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A role of her own: female cowbirds, *Molothrus ater*, influence the development and outcome of song learning

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Previous work has shown that captive female cowbirds, *Molothrus ater*, can influence the outcome of male song development by affecting retention or deletion of song elements and by stimulating improvization. Here we looked for evidence of female influence during the process of learning, as males progress from subsong to plastic song to stereotyped song. In a longitudinal study, we measured the rate and timing of vocal development in captive, juvenile male brown-headed cowbirds, *M. a. artemisiae*. Half the young males were housed with female cowbirds from their own population (South Dakota: SD) and half with female cowbirds from a *M. a. ater* population (Indiana: IN). Both populations of females prefer local songs and differ in the time of breeding, with SD females breeding 2 weeks later than IN females. The results showed significant effects of female presence on the age at which males advanced through stages of vocal development: the SD males with SD females, as opposed to SD males with IN females, developed stereotyped song earlier, reduced motor practise earlier, and produced more effective playback songs. Longitudinal observations of social interactions showed that the two groups of females reliably differed in social responses to males. Degree of social proximity of females to males in the winter predicted song maturity, rate of rehearsal and song potency. Thus, females can stimulate the progression of song learning, as well as prune song content.

In many species of songbirds, females serve as receivers of male signals, thereby providing a means for sexual selection of traits such as song or plumage. Such selection occurs on the adult phenotype of these traits. But what if female behaviour also affects the developmental trajectories of such traits? In that even seemingly minor shifts in timing of ontogenetic events can cascade into major phenotypic changes, such an epigenetic role for females would endow them even more evolutionary force (Gould 1977; Oyama 1982; Raff & Kaufman 1983; Gottlieb 1992). In some mammals, females produce extragenetic effects on the sex, size, morphology and behaviour of offspring (Michel & Moore 1995). However, with few exceptions, a female's role during the development of a potential signaller's behaviour has not been examined (but see Moore & Morelli 1979).

The issue of ontogenetic effects has immediate ecological meaning for songbirds. Appropriate timing of song readiness is crucial given the seasonal nature of breeding of many temperate zone species. It is especially important to migratory populations as they may have an even more limited time window to learn to use song on breeding grounds. Experiences that could shift a male's rate of acquisition of vocal skills could then be key to reproductive success (Nelson et al. 1995; O'Loghlen & Rothstein 1995; Kroodsma 1996; Nelson 1999).

We have already gathered considerable evidence demonstrating that captive female brown-headed cowbirds, *Molothrus ater*, affect the outcome of song learning by stimulating males to modify specific song content (King & West 1983b, 1989; West & King 1985, 1986, 1988a). The females' impact on song is all the more challenging to understand because females do not sing and cannot act as vocal models, ruling out imitative mechanisms. A cross-modal process appears to be at work in which males attend to visual cues from females to modify their own vocal production.

The effects of female cowbirds has been noted as an example of 'action-based learning' and 'selective attrition', a process by which overproduction of song material is winnowed to correspond more to local conditions (Marler & Peters 1982a, b; Marler & Nelson 1993; Nelson & Marler 1994). The strongest evidence indicating action-based learning in cowbirds comes from studies of captive males and females in early spring. We showed that female cowbirds respond to certain songs with rapid wing actions, gestures termed wing strokes. Wing strokes

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typically cannot be seen without the aid of videotape as they can be as brief as 200 ms, occurring simultaneously with the male's production of his 1-s song. Males attend to wing strokes as indicated by changes in proximity and posture and by changes in song content and frequency of repetition of specific song types. Songs that provoke wing strokes in early spring are also much more potent releasers of female cowbirds' copulation solicitation displays than songs that do not elicit wing strokes (West & King 1988a). Thus, females influence selective attrition, as is the case in other studies of action-based learning.

However, must females await males' production of relatively stereotyped song types before influencing the vocal learning system? Our research has led us to think that females may act as social facilitators at earlier points in time. We have found evidence of early female influence when males are under 4–5 months of age and are still producing primitive and variable sounds. For example, we randomly assigned acoustically naïve males from a local population to receive social stimulation from female cowbirds from a local or a distant population. Differences in the acoustic content of song were evident when the males were under 150 days of age, differences biased towards female preferences (King & West 1988). We have also found that female cowbirds discriminate between the kinds of vocal precursors (e.g. subsong and plastic song and plastic song with note clusters) produced by males of this age (West & King 1988b). Females may have the opportunity to exert these effects at many times over the year: before autumn migration, when adult and juvenile males sing after their summer moult; on wintering grounds, where singing is frequently heard in winter roosts in the southern U.S.; and after their return to breeding areas in the spring (King & West 1988).

Here we chose to look specifically at the role of females on the pace of transitions from subsong to stereotyped song. Do females influence the rate of production of song material even before they begin to participate in its pruning? The specific design of the present study drew on a recent experiment in which we found that young males housed with juvenile female cowbirds arrived at the stage of song stereotypy 2 or more weeks earlier in the spring than males housed with canaries (*Serinus canaria*). This time difference translates into 20–50% more time for yearling males to use songs of higher acoustic quality when they interact with conspecifics after migration (late February to early March in the midwestern U.S.) and prior to the onset of breeding (late April; Friedmann 1929). Yet these data do not allow us to characterize the females' behaviour in terms of facilitative effects. It could be that the differences in timing or singing rate reflected anomalous effects of housing half of the males with nonconspecifics. Such conditions may have lead those males to develop song slowly. Thus, the differences between the two groups cannot be assumed to provide any 'positive' evidence of female-based regulation of song development. We sought to clarify this issue in the present work by housing all males with female cowbirds and asking if females with different social characteristics could differentially modulate the rate of development.

To that end, we compared the social effectiveness of female cowbirds from two midwestern populations, Indiana (IN) and South Dakota (SD) on the song development of juvenile SD males. Prior work had established that captive IN and SD females both respond significantly more to playback of songs from their respective local populations. Also, captive IN cowbirds come into breeding condition 2 weeks earlier than SD birds and begin responding to song playback earlier than SD females, even when the two groups are on the same photoperiod (West et al. 1998). Thus, we reasoned that young SD males might receive different social responses from IN versus SD females, allowing us to determine whether different patterns of social responsiveness were associated with differences in song development. We measured rate of singing and transitions in song content from early autumn until late spring, and final song potency. At the same time, to find mechanisms underlying female influence, we observed the birds, recording social actions and reactions of females to a male's approach or vocalization.

METHODS

Subjects

Twelve male cowbirds served as subjects. We collected the juvenile males in Fall River and Custer Counties of South Dakota when they were between 50 and 100 days of age. The 24 females serving as social companions had been in the laboratory for one or more years and used in previous experiments in both outdoor aviaries and sound-attenuating chambers. The 12 IN females were collected in Monroe County of Indiana and the 12 SD females had been collected at the same site as the juvenile males. In August of 1995, all birds were housed in triads in sound-attenuating chambers ($1.3\ m^3$), allowing social interactions among the triad but no social or acoustic contact with other triads. Six males were randomly assigned to chambers with two SD females (hereafter, the SDH males) and six assigned to chambers with two IN females (the INH males). All birds used in the study were banded with coloured leg rings to permit individual identification. All were maintained on a modified version of the Bronx Zoo diet for omnivorous birds and were given millet, canary seed and vitamin-treated water daily. The photoperiod in the chambers followed the natural photoperiod for our location in south-central Indiana.

The same 24 females served as subjects for assessment of males' vocalizations in May and June 1996, where we scored copulatory postures displayed by the females in response to playback of the males' songs. The females were housed in their 12 original pairs, except in two cases where SD females were exchanged with one another.

Measures of Social Behaviour

We used the following measures of social behaviour throughout the study.

(1) Song: a vocalization containing any elements of cowbird song. Male song (or 'perched song', see Rothstein

et al. 1988) consists of several low-frequency tone bursts followed by a high-frequency note and whistle lasting between 200 and 1200 ms. The tone bursts are organized into notes and note clusters, with songs having one to three such clusters. We defined song as directed if the male was within 0.6 m of the female and oriented a wing-spread display towards her.

(2) Vocalizing rate: the number of minutes vocalizing in a recording session. A singing bout was determined to be over when a male produced no vocalization for 3 min.

(3) Approach: movement by a female or male to within 0.3 m of another bird or birds.

(4) Stay to male: no movement in place by a female beyond 2.5-cm shifts of the feet following a vocalization or an approach.

(5) Sidle: movement of greater than 2.5 cm using the legs either sideways or forward within 2 s of onset of a song or approach.

(6) Fly: taking to air by flapping of the wings within 2 s of onset of song or approach.

Observation Procedures

Beginning on 7 September 1995 and ending on 18 May 1996, we took social behaviour samples consisting of 10-min social interaction focal observations for each female, thus 20 min per triad. All focal observations were taken between 0730 and 1200 hours. We recorded actions and reactions between the focal female, male and other female. All but three social behaviour samples spanned a period of a week or less. The three exceptions spanned 16, 15 and 10 days. Fifteen samples began with observations from the SD social condition and 16 with the IN social condition. No more than three consecutive samples began with the same condition. Starting time of focal observations was balanced across chambers. We gathered 31 samples, representing 124 h of observation.

Audio Recording Schedules and Procedures

The SD males were recorded for 10 h every 10 days beginning on 22 September 1995 and ending 13 May 1996, resulting in 17 sessions and 170 h of recording. The vocalizations were recorded with Panasonic SV-3700 Professional DAT recorders. Vocalizations of all the males were recorded using either Sennheiser RF-Condenser or electret microphones. All recordings were made between 0715 and 1200 hours. Males were recorded in blocks over three consecutive days for 4 h, 4 h and 2 h. The 10 h of recordings were scanned to determine total minutes of singing and to obtain vocalizations used for analysis of the development of song structure for each session.

Altogether, across the 17 audio recording sessions, 50 560 min of vocalizing were recorded, 26 471 for the INH males and 24 769 for the SDH males. The median number of recorded minutes of vocalizing per session was 204 (range 15–494) for SDH males and 246 (range 45–480) for INH males.

Song Development Analysis

We categorized the vocalizations into one of six categories: plastic song, plastic song with note clusters, formatted song, stereotyped song, whistles and other.

(1) 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.

(2) Plastic song with note clusters: highly variable vocal sequences, as in plastic song, but 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 (notes between 300 and 1500 Hz) and high notes (greater than 1550 Hz) with the other voice usually in alternation and generally characterized by ascending frequency.

(3) Formatted song: vocalizations possessing definite timing and with syntactic ordering to the elements. Formatted songs last roughly between 500 and 1500 ms with variable content across renditions. They start with low-frequency tone bursts (notes) grouped into clusters and end with a high-frequency whistle.

(4) Stereotyped song: vocalizations possessing a fixed number and order of elements across renditions, with a duration of 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. These songs possess extremely precise timing and frequency of the elements such that new repetitions are essentially identical copies of one another.

(5) Whistles: vocalizations composed of one or two high-frequency (greater than 2.5 but less than 13 kHz) tones. We included in this category both flight whistles, consisting of modulated tones between 500 and 2000 ms in duration, and the whistle component of the song sung in isolation, consisting of one syllable or more and lasting between 200 and 1200 ms.

(6) Other elements: production of rattles or isolated song elements (e.g. subsong). Rattles were defined as sequences of broad-band frequency modulated syllables. The vocalization is often termed ‘chatter’, and is usually associated only with female cowbirds.

The number of sessions birds took to reach and stay at or above a criterion of 10% or more minutes singing consisting of a particular developmental category was considered the time until onset of that category. Similarly, the number of sessions until singing of a particular category dropped and stayed below 10% was considered time until decline.

Notes comprising note clusters, in additional to being produced by either the high (HV) or low voice (LV), differ in relative amplitude to each other. The amplitude of each note relative to the preceding note leads to different kinds of note sequences. For example, some note clusters contain sequences of notes such that each note is produced with greater amplitude than the previous note, thereby producing sequences of ascending amplitude

(King & West 1988). We define the LV/Notes ratio as the proportion of all notes produced in a song that are low voice notes with ascending amplitude (a note with greater amplitude than the preceding note).

We analysed a total of 37 403 vocalizations from the 12 males across the 17 sessions. The median number of vocalizations per session for the two groups was: SDH males, 181.5 (range 133–220) and INH males, 217.5 (range 140–217), a nonsignificant difference (Mann–Whitney: U=16, N_1=N_2=6, NS). To measure any acoustic correlates of song potency, we measured the acoustic structure of the 24 songs chosen for playback. To look for precursors to potency, we measured the acoustic features of six vocalizations from each male from the 8 April (the 12th) recording session.

Playback Procedures

Playback songs

Zero-crossings-analyser (ZCA) displays were used to analyse songs from the final recording session for playback. Song types (different structural patterns sung repeatedly by a male; West et al. 1979) were classified by two observers. For use in playbacks, we chose the two most frequently sung song types of each male, a total of 24 songs. One example of each was chosen on the basis of recording quality (median number of recordings/male=68, range 17–153). We then dubbed the recordings chosen for playback to an Otari MX5050 MK III half-track recorder at 38.1 cycles/s.

Playback testing

The males were removed in the third week of May and playback testing began a week later. We played songs back using an Otari MX5050 recorder, a Urei 537 1/3-octave equalizer, and a Crown D75 power amplifier through JBL 2105 speakers located in each chamber. The Urei equalizer was adjusted by playing white noise through the playback system and then recording speaker output with a Brüel & Kjaer (B&K) 2033 spectrum analyser. The sound pressure level (at 76.2 cm) was 85 ± 2 dB adjusted with a B&K 2209 sound pressure meter, set to A weighting, impulse reading.

We played six songs a day to the females, with one vocalization per trial, separated in time by 90 min. We played back each vocalization six times over the course of 24 days. Vocalizations were played in varying orders each day, but each vocalization was presented once at each time of day. We scored a positive response to a playback song if a female adopted a copulatory posture within 1 s from onset of the sound (i.e. if she arched her neck and back and separated the feathers around the cloacal area). Song potency for each male was defined as the average proportion of positive responses to playbacks of his two songs. A second observer scored responses on 4 of the days of playback. Agreement between observers on occurrence or nonoccurrence of a copulatory posture was 100%.

Statistical Analysis

We combined the 31 behaviour samples into three periods, autumn (eight samples, September–October), winter (12 samples, November–February) and spring (11 samples, March–May). We chose these times to correspond generally to cowbirds' migratory habits, with birds leaving breeding grounds in the late autumn and arriving the next spring beginning in late February. Among the measures of changes in song structure, we targeted the growth of stereotyped song for statistical comparisons as it was the behaviour of most interest and changes in other song categories (e.g. plastic or formatted song) were not independent. Because of heteroscedasticity of most behaviour and song data, we used nonparametric analyses for all but the playback potency data. Medians and ranges are presented unless otherwise noted. Mann–Whitney tests were used to test for between-condition differences of males or females. To determine whether the two groups of females displayed differing trajectories for their social reactions, we used the method of combining probabilities from tests of significance. Probability values are distributed such that $-2 \ln P$ is distributed as a chi-square with two degrees of freedom. Probabilities from multiple tests of the same phenomenon can be tested by summing $-2 \ln P$ values and determining significance based on a chi-square with degrees of freedom equal to two times the number of tests (Sokal & Rolf 1995, pp. 794–797). The P values for these comparisons are listed as 'overall' P value in the text. Spearman rank correlations and analyses of variance (ANOVAs) were also used when appropriate. All tests were two tailed.

RESULTS

Vocalizing Rate

Although SDH and INH males vocalized at about the same rate until spring, they diverged thereafter (Fig. 1). In the first recording session in April (session 12) and the last one in May (session 17), the two groups showed nonoverlapping differences in singing rates. SDH males reached their peak of singing reliably sooner than INH males, measured by the number of recording sessions until the maximum rate of singing (Mann–Whitney U test: U=0.5, N_1=N_2=6, P<0.01). As a group, SDH males averaged maximum frequency of singing in the 12th session whereas INH males were still increasing in session 17.

Emergence of Stereotyped Song

In addition to differences in rate of song activity, SDH and INH males' pace of song development differed (Figs 2, 3). The six SDH males were all producing 10% or more stereotyped song in session 12 whereas it was two more sessions before all INH males sang stereotyped song (Fig. 2). SDH males sang more stereotyped song in the spring and took fewer recording sessions to reach the criterion of 10% or more stereotyped song than INH males (median number of sessions to onset=12, range 10–12 for SDH; median=12.5, range 12–14 for INH; ties

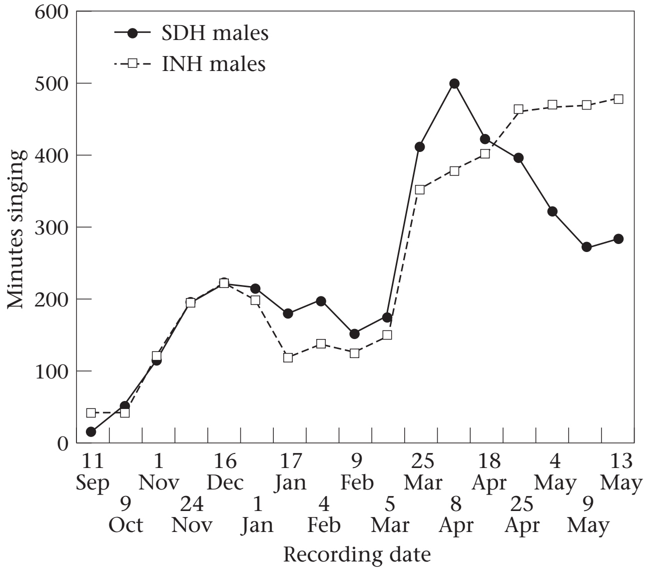

Figure 1. Average minutes singing by SDH and INH males during 10-h recording sessions from September through to May. Each of the 17 recording sessions spanned 3 days and began on the date indicated on the *X* axis.

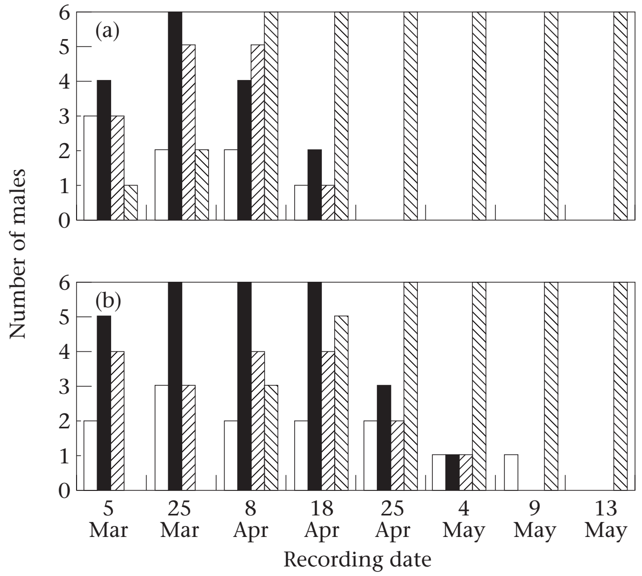

Figure 2. Number of males singing each song type in recording sessions in March, April and May (the last eight recording sessions): (a) SDH males, (b) INH males. A male was considered to be singing a song type (☐: plastic; ■: plastic plus note clusters; ▨: formatted; ▧: stereotyped) if at least 10% of his minutes vocalizing during the 10-h recording session consisted of that song type. Each recording session spanned 3 days and began on the date indicated on the *X* axis.

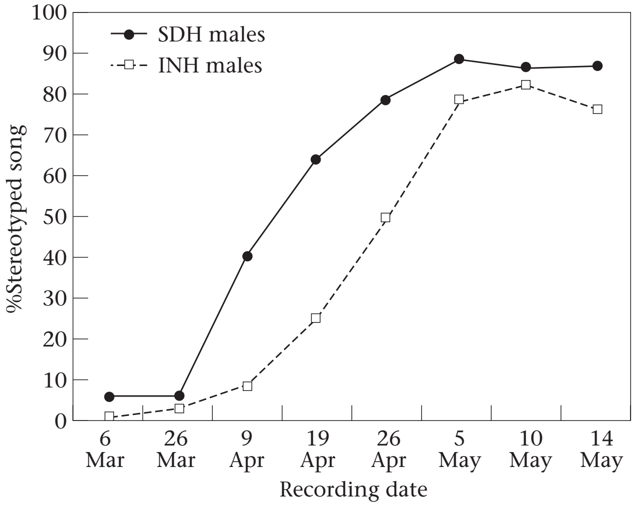

Figure 3. Average percentage of total vocalizations consisting of stereotyped song in March, April and May (the last eight recording sessions) for SDH and INH males. *Y* axis represents the average percentage of minutes singing during the 10-h recording sessions that was classified as stereotyped song. Each recording session spanned 3 days and began on the date indicated on the *X* axis.

broken by ranking the percentage of stereotyped song; Mann–Whitney *U* test: $U=0$, $N_1=N_2=6$, $P<0.01$; Fig. 3). Correspondingly, INH males retained plastic song with note clusters longer than SDH males (median number of sessions to decline=14.5, range 14–16 for INH; median=13, range 12–14 for SDH; ties broken by ranking the percentage of plastic song with note clusters; $U=1$, $P<0.01$). Once males began to sing stereotyped song or stopped singing plastic song, they did not revert to less mature forms (Fig. 2). Whistles and other elements accounted for roughly 10% (range 4–11%) of the males' vocal production in the final session.

Song Potency

The songs of the SDH males were significantly more effective releasers of copulatory postures than the INH songs. The SD females displayed copulatory responses to a mean ± SE percentage of 60 ± 5 SDH males' songs compared with 36 ± 8% of the INH songs. The IN females responded to 67 ± 5% of the SDH song compared with 45 ± 5% of the INH songs. A two-way ANOVA with replication showed potency to be significantly higher for SDH songs than INH songs ($F_{1,19}=70.28$, $P<0.0001$). As there was no effect of the females' native population on their potency rating ($F_{1,19}=0.90$, NS) and no interaction of their population with preference for SDH over INH songs ($F_{1,19}=0.13$, NS), we averaged values across the two groups of playback females for subsequent analysis.

We ranked each female's proportion of responding to each male's songs from most to least potent and found the SD and IN females' rankings to be significantly correlated (Spearman rank correlation: $r_S=0.95$, $N=21$, $P<0.001$) indicating consistent preferences for specific SDH or INH songs. The songs of five of the six SDH males were ranked in the top six. The SD and IN females did not differ in overall responsiveness to playback of songs (Student *t* test: $t_{19}=0.94$, NS): SD females responded to a mean of 48 ± 20% and IN females responded to 56 ± 18%.

Checks for other social effects

In previous work, we have not found any relationship between the responsiveness of females housed together or any evidence of females preferring the songs of the male with which they were housed (King & West 1983a; Freeberg et al. 1995). In the present study, we also found no such effects. In cases where only one female in a chamber ever responded to song (N=3 SD females), those females' mean responsiveness averaged 56 ± 5% (61%, 55% and 52%) compared to 53 ± 3% for chambers where both females responded (Student *t* test: t_{19}=0.27, NS). The average difference in overall playback responsiveness between the two females for each of the nine pairs was 16 ± 4%, compared to 19 ± 4% for nine randomly chosen pseudo-pairs (*t* test: t_{16}=0.44, NS).

To check for effects of familiarity on responsiveness, we looked at each female's ranking of songs of the six males within each condition. If a female preferred her own male's songs (i.e. ranked them first), then the mean ranking across females would be around 1 for the songs of their male. If they were biased against their male, the mean ranking would be 5. We found mean rankings of 3.4 for both groups of females.

Acoustic Differences in Playback Songs

The repertoire sizes of the two groups were similar: SDH males produced a median of two (range 1–4) song types and INH males had a median of three (range 2–5; Mann–Whitney *U* test: U=12, N_1=N_2=6, NS; for comparison, the repertoire sizes of wild cowbirds ranges from four to seven song types; O'Loghlen & Rothstein 1993). The SDH and INH males also did not differ in number of note clusters produced (INH median/song=3, range 2–3; SDH=2, range 1–3). The two groups differed only slightly in number of overall notes comprising the note clusters with INH males including more notes (median=16.5 notes for INH, range 11–22) compared to SDH males (11.5 notes, range 10–15; Mann–Whitney: U=7.5, N_1=N_2=6, P<0.15). SDH males included reliably more low-voice notes with ascending amplitude (a note with greater amplitude than the preceding note) as a proportion of all notes they produced (LV/Notes ratio): SDH median=0.20 (range 0.17–0.38), INH=0.10 (range 0.05–0.16; Mann–Whitney: U=5, N_1=N_2=6, P<0.05).

Comparison between April and May Acoustic Structure

We looked at the males' vocal production in early April (session 12) where the two groups began to diverge in singing rate and when SDH males began to use stereotyped song. We chose six song exemplars for each male, selected on the basis of recording quality. The median number of note clusters for SDH males was 2.5 (range 2–4) and for INH males was 3.0 (range 1–5). INH males produced more notes, with a median of 24 notes (range 18–28) compared with 15.5 (range 8–22) for SDH males, a reliable difference (Mann–Whitney: U=4, N_1=N_2=6, P<0.05). All six INH males produced more notes in the early April session than in May; four of the six SD males produced more notes in relation to their later songs.

The differences in the LV/Notes ratio in April was not as strong as seen in the final session, although the direction of the difference was the same with SDH males having a higher ratio (median=0.17 for SDH, range 0.11–0.28) compared to 0.14 for INH males (range 0.09–0.24; Mann–Whitney: U=11, N_1=N_2=6, NS).

Correlations among Structural and Developmental Measures

The relationship between growth of stereotyped song and production rate, as measured by time to reach peak production, was r_S=0.80 (Spearman rank correlation: N=12, P<0.01). Song potency was associated with both measures: peak singing (r_S=0.81, P<0.01) and onset of stereotyped song (r_S=0.62, P<0.05). For the acoustic characteristics of the playback songs, we found that the LV/Notes ratio was not significantly correlated with the number of notes in phrase one (r_S= − 0.09, NS), but was significantly correlated with song potency (r_S=0.75, P<0.01).

Social Experience of Males during Development

To look for differences in the social experience of the SDH and INH males, we examined four measures of female behaviour from the 31 behaviour samples: whether females flew, sidled away, or stayed when a male sang to or approached them and how often females approached males. The two groups of males did not differ in the frequency of singing to or approaching females across the samples: SDH males approached 2732 times (median=411.5, range 226–735) compared to 2899 times for INH males (median=505.5, range 260–735). The SDH and INH males also produced nearly the same number of total songs to the focal female across the 31 samples: SDH produced 1151 songs (median=149.5, range 116–421) and INH males produced 1064 (median=161, range 103–292). The frequency of singing or approaching also did not differ when grouped into the seasonal time periods (for all comparisons, Mann–Whitney: U>10, N_1=N_2=6, NS).

Responses to male song

Although the INH and SDH males did not differ in frequency of social or vocal behaviour towards females, the females differed in their responses towards the males, especially in how often they stayed or flew when males vocalized (Fig. 4). The major difference involved responses to song. SD females stayed significantly more often when males sang than IN females, especially in the winter and spring (Mann–Whitney: autumn U=5.5, N_1=N_2=4, winter, spring U=4.5, 1, N_1=N_2=6, χ^2_6=18.69, overall P<0.01), whereas IN females flew more often in response to song than did SD females (U=7.5, 6, 3, χ^2_6=14.36, overall P<0.05). Across the three time periods, SD females stayed to a median of 73% of their male's songs (range 56–80%) whereas IN females stayed to 52% of their male's songs (range 40–64%). There was also a

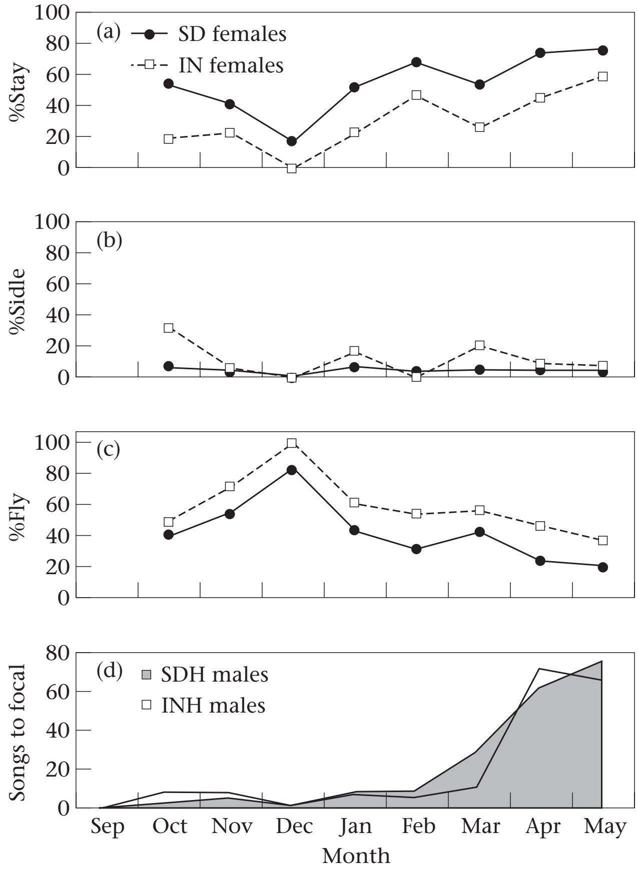

Figure 4. Female responses to male vocalization. The average percentage of responses to directed song by SD and IN focal females that were (a) stay, (b) sidle, or (c) fly (see text). Data from all social behaviour samples were combined for each month from October through to May (there were no directed songs in September). (d) The average number of songs by SDH and INH males directed to the focal female over the same time period.

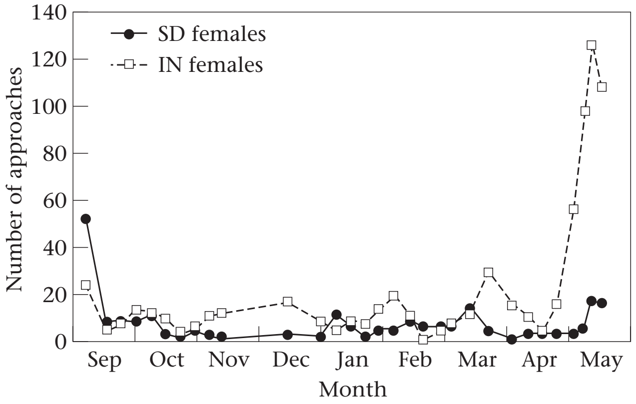

Figure 5. Total approaches to male by females in each condition. *Y* axis represents the sum of approaches by all 12 females in each condition for each of the 31 social behaviour samples. Each social behaviour sample consisted of 10-min focal observations for every female, hence 120 min of observation per condition.

tendency for IN females to sidle away from song more often (U=4.5, 17.5, 3, χ^2_6=10.91, overall P<0.10).

Responses to male approach

We found no reliable differences between groups in manner of responding to approach by males for any of the time periods, although there was a tendency for SD females to stay more often in response to male approach in the autumn and spring than IN females (Mann–Whitney: U=7, 12, 8, N_1=N_2=6, χ^2_6=11.70, overall P<0.10).

Female approach to males

Females approached males far less frequently than males approached females. Across all sessions, SD females approached males 228 times whereas IN females approached males 664 times (SDH median=32; INH=120). For IN females, the number of approaches by each female to males greatly increased in the spring whereas SD females showed little change (Mann–Whitney: spring sample: U=4.5, P<0.05). The most dramatic increase came in the final four observation sessions (May) where IN females showed a very large increase in approaches to their male companions, the same period in which INH males showed the largest increase in singing rate (Fig. 5).

Correlations between male and female behaviour

We used two measures of female staying to song, staying during the winter and during the spring, to determine whether social experience prior to (winter) or during (spring) the emergence of stereotyped song was related to vocal measures. Rate of staying to song by females during the winter was significantly correlated with the onset of stereotyped song (Spearman: r_S=0.76, N=12, P<0.01), as was staying during the spring (r_S=0.81, P<0.01). Song potency was not reliably correlated with staying during the winter, (r_S=0.47, NS) but was related to staying during the spring (r_S=0.64, P<0.05). Rate of staying during the winter was also associated with faster arrival at the peak production (r_S=0.73, P<0.01).

DISCUSSION

Taken as a whole, the data indicate that social responsiveness of female cowbirds influences multiple aspects of song ontogeny. The effects on maturation are distinct from the effects on song content. Here we found differences in rate of song development and amount of practise, events preceding production of stereotyped song. Stereotyped song is the stage of song material with the most potential to allow social shaping of content because the males' vocal responses are more stable from rendition to rendition. We found that SDH males produced stereotyped song sooner and reached a peak of vocal production sooner than INH males. The more compact and stable nature of stereotyped song may have allowed the females with the SDH males to react more consistently and more selectively. In turn, the SDH males may have reduced vocal production sooner because their songs engendered more reliable feedback from females. By contrast, INH males were slower to advance to stereotyped song and continued to increase vocal production, with some males not reaching a peak at all. The dramatic rise in the IN females' approaches to INH males during the same period may have helped to sustain higher singing rates but may also indicate that the IN females were unable to find other ways to communicate perceptual preferences.

Although the data indicate that social responsiveness throughout the year may be important, the majority of male and female interactions surrounding song coincided with the time of early spring arrival of cowbirds onto prospective breeding grounds (see Fig. 4). Stereotyped song begins to increase a week or two later. Thus, the social feedback from females escalates after birds are back on local breeding grounds.

As noted earlier, local adult males return in late February and females in early March (Friedmann 1929). Observations of 10 banded and many unbanded individuals confirm these dates. By mid-March, interactions involving song and flight whistles are common for both banded and unbanded (possibly yearling) males. Such interactions are frequent until and after actual breeding begins in late April or early May (M. J. West, unpublished data). In earlier observations of a winter roost in North Carolina, we saw social interactions of young males with both adult males and adult females from December through to February. Shifts in production from plastic to stereotyped song measured in the field corresponded well with shifts seen in captive males living with females (King & West 1988). More work is needed to clarify whether female feedback prior to return to local areas functions mainly at the level of motivating general song production and maturation, an effect that may advance males to the stage where local females can detect and respond to differences in specific song structures.

Song Potency Differences

We had expected that the playback songs of the INH males would be more stimulating to IN females than the SDH songs. We had also expected the INH males' vocal structures to shift towards IN preferred variants. These expectations were not confirmed: all females preferred the SDH song variants. As noted above, however, INH males were slower to reach the final phases of song ontogeny. Acoustic analyses indicated less vocal attrition in this group as the INH males had more notes than SDH males in early April and showed a trend in that direction even in their final playback songs. Perception by females during playback of differences in song stereotypy, apart from differences in song content, may have reduced the potential potency of INH songs. Why INH males developed more slowly remains to be explored in more detail. The INH males' pace of development may have interfered with any chance for females to fine-tune song features that serve as geographic markers between the two populations (e.g. characteristics of notes in the first phrase). IN females may be intrinsically primed to stimulate males at an earlier time than SD females because they breed earlier (Friedmann 1929; South Dakota Ornithologists' Union 1991; M. J. West, unpublished data). They could not be effective, however, because their SD male companions sing much less during the winter than juvenile IN males (King et al. 1996).

We know from other work that IN females are capable of affecting IN and SD male song development (Freeberg 1996; West et al. 1997). Thus, the capacity is there but was not engaged in the social context used here. We should emphasize that the IN females in this study were as responsive to playback as the SD females and, in a second playback test right after this experiment, they showed reliable preferences and strong responsiveness to songs from wild IN males.

The social interactions between the sexes are most likely linked to hormonal effects, although the direction of effects between changes in hormones and changes in behaviour within each sex remains to be clarified. Does more singing, in addition to photoperiodic changes, raise testosterone (T) in male cowbirds and does the faster rise contribute to earlier crystallization? Dufty & Wingfield (1986) studied hormonal responses to social cues in cowbirds in the laboratory. They found that housing males with females in cages led to a faster increase in T levels compared with when males were housed alone. Solitary males showed higher corticosterone levels than socially housed males. The two groups did not differ in peak plasma levels of T, but in rise to peak production. With respect to our study, we should note that the two groups of males did not differ in overall song production or in responsiveness to females as measured by singing or approaching, showing no obvious difference in major activities that might be expected to reflect differences in hormonal states. However, they did differ in the rate of song production, an effect that could be linked to T levels. The time of establishing social relationships between late February and late April may be a critical time to look for hormonal differences and correlated changes in song structure. Effects of T levels on song crystallization have also been reported (Nottebohm et al. 1987; Marler et al. 1988; Korsia & Bottjer 1991). This stage will also require new analyses.

We also need to learn about hormonal production in the females. Were IN females less stimulated than the SD females because the songs of males from a distant population were less appealing to them? As noted above, the IN females were as responsive to playback as the SD females. Little is known at present about changing hormonal conditions in female songbirds during the development and expression of perceptual preferences.

The ontogeny of song for many songbird species can be viewed as a timed test of competence: songs must be ready when female mates or male rivals are ready. In many species, including cowbirds, once males are in reproductive condition, they have fewer degrees of freedom in changing song repertoires. In particular, the basic frequency pattern remains stable, although male cowbirds do modulate amplitude and tempo. Thus, yearling males with less effective song structure may be at an additional reproductive disadvantage because they also have had less experience in exploring the effects of changing amplitude or tempo. Given that cowbirds may live through only two breeding seasons, developmental delays evident in their songs could be very costly (Lowther 1993; O'Loghlen 1995).

The flight whistle of cowbirds is also a learned vocalization used during courtship and copulations. In some populations, young male cowbirds do not have access to adult male models until their first breeding season, a condition associated with delayed development of whistle dialects until males are in their second breeding season (Dufty & Wingfield 1986; Rothstein & Fleischer 1987; O'Loghlen 1995). Thus, the timing of access of stimulation appears critical for both male vocal signals used during pairing and mating.

Nelson and colleagues have studied vocal development among white-crowned sparrow, *Zonotrichia leucophrys*, populations that differ in migratory status and in length of time on breeding grounds prior to breeding. Their data also show strong developmental differences in time of sensitivity to tutoring, the duration of time spent producing plastic song, and amount of overproduction (Nelson 1997, 1999; Nelson et al. 1997). Vocal development has an ecological deadline for many migratory species: reaching that deadline appears subject to social influence in cowbirds and other songbirds (Payne & Payne 1997).

Importance of Social Proximity

Our data suggest that regulation of social proximity frames the process of male–female interaction. In field settings, consortships or paired status are defined by a male's ability to direct vocalizations to the same female and to be close to her on repeated occasions (Dufty & Wingfield 1986; Rothstein et al. 1988; Yokel & Rothstein 1991). In aviary settings, Freeberg (1996, 1997) found SD female cowbirds were more likely to stay to hear a second song from a male from her own cultural background than from a male from a different experiential background. In our study, the SD females stayed significantly more and flew significantly less to directed song than the IN females.

During development, staying by a female when a male sings may mean she can hear more song or hear it more clearly. The issue of proximity has bioacoustic implications as well. The note clusters in the first phrase, which are critical for copulatory responding in playback settings, degrade rapidly at very short distances (King et al. 1981). Female proximity is also important to the male as he can obtain two kinds of feedback: general information that his behaviour is stimulating, followed by the opportunity to vocalize again and receive signals more specifically tuned to finer variation within the same vocal signal. For example, differences in social proximity may explain the higher LV/Notes ratio of SDH males and their faster reduction in the number of notes in their song. We are presently examining social proximity at a microanalytic level using videotaped interactions in March and April that occurred between the females and young males studied here to learn more about the effects of females (unpublished data).

Integrating Male and Female Effects

We are now beginning to examine how female and male stimulation work in concert. In past work, we have found clear evidence of the integration of male and female influence on yearlings. In a field study, we observed that adult females were often found in small groups with young males in the late winter. We also found generally comparable maturational rates for wild males that could hear adults compared to captive males living with females only, although the data were not analysed at a level fine enough to detect differences in precise timing (King & West 1988). We also know that females can affect song development in young males exposed to tutor tapes of adult males. For example, young males tape-tutored with multiple song types and housed with heterospecifics copied tutor songs and retained more of them in their final repertoires. But when housed with adult female cowbirds, a second set of young males learned the tutor songs, then improvised on the songs until they no longer matched the tutor material. The playback responsiveness of their female companions also affected the amount of improvisation, with males housed with less responsive females improvising more and singing more potent song (West & King 1986; King & West 1989).

In the wild and in our aviaries, males copy one another's song types when quite young (under 100 days of age; King et al. 1980; Dufty 1985) and adult males attend socially to the songs of juveniles, sometimes attacking young males if their songs are potent ones directed to females (West et al. 1981a, b). Thus, young males face a challenging balancing act: attempting to interact with females while deflecting agonistic attention from older males.

To learn more about the influence of adults of both sexes on song development, Schlossberg (2000) housed juvenile males in outdoor aviaries with either only juveniles or also with adult males and females through to late autumn, then housed half of each group with either adult or juvenile females for the rest of the year. The males could hear wild cowbird and heterospecific songs as the aviaries were located in open field habitat. Schlossberg found that housing juvenile males through late autumn with adults was associated with higher levels of formatted song (and less plastic song). He also found higher levels of song sharing among the males later housed with juvenile females compared with those housed with adult females, suggesting the latter stimulated more improvisation even though they were less socially responsive than the juvenile females, consistent with previous work in more constrained settings (King & West 1989).

In past work in aviaries, we have also found that the presence of older males and females leads to higher rates of female-directed singing and courtship competence than housing with males or females of the same age class (West et al. 1996). In ongoing work, again in outdoor aviaries, we are seeing strong differences in the singing patterns of juvenile males housed with only female cowbirds as opposed to juvenile males housed with adult males and females (unpublished data). How social contacts with both adult males and adult females interact to produce these effects remains to be investigated.

What advantages accrue to a female cowbird in her role as facilitator of male vocal ontogeny? We believe that her behaviour may allow her a more sensitive means to assess male quality, a critical task for all females but especially in parasitic species where males offer no resources. For a male to be affected by females' social signals, he needs to do more than simply sing, as we have shown in this study. He needs to be alert to changes in a female's behaviour to connect his immediate behaviour to her immediate response. The capacity to detect and act on contingencies is a basic property of learning in general and may allow females to discriminate better learners on the basis of the presence of female-stimulated traits in the males' songs. These traits need not come from the same females assessing the young males during breeding, but may come from other females with which the males interacted during early spring, as local females show strong concordance in preferred song features (West & King 1986; King & West 1989).

To explain song development in cowbirds clearly requires the elucidation of many developmental connections assembled by social experience, only some of which have been studied here (see also Payne & Payne 1997; Payne et al. 2000 for social connections in other passerines). Understanding the composite nature (i.e. multiple sensory systems) of social stimulation is also necessary and such work is underway in some species, with increasing emphasis on the correlated role of visual stimulation in auditory learning (e.g. ten Cate et al. 1993; Hamilton et al. 1998; Hultsch et al. 1999).

Given that song is a behaviourial trait subject to sexual selection, the mechanisms underlying its development cannot be studied in isolation from functional or evolutionary considerations. If traits like song are not only assessed by females, but also ontogenetically influenced by females, the need to articulate the coupling of developmental processes is indicated, as has been done for coevolutionary processes. But, of most importance, is that developmental studies of sexually selected traits such as bird song consider receivers in an ontogenetic light: females may have two roles, as ultimate arbiters of a trait's success, but also as proximate intermediaries in a trait's development. The results of our study show that the latter role is an active one, as females modulate distance, attention and responsiveness to a male's social and vocal behaviour.

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