

Do juvenile males affect adult males' reproductive success in brown-headed cowbirds (*Molothrus ater*)?

Julie Gros-Louis^{1,2}, David J. White³, Andrew P. King¹
& Meredith J. West¹

(¹ Department of Psychological and Brain Sciences, Indiana University;

³ Department of Psychology, University of Pennsylvania)

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Summary

The present study was motivated by a recent anomalous finding between individual competitive performance and reproductive output in brown-headed cowbirds (*Molothrus ater*). White et al. (2002c) found that adult males who were housed with juveniles outcompeted adults who were housed with other adults when they were brought together to compete for mating opportunities. Although the males in groups that contained both juveniles and adults appeared to be better in securing reproductive opportunities, these groups were found to produce fewer eggs than groups with all adult males (White et al., 2002c). Because adult males were housed with juveniles, it was unclear whether the lower egg production was simply due to juveniles not reproducing or whether the adult males suffered decreased reproductive output. Is the presence of juvenile males advantageous to adult males or do they suffer reproductive consequences? In the current study, we studied four groups of captive cowbirds that differed only in the presence of juvenile males to determine what influence juvenile males have on adult male reproduction. At the end of the breeding season, we performed microsatellite parentage analysis on these four groups. Females in the two groups that contained juvenile and adult males produced fewer fertile eggs compared to females in the all-adult male aviaries. Furthermore, parentage analysis revealed that female reproductive patterns were similar in the two conditions, but females in the juvenile-adult aviaries produced fewer fertile eggs. Similarly, the males in the juvenile-adult aviaries showed a similar pattern of reproductive success as the males in the all-adult male aviaries, but had consistently lower reproductive output.

Keywords: cowbird, reproductive success, parentage analysis, countersinging

²) Corresponding author's address: Department of Psychological and Brain Sciences, 1101 E.10th St., Bloomington IN 47405, USA; e-mail address: jgroslou@indiana.edu

Introduction

Most research on social influences on development focuses on how young organisms acquire abilities to survive and reproduce in an environment containing knowledgeable adult conspecifics (Boyd & Richerson, 1985; Heyes & Galef, 1996; Avital & Jablonka, 2000). The advantages obtained by young individuals maturing in a group with experienced peers or adults are apparent. By contrast, researchers rarely investigate the possible influences of inexperienced individuals on adults. Furthermore, in the context of social learning, researchers rarely consider the relative reproductive consequences for individuals living in groups with experienced compared to inexperienced individuals (but see Laland & Williams, 1998). Groups with different age and sex ratios, thus different levels of experience, represent different environments in which individuals reproduce. These differences in group composition can influence behaviour, physiology, development, and even evolution (e.g., Lefebvre & Helder, 1997; Jarvis et al., 1999; Reader & Laland, 2000; Schwartz et al., 2001; King et al., 2003a, b; West-Eberhard, 2003).

Experimental social manipulations on captive flocks of brown-headed cowbirds (*Molothrus ater*) have revealed the effects of social environment on the development of reproductive behaviour in juveniles (White et al., 2002a, c, d; King et al., 2002). Wild populations of brown-headed cowbirds show variation in social environments within and between flocks analogous to those created experimentally (Friedmann, 1929; Ortega, 1998). Findings from wild populations also highlight the importance of social environment on vocal and social development (O'Loughlen & Rothstein, 1993, 2002). While the effects of experienced individuals on juveniles are not surprising, White et al. (2002c) also discovered that adult males benefit from living with inexperienced juveniles; juvenile males enhanced adult male courtship competency. White et al. (2002c) housed one group of adult males with females and juvenile males and one group of adult males with only females from the fall through the breeding season. The two groups of adult males then were brought together in the second half of the breeding season to assess their competence in courtship without juveniles present. Adult males who had been housed previously with juveniles dominated adult males who had been housed with peers. All four adult males from the juvenile-adult condition copulated, whereas only one of the four males who competed from the all-adult male condition did. Furthermore, the one male who was successful

from the all-adult condition was slower to copulate than the male from the juvenile-adult condition.

Male competition, however, may not tell the entire story about reproductive success. Although adult males from the mixed-class aviaries outcompeted males who had been housed with peers, egg production was lower in the mixed-class aviary than in the all-adult aviary (White, King & West, unpubl. data; see also West et al., 2002). Given the big difference in the number of adult males across conditions, it is unclear what this difference in egg production means. This finding, somewhat anomalous given males' differential courtship abilities, was consistent with the results from a number of studies in recent years: female egg production correlates highly with countersinging among males in a group (West et al., 2002; King et al., 2003b). Accordingly, White et al. (2002c) found that countersinging among males was much higher in the all-adult male condition compared to the juvenile-adult condition. Without parentage analysis, however, it was impossible to determine whether the production of fewer eggs in the juvenile-adult male aviary was due to non-reproducing juvenile males or lower reproductive success of adult males. If juvenile males were unsuccessful, the enhanced competitive abilities of adult males in the mixed-class aviaries may have led to increased reproductive success that was masked by the lack of reproduction by juvenile males. Alternatively, adult males in the two aviaries may have fertilized a comparable number of eggs, masked by lower reproduction of the juvenile males. Lastly, adult males in the mixed-class aviary may have had lower reproductive success than did adult males in the all-adult male aviary.

The purpose of the present study was to determine whether the positive effect of juvenile males on the competitive abilities of adult males translated into enhanced reproductive success. We predicted that females in the aviary with both juvenile and adult males would produce fewer eggs than females housed with only adults based on prior observations (West et al., 2002). In addition, we predicted that adult males housed with juvenile males would have higher reproductive success than adult males in all-adult aviaries. We manipulated experimentally the social environments of adult males, differing only in the presence of juveniles. We conducted the study over two consecutive breeding seasons to observe the same adult males in different social environments. By doing so, we controlled for individual abilities so that we could more accurately assess how the social environment influenced adult

male reproductive behaviour. We documented male countersinging behaviour, copulations, and the number of fertile eggs produced in each condition. Finally, we performed microsatellite parentage analysis on the four groups to determine the individual reproductive success of males in the different social environments.

Methods

Subjects

There were 81 wild-caught brown-headed cowbirds in the study: 21 adult males, 47 adult females and 13 juvenile males. All individuals were caught in Monroe County, IN. Adults had lived in mixed-sex groups in large outdoor aviaries for the year or two prior to the current study except five females who were caught during the spring of 2002 (three were housed in the all-adult male condition and two in the juvenile-adult male condition). Juveniles were caught during June and July of 2001 for the first year of the study (spring 2002) and a second group of juveniles was caught during June and July 2002 for the second year of the study (spring 2003). The age of the birds was determined at the time of capture based on their amount of mature plumage (Selander & Giller, 1960). Birds were individually identified with plastic coloured leg bands.

Housing

We housed birds in two large outdoor aviaries ($9.1 \times 21.4 \times 3.4$ m) containing grass, shrubs, indoor and outdoor perches and feeding stations. The aviaries were visually, but not completely acoustically, isolated from one another. The birds experienced weather conditions and could see and hear predators and wild conspecifics. Vitamin-treated water, a mixture of white millet, red millet and canary seed and a modified Bronx zoo diet for blackbirds was provided daily.

Procedure

In Year 1, Aviary 1 housed females with both juvenile and adult males (JA condition), whereas Aviary 2 housed females with adult males (A condition). To control for aviary-specific and individual effects, we counterbalanced

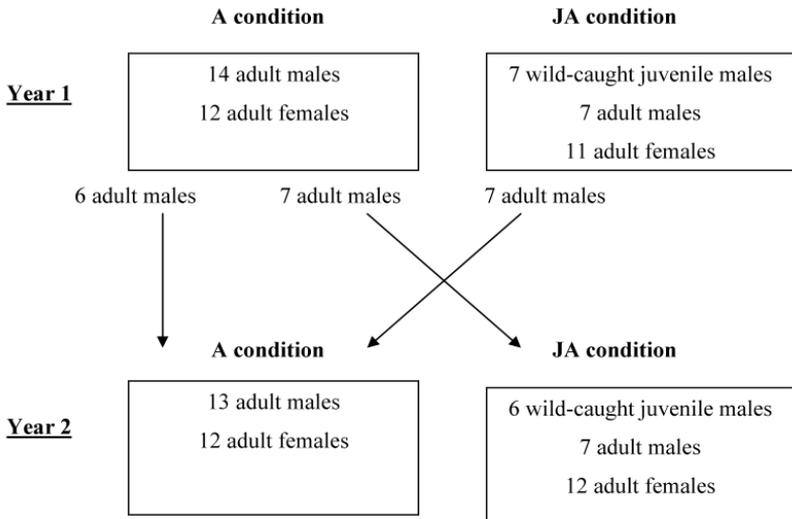


Figure 1. Schematic diagram of aviary configurations in Year 1 and Year 2.

males in the conditions in Year 2. Half of the males who were housed in the A condition in Year 1 were housed with six juveniles in the JA condition in Year 2. Six of the adult males from the A condition in Year 1 were housed with half of the adult males from the JA condition in Year 1, thus comprising the A condition for Year 2. All adult females used in Year 2 were different from those used in Year 1 (Figure 1).

In Year 1, there were 7 juvenile males, 7 adult males and 11 adult females in the JA condition and 14 adult males and 12 adult females in the A condition. In Year 2, there were 6 juvenile males, 7 adult males and 12 adult females in the JA condition and there were 13 adult males and 12 adult females in the A condition (Figure 1).

Data collection

Observers collected data in each aviary starting between 0700 and 0900. Observers collected two blocks of song data daily (see below). In both years, we collected data during the breeding season, between May 4 and late June. We collected 150 blocks of song data in Aviary 1 and 149 blocks of song data in Aviary 2 in Year 1. In Year 2, we collected 112 and 107 blocks of song data in Aviaries 1 and 2, respectively. Analyses are based on a total of 129.5 hr of data.

To document singing, we used the same method that we have used in past work (West et al., 2002; White et al., 2002a). Briefly, we documented all songs produced by males during 15-min sampling blocks. We recorded whether a song was undirected or directed. We noted the identity of the singer and recipient when a male sang a directed song, which we determined based on the orientation (0-45 degrees) and distance (within 60 cm) between the singer and song recipient.

We used directed song tallies to document males singing to females because male copulatory success correlates with female-directed singing (e.g., Hamilton et al., 1998; White et al., 2002c). In addition, we used directed song tallies to derive tallies of countersinging because countersinging is a subset of directed singing, occurring when a male responds to a song directed to him by another male. We programmed the database to determine whether or not a directed song was part of a countersinging bout. Two males were considered to countersing if each male sang at least one directed song to the other with no longer than 15 s elapsing between consecutive songs.

To record data, we used wireless lapel microphones (Telex WT 150; Telex Communications Ltd.) and voice recognition software (IBM ViaVoice Millennium, Pro Edition) loaded on a Pentium III 500-MHz IBM-compatible computer running Microsoft Windows 1998. Observers spoke the identities of the birds and behaviours into the microphone. A Telex FMR 150 receiver transmitted the vocal signal to the computer. Microsoft Word 2002 transcribed the incoming speech into text and each behavioural action was time-stamped. We exported the data into a database (4th Dimension v. 6.5.1; ACI Inc.) that we programmed to detect errors automatically (White et al., 2002b).

Reproductive and parentage analysis

We recorded copulations during morning data collection periods. To measure female reproductive output, we collected eggs throughout the breeding season. We placed 10 mock nests in each aviary. We made nests out of strainers that were 12 cm in diameter filled with grass clippings. Each nest contained three white yogurt-covered peanuts to serve as false eggs. Females removed the peanuts and deposited eggs in the mornings. We collected eggs at 0545 each morning and replaced eggs with peanuts. We changed the location of nests roughly once per week. We incubated intact eggs (Petersime Model 1 incubator: Petersime Incubator Co., Gettysburg, Ohio, USA). After 10 days

of incubation, we candled eggs to determine whether they had been fertilized.

For parentage analysis, we collected blood (50–100 μ l) from adults in the four aviaries by puncture of the brachial vein. We also extracted embryos from the fertilized eggs on day 10 of incubation. Blood and embryos were stored at -20°C until the DNA extraction was performed.

DNA was isolated from blood samples by organic solvent purification (Sambrook & Russel, 2001). Parentage was determined using four pairs of nuclear microsatellite markers, three of which (*Ma μ 20*, *Ma μ 25*, *Ma μ 29*) were developed for brown-headed cowbirds and one of which (*Dp μ 16*) was developed for yellow warblers (*Dendroica petechia*) (Alderson et al., 1999; Dawson et al., 1997). We used ABIPRISM 310 Genetic Analyzer (Applied Biosystems) to analyze amplified sequences of base pair loci. In addition, we determined heterozygosities and parentage using a likelihood-based approach in the Windows-based computer program CERVUS (version 2.0; Marshall et al., 1998; Slate et al., 2000).

All microsatellite loci were highly variable and averaged 21 alleles/locus. The observed number of heterozygotes did not differ from the expected number of heterozygotes for all four loci. Furthermore, the estimated occurrence of null alleles was also correspondingly low.

Data analysis

Due to small sample sizes and heterogeneity of variance between conditions, we performed non-parametric statistical analyses. We used Mann-Whitney *U*-tests for between-aviary comparisons. All tests are two-tailed, with significance levels of $p < 0.05$.

Results

The only difference in singing behaviour between and among males in the two conditions was found in levels of countersinging in Year 1: males in the all-adult aviary engaged in significantly more countersinging than did males in the mixed-class aviary. Adult males in the two conditions did not differ in their amount of countersinging in either year. Similarly, within the mixed-class aviary, juvenile and adult males did not differ in their amount

of countersinging. In addition, males in both conditions did not differ significantly in the number of songs that they directed to females in either year. Furthermore, males in the two conditions did not differ significantly in the number of copulations that they obtained. Nonetheless, in both years, females in the mixed-class aviaries produced fewer eggs than females in the aviaries that housed all adult males. Parentage analysis revealed that most of the females in each condition reproduced and similar reproductive patterns existed in both conditions; however, average egg production per female in the all-adult aviaries was more than twice as much as in the mixed-class aviaries. Adult males also showed a similar pattern of reproductive success in the two conditions, but adult males in the all-adult aviaries sired consistently more offspring.

Singing behaviour

Countersinging

Figure 2a summarizes countersinging interactions between males. There were more than two times as many countersinging interactions in the all-adult aviary in Year 1 and nearly twice as many in Year 2 (Year 1: 5834 vs 2611; Year 2: 3711 vs 2153). In Year 1, males in the A condition engaged in more countersinging than did males in the JA condition. This was a trend in Year 2 (Year 1: $U = 49$, $N_1 = 14$, $N_2 = 14$, $p < 0.03$; Year 2: $U = 47.5$, $N_1 = 13$, $N_2 = 13$, $p < 0.06$). When inspecting only adult male countersinging interactions in both conditions, although it appears as though there was more countersinging by adults in the A condition compared to adults in the JA condition, these differences were not significant due to wide variance in the data set (both U 's > 27 , both NS). Similarly, within the JA condition, juvenile and adult males did not differ significantly in their amount of countersinging in either year due to wide variance among juveniles and adults (both U 's > 8 , both NS).

Directed singing to females

Figure 2b summarizes directed singing by males. Males did not differ in the proportion of songs that they directed to females in the JA and A conditions in either year (both U 's > 51 , both NS). Furthermore, adult males in the JA and A conditions did not differ in the proportion of songs that they directed to females in either year (both U 's > 27 , both NS). Within the JA condition,

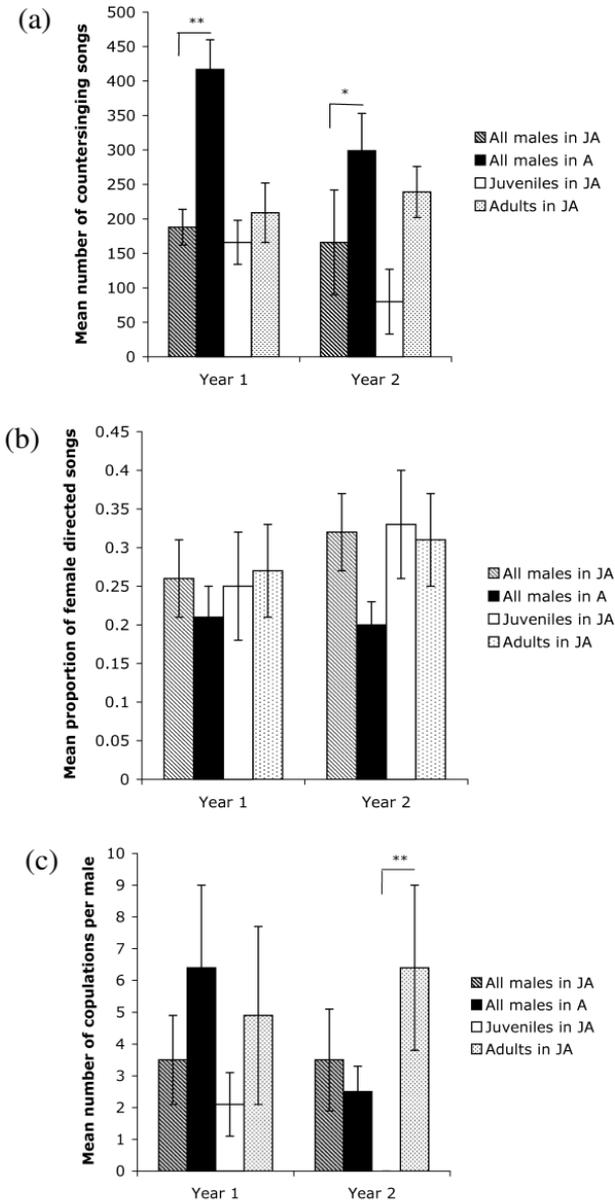


Figure 2. Means and SE's for measures of singing and reproductive behavior of males in the juvenile-adult and all-adult aviaries in Year 1 and Year 2. (a) Countersinging songs; (b) proportion of songs directed to females; and (c) copulations. J = juvenile males; A = adult males; JA = juvenile-adult condition; A = adult condition. * = $p < 0.06$; ** = $p < 0.04$.

juvenile and adult males did not differ in the proportion of songs that they directed to females in either year (both U 's > 10 , both NS).

Reproductive measures

Copulations

Figure 2c summarizes copulations by males. Males in the JA and A conditions did not differ in the number of copulations that they obtained in either year (both U 's > 77 , both NS). Similarly, adult males in the JA and A conditions did not differ in their copulatory success in either year (both U 's > 32 , both NS). Within the JA condition, adult males obtained more copulations than juvenile males in both years. In Year 1, however, juveniles and adults did not differ significantly in the number of copulations that they obtained due to wide variation in the number of copulations that adults received ($U = 22$, NS). In Year 2, adult males obtained significantly more copulations than did juvenile males, who were not observed copulating during data collection periods ($U = 9$, $N_1 = 6$, $N_2 = 7$, $p < 0.04$).

Egg production

We collected an average of 1.4 eggs per day (range 0-4) in the JA condition and 2.5 eggs per day in the A condition (range 0-7) in Year 1 and 1.3 eggs per day (range 0-4) in the JA condition and 1.5 eggs per day in the A condition (range 0-5) in Year 2. In both years, females produced fewer eggs, and fewer of which were fertile, in the JA condition compared to the A condition (Figures 3a & b).

Parentage

Females: Well over half of the females in both conditions reproduced (75-100%), except females in the mixed-class aviary in Year 1 (45%). All females reproduced in the all-adult aviary in Year 1 and all but one female reproduced in Year 2. In the mixed-class aviaries, 5 of 11 and 9 of 12 birds reproduced each year, respectively. Results of the parentage analysis demonstrated that females had similar patterns of reproductive success in the two aviaries (with the exception of one female in the all-adult aviary in Year 2 who produced over four times as many eggs as any other female in either year; Figures 4a, b); however, females in the A condition produced more

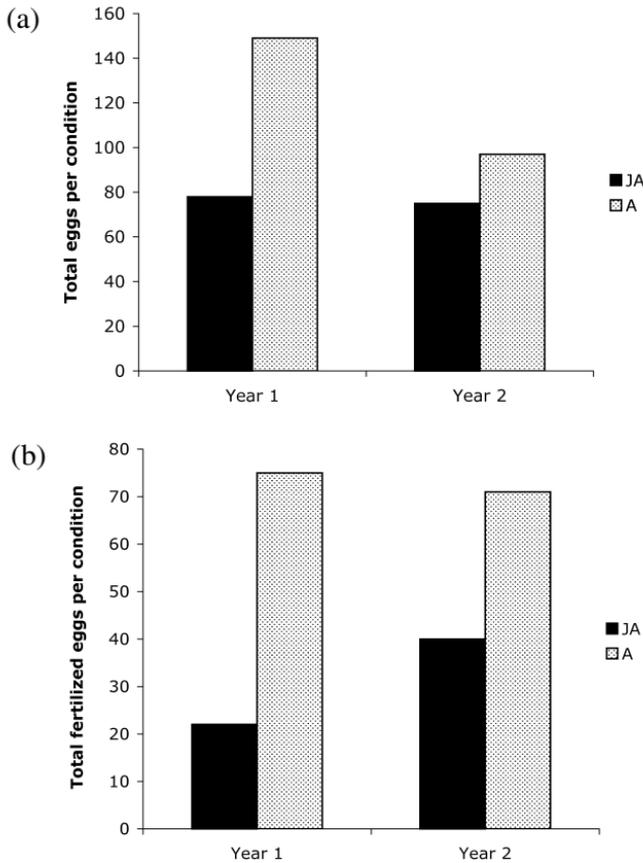


Figure 3. Egg production in the juvenile-adult and all adult aviaries in Year 1 and Year 2. (a) Total number of eggs produced and (b) total number of fertile eggs produced.

than twice as many eggs as did females in the mixed class aviary in both years (mean number of eggs per female, Year 1: 5.9 ± 1.7 vs 2.3 ± 1.2 ; Year 2: 4.9 ± 2.7 vs 2.3 ± 0.7).

Males: In each condition in both years, approximately half of the adult males reproduced. In the all-adult aviaries, 7 of 14 and 6 of 13 adults reproduced, while in the mixed-class aviaries, 4 of 7 and 3 of 7 adult males reproduced. Juvenile males did not reproduce in either year. Examination of the parentage data revealed a similar pattern of reproduction among males in an aviary, with one male in each condition outcompeting the others and a similar pattern of decreasing reproductive success across males within each condition. Due to the small number of adult males reproducing in the juvenile-

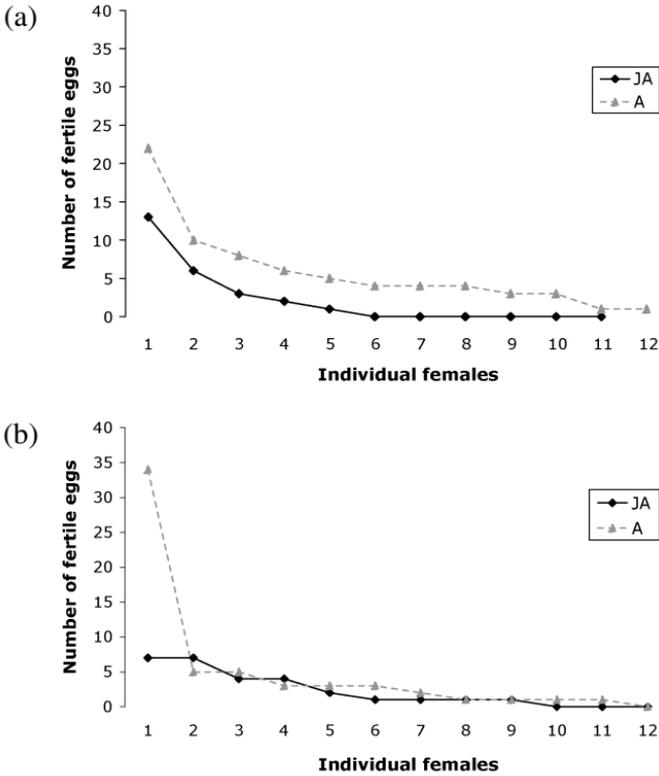


Figure 4. Individual female egg production in the juvenile-adult and all-adult aviaries based on parentage analysis in (a) Year 1 and (b) Year 2.

adult condition, statistical comparisons across conditions were not possible. Nonetheless, males in the A condition generally reproduced more than did adult males in the JA condition (mean number of offspring sired per male, Year 1: 7.5 ± 3.8 vs 0.14 ± 0.14 ; Year 2: 7 ± 5.3 vs 4 ± 1.8 ; Figure 5a, b).

Discussion

This study was designed to test the prediction that adult males accrue a reproductive advantage by living in groups that contain juvenile males, given the previous finding that males housed with juveniles exhibit superior competitive skills (White et al., 2002c). By configuring aviaries differing only in the presence of juveniles in two different years, we found that the presence of juvenile males in an aviary had a negative effect on female reproductive

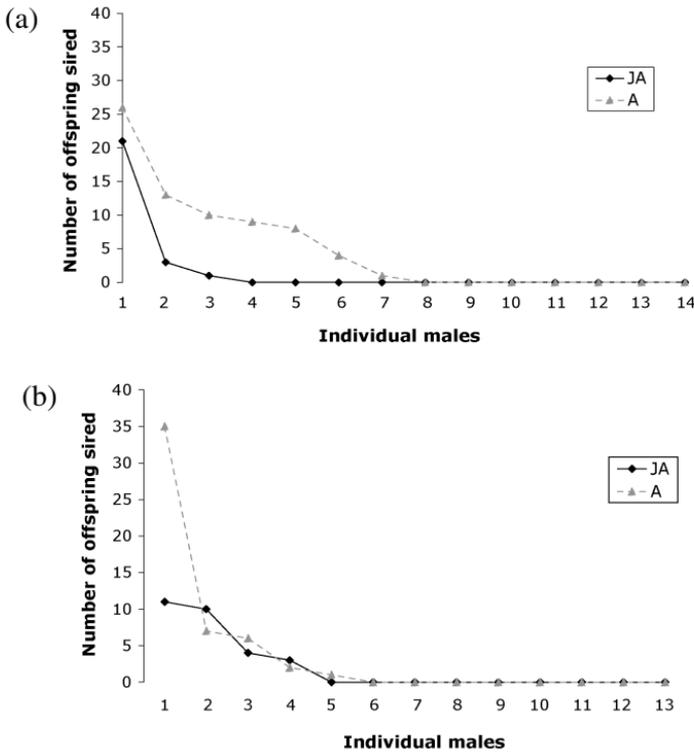


Figure 5. Individual male reproductive output for the juvenile-adult and all-adult aviaries based on parentage analysis in (a) Year 1 and (b) Year 2.

output. Egg production was lower in the aviaries that housed females with juvenile and adult males compared to the aviaries that contained all adult males. Parentage analysis indicated that most females reproduced in both conditions and exhibited similar reproductive patterns between aviaries. The egg production difference appeared to be due to overall decreased reproduction by females in the mixed-class aviaries. In addition, although reproductive output patterns were similar across males within each condition, adult males housed with juveniles had lower reproductive success than adult males housed with peers.

The difference in reproductive success between adult males in the juvenile-adult and all-adult aviaries was not due to differences in individual adult male behaviour in the two conditions. Adult males were equally successful in obtaining copulations in the mixed-class aviaries. Furthermore, adult males in the two conditions did not differ in the number of songs that they directed

to females, which has been shown previously to correlate with reproductive success (Freeberg, 1996). The presence of juveniles in a group with adult males appears to decrease the effectiveness of female reproductive stimulation.

Why does the mix of juvenile and adult males appear to ‘dilute’ female reproductive stimulation? We propose that the social chemistry that results from interactions within a group affects reproductive stimulation. One type of interaction that may vary relative to the social makeup of the group is countersinging. Countersinging is an important aspect of social interaction among male cowbirds and increases during the breeding season. We had a hint from previous observations that countersinging influences female egg production because a correlation exists in the amount of countersinging and egg production in an aviary (West et al., 2002; King et al., 2003b). In the current study, there were fewer countersinging interactions in the mixed-class aviary, significantly so in Year 1 and marginally so in Year 2, and females had lower reproductive output. In addition, the relative difference in the number of fertile eggs produced in the JA and A conditions in Year 1 was more than in Year 2, mirroring a larger difference in overall countersinging between the two conditions in Year 1 compared to Year 2.

Given that juvenile males must learn to countersing, and one way to learn how to countersing is from adult males, it is possible that inexperienced juveniles may interfere with adult males’ ability to countersing (White et al., 2002d). Juvenile males, through the process of learning how to countersing, may disrupt or prevent typical singing interactions among adult males. A second possibility is that juvenile males, in addition to differing in age and abilities, were less accustomed to living in captivity than were adult males who had spent nearly two years or more in large aviaries. However, the juveniles were caught the summer before the study and thus had spent most of their lives in the aviaries (10-11 months). In addition, observations from a study during the following year indicate that differential experience with living in captivity is unlikely to account for the results of this study. Juvenile and adult males were caught about six weeks prior to the breeding season in the following year at the same time of year that the social composition of the aviaries were configured for this study. The new wild-caught males were placed in different social housing conditions with birds who had been living in aviaries for months to years. The behaviour of the new males was indistinguishable from the behaviour of the resident males. Juveniles were

poor countersingers whether they were recently caught or caught the year before. In addition, adult males, both resident and newly caught, were better countersingers than juveniles. And, in fact, some of the newly caught adult males were the best countersingers of the breeding season.

Why would countersinging influence female egg production? Studies in a number of species indicate that females vary investment in eggs relative to the attractiveness or quality of males (see Sheldon, 2000 for an overview). We propose that countersinging may provide a way for females to assess male quality. Unlike song exchanges by songbirds on neighbouring territories (e.g., Horn & Falls, 1988), countersinging between male cowbirds occurs in close proximity. Two males perched within inches of one another exchange songs, accompanied by wing spread displays and bows in rapid succession. Thus, in an environment with less countersinging, females have fewer opportunities to assess males. If females are constrained in their mate selection and must make suboptimal choices, they may invest less in current clutches to await future reproductive opportunities (Gil et al., 2004). It has been found that females lay smaller clutches when paired with undesirable males (e.g., Reyer et al., 1999). Similarly, females lay larger clutches when paired with more attractive males (e.g., Petrie & Williams, 1993; Balzer & Williams, 1998). A recent study in lesser black-backed gulls (*Larus fuscus*) shows that maternal investment in egg content can vary with intraspecific interactions (Verboven et al., 2005). We propose that female cowbirds may control clutch size relative to levels of countersinging interactions among males.

The findings from this study, in light of those from White et al. (2002c), demonstrate that juveniles have two opposing effects on adult male reproductive behaviour. White et al. documented that adult males who had lived with juveniles subsequently outcompeted adult males who had lived with peers, thus indicating that juvenile males can enhance adult males' individual competitive abilities. An apparently inconsistent consequence of living with juveniles, however, is lower reproductive success due to lower female reproductive output. Therefore, although it appears that adult males would do best to avoid flocks with juvenile males, adults may benefit from living with juveniles in certain environments. Juvenile male behaviour is more variable than adult male behaviour and the unpredictability of juveniles may prepare adults to be more adaptable to changing social environments (White et al.,

2002c). Increased competitiveness of adult males would be advantageous in unstable environments.

The broader finding from the parentage data, when considered with the results from White et al. (2002c), demonstrates the multivariate nature of reproductive success. Reproductive success is not related to individual characteristics in a linear, stable fashion. Males may have certain individual traits that would be considered successful for reproduction if considered without observing males in the context of a social group (such as song potency). As a result of being in a particular group, however, males with good individual qualities are limited in their reproductive potential by their social environment. For example, males gain enhanced competitive abilities from living with juveniles (White et al., 2002c). Although these abilities are clearly important for males to outcompete other males to gain access to females, copulatory success alone is not sufficient for reproductive success. Males who direct more songs to females and who live in social environments with high levels of countersinging accrue greater reproductive success (White et al., 2002d). In the current study, although different social conditions did not affect males' production of female-directed song, overall levels of countersinging were higher in the all-adult male aviaries. Adult males reproduced more in these aviaries, thus countersinging thus appears to contribute to a male's reproductive success; however, countersinging is not an individual trait. Countersinging is dependent on interactions among males in the group environment. Therefore, individual reproductive success should be considered to be a product of both individual abilities and the social environment (cf Avital & Jablonka, 2000).

The results of this study provide evidence for how a social environment influences the reproductive behaviour and output of individuals in a group. The groups that we studied represent natural variation in the social ecology of cowbirds. In some populations young cowbirds may not associate with adults in their first year, while in other populations juveniles may join adults at the end of the breeding season and remain with them throughout the year (O'Loughlen & Rothstein, 1993). Furthermore, because adults and juveniles may migrate different distances, winter flocks could differ in age and sex composition (Cristol et al., 1999). The results of this study suggest that flocks containing juveniles may have different behavioural patterns than flocks without juveniles and these differences may have reproductive consequences. Similarly, the presence or absence of adults in flocks can influence juvenile reproductive behaviour (e.g., Freeberg et al., 2001).

Given that there is a close relationship among the social composition of groups, individual trait expression and the effectiveness of particular traits on mating success, future studies should try to understand the role of social environment on reproductive success. Studies should focus on determining both the proximate influences of group composition on behavioural variation and, in turn, the effectiveness of behavioural traits across social environments. Such research on both the causes and consequences of behavioural variation will result in a better understanding of the interrelated effects of individual variables and the social environment on individual reproductive success.

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