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ORIGINAL ARTICLE

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Female brown-headed cowbirds' (*Molothrus ater*) social assortment changes in response to male song: a potential source of public information

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Abstract In many species, females' behavior appears to be influenced by that of other females, particularly regarding mate choice. Females theoretically can reduce the costs associated with independent male assessment by observing conspecifics. Studies of brown-headed cowbirds suggest that females pay attention to other females' behavior. Group-housed females modify their song preferences, whereas females housed in pairs do not. What information is available to females in a group environment? To address this question, we studied two groups of juvenile (i.e. hatch-year birds) and adult female cowbirds in a naturalistic group setting. We used a longitudinal ABA design, consecutively introducing and removing males that differed in age, amount of song production and stage of song development, to isolate the male characteristics that related to changes in female behavior. Juvenile and adult females assorted by age class when singing adult males were in the aviary, but not when singing juveniles or silent males of any age class were in the aviary. Results from playback tests confirmed that adult male song alone influenced female age class assortment. Videotape analysis from playback tests revealed that females also wing stroked in response to male song. Other females sometimes approached females who wing stroked and observed them. We hypothesize that group-level changes in social organization and individual females' responses can serve as visual signals for other individuals.

Keywords Cowbird · Preference · Public information · Social assortment · Wing stroke

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Introduction

In many species, females appear to attend to the behaviors of female conspecifics. Most often studied in the context of mate choice, females' grouping patterns, preferences and even mate choices can be influenced by other females (Gibson et al. 1991; Shuster and Wade 1991; Dugatkin 1992; Gibson and Hoglund 1992; McComb and Clutton-Brock 1994; Jennions and Petrie 1997; Hoglund et al. 1995; White and Galef 1999; Westneat et al. 2000). By observing conspecifics, females theoretically can reduce the costs of sampling or errors associated with choosing a mate and, in some cases, they can gain information from more knowledgeable individuals (Losey et al. 1986; Wade and Pruett-Jones 1990; Gibson and Hoglund 1992; Pruett-Jones 1992; Stohr 1998; Agrawal 2001; Sirot 2001). Female brown-headed cowbirds (*Molothrus ater*) appear to be influenced by other females' preferences when housed in a group environment (Freeberg 1998; Freeberg et al. 1999), whereas laboratory studies have been unable to find evidence of such malleability (King and West 1983; see also Baptista et al. 1993for parallels in female song learning in white-crowned sparrows *Zonotrichia leucophrys*). Thus, a group setting appears to provide opportunities for learning that are unavailable to females living in more restrictive housing. But what is the mechanism that can account for this difference? Do females' responses in a group provide different information than their responses in pairs?

We were led to consider social assortment as a measure of responsiveness based on a series of studies looking at social development of cowbirds housed in large aviaries. In 12 groups in previous studies, we have found that social organization by age ad by sex is a robust measure of social influence on the development of male courtship behavior in cowbirds living in large aviaries (Freeberg 1999; Smith et al. 2002; King et al. 2002; White et al. 2002b; Whiteet al. 2002c). In addition, West et al. (2002) found that social assortment of females varied as a function of the age-sex class of birds with whom

they were housed. Females showed segregation by age class when housed with males (see also Smith et al. 2002; King et al. 2002) but not when housed only with females. In conditions with adult males, females had more male neighbors, approached males more often, and assorted more strongly by age than when housed with juvenile males (White, unpublished data). Furthermore, in the breeding season, the females in conditions with adult males copulated more and produced more fertile eggs as compared to the females who were housed with juvenile males.

Taken as a whole, the results of West et al. (2002) indicated that females are sensitive to the variables of sex and age and correlated behaviors when housed in flocks and that this sensitivity has reproductive consequences. The design of the West et al. study did not allow us to determine proximate influences on social responsiveness because the females remained in the same social groups all year. For this reason, in this study, we turned to a longitudinal ABA design to examine how different types of male stimulation affected social organization of females in the fall.

In addition to documenting changes in females' group behavior, we sought to identify behavioral responses that may reflect females' assessment of males. Do females respond in particular ways that are publicly informative about males? Do females perhaps also perform species-typical signals, seen in other contexts, when females interact in groups? For example, we know from laboratory studies that females respond to a small percentage of songs with rapid flicks of their wings, termed wing strokes (West and King 1988a). If a female exhibits a behavioral response such as this in a more social context, not only does the male receive feedback, but so might females who are in close proximity.

To explore the nature of female responsiveness to males, we studied two groups of juvenile (i.e. hatch-year birds) and adult females in outdoor aviaries during the fall. We consecutively introduced and removed males that differed in age, amount of song production and stage of song development, to isolate which characteristics of males related to changes in female behavior. Widowski et al. (1990,1992) successfully used a similar within-subjects experimental design to determine the male characteristics that influenced female reproductive condition in cotton-top tamarins (*Saguinus oedipus*). Because we needed to compare the relative influence of particular male characteristics on female behavior, we used the same females to avoid a confound due to inter-female variability in responsiveness (King and West 1989). We asked how females responded to male presence and, in the absence of males, how females responded to male song as determined by playback tests.

Methods

General

Subjects

We used 62 wild-caught brown-headed cowbirds from Monroe County, Indiana as subjects in experiments conducted between 7 September and 14 December 2001. We trapped all of the juveniles between 12 July and 19 August 2001. We determined the sex and age of the juveniles based on the mature plumage that had emerged (Selander and Giller 1960). We judged juveniles to be between 40 and 50 days old. We trapped four adult males (>2 years) between 5 and 10 July 2001. We trapped the other adult birds in the previous 2 years and housed them with birds of different age-sex classes for various experiments. We used unique combinations of colored plastic leg bands to identify individuals.

The subjects of the experiments were 13 juvenile females and 16 adult females. We randomly assigned six juveniles and eight adults to one aviary (aviary 1), and seven juveniles and eight adults to the other (aviary 2). We consecutively added and removed other individuals, 6 adult females, 18 adult males, and 9 juvenile males, over the course of five experiments.

The two aviaries were large outdoor enclosures (9.1×21.4×3.4 m) containing grass, trees, indoor and outdoor perches, and feeding stations. A shelter building separated the aviaries and thus birds were visually but not acoustically isolated from one another. Birds experienced weather conditions and were able to see and hear wild local conspecifics and predators. We provided the birds daily with vitamin-treated water, a modified Bronx zoo diet for blackbirds, and a mixture of white millet, red millet, and canary seed. In addition, the birds foraged freely.

Procedure

The study consisted of 15 rounds of data collection within a series of five experiments to observe changes in female social organization and behavior in response to the introduction of males with different characteristics into the aviaries. Each round represented a different phase within an experiment and thus will be explained below for each experiment. However, here we provide a general overview of the procedure.

In the first experiment, we observed only one aviary. We first took baseline data to document levels of female age class assortment in the absence of males. We then introduced males to the females to observe changes in female age class assortment in response to male presence. For the final four experiments, we used a modified ABA design in the two aviaries (baseline-experimental introductions-reversal of introductions-return to baseline) to document the immediate effects of introducing males with different characteristics on female age class assortment. We first collected baseline data to document female age class assortment before male introductions into the aviaries. We sequentially added and removed males who were either 'singing' or 'non-singing' (see below) using a counter-balanced design to control for order effects. Lastly, we removed the males and collected data to document whether females returned to baseline levels of age class assortment. For each social manipulation, we added or removed birds one day prior to the commencement of data collection. We did not use the same males in more than one experiment.

In rounds 12–15, we performed playback tests within the aviaries to determine more precisely what role male song had on female age class assortment. First we performed playbacks in the presence of 'non-singing' juvenile males (as controls) and then in the absence of males.

Data collection

To measure age class assortment, we recorded near neighbor (NN) associations in 7-min sampling blocks. We defined near neighbors

as two birds within approximately 30 cm of one another. Observers identified one bird (the "target") and recorded the identity of any bird within 30 cm (the "near neighbor") and then located another target bird. The same individuals could not be recorded as near neighbors again in the same block unless they moved away and re-associated. For example, if A and B were within 30 cm of one another, they were counted as near neighbors only once in a data block (A as B's neighbor or B as A's neighbor, but not both) unless they moved apart and came to within 30 cm of one another again during that block. Individuals could serve as the target multiple times in the same block.

To document singing behavior, we collected data ad libitum on all songs produced by males during the 7-min sampling blocks (Altmann 1974). A solo bout was defined as a series of ten undirected songs in a minute. If a male sang a solo bout, we noted it and stopped collecting song production data for that male during that block.

Three to four observers sequentially collected typically four blocks of data each over a period of 3–9 days for every round of data collection (see below for the exact numbers of days and data blocks within each round). Due to weather conditions, the numbers of days varied between experiments, but were roughly equal within experiments. We started each round of data collection on the morning following the introduction of new birds into an aviary. We collected a total of 94.4 h of data totaling 32,266 NN points.

Observers spoke the color band acronyms of birds that were NN into omni-directional, wireless lapel microphones (Telex WT 150; Telex Communications). A receiver (Telex FMR 150) transmitted each observer's vocal signal to a Pentium III 500-MHz IBM-compatible computer running Microsoft Windows 1998. We used voice recognition software (IBM ViaVoice Millenium Pro Edition) and Microsoft Word 2000 to transcribe the speech into text. We exported data into a database (4th Dimension v. 6.5.1; ACI) that we programmed to compare incoming bird identification bands and data codes with a list of possible acronyms to detect and correct errors automatically (White et al. 2002a).

Statistical analysis

Due to small sample sizes and heterogeneity of variance, we performed non-parametric statistical analyses throughout. In addition, because of small samples sizes, we combined the results from the two aviaries for statistical analysis. We used each female's proportion of NN associations with adult females in Wilcoxon signed-ranks tests to document changes in individual females' assortment within and between rounds in each experiment. Using this experimental design, each female served as her own control. We report the mean change (±SE) in the proportion of NN associations for females within each age class for each comparison to illustrate changes in female assortment. Although we combined data from the two aviaries, we provide separate figures for each aviary (Fig. 1a, b) to illustrate the variance. See Table 1 for an overview of the experimental manipulations performed in each aviary.

Experiment 1: presence of adult males

We had documented in a previous study that females organized themselves by age class in the presence of adult males, but not in their absence (West et al. 2002). We wanted to replicate and extend these findings to determine whether females were influenced by mere visual contact with adult males or whether adult males needed to be physically present in the aviary with females. Therefore, the purpose of the first experiment was to investigate how the presence of adult males influenced female age class assortment.

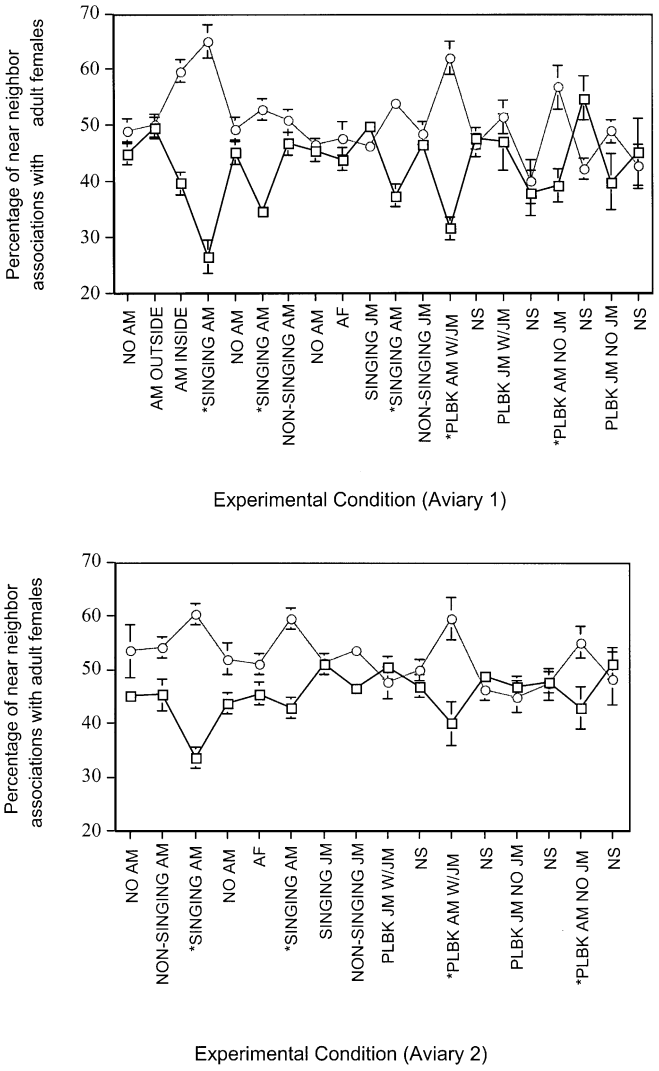

Fig. 1 The percentage of juvenile and adult female near neighbor associations with adult females for each round of the five experiments in **a** aviary 1 and **b** aviary 2. Percentages were calculated by averaging each female's mean number of near neighbor associations with adult females. *Asterisks* mark the introduction of 'singing' adult males into the aviary and the presentation of adult male song during playback trials. *AM* Adult male, *AF* adult female, *PLBK* playback, *NS* no song (baseline), □ juvenile female, ○ adult female. See text for further explanation

Methods

Procedure

We collected NN association data in aviary 1 for 7 days, for a total of 47 blocks, to determine the level of female age class assortment in the absence of adult males. We then placed three adult males in a mobile cage (2.5×1.5×1.4 m) just outside of the aviary. The cage was within 2 m of where the females frequently perched. We collected 31 data blocks during the 5-day collection period. We recorded no singing from the males until one male sang a solo bout at the end of the last 7-min data block. In the final round of this experiment, we intro-

Table 1 Summary of experimental manipulations, number of days and number of data blocks per experiment. *AM* adult male, *AF* adult female, *JM* juvenile male, *PB* playback

Experiment	Round	No. of data blocks	Days	Manipulation	
				Aviary 1	Aviary 2
1	1	47	7	No AM present	
	2	31	5	3 AM outside aviary	
	3	56	5	3 AM inside aviary	
2	1	25	8	No AM	No AM
	2	45	5	3 singing AM	3 non-singing AM
	3	41	5	3 non-singing AM	3 singing AM
	4	41	4	No AM	No AM
3	1	19	7	3 AF	3 AF
4	1	45	5	3 singing JM	3 singing AM
	2	57, 58 (av. 1,2)	5	6 singing AM	6 singing JM
5	1	44	4	Non-singing JM	Non-singing JM
	2	37	3	PB AM song with JM	PB JM song with JM
	3	26	3	PB JM song with JM	PB AM song with JM
	4	12	3	PB AM song without JM	PB JM song without JM
	5	12	3	PB JM song without JM	PB AM song without JM

duced the three adult males from the mobile cage into the aviary with the females to determine the effect of the presence of males on age class assortment. Thus, in this round, females could interact with adult males rather than merely being in visual contact with them.

Once in the aviary, two of the three adult males sang solo bouts in 17 of the 56 7-min data blocks. We analyzed the NN association data separately for blocks with song (n=17) and blocks without song (n=39).

Results

The juvenile and adult females assorted by age class only when adult males were present in the aviary, particularly when they were singing. Baseline levels of age class assortment showed that the juvenile and adult females (JF and AF respectively) did not associate preferentially with one age class (mean proportion of JF-JF associations=0.55±0.02; AF-AF mean=0.49±0.02; Fig. 1a). The juvenile and adult females did not increase their NN associations with females of the same age class in response to the visual presence of males outside of the aviary (JF-JF mean change from baseline=–0.05±0.03: Wilcoxon T=3, n=6, P>0.5; AF-AF=0.01±0.03: Wilcoxon T=20, n=8, P>0.8). When we placed males inside the aviary, both the juvenile and the adult females associated significantly more with individuals of the same age class than when males were outside of the aviary (JF-JF mean increase=0.07±0.02: Wilcoxon T=21, n=6, P<0.04; AF-AF=0.09±0.03: Wilcoxon T=35, n=8, P<0.02).

Male song appeared to have the strongest effect on female social organization. Based on observations during which males were singing (mean no. of solo bouts = 6.3±4.9), the juvenile females significantly increased their NN associations with juvenile females compared to when males were not singing (JF-JF mean increase= 0.17±0.03: Wilcoxon T=21, n=6, P<0.04). Adult females also tended to associate more with adult females in response to male song (AF-AF mean increase=0.08±0.03: Wilcoxon T=31, n=8, P<0.08).

Experiment 2: effect of singing males

In experiment 1, we had observed that females assorted by age class when adult males were present in the aviary but more so during blocks when the males were singing. Furthermore, females responded immediately to male song; we saw effects within the 7-min blocks when song was present. Because the males were singing throughout the experiment, it was hard to isolate the effects of male presence and male song. The purpose of the second experiment was to determine whether the presence of males, or singing males specifically, was responsible for female age class assortment by introducing ‘singing’ or ‘non-singing’ males into each aviary.

Methods

Procedure

We selected ‘singing’ and ‘non-singing’ males based on 4 days of observations between 10 and 17 October 2001 conducted in the home aviary of adult males. We collected data ad libitum to note all songs produced by males (Altmann 1974). The number of songs produced by 40 adult males ranged from 0 to 157. We defined ‘singing’ males as those males who sang often, compared to other males in their home aviary (median no. of songs = 130). ‘Non-singing’ males were those males who never sang in their home aviary. In the fall, unlike in the spring, singing behavior has no obvious relationship to dominance (Dufty 1986).

We first collected NN association data on females in both aviaries for 8 days to document baseline levels of age class assortment. After 8 days, we concurrently introduced three 'singing' adult males into aviary 1 and three 'non-singing' adult males into aviary 2. We observed individuals for 5 days and collected 45 blocks of NN data in each aviary. We then switched the adult males housed in the two aviaries and again observed the birds for 5 days and collected 41 blocks of NN data in each aviary. Lastly, we removed the adult males from both aviaries and collected 41 blocks of data over a 4-day period to determine whether in the absence of the males, females returned to baseline levels of age class assortment.

Results

The presence of 'singing' adult males generally resulted in female age class assortment, whereas the presence of 'non-singing' adult males did not. During the baseline period, females did not assort by age class (JF-JF= 0.55±0.02; AF-AF=0.51±0.03). The juvenile and adult females showed a significant increase in NN associations with individuals of the same age class compared to baseline levels when we introduced 'singing' adult males (mean no. of solo bouts across all data blocks = 7.8±2.1) (JF-JF mean increase=0.11±0.02: Wilcoxon T=91, n=13, P<0.0005; AF-AF=0.05±0.02: Wilcoxon z=2.28, n=16, P<0.03). When we introduced 'non-singing' adult males (n=0 songs each across all data blocks) into the aviaries, NN associations for the juvenile and adult females returned to levels that were not significantly different from baseline (JF-JF mean change=–0.01±0.02: Wilcoxon T=31, n 13, P>0.5; AF-AF=0.01±0.02: Wilcoxon z=0.78, n=16, P>0.4). In addition, NN association patterns remained at levels indistinguishable from baseline in the final phase of the experiment when we removed the 'non-singing' adult males from the aviaries (JF-JF mean change=0.01±0.02: Wilcoxon T=52, n=13, P>0.5; AF-AF=–0.02±0.02: Wilcoxon z=1.03, n=16, P>0.3).

Experiment 3: presence of adult females

We conducted a third experiment to control for the possibility that the mere introduction of any novel birds could influence female age class assortment. We introduced three adult females into each aviary to determine whether they influenced the social organization of juvenile and adult females, as did the adult males.

Methods

Procedure

We randomly selected six adult females from an all-adult female aviary and randomly assigned three to each test aviary. We collected 19 blocks of NN data over a 7-day period. We compared levels of age class assortment after the female introductions to baseline data taken at the end of the previous round.

Results

When we introduced the adult females into the aviaries, the juvenile and adult females did not show a significant increase in the proportion of their NN associations with females of their own age class compared to baseline levels (JF-JF mean increase=–0.003±0.01: Wilcoxon T=24, n=13, P>0.5; AF-AF=–0.001±0.02: Wilcoxon z=0.05, n=16, P>0.8).

Experiment 4: effect of juvenile versus adult males

The purpose of this experiment was to compare the effects of juvenile and adult males on female age class assortment. We had seen an effect of singing adult males on female assortment in experiments 1 and 2. Therefore, we wanted to determine whether females responded to singing males in general, regardless of their age.

Methods

Procedure

We selected 'singing' males using the same procedure as described in experiment 2. We based our selections on 5 days of observations of juveniles in an all-juvenile aviary and 9 days of observations of adults in an all-adult aviary between 10 October and 7 November 2001. The number of songs produced by 26 juvenile males ranged from 0 to 150 (median no. of songs=89), whereas the number of songs produced by 40 adult males ranged from 0 to 259 (median no. of songs=160).

We first introduced three 'singing' juvenile males (median no. of songs=130) into aviary 1 and three 'singing' adult males (median no. of songs=189) into aviary 2. We collected 45 blocks of NN associations over a 5-day period. For the reversal phase, we introduced new males rather than switching the males between aviaries because of low levels of singing by the original males. We selected three new juvenile and three new adult males from the all-juvenile and all-adult male aviaries. We placed three new 'singing' adult males (median no. of songs=163) into aviary 1 and three new 'singing' juvenile males (median no. of songs=71) into aviary 2.

During the first two days of observation, none of the juvenile males produced any songs, and two of the three adult males sang 10 and 20 songs, respectively, in 3 of 32 blocks. Therefore, we decided to add three more males to each condition. We selected three more 'singing' juvenile and adult males (median no. of songs=71 and 54, respectively). We observed the birds for an addi-

tional 5 days for a total of 58 and 57 blocks of data respectively for aviaries 1 and 2. We compared levels of age class assortment in the presence of 'singing' juvenile and adult males to baseline levels obtained at the end of the previous round.

Results

The juvenile and adult females assorted by age class in the presence of 'singing' adult males but not in the presence of 'singing' juvenile males. When we introduced the 'singing' juvenile males (mean no. of solo bouts across all data blocks=4.7±1.7) into the aviaries, the juvenile and adult females allocated roughly equal proportions of NN associations to females of each age class that were not significantly different from baseline levels (JF-JF mean change=–0.06±0.01: Wilcoxon T=4, n=13, P>0.5; AF-AF=0.007±0.02: Wilcoxon z=0.31, n=16, P>0.6). When we introduced 'singing' adult males (mean no. of solo bouts across all data blocks=2.5±0.65) into the aviaries, the juvenile females tended to increase their NN associations with other juveniles but the change was not significant (mean increase=0.04±0.02: Wilcoxon T=70, n=13, P>0.09). The adult females allocated a significantly greater proportion of their NN associations to adult females compared to baseline levels in the presence of 'singing' adult males (mean increase=0.08±0.02: Wilcoxon z=3.15, n=16, P<0.002).

'Singing' adult males had a greater effect on NN associations than did 'singing' juvenile males. Juvenile and adult females increased their within-age class NN associations in response to the presence of 'singing' adult males compared to 'singing' juvenile males (JF-JF mean increase=0.10±0.01: Wilcoxon T=20, n=13, P<0.001; AF-AF mean increase=0.08±0.01: Wilcoxon z=3.21, n=16, P<0.0002).

Experiment 5: effect of juvenile and adult male song in the absence of singing males

The differential effect of adult males and juvenile males on female age class assortment led us to question what age-related cues were driving social reorganization among females. Males' size and morphological characteristics did not seem to be a reliable cue; males varied slightly in size and/or plumage coloration. By contrast, juvenile and adult males clearly differed in their stage of song development. In addition, juvenile and adult males may have differed in their non-vocal behavior associated with singing. Females could have been responding differently to juvenile and adult males because of differences in their vocal or their non-vocal behavior. We designed a series of playback tests to distinguish between these two possibilities.

Methods

Subjects

The original two groups of females in aviary 1 and aviary 2 served as subjects with the exception of one juvenile female in aviary 1 who died during the course of playback tests. In addition, we introduced six 'non-singing' juvenile males, three in each aviary, to serve as controls for male presence during some of the playback tests (see Procedure).

Playback stimuli. We created two CDs of juvenile male song and two CDs of adult male song to be used as playback stimuli. We used songs that were recorded from adult and juvenile males during the first week of October 1999. We recorded songs using a Sennheiser RF condenser microphone and a Sony TCD-D10 PRO II DAT recorder at a distance of approximately 30 cm. We selected, based on recording quality, a sample of 23 songs from four juvenile males and 23 songs from four adult males to use in playback sequences.

We only used songs from four juvenile and four adult males because we wanted to simulate the introduction of 'singing' and 'non-singing' males that we had conducted in previous experiments. The four adult males were selected based on the amount of song they produced such that they were representative of the distribution of total song production by adult males (few–many). Their songs were judged to be typical Indiana songs, containing common whistle types. The four juvenile males were hatch-year birds, and therefore, we did not have any data on their singing history. Adult and juvenile song differed in that all of the adult songs contained both note clusters and whistles, whereas the juvenile song was more variable in its elements, structure and rhythm (see West and King 1988b; Smith et al. 2000for a description).

To create playback sequences, we first digitized the 46 selected songs by playing them on a Panasonic SV-3700 professional DAT recorder that was connected to an Apple 500 MHz G3 Powerbook running Sound Edit 16 version 2.0.7. We digitized the calls at a sampling rate of 44.1 kHz and created a sequence of 23 songs covering a 7-min period. Within the 7 min, we created one solo bout, while the remainder of the songs occurred at different intervals so that playback sequences reflected a natural rate of singing by males at this time of year. We used the same juvenile male and adult male songs to make two different temporal sequences of song for the juvenile and adult male playback stimuli.

Playback setup. We placed a speaker (AIWA LCX-350) in each aviary 2 days before the experiment for a few hours each day to habituate the birds to its presence. On the days of playback tests, we placed the speakers in the aviaries half an hour before the commencement of the tests. To enhance the credibility of the playback stimuli, we chose a position for the speakers where it would be feasible for a bird to be perched out of view of the group.

We positioned the speaker close to perches that the birds frequently used. There were enough perches within one meter of the speaker that potentially all of the birds could position themselves in close range of the speaker.

We broadcast the playback stimuli with an AIWA LCX-350 portable audio system. We selected a volume level for broadcasting that produced realistic renditions of the songs in the playback sequence and then measured sound pressure levels to ensure that the amplitude for all of the songs was similar to naturally occurring song. The mean sound pressure levels of the 23 songs in each of the playback sequences were 85.1±1.1 dB for juvenile song and 88.3±0.83 dB for adult male song, as measured at 1 m using a K & B 2209 sound pressure meter, A-weighting, impulse reading.

Experimental procedure. We introduced three juvenile males who had been in aviary 1 and had not sung during experiment 4 into aviary 2. Similarly, we introduced three juvenile males who had been in aviary 2 and had not sung during experiment 4 into aviary 1. We did not use new 'non-singing' males from the home aviaries of all males because we wanted to be sure that the males would not sing during the playback tests. We first collected NN association data for 4 days to document the baseline levels of female age class assortment in the presence of the juvenile male controls.

We randomly assigned the playback stimuli (either juvenile or adult male song) to each aviary for the first 3-day playback round. We then alternated the stimuli between the aviaries for each 3-day round that followed. Subjects heard one playback sequence per day during the 3 days of playback tests. We presented playback stimuli in the first block of four 7-min data blocks.

We next performed the reversal phase of the experiment for replication by switching which playback stimuli the females heard first in each aviary. During this round, we alternated temporal playback sequences each day during the 3-day round to reduce habituation to the sequences.

As a final test of the effect of male song on female age class assortment, we removed the juvenile males from each aviary and repeated the playback tests using juvenile and adult male song in both aviaries. We followed the same playback procedure as described above.

Playback observations. Three observers sequentially collected NN association data for four 7-min blocks each day during the first round of playback tests (with the playback presented in the first of the four blocks as noted above). For the last three rounds of playback tests, we changed the data collection protocol to try to document additional behavior of the females. Two observers simultaneously collected data during the four 7-min data blocks each day. One observer recorded NN associations, while the other observer recorded approach data ad libitum (Altmann 1974). Approaches documented the initiation of NN associations. When one bird came to within 30 cm of a second bird, we recorded the band of the approaching bird and the band of the bird that was approached. In the first of the last three rounds of playback tests, the third observer collected four 7-min blocks of NN association data when the two observers finished their four blocks of simultaneous data collection. In the final two rounds of playback tests, the third observer recorded the females' behavior using a Sony Hi-8 DCR-TRV330 video camera with a Sony ECM-737 electret condenser microphone while the two observers were recording data simultaneously.

Statistical analysis. The 7-min block of data occurring during playback and the 7-min block of data collection immediately following playback served as the experimental data set (called 'song blocks'). The final two 7-min data blocks served as data blocks to calculate levels of age class assortment in the absence of song ('post-song blocks'). For those rounds in which the second and third observers entered the aviaries sequentially after the first observer conducted the playback experiment and collected four blocks of data, their NN association data were included with the 'post-song' data.

We used Wilcoxon signed-ranks tests to compare females' NN associations in the song blocks to their NN associations obtained during the baseline round prior to the playback tests. In addition, we compared NN associations in 'song' and 'post-song' data blocks within each round. We also compared the proportion of each female's approaches to other females in 'song' blocks and 'post-song' blocks. As with the first four experiments, we combined data from the two aviaries for statistical analyses although the data from the aviaries are presented separately in Fig. 1a and b.

We scored the behavioral responses of females that we videotaped ad libitum (Altmann 1974) during the experiment. We were constrained in our sampling procedure because we had to be able to see the bands of the birds for identification. Therefore, we opportunistically sampled those females who were in the best position for videotaping. Throughout the experiment, females often moved in and out of view of the camera. Because females were not equally sampled, we were unable to conduct extensive statistical tests on the behavioral responses of females. We report the behavioral changes that we observed for descriptive purposes.

Results

Near neighbor associations

We observed changes in female age class assortment in response to the playback of adult male song but not in response to juvenile male song. During the baseline period, the juvenile and adult females in both aviaries did not assort by age class in the presence of the 'non-singing' juvenile male controls (JF-JF=0.53±0.01; AF-AF= 0.51±0.01). When we performed the playback of adult male song, the females associated significantly more with females from the same age class compared to baseline association patterns in the days prior to the start

of the playback experiment (JF-JF mean increase= 0.11±0.03: Wilcoxon T=85, n =13, P<0.004; AF-AF mean=0.10±0.02: Wilcoxon z=3.05, n=16, P<0.003). By contrast, the juvenile and adult females did not increase their proportion of NN associations with females of the same age class from baseline levels when we presented juvenile male song (JF-JF mean change=–0.03±0.02: Wilcoxon T=24, n=12, P>0.5; AF-AF mean=-–0.01± 0.03: Wilcoxon z=0.78, n=16, P>0.4).

As a more precise analysis of females' responses to the broadcast of adult male song, we analyzed changes in association patterns within the playback test. We found that within consecutive data blocks females showed rapid changes in NN association patterns. Females associated significantly more with females of the same age class in song blocks in which we played adult male song, compared to post-song blocks (JF-JF mean increase= 0.12±0.02: Wilcoxon T=90, n=12, P<0.0005; AF-AF= 0.16±0.04: Wilcoxon z=3.15, n=16, P<0.002).

After removing the juvenile male controls from both aviaries, we still observed significant changes in female social organization in response to the playback of adult male song. For these analyses, we compared data within playback tests from song blocks and post-song blocks. Both juvenile and adult females allocated more NN associations to other adult females in response to adult male song compared to when song was absent (JF-JF mean increase=0.11±0.03: Wilcoxon T=90, n=12, P<0.0005; AF-AF=0.11±0.03: Wilcoxon z=2.69, n=16, P<0.008).

As in the playback tests with the juvenile male controls present in the aviaries, the juvenile and adult females did not assort by age class in song blocks with juvenile song compared to post-song blocks (JF-JF mean change=0.03±0.03: Wilcoxon T=43, n=12, P>0.5; AF-AF=0.02±0.03: Wilcoxon z=0.47, n=16, P>0.6).

Approaches

We analyzed female approach data for the two playback rounds where juvenile males were not present. We found that both juvenile and adult females approached adult females significantly more during song blocks than post-song blocks (JF-AF mean number of approaches: 1.96±0.30 vs. 1.41±0.21: Wilcoxon T=69, n=12, P<0.02; AF-AF mean=1.29±0.23 vs. 0.94±0.14: Wilcoxon z=100, n=15, P<0.03). Furthermore, juvenile females approached adult females more when they heard adult male song compared to when they heard juvenile male song (2.09±0.36 vs. 1.26±0.24: Wilcoxon T=51, n=10, P<0.02). Adult females also approached adult females more when they heard adult male song, but this finding was not significant (1.35±0.12 vs. 0.86±0.22: Wilcoxon T=92, n=15, P>0.07).

Individual behavior

Although changes in female NN association patterns occurred in response to male song, observations of individual female behavior suggest that these changes emerged over the course of the two song blocks. The videotaped responses of individual females revealed that they typically did not change their behavior during or immediately following male song playback (n=518 of 592 observations of individual females). For example, if a female was hopping down a perch prior to the playback, she continued this behavior during the playback. In the 98 behavioral responses that occurred, we recorded 11 different behaviors, 9 of which occurred infrequently (less than 3 times each) and thus will not be discussed.

The majority of the females responded to the playbacks of juvenile and adult male song. We were surprised to record wing stroking responses by females, because we had observed this behavior previously only in early spring in response to live males singing at close range (King and West 1988). In response to the playback of male song, we observed wing stroking by 7 of 12 different juvenile females and 10 of 16 adult females (n=33 occurrences). Although a larger proportion of adult females wing stroked to adult male song than did juvenile females (AF=0.31; JF=0.08), this result was not significant (Fisher's exact test, n=28, P>0.2). A roughly equal proportion of adult and juvenile females wing stroked to juvenile male song (AF=0.56; JF=0.50). In addition, of the 17 females who responded with wing strokes, there were four adult females who were more responsive than the other 13 females. The mean number of wing strokes performed by these four females was significantly greater than the mean number of wing strokes by the other 13 females (mean number of wing strokes=4.3±0.6 vs. 2±0.3; Mann-Whitney U=62, n_1=4, n_2=13, P<0.002, corrected for ties).

We also documented females moving either laterally along a perch or hopping to a different perch in response to male song (n=48 occurrences). Seven of 12 juvenile female and 9 of 16 adult females moved in response to song. Similar to the results obtained for the wing stroking data, a non-significantly larger proportion of adult females moved in response to adult male song than did juvenile females (AF=0.25; JF=0.08; Fisher's exact test, n=28, P>0.4) whereas a roughly equal proportion of adult and juvenile females moved when they heard juvenile male song (AF=0.44; JF=0.50).

Discussion

We documented different patterns of association and individual behavior in response to different male characteristics in two groups of juvenile and adult female cowbirds. The results from male introduction and playback experiments indicate that female social organization changed specifically in response to adult male song; females showed no changes in association patterns in response to the presence of silent males of either age class. When we introduced singing adult males into the aviaries, juvenile and adult females associated more with

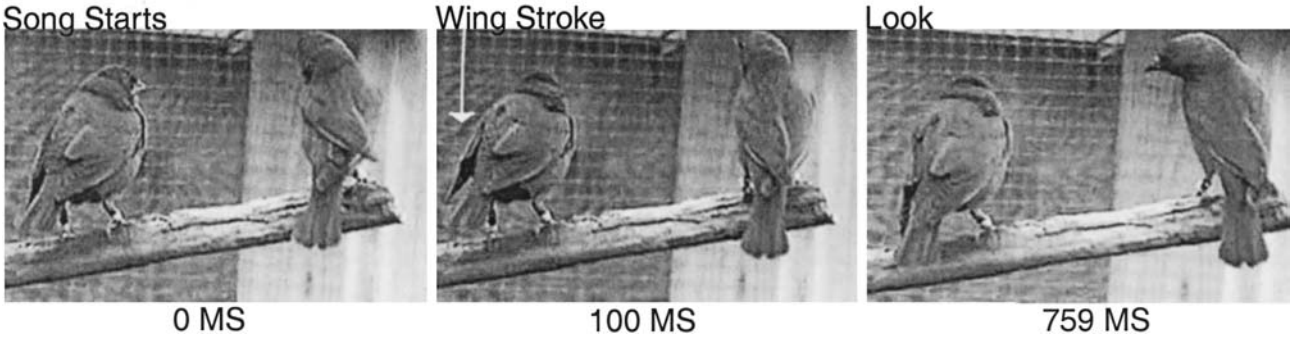

Fig. 2 Photographs depicting a videotaped sequence of a female's wing stroke response, followed by a neighboring female observing her. The *first frame* shows the females at song onset. The *second frame* shows one female wing stroking 100 ms after song onset. The *last frame* shows a second female observing the female 659 ms after she wing stroked. Photographs were made using Strata Videoshop 4.5.1 to capture the frames of the video recorded during the playback experiment

females of their own age class. By contrast, females did not preferentially associate with females of the same age class when we placed singing juvenile males in the aviary. Playback experiments confirmed the results from introduction experiments; adult song caused female age class assortment.

Why would females assort by age class exclusively in response to adult male song? Because near neighbor associations are an outcome measure of female behavior, we cannot determine what drove age class assortment. Changes in social organization could result from quantitative or qualitative differences in responses between age classes. For example, one age class may respond more than the other class. Or, it may be that one age class responds in a distinct way from the other age class, such as moving toward or away from a singing male (or in this case, the speaker).

Although we cannot identify the mechanism for age class assortment, there are several possible functional causes of assortment. In several species, females aggregate to avoid harassment from males (e.g. McComb and Clutton-Brock 1994; Cassini 2000). Adult females, who have had experience with adult males in previous years, may cluster together upon hearing adult male song, which would leave juvenile females primarily with juvenile females. Age class assortment may also arise from female-female mate competition (e.g. see Dugatkin 1992; Gibson and Hoglund 1992; Jennions and Petrie 1997). Lastly, age-specific responses by females to particular song characteristics that are independent of other females' responses could lead to age class assortment (e.g. Grant and Green 1996; Gibson et al. 1991; Slagsvold and Viljugrein 1999).

Our observations of the behaviors of females during the playback phase suggest to us that the changes in social organization could function in the shaping of female preferences (Freeberg 1998; Freeberg et al. 1999). We base this conclusion on the fact that females approached and observed females who wing stroked (Fig. 2). West and King (1988a) showed that females wing stroked to high quality songs, i.e., those songs most likely to stimulate copulatory responding later in the breeding season. Wing strokes and song occur simultaneously, as do the reactions of observers to them (Fig. 2). As a result, song quality can potentially be communicated between non singing females. What might be the consequences of this communication? Juvenile females show significant variability in their copulatory responsiveness to adult songs whereas adult females show strong agreement as to the relative quality of the breeding season songs (King et al., submitted). Female wing stroking and approach could provide the information necessary to fine tune individual preferences, thereby reducing variability. Thus, juvenile females may become more discriminating in their preferences through a longitudinal process of observing responses by adult females (e.g., see also Dugatkin and Godin 1993; Stohr 1998).

It is not necessary to assume that the primary function of wing strokes is to communicate about preferences; rather, visual signals such as wing stroke responses may function as an intersexual communicative signal that can be co-opted by other females. Thus, wing strokes and changes in social organization serve as a form of 'public information' that is readily available to others (cf. Doligez et al. 2002; Nordell and Valone 1998; Templeton and Giraldeau 1996; Valone 1989, 1996). Individuals in a number of species are known to 'eavesdrop' on song contests and fights between males. Information obtained in these contexts appears to be used to assess mates (Doutrelant and McGregor 2000; Mennill et al. 2002; Otter et al. 1999) and competitors (Earley and Dugatkin 2002; Naguib et al. 1999; Oliveira et al. 1998; Peake et al. 2001). Recent studies demonstrate that female songbirds appear to assess males based on their song, possibly because it indicates something about their song learning ability (cf. Searcy et al. 2002; Nowicki et al. 2002). Therefore, female cowbirds may obtain information through 'eavesdropping' on female responses to male song which may, in fact, be directed to males given that wing strokes influence the development of male song (West and King 1988a). Wing strokes during the fall months may provide feedback to males at a time when their songs are developing but, at the same time, wing strokes also may have the potential to inform females about other females' preferences.

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