58	4–47	0–23
Stereotyped song (%)	28	44	55	73
Range	14–40	26–78	30–70	35–98
No. of sessions to >10% stereotyped song	7	7	5	2
Range	5–8	4–8	4–7	0–6

Note. The differences and ranges included here are of selected vocal categories for South Dakota and Indiana male cowbirds housed with canaries or female conspecifics.

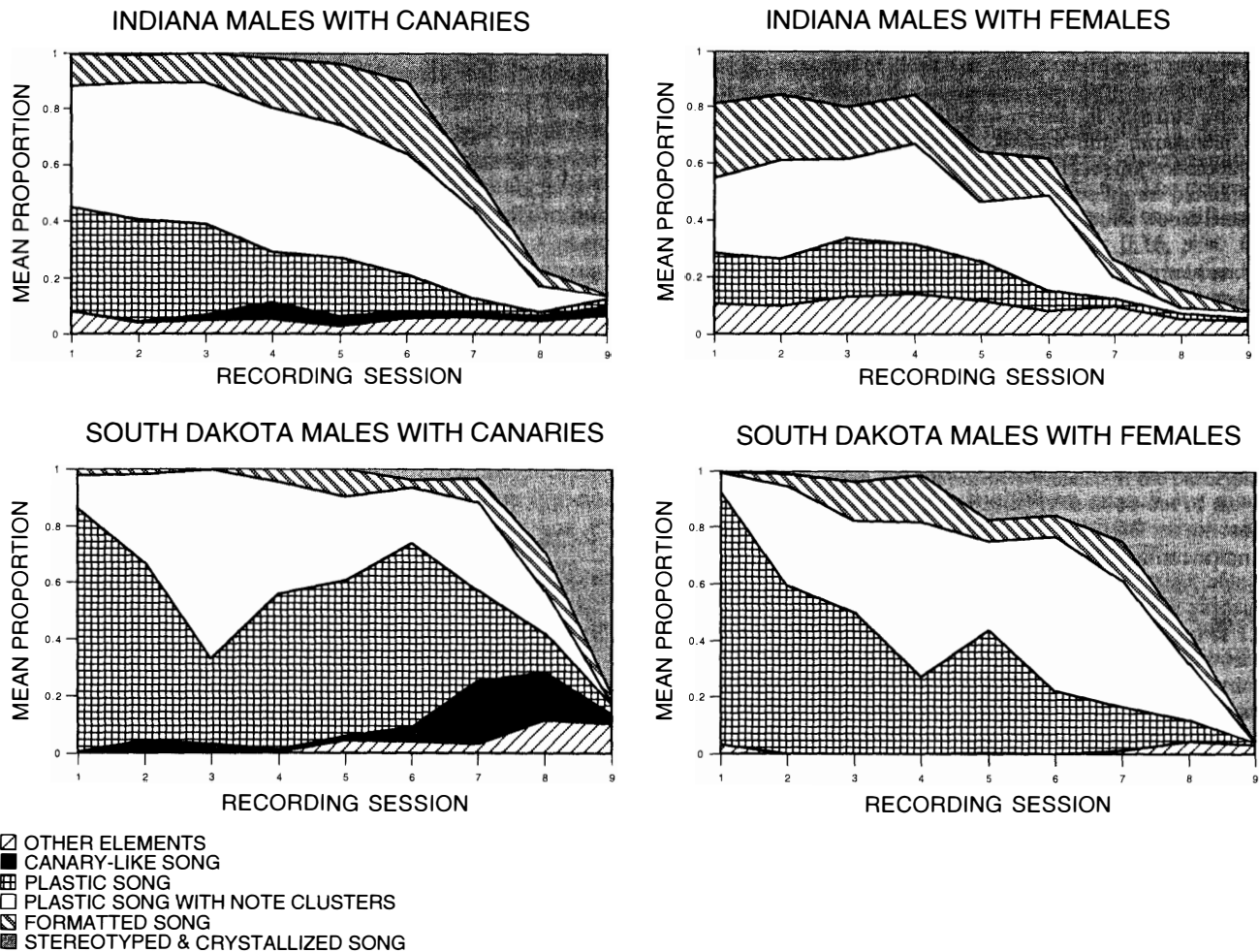


Figure 3. Changes in the mean proportion of production of the vocal categories for the four groups across the nine recording sessions.

a median of 13% (Range, 2–18) canarylike song for Sessions 6–9 compared with 1% (Range, 0–6) for the IN-FH males,  $U = 4, p < .02$  (Figure 3).

*Plastic Song and Plastic Song With Note Clusters*

Over all nine sessions, the SD males averaged more plastic song compared with the IN males, 45% (Range, 22–65) compared with 15% (Range, 3–43; Figure 3). Significant differences in the amount of plastic song produced by the four groups occurred for Sessions 6–9,  $H(3) = 19, p < .001$  (Table 1). The two IN groups did not differ from one another,  $U = 22, ns$ . However, the SD-CH males produced reliably more plastic song than did the IN-CH males in Sessions 6–9, Table 1;  $U = 3, p < .0035$ , significant with Bonferroni adjustment of  $\alpha = .01$ . The two SD groups also tended to differ from one another, with SD-FH males producing less plastic song than SD-CH males,  $U =$

4,  $p < .048$ , not significant with sequential Bonferroni adjustment of  $\alpha = .025$ .

Group differences also occurred in the decline of plastic song,  $H(3) = 10.6, p < .02$  (Figure 3). Plastic song declined below 10% reliably later in the SD-CH males compared with the IN-CH males, Table 1;  $U = 2, p < .002$ , significant at Bonferroni adjustment of  $\alpha = .01$ , with a similar trend in the SD-FH versus IN-FH males,  $U = 7.5, p < .04$ , not significant with sequential Bonferroni adjustment of  $\alpha = .017$ . Declines in plastic song production between IN-CH and FH males were not significantly different ( $U = 21, ns$ ) but close to significant for the SD-CH males who showed a slower decline than SD-FH males,  $U = 3, p < .028$ , with sequential Bonferroni adjusted at  $\alpha = .025$ .

The amount of plastic song with note clusters sung during Sessions 6–9 did not differ reliably across the four groups,  $H(3) = 5.8, p > .10$ . The IN-CH males did produce reliably more plastic song with note clusters during Sessions 1–5

than the IN-FH males, which were already advanced beyond this stage (see Figure 3),  $U = 7$ ,  $p < .005$ .

### *Stereotyped Song*

The SD males produced virtually no stereotyped song until Session 5. One SD-FH male accounted for all stereotyped song before this time (Figure 3). One SD-CH male never produced stereotyped cowbird song, although he did crystallize two canary-like vocalizations. In contrast, the IN-FH males produced reliably more stereotyped song in Sessions 1–5 compared with the IN-CH males (19% vs. 1%),  $U = 2$ ,  $p < .001$ . Differences in the onset of stereotyped song also yielded significant group differences,  $H = 9.5$ ,  $p < .05$ , with the IN-FH beginning to sing stereotyped song reliably sooner than the IN-CH males,  $U = 7$ ,  $p < .006$ , significant at Bonferroni adjusted  $\alpha = .01$  or the SD-FH males,  $U = 2$ ,  $p < .005$ , significant at Bonferroni adjustment of  $\alpha = .013$ . The onset of stereotyped song did not differ for the two CH groups ( $U = 17$ , *ns*) or between the two SD groups ( $U = 6$ , *ns*).

The amount of stereotyped song produced during Sessions 6–9 also varied by population,  $H(3) = 11.8$ ,  $p < .01$ . The SD-CH males' production was significantly less than that of the IN-CH males,  $U = 4$ ,  $p < .006$ , significant at Bonferroni adjusted  $\alpha = .01$ , and the SD-FH males tended to produce less stereotyped song than the IN-FH males,  $U = 4$ ,  $p < .048$ , not significant with Bonferroni adjustment of  $\alpha = .025$ . Differences within population with respect to housing condition showed similar trends: SD-CH males sang less stereotyped song than SD-FH males,  $U = 4$ ,  $p < .048$ , not significant at Bonferroni adjustment of  $\alpha = .025$ , and IN-CH males tended to sing less of the category than IN-FH males,  $U = 6$ ,  $p < .037$ , not significant at Bonferroni adjustment of  $\alpha = .017$ .

As noted earlier, we included songs composed only of note clusters into the category of stereotyped song. Such songs were sung primarily by the IN males in Sessions 6–9 and were produced more frequently by the IN-FH males, 16% (Range, 0–48) versus 7% (Range, 0–29) for the IN-CH males. One SD-FH male produced this one-note-cluster variant during Sessions 1–5 and then deleted it.

Many of the songs produced in Session 9 exceeded the criterion for stereotyped song, qualifying as crystallized song (Figure 1). The mean percentages of crystallized songs for the four groups were similar. The SD-CH males averaged 86% crystallized song (Range, 53–100), the SD-FH males averaged 90% (Range, 77–100), the IN-CH males averaged 85% (Range, 70–100), and the IN-FH males produced an average of 90% (Range, 60–96).

### *Correlations Between Vocal Rate and Song Progression*

The differences in the pace of song development were correlated with the decline in plastic song and the increase in stereotyped song. For the 26 males as a whole, rate of vocalizing (number of songs produced per hour of record-

ing) was positively correlated with the decline in plastic song and the onset of stereotyped song,  $r_s = .63$ ,  $p < .01$ , for both comparisons. For the four groups, the correlations indicated a more positive relationship for the FH males in both populations. For the decline in plastic song, the correlation for the SD-CH males was  $r_s = .50$ , *ns*, and  $r_s = .8$ ,  $p < .10$ , for the SD-FH males. For the IN males, the correlation for IN-CH males was  $r_s = -.10$ , *ns*; for IN-FH males, the correlation was  $r_s = .93$ ,  $p < .01$ . For the onset of stereotyped song, all correlations were positive and significant, SD-CH,  $r_s = .90$ ,  $p < .05$ ; SD-FH,  $r_s = .95$ ,  $p < .025$ ; IN-CH,  $r_s = .86$ ,  $p < .03$ ; and SD-FH,  $r_s = .98$ ,  $p < .001$ .

### *Growth of Other Vocal Elements*

Subsong occurred rarely. It was sung by 1 IN-CH male in Session 1 and by 4 SD-CH males between Sessions 1–4. Whistles accounted for an average of less than 10% of all vocalizing in all four groups across sessions. The SD-CH males whistled most during Sessions 6–9, averaging 6% (Range, 1–10) compared with 1% (Range, 0–7) for the SD-FH males, with 1 SD-FH male accounting for all the whistles. The IN-CH and FH males whistled roughly comparable amounts: 5% (Range, 0–12) and 7% (Range, 2–12) across all sessions. The males possessed 0–3 whistle types: SD-CH males produced 0–2 types, SD-FH males produced 1–3 types, IN-CH males produced 0–3 types, and IN-FH males produced 0–2 types. Other vocal elements, primarily rattles and single notes, accounted for less than 10% of singing in any session for any male.

### *Final Song Features: Repertoire Size and Number of Note Clusters*

We looked at general differences in final song structure, although the functional outcome was known: When played back to females from their respective populations, the songs of FH males elicited significantly more copulatory postures than did the songs of the CH males (Freeberg et al., 1995; West et al., 1996). Repertoire size differed among the four groups,  $H(3) = 9.4$ ,  $p < .05$ . The IN-FH males had larger repertoires of songs (excluding whistles) ranging from 3 to 4, with a median of 4 song types compared with 2 song types (Range, 1–3) for the IN-CH males,  $U = 4.5$ ,  $p < .001$ , significant at Bonferroni adjustment of  $\alpha = .01$ . The SD-FH each produced 2 song types and the SD-CH males ranged from 1 to 3, averaging 2 song types,  $U = 12.5$ , *ns*.

The number of different note clusters within a male's repertoire also tended to differ by group,  $H(3) = 12.9$ ,  $p < .01$ . The IN-FH males averaged the most number of different note clusters, producing a median of 5 (Range, 3–7), followed by the IN-CH males with an average of 4 (Range, 2–5), the SD-FH males with 3 (Range, 2–5), and the SD-CH males, with an average of 2 clusters (Range, 1–4).

## Discussion

We focused on female and heterospecific stimulation as these influences have been studied less often in songbirds. The paucity of information on the effects of social companions on the *process*, as opposed to the *outcome*, of vocal learning may explain the greater emphasis on imitative mechanisms as the sole means by which vocal material is acquired (Marler & Nelson, 1992). The data presented here and in previous studies of cowbirds challenge the generality of this view (King & West, 1988; see also Payne & Payne, in press). The data indicate that vocal ontogeny can also be the epigenetic product of social learning and imitation.

The data also suggest some populations of cowbirds may accept heterospecifics as sources of vocal influence—a finding hard to reconcile with concepts of preprogramming and templates. The SD-CH males incorporated both phonological and structural patterns from their canary companions: Not only were canary syllables recognizable, but repetition rates of some vocalizations mimicked canary songs as well. Some of the males' flight whistles also revealed the influence of canaries, further evidence of social malleability. We chose canaries as companions because, from previous observations, we knew they would interact socially with cowbirds (West & King, 1986b). In particular, vocal overtures by the male cowbirds received a variety of responses including approach, departure, lunging, ignoring, and the use of calls. The possibility for differential social reinforcement, therefore, seemed to be present.

Our use of canaries was also driven by the need to rule out prior acoustic experience in the field as a source of vocal influence. The results suggest that some populations are very open to social influence, suggesting the real possibility that contact with other cowbird subspecies, which naturally occurs, could also affect development. New evidence supporting such a prediction comes from work in progress in which juvenile male and female SD cowbirds were housed together either with an adult aviary of IN or SD cowbirds (Freeberg, in press). At the end of their first year, the SD males' songs showed clear evidence of incorporation of IN or SD vocal patterns. In addition, social effects were evident: The mating preferences of the juvenile SD birds, as tested in captive aviaries, could be predicted by their social experience in the laboratory, not by their place of origin. Thus, the SD juveniles' experience with another subspecies paralleled the effects found here with SD males and canaries.

The finding of experiential influences on the mating preferences of SD individuals is also important in thinking about the nature of female influences on vocal ontogeny. Previous attempts to modify female song preferences in eastern populations of *M. a. ater* have provided very little evidence of malleability (West & King, 1986a). Thus, SD females may differ from other populations in the origins of their song preferences, with postnatal experience playing a definite role. Such malleability in females may have behavioral consequences for males' vocal ontogeny. Juvenile SD females may be less effective social stimulators in their first year as their own preferences are still developing and

changing. Malleability in females may mean that SD males must be prepared to modify and to improvise song structures at basic levels quite late in their first year to appeal to changing preferences of returning females. Such reasoning suggests that second year SD males should show considerable evidence of vocal change from their first to second year, and they do. In captive and field settings, substantial degrees of vocal plasticity in both songs and flight whistles have been documented (Freeberg, in press; O'Loughlen & Rothstein, 1993). Such plasticity also affords a continuing role for males as vocal tutors, a topic not addressed here, but ultimately important, as males represent naturally complementary sources of vocal and social stimulation (Freeberg et al., 1995; West et al., 1996).

Geographic differences in the timing of exposure to adult male cowbirds have been suggested as a mechanism explaining differences in the size of song and flight whistle repertoires in a western population of *M. a. artemisiae* (Kroodsma, 1988; O'Loughlen, 1995; O'Loughlen & Rothstein, 1993). Two likely (and correlated) differences between the IN and SD populations studied here are the length of residence of males and females before the breeding season and the timing of the breeding season in relation to migration (South Dakota Ornithologists Union, 1991). The more northern latitude for SD (43° as opposed to 39°) is associated with later arrival times for yearlings and adults and represents a harsher climate that may affect the timing of nesting of hosts, a critical stimulus for breeding in this parasitic species (Friedmann, 1929). By contrast, IN yearlings and adults arrive earlier, and more young cowbirds may hatch earlier because of the milder climate. Some of the IN males studied in this research were collected while resident adults were still present and singing.

Several field reports for eastern populations of *M. a. ater* also suggest more exposure to adult males and females in a juvenile's first summer than in other populations (Dufty, 1982, 1985; Hahn, & Fleischer, 1995). Thus, it is quite possible that the IN and SD juvenile males entered the experiment with quite different amounts of exposure to species-typical signals. The IN males probably had greater auditory and social contact with conspecific adults, thus setting into motion different ontogenetic trajectories.

The overall pattern of populational differences complement those of Nelson, Marler, and Palleroni (1995) for two subspecies of white-crowned sparrows, *Zonotrichia leucophrys oriantha* and *Zonotrichia l. nuttalli*. Their investigation used hand-reared males, which were virtually acoustically naive, and were housed in the laboratory in social isolation. They found reliable differences in the timing of shifts from primitive to stable song, with the migratory *oriantha* males singing subsong and plastic song later and crystallizing song a full month later than the sedentary *nuttalli* sparrows. Nelson et al. viewed the differences as adaptations to environmental differences including the harsher climates faced by *oriantha* males, producing a shorter singing season, and differences in the timing and length of exposure to adult male tutors. Intraspecific variation in developmental parameters of song acquisition has also been documented in several other songbird species in

which ecological variations such as hatching time, dispersal, or migratory patterns affect exposure to song material from adult tutors (DeWolfe, Baptista, & Petrinovich, 1989; Kroodsma, 1974, 1982, 1983; Kroodsma & Pickert, 1980).

What is required to produce the raw material for such intraspecific comparisons are detailed descriptions of changes in behavior during development. Simply comparing the vocal outcomes of young learners provided with access to different vocal or social stimulation is inadequate. The time at which such stimulation begins to affect the nature of vocal production must also be identified. Only with such information can researchers hope to understand the specific variables actually responsible for the generation of the vocal material that subsequently is subjected to improvisation, shaping, or selection. The results presented here suggest that in some species, the emergent acoustical organization of the notes may not arise solely from "extensive pre-encoding of information about species-typical structure, embodied in innately-specified brain circuitry" (Marler & Nelson, 1992, p. 415). Vocal precursors of song may also be the ontogenetic products of socially set preferences for sounds made by the learner or his or her companions, preferences reinforced and perhaps modified throughout development by the behavior of listeners.

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