# PLASTICITY IN ADULT DEVELOPMENT: EXPERIENCE WITH YOUNG MALES ENHANCES MATING COMPETENCE IN ADULT MALE COWBIRDS, MOLOTHRUS ATER

by

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(Acc. 5-III-2002)

**Summary**

The social environment can play an important role in organizing organisms' behavioural development. We studied the effect on adult male cowbirds' communication and mating-related behaviour of being housed in social groups with juvenile males. In two large outdoor aviaries, we housed adult males, juvenile females and adult females either with or without juvenile males. Conditions remained intact from September 1999 through the first half of the breeding season in May 2000. We observed them throughout this time, documenting singing interactions, patterns of affiliation, and song production. We then brought the two groups of adult males together by rotating individuals from the groups into a mating competency tournament, allowing the males to compete with each other for mating opportunities with a new group of females. Throughout the study prior to the mating competency test, there were few differences among adult males in the two conditions as measured by amount and use of song, the quality of their songs, or number of copulations they received. In the mating competency tournament however, significant differences among males in the two conditions emerged. Compared with adult males that had been housed without juvenile males, adult males that had formerly been housed with juvenile males were more successful in the mating competition as measured by: success in getting copulations, number of copulations received, and latency to get copulations. They also engaged in more male-male singing interactions. These results provide evidence to suggest that development of mating competency is malleable throughout life in response to the social environment that individuals experience.

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[2)] The work was supported by NSF. DJW Received support from an NSERC post doctoral fellowship. Sue Linville assisted with data collection. C. Snowdon and two anonymous reviewers made valuable comments on earlier draft of the manuscript.

## Introduction

Traditionally, investigations of social learning, information transmission, and social development consider how young, naive individuals learn from older, more experienced conspecifics (Boyd & Richerson, 1985; Heyes & Galef, 1996). Little attention, however, has been paid to the role experience with young can have on older conspecifics. The presence of young in a social group can change the environment for adults in several ways. Young organisms are a potential source of behavioural variability; they play, explore, and can behave in ways contrary to existing behavioural traditions. Young can provide adults with consistently changing social relationships as well as serving as a source of behavioural innovations (West & King, 1987). Social environments differing in the age classes of conspecifics present can provide individuals in those groups with very different experiences. Different types of information may pass through subsets of the group, at different rates, or at different times (*e.g.* Reader & Laland, 2001), potentially favouring the development of different behavioural repertoires.

This study is part of a larger investigation into how the composition of a social group can impact the development of functionally important behaviour of the group members. We study brown-headed cowbirds (*Molothrus ater*) because the species experiences large variation in social ecology. In the wild, flock composition can vary by age class and sex (Friedmann, 1929). In some populations, adult movement patterns do not overlap with juveniles (O'Loghlen & Rothstein, 1993); in others, the age classes do overlap (King & West, 1988). Thus, across populations, both within and between subspecies there can be large differences in the sex and age class composition of social groups (Smith *et al.*, 2000).

In captive flocks, we have found that social ecology can have a powerful influence on development in cowbirds. In a series of experiments, we have modified the social ecology of flocks by manipulating the age classes of birds present. As a result, we affected the developmental trajectories of juvenile males' reproductive behaviour patterns. We housed juvenile males in large social groups in outdoor aviaries with females and either with or without adult males. Juvenile males, differing only in exposure to adult males, developed very different courtship and communicative skills (White *et al.*, in press). Compared with juvenile males housed with adults, the juvenile males housed without adults (1) developed courtship song faster

that was structurally different and was more effective at eliciting females' copulatory postures, (2) engaged in fewer singing interactions with males and with females, and (3) courted and copulated with females unselectively, showing little mate guarding or intrasexual competition. These differences emerged rapidly and were present at a very young age, within the first few weeks of independence from their hosts (White *et al.*, 2002). In summary, we found that the process of development in juvenile males was facultative, rather than fixed, constructed from patterns of interaction with conspecifics in the social environment.

In the current study, we examine whether adult male development could be influenced by the composition of the social environment. We were interested in effects on all aspects of reproductive behaviour. We use the term mating competence to incorporate all components of the courtship system that lead to successful mating, including effective interactions with females (singing potent courtship songs persistently to individual females) as well as effective interactions with males (establishing dominance relationships though song). Other work has shown that interactions in a social environment can influence adult male competitive behaviour, courtship success, and mate choice (Chase *et al.*, 1994; Jones *et al.*, 1996; White & Galef, 1999; Fernald & White, 2000; Nelson, 2000; Pfaus *et al.*, 2001). Also, there is some evidence from cowbirds that adult males show evidence of malleability in song learning. In adulthood, cowbirds have the potential to change song repertoires, as well as to improve their courtship competency (West *et al.*, 1996). That study however was conducted with birds that had abnormal experiences in early life, such as being housed only with canaries. Nevertheless, the potential existed for modifiability in adulthood. Here we asked whether we could detect any significant changes in the mating competence of two groups of adult males when the only difference between the groups was whether or not they had been housed with juvenile males.

We set up groups of adult males living in social groups in large outdoor aviaries. The groups contained juvenile and adult females and either juvenile males or no juvenile males. While the aviaries were large, they could not, of course, be considered analogous to the wild. Social compositions of this sort (*i.e.* adults living in the presence or absence of juvenile males), however, do occur naturally (Friedmann, 1929; King & West, 1988). We left the adult males in their conditions for 10 months and observed them throughout the study. We measured association patterns within the groups

using near neighbor associations. To document male intrasexual interactions we measured their vocalizing patterns with other males. Vocalizations by males are their major form of interaction with other males and with females. Males sing to other males to establish dominance relationships (Dufty, 1986) and they direct vocalizations to females in the breeding season to elicit copulatory postures. We also recorded their songs to document structural and song potency differences. In the breeding season we measured their courtship abilities in their home aviaries. We then directly compared the two groups of males by rotating males of both groups through a new social environment in the presence of a new group of females.

## Materials and methods

### *Subjects*

We collected 7 juvenile male, 10 juvenile female, 17 adult male, and 14 adult female brown-headed cowbirds in Monroe County, IN to serve as subjects throughout the experiment. We determined juveniles to be between 50 and 70 days of age by the amount of mature plumage present at the time of capture (Selander & Giller, 1960). Adult birds were at least one year old at the beginning of the experiment, also determined by plumage (Selander & Giller, 1960). We trapped birds at three locations and randomized location and date of capture when assigning birds to conditions. To permit individual identification, we marked all birds with unique combinations of coloured leg bands. We housed birds in two large 9.1 × 21.4 × 3.4 m indoor/outdoor aviaries, visually and acoustically isolated from each other. Both aviaries contained vitamin-treated water, white millet, red millet, canary seed, and a modified Bronx zoo diet for blackbirds available *ad libitum*. Both aviaries contained trees, perches, feeding stations, a grass covered ground surface and shelters. In the aviaries, birds experienced weather conditions, wild local cowbirds, and the attention of predators.

We randomly assigned birds to the two aviaries in the following numbers. In both aviaries, we housed seven adult and five juvenile females. In one aviary, referred to as the juvenile-male-adult-male condition (JA), we housed eight juvenile males and five adult males. In the second aviary, referred to as the adult-male condition (A), we housed 12 adult males and no juvenile males. We created groups of these sizes to keep the same amount of males in each condition in order to maintain the same sex ratio and density in the two conditions. All birds remained in their home aviaries from September 1999 through June 2000. Across the entire year, two juvenile males, one adult male, and one adult female died in the JA condition and one juvenile female, one adult female, and two adult males died in the A condition.

### *Procedure*

For 404 total observation hours, from September through June, two observers recorded birds' vocal behaviour and social assortment for 0.5 to 1.5 h per aviary, starting between 600 h and 800 h and ranging from five to seven days per week. We divided observations into four phases of approximately equal sample size: fall (Sept 22 through Nov 27), winter (Jan 10 through

Mar 1), spring (Mar 2 through Apr 27), and breeding season (April 28 through June 1). At the end of the breeding season phase, we removed birds from their home aviaries and conducted a mating competency tournament, rotating adult males from the two conditions through a new aviary with a new group of females.

To measure song production and song use, we conducted 15 min song census blocks in which observers used ad lib sampling in the aviaries (Altmann, 1974), 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 vocalization, the bird had to vocalize with either a song or a flight whistle toward a recipient, oriented on axis plus or minus approximately 45°. The distance between vocalizing bird and recipient could not exceed 60 cm. We considered vocalizations produced that were not oriented to another bird as undirected.

To measure the social organization within the aviaries, we recorded near neighbor associations for each bird in the study. In seven min blocks we sampled each bird (referred to as the 'target') in an aviary and noted any other bird (referred to as the 'near neighbor') within 30 cm. Once we recorded a pair as near neighbors, they could not be recounted as another near neighbor association unless the pair moved apart and then re-associated.

Interobserver reliability for the prebreeding season was high for song census measures of number of songs per male and for near neighbor associations per bird (both $r_s \geqslant 0.87$, both $p_s < 0.005$).

For the first eight months, we manually recorded measures on data sheets. During the breeding season and mating competency tournament, we developed and began using a system for automated data collection using voice recognition (White *et al.*, 2002). 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 Ltd.) and receiver system (Telex FMR 150). Microsoft Word 2000 word processing software transcribed speech into text. We then exported text into a database (4$^{th}$ Dimension v. 6.5.1; ACI Inc.) that we programmed to match incoming text to a list of possible codes to detect and correct errors automatically.

Interobserver reliability was high using voice recognition for song censuses (songs per male; $r = 0.98$, $p < 0.001$) and for near neighbor associations (associations per bird; $r = 0.87$, $p < 0.005$). Voice recognition provided a doubling in the amount of data collected over the manual method (White *et al.*, 2002).

The amount of observation time in each of the four phases was approximately equal at 37.5 h (36.25 h for the breeding season) per condition for song censuses and 9.33 h (13.53 h for the breeding season) for near neighbor measures. At the end of each phase, we calculated for each adult male the number of undirected vocalizations, vocalizations directed to males (male-directed song), and vocalizations directed to females (female-directed song). We also measured during song censuses any instance of females approaching to within 30 cm of singing males.

The breeding season phase commenced on the day of the first observed copulation and continued for the first half of the cowbird breeding season, which usually lasts from late April until early July in the Midwest United States (Lowther, 1993). We observed birds each day between 600 and 1000 h, the time when virtually all copulations occur (Rothstein *et al.*, 1986). We took song census and near neighbour samples using the same methods as in the prior phases. During both types of samples, we recorded all copulations that occurred and noted the individuals involved.

We also examined the quality of songs of males in the two conditions. To do so, we recorded vocalizations from each of the adult males in the two conditions when their songs had crystallized in early May 2000. We made the recordings in their home aviaries using Sennheiser RF condenser microphones recorded into a Sony TCD-D10 PRO digital audiotape recorder. To measure the quality of the songs, we played the recordings to females in sound attenuating chambers and we measured each song's efficacy in eliciting a copulatory response from the females.

We dubbed the breeding season recordings that we selected for playback onto an Otari MX III half-track recorded at 36 cm/s. We played back songs using an Otari recorder, a Urei 537 1/3-octave equalizer, and a Crown D75 power amplifier through JBL 2105 speakers located in each sound-attenuating chamber. The sound pressure levels of the songs were $85 \pm 2$ dB (a weighted impulse reading at 0.8 m from the speaker as recorded by a B & K 2209 sound pressure meter). We selected one song from each male in the two conditions based on recording quality from a selection of approximately 30 songs per male. We did not get usable recordings of four males in the A condition, thus leaving songs from 6 A males. We tested songs from all 4 JA males. To equate for the number of songs played back per condition, we played back an additional song from two males in the JA condition and took the mean response rate of the two songs for the males' scores. Signal to noise ratios, measuring peak noise to peak signal, did not differ between songs from the JA and A conditions (means 48.84 and 49.38 respectively Student's $t$-test, $t(10) = 0.54$, NS).

Starting on May 15, 2000, we played the songs to a group of eight adult and six juvenile females. We had housed these females in an outdoor aviary from September 1999. The females were housed without males in the aviary but could see and hear wild resident cowbirds. On April 27, 2000 we brought the females into the lab and housed them in pairs in 1.3 $m^3$ chambers. Housing females in pairs served to reduce potential stress induced by being housed in chambers and has been shown to have no influence on females' responses to played back song (West *et al.*, 1996; Smith *et al.*, 2000). We played six songs per day to females. Each song trial was separated by 90 min. We alternated the order in which we played back songs with each presented 6 times over the course of the experiment. We scored a positive response if the female adopted a copulatory posture within one second from the onset of the song. To calculate potencies, we computed mean number of responses per female for each song and averaged over all males in each condition. We removed one adult female from the experiment who never responded to any playbacks.

### *Mating competency*

*Part a.* Starting on June 5 we began removing birds from their home aviaries to test in the mating competency tournament. Though we did begin the test in the second half part of the breeding season, throughout the tournament females were laying eggs and copulations were occurring in other aviaries. Past work in aviaries has shown that 30 percent of eggs are laid after June 5. We combined a random selection of three adult males from both conditions in a new test aviary, identical to their home aviaries, and observed their mating success with a group of three juvenile and four adult females that had formerly been housed in an aviary with juvenile males. We used this number of subjects for sampling purposes as it allowed us to document the majority of courtship behaviour in the aviary. In the wild, social composition of flocks is dynamic and it is not uncommon for new males to enter social groups late into the breeding season (Friedmann, 1929; Darley, 1982; Dufty, 1982). Once we determined that

a male had reached a criterion for mating success or mating failure in this aviary (see below), we replaced him with another adult male from his home aviary. We observed birds each morning from 600 h to 1000 h for a total of 42.25 observation hours. We used song censuses procedurally identical to the breeding season censuses. To test the possibility that scan sampling vocalizing males was systematically biasing our observations of song production or song use, we also took 15 min focal samples on each male in the competition each day, recording the same measures as in song censuses. During these focal samples, we continued to scan for and record any copulations that occurred in the aviary. Focal and scan sampling measures produced similar patterns of results ($r = 0.92$, $p < 0.001$). We collected 3.84 times more data in scan samples than we did in focal samples.

We considered a male a success in the tournament if he copulated more than three times, or had consort days with the same female for three days in a row. We considered a male to have obtained a consort day with a female if he either copulated with her or sang the majority of his female-directed songs to her (previous studies using this type of tournament have shown consort persistence to be a predictor of copulatory success; West *et al.*, 1996). We considered males to be failures if they sang less than ten female-directed songs per day over a four-day period and also failed to copulate. Once a male reached criterion for success or failure, he was removed and another male from his condition took his place. The test continued until we had determined the success or failure of all males in one condition. We recorded the number of copulations each male received, the latency to copulate based on the number of days spent in the competition, directed songs to males and females, and consort persistency (CP), defined as the number of consort days divided by the number of days in the competition.

*Part b.* Due to differences in the number of subjects in the two conditions, 4 males in the A condition had not been tested at the point when all males from the JA condition had been tested. Thus in part b of the mating competency test, we tested these four untested A males against four juvenile males in the JA condition following the procedures from part a above.

*Statistical analysis.* Due to small sample sizes and heterogeneity of variance between conditions, we used non-parametric statistical analyses throughout. For the work leading up to the mating competency tournament, we compared singing and association patterns for males from the two conditions each season with Mann-Whitney $U$-tests using a Bonferroni correction for the number of tests conducted across the phases, resulting in a two-tailed critical alpha level of 0.0125. We report as trends situations where the obtained alpha levels were below a two-tailed $p$ of 0.05. For illustrative purposes, we depict means, standard errors, and ranges in results.

We found no significant differences between juvenile and adult females between or within conditions for measures across this study. We thus combined classes of females in analyses.

## Results

Throughout the phases of the study leading up to the mating competency tournament, there were few significant differences among males in the two conditions. Within the mating competency tournament, however, differences in competency emerged favouring the JA males. Patterns of behaviour prior to the mating competency test are summarized briefly below.

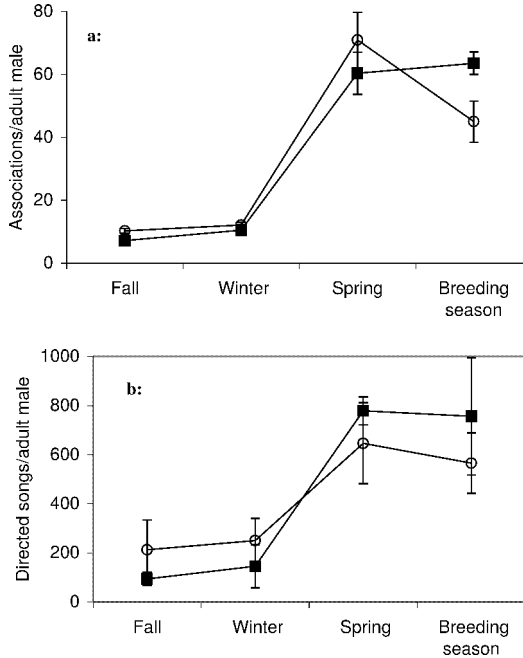


Fig. 1. Interactions among adult males in the JA (■) and A (○) conditions for the fall, winter, spring and breeding season. (a) Mean (± SEM) near neighbor associations with other males per adult male and (b) mean (± SEM) male-directed song sung per adult male.

There were no differences in near neighbour associations of adult males with other males before the breeding season (all $U_s > 8$, all NS). In the breeding season phase, however, JA adult males showed a trend to have more near neighbour associations with other males than did A adult males ($U = 5$, $p = 0.036$; Fig. 1a). There was no significant difference in near neighbour associations with adult males in the two conditions (*i.e.* near neighbour associations with juvenile males removed from the analysis from the JA condition).

There were no significant differences in the amount of undirected song sung or male-directed song sung by adult males in the two conditions for any sampling period over the entire study (undirected song, all $U_s > 9$, all NS; directed song, all $U_s > 7$, all NS; Fig. 1b). JA adults sang on average 60 (± 7)% of their male-directed song to adult males in the fall, 33 (± 10)% to adult males in the winter, 48 (± 12)% to adult males in the spring, and 53 (± 10)% to adult males in the breeding season.

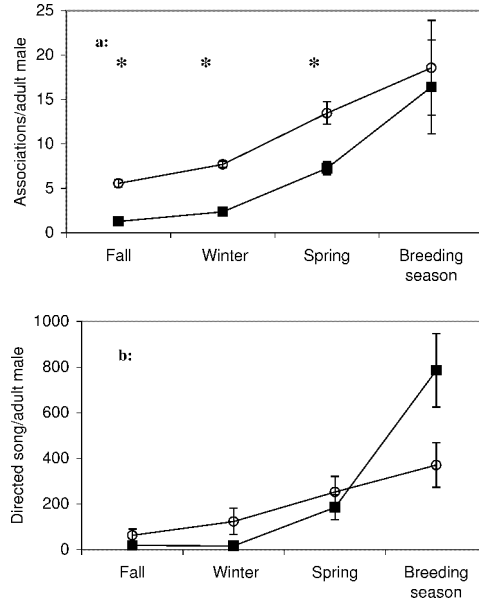


Fig. 2. Interactions with females for adult males in the JA (■) and A (○) conditions for the fall, winter, spring and breeding season. (a) Mean (± SEM) near neighbor associations with females per adult male and (b) mean (± SEM) female-directed song sung per adult male. * indicates significant difference at $p < 0.0125$.

One of the most distinctive differences in the two conditions before the mating competency phase was in male — female interactions. A males affiliated significantly more with females than did JA adult males throughout the fall, winter, and spring (all $U_s = 0$, all $p_s < 0.005$; Fig. 2a), but not in the breeding season ($U = 16$, NS). A males also showed a trend to sing more female-directed song in winter than did JA adults ($U = 3$, $p = 0.014$; Fig. 2b) and had similar trends in the fall and spring. In the breeding season however, it was the JA males that showed a trend in singing more female-directed song than did A males ($U = 5$, $p = 0.036$). Females approached singing males more often in the A condition than in the JA condition across all sampling sessions before the breeding season (all $U_s = 0$, all $p_s < 0.001$; Fig. 3).

We found no significant differences in song potency of males in the A condition (mean potency 0.40 ± 0.06) and JA condition (mean potency 0.44 ± 0.06; Wilcoxon paired signed ranks test, $T = 28.5$, NS). Nor did we find differences in amount of copulations received by adult males in the two

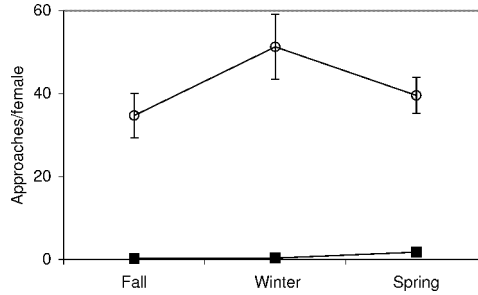


Fig. 3. Mean (± SEM) female approaches per female to singing adult males in the JA (■) and A (○) conditions for the fall, winter, and spring. * indicates significant difference at $p < 0.0125$.

conditions (mean copulations per male, A males: 16, range 0-58; JA males 15.75, range 7-36; $U = 15$, NS). Within the JA condition, juvenile males received a mean of 6.33 (range 0-26) copulations per male (see White *et al.*, in press for analysis of juvenile behaviour).

In the A condition, males' song potency, as measured in the playback experiment correlated positively with number of copulations received from females in the aviary during the breeding season ($r_s = 0.60$). In the JA condition, the correlation was negative ($r_s = -0.269$). This difference however did not reach statistical significance.

*Mating competency*

*Part a.* While differences among males in the two conditions were not pronounced when we compared them in their home conditions, large differences emerged when we placed males from the two conditions into direct competition with each other. As depicted in Table 1a, in the mating competency tournament JA adult males were more successful than A males as measured by: number of copulations received, number of males receiving copulations, latency to get copulations, and consort persistence. In addition, JA adults sang significantly more female-directed and male-directed song than did A adults.

There were no significant correlations of the behaviour of JA adults in the breeding season with their behaviour in the mating competency test for male-directed song ($r_s = -0.185$), female-directed song ($r_s = 0.632$), or how copulation success in the breeding season correlated with: number of copulations in the mating competency test ($r_s = -0.673$), latency to get a

TABLE 1. *Performance of males in mating competency tournament*

| | Female directed | Male directed | Days to first copulation | CP | # cops | Prop males successful |
|---|---|---|---|---|---|---|
| (a) | | | | | | |
| A | 4.84 | 4.19 | 5+ | 0.10 | 0.80 | 0.20 |
| | (4.26) | (3.38) | – | (0.10) | (0.80) | (1/5) |
| JA adults | 43.71 | 41.56 | 3.25 | 0.85 | 3.00 | 1.0 |
| | (8.17) | (15.63) | (0.48) | (0.10) | (0.71) | (4/4) |
| | $U = 0$ | $U = 0$ | $U = 0$ | $U = 0$ | ns | Fisher |
| | $p < 0.02$ | $p < 0.02$ | $p < 0.02$ | $p < 0.02$ | | $p < 0.05$ |
| (b) | | | | | | |
| A | 36.98 | 18.72 | 2.67 | 0.65 | 2.00 | 1.00 |
| | (16.31) | (6.10) | (0.67) | (0.24) | (1) | (4/4) |
| JA juveniles | 0.56 | 0.54 | > 5 | – | 0.00 | 0.00 |
| | (0.41) | (0.41) | – | – | (0) | (0/4) |
| | $U = 0$ | $U = 0$ | $U = 0$ | $U = 0$ | $U = 0$ | Fisher |
| | $p < 0.05$ | $p < 0.05$ | $p < 0.05$ | $p < 0.05$ | $p < 0.05$ | $p < 0.05$ |

Means per adult male (numbers in brackets denote standard errors) for number of songs sung to females and males per day in competition, number of days to first copulation, consort persistence (CP), and number of copulations (# cops) in part a and b of mating competency tournament. Prop males successful indicates proportion of males from each condition that competed successfully in tournament (successful/total provided in brackets).

copulation ($r_s = -0.389$), or consort persistence ($r_s = 0.889$). We could only examine the correlations for the JA males because so few males were successful in the A condition.

*Part b.* All A adult males were more successful at getting copulations than were juvenile males. Table 1b provides the results of this part of the mating competency test. A adult males sang more to females and other males than did the JA juveniles. The adults also were more successful than juveniles in the tournament as measured by number of copulations received, number of males receiving copulations, latency to copulate, and consort persistence. Comparing the behaviour of A males in the breeding season with their behaviour in the mating competition produced no significant correlations for directed song to males and females, and copulation success ($r_s$ range $= -0.4$ to 0.632, all NS).

## Discussion

While the two groups of adult males in this study did not display dramatic differences over the year as measured by male interactions or copulatory success in their home aviaries, once they were brought together in direct competition, large differences emerged. Adult males formerly housed with juveniles were far more successful in competing for females against adult males formerly housed with peers. Every single JA male got copulations faster than every single A male, only one of which ever managed a copulation. Lack of copulatory success in the competition by the A males could not be attributed to their inability to court females in the new environment since A males, once given the opportunity to court females with less competent (juvenile) males, were successful.

We offer three, non mutually exclusive hypotheses explaining the observed effects from the mating competency tests, (1) the competitive abilities of the JA adult males were enhanced, (2) the timing of mating behaviour in the two groups was different, and (3) the JA males were more adept in dealing with a new social environment. The first hypothesis seems the most obvious. On this theory, the JA males, as a consequence of living in an environment where they could consistently outcompete the other males became more dominant and were more effective in intrasexual interactions, possibly through winner effects (*e.g.* Chase *et al.*, 1994). This hypothesis is strengthened by the results of part b of the competition, showing that the A males could mate successfully when the JA adult males were not present. One lesson learned from past work in our lab, however, has been that the role of the female should not be ignored. It is possible that females preferred the more vigorous courters, in turn stimulating courting from the males. Females could perhaps have preferred JA adults over A adults, but preferred A adults over JA juveniles. Because we were interested in effects on the entire system of mating related behaviour, we tested the birds in groups. Isolating social effects on inter and intra sexual interactions will be the topic of future studies.

On the second hypothesis, the males in the two conditions engaged in patterns of reproductive behaviour along different timeframes. Although the differences before the mating competency test were not pronounced, they revealed differences in the timing of social interactions in the two conditions. In the A condition, females were more visible and more interactive with

males throughout the year. Females associated more with A males (Fig. 2a) and approached singing A males frequently (Fig. 3), a behaviour almost unseen in the JA condition. By the spring, A adult males were pairing up with their consorts and not singing as much overall to females (Fig. 2b), and were associating (Fig. 1a) and singing less with other males (Fig. 1b). In the JA condition, males were still aggregating in competitive interactions and were singing more to females later into the breeding season. This suggests the possibility that JA adults were more likely to be ready to compete and court later in the breeding season, the time at which we conducted the mating competency test. In future tests we will conduct mating competency tests at other times of the breeding season to test this hypothesis.

Finally, the JA adult males might have become more adept at dealing with a change in the social environment due to juvenile male influence. Over the year, juvenile males changed dramatically their plumage, song potency, song repertories and the ways they used their songs (White *et al.*, in press). These differences may have provided adults with challenges to the social order of the group, requiring more intrasexual interactions later into the breeding season to navigate fluctuating relationships within the group. When placed into the mating competition test, these adults were prepared once again to deal with another change in the social environment. A adults in comparison lived in a stable environment where the social relationships within the group changed little over time. Thus when these males were placed into a new social environment, they were at a disadvantage to the JA adults. Further study of fluctuating versus stable social environments will determine whether social change can mediate mating competence.

One difficulty in determining the mechanisms of effect on adult male behaviour is the difference in numbers of males in each condition. We created groups with equal sex ratios and equal densities. Unfortunately, as a consequence, adult males in the two conditions had different numbers of peers with which to interact. It is possible that living in a social group containing more adults requires more competition among males and by the mating competency test the A males were exhausted. There were no measures, however, that showed on a per male basis that A males engaged in more competition than JA males.

Another potential difficulty in determining the mechanism of effect in this study is the possibility that there was another unmeasured variable controlling the differences in male behaviour that has nothing to do with

the juvenile males or influencing adult male development. An independent replicate of the A condition (King *et al.*, in press) and a study examining a group of birds in a social composition similar to the JA condition (Smith *et al.*, 2002) revealed similar patterns of behaviour as the ones provided here both before and into the breeding season, including patterns of male-male and male-female interactions and female approaches. We have not at this point replicated the mating competency effect.

Whatever the mechanism may be, the consequences are clear. Adult males in the two conditions systematically differed in their competency. The implications of the observed patterns are twofold. First, mating success must be considered in relation to the social group in which it is observed. Here, the correlates of mating success in one group were not the correlates of success in another social group (song potency for example). Comparison of the males only in their home conditions would have resulted in a conclusion that the two groups of adult males had similar abilities. Furthermore, an individual's success in one social environment was not predictive of that individual's success in another social environment. For example, the male that received the fewest copulations (7 copulations) in the JA condition in the breeding season phase of the experiment out competed the A male that received the overall greatest number of copulations in the breeding season phase (58 copulations). Also, measures of relative success in the breeding season did not correlate with relative success in the mating competition, while the power of these correlations was limited, no trends or patterns emerged (correlations ranged from −0.67 to 0.89). We suggest that mating success must be considered as conditional to the social environment and caution should be taken when attempting to determine general phenotypic correlates of mating success from one social group.

The second implication of this work is that into adulthood there is significant malleability in the development of functionally important behaviour. Currently in most research in learning and development, plasticity of adult behaviour has been understudied. This is especially important considering that in many species the most significant contributions to an individual's reproductive success occur in adulthood (Clutton-Brock, 1988).

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