



Female social networks influence male vocal development in brown-headed cowbirds, *Molothrus ater*

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Previous work has found that adult female brown-headed cowbirds, who do not sing, shape male vocal structure when in restricted housing. The present work extends this finding to a flock setting to examine the role of social behaviour in shaping male vocal development. We housed juvenile males with either adult or juvenile females in large flocks. Over the course of a year, we recorded their song and social behaviour. We found in early autumn that juvenile males housed with adult females improvised more song elements than males housed with juvenile females. During late autumn, we switched the males across female age-class conditions for 6 days. The males switched to the adult female flocks increased the number of improvised elements in their vocal repertoires. Analysis of the sequences of female–male social contact revealed that juvenile females, but not adult females, interacted indiscriminately with the males. Social network measures such as betweenness and closeness centrality further showed that adult females are more selective in their interactions with males than juvenile females. This study suggests a systemic role for selective social behaviour in shaping male vocal development.

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Studying the development of behaviour is a necessary precursor to understanding how individual variation contributes to natural selection. Song learning, a system that generates a large amount of individual variation, is one of the best-studied nonhuman learning systems. Understanding the developmental processes of song learning is especially significant because song is used in reproductive contexts. Most theories of song learning are primarily based on imitation or acoustic stimulation (Kroodsma 1996).

We have found that the behaviour of female brown-headed cowbirds, who do not sing, can shape male vocal structure throughout development (King & West 1983a, 1988; West & King 1988). This work is noteworthy because it shows a means for male song variation to develop through noncopied social stimulation from nonsinging females. Females can use a variety of nonvocal social behaviours to shape song development; wing strokes and

gapes, in particular, are associated with vocal changes in males (West & King 1988; Smith et al. 2000). Wing strokes are rapid flicks of a wing in response to song; gapes are a rapid opening and closing of the beak with a neck extension. Wing strokes and gapes are infrequent behaviours and occur in reaction to only about 2–4% of songs. Because of the infrequency of these behaviours, it seems likely they are salient to males. Levels of wing strokes and gapes in response to song influence both song usage and the rate of vocal development leading to earlier onset of stereotyped song (King et al. 2005). For example, songs that elicit wing strokes in the winter and spring have a higher probability of developing into songs that elicit the female copulatory display than songs that do not elicit wing strokes.

However, these studies were conducted in restricted housing (sound-attenuation chambers in pairs or trios of birds), which gave males unrestricted access to females and also removed typical social stimulation from other group members. Specifically, in restricted housing, when a male sings to a female, she cannot leave and there is little else for the male to attend to other than the female's reaction, or lack thereof, to his song. This leaves open the

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question of whether females can influence male vocal development in seminaturalistic settings such as in large aviaries. In large aviary settings, females as well as other flock members can control male access and provide feedback. Thus, how do these increased levels of social and spatial opportunities influence male song development? To answer this question, we studied the song development of male cowbirds housed in flocks in large aviaries to see whether female social behaviour could shape male song structure. Furthermore, if social shaping occurred, how was the flock structure organized to allow the flow of selective social feedback to foster learning?

White et al. (2006) found that juvenile females housed in flocks responded indiscriminately with wing strokes to the playback of immature and mature song in the autumn. However, adult females, also housed in flocks, responded selectively with wing strokes to advanced song. Freed-Brown et al. (2006) found flock-housed juvenile females to be much more socially interactive with juvenile males in the autumn than similarly housed adult females. These two findings suggest that juvenile or adult female social behaviour and reactions to song could differentially influence male song development in flocks.

Cowbirds are a gregarious species, gathering in flocks throughout the year (Friedmann 1929). Female song preferences change when females are housed in flocks (King et al. 2003a; West et al. 2006). By contrast, when females live in chambers they fail to modify their song preferences by either live or tape tutoring (King & West 1983b; West & King 1986b). In flocks, however, female song preferences are predicted by experience with male song, thus potentially linking male vocal development to the formation of female song preferences (West et al. 2006).

In flock settings, birds are given the opportunity to meter their distances from one another, which allows individuals to deny access to or form bonds with others. The bonds individuals form may influence attentional or motivational states, leading to differences in development. These options also afford different learning opportunities, creating individual variation within a group (Beecher 1996). For example, a young male may not be able to get close enough to a dominant male to hear his song in sufficient detail to copy. Likewise, males or females may not see the rapid responses of females to male song depending on their location in a flock (Gros-Louis et al. 2003). To understand flock social organization and flow of information within a flock, we use social network analysis.

Social network analysis describes the relations among individuals and the potential consequences of these relations. The network perspective assumes (1) individuals in a network are not independent, they are interdependent; (2) information can flow between individuals through social relations; and (3) the network can provide opportunities or constraints for learning (Wasserman & Faust 1994). By using a network perspective, we assume that the collection of individuals and relations between individuals that comprise a network have characteristic social dynamics and consequences. Social network analyses have been used to describe network structure in a variety of other species. For example, Croft et al. (2005) found that guppies (*Poecilia reticulata*) and threespine stickleback

(*Gasterosteus aculeatus*) were more likely to interact with others with similar body length and similar shoaling tendencies and also appeared to be discriminating in their social interactions by interacting with particular individuals. Lusseau and colleagues (Lusseau 2003; Lusseau & Newman 2004; Lusseau et al. 2006) found that individuals in networks can assort by sex and form long- or short-term associations in multiple networks of bottlenose dolphins (*Tursiops* spp.).

In addition to describing network structure, these analyses can also show how social relations can enhance or restrict the flow of information among the individuals in a flock (e.g. ability to hear a song or observe a wing stroke or gape). We used the network properties of betweenness and closeness centrality to characterize an individual's ability to access or block information from other individuals in the flock. We also used density to measure the actual number of relations present out of all the possible relations. In addition, we analysed sequences of behaviour to capture variation in dynamic interactions between flocks. Our hypothesis was that there would be differences between the juvenile and the adult female social structure and that these differences would systematically influence variation in male vocal development.

METHODS

Subjects and Housing

We used the same individuals that were used in the Freed-Brown et al. (2006) study. All birds were collected and housed in Monroe County, Indiana, U.S.A. We captured a total of 45 juveniles (24 juvenile females and 21 juvenile males) during June and July 2004. We estimated their age to be between 30 and 50 days upon capture based on plumage (Selander & Giller 1960). In addition, we used 24 adult females that were captured at the same site in previous years with an estimated age range of 516–2713 days. In previous years, all adult females were housed in mixed-age and -sex flocks in outdoor aviaries with extensive breeding season experience, except for eight females who were used in a playback study during the 2004 breeding season (West et al. 2006).

In September 2004, we composed four flocks. Each flock contained juvenile males and either juvenile or adult females. Two flocks (AJ1 and AJ2) each contained 12 adult females; AJ1 had five juvenile males and AJ2 had six juvenile males. The other two flocks (JJ1 and JJ2) each contained 12 juvenile females and five juvenile males. We used a skewed sex ratio favouring females to increase the opportunity for female–male interactions. Skewed sex ratios favouring either males or females are commonly reported from field observations of cowbirds (McKenny 1940; Rothstein et al. 1987; Woolfenden et al. 2001).

We housed each flock in an outdoor/indoor aviary measuring $9.1 \times 20.75 \times 3.4$ m. Ecological conditions were similar in each aviary, comprising trees, perches, feeding stations, grass-covered ground and shelters. Birds were exposed to sights and sounds of the area, which included wild conspecifics and the sight and attention of

predators. We provided all birds with white and red millet, canary seed, vitamin-treated water (Aqua-Vite; Nutritional Research Associates, Inc., South Whately, Indiana, U.S.A.) and a modified Bronx zoo diet for blackbirds, which included Avia (Nutra-Vet Research Corp., Poughkeepsie, New York, U.S.A.). The birds wore coloured leg bands to permit individual identification.

Audio Recordings

We recorded each flock of birds four times during autumn 2004 and spring 2005 between 0800 and 1200 hours Eastern Standard Time. We recorded vocalizations using a Sony TCD-D10 Pro II DAT recorder sampled at 48 kHz. We placed two to six Sennheiser RF condenser microphones around the aviary near perches to enhance our chances for optimal recordings from the birds. See [Supplementary Table S1](#) for recording dates and social behaviour data collection.

Flock Manipulations

During the autumn, we kept the birds in their basic adult–juvenile (AJ) and juvenile–juvenile (JJ) conditions with the exception of one episode. For the second recording, we exchanged males from JJ1 and JJ2 with the males from AJ1 and AJ2 so that all males initially housed with adult females were now housed with juvenile females and vice versa. The second recording occurred during this 6-day period. After the second recording, we returned all birds to their original condition (for more information on autumn housing conditions, see [Freed-Brown et al. 2006](#)). During the spring, we kept all flocks in their original September configuration. Recordings 3 and 4 took place during the spring.

Social Behaviour

We recorded social behaviour, as indexed by near-neighbour data, from August 2004 to June 2005 in each

flock (for more autumn 2004 details see [Freed-Brown et al. 2006](#)). Two or three trained observers collected behavioural data using a near-neighbour protocol. We scored a near-neighbour point for each individual bird when two birds were within 15 cm of each other ([Smith et al. 2002](#)). A point was rescored if two birds were within 15 cm of each other for more than 1 min. A point was scored if two individuals moved apart from one another and later rejoined. We did not collect data while birds were on the ground or by food or water stations to avoid incidental points. We collected near-neighbour data in 7-min blocks. Across the entire autumn, the observers differed by less than 3% in the amount of social behaviour collected.

We analysed near-neighbour data at five different points in time: a baseline that occurred after flock formation and four additional times occurring around each recording session (see [Supplementary Table S1](#)). We collected data using voice recognition technology ([White et al. 2002b](#)). Observers spoke leg-band acronyms into wireless microphones (Telex WT 150; Telex Communication Ltd). We used IBM ViaVoice Millennium Pro Edition voice recognition software operating on a Pentium III, 500-MHz IBM compatible computer, running Microsoft Windows 98 and Microsoft Word 2000 to receive the voice signal and transcribe speech into text. Text was exported into a database (4th Dimension version 6.8; ACI, Inc.).

Analyses

Acoustical analysis

[Figure 1](#) shows a spectrogram of a prototypical cowbird song recorded during the breeding season. Cowbird song typically starts with two note clusters followed by a high-frequency whistle. Each male typically has between two and six song types in his breeding season repertoire ([Rothstein et al. 1988](#)). The introductory note clusters of cowbird song are of particular interest as they elicit wing strokes during the autumn and winter and copulatory postures during the breeding season ([West et al. 1998](#)). We

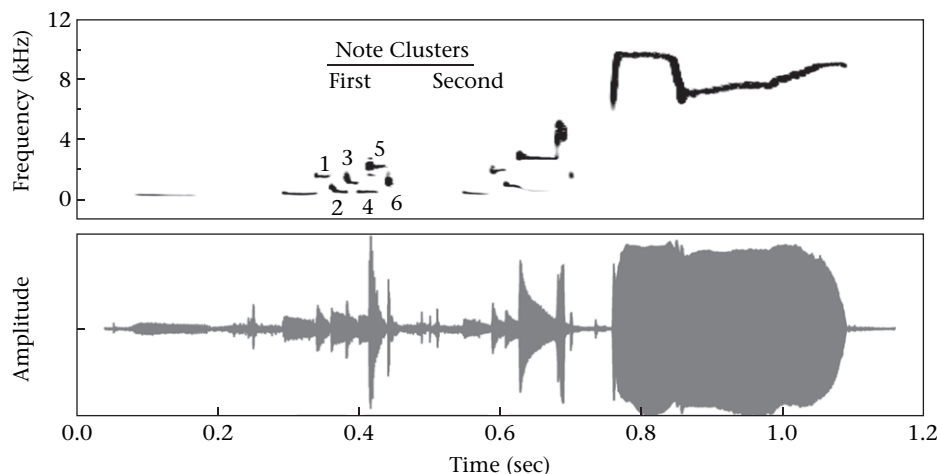


Figure 1. An exemplar of a stereotyped song. A typical cowbird song has two note clusters and one whistle; each note cluster consists of low and high voice notes. The first note cluster contains six notes; we do not count the first low voice note because it is a low amplitude note and we cannot reliably record it.

traced the structural development of the note clusters for all the males in this study. We analysed all vocal recordings using Bsound with IGOR Pro version 4.1 (<http://homepage.mac.com/bsnelson/Igor/BSound.html>). All songs were printed on paper and transparency film. We used a light table to compare spectrograms with the copied transparencies. We used unambiguous categories established by observer agreement in previous studies. For note clusters to be scored as the same, the structure of the note cluster had to be at least 85% matched in the autumn and 100% matched in the spring. We measured the following song parameters for each male during all four rounds of recording: note cluster repertoire, average number of notes per note cluster and proportion of improvised note clusters (autumn) or unique song types (spring) within a flock. We determined the total number of different note clusters for each male. We also calculated the number of notes in each note cluster. We categorized each note cluster as a copied or an improvised vocalization relative to the other males in their flock. A copied note cluster was defined as a vocalization that was shared by more than two males. An improvised note cluster was defined as a note cluster that was not present in any other male's vocal repertoire in the flock. In the spring, a copied song consisted of the same patterning of note clusters and whistle for two males. A unique song was sung by only one male in a flock and consisted of a unique pattern of note clusters and a whistle. We found no song sharing across flocks (see [Supplementary Table S2](#) for number of males recorded and number of songs analysed).

Social behaviour analyses

We analysed the following network measures using UCInet version 6.178 (Borgatti et al. 2002): betweenness centrality, closeness centrality, density and centralization index (see [Supplementary Table S3](#) for examples). Betweenness centrality is the extent to which an individual falls on the shortest path between two other individuals (Freeman 1977). This measure relates to the idea of information flow throughout the network. If two individuals are indirectly connected to one another, other individuals between the two individuals may control the probability of an interaction. Closeness centrality measures how directly or indirectly connected an individual is to all the nodes in a network (Freeman 1979). This measure relates to the idea of how quickly individuals can interact with other individuals in a network. If individuals are close together, information can spread faster and more easily throughout the network. Density is measured as a percentage that calculates the actual number of relations present of all the possible relations. We examined only the female–male density in each flock. The centralization index takes into account the variation of betweenness centrality in individuals (Freeman 1977). A high centralization index indicates that individuals in the network have a wide range of betweenness centrality. A low centralization index shows that all individuals have similar betweenness centrality.

We chose closeness and betweenness centrality because these measures are sensitive to the set of individuals the

birds choose to interact with. The centrality measures (betweenness and closeness) for each individual are dichotomized (all numbers greater than 1 are transformed to 1); that is, they are binary. Thus, the frequency of interactions was not taken into account for the centrality statistics. By dichotomizing the social behaviour, we can use the centrality measures to examine low levels of behaviour, similar to wing strokes and gapes that occur at a low frequency (responses to 2–4% of songs) during vocal development. Density takes into account the number of ties present in the network. We calculated density only on female–male ties; however, the density can be calculated on same-sex ties as well.

In addition to the social network statistics, we calculated the subsequent levels of female–male interaction after an initial female–male contact (see [Supplementary Table S3](#)). All near-neighbour data were time stamped, allowing us to analyse sequences of behaviour. Near-neighbour sequences were defined in the following manner. After an initial female–male contact, we tabulated all near-neighbour points between birds who came into contact with the initiators of the original male–female point within 15 s and referred to those points as a near-neighbour sequence. In addition, if a new individual arrived and made a near-neighbour point with any sequence participant, we reset the clock for another 15 s and counted that point as part of the sequence. For example, male 1 and female 1 make a male–female contact. If female 2 makes a point with male 1 within 15 s of the original male–female contact, this second male–female contact would be scored as part of a sequence. Then, if within 15 s of this first contact a third bird arrived and made a near-neighbour contact with any of the other birds, it was scored as part of that sequence. When 15 s elapsed without a new sequence contact, no additional contacts were scored as part of that sequence. The first male–female contact was not tabulated in the sequence, only points subsequent to the initial point were tabulated, thus reflecting levels of activity after a male–female near-neighbour point.

Statistics

Due to small sample sizes and nonheterogeneity of variance, we performed nonparametric tests on individual measures. We used Kruskal–Wallis ANOVAs across the four groups for song structure and social behaviour measures. We had a priori predictions that significant differences in female–male interactions would exist between the adult–juvenile and the juvenile–juvenile conditions. Thus, we did not correct for multiple comparisons and conducted a finite set of analyses (Howell 2002). We conducted tests between conditions with Mann–Whitney *U* tests; we combined AJ1 and AJ2 as well as JJ1 and JJ2 for comparisons. We used individual measures as our unit of analysis because we were interested in examining variation in individual learning within a group. By looking at group level variables, we would be unable to identify individual differences. [Tables 1 and 2](#) contain the results for all statistical tests.

Table 1. Social network measures

	Betweenness centrality (males)		Betweenness centrality (females)		Closeness centrality (males)		Closeness centrality (females)		NN sequences—proportion		NN sequences—average	
	KW†	MW‡	KW†	MW‡	KW†	MW‡	KW†	MW‡	KW†	MW‡	KW†	MW‡
Baseline	NS	NS	6.75	A>J**	16.71**	A<J**	37.14**	NS	17.58**	A<J*	24.68**	A<J**
1: Early autumn	4.38	P=0.02	A>J**	A>J**	21.52**	A<J**	19.46**	A<J**	15.71**	A<J**	28.62**	A<J**
2: Late autumn	11.48*	A>J	P=0.03	A>J**	15.58**	A<J**	18.60**	A<J**	17.02**	A<J**	23.08**	A<J**
3: Early spring	11.51*	A>J*	NS	A>J*	15.73**	NS	31.07**	NS	NS	NS	13.53*	A<J**
4: Late spring	NS	NS	NS	NS	14.45*	NS	28.25**	A<J*	NS	NS	NS	NS

Across-conditions tests (AJ1, AJ2, JJ1, JJ2) were done using a Kruskal–Wallis (KW) test. Within-condition tests (AJ1 and AJ2; JJ1 and JJ2) were conducted using a Mann–Whitney (MW) test. NS: nonsignificant. NN: near-neighbour.

* $P < 0.010$; ** $P < 0.001$.

†Flocks $N = 4$.

‡AJ males $N = 11$, JJ males $N = 10$.

§AJ females $N = 24$, JJ females $N = 24$.

Table 2. Statistical test conducted between note clusters (NC), number of notes in note clusters and proportion of improvised elements for males within condition

Recording	Note clusters†	Number of notes in NC†	Proportion of improvised elements
1	AJ>J**	AJ>J**	AJ>J**
2	AJ>J**	AJ>J**	NS
3	NS	AJ>J**	NS
4	NS	AJ>J**	NS

AJ: juvenile males housed with adult females; JJ: juvenile males housed with juvenile females.

* $P < 0.050$; ** $P < 0.02$.

†All $H_3 > 7.882$ and significant at the $P < 0.050$ level.

RESULTS

Baseline: Autumn Flock Formation

For the baseline, we established significant differences in social structure between the AJ and the JJ flocks (Fig. 2a). Near-neighbour (NN) sequences revealed that juvenile females had more, and longer, interactions with males than did adult females. There were more female–male sequence points in the JJ condition compared to the AJ condition (AJ1: 0.0708 ± 0.025 ; AJ2: 0 ± 0 ; JJ1: 0.450 ± 0.060 ; JJ2: 0.1833 ± 0.67). In addition, the juvenile females had a higher proportion of female–male points in NN sequences than adult females (AJ1: 0.273 ± 0.104 ; AJ2: 0 ± 0 ; JJ1: 0.570 ± 0.077 ; JJ2: 0.2867 ± 0.105).

There were also large differences in centrality measures across the four flocks. Network statistics revealed significant differences in closeness centrality between the males and the females across the four flocks during baseline. JJ males had higher closeness centrality than AJ males; however, there were no differences in closeness centrality between adult and juvenile females. There was also a trend for differences in betweenness centrality for females, but not for males, across the four flocks. Adult females had a higher betweenness centrality than the juvenile females, whereas there were no differences between AJ and JJ males. Thus, although both juvenile and adult females were equally close to all individuals in the flock, the adult females had a greater potential to transmit or block information throughout the flock than juvenile females. See Fig. 2a for an example of individuals with high and low betweenness and closeness centrality.

There were large differences in the network centralization index and density across the four flocks. The AJ flocks had a higher betweenness centralization index than the JJ flocks (AJ1: 8.68%; AJ2: 42.11%; JJ1: 0.39%; JJ2: 0.84%). Female–male density was higher in JJ flocks than in AJ flocks (AJ1: 0.375; AJ2: 0.050; JJ1: 1.733; JJ2: 1.166).

Recording 1: Early Autumn

Vocal structural differences

In recording 1, the males, estimated to be between 128 and 172 days of age, produced highly variable

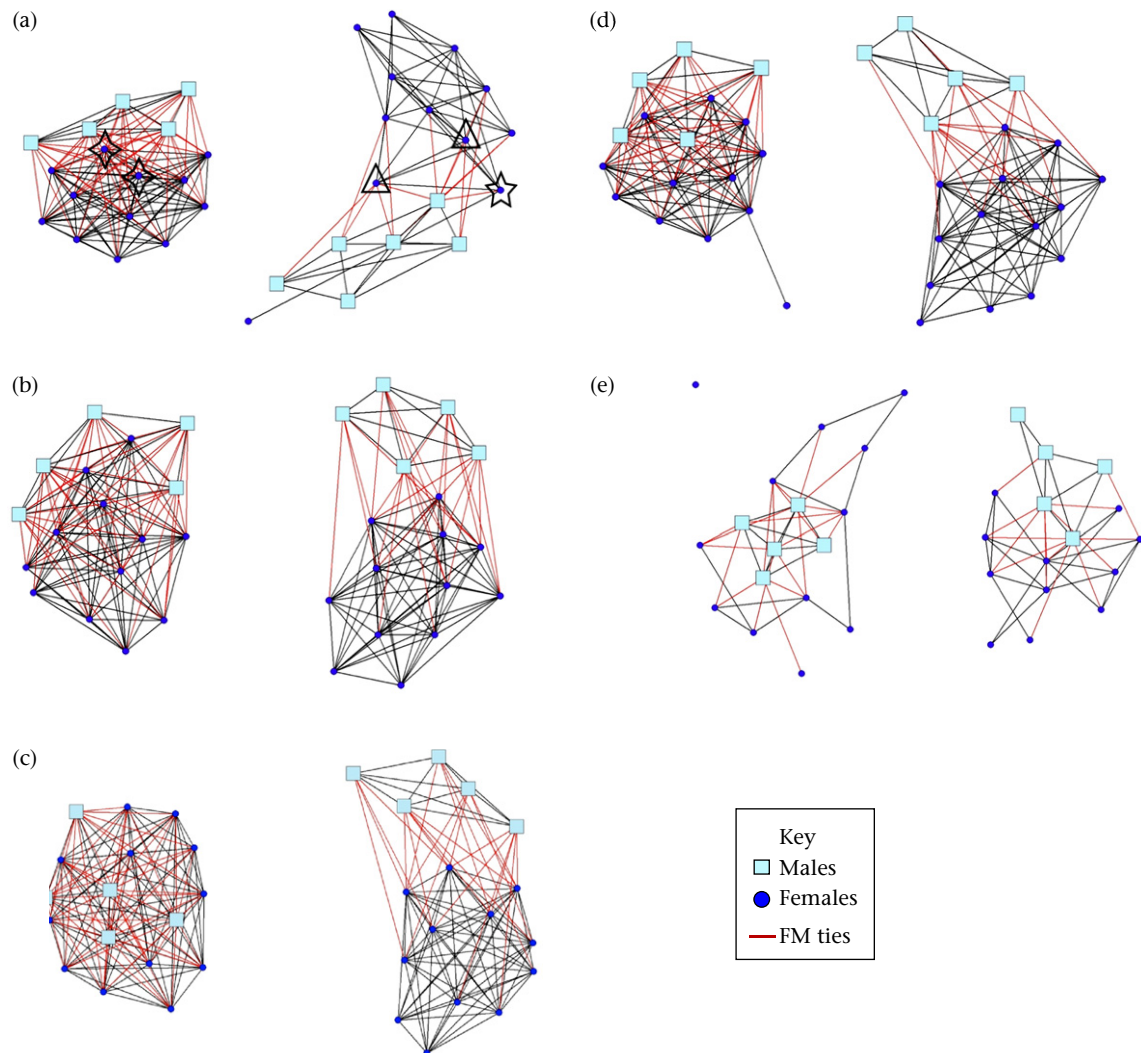


Figure 2. Illustration of cowbird networks constructed at each time period (baseline–recording 4) using Netdraw (Borgatti et al. 2002). In each set of networks, the flock on the left is a representation of a JJ flock and the flock on the right is a representation of an AJ flock. In (a), on the left, the diamonds represent the juvenile females with the highest betweenness and closeness centrality and on the right, the triangles represent the two females with the highest closeness centrality, whereas the star represents the female with the highest betweenness centrality. In all networks, the red lines represent female–male interactions (FM). Black lines represent within-sex interactions, male–male and female–female. (a) Baseline, (b) recording 1, (c) recording 2, (d) recording 3, (e) recording 4.

vocalizations consisting of at least one note cluster. Males differed across groups in the nature of their repertoires: specifically, the AJ males produced a higher number of note clusters and higher number of notes within note clusters than JJ males. AJ males had a higher proportion of improvised note clusters in their repertoire than did JJ males.

Social behaviour statistics

Significant differences persisted in social behaviour between the AJ and the JJ flocks (Fig. 2b). NN sequences revealed that juvenile females had more, and longer, interactions with males than did adult females. There were more female–male sequence points in the JJ condition compared to the AJ condition (AJ1: 0.5167 ± 0.135 ; AJ2: 0.055 ± 0.031 ; JJ1: 1.016 ± 0.121 ; JJ2: 1.23 ± 0.159). In addition, the juvenile females had a higher proportion

of female–male points in NN sequences than adult females (AJ1: 0.346 ± 0.077 ; AJ2: 0.191 ± 0.103 ; JJ1: 0.547 ± 0.052 ; JJ2: 0.670 ± 0.036).

There were also large differences in centrality measures across the four flocks. Network statistics revealed significant differences in closeness centrality between the males and the females. Juvenile females had a higher closeness centrality than adult females, whereas JJ males had a higher closeness centrality than AJ males. There were also significant differences in betweenness centrality across the four flocks. Adult females had a higher betweenness centrality than juvenile females and AJ males had a higher betweenness centrality than JJ males. Thus, although juvenile females could interact with birds at a closer distance than did adult females, the adult females had a greater potential to transmit information throughout the flock.

There were large differences in the network centralization index and density across the four flocks. The AJ flocks had a higher betweenness centralization index than the JJ flocks (AJ1: 1.38%; AJ2: 4.05%; JJ1: 0.06%; JJ2: 0.11%). Female–male density was higher in JJ flocks than in AJ flocks (AJ1: 2.716; AJ2: 0.597; JJ1: 3.316; JJ2: 4.08).

Recording 2: Late Autumn—Males Exchanged across Female Age Class

Vocal structural differences

In recording 2, the males, estimated to be between 169 and 191 days of age, produced highly variable vocalizations consisting of at least one- or two-note clusters.

From recording 1 to recording 2, the JJ males significantly increased their number of note clusters ($T=0$, $N=9$, $P<0.02$; Fig. 3); however, there was no change in the number of notes within note clusters ($T=4.20$, $N=9$, $P=0.674$; Fig. 4). In addition, from round 1 to round 2, the AJ males significantly decreased the average number of notes in their note clusters ($T=0$, $N=7$, $P<0.030$), but not the number of note cluster types ($T=3.20$, $N=7$, $P<0.249$).

Males differed across groups in the nature of their repertoires: males that were switched to the juvenile female condition had a larger number of note cluster types and higher number of notes within note clusters than males that were switched to the adult female condition. The AJ and JJ males had on average the same proportion of improvised note clusters in their repertoires.

Social behaviour statistics

Significant differences persisted in social behaviour between the AJ and the JJ flocks (Fig. 2c). There were significant differences in both the average and the proportion of female–male sequence points between the four flocks during the second recording. There were more female–male sequence points in the JJ condition compared to the AJ condition (AJ1: 0.0667 ± 0.037 ; AJ2: 0.1500 ± 0.060 ; JJ1: 0.3833 ± 0.121 ; JJ2: 0.8208 ± 0.141). In addition, the juvenile females had a higher proportion of female–male points in NN sequences than did adult

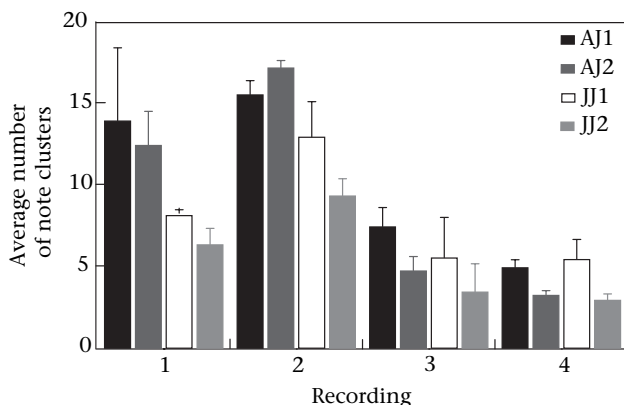


Figure 3. Average number of note clusters per flock for recordings 1–4. Data are displayed as means + SE.

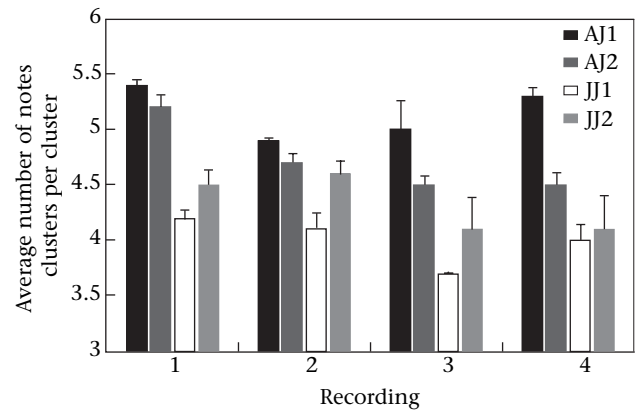


Figure 4. Average number of notes per note cluster for recordings 1–4. Data are displayed as means + SE.

females (AJ1: 0.1775 ± 0.097 ; AJ2: 0.229 ± 0.091 ; JJ1: 0.431 ± 0.067 ; JJ2: 0.656 ± 0.041).

Large differences in centrality measures persisted across the four flocks. There were significant differences in closeness centrality between the females and the males. Juvenile females had higher closeness centrality than adult females and JJ males had a higher closeness centrality than AJ males. There were significant differences in betweenness centrality across the four flocks. Adult females had a higher betweenness centrality and there was a trend for AJ males to have higher betweenness centrality than JJ males. Thus, although juvenile females could interact with birds at a closer distance than did adult females, the adult females had a greater potential to transmit information throughout the flock.

There were large differences in the global structure across the four flocks. The AJ flocks had a higher betweenness centralization index than the JJ flocks (AJ1: 3.12%; AJ2: 6.22%; JJ1: 0.62%; JJ2: 0.14%). Female–male density was higher in JJ flocks than in AJ flocks (AJ1: 0.716; AJ2: 0.850; JJ1: 1.916; JJ2: 2.805).

Recording 3: Early Spring

Vocal structural differences

In recording 3, the males, estimated to be between 276 and 298 days of age, produced typically formatted cowbird song with two or three introductory note clusters followed by a whistle. Males differed across groups in note cluster repertoire size and number of notes produced in note clusters (Figs. 3, 4). AJ males produced a greater number of notes in their note clusters than did JJ males but there were no differences in number of note clusters per male. There were no differences in the proportion of unique song types between the AJ and the JJ males.

Social behaviour statistics

Significant differences persisted in social behaviour between the AJ and the JJ flocks (Fig. 2d). There were significant differences in the average, but not the proportion, of female–male sequence points between the four flocks. There were more female–male sequence points in the

JJ condition than the AJ condition (AJ1: 0.114 ± 0.058 ; AJ2: 0.166 ± 0.054 ; JJ1: 0.666 ± 0.169 ; JJ2: 0.350 ± 0.089). In addition, there were no differences in the proportion of female–male sequence points between the adult and the juvenile females (AJ1: 0.330 ± 0.124 ; AJ2: 0.503 ± 0.147 ; JJ1: 0.447 ± 0.073 ; JJ2: 0.420 ± 0.081).

There were significant differences in closeness centrality across the flocks. However, there were no differences between AJ and JJ males nor were there any differences between juvenile and adult females in closeness centrality. There were significant differences in betweenness centrality. Adult females had a higher betweenness centrality than juvenile females and AJ males also had higher betweenness centrality than JJ males. Thus, whereas both juvenile and adult females were close enough to interact with all members of the flock, adult females had a greater potential to transmit information throughout the flock.

There was one global difference between the four flocks. Female–male density was higher in JJ flocks than in AJ flocks (AJ1: 0.642; AJ2: 0.708; JJ1: 2.833; JJ2: 1.583). There were no differences in the betweenness centralization index between the AJ and the JJ flocks (AJ1: 8.04%; AJ2: 11.25%; JJ1: 12.99%; JJ2: 0.13%).

Recording 4: Breeding Season

Vocal structural differences

Males, estimated to be between 342 and 364 days of age, produced stereotyped song. Males differed across groups in note cluster repertoire size and number of notes produced in note clusters. AJ males produced more notes in their note clusters than did JJ males; however, the number of note clusters did not differ between AJ and JJ males. There were no differences in the proportion of unique song types between the AJ and the JJ males.

Social behaviour statistics

Differences persisted in the social behaviour between the AJ and the JJ flocks (Fig. 2e). There were no differences in average or proportion of female–male sequence points between the four flocks. Furthermore, there were no differences in number or proportion of female–male sequence points between the AJ and the JJ conditions (average: AJ1: 0.116 ± 0.051 ; AJ2: 0.194 ± 0.057 ; JJ1: 0.090 ± 0.041 ; JJ2: 0.325 ± 0.083 ; proportion: AJ1: 0.312 ± 0.119 ; AJ2: 0.424 ± 0.113 ; JJ1: 0.303 ± 0.130 ; JJ2: 0.712 ± 0.132).

Differences in centrality measures persisted across the four flocks. There were significant differences in closeness centrality. Specifically, juvenile females had significantly higher closeness centrality than did adult females; however, there were no differences between the AJ and the JJ males in closeness centrality. There were also no differences in betweenness centrality. Thus, although juvenile females could interact with birds at a closer distance than did adult females, there were no differences in the capacity to transmit information. There were no global differences in the betweenness centralization index (AJ1: 15.79%; AJ2: 10.98%; JJ1: 20.33%; JJ2: 13.15%) or density

(AJ1: 1.333; AJ2: 2.347; JJ1: 1.272; JJ2: 2.075) between the AJ and the JJ flocks.

DISCUSSION

To our knowledge, this is the first experimental demonstration of female nonvocal social behaviour to shape male song structure in a flock setting. This study extends findings from previous song learning studies conducted in highly controlled settings (King et al. 1986, 2005; King & West 1989; Smith et al. 2000). In this study, birds were housed in large aviaries allowing the self-organizing properties of the flock, not the experimenter, to control patterns of affiliation and opportunities to learn. Adult and juvenile females organized their flocks very differently. The adult females' flock organization allowed for limited but selective interaction with males as suggested by high betweenness centrality and relatively low closeness centrality measures in conjunction with low flock density. This social pattern would seem to be consistent with effective social shaping, as females must selectively reinforce specific vocal variants and males must be attentive to subtle female reactions. Throughout the fall and spring, males exposed to the selective adult female flock structure produced more note clusters containing more notes, resulting in higher levels of improvisation during the fall, than the males housed with juvenile females. The juvenile female flock structure showed high closeness centrality and low betweenness centrality in conjunction with high female–male density. This structure would seem likely to present the males with sensory overload, making it difficult for a male to attend to subtle and specific social feedback. This point is reinforced by the extended male–female sequences, which occurred after a female–male near-neighbour point in the juvenile flocks, but not in the adult flocks.

When the juvenile-female-housed males were exposed to the adult females for only 6 days, the adult females maintained their flock organization of high betweenness centrality and relatively low closeness. The newly introduced males began to produce higher levels of improvisation, revealing real-time sensitivity of vocal production to the adult flock structure. The differences in flock organization between the juvenile and the adult females persisted throughout the fall and into the early spring and were paralleled by differences in the vocal structure of the males. As the breeding season approached, differences in flock structure disappeared as the males began singing species-typical song with two note clusters and a whistle. However, the males with the adult females retained note clusters with more notes than the males with the juvenile females.

For the cowbird, the nature of social organization exerts critical influences on male vocal development at least in the first year (White et al. 2002a) and most likely on female song preferences during the first year and beyond (King et al. 2003a; West et al. 2006). We do know that captive cowbirds assort by age and sex (Smith et al. 2002) but the degree of assortment varies widely as a function of the age class of the individuals present (White et al. 2002a, c),

sex ratio (Freed-Brown et al. 2006), presence of male song (Gros-Louis et al. 2003), variation in individual traits (King et al. 2003b) and age of individuals (Miller et al. 2006). Social network statistics hold the promise of integrating these different variables in a framework that can be used to understand the role of social ecology in structuring male vocal production and female preferences.

The social network analyses we used revealed differences in centrality at the individual and flock level. These differences reflected the degree of selectivity among the individuals between the flocks. The statistics we used did not take into account the strength of relations between individuals. Future analyses should consider how the frequency of the interaction may influence the flow of information. In this study, we used undirected networks, that is, we did not know the direction of effect. Were the females or the males responsible for initiating the interactions? Were particular individuals responsible for creating and sustaining network structures (King et al. 2003b)? Directed graphs, networks that take into account who initiated the interaction, can provide additional information such as singing relationships. Social network analyses are not limited just to relations between birds; network analyses can be applied to a wide range of phenomena, including dominance hierarchies, mating, grooming and migratory patterns. The flexibility of these different kinds of graphs (undirected, directed) and behavioural relations make this technique applicable to many studies of social behaviour. Studies in animal behaviour using social networks have ranged from birds to fish to mammals (including dolphins, primates, whales and cows; Faust & Skvoretz 2002; for reviews see Krause et al. 2007; Wey et al. 2008).

Currently, most theories of bird song are based on auditory stimulation and copying; the current study indicates that the role of social stimulation apart from auditory stimulation may be an important part of male song development (Marler 1997; Beecher & Brenowitz 2005). Furthermore, the influence of social stimulation on male song structure was systemic, that is, males were shaped by female feedback throughout the entire year. This is in contrast to Marler & Nelson's (1993) action-based learning in which social influences play a role during the spring to form a male's final song repertoire. The role social influences play throughout song development may be missed due to the lack of social stimulation in restricted housing or the difficulty of observing birds in field settings (except see Nordby et al. 2007). Both settings have disadvantages in detecting the role of global social structure to account for individual variation. In the lab, the setting is too simple to allow social complexity to be manifest. In the field, social relationships are hard to detect due to difficulties in tracking birds and recording social behaviour. We used a seminaturalistic setting, large outdoor aviaries, with these shortcomings in mind. In this setting, we can see what is not visible in the other contexts: species-typical rules of social organization.

The differences in song structure we found are striking because they are used by females to delineate geographically distinct populations. Playback tests of male song from different populations reveal that females prefer songs

with more notes within note clusters (King & West 1983b; West & King 1986a). King et al. (1986) found rhythm differences in note clusters between Oklahoma and Texas populations to be the basis of song discrimination at a subspecies border. A study of South Dakota and Indiana cowbirds found the numbers of note clusters and notes in a note cluster differentiated the two populations (Freeberg et al. 2001). Most species also have acoustic differences across populations (e.g. Marler & Tamura 1962; Baptista 1977; Baptista & King 1980; Kroodsma & Byers 1991). These differences have been suggested to have an important function as a recognition mechanism within a population (Freeberg et al. 2001). In the previous studies, the song structure differences were from distant populations, but in this study, all of the birds were captured from the same location. Thus, females' social stimulation from the same population was able to generate structural variation characteristic of macrogeographic differences. This is consistent with the finding that housing cowbirds in different social ecologies can lead to different patterns of social behaviour that are as divergent as macrogeographic differences. Such differences are sometimes assumed to be genetically based, whereas these data show learning can produce the same structural differences within a population (West et al. 2003).

Taken as a whole, these results show that female selectivity, as measured by betweenness, may control the opportunity for social shaping of vocal development (West et al. 2003). In a social group, individuals can channel or gate information. The changes we found in male vocal structure paralleled systematic changes in the social structure. The finding that during development vocal variation is sensitive to complex social stimulation points to the importance of studying development in ecologically relevant settings. These findings indicate a systemic role for a complex social ecology in shaping vocal behaviour.

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Supplementary Material

Supplementary material associated with this article can be found in the online version, at [doi:10.1016/j.anbehav.2008.05.011](https://doi.org/10.1016/j.anbehav.2008.05.011).

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