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6 The development of local song preferences in female
7 cowbirds (Molothrus ater): Flock living stimulates learning
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Abstract

32 We carried out two experiments across two years on song perception in female
33 cowbirds (Molothrus ater). In the first experiment, juvenile and adult female brown-
34 headed cowbirds, living in same sex flocks in outdoor aviaries, were periodically tutored
35 with recordings of local male cowbirds' songs. In the spring, four adult male cowbirds
36 were placed with half of the females for a 12-day period. We then tested song preferences
37 of all females by measuring copulation solicitation displays during the breeding season.
38 We found that the females exposed only to tape-tutor songs preferred those songs to those
39 of the unfamiliar males used as companions and that the females allowed to interact with
40 males preferred their songs over the familiar tape-tutor songs. These data establish the
41 modifiability of female cowbirds' song preferences at the level of local song. In a second
42 experiment, we studied the playback responses of juvenile females, hand-reared from the
43 egg, who were tape tutored only in the spring in the presence or absence of adult females.
44 There were no differences between the responses of juveniles housed with or without
45 adult females and the hand-reared juveniles were significantly less responsive to song
46 than adult females. Adult females responded more to familiar songs than to the unfamiliar
47 songs: juvenile females made no such distinction. Taken as a whole, these data are the
48 first to document that female cowbirds' song preferences for local song can be re-shaped
49 by postnatal experience. These data complement recent work in cowbirds and other
50 species showing that socially more complex contexts reveal plasticity in female song
51 preferences that are not apparent when learning opportunities are constrained by
52 impoverished laboratory settings.

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Introduction

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Understanding the communicative capacities of female songbirds is critical to understanding the function of male song in mate choice and to exploring how vocal cultures are transmitted from one generation to the next (Searcy & Yasukawa 1996). Studies of female song preferences have increased as techniques for measuring responsiveness have been developed (King & West 1977; Searcy 1992; Riebel & Slater 1998; Payne et al. 2000; Depraz et al. 2000; Nagle et al. 2002; Lauay et al. 2004). These studies focus on different levels of responsiveness, from recognition of conspecifics to discrimination of fine acoustic structure within songs. The results indicate that female song preference, like male song production, has a learned component in many songbird species (for reviews, see Riebel 2003 a& b). Such findings are critical to begin the task of uncovering the mechanisms integrating male and female behavior within communication networks (King et al. 2003a; Sturdy et al. 2001; West & King 1986).

Much remains to be learned about the determinants of female song preferences, especially with regard to the developmental context in which song preferences are acquired and/or modified. Many studies of female song preferences, like studies of male song production, have occurred in socially impoverished contexts in which opportunities to learn have been restricted due the absence of chances to interact with multiple conspecifics (Riebel 2003a &b). As in the study of male song production, studying females in simplified environments has been necessary to control song experience but such restrictions may affect components of song perception. Along these lines, Sturdy et al. (2001) found that reduced auditory exposure in female zebra finches (*Taeniopygia guttata*) led to deficits in frequency range discrimination. Riebel (2000) found that

76 isolated female zebra finches showed less repeatability in their operant responses to tutor
77 songs. Tutored females repeatedly chose the same tutor song while isolates varied in their
78 choices from trial to trial.

79 Studies of naïve female cowbirds housed in auditory isolation show that postnatal
80 experience is not necessary for species recognition or discrimination of geographic song
81 variants (King & West 1977; King & West 1983; King & West 1987). Studies of females
82 housed with males for many months also reveal no evidence of male influence, except in
83 one border population where such experience led to a broadening of the females'
84 preference for songs on both sides of the border (King et al. 1986). Such lack of
85 malleability would seem to be consistent with the needs of a female brood parasite, where
86 early experience with foster species might facilitate species-atypical song preferences
87 leading to inappropriate mate choice.

88 Further evidence suggesting female cowbirds' lack of sensitivity to male vocal
89 stimulation came from examining the individual playback preferences of females housed
90 with individual males from local or distant populations during the fall, winter, and spring.
91 When exposed by playback to the songs of their (now absent) male companion versus
92 unfamiliar but identically housed males, females show no preference or aversion to the
93 specific songs of their companion male, (e.g., West & King 1980; King & West 1983;
94 King et al. 1986; King & West 1987; Smith et al. 2000). Thus, long-term exposure to the
95 same male did not modify female preferences. Observations of the females indicated,
96 however, that the two sexes interacted, especially in the spring, leading to changes in the
97 males' repertoires (Smith et al. 2000; King et al. 2005).

98 The first evidence of female plasticity in cowbirds came from studies of mate
99 choice in captive colonies (Freeberg 1996; Freeberg 1997; Freeberg et al. 2001). When
100 juvenile females were housed in large aviaries with males and females from a local or
101 distant population, Freeberg found that females preferentially paired and mated with
102 males from the same cultural background, even if males from their local population were
103 available as potential mates. The enculturated females were also able to pass on their
104 preferences to a second generation of young females. The basis for mate choice was
105 partially explained by different preferences for male song (Freeberg et al. 2001). Given
106 the importance of male song to mate choice in this species, these data indicated
107 considerable plasticity in females' song preferences and suggested that the prior methods
108 had not been sensitive to developmental parameters in females.

109 We obtained more direct evidence of female plasticity in regard to
110 macrogeographic song preferences in a study of females housed with or without males in
111 large outdoor aviaries (King et al. 2003a). Juvenile and adult females, housed throughout
112 the fall, winter, and spring without male companions in all-female flocks, showed no
113 playback preferences during the breeding season for local versus distant song, whereas, in
114 previous studies, both ages had displayed strong local preferences after year-long housing
115 without males in sound attenuating chambers. The broadening of the aviary females'
116 preferences to include distant song might have resulted from females hearing a range of
117 song from local and migratory males singing outside the aviaries. When local males were
118 placed inside the aviaries, the females showed a preference for local versus distant song.
119 Thus, females appeared to be sensitive to postnatal stimulation when housed in social
120 groups.

121 In King et al. (2003a), we demonstrated influences on song preferences between
122 populations that do not ordinarily interact with one another during the breeding season.
123 But mate choice involving discrimination and plasticity at the microgeographic level is
124 essential to understanding the function of female song preferences. Prior to the breeding
125 season, females show sensitivity to male songs and flight whistles (O'Loughlen &
126 Rothstein 1995; West et al. 1998). But females also observe other male behaviors such as
127 counter-singing (White et al. 2002) that draws attention to males and their songs and
128 affects females' production of eggs (West et al. 2003b). Young females may also watch
129 older females' interactions as a basis for male assessment (Gros-Louis et al. 2003). Thus,
130 sources of influence on females' preferences for songs may be based on diverse forms of
131 experience.

132 Here we explored female plasticity by exposing females to song by tape tutoring,
133 by live tutoring, and by manipulating adult female presence. In the first experiment, we
134 tutored flock-housed juvenile and adult females with recordings of local adult males in
135 three sessions during the year. We examined whether adult and juvenile females'
136 responsiveness and preferences for the song sets were the same and whether the addition
137 of males to a group for a short period in the spring would affect preferences for the taped
138 songs or the songs of the male companions. In a second experiment in the following
139 year, we compared responses of a new set of hand-reared juvenile females tutored with
140 the same songs used in Experiment 1, either in the presence or absence of a new set of
141 adult females. We wanted to see if juvenile females with no physical contact with adult
142 males could acquire preferences and we wanted to see if housing with adult females had
143 any effect on juveniles' preferences. Previous observations suggested that adults showed

144 more concordant preferences than juveniles which might make them stable sources of
145 information about song. Stability of preference for specific songs would seem to be
146 critical to repeatable mate choice if male song traits are actually reliable indicators of
147 male quality and affect parameters of heritability (Riebel 2000). In contrast to the
148 previous year, exposure to the tape-tutor songs was limited to one 12-day session in late
149 April to see if massed exposure would lead to learning from the tutor song sets.

150 In the first experiment, we chose to tutor the females in late fall and early spring.
151 We chose these times because they coincided with periods in which we had seen
152 evidence of female influence on male song structure (King & West 1988; West & King
153 1988). Even though they cannot sing, female cowbirds can shape male song by emitting
154 visual displays to preferred song variants. The process appears to begin in late November
155 and ends in April. This period coincides with juvenile males' proceeding from plastic to
156 stereotyped song, the pace of which is also affected by female stimulation.

157 In all experiments, females could, of course, see and hear wild males and other
158 species outside the aviary. Based on past work with flocks, we wanted to see if inanimate
159 or live tutoring inside the aviary provided a robust form of stimulation when pitted
160 against the backdrop of an acoustically rich environment. We chose very experienced
161 adult females under the assumption that the ample experience they had had with male
162 songs would approximate species-typical contexts in the wild and that it would be a fair
163 assumption that all adult females could already discriminate local variants and show
164 preferences for some songs over others as we and others have found in playback and
165 mate choice tests (West & King 1985; O'Loughlen & Rothstein 1995; Freeberg, 1996).

188 In October of 2002, 12 adult and 12 juvenile females were assigned to 4 outdoor
189 aviaries, each measuring 2.4 x 6.1 x 2.3 m. Each aviary housed three juveniles and three
190 adults (Table 1). In April of 2003, the four groups were collapsed into two flocks, with
191 equal numbers of adult and juvenile females. On April 16, 2003, four local adult males
192 from our aviaries (hereafter the MC males) were introduced to one of the two groups and
193 remained for 12 days. The two aviaries were situated on either side of a wood building so
194 that only the one group heard the MC males. After the males' removal, the females were
195 reconfigured into four flocks with equal numbers of juveniles and adults. The juvenile (J)
196 and adult (A) females exposed to the four males are hereafter referred to as the JA+MC
197 females, as opposed to JA females who received no experience with males in aviaries.
198 Three females (two adults and one juvenile) died during the course of the experiment and
199 no data are reported from them.

200 Song/male experience between fall 2002 and spring 2003. The four groups of
201 females were exposed to tape recordings of cowbird song beginning in the fall of 2002
202 and ending in the spring of 2003 (Table 1). Each session consisted of four days of
203 tutoring with recordings of 10 unfamiliar, wild-caught adult Indiana (IN) males. There
204 were five seconds of silence between the songs in the playback. After the first 5
205 playbacks each day, 30 minutes elapsed before playback of the second five songs. Thus,
206 in each 4-day session, the females heard each song 4 times for a total of 40
207 playbacks/session. The 10 songs were presented in a different order each day. The
208 females heard the ten-song set, hereafter the TT-10 set, once in the fall and twice in the
209 spring while housed in the four aviaries in groups of six. Among the songs on the TT-10
210 set, three were shared, i.e., showed the same frequency structure and timing. In that song

211 playback to females had not been carried out at these times before, we chose the number
212 of songs and amount of tutoring based on our best guesses about balancing exposure with
213 habituation.

214

215 On two occasions in the fall and winter of 2002, all the females heard playbacks
216 of plastic and formatted song recorded from unfamiliar IN males housed with
217 nonconspecifics as part of another study (Table 1). Plastic song contains note clusters and
218 whistles sung in varying arrangements from rendition to rendition; formatted song shows
219 variable content but contains a stable syntactic structure. Females in the wild would hear
220 these forms of song in the late winter and early spring.

221 The 4 MC males' songs were heard for 12 days on April 16-30 by one group of 6
222 juveniles and 6 adults when the females were divided into two flocks of 12. During that
223 time, we recorded each male. From the recorded songs, eight songs, two from each male,
224 were combined with eight of the TT-10 songs into one test tape, hereafter the TT-8/MC-8
225 song set. We dropped the two songs receiving the fewest playback responses. Three of
226 the TT-8 songs were shared and none of the MC songs were shared.

227 Recording and playback procedures. We recorded TT-10 male song in aviaries
228 during the breeding season of 2002 (all TT songs) and 2003 (MC males). We placed 2-4
229 Sennheiser RF condenser microphones in locations to maximize our chances of obtaining
230 recordings from males vocalizing less than 0.3 m on axis with the microphones. The
231 vocalizations were recorded with a Sony TCD-D10 PRO II DAT recorder, sampled at 48
232 kHz. Songs were then digitally converted to 44.1 kHz files. Songs were selected on the
233 basis of recording quality. Using Peak LE and Bsound with Igor Pro

234 V.4.1(<http://homepage.mac.com/bsnelson/Bsound.html>), we filtered songs with a
235 Hanning window high pass (75 kHz) filter to remove low frequency noise below the
236 range of cowbird song.

237 During the year, the songs were played back through AIWA LCX-350 speakers,
238 attached in one corner of each aviary, positioned so that they broadcast away from the
239 other aviaries. Sound was played using a NAD compact disc player and songs were
240 broadcast at a level approximating the amplitude of songs sung within an aviary.

241 Breeding season playback. On May 2, 2003, all females were placed in two
242 indoor flight cages (2.4 x 6.1 x 2.3 m) out of contact from males. JA+MC females were
243 housed in one cage and JA females in the other. All were moved into sound attenuating
244 chambers on May 13, 2003 and playbacks began on May 15. The sound attenuating
245 chambers are 1m³ with the playback speaker placed to the left of the door. Some females
246 were housed in pairs and some alone. No effects of pair housing have been found in past
247 work in over 20 years of testing (King & West 1983; Smith et al. 2000; West & King
248 1985).

249 Beginning on May 15, 2003, song playbacks took place (Table 1). Between the
250 tests of the TT-10 and TT-8/MC-8 songs, the females heard six unfamiliar local songs
251 from a set of 14 songs across the day to reduce the chances of a recency or frequency-
252 dependent effect favoring the TT songs during the June playback of TT-8/MC-8 songs.

253 Measuring playback responsiveness. For both test tapes, we played six songs
254 daily to the females, with one song per trial and each trial separated in time by 90 min,
255 beginning at 0700 h. We played back each song six times to each female over the course
256 of the experiment. The females heard the vocalizations in varying orders each day and

257 each vocalization was presented roughly an equal number of times at different times of
258 the day.

259 We scored a positive response if a female adopted a copulatory posture (if she
260 arched her neck and back and separated the feathers surrounding the cloacal area) within
261 1 s from onset of the song. We played songs using a Denon DN-C680 compact disc
262 player, a Crown D75 power amplifier and JBL 2105 speakers located in each chamber.
263 The SPL was 85 +/- 2 dB adjusted with a B&K 2209 sound pressure meter, set to A
264 weighting, impulse reading, measured 75 cm. from the speaker.

265 Data analysis. Due to small samples sizes and heterogeneity of variance, we used
266 nonparametric tests. We used Mann Whitney tests for comparisons across groups,
267 Wilcoxon signed-rank tests for comparison within groups, Kendall's coefficient of
268 concordance for measures of inter-female agreement, and Kruskal-Wallis tests for
269 comparisons of 3 groups, using a Bonferroni-adjusted alpha of $p < .01$ (Siegel &
270 Castellan 1988). All tests were two-tailed. Some females did not respond at all to song
271 reducing the N in each group as shown in Table 2.

272

273 Results

274 Experiment 1

275 Response to local song. Within each group, the playback responsiveness of adults
276 and yearlings to the local song variants on the TT-10 song set did not differ (Table 2,
277 JA+MC, $U=5$, $n_1=4$, $n_2=4$, $p < .48$ and JA, $U=10.5$, $n_1=4$, $n_2=6$, $p < .76$). As a result, the
278 responses of the two ages were averaged together. Experience with the MC males did not
279 affect the mean proportion of responses to the TT-10 song set (Table 1, $U=26$, $n_1=10$,

280 $n_2=8$, $p < .21$). The females also did not differ in their responding to shared versus unique
281 songs (JA+MC, mean shared song =.52 (.10) vs. unique song=.43 (.08), $T=8$, $n=8$, $p <$
282 .16; JA, mean shared song=.24 (.11) vs. unique songs =.35 (.07), $T=8$, $n=10$, $p < .09$).

283 Concordance. Experience with the MC males did, however, affect the
284 concordance of female responding to the individual songs within the TT-10 set (Table 3).
285 JA+ MC females exposed in their aviary to males showed significant concordance in
286 their rankings of the 10 songs ($W=.46$, $n=8$, $p < .001$), but unexposed JA females did not
287 ($W=.14$, $n=10$, $p < .20$).

288 Responses to familiar and unfamiliar song. There were no age differences in mean
289 responsiveness to the TT-8/MC-8 set and so data were combined across age: for the
290 JA+MC group, $U=2$, $n_1=3$, $n_2=3$, $p < .40$ for TT-8 and $U=3$, $n_1=3$, $n_2=3$, $p < .70$ for the
291 MC songs; JA group, $U=12$, $n_1=5$, $n_2=5$, $p < .50$ for TT-8 songs and $U=10$, $n_1=5$, $n_2=5$,
292 $p < .68$ for MC songs). There were no significant differences in responding to the shared
293 versus unique songs in either group of females. The mean response for the JA group was
294 .41 to shared songs and .42 to unique songs. The mean response for the JA+MC group
295 was .37 to the shared songs and .38 to the unique songs.

296 The two groups of females responded significantly differently to the songs
297 presented by tape tutoring as opposed to those from the male companions (Table 2).
298 Within the JA+MC group, all females responded more to the songs of the male
299 companions ($T=0$, $n=6$, $p < .027$) while all but one of the JA females responded more to
300 the tutor-tape songs ($T=1$, $n=10$, $p < .024$). Between groups, JA+MC and JA females did
301 not differ in their mean responsiveness to the TT-8 songs ($U=29$, $n_1=6$, $n_2=10$, $p < .64$),

302 however, JA+MC females responded significantly more to MC songs than did JA
303 females ($U=5$, $n_1=6$, $n_2=10$, $p < .007$).

304 Concordance. We examined concordance of individual song rankings within the
305 two groups (Table 3). The JA+MC group showed significant concordance across the
306 entire set of 16 songs, $W=.35$, $n=6$, $p < .01$). The JA group also showed concordance,
307 $W=.28$, $n=10$, $p < .02$).

308 Discussion

309 The results show for the first time that female cowbirds' song preferences for
310 local songs are affected by postnatal experience when females are tutored outdoors in
311 groups. The different experiences afforded the two groups of females lead to a divergence
312 in their preferences. The JA females responded more to the familiar tape-tutor songs
313 compared to songs of unfamiliar males, while the JA+MC females preferred the male
314 companions' songs to the tape-tutor songs. Sensitivity to song tutoring from animate or
315 inanimate sources contrasts with all previous work studying female cowbirds housed in
316 pairs or triads in sound—attenuating chambers: under those circumstance, naïve or
317 experienced juvenile or adult females showed absolutely no evidence of postnatal
318 influence at microgeographic levels of song structure even after nine months of co-
319 habitation with males (King & West 1980; Smith et al. 2000; King et al. 2003a). Here, we
320 found sensitivity to acoustic and social influence with far less extended exposure. The
321 data from the present experiment do not allow us to tell if live tutors are more effective
322 than tape tutors and leave open many questions about the effects of timing of exposure.
323 The females with the 4 MC males almost certainly heard more song in the 12 day period
324 in late spring compared to the 120 total exposures to the TT-10 set during the year.

325 Further work is required to discover if one form of exposure is more effective than the
326 other, but our goal here was to see if *any* form of postnatal experience would affect
327 microgeographic preferences and the answer was that both sources were effective.

328 The tests of the MC vs. TT songs occurred later in the breeding season than the
329 tests of the TT songs alone, leaving open the possibility that the level of physiological
330 responsiveness could have changed. There was no evidence that females were more or
331 less responsive in the June test (Table 2). For the May test, the JA+ MC females' mean
332 proportion of responding was .46 compared to .49 for June tests; for JA females, the
333 mean proportion of responding was .32 in May and .33 in June. Two TT songs were
334 removed to form the TT-8 song set: the deleted songs were the least potent songs from
335 the first playback test. Could this exclusion have affected preferences when the TT and
336 MC songs were tested together? It does not seem likely to be the case as the two groups
337 of females did not differ in their playback responses to the TT-8 songs, responding to a
338 mean proportion of .38 versus .42 of the TT-8 songs (Table 2).

339 These data from aviary-housed birds stand in contrast to the results of previous
340 studies indicating no effects of postnatal experience on preferences in females housed in
341 sound-attenuating chambers who were tape tutored or housed with individual males
342 (West & King 1980; King & West 1983; King et al. 2003a). The preferences shown by
343 the females in the present experiment are all the more impressive when taking into
344 account the acoustic surroundings of the aviaries; we regularly observed singing male
345 cowbirds outside the aviaries throughout the fall and spring. In contrast, during the same
346 time frame, the females in the two groups heard each of the TT songs only 12 times (for a
347 total of 120 playbacks) and half of the females experienced the MC songs from the added

348 males for only 12 days. Thus, female cowbirds do not appear to need extensive
349 experience with specific songs in order to develop specific preferences. Both juvenile and
350 adult females were affected by the tutoring regimes, indicating that adult females can
351 learn new preferences beyond the first year, as has been found in some other songbird
352 species (Nagle et al. 2002; Riebel, 2003a).

353

354 Experiment 2: Comparison of hand-reared juveniles and experienced adult females

355 We conducted a second study to see if social experience with or without adult
356 females during the time of tape tutoring would affect juvenile females' song preferences.
357 The question was of interest because we thought it was possible that juveniles were
358 acquiring their preferences by observing how adult females responded to song during the
359 tutoring. We also used juveniles females that had been hand-reared from the egg and thus
360 had had no exposure to host species or to cowbirds until they were 30 or more days of
361 age. All previous work on female perception in cowbirds had been carried out with wild-
362 caught birds, making these fully hand-reared females a new developmental end point.

363 We also examined whether adults and juveniles would show a preference for tutor
364 songs when given massed playback exposure in relation to the first experiment. In this
365 test, we restricted the period of tutoring to one interval in the spring, at the time when
366 females in nature would be interacting with local males prior to pairing and breeding in
367 May. The females heard the TT songs an equal number of times but over the course of
368 two weeks, not six months.

369

370 Methods

371 Subjects and procedures. Twenty-two females were used. The eight adult females
372 had been wild-caught at the same collection site as Experiment 1 in 2001 and 2002. They
373 had lived in mixed sex aviaries until summer 2003 and then in aviaries with only
374 juveniles until March of 2004. They had not been subjects in any other playback tests.
375 The juveniles were hatched from eggs collected from aviaries at the laboratory in 2003.
376 Upon hatching, they were hand fed until independence, which generally occurred
377 between Day 18 and 25. Around Day 30, adult female cowbirds were added to the
378 outdoor aviary containing all the juveniles to facilitate independent foraging in the young
379 birds. The hand-reared juveniles (male and female) and adult females remained together
380 until the spring. On March 8, 2004, the 14 juvenile females and 8 adult females were split
381 into two groups. The first group consisted of the eight adult females and six juveniles (JA
382 condition). The second group consisted of eight juveniles (J condition). They were
383 placed in two of the same aviaries used in Experiments 1. All other details of care follow
384 Experiment 1.

385 Tutoring protocol. Both groups of females were tape tutored for 12 days
386 beginning on April 18, 2004 (Table 1). They heard the entire TT-10 song set once per day
387 using the previously described equipment.

388 Playback procedures. On April 30, 2004 the birds were moved into indoor flight
389 cages with juveniles in one cage and adults in the other. The juvenile females were placed
390 in sound attenuating chambers beginning on May 15, and playbacks occurred between
391 May 16-June 8 (Table 1). With the exception of one pair, we housed juvenile females
392 alone. From May 31 to June 10, the adults were housed in chambers and played the TT-
393 10 song set. On June 11-24, the TT-8/MC-8 playback occurred for all females. All

394 playback and statistical procedures followed those described earlier for Experiments 1.
395 One juvenile became ill and was taken out of the experiment.

396

397 Results

398 Responses to local song. A Kruskal-Wallis analysis of variance indicated
399 significant differences in responsiveness among adults, juveniles with adults, and
400 juveniles without adults for the TT-10 song set ($H=8.4$, $n_1=4$, $n_2=6$, $n_3=8$, $p < .015$).
401 Adults with juvenile females were reliably more responsive than juveniles alone (A vs. J
402 with A, $U=1$, $n_1=8$, $n_2=4$, $p < .018$; A vs. J only, $U=8$, $n_1=8$, $n_2=6$, $p < .04$; Table 2).
403 The adults' song preferences for the tutor songs were concordant ($W=.34$, $n=8$, $p < .01$).
404 The juveniles' preferences were not concordant (JA: $W=.19$, $n=4$, $p < .60$; J: $W=.28$, $n=6$,
405 $p < .20$).

406 In the second playback, all of the adult females responded more to the familiar
407 TT-8 songs (Table 2; $T=0$, $n=7$, $p < .018$). The juvenile females showed more variability,
408 with the three J+A and 1 J-A juveniles responding more to TT-8 songs and 3 J only
409 females responding more to the K1 songs. The adults also showed concordance in their
410 responses to the entire TT-8/MC-8 song set, $W=.46$, $n=7$, $p < .001$ (Table 3). Too few
411 juveniles responded in the two groups to compare concordance.

412 Year-to-year correlations. In both 2003 and 2004, we tested cohorts of adult and
413 juvenile female cowbirds housed together without males but tutored with the TT-10 song
414 set (JA condition), although at different points in time. For the two independent sets of
415 JA adult females, the year-to-year rankings of the TT-10 songs were highly correlated,
416 $r_s=.79$, $p < .01$; their rankings of the TT-8/MC-8 song sets were also highly correlated,

417 $r_s=.80$, $p < .001$. For JA juvenile females, the rankings were not correlated: for the TT-10
418 song set, $r_s=.24$, $p < .5$ and for the TT-8/MC-8 song set, $r_s=.51$, $p < .053$.

419

420

Discussion

421 Hand-reared juveniles were less responsive, less discriminating and less
422 consistent than adults when reacting to playbacks of familiar and unfamiliar song. The
423 data suggests that the naïve juveniles either needed song stimulation to occur much
424 earlier in the year or needed direct social contact with males. It may also be that some
425 other aspect of hand-rearing affected responsiveness. The social and acoustic experiences
426 of the hand-reared juveniles versus wild-caught juveniles in Experiment 1 differed as the
427 wild caught females could have heard adult song and interacted with adult males prior to
428 capture while the hand-reared birds could only have heard adult male song from outside
429 the aviary after day 18. They also may have heard more immature song from their male
430 flock mates in the fall and winter. Further investigation is required to sort through these
431 differences but the finding that the wild-caught juveniles in Experiment 1 did develop
432 reliable preferences for TT-10 or MC-8 songs shows that new preferences can be learned
433 even after 30-50 days of species-typical experience during the first year and after only
434 relatively brief periods of tutoring. The lack of discrimination by hand-reared birds even
435 with tutoring suggests that early experience with males is important to forming a
436 preference. We found a parallel dependence in wild-caught juveniles tested with
437 macrogeographic songs variants (King et al, 2003). Zebra finches also appear to need
438 experience with adult males to develop preferences for high quality songs (Lauay et al.
439 2004).

440 The Experiment 2 juveniles did not show concordance in their song rankings of
441 the TT-10 songs. Nor did their responses correlate with those of the JA juveniles in the
442 first experiment. The results add to the conclusion that juvenile females may require
443 actual experience with singing males before they can form significantly concordant
444 preferences (West et al. 1998; King et al. 2003a). The lack of correlation between the
445 2003 and 2004 juveniles housed with only adult females also suggests that more learning
446 is required. By contrast, the adult females' preferences were highly correlated, suggesting
447 song experience brings with it repeatability, even for songs heard for brief amounts of
448 time. In zebra finches, early exposure to song leads to more repeatable preferences of
449 songs using an operant response (Riebel 2000).

450 Looking collectively at the two groups across two years also adds weight to the
451 finding that exposure to tutor songs alone affects song discrimination. Across the two
452 years, all 12 JA adults from two different cohorts responded more to the familiar TT-8
453 songs versus the unfamiliar MC-8 songs and 7 of 8 JA juveniles responded more to TT-8
454 songs.

455 Learning by females may not be limited to the male's song. In other parts of the
456 cowbird's range, female cowbirds display copulatory preferences for playbacks of local
457 flight whistle dialects. These dialects are often not learned by males until their second
458 breeding season and there is some suggestion that females also may have to learn flight
459 whistle dialects after their first summer as they most likely learn them from males
460 (O'Loughlen 1995; O'Loughlen & Rothstein 1995). Thus, contact with adult males, not just
461 juvenile males, may enhance females' discrimination of song and whistle types.

462 Studies in white-crowned sparrows (*Zonotrichia leucophrys oriantha*) indicated
463 that wild-caught juvenile females did not exhibit greater physiological responses to natal
464 versus foreign song at the end of their first year but did respond with more copulatory
465 responses to natal song when tested at the end of their second year (MacDougall-
466 Shackleton and MacDougall-Shackleton 2001). Exposure to foreign song at the end of
467 their first year also affected responding to natal dialects the following spring. These data
468 indicate the importance of testing females beyond their first breeding season and raise the
469 possibility that song heard during the breeding season can also be considered as
470 additional auditory experience leading to song learning. Thus, in the present work, the
471 May playback of TT-10 songs might also be considered as further auditory learning. It
472 was not sufficient to preclude the JA+MC females' preference for MC songs but may
473 have consolidated the JA females' preferences. Future work is needed to look at the
474 physiological responses to song playback and to compare females' responses to songs in
475 June that were not preceded by the opportunity for further learning earlier in the breeding
476 season.

477

478 As measured here, adult females did not affect juvenile females' preferences for
479 tutored song as we had thought possible. It may be that the low response rate of the
480 juveniles masked any effect. It may also be that hand-reared females were too naive to
481 take advantage of observing adult females. The juveniles were housed in only two
482 aviaries; there could have been other factors besides the presence or absence of adult
483 females that contributed to their postnatal experience. Thus, the data must be viewed with
484 some caution until more groups are tested.

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General Discussion

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The results of the present work showing preferences for local song variants as a function of song experience complement those carried out on preferences for macrogeographic song variants (King et al. 2003a). In both studies, flock housing revealed postnatal plasticity in adult and juvenile females where chamber housing had indicated no plasticity. Concordance in song discrimination was affected by male experience and age. In both studies, adult females of two or more years of age with courtship experience and previously formed song preferences showed evidence of new learning, developing preferences for new songs experienced either by song or live tutoring. Thus, female cowbirds appear to show an extensive period of sensitivity to song stimulation and may, in fact, be more open-ended as learners than male cowbirds, whose ability to add song types does not appear to go past the second year (Hamilton et al. 1998).

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In past studies of seven populations within and across the three subspecies, we found that acoustically- isolated juvenile and adult females showed strong local preferences, even after complete deprivation from local song or many months of exposure to distant song (West et al. 1998; King & West, 1990; Smith et al. 2000; King et al. 2003a). The presence of species-typical song preferences when housing is in sound-attenuating chambers suggests that the development of song preferences proceeds through the modification of innate perceptual biases as opposed to de novo postnatal formation of preferences. In that regard, the data gathered here on young females suggests some similarities with the male cowbird's development of song. Males with no

508 postnatal experience produce songs that elicit copulatory responses, just as females with
509 no postnatal experience discriminate cowbird song from heterospecific song (King &
510 West 1977; 1980). These findings by themselves suggest that the species possesses a
511 safety net for song recognition, a seemingly appropriate adaptation for a brood parasitic
512 species. But such a conclusion is wrong because it is based on a performance in a
513 physical context cowbirds and other songbirds never experience, i.e. no social contact
514 with conspecifics. Cowbirds naturally form social groups as juveniles and that experience
515 leads young males to sing less potent song than isolates and as the first experiment
516 shows, appears to lead young females to override perceptual biases in favor of current
517 exemplars of local song (West & King 1980). In sum, for both females and males, social
518 interactions affect initial sensory states leading to different communicative outcomes.
519 The dynamic pattern of initial bias, social perturbation, and rapid assembly of new
520 preferences through active engagement with the environment is one that also describes
521 developmental change in song preference learning in some other songbirds (Marler &
522 Nelson 1993; Riebel 2003 a & b; West & King 1996) and sensory-motor development in
523 many species for many motor behaviors (Thelen & Smith 1994).

524 Much more is known about the contextual properties that cause transitions in male
525 song production and use than the transitions in female perception and choice. Recent
526 work in the laboratory has begun to outline the contextual properties important to female
527 development. In a series of studies conducted in outdoor aviaries, we have observed the
528 nature of female social organization and how it is affected by the presence of males,
529 females, or the presence of songs (Gros-Louis et al. 2003; King et al. 2003b; West et al.
530 2003a; White et al. 2002). Briefly put, these studies show that juvenile females' social

531 interactivity with adult females varies as a function of male presence. If males are absent,
532 females show no particular pattern of social organization by age, but they rapidly
533 segregate by age when adult males are introduced. Females also show immediate re-
534 organization into age-segregated groups when male song is played into an aviary, with
535 the age segregation disappearing when playbacks cease, and returning when playbacks
536 resume. These changes occur as early as the fall of the female's first year. Both juvenile
537 and adult females also use visual displays in response to song, especially rapid flicks of
538 the wing, termed wing strokes (Gros-Louis et al. 2003). In other work with the birds
539 studied here, White (unpublished data) found that the adult and juvenile females wing
540 stroked differently to primitive versus more mature song. Females also appear to observe
541 each other's wing strokes and appear to compete by approaching males and displacing
542 each other (Gros-Louis et al. 2003). Females who approach males stimulate counter-
543 singing, which, in turn, appears to affect egg production (King et al. 2003b). Ongoing
544 work also suggests that juvenile and adult females differ in their levels of interactivity.
545 Juvenile females are more interactive with each other and with juvenile males, compared
546 to adult females who segregate themselves from young males, When adult females are
547 introduced into juvenile flocks, they significantly increase their affiliations with young
548 males, suggesting they see juvenile females as possible competitors. In the wild, flocks
549 vary in composition with some containing only juveniles and some containing adults as
550 well. Young females then may learn to attend to some attributes of males by
551 eavesdropping on adult female-juvenile male interactions.

552 In sum, females' reactions to song and to males affect patterns of affiliation and
553 individual behaviors well before the breeding season. Group dynamics such as changing

554 patterns of flock assortment cannot occur when females are housed in sound attenuating
555 chambers with one or two females and one or no males. In nature, during the fall and
556 winter, juveniles join large flocks. But within these settings, we have observed that small
557 groups of males and females (under 20 birds) can be found in association across time
558 (King & West, 1988). Thus, opportunities for interactions like those studied here map
559 roughly onto natural contexts. The chamber setting precludes the formation and
560 maintenance of communication networks as described by McGregor & Peake (2000) and
561 Sturdy et al. (2001). The rapid changes in group patterns reveal the sensitivity of network
562 members to one another; the diversity of behavior within the network indicates the
563 possibilities for direct and indirect learning. At present, we do not know the precise
564 parameters of individual versus flock housing that affect plasticity. The ambient
565 environment in outdoor aviaries is likely to be more arousing as a result of shifts in
566 weather, challenges from aerial predators, and changes in the acoustic environment
567 created by resident and migrating birds. This state of arousal is likely much higher than in
568 the stable state of chamber housing, and thus more likely to lead to behavioral transitions.

569 The data collected here document changes in song preferences. How these
570 preferences affect actual mate choice is yet to be understood. Such studies are essential in
571 that song structure represents only one means of male assessment. Studies in canaries and
572 sparrows indicate that reproductive activity such as nesting or egg laying may be
573 stimulated by other cues (e.g., Depraz et al. 2000; MacDougall-Shackelton &
574 MacDougall-Shackleton, 2001). In studies of flocks of cowbirds, we have found that
575 female cowbirds' egg production and the hatching success of her eggs are best predicted
576 by male counter-singing, not potency of particular song types. Female-directed singing

577 by males is also an important metric (White, unpublished data). Both of these behaviors
578 involve song embedded in a social context. Thus, the next step is to see how plasticity in
579 song preference relates to mate choice and reproductive success.

580 The data presented here show that song preferences are malleable traits, which
581 might seem to be a contradiction in terms as “traits” typically refers to behavioral or
582 morphological properties that are relatively fixed within individuals across their lifetimes
583 (Stamps 2003). In cowbirds, and probably other songbirds, females’ preferences for
584 songs do not appear to be stable over time and context. Perhaps, they are best not classed
585 as traits at all, or qualified as state-dependent traits, where knowledge of context is
586 required to answer functional and evolutionary questions. What is stable over lifetimes
587 and individuals is the certainty that the ontogeny of preferences is situated in a social
588 ecology. It is similarities and differences in the traits of a species’ ecology that must be
589 identified to understand how selection operates on the development and evolution of
590 communicative capacities (West et al. 2003a).

591

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710
 711 Table 1. Dates for aviary and breeding season playbacks. For aviary playbacks, the
 712 females heard 10 songs per day in different orders for four days; for sound-attenuating
 713 chamber playbacks, the females heard 6 songs per day in different orders. All fall and
 714 spring playbacks took place in each of four aviaries; male exposure took place in two
 715 combined aviaries.

716

717

EXPERIMENT ONE

718

719

720 FALL and SPRINGSONG SETS in OUTDOOR AVIARIES

721

722 Nov. 11-14, 2002

TT-10

723

724 Nov. 26-Dec. 4, 2002

Plastic Song

725 Dec. 16-20, 2002

Plastic and Formatted Song

726

727 April 8-12, 2003

TT-10

728

729 *April 14-28, 2003**4 adult Indiana males (MC) housed
with 6 J and 6 A females and then removed*

730

732 April 29-May 2, 2003

TT-10

733

734 BREEDING SEASONPLAYBACKS in SOUND ATTENUATING CHAMBERS

735

736 May 15-25, 2003

TT-10

737

738 May-26-June 8, 2003

14 Local Indiana Songs

739

740 June 8-24, 2003

TT-8/MC-8

741

742

743

EXPERIMENT TWO

744

745 SPRINGSONG SET in OUTDOOR AVIARIES

746

747 April 18-30, 2004

TT-10

748

749 BREEDING SEASONPLAYBACKS in SOUND ATTENUATING CHAMBERS

750

751 May 16-June 8, 2004

TT-10 to J females

752

753 May 31-June 10, 2004

TT-10 to A females

754

755 June 11-24, 2004

TT-8/MC-8 to J and A females

756 Table 2. Mean proportion and standard error of copulatory responses in the two
 757 experiments. Numbers in bold connected by brackets indicate significant differences as
 758 tested by Wilcoxon signed-rank tests (T) for within group comparisons; Mann Whitney
 759 tests (U) for between group comparisons; and Kruskal-Wallis (H) ANOVA for
 760 comparison of the three groups.

761

762

2003 PLAYBACK SETS: Experiment 1

763

764

Test One

Test Two

765

TT10

TT-8 versus MC-8

766

767

T=0, p < .027

768

769 J+A FEMALES
 770 (w/ MC MALES)

.46 (.08)
 n=8

.38 (.08) **.61 (.07)**
 n=6 n=6

771

772

773

T=1, p < .024

774

775 J+ A FEMALES

.32 (.07)
 n=10

.42 (.04) **.25 (.06)**
 n= 10 n=10

776

777

778

779

780

2004 PLAYBACK SETS: Experiment 2

781

782

783

Test One

Test Two

784

TT-10

TT-8 versus MC-8

785

786

787 J FEMALES
 788 (w A's)

.30 (.08)
 n=4

.19 (.04) .27 (.06)
 n=4 n=4

789

790 J FEMALES
 791 (w/o A's)

.46 (.07)
 n=3

H=8.4
p < .015

.59 (.09) .31 (.03)
 n=3 n=3

792

793

794

795 A FEMALES
 796 (w J's)

.72 (.07)
 n=8

.67 (.06) **.53 (.04)**
 n= 7 n=7

797

798

799

800

801

U= 1
p < .008

T=0, p < .02

802

803

804

805 Table 3. Kendall's co-efficient of concordance for juvenile and adult females

806 for Experiments 1 and 2. Values significant at $p < .05$ or lower are indicated by a "yes"

807 and non-significant values with "no".

808

809

810

SONG SETS

811

812

TT10TT8-MC8813 CONCORDANCE 2003

814

815 J+A FEMALES816 w/ MC MALES

Yes

Yes

817

818

819 J+A FEMALES

No

Yes

820

821

822 CONCORDANCE 2004

823

824 J FEMALES

825

826 With adults:

No

*

827

828 Without adults:

No

*

829

830 A FEMALES

Yes

Yes

831

832 *Concordance not computed due to low N's.

833

834

835

836