



Female brown-headed cowbirds', *Molothrus ater*, organization and behaviour reflects male social dynamics

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In four large aviaries, we studied social assortment and reproductive behaviour of female brown-headed cowbirds housed with males differing in age class and in corresponding levels of intrasexual interaction. Juvenile and adult females resided with either (1) adult males, (2) juvenile males, (3) adult and juvenile males, or (4) no males. We observed social behaviour of males and females from September 1999 through to the 2000 breeding season. Throughout the year, males in the different conditions showed different levels of social interaction, with adult males being most engaged in male–male interactions and juvenile males being least engaged in male–male interactions. Females in the four conditions differed in their associations with males and with other females. In conditions with adult males, females spent more time near males, approached males more often, and associated with females less. During the breeding season, females in conditions with more adult males copulated more and produced more fertile and viable eggs. In the condition where females were housed with juvenile males, they copulated less, laid fewer eggs and destroyed more of their eggs. Results indicate that throughout the year, females are sensitive to male age and behaviour in their social group, and that this sensitivity can have reproductive consequences.

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Given the role accorded to females of many species with respect to sexual selection of male traits, the nature of female attention to and assessment of males is of considerable importance (Janetos 1980; Bradbury & Andersson 1987; Real 1990, 1991; Andersson 1994; Andersson & Iwasa 1996). It has now been well established that in several species females attend to and choose mates during courtship (Bateson 1983; Andersson 1994). Here we study whether female cowbirds are sensitive to male behaviour at other times of the year. Moreover, if they do attend to males at other times, is there an influence on their future functionally relevant mating behaviour?

We studied social behaviour of captive female brown-headed cowbirds for 1 year. In the wild, throughout the autumn, winter and spring, cowbirds live social groups (Friedman 1929; King & West 1988), contexts that afford the potential for learning about behaviour of conspecifics prior to the time of courtship in late spring and summer. Female cowbirds are potentially witness to many activities by males: males sing to females and also sing to other males. Males engage in singing interactions with one another in groups to establish dominance hierarchies (Dufty 1986). If dominance in male–male interactions is

an indicator of male quality (e.g. Zuk & Johnsen 2000), then females could use male singing interactions to learn about the quality of males in a group. The goal of the present study was to look for evidence that differences in males in a group setting influence females' social behaviour in ways potentially relevant to their roles as perceivers of male traits.

We studied birds in large aviaries. We have evidence that observations in such settings can reveal social sensitivities not seen in females housed with males in small cages or in small social units such as pairs or triads. Freeberg (1996, 1998), for example, has shown that female cowbirds' preferences for mates can be predicted by postnatal social experience. Freeberg's findings were obtained in cowbirds that were housed in large aviaries where they quickly formed social associations as evidenced by stable near-neighbour patterns (Freeberg 1999). Females associated more with females, and males associated more with males. Females' eventual courtship preferences for certain males developed via experiences that were transmitted through a network of self-organized female groups.

The malleability in female preferences seen by Freeberg stands in contrast to previous studies in our laboratory where we had found little malleability of song preferences in female cowbirds in studies of seven populations (King & West 1990). Only in one population in Oklahoma

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(U.S.A.) did we find evidence of malleability, in this case a broadening of preferences to include Oklahoma songs from the females' natal population and Texas (U.S.A.) songs from the population of males housed with the females (King & West 1990). In these laboratory studies, the housing conditions consisted of pairs or triads of females with one male residing in sound-attenuation enclosures (1.3 m³ in size).

We now suspect that the spatially and socially restricted setting used in these laboratory studies contributed to our failure to see malleability in the song preferences of females. Freeberg's socially more complex setting may have revealed such learning because the setting provided females the opportunity to regulate physical access to males according to the females' motivation, not the males'. In a series of recent studies, we have found strong evidence for self-organized social assortment in captive groups of males and females (Smith et al. 2002; White et al. 2002a). That is, particular patterns of assortment were not imposed upon the birds by the experimenter, but emerged from the birds' behaviour. Neither the design of the aviary nor the location of perches or food in these studies favoured any particular social aggregation.

Self-organization may serve to provide distinct social environments within a larger group in which different opportunities for learning and experience may come about first by indirect, and then direct means. Young females may observe older females interacting with males and use the acquired information to learn about the quality of males. These experiences provide a public forum potentially giving females predictive information about the nature of males' responsiveness to females and knowledge of how other females interact with males.

If behaviour of females in social groups is related to learning about males, settings containing males of different social experience and patterns of behaviour might be reflected in the females' social organization and behaviour. To test this idea, we manipulated male presence in social groups in large outdoor aviaries and compared behaviour of females living within those groups. We manipulated male presence by housing females with adult males, juvenile males, both adult and juvenile males, or no males. While adult and juvenile males look alike, they behave differently in interactions with other males and with females. By measuring the behaviour of both sexes throughout the year, we sought to isolate how the presence of males of different age classes affects group and individual behaviour of females.

We documented patterns of male-male, male-female and female-female social interactions in the aviaries at several levels of analysis: first, we measured how males of different age classes interact with song by recording song production and use in the aviaries. We also measured the social composition of female groups to determine whether differences in male presence affected basic states of assortment such as near-neighbour patterns. In addition, we looked for active attempts by females to initiate interactions with males. Finally, we documented patterns of egg laying during the breeding season as an indirect indicator of reproductive stimulation.

GENERAL METHODS

Subjects

Twenty-one juvenile female, 19 juvenile male, 29 adult female and 17 adult male brown-headed cowbirds served as subjects throughout this experiment. We captured birds in summer 1999 in Monroe County, Indiana, U.S.A. We determined juveniles to be between 50 and 70 days of age by the amount of mature plumage that had emerged at date of capture (Selander & Giller 1960). Adult birds were at least 1 year old at the beginning of the experiment, also determined by plumage (Selander & Giller 1960). We marked birds with unique combinations of coloured leg bands to permit individual identification. We housed birds in four large indoor/outdoor aviaries (9.1 × 21.4 × 3.4 m) where we provided them daily with vitamin-treated water and white and red millet and canary seed plus a modified Bronx zoo diet for blackbirds. Being approximately 200 m apart, the four aviaries were acoustically and visually isolated from each other. All aviaries contained feeding stations, trees, perches, a grass covered ground surface and shelters (for details of aviary design see Smith et al. 2002). Observers were located on a platform at the centre of the east wall of each aviary where all perches were in sight. Observers could not view the insides of the shelters, but birds rarely entered the shelters during the day. In the aviaries, birds were exposed to weather and the attention of predators. Occasionally, wild local cowbirds were attracted to the aviaries. We observed wild cowbirds on each of the four aviaries over the year with no one aviary receiving more wild cowbird contacts than the others.

Social composition of groups in the four aviaries differed only in the age class of males present. We randomly assigned birds to the four aviaries in the following numbers. In three aviaries, we housed seven adult and five juvenile females. In one of these aviaries, referred to as the 'Juvenile male-Adult male' condition (JA), we added seven juvenile males and five adult males. In the second aviary, referred to as the 'Juvenile male' condition (J), we added 12 juvenile males and no adult males. In the third aviary, referred to as the 'Adult male' condition (A), we added 12 adult males and no juvenile males. In a fourth aviary, referred to as the 'No male' condition (No), we housed eight adult and six juvenile females without males. Density and sex ratio were the same across conditions (except for the No condition). All birds remained in their home aviaries from September 1999 to June 2000. Across the entire year, three juvenile birds died (one JA male, one J female and one A female) and seven adults died (one JA male and one JA female, one J female, three A males and one A female).

Procedure

From September to April, two observers recorded birds' social assortment (using near-neighbour associations, see below) and males' vocal behaviour (using song censuses, see below) for 0.5–1.5 h per aviary, starting between 0600 and 0800 hours depending on seasonal variation in

sunrise, ranging from 5 to 7 days per week (totalling 450 h). We observed birds in three phases: autumn (22 September–27 November), winter (10 January–1 March) and spring (1 March–28 April).

To assess social assortment, we measured near-neighbour associations for birds in each condition. We recorded near-neighbour associations by sampling each bird (referred to as the 'target') in an aviary and noting any other bird (referred to as the 'near neighbour') that was observed to be within approximately 30 cm. Once we recorded a pair as near neighbours, they could not be recounted as another near-neighbour association unless they moved apart and then reassociated. For the first 8 months, we manually recorded near-neighbour measures on data sheets. For the spring, we developed and began using a system for automated data collection using voice recognition. We used IBM ViaVoice Millennium Pro Edition voice recognition software operating on a Pentium III, 500 MHz IBM-compatible computer (Compaq Deskpro EP), running Microsoft Windows 98. We used a solid-state, wireless, omni-directional lapel microphone (Telex WT 150; Telex Communications Inc., Burnsville, Minnesota, U.S.A.) and receiver system (Telex FMR 150). Microsoft Word 2000 word-processing software transcribed speech into text. We then exported text into a database (4th Dimension v. 6.5.1; ACI Inc., San Jose, California, U.S.A.) that we programmed to match incoming text to a list of possible codes to detect and correct errors automatically (for further description of the system see White et al. 2002b).

We conducted song censuses to measure production and use of vocalizations by males in the A, JA and J conditions. Song censuses consisted of 15-min blocks in which observers occasion-sampled aviaries, noting any male that vocalized. For each vocalization, we recorded whether it was directed to another bird or was undirected. To be scored as a directed song, the male had to whistle or sing towards a recipient, oriented on an axis between approximately 0° and 45°. The distance between the vocalizing bird and the recipient could not exceed 60 cm. We considered songs and whistles that were not oriented to another bird as undirected song. We also noted females' behaviour to singing males. If a female approached within 30 cm of a singing male, we recorded an 'approach' from that female.

The amount of observation time for near-neighbour measures in each of the autumn, winter and spring samples was equal at 9.33 h for each condition. We conducted 37.5 h of observations for song censuses for each of the three conditions that contained males. Interobserver reliability was high for song census measures of number of songs per male and for near-neighbour measures of number of associations per bird (both $r_s=0.89$, both $P_s<0.001$). Interobserver reliability was also high using voice recognition for near-neighbour associations per bird ($r=0.87$, $P<0.005$).

To measure females' reproductive behaviour and stimulation, we counted copulations in the breeding season and we collected all eggs laid. Each morning in the breeding season (28 April–1 June) from 0600 to 1000 hours we recorded all copulations that occurred in

aviaries containing males, noting the individuals that were involved for each copulation. At the beginning of the breeding season we removed females in the No aviary and placed them into sound-attenuation chambers to be used for a separate playback study (unpublished data).

We placed 10 nests in each aviary. We used as nests 12-cm diameter tea strainers filled with grass clippings and three white, yogurt-covered peanuts. Females would remove peanuts and deposit eggs in these nests each morning. At 545 h each day we would collect eggs and replace removed peanuts. We moved nests that did not receive eggs for more than 1 week to other locations in the aviaries. We also collected any eggs found on the ground. We counted all eggs, whether broken or not, as long as we located the majority of the egg.

We incubated all intact eggs that we collected using a Petersime Model 1 incubator (Petersime Incubator Co., Gettysburg, Ohio, U.S.A.). After 10 days of incubation we candled eggs to determine whether they had been fertilized. Of the fertilized eggs, we considered them to be viable if after 10 days of incubation the embryo had developed to more than 50% of the eggs' content.

Statistical Analysis

Due to small sample sizes and heterogeneity of variance among conditions, we used non-parametric statistical analyses throughout. For post hoc Mann–Whitney U tests and Kruskal–Wallis analyses of variance (ANOVA), we used Bonferroni corrections for familywise error rates. Thus, we used α levels of 0.01 where we compared three groups and 0.008 where we compared four groups. For descriptive purposes, we depict means, standard errors and ranges.

RESULTS

Male–Male Behaviour

Near neighbour

Throughout the three seasons there were differences in the rate at which males in the three conditions interacted with other males as measured by the frequency of male–male near-neighbour associations over each season (Kruskal–Wallis ANOVA: all $H_{2s}>21.43$, all $P_s<0.0001$; Fig. 1). In all seasons, there were significantly more near-neighbour associations among males in the two conditions that held adult males (A and JA) than in the condition that held only juveniles (J) (Mann–Whitney U tests: all $U_s=0$, $N_1\geq 9$, $N_2=12$, all $P_s<0.001$). There were no significant differences in the number of associations between males in the JA and A conditions, although in the spring there was a tendency for males in the A condition to have more associations ($U=16$, $N_1=10$, $N_2=9$, $P<0.018$).

Within the JA condition, juvenile males had more near-neighbour associations with other juveniles than adult males had with other adult males in the autumn and winter (both $U_s=0$, $N_1=6$, $N_2=4$, $P<0.02$), but in the spring adult males had significantly more near-neighbour

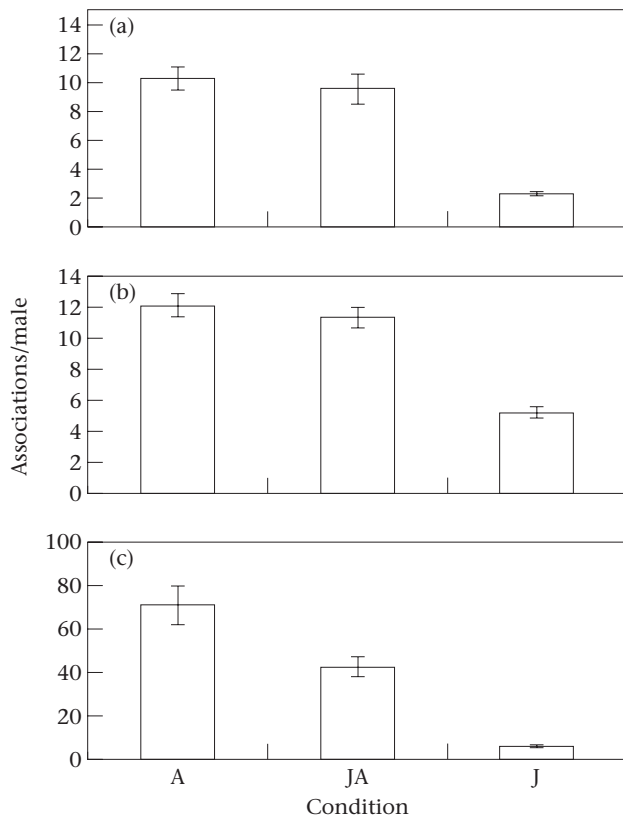


Figure 1. Mean male-male near-neighbour associations per male (\pm SE) in each male condition, during (a) autumn, (b) winter and (c) spring. A: Adult males; J: Juvenile males.

associations with other adults than juveniles had with other juveniles ($U=0$, $N_1=4$, $N_2=6$, $P<0.02$). In all seasons, juvenile males associated with adult males at rates similar to the rates of juvenile male-juvenile male associations in the given season.

Song

We observed significant differences among males in the three conditions in amount of song directed to other males in autumn ($H_2=9.58$, $P<0.01$) and spring ($H_2=14.72$, $P<0.001$) but not in winter ($H_2=1.30$, NS; Fig. 2). There were significantly more songs directed to males in the A condition than in the J condition in the autumn and spring (both $U_s<14$, $N_1=9$, $N_2=12$, both $P_s<0.005$). In spring, males in the JA condition also sang significantly more directed songs to males than did males in the J condition ($U=6$, $N_1=10$, $N_2=12$, $P<0.001$).

We also observed differences across conditions and across seasons in the number of undirected songs produced ($H_2=15.05$, $P<0.001$). J males sang significantly more undirected song than either the JA ($U=13$, $N_1=12$, $N_2=10$, $P<0.002$) or A males ($U=8$, $N_1=12$, $N_2=9$, $P<0.001$).

Within the JA condition, juvenile males sang significantly more undirected song than adult males in the autumn and winter (both $U_s<1$, $N_1=6$, $N_2=4$, $P<0.02$), but

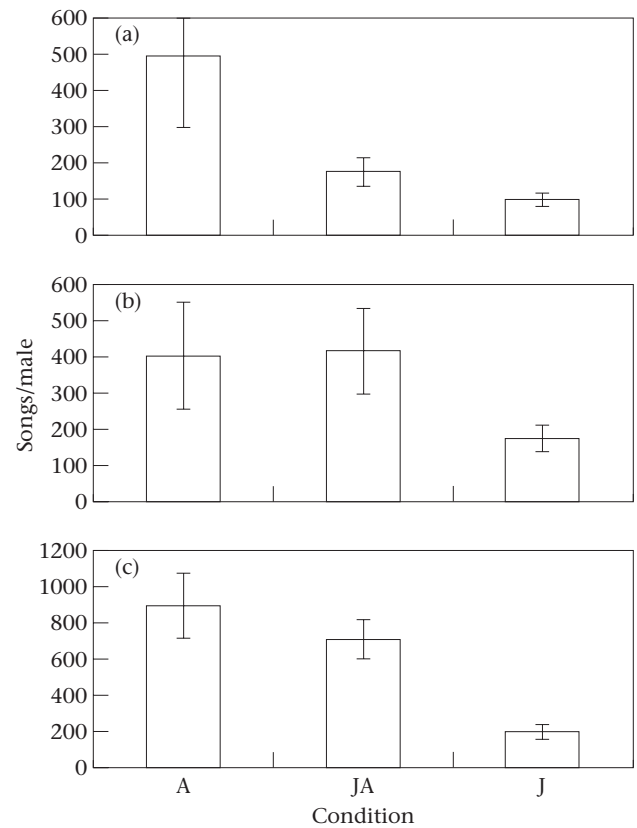


Figure 2. Mean songs per male (\pm SE) directed to other males in each male condition during (a) autumn, (b) winter and (c) spring. A: Adult males; J: Juvenile males.

not in spring ($U=12$, $N_1=6$, $N_2=4$, NS). There were no significant differences in the amount of directed song produced by juveniles and adults in the JA condition (all $U_s\geq 4$, $N_1=6$, $N_2=4$, NS).

Male-Female Behaviour

Near neighbour

In all three seasons, there were differences across conditions in the amount of male-female near-neighbour associations (all $H_2>20.65$, all $P_s<0.0001$; Fig. 3). Females in the A condition had significantly more near-neighbour associations with males than did females in either the J or JA conditions in each season (all $U_s<5$, $N_1=11$, $N_2\geq 10$, all $P_s<0.0001$). Females in the JA condition had significantly more near-neighbour associations with males than did females in the J condition in autumn ($U=1$, $N_1=12$, $N_2=10$, $P<0.0001$), winter ($U=5$, $N_1=12$, $N_2=10$, $P<0.0001$) and spring ($U=26$, $N_1=12$, $N_2=10$, $P<0.01$).

Within the JA condition, there were no significant differences in the amount of near-neighbour contacts that females had with adult and juvenile males throughout the study until the breeding season. In the breeding season females had significantly more near-neighbour contacts with adult males than with juvenile males

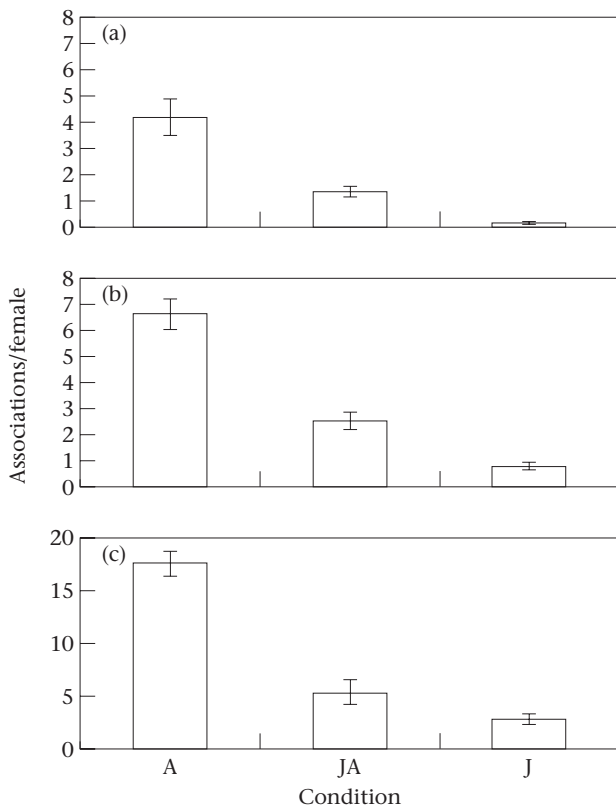


Figure 3. Mean female-male near-neighbour associations per female (\pm SE) in each male condition during (a) autumn, (b) winter and (c) spring. A: Adult males; J: Juvenile males.

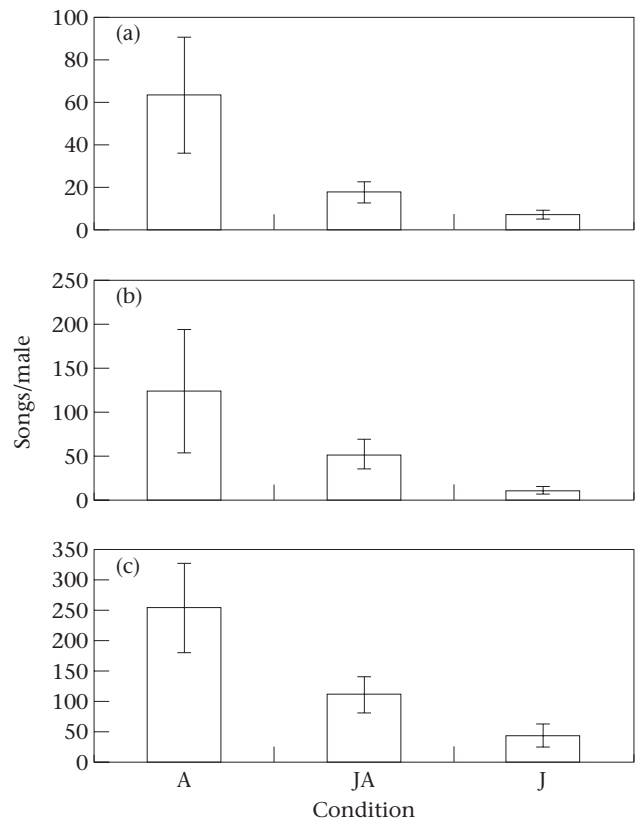


Figure 4. Mean songs per male (\pm SE) directed to females in each male condition during (a) autumn, (b) winter and (c) spring. A: Adult males; J: Juvenile males.

(Wilcoxon matched-pairs signed-ranks test: $T=1$, $N=11$, $P<0.001$).

Directed song

There were significant differences across conditions in the number of songs sung to females (all $H_2s>9.52$, all $Ps<0.01$; Fig. 4). Males in the A condition sang significantly more directed songs to females than did males in the J condition in all seasons (all $Us<6$, $N_1=9$, $N_2=12$, all $Ps<0.005$). Males in the JA condition sang more directed songs to females than did males in the J condition in the spring only ($U=18$, $N_1=10$, $N_2=12$, $P<0.006$). Within the JA condition, there were no significant differences between juveniles and adults in the number of songs sung to females in the autumn or winter (both $Us\geq 3.5$, $N_1=6$, $N_2=4$, NS), but in the spring, adult males sang more directed song to females than did juveniles ($U=2$, $N_1=4$, $N_2=6$, $P<0.05$).

Throughout the three seasons, females across conditions approached singing males at different rates (all $H_2s>23.2$, all $Ps<0.0001$; Fig. 5). In all seasons, females in the A condition approached singing males significantly more often than did females in any other condition (all $Us=0$, $N_1=11$, $N_2\geq 10$, all $Ps<0.0001$). In the spring, JA females approached singing males significantly more often than did J females ($U=18.5$, $N_1=12$, $N_2=10$, $P<0.006$).

Female-Female Behaviour

Near neighbour

In all seasons, rates of female-female associations differed across conditions (all $H_3s>26.56$, all $Ps<0.0001$; Fig. 6). In winter and spring, females in the A and JA conditions had fewer associations with other females than did females in the J and No conditions (all $Us<4$, N_1 , $N_2\geq 10$, all $Ps<0.0001$). In the autumn, females in the A and JA conditions had significantly fewer near-neighbour associations with other females than did females in the No condition (both $Us<6$, $N_1\geq 10$, $N_2=14$, both $Ps<0.0001$) but not the J condition (both $Us>14$, $N_1\geq 10$, $N_2=10$, both NS).

There were also differences in how females of the two age classes assorted with other females when males were present compared to when males were absent. We compared each age class of females housed in the three conditions where males were present with the same class of females in the No group. We combined data for females in the A, JA and J conditions in order to attain statistical power. Females associated by age class only when males were present. Juvenile females housed with males had a significantly higher proportion of female near-neighbour associations with other juvenile females (0.555 ± 0.02) than did juvenile females in the No condition (0.493 ± 0.007 ; $U=18$, $N_1=14$, $N_2=6$, $P<0.03$). Similarly, but not as pronounced as juveniles, adult females

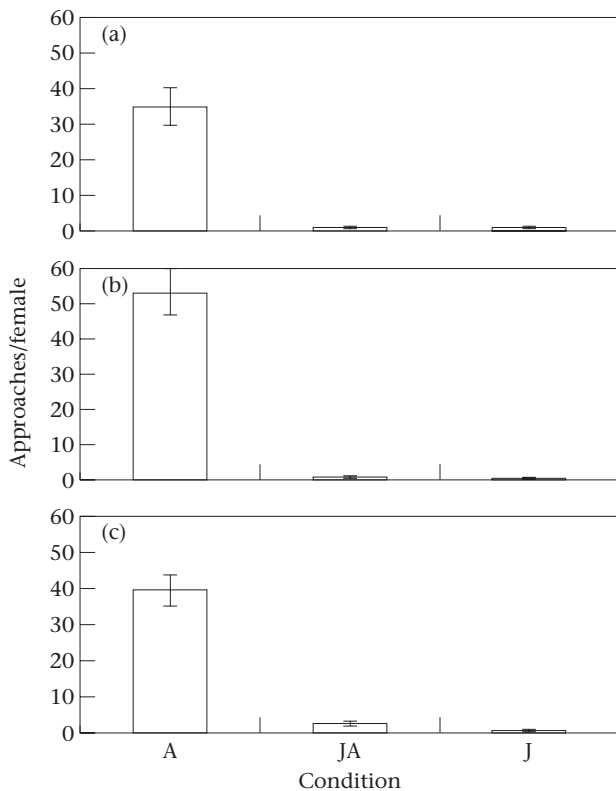


Figure 5. Mean approaches per female (\pm SE) in each male condition during (a) autumn, (b) winter and (c) spring. A: Adult males; J: Juvenile males.

housed with males had a significantly higher proportion of female near-neighbour associations with adult females (0.521 ± 0.012) than did females in the No condition (0.478 ± 0.012 ; $U=31$, $N_1=18$, $N_2=8$, $P<0.05$). Small sample sizes precluded testing intergroup variation in female assortment by age class among groups with males present.

Breeding Season

Copulations

Females differed across conditions in number of copulations received (means: A females= 9.9 ± 1.51 ; JA females= 7.11 ± 1.69 ; J females= 3.6 ± 0.95 ; $H_2=8.58$, $P<0.02$). Females in the A condition copulated significantly more often than females in the J condition ($U=13$, $N_1=N_2=11$, $P<0.005$). There was also a difference across groups in females' number of sexual partners ($H_2=15.35$, $P<0.001$). Females in the J condition copulated on average with $2.11 (\pm 0.43)$ partners, which was significantly higher than females in the JA or A conditions, who never copulated with more than one partner ($U_s<15$, $N_1=10$, $N_2 \geq 10$, $P_s<0.005$).

Eggs

We collected a mean of 2.7 eggs per day (range 0–5) in the A condition and 1.7 eggs per day (range 0–3) in each of the JA and J conditions. Data on egg production is

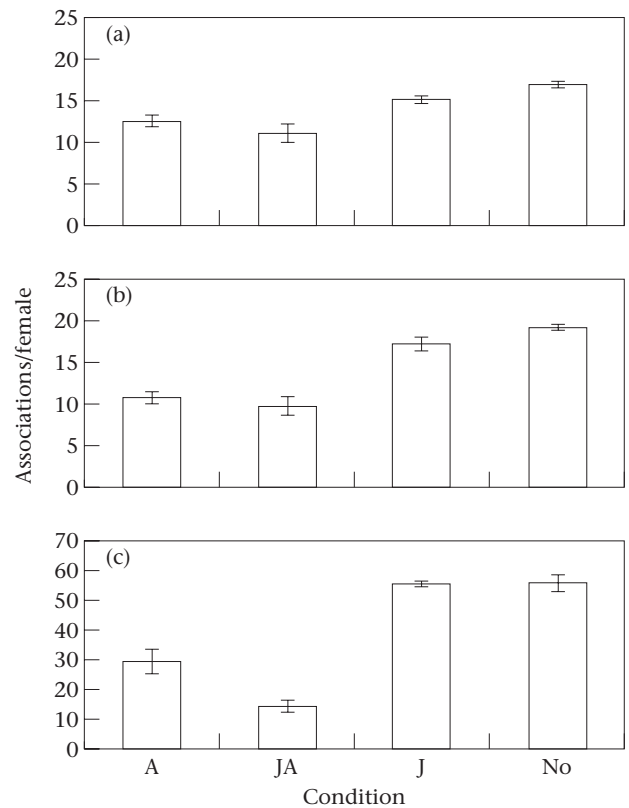


Figure 6. Mean female-female near-neighbour associations per female (\pm SE) in all conditions, during (a) autumn, (b) winter and (c) spring. A: Adult males; J: Juvenile males; No: No males.

Table 1. Eggs produced in each male condition

Condition	Eggs laid	Broken	Fertilized	Total viable/female
A	81	14 (0.173)	50 (0.617)	4.3 (0.551)
JA	52	18 (0.346)	25 (0.481)	2.5 (0.481)
J	47	33 (0.635)	9 (0.173)	0.55 (0.115)

Total number of eggs laid, number of eggs broken, number of eggs fertilized and number of viable eggs produced by females in each condition. Numbers in brackets indicate proportion of total eggs laid. A: Adult males; J: Juvenile males.

provided in Table 1. Females in the A condition laid more eggs than did females in the other conditions. While females in the J and JA conditions laid the same number of eggs, in the J condition we found more eggs broken on the ground and pecked in nests (proportion broken in Table 1) than in the other conditions. Of the eggs produced that were not broken, J condition females had a lower proportion of their eggs fertilized and viable than did females in the other conditions. Overall, after 1 month of collecting eggs, J condition females produced in total only six viable eggs; one-seventh the number of eggs that were produced by females in the A condition and one-fourth the number of eggs produced by females in the JA condition.

GENERAL DISCUSSION

Across the three seasons of this study, females housed in groups with males of different age classes differed in their social behaviour. Across conditions, females associated differently with both males and females starting as early as autumn and continuing through the year into the breeding season. Furthermore, in the breeding season, females differed in their frequency and patterns of copulations and in their egg production and laying behaviour.

The main variable that corresponded to the differences in female behaviour was the amount of male social interactions in the different conditions. The J condition was characterized by low levels of male social association and singing interaction. Males rarely came near other males and did not direct song to one another; instead they sang undirected song predominantly. Here females rarely associated with males and affiliated with other females as much as did females in the condition where no males were present. In the breeding season, J females' reproductive behaviours differed from those of females in the A or JA conditions. J females copulated with multiple partners, produced fewer eggs than the A condition females, and broke more eggs, resulting in the production of fewer viable eggs.

The A condition was characterized by high levels of male–male social interactions. Here females associated more with males than did any females in the other conditions and they associated less with other females than did females housed with only juvenile males or no males. Females in the A condition received more directed song from males and actively approached singing males, a behaviour that very rarely occurred in the other conditions. In the breeding season they copulated more often, and produced more eggs.

Compared to the A and J conditions, the JA condition was characterized by moderate levels of male interactions. Here, measures of female behaviour were at levels between the two extremes of the A and J females with respect to associations with males, associations with females, copulations and viable eggs produced.

In the No condition, where females had no interactive contact with males, we observed no social assortment by age class. The absence of organization suggests to us that the presence of males produces motivational constraints on female assortment.

The possibility that females were sensitive to and reacting to particular morphological characteristics of juvenile versus adult males seems unlikely. Females responded to the two groups of juveniles differently (for an analysis of differences in behaviour between juvenile males in the JA and J conditions see White et al., in press). In addition, females responded differently to adult males depending on whether there were juveniles present in the group. These patterns suggest the behaviour of the males was the important factor influencing female behaviour. That being said, however, it is impossible at this point to establish the direction of effects. Females, for example, may react differently to different male behaviour and these differences may stimulate males to alter their

behaviour (King & West 1987). We believe, however, that the heuristic value here is in understanding (1) how the effects of numerous differences in female and male behaviours across conditions can cascade across time to produce different social environments and (2) the functional consequences for individuals living within those different social environments. Future work will be directed to determining the mechanisms and the directions of the social effects on learning and development seen here.

Since there was only one group in each condition in this study, the possibility exists that an unmeasured variable contributed to the observed differences in male and female behaviour. We have very recently replicated each of these conditions with independent groups of cowbirds in different aviaries. Smith et al. (2002) replicated the JA condition in a larger aviary complex with a larger group size. They found similar patterns of near-neighbour association, with females assorting by age and sex throughout a year. Recently, we have replicated the A condition (see King et al., in press) and have found female assortment by age and sex, high levels of female near-neighbour contacts with and approaches to males, as well as high levels of copulations and eggs produced. We conducted a replicate sample of the No condition by placing a new group of adult and juvenile females in an aviary and then recording 1532 near-neighbour associations during autumn 2001. Similar to patterns reported here, we found no significant assortment by age class (A. P. King & D. J. White, unpublished data). We have also replicated the J condition four times (see King et al., in press). Combining across these four replicates, we found similar patterns of behaviour as reported here for the J males, including age and sex of near-neighbour associations for females, low levels of female near-neighbour associations with and approaches to males, few copulations and eggs produced. Notably however, across these four conditions the amount of female association with males corresponded to the amount of male–male social interaction observed, suggesting that even within an age class of males, social behaviour of females is related to male intrasexual interaction. Results from all of these replicate trials are similar to patterns of behaviour observed in the current experiment and are consistent with the hypothesis that social organization and behaviour of females is related to male–male interactions.

Our aim in this study was to document functional effects of social groups on behaviour, which required maintaining the groups from the beginning of the study through to the breeding season. But is this stability we imposed on the captive groups in any way representative of cowbird social groups in nature? Obviously, while our aviaries are large and, being outside, expose subjects to many aspects of the real world, they cannot simulate many of the experiences cowbirds would be exposed to in the wild. Attempting to determine whether we have captured a representative social ecology is difficult because it is impossible to characterize a cowbird's species-typical social structure. Cowbirds inhabit a variety of ecologies across which differences have been reported in density, timing of migration and breeding, sex ratios

and mating system (Friedmann 1929; Rothstein et al. 1980, 1986; West & King 1988; O'Loughlen & Rothstein 1993; Ortega 1998; Rothstein & Robinson 1998). Currently, we have begun investigating the effects of group stability on cowbird behaviour. We are studying female responses to males in more dynamic social groups where individuals are frequently exchanged. A robust finding thus far has been that female behaviour responds rapidly to different male characteristics (for example, their stage of song development) and we have been able to measure changes in female behaviour in real time (e.g. when males are singing versus when they are not; J. Gross-Louis, D. J. White, A. P. King & M. J. West, unpublished data).

In many species (cowbirds among them; Freeberg 1998), female mate selection can be influenced by social factors. For example, mate choice or mate preferences can be modified by opportunities for sampling potential mates (Janetos 1980; Real 1990, 1991; Riebel 2000), learning about potential mates from observing other females (White & Galef 1999), or exposure to developing song (West & King 1988; Casey & Baker 1992; Payne et al. 2000). The present study indicates a potentially significant source of variation in mating patterns among females: differential opportunities to interact with and learn from other females and males prior to a breeding season. The data also suggest that females are sensitive to behaviours associated with male quality from an early age. They may witness the formation, as well as the eventual use, of sexually selected traits. These findings argue for more attention to be paid to the developmental ecology of females. The work reported here is a first step in exploring how variation in social ecology can be related to differences in mating-related behaviours.

It suggests the need to look closely at female social organization as it may contribute to maintenance of variation in female preferences, mate choice and reproductive success.

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