

Female Cowbird Song Perception: Evidence for Plasticity of Preference

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Abstract

The goal of the research reported here was to look for evidence of modifiability of preference for male song in female cowbirds, *Molothrus ater*. To this end, we investigated whether social experience affected the breadth and consistency of females' playback preferences for geographic variants of male song. In three experiments, we varied female cowbirds' exposure to males. Wild-caught juvenile females showed a preference for local song in their first year when housed without males in sound-attenuating chambers, as we had found previously with adult females. But we found that neither adult nor juvenile females showed a preference for local over distant song after they had been housed in large, outdoor aviaries with other females but without male residents. Aviary housing with local males did lead to preferences for local songs. These data represent the first unqualified evidence that adult and juvenile female cowbird preferences for song are modifiable. These data add to the growing body of literature suggesting that receivers, as well as signalers, rely on learning during development of their communication system.

Introduction

Male songbirds show considerable malleability in song learning. Learning has been found to play a role in the development of vocal communication in all songbirds studied to date (Kroodsma 1996). Such learning allows rapid cultural transmission of song variants, which can affect mating success and possibly the reproductive isolation of populations. Less is known about the plasticity of song preferences in receivers of song but growing evidence suggests that preferences for song may also be sensitive to an animal's social and acoustic history. Indeed, there may be an evolutionary link between male and female plasticity. Payne et al. (2000) proposed that one might expect to find plasticity in female songbirds to parallel that found in males based on the idea of a 'developmental correlation between the two sexes, which in females entails attraction to song and in males, the learning and production of song' (p. 78). Sturdy et al. (2001)

have expressed a similar concept, proposing the idea of communication networks between males and females, adults and young, or neighbors and strangers. Evidence of male and female plasticity has been found in the imprinting of female village indigobirds, *Vidua chalybeata* (Payne et al. 2000). There is also evidence for perceptual song learning in female zebra finches, *Taeniopygia guttata* and white crowned sparrows, *Zonotrichia leucophrys*, (Baptista & Petrinovich 1986; DeWolfe et al. 1989; Clayton 1990; Casey & Baker 1992; ten Cate & Vos 1999; Riebel 2000; MacDougall-Shackleton et al. 2001; Sturdy et al. 2001). In domesticated canaries (*Serinus canaria*), there is evidence of modifiability of song preferences in both juvenile and adult females, perhaps paralleling the open-ended patterns of male canary song learning (Nagle & Kreutzer 1997a,b).

Despite the considerable plasticity seen in male cowbirds' learning of both songs and flight whistles, we have found little evidence for plasticity in female cowbirds' preferences for song (but see O'Loughlen & Rothstein 1995 for such a suggestion regarding flight whistles). Most of our work has involved captive females acoustically isolated or exposed to geographic variants of cowbird songs and tested using playback of song. We have found no evidence that social or acoustic experience was necessary to elicit local geographic preferences (e.g. King & West 1983a,b; King & West 1990; West et al. 1998). These data led us to propose that female preferences at a geographic level do not change across ontogeny (King & West 1983b). This conclusion was consistent with predictions made by Lehrman (1974) and Mayr (1974) about the constraints necessary for brood parasitic cowbirds to avoid errors in mate choice.

1 Work by Freeberg (1996) in cowbirds, however, led us to question whether these playback findings were sufficient to support the conclusion that female perception of song is closed to experience. Freeberg carried out a longitudinal study of mate preferences in large aviaries in two captive populations of cowbirds. He found that the females chose as mates males with the same cultural background as their own. The effect on mate choice persisted into the female's second year and the females were able to pass on their acquired preferences to a new generation of juvenile females. Given that mate choice depends heavily on the use of vocal signals, Freeberg's data suggested that song preferences could be modified.

We speculated that the housing in large aviaries used by Freeberg could be a factor in facilitating female perceptual modifiability. In these settings, the females can participate in and observe diverse social interactions, a more stimulating experience than residence in sound-attenuating chambers with only one or two conspecifics [see Gottlieb (1993) for effects of social housing on imprinting in ducklings]. In light of these findings, we chose to re-examine the question of plasticity of female perception with respect to geographic differences in song.

To test the proposition that female preferences for song can be modified by their social environment, we studied juvenile and adult females living in large aviaries or sound-attenuating chambers. We used the copulation solicitation assay

as our outcome measure. We chose playback songs to represent local and distant populations. We focused on two measures. The first was song preference: did females respond more to local vs. distant playback songs? The second was group concordance which is a measure of whether females ‘agree’ as to the ranking of songs from most to least effective. We consider concordance to be a critical measure because it indicates the reliability of the females’ preferences, an important factor if selection occurs on male song. Early experience with song has been shown to consolidate the repeatability of preferences in female zebra finches (Riebel 2000).

Experiment 1. Song Perception in Male-Deprived Female Cowbirds

Purpose

We asked to what extent juvenile and adult female cowbirds would show local vs. distant song discrimination if they had been housed without males in one of two settings. First, we tested a group of juvenile females housed in sound-attenuating chambers to compare their discrimination to adults we had studied earlier in West et al. (1998). In that study, wild-caught adult females, collected in Indiana (IN) and housed in sound-attenuating chambers, preferred local over distant song. Secondly, we housed a group of IN juvenile and adult females in a large indoor-outdoor aviary with no male residents. See Table 1 for a summary of the experimental design.

Playback Subjects

Nine juvenile females served as sound-attenuating chamber subjects and eight adult and six juvenile IN female cowbirds were used as aviary subjects. All females had been collected between Jun. and mid-Aug. from the same site in Monroe County, IN. Age was determined by juvenile plumage (Selander & Giller 1960). All the juveniles had presumably heard cowbird song and were collected from small flocks of cowbirds. All but two adult females were wild caught the summer before the experiment: the other two had been housed in aviaries with

Table 1: Experimental conditions

| | Condition | | Males | Test songs |
|------------------|-----------------------------------|----------|-------|-----------------|
| West et al. 1998 | Adults n = 11 | Chambers | No | IN1-SD1 |
| Expt 1 | Juveniles n = 9 | Chambers | No | IN1-SD1 |
| | Adults n = 8 with juveniles n = 6 | Aviary | No | IN1-SD1 |
| Expt 2 | Juveniles n = 12 | Aviary | No | IN2-SD2 IN1-TX1 |
| | Adult n = 12 | Aviary | Yes | IN2-SD2 IN1-TX1 |
| Expt 3 | Juveniles n = 11 with adults | Aviary | Yes | IN2-SD2 |

males and females for 2 yr. The birds wore colored leg bands to permit individual identification.

Housing

The sound-attenuating chambers (1.3 m^3) were made from plywood and sheetrock and each contained several perches and housed two juveniles (King & West 1977). The indoor–outdoor aviary ($9.1 \times 21.4 \times 3.4 \text{ m}$) each contained an enclosed shelter and an outdoor section containing perches, trees, a pond, a grass covered surface, and an observation deck [see Smith et al. (2002) for details]. In the aviary, females could see and hear male cowbirds outside the aviary, which meant hearing males from different geographic areas because, during the fall and spring, the laboratory aviaries attracted both resident and migratory cowbirds. All the birds were provided daily with vitamin treated water, canary seed, red and white millet, and a modified version of the Bronx Zoo diet for blackbirds.

In early May, we transferred all aviary females indoors, first into a flight cage ($1.8 \times 2.4 \times 1.8 \text{ m}$) to acclimate them to smaller quarters and then 2 wk later we transferred them in pairs or singletons into sound-attenuating chambers (1.3 m^3) for playback testing. No effects of social or solitary housing in the chambers have been found on female playback responsiveness, selectivity, or concordance in previous studies (King & West 1983a,b; Smith et al. 2000).

Playback Procedure

Beginning on May 15, we played six vocalizations daily to the females, with one vocalization per trial and each trial separated in time by 90 min, beginning around 07.00 hours. We played back each vocalization eight times to each female over the course of the experiment. We scored a positive response if a female adopted a copulatory posture (if she arched her neck and back and separated the feathers around the cloacal area) within 1 s from onset of the sound. The females heard the vocalizations in varying orders each day and each vocalization was presented roughly an equal number of times at different times during the day.

We played back songs 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 recording speaker output with a B & K 2033 spectrum analyzer. The SPL was $85 \pm 2 \text{ dB}$ adjusted with a B & K 2209 sound pressure meter, set to A weighting, impulse reading, measured 75 cm. from the speaker.

Selection and Recording of Songs

The songs played back in expt 1 were obtained in a previous year during the breeding season from six adult IN males captured at the laboratory in Monroe County, IN and from six South Dakota (SD) adult males captured in Fall

River and Custer Counties, SD. The males had lived in large aviaries ($11.3 \times 9.1 \times 3.4$ m) with consubspecific males and females from their respective collection sites. We placed 4–6 Sennheiser RF condenser microphones in locations within the aviaries to maximize our chances of obtaining recordings from males vocalizing less than 0.3 m on axis of the microphones. The vocalizations of the males were recorded with either a Nagra IVS recorder at 38.1 cm/s or a Sony TCD-D10 PRO II DAT recorder. Twelve vocalizations, six from each population, constituted the playback set. One song from each of 12 males was used. Particular vocalizations were chosen for playback on the basis of acoustic quality and to sample the range of different song types in the two populations. For inclusion, the unweighted signal-to-noise ratio measured peak-to-peak had to be at least 53 ± 2 dB measured between 300 and 12 000 Hz.

Data Analyses

The dependent variable was each female's mean percentage of responses to each set of playback songs. We used paired t-tests and Kendall's coefficient of concordance to test for differences between song sets (Siegel & Castellan 1988). All tests were two-tailed.

Results and Discussion

The juvenile females housed in the sound-attenuating chambers responded significantly more to IN than to SD songs ($t = 3.58$, $df = 8$, $p < 0.0073$). They responded to a mean of 68% of the IN songs ($SE = 4.3$) and 49% of the SD songs ($SE = 5.5$). They did not, however, show significant concordance in their responding, $W = 0.137$, NS.

Neither group of aviary females showed a preference for IN or SD songs. The adult females responded to a mean of 40% ($SE = 4.5$) of IN songs and 49% ($SE = 9.3$) of SD songs ($t = 1.258$, $df = 7$, $p < 0.2488$). The juvenile females responded to a mean of 42% ($SE = 10.3$) of IN songs and 40% ($SE = 8.4$) of SD songs ($t = 0.247$, $df = 5$, $p < 0.8146$).

The adult aviary females did, however, show concordance with respect to song types, responding most often to one IN and two SD songs respectively, $W = 0.39$, $p < 0.001$. The juvenile females did not show concordance, $W = 0.20$, NS. We also looked at a Spearman correlation between the rankings of the aviary adult and juvenile females and found no relationship, $r = 0.035$, NS.

In sum, wild-caught juvenile female cowbirds, housed in sound-attenuating chambers, showed a geographic preference for IN song, as had identically housed IN adults listening to the same playback tape (West et al. 1998). Unlike the adults, however, the juveniles did not agree as to the rankings of the particular song types from most to least potent. Thus, although they could tell the populations apart, they showed little evidence of the reliability of preference shown by adults. It could be that the absence of hearing any song led to reduced discrimination ability as has been found in zebra finches, even

7 though they show a natal preference for male song (Braaten & Reynolds 1999; Sturdy et al. 2001).

The juvenile and adult female cowbirds, housed without males in an outdoor aviary, did not show local over distant song preferences. Thus, the aviary experience without males appeared to modify female preference by eliminating a preference for local song as had been found in the chamber-housed birds. The aviary-housed adults showed significant concordance, the juveniles did not, which also parallels the findings with chamber-housed birds.

Experiment 2. Geographic Preferences in Aviary-Housed Females

To learn more about the development of juvenile and adult female perception, we housed a new group of wild-caught adults in outdoor aviaries but provided them with IN male companions. We also studied a new group of juvenile females, wild caught in their first summer, housed without males. We predicted that the adult females housed with males would show local preferences and the juveniles without males, would not. (We attempted to run a third condition of juveniles with males but this condition had to be aborted because of disease).

Subjects

Twelve juvenile females served as playback subjects: they were housed in an indoor/outdoor aviary without males. Twelve adult females were housed in an indoor-outdoor aviary with eight adult males. All other details followed expt 1 (Table 1).

Playback Songs

We constructed two new sets of playback songs (see Table 1). The first set was composed of six songs from six different IN males (the same songs and males used in expt 1) and six songs from six wild males from the Chaparral Wildlife Management Area near Artesia Wells, TX. The second set contained six new songs from six SD males living in our aviaries with other SD individuals who were originally wild-caught in Custer County, SD and six songs from a new group of wild-caught IN adults. Songs were recorded following the procedures outlined for expt 1. For the field recordings in TX, using a Nagra IV-S recorder and Sennheiser electret microphones, males were held temporarily in a portable flight cage ($2 \times 0.5 \times 2$ m) to obtain high-quality recordings. All playback procedures followed expt 1.

Results and Discussion

Not all females responded to each playback set, reducing the N for the various analyses.

The adult IN females, housed with IN males, reliably discriminated local from distant song for both playback sets: SD vs. IN and IN vs. TX. Moreover, they showed significant concordance for both sets. The females responded to a mean of 47% (SE = 6.2) of IN songs compared with 36% (SE = 5.1) of SD songs, $t = -2.448$, $df = 10$, $p < 0.0344$; the concordance value was $W = 0.33$, $p < 0.01$. The mean preference for IN over TX was even stronger, 57% (SE = 5.0) compared with 30% (SE = 5.4), $t = 9.028$, $df = 9$, $p < 0.0001$ with concordance also significant, $W = 0.82$, $p < 0.0001$.

As in expt 1, the yearling females without males showed neither local vs. distant discrimination nor concordance for either comparison. For IN vs. SD, six of seven females responded more to SD song, yielding means of 45% (SE = 3.9) for SD and 35% (SE = 4.1) for IN, $t = 1.085$, $df = 6$, $p < 0.3195$. Concordance was not significant, $W = 0.19$, NS. For IN and TX, 6 of 10 females responded more to IN, with means of 48% (SE = 5.5) for IN compared to 46% for TX (SE = 3.2), $t = .347$, $df = 9$, $p < 0.7365$. Concordance was not significant, $W = 0.15$, NS.

Replicating the first aviary experiment, juvenile females housed without males in large aviaries showed no geographic discrimination of song variants. But adult females, housed with males inside the aviaries, did show significant IN preferences and concordance for both comparisons.

Experiment 3. Effects of Limited Exposure to Male Song

Because of the failure in expt 2 to get data from juvenile females housed with males, we decided to repeat that condition in the next year. Given the results with the adult females, it seemed highly likely that year round exposure would produce macrogeographic preferences in juveniles. We therefore asked a more specific question about the timing of female learning. Given the ecology of cowbirds, young females in the wild probably hear the most song from local males in late spring once the birds have returned from migration and are settled on breeding grounds (Friedmann 1929). The spring period would seem to be the most likely to provide young females with experience with local song. Thus, we chose to concentrate the bulk of the females' exposure to males to a 6-wk period in the late spring.

Subjects and Methods

Eleven juvenile females served as subjects. They had been captured from the same site as all other juveniles in the study. They were housed with adult females in two indoor-outdoor aviaries from Aug. until Mar. without males (but see below). Starting in Mar., they were divided into four groups and moved into one of four comparably sized aviaries with IN adult and juvenile males and IN adult females. Each aviary held approx. 26 birds. The sex ratio was approx. 1:1.

Procedure

In the fall, all of the females were exposed to males for brief periods as part of another experiment (Gros-Louis et al. 2003). Between Sep. 7 and Dec. 14, they were exposed to IN males for four 3–5-d periods. They also heard aviary playbacks of song for a 12-d period and juvenile males were present in the aviary for six of 12 playback days. The playbacks lasted 7 min each day comprising of 23 songs.

On Apr. 29, the juvenile females were moved indoors to a flight cage and then into sound-attenuation chambers on May 15. Playbacks began on May 17. We played back the IN-SD test tape used in expt 2. All other procedures followed expts 1 and 2.

Results and Discussion

The juvenile females showed a reliable preference for IN song, with all females responding more to the IN variants, $t = -6.312$, $df = 6$, $p < 0.0007$. The females responded to a mean of 58% (SE = 8.4) of IN songs and 29% (SE = 10.7) of SD songs. For the first time in the series of experiments, the juvenile females also showed concordance in the rankings of the songs, $W = 0.53$, $p < 0.001$.

We also looked at the correlation between the rankings of the expt 3 juveniles and expt 2 adults when responding to the same IN–SD test tape. Their responses were positively correlated across the 2 yr, $r = 0.74$, $p < 0.02$.

Thus, experience with adult males and females led to local discrimination and concordance for IN over SD song. It also led to agreement between juveniles and adults from the previous year as to the most potent songs although the females were housed with different males in the 2 yr. Moreover, juveniles in the third experiment were not all exposed to the same adult males as they were housed in the spring in four different aviaries, with no song sharing among the aviaries. Thus, females must learn to listen to generic features in male song that helps order differences in song effectiveness.

Discussion

Figure 1 summarizes the findings across the different housing conditions. The lines labeled as ‘a’ highlight the evidence for plasticity in macrogeographic preferences. Adult and juvenile females, when housed in flocks in aviaries without males, lost or did not develop a preference for natal song while females housed in chambers did maintain or develop a macrogeographic preference.

The lines labeled ‘b’ in Fig. 1 point to the evidence for plasticity in local song preferences, as measured by concordance. The data indicate that, regardless of housing, adults demonstrate concordance for song, while juveniles need to have experience with males to acquire local song concordance.

Several of the comparisons yielded a finding of ‘no difference’ between playback sets. Given that the sample sizes are relatively small, these data must be

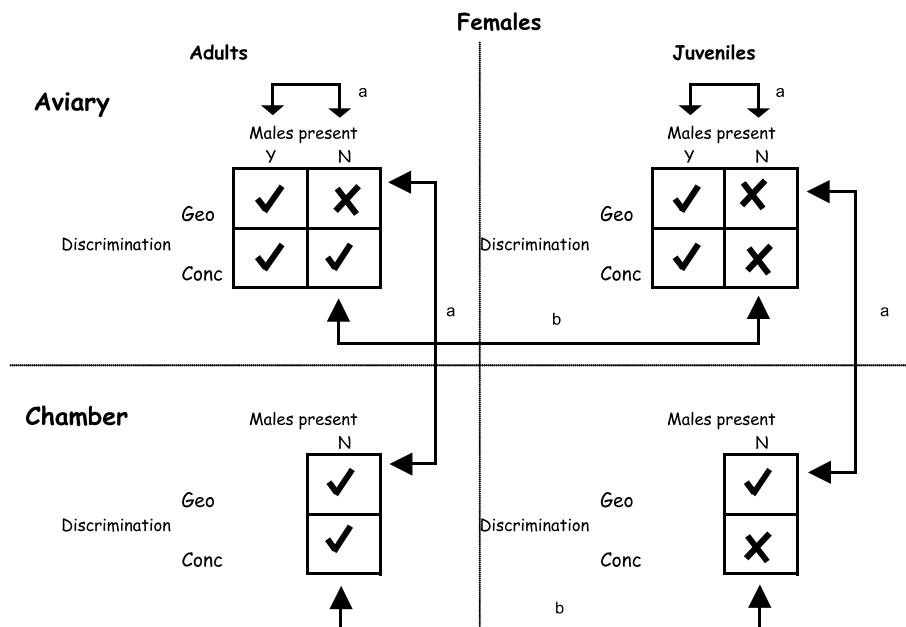


Fig. 1: Results of geographic and local song discrimination by adult and juvenile females housed in aviaries or chambers, housed either with or without males. Checks indicate significant effects of either geographic discrimination (GEO) or concordance (CONC) among females. Crosses indicate no significant discrimination or concordance. The 'a' indicate malleability in geographic discrimination and the 'b' indicate malleability in local song discrimination

viewed cautiously. But, with the juvenile females, we obtained the effect in two samples using three different playback tapes. The same size samples were also sufficient to detect differences between playback sets in other comparisons.

In previous work in our laboratory, we have found preferences for local song in all three subspecies, in seven distinct populations (King & West 1990; West et al. 1998). It was therefore very surprising to uncover conditions that erased macrogeographic preferences. We can only speculate as to the conditions in the all female flocks that produced this effect. In that the presence of singing males housed with females in sound-attenuating chambers has never produced evidence of modifiability of female preference, we conclude that female–female interactions and reactions to song are likely responsible for the modifiability. That is, when song is present, females may learn by observing one another's reactions to the song. The aviary females' exposure during the year to song outside the aviary from males included a broad geographic range of song types, including migratory individuals. In the fall, the females heard local males, and then migrant males moving south and the reverse in the spring. The chronic absence of males inside the aviary may have made the females sensitive to these occasional bursts of male stimulation, a sensitivity communicated among the group by wing stroking and

approaching, as we saw when song was presented alone to a flock of females (Gros-Louis et al. 2003).

The data indicate that females must learn their preferences for local song, as juvenile females housed without males did not show concordance. The only condition showing concordance was when juvenile females were housed with both adult males and females. Thus, we do not know whether acoustical stimulation alone would be sufficient for concordance to develop. Like male song, female cowbird song perception is sensitive to developmental experience, undergoing transitions in its nature depending on what the specific environment offers. Changes in song preferences with different kinds of social housing have also been shown in mountain white-crowned sparrows and canaries (Nagle & Kreutzer 1997b; MacDougall-Shackleton et al. 2001).

Limited social environments, such as housing in sound-attenuation chambers, may leave song preferences unchanged because modifiability of preferences is stimulated by competitive female–female interactions found in flocks. Complex social environments, such as those used here or in Freeberg (1998) and Gros-Louis et al. (2003) may induce malleability because the amount of social activity leads females to attend to different dimensions of sound in conjunction with dynamic visual stimulation. Thus, the present data suggest that song preferences can only be predicted by knowledge of the female's social circumstances: the preferences are not an exclusive product of internal sensory states, but the interplay between such states and ongoing external stimulation during the year. O'Loghlen & Rothstein (1995) suggest such an interplay for the perception of culturally correct male flight whistles by female cowbirds. The present data also suggest that this learning process goes on in adulthood, as well as during the female's first year. The patterns of concordance found suggest that song discrimination is a multilevel process and thus degree and kind of exposure may affect one level and not the other, as was found here with respect to geographic discrimination vs. concordance.

What function might female plasticity serve? The most likely answer is that it links male and female behavior to coordinate mate choice. We know that male cowbirds can learn new song patterns as adults and thus females may need a way to adjust their perception of song features (King & West 1990).

Cowbirds, like other organisms, inherit environments as well as genes (West & King 1987). These environments are correlated with genetic inheritance so that, for example, SD or IN cowbirds show both stable genetic and ecological differences. In SD, for example, young birds appear to be less likely to interact with adults during their hatching summer (Freeberg, pers. comm.). The inheritance of environments, along with genes, may explain how such a facultative system, where both males and females are plastic, can operate effectively. In flocks where females get sustained exposure to males, there may be a high population density, necessitating a finer sense of song discrimination, as there would be many male competitors for the female's attention. In less dense populations, male–female interactions may be more scarce, but so would potential mates meaning

that a developmental bias toward general features of local vs. distant song may be sufficient for effective mate choice.

At this point, we cannot make a definitive statement as to the mechanism of effect leading females to retain, gain or lose local and geographic preferences for male song. Irrespective of the mechanism however, plasticity in mating preferences can play an important role in influencing sexual selection (Cavalli-Sforza 1974; Qvarnstrom et al. 2000; Agrawal 2001). In species where fitness can be context dependent, as we have found repeatedly in our cowbird flock experiments (West et al. 2002; White et al. 2002; King et al. in press), it would serve females to have preferences that were also contextually influenced. Such malleability in female preferences may provide a means for females to make locally adaptive mate choices.

This work, in concert with others (Nagle & Kreutzer 1997b; Riebel 2000; Kodrick-Brown & Nicoletto 2001; Riebel et al. 2001; Badyaev & Qvarnstrom 2002) suggests that tests of mate choice and mate preferences must take into account the developmental context of both the signaler and the receiver. Not doing so runs the risk of misidentifying the source and result of selection (West et al. in press).

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