

Non-Vocal Shaping of Avian Song Development: Parallels to Human Speech Development

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Abstract

Vocal development in young male cowbirds (*Molothrus ater*) is sensitive to acoustical stimulation from males, but also to social feedback from female cowbirds, even though females do not sing. Juvenile males show different vocal trajectories if housed with local or distant population females. The major goal of the present study was to identify differences in the form and timing of non-vocal cues from females during the period in early spring when juvenile males begin to sing stereotyped song and to finalize their repertoires. We housed juvenile males with either local or distant population females and no adult males. We found significant differences between the two groups of females in the use of wing stroking and in male reactions to wing strokes and gapes. There were also differences between the groups in male song performance. To understand further the potential consequences of these differences, we correlated measures of male and female responsiveness to results reported in Smith et al. (2000) on vocal ontogeny and song potency. We found that wing stroking by females was associated with a faster rate of song development and tended to relate to differences in song potency. The non-vocal shaping seen here may represent a general mechanism for the development of vocal communication, as similar processes influence phonological development in human infants.

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Introduction

Studies of song learning in passerines typically focus only on male behavior, such as the processes of vocal imitation and improvisation of song. The crucial form of stimulation for song ontogeny is usually thought to be auditory in nature, and the key social agents are assumed to be male learners and male tutors (Kroodsma 1996). Neurobiological studies of the song control region in the avian

brain also focus almost exclusively on auditory pathways (Brenowitz & Kroodsma 1996). In brown-headed cowbirds (*Molothrus ater*), however, the presence of non-singing female cowbirds during song ontogeny has been shown to have the potential to influence the process of song learning: both the structure and function of songs are affected (King & West 1983, 1988; West & King 1988; Smith et al. 2000). Thus, female behavior is implicated in a social learning system whereby males attend not only to vocal and visual feedback from other males, but also to visual feedback from females.

Here we focused on two visual signals produced by female cowbirds during vocal performances of young male cowbirds in the final phase of song learning in their first year (Smith et al. 2000). We asked how contingent relationships between such signals and male singing affected song development. One form of visual signaling had been identified by West & King (1988) in a study of videotaped interactions between juvenile male cowbirds housed individually with adult female cowbirds in early spring. The videotapes revealed the females' use of a rapid wing action, a response termed a wing stroke. Wing strokes were as brief as 200 ms and co-occurred with the male's production of his 1-s song. Wing strokes happened infrequently, about once for every 100 songs produced. The juvenile males responded to wing strokes by retaining song material that had elicited the females' responses (West & King 1988). Songs eliciting wing strokes developed into effective courtship signals, as measured by subsequent playback testing of the songs' effectiveness at eliciting copulatory postures in females in breeding condition. Songs associated with wing strokes were significantly more potent than songs produced in the same singing bout but unaccompanied by a wing stroke.

Informal observation during the West & King (1988) study also revealed that when males saw wing strokes, they moved toward the female, looked at her wings, and sang again, often repeating the specific song pattern that elicited the wing stroke. The infrequency of wing strokes may have made them more conspicuous to the males. Subsequent observations revealed another visual behavior, a female gape, a rapid and wide opening and closing of the bill with the beak turned upwards. It too appeared to be related to males' vocal behavior but its specific relationship was unknown.

These informal observations suggested the possibility that female visual behavior is used to reinforce song practice in a process of non-vocal shaping. Behavioral shaping occurs when animals come to make connections between the production of different behaviors and the contingent occurrence of different responses or reinforcers, leading the animal to retain those behaviors that are the most associated with a positive response (Catania 1984). A possible form of vocal shaping identified in songbirds is termed action-based learning (Marler & Nelson 1993). Action-based learning has been described in several sparrow species in which young birds go through a phase of overproduction of song material from which learners select specific song patterns to be retained in their final repertoire. The selection process is guided by 'reinforcement' such as song contingent matching between a tutor and learner. A key feature defining action-based

learning is that the song material being reinforced is already possessed by the male, having been acquired earlier during the sensory phase of song learning guided by a species-specific innate template.

Cowbird song development differs in two important ways from action-based learning. First, social reinforcement occurs throughout the stages of song ontogeny, not just during the final winnowing phase. Rather, from as early as song production can be measured in late fall, there is evidence of female influence on song structure (King & West 1988). Even when the birds are only producing the variable and inarticulate sounds termed subsong and plastic song, they are affected by social interaction with females. Thus, non-vocal shaping appears to be a systemic feature of song ontogeny in this species. Second, the non-vocal stimulation from females represents a source of learning that does not involve imitation. Males do not copy the behavior they see females produce, but learn from the contingencies between their behavior and the female's behavior to alter their singing. Third, males elicit non-vocal feedback by singing directed songs to females. Male song can be undirected, i.e. oriented toward no individual, or directed, i.e. physically oriented toward a particular male or female. In a series of investigations, we found that songs directed to females enhance copulatory success in captive colonies. The degree of use of female-directed song during the breeding season also correlates with song potency and neural changes in the anterior song pathway and the visual thalamic nucleus, Rt (West et al. 1996; Hamilton et al. 1998; Freeberg et al. 2003). The observation of directed song is also used in the field to indicate mated pairs (Yokel & Rothstein 1991). Thus, the ingredients for developmental change appear to be present in the nexus between directed singing by males and non-vocal signaling by females.

A comparative analogue to shaping by non-vocal stimulation has recently been described in humans. In a study of 8-mo-old human infants, we tested the hypothesis of non-imitative non-vocal involvement in pre-linguistic vocal development (Goldstein et al. 2003). This developmental period (often called babbling) has been proposed as a parallel to the period of production of vocal precursors called subsong and plastic song in songbirds (Marler 1970; Petrinovich 1972). These early forms of vocal production are characterized by variable phonological structure and articulatory quality, as is the case with vocal precursors to birdsong. We found that mothers' use of non-vocal signals such as touching and smiling, when infants babbled, were sufficient to produce immediate phonological advances in the 8-mo-old infants' vocal repertoire. The mothers' behaviors had to be contingent on the infants' vocal production for the effect to occur. Infants who received equivalent amounts of non-contingent stimulation did not change the quality of their vocalizations. These data are significant because, as in songbirds, the vast majority of studies of infant vocal development focus on imitation of sounds, a purely auditory process.

The purpose of the present study was to look for evidence of non-vocal shaping during the song learning process. Specifically, we explored the contingent relationship between female visual signals such as wing strokes and gapes and male vocal behavior. We looked for such effects many weeks before courtship actually

begins, i.e. during the time period when birds first return to breeding grounds by early spring. We used as our sample of birds the 12 males that had been studied in Smith et al. (2000). The males had been divided into two experimental groups. In the first group, young males were housed individually with two adult females from their local South Dakota population (LP); in the second group, young males from the same LP capture site were housed with females from a distant Indiana population (DP). The two female populations came from different subspecies, characterized by differences in female song preferences (King et al. 1996; West et al. 1998). The housing began in Jul. and ended the following May. The results of the Smith et al. (2000) study demonstrated the long-term consequences of female presence. First, the LP-housed males developed stereotyped songs sooner and produced more potent playback songs than did the DP-housed males. Second, the LP females stayed closer to the male after song delivery more frequently than did the DP females. Third, neuronal volume of the visual thalamic nucleus Rt was larger in the LP-housed males than the DP-housed males (Freeberg et al. 2003). Finally, the LP songs differed from the DP songs in the nature of amplitude relationships on the low voice notes in the song's first phrase (Smith et al. 2000).

Although we suspected that visual communication was important to the differential vocal development in the two groups, we had not measured the frequency of female signaling or differences in male song use. Wing strokes and gapes are very rapid and could not be seen via the methods used in Smith et al. (2000) where observations were made in real time and males were sampled only 20 min/wk. Here, we used slow motion videography to capture visual and vocal signals used by males and females. We videotaped the birds in early spring during the period Smith et al. suggested was critical to the selection of songs to be retained in the bird's final repertoire. By studying males from a single population whose development diverged as a consequence of different social companions, we hoped to isolate key behavioral patterns that might account for the different developmental trajectories prior to the breeding season.

We asked the following questions about activity occurring in the early spring: (1) did the two groups of males differ in song use, i.e. the prevalence of directed or undirected vocalizing? (2) did the two groups of females differ in the use of wing strokes or gapes in response to directed and undirected songs? (3) did males differ in their responses to wing strokes or gapes? and (4) did individual differences in female visual signals or male singing relate to the developmental outcome variables identified in Smith et al. (2000), i.e. onset of stereotyped song and song potency? Based on previous work (West & King 1988), we predicted that wing strokes would be related to the outcome measures; we could not predict how gapes would relate to these same variables.

Methods and Subjects

The subjects were the same individuals used in Smith et al. (2000). We had collected 12 juvenile male cowbirds (*M. ater artemisiae*) in Aug. 1995 to serve as subjects. They came from Fall River and Custer Counties of South Dakota when

they were between 50 and 100 d of age. The 12 adult LP females serving as social companions had lived and bred in outdoor aviaries for 2 yr with South Dakota males; all had been collected as adults at the same site as the males in Aug. of 1993. The 12 adult Indiana (DP) females (*M. ater ater*) were collected as adults in Aug. of 1993 in Monroe County of Indiana and had lived and bred in outdoor aviaries with other Indiana males until the onset of the current work. All birds were housed in triads in sound-attenuating chambers (interior dimensions: 1.3 m³) beginning in Jul. 1995 and ending in May 1996. The males were randomly assigned to 12 individual chambers, six with two LP females and six with two DP females. All birds were banded with colored leg rings to permit individual identification. They were fed a modified version of the Bronx Zoo diet for omnivorous birds, supplemented daily with red and white millet, canary seed, and vitamin-treated water.

Procedures for Collecting and Analyzing Data

We videotaped the triads between Mar. 12 and Apr. 4, 1996. Each chamber was videotaped for 2 h every morning between 0800 and 1000 h for 5–10 d, as on some days there was no vocal behavior by the DP group. This 2-h window in the morning was chosen as it is the time of the most vocal activity. We analyzed 8 h of recording for each triad, choosing tapes so that the median recording date was the same for both groups. We divided singing into two categories: undirected and directed. We included male flight whistles and plastic song into the category of undirected song because males showed no orientation toward the female when producing them and because they occurred infrequently, accounting for less than 8% of all singing. When a song occurred, the observer recorded the type of song and each female's reaction as listed in Table 1. If neither female changed her behavior during the song or within 1 s of the offset of the song, the sequence was terminated and a 'no response' was scored for each female. But, if one or both females produced a response within 1 s of the song, we scored that event and all subsequent reactions by either bird within 1 s of the preceding reaction.

Other forms of social interactions occurred in the triads, not initiated by song, but we did not use these measures in the present study as our focus here was on responses to song overtures. Two observers viewed six 2-h tapes, three from each group to finalize the measures and establish reliability, which was above 90% agreement for all behaviors. For behavioral coding and reliability, the tape was slowed down and analyzed frame-by-frame using a JVC BRS-800 U video deck (JVC Co. of America, Wayne, NJ, USA). Data from the present study were subsequently correlated with two measures from Smith et al. (2000). The measures were onset of stereotyped song and song potency. Stereotyped song was defined as vocalizations possessing a fixed number and order of elements across renditions, with a duration of approximately 1 s. These songs were characterized by extremely precise timing and frequency of the elements such that new repetitions were essentially identical copies of one another. Onset was defined as the first recording session in which 10% or more of the male's songs were stereotyped. As reported in Smith et al. (2000), the LP group began singing

Table 1: Definitions of male and female behaviors

Undirected song	A song beginning with note clusters followed by a whistle, not oriented toward any individual, with or without a wing spread display; flight whistles consisting of a pure modulated tones, sometimes with more than one syllable, generally between 4 and 14 kHz; or immature song including male rattling. To be scored as undirected, the male could not be oriented toward another individual.
Directed song	To be coded as directed singing, the male had to be oriented within a 30° axis to the female. The 30° rule did not apply if the male was less than 15 cm from the female. In most cases, the male also performed a wing-spread display while singing.
Look/Approach	Movements after a song decreasing the distance between the male and female by a body width or change in body orientation so that the male was on axis with the female.
Other male action	Movements after a song such as preening or stretching, flying, wing movements, lunging, pecking, or chasing.
Gape	Female opens beak widely generally with a vertical head movement during or following the end of a song. No vocalization accompanies the gape and the beak opens much wider than during the female vocalization of rattling.
Wing stroke	Rapid wing movement by a female during a song or within 200 ms of the end of the song.
Move away	Females flies or moves more than one body width away from the male.
Move to	Female moves to within 15 cm of the male or makes three consecutive movements toward the male and is then within 30 cm of the male.
No response	No movement or failure to meet the criterion for any other reaction.

stereotyped song between Mar. 5, 1996 and Apr. 8, 1996; the DP males began between Apr. 8 and Apr. 25, 1996. The LP songs were significantly more potent than the DP males' songs. Playback song potency was defined as the frequency of copulatory postures elicited from male deprived females during the breeding season (see Smith et al. 2000 for more details). Repertoire size did not differ between the two groups, with a median of two songs for LP males and three songs for DP males (see Smith et al. for more details).

Data Analysis

The responses of the two females in each chamber were averaged into one score. Thus, all comparisons are based on N's of six. Because of the small sample size and heterogeneity of variance, we used non-parametric analyses: Mann-Whitney U-tests for between group comparisons and Spearman rank-order

correlations for analysis of individual differences; all p-values are two-tailed. Bonferroni adjustments were made when conducting multiple comparisons as noted in the text (Sokal & Rohlf 1995, p. 240). p-Values less than 0.05 were noted as trends. Means and standard errors are provided for descriptive purposes.

Results

Song Production in Males

Directed and undirected song occurred very frequently, totaling 27 172 vocalizations, 10 014 by the DP males and 17 158 by the LP males, or 3.5 songs/min for DP males and 5.9 songs/min for LP males. The two groups of males did not differ in the production of undirected songs, 7821 (range: 610–2114) for the DP group and 9621 (range: 1162–2114) for the LP group (Mann–Whitney U-test = 18, ns). Directed songs were produced more frequently by the LP group, totaling 7537 (range: 677–2083) songs compared with 2193 (range: 38–981) for the DP group ($U = 2$, $p < 0.01$). The males also differed in the proportion of songs that were directed or undirected, with LP males singing more directed songs than DP males ($U = 2$, $p < 0.01$). Undirected and directed songs were not correlated with each other: for number of songs, the correlation was $r_s = 0.231$ (ns) and for proportion of songs, $r_s = -0.301$ (ns). Tables 2 and 3 present means and standard errors for number and proportion of directed and undirected songs across the entire 8 h of recording.

Table 2: Mean number and standard error of male and female behaviors across 8 h of recording

	Distant population triads (n = 6)	Local population triads (n = 6)
Undirected songs	1304 (307)	1603 (271)
Directed songs	365 (147)	1226 (187)*
Female no response		
Undirected song	1478 (428)	1986 (322)
Directed song	348 (150)	1196 (288)**
Female wing strokes		
Undirected song	36 (9)	37 (17)
Directed song	4 (2)	40 (10)***
Female gapes		
Undirected song	36 (7)	70 (10)****
Directed song	12 (8)	66 (25)**
Female move to		
Undirected song	39 (15)	20 (7)
Directed song	16 (9)	28 (6)
Female move away		
Undirected song	255 (65)	141 (30)
Directed song	156 (51)	436 (32)*****

* $p < 0.01$; ** $p < 0.025$, trend; *** $p < 0.005$; **** $p < 0.037$, trend; ***** $p < 0.004$.

Table 3: Mean proportion and standard error of male and female behaviors across 8 h of recording^a

	Distant population triads (n = 6)	Local population triads (n = 6)
Undirected songs	0.813 ± 0.04	0.564 ± 0.04
Directed songs	0.187 ± 0.05	0.436 ± 0.04*
Female no response		
Undirected song	1.09 (0.11)	1.24 (0.03)
Directed song	0.792 (0.11)	0.930 (0.05)
Female wing strokes		
Undirected song	0.010 (0.004)	0.020 (0.005)
Directed song	0.010 (0.004)	0.033 (0.005)**
Female gapes		
Undirected song	0.035 (0.009)	0.047 (0.005)
Directed song	0.041 (0.009)	0.048 (0.012)
Female move to		
Undirected song	0.032 (0.012)	0.012 (0.003)
Directed song	0.049 (0.015)	0.022 (0.063)
Female move away		
Undirected song	0.208 (0.035)	0.095 (0.024)
Directed song	0.581 (0.106)	0.382 (0.040)***

^aBecause each female in the pair could contribute one or more responses to a given song, the proportions do not add up to one.

* $p < 0.01$; ** $p < 0.004$; *** $p < 0.043$, trend.

Number of Female Responses to Song

We measured five female contingent reactions to song: no response, wing stroke, gape, move toward the male and move away from the male. Separate analyses were carried out for undirected and directed song as the two measures were not correlated ($r_s = 0.231$, ns).

The critical alpha for significance was set at $p < 0.01$ for each analysis. Most often, both females failed to respond to a song (Table 2). LP females tended to show no behavioral response more often than did DP females to directed song ($U = 4$, $p < 0.025$). The LP females produced a total of 462 wing strokes and the DP females produced 241. The number of wing strokes between the groups did not differ significantly for undirected song ($U = 12$, ns), but did for directed song, with LP females producing a mean of 40 (SE = 10) wing strokes compared with 4 (SE = 2) for DP females, ($U = 36$, $p < 0.005$). During sequences initiated by a vocalization, LP females produced a total of 816 gapes and DP females produced 290. Eighty-one additional gapes (50 in LP-housed birds and 31 in DP-housed birds) occurred during sequences not initiated by a vocalization but were not analyzed further.

The LP females showed a tendency to gape more to undirected songs (70; SE = 10) than did the DP females, (36, SE = 7) gapes ($U = 5$, $p < 0.037$). The LP females also tended to gape more to directed songs than did the DP females,

66 (SE = 25) vs. 12 (SE = 8) gapes ($U = 4$, $p < 0.025$). Movement toward the male was much less frequent than moving away ($U = 7.5$, ns). There were no group differences in the number of times females moved toward the male ($U = 13.5$, ns). The females also did not differ in the number of times with which they moved away when the male sang undirected song, but they showed a significant difference when males produced directed song, with LP females moving away more often ($U = 0$, $p < 0.004$).

Proportion of Female Responses to Male Song

We also examined the mean proportions of vocal responses to the same five female variables in light of the large difference in the number of directed songs between the two groups (Tables 2 and 3). The statistical analyses of the five responses to directed vs. undirected song were considered separately because the frequencies of directed and undirected songs were not correlated ($r_s = 0.301$, ns). The critical alpha was $p < 0.01$. No differences between groups for the category of 'no response' for neither type of song (U 's = 11.5 and 14, ns), nor did the groups differ in the mean proportions of wing strokes to undirected song ($U = 12$, ns). The LP females displayed a higher proportion of wing stroking to directed song than did DP females, 0.03 (SE = 0.005) vs. 0.01 (SE = 0.004), ($U = 0$, $p < 0.004$). The mean proportion of gapes and moves toward males did not differ between the groups for either song category (U 's between 8 and 10, ns). Finally, the LP females, compared with the DP females, tended to move away less often from undirected song ($U = 5.5$, $p < 0.043$) but showed no difference for moving toward the male ($U = 10$, ns).

Male Response Following Wing Strokes and Gapes

Figure 1 shows the four categories of male behaviors scored following the females' production of wing strokes or gapes. The critical alpha was set at $p < 0.0125$ for each of the two analyses. The LP and DP males differed in their reactions. LP males sang proportionately more directed songs after wing strokes than did DP males ($U = 2$, $p < 0.01$) and LP males looked at and/or approached the females more often ($U = 1$, $p < 0.007$). The two groups did not differ in the proportion of male acts and undirected songs ($U = 8$ and 12, ns). Reactions to gapes differed by group. The LP males sang proportionately more directed song following gapes than did the DP group ($U = 2$, $p < 0.01$), looked at/approached females proportionately more often ($U = 2$, $p < 0.01$) and showed a tendency to produce more undirected song ($U = 4$, $p < 0.025$). They showed no difference in the proportion of male acts ($U = 15$, ns).

Relationship to Developmental Outcomes

We looked at individual differences among males and females in the production of undirected and directed song and use of wing strokes and gapes in

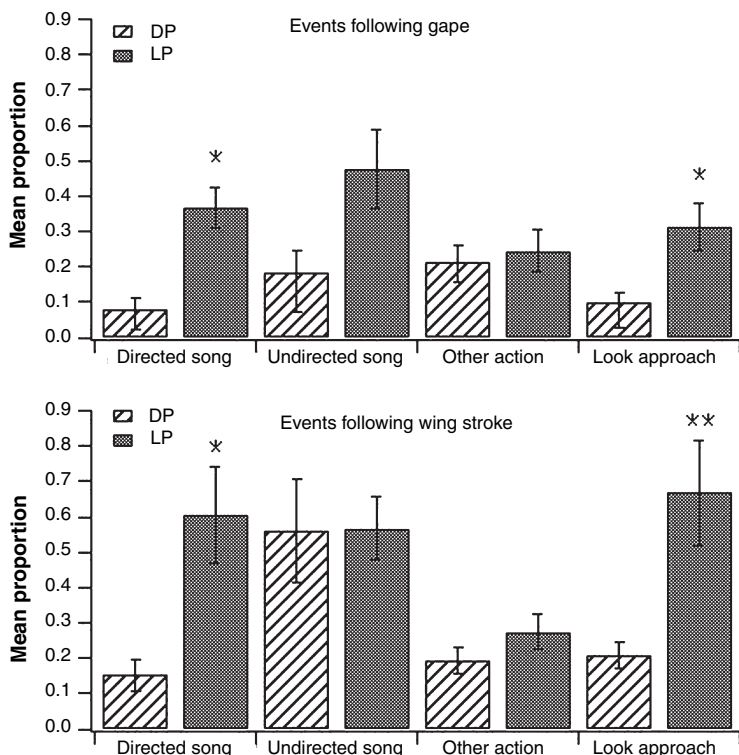


Fig. 1. Mean proportion and standard error of the male's responses following a female gape or wing stroke. * $p < 0.01$; ** $p < 0.004$. See Table 1 for definitions. The proportions do not add to 1.0 because a single male behavior could follow multiple gapes or wing strokes by the pair of females or the male could follow the wing strokes or gapes with more than one behavior as long as the events occurred within 1 s of one another

relation to two developmental variables from Smith et al. (2000): onset of stereotyped song and playback song potency (Fig. 2). We set the critical alpha level at $p < 0.025$ for correlations between (a) onset of stereotyped song the two song types and (b) between song potency and the two song types. For the males, the correlation was $r_s = -0.87$ ($p < 0.004$) between number of directed songs and advancement to stereotyped song whereas the correlation was -0.42 (ns) for undirected song. Thus, males that produced more directed song required less time to reach the onset of stereotyped song. For song potency, there was a tendency for directed song to be related, $r_s = 0.64$ ($p < 0.034$) and no correlation for undirected song, $r_s = 0.32$ (ns). For females, we looked at whether production of wing strokes and gapes to directed or undirected song related to the two developmental measures. We set the alpha level at $p < 0.0125$ as there were four correlations for each of the two outcome variables. The rate of wing stroking to directed song correlated with onset of stereotyped song, $r_s = -0.78$ ($p < 0.009$) and showed a tendency to be related to song potency, $r_s = 0.64$ ($p < 0.03$)

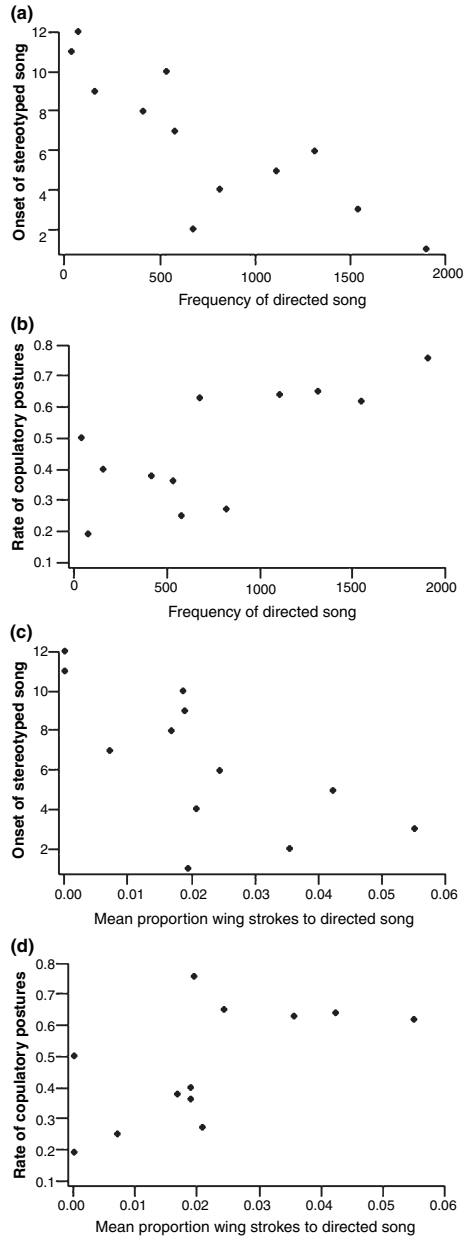


Fig. 2: Scatterplots of the relationship between (a) frequency of directed song and the time of onset of stereotyped song where faster onset is expressed as a lower rank; (b) frequency of directed song and the mean rate of responding with copulatory postures to the 12 males' songs; (c) time of onset of stereotyped song and the proportion of wing stroking during directed song; and (d) mean rate of responding with copulatory postures and mean proportion of wing strokes to directed song. See Smith et al. (2000) for more details on onset of stereotyped song and copulatory responding

(Fig. 2). Rate of gaping to undirected or directed song did not correlate with either outcome variable ($r_s = -0.37$ and 0.13 , ns).

Discussion

The local and distant population females stimulated different patterns of male song use, even though all males originated from the same local population. Specifically, the males in the two groups differed in their production of directed song, and the two subspecies of females varied in their use of two visual signals; wing stroking and gaping. Local population females produced more wing strokes and gapes to directed songs compared with distant population females, while the two groups produced the two signals equally when songs were undirected. When the data were corrected for differences in opportunity to respond to directed songs, the LP females displayed a reliably higher rate of wing stroking than did DP females, even given the very large difference in frequency of directed songs. Both female visual responses were infrequent in comparison to the frequency of vocalizing. On the other hand, the amount of vocalizing was extremely high: the 12 males averaged 4.7 songs for each minute of observation. The infrequency of wing strokes and gapes could have made their occurrence quite conspicuous to the males. The LP males saw more wing strokes and gapes when they directed songs to females than did the DP males. These differences in perception correlated with differences in developmental outcome for the LP group, where more directed singing and wing stroking were related to a faster onset of stereotyped song and higher song potency. We do not know whether male or female differences are responsible for the relationship between responsiveness and the developmental outcome measures. Given that all the males were collected at the same time from the same population and randomly assigned to the two groups, the differences suggest the females' behavior is critical to creating differences in male singing.

As a whole, the data provide evidence of the operant nature of non-vocal shaping. The operant response, directed singing, is very frequent and is reinforced periodically. An intermittent reinforcement schedule is known to produce highly reliable responses across many behaviors in many taxa (Catania 1984). Evidence that males attend to the reinforcement is seen in Fig. 1. which shows how frequently males sang after receiving a wing stroke and/or attempted to look and approach the female. The necessary role of attention in the process is indicated by the findings of relationships between female responses and directed, but not undirected, singing. During undirected singing, the male may be at a distance from the female, may be facing away, and thus not able to see the female signals.

Like a wing stroke, the gape is rapid, difficult to record in real time, and an infrequent response to song. While the wing stroke and gape generally produce an immediate vocal or approach reaction from the male, wing strokes appear to be a more sensitive measure of the female's responsiveness. The similarity of the wing stroke to a pre-copulatory posture may explain its greater potency. Gapes may signal general interest in singing on the part of females but not attention to

specific song structure or use. Possibly in this context, gapes serve to attract the male's attention and foster orientation toward the female, inferences supported by the data shown in Fig. 1.

The females' differential responses to song most likely began long before the observation period in Mar. As noted earlier, we have evidence of female influence on male song structure from as early as Nov., when males are producing primitive and extremely variable vocalizations (King & West 1988). We can only speculate as to the origin of differences in female responsiveness found here, but it seems likely that the earliest vocalizations of the males in the fall reflect subspecies variation in song structure (King & West 1988; Freeberg et al. 2001). It is doubtful that the males had experience with adult males in South Dakota before being captured because adults were not seen in the capture area prior to collection (T. M. Freeberg, pers. comm.). Given these circumstances, the subspecies variation in the LP males' songs was probably not learned. The LP females may have been more interested and reactive to the 'population appropriate' song elements than the DP females for whom these elements represented foreign acoustic patterns. As noted earlier, the two groups differed in the amount of amplitude placed on the note in the song's first phrase. The females were all several years old and were experienced with local song variants in the field prior to capture and in aviaries thereafter. Previous work shows that females from these two populations show local preferences for playback songs from their respective populations and differences in final song structure have been identified (West et al. 1998; Freeberg et al. 2001).

Across the triads, the frequency of directed song and wing stroking correlated with two outcome measures from Smith et al. (2000), onset of stereotyped song and song potency. The results suggest that there is a synergistic relationship between components of social interactions and the progression of vocal development. Previously, we found that vocal precursors of song that received wing strokes elicited more copulatory postures 2 mo later during the breeding season (West & King 1988). The faster onset of stereotyped song in the LP males, a time span of 2–4 wk, may have allowed them to crystallize their repertoires sooner and/or to receive positive feedback about more advanced forms of singing (see Smith et al. 2000 for more details). The males may also be more successful at acquiring mates as they may be able to pair at an earlier date.

Because of the difficulty of seeing and recording wing strokes and gapes, it is difficult to study them in nature. We do know, however, that they occur outside of the environment of sound attenuating chambers, i.e. in flocks in large indoor–outdoor aviaries. Female wing stroking and gaping to playbacks of male song were videotaped in flocks of females during the fall, and female wing stroking appeared to play an important role in fostering female social interactions but gaping was only observed on two occasions (Gros-Louis et al. 2003). Thus, males may need to be present for females to use the gape behavior regularly.

Male cowbirds in nature, and in our aviaries, sing frequently to other males and show evidence of song sharing. These vocal interactions affect song structure and are important for reproductive success (White et al. 2002). Thus, the

processes described here with females represent only one potential component of vocal learning, but one that has been understudied. The time period we chose for analysis coincides with the return to breeding grounds and the beginnings of frequent interactions between males and females in the field. Although males also sing often to each other during this time, observations of cowbirds in the field, and in aviaries, reveal considerable singing to females (Friedmann 1929; White et al. 2002; M. J. West, pers. obs.). Thus, the kinds of stimulation studied here are likely to represent learning opportunities in nature that supplement those gained through male–male interactions.

More evidence for the likelihood of this occurring in nature comes from a study of a flock of 74 Indiana cowbirds in a multi-compartment aviary (Smith et al. 2002). We found that young males sought out associations with adult females, even when males were present. Young males with the most frequent associations with adult females showed signs of advanced song development relative to males who spent less time with females. Under these conditions, males had many choices as to companions and yet we still saw associations between young males and adult females. We have also observed juvenile males repeatedly associating with adult females during late winter in an overwintering roost in the field (King & West 1988). Moreover, the males in the field were singing the same proportions of plastic and formatted song as were males of the same age housed alone with females in captivity.

As noted earlier, a potentially important feature of female influence on learning is that it is entirely non-imitative in nature. Cowbirds are the only songbird species in which female shaping has been documented, but cowbirds are also one of the only species in which the potential process has been studied. Others have however found roles for visual or contingent stimulation in conjunction with auditory stimulation (e.g. Bischof & Engelage 1985; Hultsch et al. 1998; Houx & ten Cate 1999; Houx et al. 2000; Balsby & Dabelsteen 2002). Thus, there is evidence of the power of visual stimulation during song learning and of the possibility of non-vocal shaping. It seems unlikely that the brood parasitic habit of the cowbird is uniquely associated with female song influence as other aspects of song learning in cowbirds such as song sharing, response to tutoring, and song maturation are similar to those found in non-parasitic species (King & West 1988; White et al. 2002).

What function might female stimulation of song learning serve? It may be that female stimulation of song learning affects subsequent choice of mates, in that females may prefer males that have learned to be maximally attentive to them. They need not be associating with the males they encountered in the spring. Rather, they may be affiliating with other local males who also show the same trait, that of sensitivity to female signals. Given that females in a local area show significant concordance for the songs they prefer, individual females may all be shaping male vocal content in the same direction. Females may also benefit from interactions prior to the breeding season: we now have evidence that exposure to males in the spring can alter female preferences (King et al. 2003). Thus, a synergistic system may exist whereby females attend to preferred adult males and then transmit these preferences to juvenile males.

Given that attentive behavior by the males is associated with a more rapid achievement of song stereotypy and higher song potency, females that choose males whose songs were influenced by female stimulation may be selecting mates that are more likely to respond to social contingencies, an attribute that may distinguish a high quality male. Nowicki et al. (1998) have shown that quality of song learning may be a factor in sexual selection of mates. We know from other studies that reproductive success is higher in males that show evidence of social learning of critical courtship behaviors from other males such as the use of counter-singing or female-directed song (White et al. 2002).

The generality of vocal shaping awaits testing in other species. Although imitation will continue to be one of the major vehicles for the cultural transmission of vocal signals, it may not be the only one. The presence of social companions affects many aspects of vocal learning and thus it seems quite likely that the social dynamics of interactions involving vocal precursors will uncover new mechanisms of learning in other species (Marler & Nelson 1993; Baptista & Gaunt 1997; Snowdon & Hausberger 1997; Elowson et al. 1998). To do so, however, may require methods such as those used here, involving precise documentation of the nature of social experience and experimental manipulations of social contingencies as was carried out here and in Goldstein et al. (2003).

Non-vocal signals are common responses to mature vocal communication in many species including humans (Argyle 1972). But the focus here is on non-vocal signals used by social companions during the young learner's *acquisition* of an auditory communication signal, i.e. before the time it assumes its adult form and function. At this phase in ontogeny, the prevailing assumption has been that human babbling represents only motoric practice (Jakobson 1941/1968; Lenneberg 1967), but not communication (but see Elowson et al. 1998 for a social role for babbling in non-human primates). New perspectives are emerging, however, as more is learned about the acoustic nature of vocal precursors and the potential for social interaction (Papousek & Papousek 1987; Oller 2000).

The studies of female influence in cowbirds suggest that communication between the sexes begins early and that vocal precursors have functional properties beyond practice. The time period for such communication is analogous to the period of pre-linguistic vocal development in humans and it is during this time period that we found similarities between the two species. In playback studies, for example, Goldstein & West (1999) found that mothers responded consistently to the pre-linguistic vocalizations of unfamiliar infants, suggesting that the sounds conveyed a social function beyond practice. Mothers also became more sensitive to vocal cues as the infants' vocal repertoires advanced in articulatory quality, similar to the change in responsiveness to stereotyped song in cowbirds. And, in Goldstein et al. (2003), we found that differential non-vocal responding to infants' vocal signals brought about rapid changes in phonological output. Even when human mothers were silent partners in interactions with their children, infants modified the nature of their speech. Thus, we propose that non-vocal shaping represents a comparative similarity between humans and songbirds in which non-vocal cues are used to enhance the task of learning how to communicate.

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