



ARTICLES

Female proximity stimulates development of male competition in juvenile brown-headed cowbirds, *Molothrus ater*

ANDREW P. KING, DAVID J. WHITE & MEREDITH J. WEST

Department of Psychology, Indiana University

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We investigated how individual variation in social behaviour among group members interacts to affect social structure and development of reproductive skills. We randomly assigned juvenile male and juvenile and adult female cowbirds to four aviaries and observed patterns of singing and social assortment in each. Although social composition of each aviary was the same, juvenile males in one aviary engaged in more intra- and intersexual affiliation and singing interactions. We designed a series of rotations of individuals among the aviaries to determine which individual traits were responsible for the observed group differences. First, we rotated groups of three males from a less interactive aviary into a more interactive aviary, replacing interactive males. Within 4 days, the rotated males changed their behaviour to match the aviary into which they had been moved (i.e. interactive males became less interactive and vice versa). Next, we rotated juvenile females through the aviaries. After this rotation, the behaviour of the juvenile females remained the same, but the behaviour of the resident males changed, becoming like the males in the females' former aviaries (i.e. when juvenile females were moved from an interactive aviary into a noninteractive aviary, the males in the new aviary became more interactive and vice versa). Across the aviaries, the amount of female–male associations correlated positively with male–male competition. During the breeding season, males that had experienced more competition over the year received more copulations than males that had experienced little competition. Furthermore, more eggs were produced in aviaries containing competitive males than in aviaries containing less competitive males. Past work has shown that females can influence male vocal development; here we show that they can also influence male social development.

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Social environments have fundamental influences on behaviour, physiology, development, gene expression and evolution (West-Eberhard 1983; Gottlieb 1991; Heyes & Galef 1996; Snowdon & Hausberger 1997; Jarvis et al. 1999; Fernald & White 2000; Agrawal et al. 2001). Although a social environment can serve as a source of natural and sexual selection (West-Eberhard 1983), selection itself acts on the individual. Thus, to understand group processes requires understanding the reciprocal relationship between the effects of social environments on individuals and how patterns of behaviour of individuals interact to produce social environments.

Correspondence and present address: D. J. White, Department of Psychology, University of Pennsylvania, 3815 Walnut Street, Philadelphia, PA 19104, U.S.A. (email: whitedj@psych.upenn.edu). A. P. King and M. J. West are at the Department of Psychology, Indiana University, 1101 E. 10th Street, Bloomington, IN 47405, U.S.A.

We have used brown-headed cowbirds, *Molothrus ater*, to investigate effects of group composition on social learning and development. We have documented different trajectories for the ontogeny of reproductive skills of cowbirds exposed in group settings to birds with different patterns of social behaviour. Work in the laboratory has manipulated groups by introducing birds of different species (Freeberg et al. 1995; West et al. 1996), distant populations (Freeberg 1998; Freeberg et al. 1999) and different age classes (Smith et al. 2002; West et al. 2002; White et al. 2002a, c, d).

One of the major insights emerging from studying groups has been that the acquisition of social information, in contrast to the processing of social information, has consequences for development of effective behaviour. Behaviour patterns of individuals within a group interact to create different social environments in which different opportunities to learn can emerge. For

example, we have found that opportunities to learn effective breeding behaviour for juvenile males are influenced by the presence of adult males in the social group. We reared juvenile males with females and either with adult males (Juvenile male–Adult male, JA, condition) or without adult males (Juvenile male, J, condition; White et al. 2002c). Juvenile males in the J condition associated and interacted with other juveniles and with females significantly less than did juvenile males in the JA condition. J juveniles engaged in long bouts of undirected singing throughout the year, whereas JA juveniles engaged in more directed singing with other males and with females. In the breeding season, J juveniles were less competitive and less aggressive with other males in the breeding season than were JA juveniles. J juveniles did, however, produce more effective breeding season songs and developed them more rapidly than JA juveniles. This difference in song development is consistent with past work showing that males isolated from male–male competition develop highly effective courtship song (King & West 1977). In summary, the presence of adult males produced a social environment conducive to learning about male competition (see also White et al. 2002a). There was no single experience that could account for the differences between groups. Rather, a cascade of effects involving social affiliations and song use occurring throughout the birds' first year propelled the two groups along different developmental trajectories. However, because the birds were maintained in the same conditions throughout most of a year, it was impossible to determine how quickly these cascades occurred or how resilient they were to changes to the social environment.

Also, because both groups of juvenile males copulated, it was unclear which strategy, either being competitive or not competitive, was more successful. We had some evidence from females, however, suggesting that the competitive strategy was more effective. Female egg production correlated with contact with competitive males (West et al. 2002). Females housed with competitive (JA) juvenile males produced more fertile eggs than did females housed with noncompetitive (J) juvenile males. In another group composed of adult males and females, adult males engaged in more competition with other males than did males in the other two groups, and females in this group approached singing males and affiliated with males more often than did females in the other groups. In the breeding season, these females laid more eggs than the females in the other two groups and produced more fertile eggs than the other two groups combined. If male competition produces an environment where females lay more eggs, then learning to engage in male–male singing interactions would be important for juvenile males in order to stimulate the females within the group.

Past work established that there is significant malleability in development of reproductive skills in brown-headed cowbirds that is influenced by social group composition. The next step was to determine the particular behaviours of individuals that caused the cascades of effects producing such different social environments. Cowbirds have a considerable number of social behav-

iours that they use in communication. The best documented communication signals are flight whistles and songs produced by males. Flight whistles are most often given while moving in response to disturbances such as predators, while following certain individuals, during courtship (in close association with songs), and also when taking off and landing (Rothstein et al. 1986). Males use songs in competitive interactions with one another to establish dominance hierarchies (Dufty 1986) and also to sing to females in the breeding season to elicit females' copulation solicitation displays.

Females also have social signals, to which males pay considerable attention. Female social reactivity does not revolve around vocalizing, as females do not sing. Instead of singing, females can respond to male songs with very rapid gestures, such as flicks of the wing (wing strokes) or gapes, that can only be measured with the aid of frame-by-frame videography (West & King 1988; M. J. West, A. P. King & M. H. Goldstein, unpublished data). These signals are low-frequency events, occurring 7% of the time to male vocalizations. The most common signals used by females appear to centre on physical regulation of proximity to males and other females. In general, males approach females, but females rarely approach males. Physical approach by the female is one of the only behaviours that can be observed in real time indicating conspicuous interest or tolerance of proximity of males. In past work in aviaries we documented females approaching singing males in conditions where all the males were adult. When juvenile males were present, females rarely approached singing males (West et al. 2002).

We know much about these signals from studies of pairs or trios of individuals in confined enclosures. However, we know little about how these signals combine when birds interact in larger groups in more natural environments. Here, we investigated what social signals males and females use and what consequences these signals have at the group level to foster social behaviour and social learning. We began by creating four independent replicates of the J condition used in White et al. (2002c). This was the condition where juvenile males engaged in few social interactions, and consequently where few opportunities for social learning emerged. In the wild, cowbirds experience wide variation in social composition of flocks, including situations where juveniles do not come in contact with adult males for extended periods (Friedmann 1929; O'Loghlen & Rothstein 1993). Thus, although the aviary setting cannot be considered analogous to natural conditions, the social composition of the groups in this experiment can occur naturally for at least some parts of a year.

We documented variation in behaviour of individuals across the four conditions and then moved individuals with specific characteristics in and out of the groups (for example, males that engaged in high levels of directed singing or females that approached males frequently) to determine what characteristics of individuals served to promote social interactions and the development of competitive male behaviour and reproductive competency. Throughout the experiment, we documented

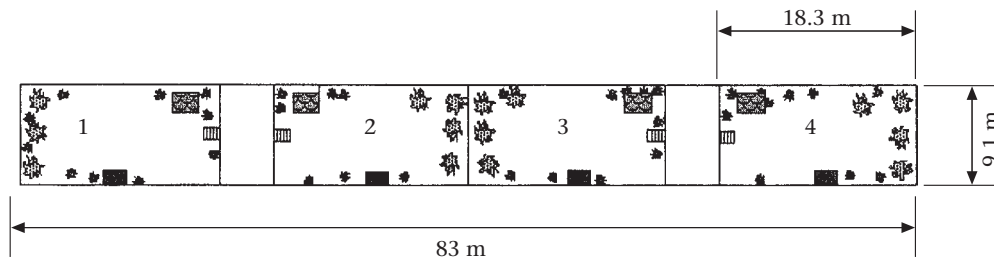


Figure 1. Scale overhead schematic of the aviary complex.

the processes of learning and development by measuring social affiliations and song use as well as outcomes of learning and development in the breeding season by measuring copulations, egg production and song quality. This allowed us to determine the dependence or independence of individuals' traits on the social environment in which they were expressed and how those traits influenced others in the groups. Thus, we could examine not only how group composition influenced the development of individuals' behaviour, but also how variation in the behaviour of individuals interacted to produce differences in groups.

GENERAL METHODS

Subjects

We captured 40 juvenile male, 14 juvenile female and 28 adult female brown-headed cowbirds from two trapping locations approximately 15 km apart in Monroe County, Indiana, U.S.A. We aged and sexed birds at capture based on the amount and coloration of adult plumage that had emerged (Selander & Giller 1960). Juvenile birds (approximately 30–50 days of age at capture) had not experienced a breeding season, whereas adults had experienced at least one breeding season. Before the experiment, birds participated in an early experience experiment in aviaries where half received brief exposure (4–28 days) to adult males and females in July and August (see White et al. 2002a). Prior to this, all juveniles had at least some experience with adult cowbirds, because they were caught in our traps with adults. We randomly assigned birds to four large aviaries in September 2000 in the following numbers: 10 juvenile males, seven adult females, and either three (aviaries 1 and 2) or four (aviaries 3 and 4) juvenile females. Throughout the experiment we found no systematic differences between birds that had been exposed to adults and those that had not been exposed to adults during the summer experiment. Across the entire experiment, two juvenile males from aviary 4, one juvenile male from aviary 3 and one adult female from each aviary died. We removed one juvenile male from aviary 2 during the breeding season because of injury.

The aviaries were large outdoor enclosures measuring $9.1 \times 20.75 \times 3.4$ m (see Fig. 1). Aviaries 2 and 3 were divided by wire mesh and only partially occluded by trees and wood. Thus, the birds in these two aviaries could see

and hear each other. Aviaries 1 and 4 were separated by sheds and thus were visually but not completely acoustically isolated from the other aviaries. All aviaries contained trees, perches, grass, indoor shelters and food stations. Being outside, birds were exposed to weather conditions, the sight of predators and wild cowbirds. We provided birds daily with vitamin-treated water, white and red millet, canary seed and a modified Bronx zoo diet for blackbirds *ad libitum*.

Measures

We documented social assortment by sampling near-neighbour associations, following procedures we have used previously (Smith et al. 2002; West et al. 2002; White et al. 2002a, c, d). In the past, we have used near-neighbour patterns as a diagnostic measure of the amount and pattern of social behaviour occurring in groups. These measures for individuals have correlated with developmental effects on mating and singing competence (Smith et al. 2002; White et al. 2002c). To measure near-neighbour associations, we scanned all birds in each aviary during 15-min sampling blocks between 0700 and 0800 hours each day, and noted any bird within 30 cm of any other bird. Associations could only be sampled once. Birds had to move apart and reassociate to be recorded as another association. We sampled as many near-neighbour associations as we could for the block.

We also documented male vocalization patterns in the four aviaries. Song censuses consisted of 15-min blocks in which observers used *ad libitum* sampling (Altmann 1974) to document 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 towards a recipient, oriented at no greater than a 45° angle off-axis from the recipient. The distance between the vocalizing bird and the recipient could not exceed 60 cm. We considered vocalizations produced that were not oriented to another bird as undirected. We recorded a soliloquy from any bird that produced 10 consecutive undirected vocalizations within approximately 1 min. Once a bird sang a soliloquy, we did not record any more undirected vocalizations from him for the duration of the census block. During song censuses, we scored an approach whenever a female moved to within 30 cm of a singing male.

We used voice recognition to record all observations. We spoke birds' leg band acronyms, behavioural codes and preprogrammed macros into a wireless microphone

Table 1. Assortment and singing patterns in autumn and winter

Aviary	NN _{males}	NN _{females}	PD	D _{males}	D _{females}	UD	Approach
Autumn							
1	4.95	0.75	0.27	27.55	5.09	78.91	0
	0.34	0.11	0.03	5.92	1.63	10.56	
2	2.20	0.11	0.26	14.80	0.90	55.10	0
	0.32	0.03	0.02	3.42	0.41	9.79	
3	7.33	1.97	0.24	30.60	9.30	121.50	0
	0.71	0.74	0.03	8.71	4.78	19.38	
4	4.31	0.58	0.23	15.60	5.70	64.20	0
	0.22	0.09	0.02	4.25	2.15	10.41	
	$H_3=20.97$	$H_3=23.47$	NS	NS	NS	$H_3=10.49$	NS
	$P<0.001$	$P<0.001$				$P<0.025$	
Winter							
1	2.20	0.17	0.36	69.91	3.82	133.82	0
	0.20	0.07	0.03	6.59	1.00	10.88	
2	5.04	0.26	0.36	77.90	2.60	169.30	0
	0.33	0.03	0.04	13.22	0.67	20.61	
3	3.77	0.93	0.56	98.44	23.00	93.22	8
	0.36	0.33	0.06	18.28	9.80	18.93	
4	3.51	0.62	0.29	92.20	5.80	175.70	0
	0.56	0.14	0.06	24.25	1.80	27.14	
	$H_3=17.48$	$H_3=12.99$	$H_3=8.30$	NS	$H_3=9.2$	NS	$H_3=12.73$
	$P<0.001$	$P<0.005$	$P<0.002$		$P<0.025$		$P<0.005$

Values are means±SE per male for the four aviaries for the autumn and winter samples. NN_{males}: near-neighbour associations per male with other males; NN_{females}: near-neighbour associations per male with females; PD: proportion of total song produced that was directed; D_{males}: songs directed to other males; D_{females}: songs directed to females; UD: undirected song; Approach: approaches to singing males by juvenile females. Numbers in bold represent a significant difference across aviaries.

and receiver system (Telex WT 150 & Telex FMR 150; Telex Communications Ltd, Burnsville, Minnesota, U.S.A.). The sound was transcribed to text using IBM voice recognition software (Millennium Pro Edition) in Microsoft Word 2000 running on a PC compatible computer (Compaq Deskpro EP, Pentium 3, 500 MHz). The text was then downloaded into a database (4th Dimension v. 6.5.1; ACI Inc., San Jose, California, U.S.A.) that we programmed to check for errors, organize the data and summarize results automatically (White et al. 2002b).

Interobserver reliability, based on sample data from 10 males, was high for song census measures of mean number of songs per male (Pearson correlation: $r_9=0.98$, $P<0.001$) and for near-neighbour associations per bird ($r_9=0.87$, $P<0.005$).

PHASE 1: DOCUMENTING VARIATION

We began by measuring the assortment and vocalizing patterns of birds in the four aviaries in two samples; one during autumn 2000 and one during winter 2001.

Procedure

Two observers sampled social assortment and singing patterns in each of the four aviaries in each sample session. Observers were never in the same aviary at the same time, but each observer sampled each aviary each day. We took 30 h of samples in both the autumn and winter sessions spanning 15 days in the autumn (15 September–1 October) and 23 days in the winter (17

February–11 March). For both the autumn and winter samples, we took 10 near-neighbour blocks and 20 song censuses.

Due to heterogeneity of variance in most measures (Levine test: $F_{3,3} \geq 4.36$ across comparisons, $P \leq 0.01$), inequality of covariance ($F_{3,34} \geq 5.142$, $P \leq 0.001$) and unequal sample sizes, we used nonparametric statistics throughout (although we report means and standard errors for descriptive purposes). We used Kruskal–Wallis analyses for each measure across the four groups, using a critical alpha of 0.025 to correct for multiple comparisons over the two seasons.

Results

Table 1 depicts assortment and singing patterns across the four aviaries for the autumn and winter samples. Aviary 3 emerged as significantly different from at least one other aviary on several measures including near-neighbour associations, directed and undirected singing and the proportion of total vocalizations directed to other birds (directed song/(directed+undirected song)). The only approaches we observed came from juvenile females in aviary 3 in the winter.

PHASE 2: MALE MANIPULATIONS

The patterns we had documented in the autumn and winter were similar to those we had seen in past work. Three of the aviaries replicated the patterns of behaviour of juvenile males housed without adult males that we

had seen the year before, characterized by little intra- or intersexual singing interactions or near-neighbour associations and more undirected singing (White et al. 2002c). However, juvenile males in aviary 3 unexpectedly behaved more like juvenile males housed with adult males, interacting more with members of both sexes. To determine which traits were responsible for the differences in this group's behaviour, we designed a series of manipulations in which we rotated individuals with particular traits among the aviaries.

First, we focused on the juvenile males in aviaries 2 and 3. We ranked them within their aviaries by their proportion of directed song sung during the winter sample in each aviary. We exchanged the top three directed-song-singing males from aviary 3 for the top three undirected-song-singing males from aviary 2. We then measured affiliation and singing in the two aviaries for 4 days (25 song censuses and 10 near-neighbour blocks; 13–16 March). Next, we rotated the next three highest directed- and undirected-song-singing males between aviaries 3 and 2, respectively (not including the males from the previous move) and resampled the aviaries for 4 days (21, 23–25 March). Finally, we exchanged the remaining four males from aviaries 2 and 3 and took 4 more days of data (26–29 March). Thus, by this final manipulation, all males that had initially been in aviary 3 were in aviary 2 and vice versa. We measured the change in a suite of behaviours that were related to social interactions. These behaviours included the proportion of directed song produced, amount of directed singing to males (male-directed song), amount of directed singing to females (female-directed song) and amount of near-neighbour associations with males and with females.

Results

Figure 2 depicts a diagram of the manipulations conducted throughout the experiment as well as the proportion of total vocalizations directed to other birds for the juvenile males in each aviary for each manipulation. For phase 2, the singing patterns in the aviaries did not change significantly as the males were rotated (Fig. 2b). After all three rounds of moves were completed (i.e. after all males had been rotated between aviaries 2 and 3), we compared the change in affiliation and singing for each male to their patterns from the sample immediately before their move. Males that were moved into the new aviaries significantly changed their song use and association patterns (Fig. 3). Males that were moved into aviary 2 from aviary 3 significantly decreased their proportion of directed song ($\bar{X} \pm \text{SE}$ decrease = 0.23 ± 0.06 songs per male; Wilcoxon matched-pairs signed-ranks test: $T=1$, $N=9$, $P<0.02$) and their amount of male-directed song ($\bar{X} \pm \text{SE}$ decrease = 70.11 ± 19.40 songs per male per sampling session; $T=1$, $N=9$, $P<0.02$), but not female-directed song ($\bar{X} \pm \text{SE}$ decrease = 17.78 ± 10.83 songs per male; $T=9$, $N=9$, NS). They also significantly decreased their amount of near-neighbour associations both with other males ($\bar{X} \pm \text{SE}$ decrease = 1.43 ± 0.36 associations per male; $T=0$, $N=9$, $P<0.01$) and with females ($\bar{X} \pm \text{SE}$ decrease = 1.02 ± 0.41 associations per female; $T=1$, $N=9$,

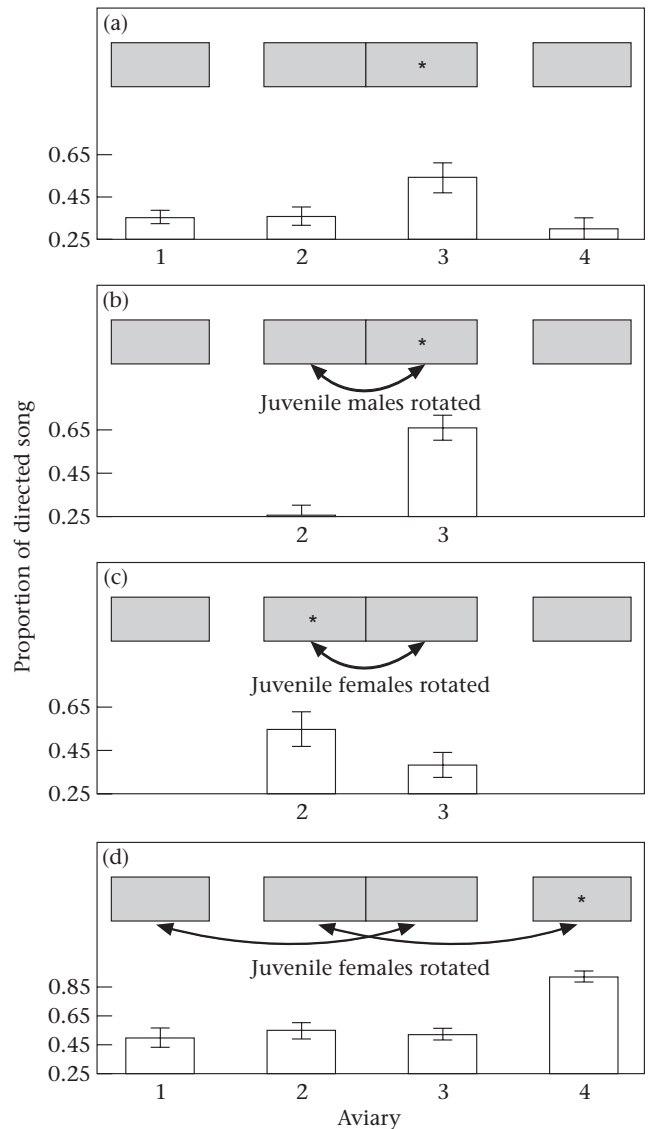


Figure 2. (a–d) Diagram of major manipulations throughout phases 1–4, respectively, and the corresponding mean \pm SE proportion of directed song produced per male in each aviary. *Aviary in which interactive females were housed during data collection.

$P<0.02$). Males that were moved from aviary 2 into aviary 3 significantly increased their proportion of directed song ($\bar{X} \pm \text{SE}$ increase = 0.20 ± 0.05 ; $T=0$, $N=10$, $P<0.005$) and their amount of male-directed song ($\bar{X} \pm \text{SE}$ increase = 64.2 ± 15.34 songs; $T=0$, $N=10$, $P<0.005$), but not their proportion of female-directed song ($\bar{X} \pm \text{SE}$ decrease = 1.2 ± 4.73 songs; $T=17$, $N=10$, NS). They also significantly increased their near-neighbour associations with females ($\bar{X} \pm \text{SE}$ increase = 0.68 ± 0.29 associations per female; $T=6$, $N=10$, $P<0.03$) and showed a similar tendency to increase their associations with males ($\bar{X} \pm \text{SE}$ increase = 0.80 ± 0.57 associations per male; $T=13$, $N=10$, $P=0.14$). Similar to the winter data sample, juvenile females in aviary 3 were the only juvenile females to approach singing males ($\bar{X} \pm \text{SE}$ = 2.06 ± 0.30 approaches per juvenile female per move). Across the rotations, we scored

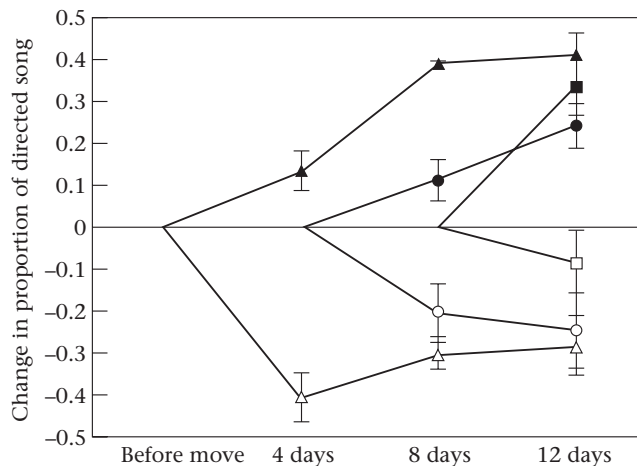


Figure 3. Change in the mean \pm SE proportion of directed song sung per male before aviary rotations and during 4-day periods beginning 4, 8 and 12 days after aviary rotations in phase 2. \triangle , \circ , \square : Highest directed-song-singing males rotated from aviary 3 to aviary 2; \blacktriangle , \bullet , \blacksquare : highest undirected-song-singing males rotated from aviary 2 to aviary 3.

five approaches from adult females, all of which occurred in aviary 3.

PHASE 3: FEMALE MANIPULATIONS

One hypothesis explaining the remarkably quick change in the singing and assortment patterns of the males that were rotated is that males matched their behaviour to the average behaviour of males in their environment. Alternatively, something else was contributing to the observed differences in aviaries 2 and 3.

One pronounced difference between aviaries was the behaviour of juvenile females. There was wide variation in near-neighbour associations among juvenile females with males across the aviaries. Furthermore, in the winter sample, the amount of male–female near-neighbour associations per aviary correlated positively with the proportion of directed song produced per aviary (Spearman rank correlation: $r_s=0.949$, $N=4$, $P=0.051$). Juvenile females in aviary 3 interacted more with the males, having more near-neighbour associations with males and approaching singing males more often than juvenile females in aviary 2. The difference in female affiliative behaviour could have been an effect of the different behaviour of the males or it could have been a cause of the differences in males' behaviour. We therefore exchanged the four juvenile females from aviary 3 (henceforth referred to as the 'interactive' females) with the juvenile females from aviary 2 and measured the changes in singing and assortment for 4 days (20 scan censuses and 10 near-neighbour samples; 30 March–2 April).

Results

After the juvenile females were rotated, males in the two aviaries reversed their singing and assortment pat-

terns (Fig. 2c). After the replacement of the interactive females, males in aviary 3 decreased their social activity, decreasing their proportion of directed song ($\bar{X} \pm \text{SE}$ decrease = 0.28 ± 0.04 ; $T=0$, $N=10$, $P<0.001$), male-directed song ($\bar{X} \pm \text{SE}$ decrease = 52.3 ± 20.65 songs; $T=5$, $N=10$, $P<0.025$), male near-neighbour associations ($\bar{X} \pm \text{SE}$ decrease = 2.08 ± 0.29 associations per male; $T=0$, $N=10$, $P<0.005$) and female near-neighbour associations ($\bar{X} \pm \text{SE}$ decrease = 0.83 ± 0.26 associations per female; $T=1.5$, $N=10$, $P<0.01$). They did not, however, significantly change levels of female-directed song ($\bar{X} \pm \text{SE}$ increase = 6.3 ± 4.34 songs; $T=11.5$, $N=10$, NS). When the interactive females were moved into aviary 2, the males there increased social activity, increasing their proportion of directed song ($\bar{X} \pm \text{SE}$ increase = 0.30 ± 0.05), their male-directed song ($\bar{X} \pm \text{SE}$ increase = 33.56 ± 11.66 songs; $T=3$, $N=9$, $P<0.021$), female-directed song ($\bar{X} \pm \text{SE}$ increase = 22.33 ± 5.30 songs; $T=0$, $N=9$, $P<0.01$), male near-neighbour associations ($\bar{X} \pm \text{SE}$ increase = 3.55 ± 0.47 associations per male) and female near-neighbour associations ($\bar{X} \pm \text{SE}$ increase = 3.02 ± 0.86 associations per female; all T s = 0, $N=9$, all P s < 0.01). The behaviour of the juvenile females did not change after they were moved. Interactive females approached males a mean of 2.25 ± 0.75 times per female before the move and 1.75 ± 0.75 times per female after the move. Juvenile females who moved from aviary 2 to aviary 3 never approached a singing male. After the manipulation, we scored five approaches from adult females; all of these approaches occurred in aviary 2.

PHASE 4: ALL AVIARIES

The results of the previous two phases suggested that the juvenile females were influencing the males' behaviour. For phase 4, we added aviaries 1 and 4 to the manipulations as independent replicates. We took baseline data in all aviaries to characterize the degree of directed song and the nature of social assortment in the groups (10 song blocks and 10 near-neighbour blocks in aviaries 1 and 4, and five song blocks and 10 near-neighbour blocks in aviaries 2 and 3; 3–8 April). We then exchanged the interactive juvenile females from aviary 2 with the juvenile females from aviary 4. Similarly, we switched the juvenile females between aviaries 1 and 3. Immediately after each move we sampled all aviaries for 4 days (9–12 April) to document the changes in male social and vocal behaviour. We then waited 11 days and resampled the aviaries (23 April–4 May).

Results

Juvenile females from aviaries 1 and 4 had similar mean \pm SE baseline measures of near-neighbour associations with males (1.55 ± 0.24 and 1.13 ± 0.52 associations per male, respectively, over 10 sampling blocks), falling between those of juvenile females from aviaries 2 and 3 (4.36 ± 0.95 and 0.63 ± 0.43 associations per male, respectively, over 10 sampling blocks; Fig. 4). Baseline levels of the proportion of directed singing for males in

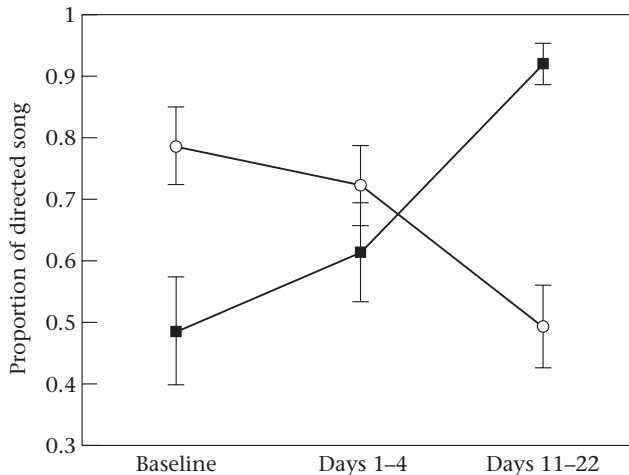


Figure 4. Mean \pm SE proportion of total song sung per male that was directed to other birds in aviaries 1 (○) and 4 (■) before juvenile females were rotated in phase 4 (baseline) and during the first and last sampling sessions after the manipulation (days 1–4 and 11–22, respectively).

aviary 4 were lower than those for males in aviary 1. After we rotated the juvenile females across aviaries, the changes in male singing patterns after the initial 4-day sample were marginal but became pronounced at the 11-day sample. Data from both samples are shown in Fig. 4, but for statistical purposes we compared baseline levels to the 11-day sample. Similar to the results from phase 3, when we moved the interactive females into a new aviary (aviary 4), the males in that aviary increased their social activity, increasing their proportion of directed singing ($\bar{X} \pm \text{SE}$ increase = 0.31 ± 0.06 ; Wilcoxon matched-pairs signed-ranks test: $T=0$, $N=8$, $P<0.02$) and their near-neighbour associations with males ($\bar{X} \pm \text{SE}$ increase = 3.96 ± 1.29 associations per male; $T=3$, $N=8$, $P<0.02$) but not their associations with females ($\bar{X} \pm \text{SE}$ decrease = 0.01 ± 0.52 associations per female; $T=25$, $N=8$, NS). When the juvenile females from aviary 3 replaced the juvenile females in aviary 1, the aviary 1 males decreased their proportion of directed singing ($\bar{X} \pm \text{SE}$ decrease = 0.26 ± 0.08 ; $T=5$, $N=10$, $P<0.05$) and their near-neighbour associations with males ($\bar{X} \pm \text{SE}$ decrease = 2.71 ± 0.18 associations per male; $T=0$, $N=10$, $P<0.005$) but not their associations with females ($\bar{X} \pm \text{SE}$ decrease = 0.31 ± 0.29 associations per female; $T=15$, $N=10$, NS).

Males in aviaries 2 and 3 continued along the trajectories from the previous manipulation in the baseline sample, with aviary 2 males singing a higher proportion of directed song than aviary 3 males (recall that during this baseline session, the interactive females were in aviary 2). After the juvenile females were replaced in aviaries 2 and 3 with the juvenile females from aviaries 4 and 1, respectively, males in aviary 3 increased their social activity, significantly increasing their proportion of directed singing ($\bar{X} \pm \text{SE}$ increase = 0.31 ± 0.05 ; $T=0$, $N=9$, $P<0.01$), directed songs to females ($\bar{X} \pm \text{SE}$ increase = 5.37 ± 1.95 songs; $T=0$, $N=9$, $P<0.01$) and directed songs to males ($\bar{X} \pm \text{SE}$ increase = 9.42 ± 3.42 songs; $T=4$, $N=9$, $P<0.05$). Aviary 2 males did not significantly decrease

their proportion of directed singing ($\bar{X} \pm \text{SE}$ decrease = 0.26 ± 0.11 ; $T=5$, $N=10$, NS) or the number of songs they sang to females ($\bar{X} \pm \text{SE}$ decrease = 0.13 ± 1.65 songs; $T=13$, $N=10$, NS) and they maintained their rates of directed singing to other males ($\bar{X} \pm \text{SE}$ increase = 14.02 ± 5.97 songs; $T=6$, $N=10$, NS). Males in aviary 2 also did not significantly decrease their near-neighbour associations with males ($\bar{X} \pm \text{SE}$ decrease = 0.47 ± 0.79 associations per male; $T=18$, $N=10$, NS) but did significantly decrease their associations with females ($\bar{X} \pm \text{SE}$ decrease = 2.75 ± 0.90 associations per female; $T=5$, $N=10$, $P<0.05$). Similar to the winter sample, in the 11-day sample, the correlation between female–male near-neighbour associations and the proportion of directed song per aviary was significant (Spearman rank correlation: $r_s=1.0$, $N=4$, $P<0.01$).

As the breeding season drew near, females began approaching males more often. After the manipulation, we scored female approaches in all aviaries. We scored one approach from a juvenile female and three approaches from an adult female in aviary 1, four approaches from an adult female in aviary 2, one approach from each of two juvenile females and four approaches from an adult female in aviary 3. In aviary 4, which held the interactive females, we scored 23 approaches; however, most approaches were from adult females (four approaches from one juvenile and 19 approaches from six adults).

PHASE 5: BREEDING SEASON

Thus far, in every aviary into which we moved the interactive juvenile females, males increased their intra-sexual interactions (see Fig. 2) and also, although less robustly, increased their intersexual interactions. We left the groups intact from the end of phase 4 into the breeding season to see whether the differences in social behaviour would have reproductive consequences. We sampled the four aviaries from 5 May (the day of the first observed copulation) until 15 June. We observed birds daily between 0600 and 1000 hours, the time when virtually all copulations occur (Rothstein et al. 1986). We sampled near-neighbour associations for 26 blocks. We also took 65 song censuses. During both types of samples, we recorded all copulations that we observed in aviaries and all fights that occurred. As a more sensitive measure of male–male singing interactions than overall levels of male-directed song, we measured the amount of countersinging in which males engaged. Countersinging occurs in the late spring and in the breeding season and is characterized by males singing back and forth to one another in directed song bouts. We programmed the database to calculate the amount of countersinging for each male from the directed song data. Countersinging bouts were recorded when two males sang to one another with no more than 15 s elapsing between directed songs.

To measure females' reproductive stimulation, we collected all eggs laid. We placed 10 nests in each aviary. We used as nests 12-cm-diameter strainers filled with grass clippings and three white, yogurt-covered peanuts. Females removed the peanuts and deposited their eggs in

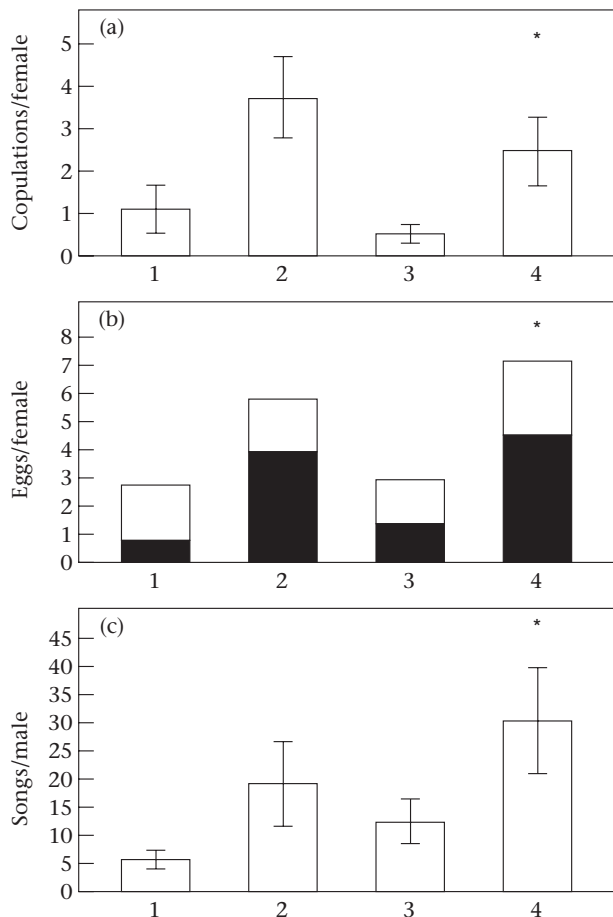


Figure 5. Breeding season patterns across the four aviaries. (a) Mean \pm SE copulations per female. (b) Mean eggs produced per female (mean fertile eggs produced per female inset). (c) Mean \pm SE number of songs sung in countersinging bouts per male. *Location of interactive females during the breeding season.

these nests each morning. At 0545 hours each day, we collected eggs and replaced any peanuts that had been removed. 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 the eggs to determine whether they had been fertilized.

Results

There was a significant difference in copulatory success across aviaries (Kruskal–Wallis test: $H_3=12.871$, $P<0.005$; Fig. 5a). More copulations occurred and more eggs were produced (3.9 and 4.3 times as many, respectively) in aviaries 2 and 4 than in aviaries 1 and 3 (Fig. 5b). In addition, females in aviaries 2 and 4 produced more fertilized eggs as a proportion of total eggs laid than did females in aviaries 1 and 3 (proportion fertile: aviary 2=0.67, aviary 4=0.62, aviary 1=0.28, aviary 3=0.45).

We tested whether the interactive juvenile females in aviary 4 received more copulations than other females. They did not. Across all aviaries, juvenile females received 22.4% of the copulations (juvenile females represented 36.8% of the female population in the aviaries). In aviary 4, the interactive juvenile females received 21.0% of the copulations in that aviary, with one of the juvenile females not copulating during the breeding season.

There were no significant differences across aviaries in total song produced (Kruskal–Wallis test: $H_3=0.065$), directed song produced ($H_3=1.66$), female-directed song produced ($H_3=1.75$) or male-directed song produced ($H_3=2.96$). There was a significant difference in undirected song across aviaries ($H_3=8.51$, $P<0.05$). Multiple comparison Mann–Whitney U tests (corrected for number of tests conducted) did not have power enough to reveal any differences between aviaries, although there was a tendency for males in aviary 1 to sing more undirected song than those in aviary 4 ($U=9$, $N_1=10$, $N_2=8$, $P=0.016$). There was a significant difference across aviaries in the proportion of directed song sung ($H_3=18.48$, $P<0.001$), with males in aviary 4 producing a significantly higher proportion of directed song than those in aviary 1 ($U=0$, $N_1=8$, $N_2=10$, $P<0.001$) or in aviary 3 ($U=2$, $N_1=8$, $N_2=10$, $P<0.001$). Aviary 2 males also had a higher proportion of directed song than males in aviaries 1 or 3, but not significantly higher (both $U>16$, $N_1=10$, $N_2=9$, NS). We scored more fights in aviary 4 ($\bar{X} \pm \text{SE}=5.88 \pm 1.99$ fights per male) and aviary 2 (3.11 ± 0.96) than in aviary 1 (1.6 ± 0.56) and aviary 3 (2.33 ± 0.95), but this difference was not significant ($H_3=5.83$, $P=0.12$).

There was a significant difference in the amount of countersinging across aviaries (Kruskal–Wallis test: $H_3=9.27$, $P<0.026$; Fig. 5c). Males in aviary 4 countersang significantly more than did males in aviary 1 (Mann–Whitney U test: $U=12$, $N_1=8$, $N_2=10$, $P<0.012$). No other countersinging differences across aviaries were significant.

PHASE 6: SONG ANALYSIS

Past work has shown that the song produced by juvenile males that experience more male–male competition is less effective at eliciting copulatory responses from females than is the song produced by juvenile males that experience less male competition (White et al. 2002c). However, in that study, the juvenile males that had experienced more male competition were group-housed with adult males and thus the presence of adult males may have suppressed the juveniles from singing their more effective songs. In the present experiment, we tested the breeding season songs of males to determine whether song effectiveness correlates with male competition and to determine the size of males' repertoires and the degree of song sharing in each aviary. We recorded juvenile males' vocalizations in the breeding season (10 May 2000). We made recordings of the males in their home aviaries using Sennheiser RF condenser microphones recorded into a Sony TCD-D10 PRO digital audiotape recorder. We analysed songs in two ways. First, we

conducted a structural analysis of the song repertoires of each male in each of the four aviaries. We printed out zero crossing frequency by time displays of recorded songs and characterized song types based on the similarity of note frequencies and timing. We considered songs to be of the same type if all notes were represented and no more than one note or whistle differed in frequency or timing. This allowed us to measure the amount of sharing of each type of song among males and the number of song types in each male's repertoire.

Second, we played recordings of males' songs in aviaries 1 and 4 to females in sound-attenuating chambers, measuring each song's efficacy in eliciting a copulatory response from the females. We only tested songs from two of the aviaries because we did not have enough time in the breeding season to play back songs from all aviaries. We thus chose the two aviaries that differed most in male-male singing interactions. We dubbed the breeding season recordings 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 mean sound pressure level of the songs was 85 ± 2 dB (A-weighted impulse reading at 0.8 m from the speaker as recorded by a Brüel & Kjaer 2209 sound pressure meter). We selected one song from each male in the two aviaries based on recording quality from a selection of approximately 30 songs per male.

Starting on 12 May 2001, we played the songs to a group of females composed of nine adults and 10 juveniles that had previously been housed in outdoor aviaries since September 2001. On 1 May 2001, we brought the females into the laboratory and housed them in pairs in 1.3-m³ chambers. Housing females in pairs reduces stress in chambers and has been shown not to influence 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 six times over the course of the experiment. We scored a positive response if the female adopted a copulatory posture within 1 s from the onset of the song. To calculate potencies, we computed the mean number of responses per female for each song, averaged over all males in each condition. We removed one adult female from the experiment that never responded to any playbacks.

Results

Song structure analysis revealed a significant difference across aviaries in repertoire size (Kruskal-Wallis test: $H_3=13.81$, $P<0.005$). Males in aviary 4 had more song types than did males in aviary 1 (Mann-Whitney U test: $U=6$, $N_1=8$, $N_2=10$, $P<0.001$). Sharing was similar within the four aviaries (proportion of songs shared by at least two males: aviary 1=0.50, aviary 2=0.55, aviary 3=0.27, aviary 4=0.75; $H_3=6.13$, NS). There was no sharing across aviaries, not even between aviaries 2 and 3, in which males were in acoustic and visual contact with each

other. Results of the playback trials revealed that the songs of males who engaged in fewer male-male singing interactions (aviary 1) were significantly more effective at eliciting female copulatory postures than were the songs of males who engaged in more male-male singing interactions (aviary 4) (mean proportion of playback songs to which females responded with postures: aviary 1= 0.51 ± 0.04 , aviary 4= 0.33 ± 0.05 ; Wilcoxon matched-pairs signed-ranks test: $T=0$, $N=18$, $P<0.0001$).

DISCUSSION

Juvenile males reorganized their singing patterns and social behaviour rapidly in response to changes in the social environment. Juvenile females maintained their social propensities as they moved through the different aviaries. Female proximity served as a catalyst for male-male singing interactions. Males in the two aviaries where interactive females were housed for the greatest duration (aviaries 4 and 2) achieved the greatest mating success, as measured by the number of copulations, eggs laid and fertile eggs produced in their aviaries. Aviary 4 males were exposed to the interactive females before and during the breeding season and aviary 2 males were housed with the interactive females from autumn to early spring (recall they were originally housed in aviary 3 before phase 2).

The findings that females laid more eggs and copulated more often with males that engaged in more intrasexual competition are in concordance with our past work showing that (1) adult males that engage in more competitive singing behaviour achieve more copulations than adult males that engage in less male-directed song (White et al. 2002d), and (2) females housed with (more competitive) adult males lay more eggs than females housed with (less competitive) juvenile males (West et al. 2002). Furthermore, the finding that the more competitive juvenile males produced less effective courtship song replicated our past work (King & West 1977; White et al. 2002c). That females copulated less and laid fewer eggs in the presence of males with more potent song suggests that the actual performance of a sexually selected trait (here, engaging in singing with other males) can be more important than the quality of the trait itself (see also King et al. 1981; Trainer & McDonald 1995; Vinnedge & Verrell 1998; Otter et al. 2001; Schwartz et al. 2001; Mennill et al. 2002).

Our previous work showing the effects of male competition on juvenile male development did not allow us to remove the many potential confounds of the presence of adult males. For example, introducing adult males may indeed introduce birds that differ in competitive ability, but it also introduces birds that differ in song quality and social experience. Here, by focusing on variation in behaviour of individuals of the same age class, we were able to determine how patterns of behaviour of individuals were expressed in different social groups and how social interactions led to the development of effective mating skills. The experiment also revealed that juvenile males could develop effective mating behaviour on their own (i.e. without experience with

adult males), given the right social circumstances. Here, the stimulus for juvenile male competitive development was juvenile female affiliative behaviour. In fact, the same mechanism may have been responsible for the observed effects in the previous work (White et al. 2002c). Because females tend to affiliate more often with males in groups when adult males are present, juvenile males may learn to compete with adult males only to gain access to females.

In the present experiment, we had only one group of interactive females. Thus, it is impossible to determine with certainty the characteristics that produced the changes in the male behaviour. For example, there may have been an unmeasured idiosyncratic trait or behaviour in the group of interactive females that influenced the males. Indeed, it is even possible that the effects in the study were caused by only one of the interactive females. The focus of this experiment, however, was on the potential for social groups to change and to reorganize and the subsequent effects on the development of reproductive competence, not specifically on what caused the rapid changes. We therefore designed the experiment to have independent replicates of the groups and used the discovery of the group of interactive females as a single controlled probe. With the focus on the group organization, it would be no less interesting if only one female could have had such a large organizing effect on an entire group. One negative aspect of increasing the number of independent replicates is that it trades off against the ability to study conditions in great detail (Bart et al. 1998). Had we set up these conditions and not taken detailed observations of behaviour throughout the year, we would have had four independent conditions that were identical in composition displaying very different patterns of behaviours, and we would not have had any idea why. Although independent conditions are required for the ability to generalize results from a sample to the population under study, the ability to gain detailed observations on behaviour also plays an important role in scientific discovery.

Although we did not have replicates of interactive females, we did have more than one independent group of females in the study. The relationship across aviaries in the winter and in the spring, showing that the proportion of directed song per aviary correlated with the number of male–female near-neighbour associations, suggests that female proximity to males may have a more general relation to male competition. That is, it was not just the one group of interactive females that had an effect on male competition; it was all four groups of females. The interactive females just happened to be so far on one end of the continuum of affiliating with males that they allowed us to notice the relationship.

Observations during this study as well as results from past work (West et al. 2002) suggest that females affect the singing behaviour of males by either approaching or flying away in response to a male's directed song. Although approaches are low-frequency events, they are the logical precursor to other female social signals, such as wingstrokes, because they tend to occur at close proximity when males sing directed songs.

It is possible that juvenile females are more likely to approach juvenile males than are adult females. We have found in the past that some juvenile females in playback tests tended to be less discriminating in responding to male songs. That is, they often responded to songs to which adult females did not respond (M. J. West & A. P. King, unpublished data). Differences in song selectivity have neural correlates. Hamilton et al. (1997) found that among adult females, the volume of IMAN, a nucleus in the anterior pathway of the song control region, positively correlates with song selectivity. Thus, females may have or acquire stable but idiosyncratic differences in their level of responsiveness to song. The approaches by the juvenile females may reveal an aviary analogue of such nondiscriminating behaviour. In past work we have found that females will readily approach adult males but not juvenile males (West et al. 2002; White et al. 2002c); less discriminating (juvenile) females may not draw these age class distinctions.

In addition, females tend to move in nonindependent patterns (West et al. 2002). Thus, one female approaching a male may increase the probability of other females approaching him. During the early manipulations, the only adult females ever to approach males were those housed with interactive juvenile females. Less discriminating preferences of juvenile females and nonindependence of female movement patterns combined may result in fewer females being likely to approach juvenile males. Current work is focused on determining differences in adult and juvenile female responses to males and male song (Gros-Louis et al. 2003).

Housing birds in large social groups revealed the value of studying mating behaviour as a developmental system. Sexually selected traits, such as song or mate competition, are typically considered to be characteristics that males must develop independently but that females subsequently judge. This work, however, shows that females can affect development of song use as well as song quality (see also Smith et al. 2000). Development is a social endeavour and investigations conducted under asocial housing conditions or with respect to only one sex may miss important influences on the mechanistic and functional basis of sexually selected characteristics. Studying the system instead of the elements of mating behaviour in isolation from one another revealed that the interaction of these elements had nonadditive (and non-intuitive) properties. For example, work in confined enclosures has shown that females' interactions with males can influence male song development by increasing song potency (West & King 1988; Smith et al. 2000). In the present study, however, the presence of females near males stimulated male competition, which had the effect of decreasing potency.

Group-level processes also emerged that influenced information flow within aviaries. For example, even though aviaries 2 and 3 were in acoustic and visual contact with each other and the birds had had interactive experience with each other (during the manipulations in phases 2 and 3), birds in the two aviaries developed along different social and vocal trajectories. There were differences between the groups in assortment, singing,

copulations and eggs produced, and there was no song sharing between groups. The social group acted as a perceptual, attentional, or motivational filter that excluded information coming from outside the immediate social group (see also White et al. 2002a).

This experiment highlights the challenges involved in studying a system so dynamic that the particular individuals present can influence the developmental trajectories of others in a group. Indeed, such malleability raises the concern that there may be nothing reliable enough within the system to be heritable. We have, however, identified some aspects of stability in the cowbird social system. Adult behaviour tends to be (somewhat) more consistent across social groups than juvenile behaviour (White et al. 2002d) and here we have shown that female behaviour is less malleable than male behaviour across conditions. We believe, however, that it is the rules of social interactions that hold the most stability in the system; for example, how a male responds to a singing male or an approaching female is reliable and predictable. Our task now is to examine parameters of variation surrounding the propensities of different classes of individuals. For example, we need to quantify the probability of an adult female approaching a male in a given situation, or a juvenile male singing a directed or undirected song. We are beginning to use computer simulations to assist in this task (Smith 2001) to integrate these parameters and give us insights into the higher levels of organization that can emerge from the interactions of individuals affiliating in social groups.

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