



# The context of social learning: association patterns in a captive flock of brown-headed cowbirds

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Much work on social learning has involved behaviour transmission between pairs of individuals, but recently the need to examine the social context in which learning occurs has been recognized. Previous studies using small numbers of animals have shown social influence on the behavioural development of juvenile male brown-headed cowbirds, *Molothrus ater*. Here we looked at the larger social context that forms the framework for such influence in more natural settings. We allowed a captive group of over 70 cowbirds, comprising adult and juvenile males and females, to associate freely in a large complex of connected aviaries. Highly organized social assortment emerged in the group, with individuals associating with others based on similarity in age and sex. Juvenile males that associated more with adult males had higher courtship success. Juvenile males that associated more with females sang less over the year. These results indicate that the social context of social learning for juvenile males is not just random association with all other birds in the social group, but is a selective and structured pattern of interaction. Differences in navigating this social structure correlated with courtship success and vocalization, behaviour known to be affected by social learning. Studies such as this, using large groups with free assortment of individuals, are the first step towards understanding the effects of the larger social context surrounding social learning.

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To tease apart social effects on behaviour, investigations are often carried out in highly controlled social situations in which only a few animals participate (see reviews in Galef 1988; Laland et al. 1993; Galef 1995). Traditional studies of social learning typically involve a single individual, the demonstrator, performing a novel behaviour and interacting with one or a few naïve individuals, the observers, which are then tested individually for evidence of the novel behaviour. But many animals, such as gregarious birds, schooling fish and colonial species, live in highly complex surroundings of tens or hundreds of interacting individuals. A social group, not the individual, forms the backdrop for social learning.

More recently, however, researchers have suggested that studies of social learning should consider the influence of social groups during the learning experience (Laland et al. 1993; Coussi-Korbel & Fragaszy 1995). Some studying social learning have begun to do so. For example, Galef and colleagues introduced a new method for studying transmission of diet preferences in groups of

Norway rats, *Rattus norvegicus*, modelled on the natural situation in rat colonies where single individuals may enter or leave a group. The initial group consisted entirely of demonstrators, replaced one at a time by naïve observers, until no demonstrators remained. Variables such as the number of initial demonstrators and the frequency of replacement affected longevity of the novel behaviour, findings that could not have been extrapolated from studies on individual transmission (Galef & Allen 1995; Galef & Whiskin 1997). Laland & Williams (1997) used the same method for studying preference of foraging routes in guppies, *Poecilia reticulata*, and determined it to be preferable to the traditional method in both the ability to make analyses of the behaviour in the population after removal of all demonstrators and the avoidance of stress-related behaviour associated with individual testing in this social species.

In another step towards examining the spread of social learning through a group of animals, Curio et al. (1978) showed cultural transmission of mobbing behaviour in blackbirds, *Turdus merula*. An initial observer learned to mob a novel stimulus using traditional methods (exposure to a demonstrator mobbing an owl that was obstructed from the observer's sight), and was then used to transmit this behaviour along a chain of six birds with

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no reduction in intensity of the response. However, this work still used pairs of individuals in the transmission paradigm.

Giraldeau & Lefebvre (1987) discovered that while pigeons, *Columba livia*, in traditional studies of behaviour transmission would learn a novel food-finding technique, a flock situation changed the dynamics such that observers scrounged the food made available by the demonstrator rather than learning to obtain it themselves. In addition, individuals that scrounged when alone with a demonstrator were more likely to learn the task than individuals that scrounged in a group (Lefebvre & Helder 1997). When scrounging was prevented, the simple presence of multiple demonstrators produced faster learning, but the addition of bystanders produced slower learning (Lefebvre & Giraldeau 1994). Similar to the scrounging results in pigeons, Beauchamp & Kacelnik (1991) found that female zebra finches, *Taeniopygia guttata*, were less likely to learn the pairing of a light with food when housed with males already trained in the task, because the behaviour of their companions was a reliable and more salient cue to finding food than the light cue. In regards to learning bird song, Tchernichovski & Nottebohm (1998) found that young zebra finches produced shorter song motifs and copied fewer notes from their fathers when housed with their father plus other male siblings than when housed alone with their father.

Social groups can also affect the propensity to display a learned task. Drea & Wallen (1999) found that low-status rhesus monkeys, *Macaca mulatta*, would learn a task when the social context included both high- and low-ranking monkeys, but would only perform the behaviour when tested in the absence of higher-status individuals. The failure to perform the task in the presence of high-ranking individuals was not due to overt aggression towards the low-status monkeys but due to the dynamics of the social group. Visalberghi (1990) also presented evidence of social groups inhibiting the performance of a learned task in capuchin monkeys, *Cebus apella*.

The effects of groups on social learning is not always inhibitory. Visalberghi & Fragaszy (1995) found that individual capuchins consumed more novel food when presented with it in a group than when alone. Nicol & Pope (1999) showed that socially dominant demonstrator hens in a pecking task stimulated more pecking by observers than did socially subordinate demonstrators. Freeberg (1996, 1998) housed brown-headed cowbirds, *Molothrus ater*, in social groups of over 30 birds, half of which were adult demonstrators, to transmit patterns of assortative mating through two generations. In the context of the large group, females demonstrated modification of mating preference, whereas no signs of such plasticity were seen in dyads or triads (King & West 1987). Beecher (1996) found that field-reared song sparrows, *Melospiza melodia*, learned whole songs from neighbours, whereas laboratory-reared birds pieced together parts of songs copied from up to four different tutors, the number made available in the laboratory. Beecher emphasized the difference in self-regulated access to song in laboratory birds: 'The young birds themselves had no control over this exposure [to song or tutor], in contrast with the

situation in the field. In particular, they could not concentrate on one of the tutors, get away from others, or interact with more than those four' (Beecher 1996, page 69).

Taken as a whole, the above studies indicate that social learning can operate differently in the context of a group. However, the complexity of studying social learning increases exponentially as group size increases. Who is learning from whom? Can we even assume that two individuals in the same group have similar social experiences? The current study was designed to open the way towards tackling such questions by examining the social dependence of development within the framework of a complex environment in which the animals themselves control proximity to other individuals. We focused on the relationship between associations after fledging and the development of courtship competency and singing of juvenile males, behaviour whose social dependence has been extensively studied and demonstrated in laboratory and aviary settings (O'Loughlen & Rothstein 1993, 1995; Freeberg 1996, 1998; West & King 1996; West et al. 1997; Smith et al. 2000).

The effects of the proximate physical and social environment are rarely addressed in studies of avian social and vocal development, although issues of crowding and dominance have been discussed (Thorpe 1958; Mulligan 1966). Beecher (1996) showed effects on number of tutors chosen and whether whole or partial songs were copied, as discussed above. Freeberg et al. (1995) found that juvenile male cowbirds that had been previously housed with female cowbirds in sound-attenuation chambers (ca. 1 m<sup>3</sup>) displayed apparently typical female-directed behaviour when placed, one at time, in flight cages containing multiple cowbird females and canaries (ca. 7.8 m<sup>3</sup>), but they failed to court females successfully when group housed in a large mixed-sex aviary (ca. 556 m<sup>3</sup>), devoting most of their time singing to other males. The smaller size of the individual flight cages may have contributed to the males' ability to court females, by constraining the distance females could be from the males; whereas, the opportunity to interact with other males may have contributed to the males' lack of attention to females in the aviary.

The difference between living in an aviary with many other individuals and living in a small enclosure with one or two birds also has bioacoustic implications for cowbirds. The female-salient elements of male cowbird song degrade rapidly at distances beyond 0.3 m (King et al. 1981). Males living in the 1-m<sup>3</sup> chamber could not sing without having a clear rendition of their vocalization transmitted to their social companions, and their companions could not leave the area of singing. But even in such controlled circumstances, proximity mattered during song delivery. Males housed with females that remained in close proximity during song delivery developed more effective songs than males housed with females that flew away (Smith et al. 2000). In a larger aviary, females could spatially separate themselves from young males even more dramatically, bringing up the question of whether they would associate closely enough with the juveniles to hear the female-salient elements of

the song at all. Bioacoustics has implications for interactions with males as well. When socially naïve adult males were group housed with socially experienced adult males and females for a 4-h period during the breeding season, the naïve males' songs were especially stimulating to females, but provoked attack by the experienced males, because the naïve males had not yet established dominance (West & King 1980). Thus, juvenile males may need to separate themselves from adult males while practicing song to avoid aggression provoked by the adult males' reaction to the female-salient elements.

Thus, social proximity is a significant parameter of social dynamics in this species. In the present work, we measured the proximal relations of juvenile males with adult males and females. We housed adult and juvenile male and female cowbirds together in a spacious aviary complex large enough that individuals at opposite ends were socially and acoustically separated. As a way of gauging the difference in size of the housing environment between this and previous experiments, we measured the cubic space available per individual bird. Our sound-attenuation chambers have a volume of 1.3 m<sup>3</sup>, providing three birds with 0.4 m<sup>3</sup> per bird (as in Freeberg et al. 1995; Smith et al. 2000). The aviary complex used in this study has a volume 2511.5 m<sup>3</sup>, giving our 74 birds each 33.9 m<sup>3</sup>, over 80 times the volume available per bird in a sound-attenuation chamber. Cowbirds are known to overwinter in single-age and mixed-age and -sex flocks of near one hundred to thousands of birds (Friedman 1929; King & West 1988). By allowing free movement throughout the complex, we hoped to produce a seminatural approximation of an overwinter group, where behavioural interactions between individuals, as opposed to spatial constraints, would dictate social associates.

We recorded near neighbours of individuals, all birds within a certain radius, or proximal zone, following the reasoning that animals that are near each other have the opportunity to engage in interaction (Coussi-Korbel & Fragaszy 1995; Holekamp et al. 1997; Freeberg 1999). Near-neighbour measures have been used in this manner in birds and primates (Boinski & Mitchell 1994; Digby 1995; Latta & Wunderle 1996; Freeberg 1999). Birds within the proximal zone can also hear the female-salient elements of song with high fidelity (King et al. 1981). While it does not necessarily follow that an individual interacts with all birds in its proximal zone, the collection of these birds forms the frame in which social behaviour occurs. We called this collection the proximal network of an individual. The composition of the proximal network represents the backdrop of social opportunities navigated by an individual in the group. To look at opportunities for and evidence of social learning, we recorded singing behaviour of adult and juvenile males over the year and measured their courtship success at the end of the experiment.

We focused specifically on juvenile males, which must learn social and courtship skills before their first breeding season. Given a broad range of possible companions and given the ability to separate spatially, what is the nature of juvenile males' proximal networks? Do differences in

the amount of association with specific age and sex classes correlate with differences in the developmental variables of singing and courtship success?

## METHODS

We housed adult and juvenile male and female cowbirds together in a large complex of connected aviaries during September–May, and recorded proximal associations and singing behaviour throughout this period. We then divided the birds into smaller groups for the breeding season assessment, where we measured the courtship success of adult and juvenile males.

### Subjects

The subjects were 74 brown-headed cowbirds, *Molothrus ater ater*, captured in Monroe County, Indiana. The birds fell into four age and sex classes: 20 adult males, 23 adult females, 14 juvenile males and 17 juvenile females. The adult males and females were at least 1 year old at capture; the juvenile males and females were between 50 and 70 days old. Two birds, one adult male and one adult female, had been captive for 4 and 5 years, respectively. The remaining birds were captured in the summer of 1997. Nine of the 74 birds did not finish the course of the experiment: six died and three escaped. The birds were maintained on a modified Bronx Zoo diet for omnivorous birds and were provided white millet, red millet, canary seed, cracked corn and vitamin-treated water. Each bird was banded with coloured plastic leg rings for individual identification.

### Overwinter Housing

#### *Housing prior to experiment*

The subjects resided in several different facilities between initial capture and the start of the experiment. Adults were housed in either single-sex or mixed-sex outdoor aviaries after capture (range 2 × 3 × 2 m–9.1 × 18.3 × 3.4 m). After 12 July, all adults were placed together in a large outdoor aviary (section 4 of Fig. 1). Juvenile males and females were housed together in an indoor cage measuring 1.8 × 2.4 × 1.8 m until six individuals had been captured. These six were moved to a large outdoor aviary on 11 July (section 1 of Fig. 1) and additional juveniles were added to this location as they were captured.

#### *Introduction of birds to the experimental complex*

The experimental complex consisted of five outdoor aviaries and three indoor shelters (Fig. 1). All sections of the complex could be isolated from others or opened to allow movement of birds between sections. The outdoor aviaries contained trees, perches (sticks and branches suspended by wire from the roof mesh), feeding stations, water bowls and a grass and weed covered ground surface. All indoor shelters contained perches and some contained seed or water bowls. There was a total of nine water bowls and four covered and one uncovered feeding stations. Birds in the complex could see and hear wild



**Table 1.** Definitions of terms used in collection and analysis of data

Term	Definition
Age and sex class	Whether an individual was a male or female and was an adult (1 year of age or older) or a juvenile in the summer of 1997.
Data block	A 10-min period in which data were taken in the overwinter data collection period. Time, location in complex and number of birds in that location were recorded at the start of each data block. The number of birds in the location was also recorded at the end of each data block.
Target bird	Bird chosen by observer; object of collected data.
Near neighbour	Identity of individual within 0.3 m without obstruction (leafy branch, wooden pole, other bird, etc.) of target bird. A near-neighbour point was scored for both individuals in a pair.
Song point	Occurrence of singing by a male during a 10-min data block, including both discrete songs approximately 1 s in length, characterized by several low-frequency notes followed by a high-frequency whistle, and warbling streams of song several seconds to several minutes in length. Song points provided a rough estimate of the amount of singing for each male.
Directed song	A discrete song by a male accompanied by a wing-spread display and oriented towards another bird within 0.6 m of the male.
Undirected song	A discrete song by a male not oriented towards any other individual within 0.6 m. An undirected song may or may not be accompanied by a wing-spread display.
Flight whistle	A high-frequency modulated tone of one or more syllables.
Copulatory posture	Posture displayed by the female in which the back was arched and feathers around the cloacal area were separated. Usually displayed in response to a directed song by a male.
Copulation	Male mounted female while she displayed copulatory posture.
Focal sample	A 20-min period during which the behaviour of a single male, including all directed songs, undirected songs, whistles, copulations and copulatory postures received, were noted during breeding season assessment.
Consort day	Day during breeding season assessment on which a male sang at least seven directed songs to one female during his 20-min focal sample or received a copulatory posture from her during the morning. The male was scored a consort day for each female for which he met these criteria. Directed singing to females and receipt of copulatory postures is known to be highly correlated (Eastzer et al. 1985).
Consortship	A male was scored a consortship with a female when he had received a consort day with that one female for 3 out of 4 consecutive days.
Latency to consortship	A measure to compare how quickly males achieved consortships, calculated by summing the number of days before a consortship was achieved and dividing by the number of days the male was observed in that social group. Thus, it represents the fraction of total days a male was observed that were days before consortships. Because a consortship took at least 3 days to achieve, all males had latencies above zero (there were always some days before a consortship). A male who never achieved a consortship would have a latency of 1 (all days before consortship).
Copulations/day	Used to compare number of copulations between males. Copulations per day were calculated by dividing the total number of copulations by number of days a male was observed.
Songs to female/min	Used to compare vocal attention to females between males. Songs/min were calculated by dividing the total number of directed songs to females during all of a male's focal samples by the sum of minutes in the focal samples.

that remained in or travelled through the observer's aviary during the data block (average number of birds at start of block=31, range 2–74; average number of birds at end of block=29, range 1–74).

The aviary in which to observe was chosen by the observer based on where the birds were located. If the birds were not all in the same aviary, the choice of aviary was up to the observer and generally corresponded to where the observer perceived the most birds to be located. The observer could move among aviaries in the complex between data blocks at his or her discretion. The observer could only move between aviaries within a data block if all the birds left the aviary.

#### *Amount of data*

Over the entire year, we collected 26 833 near neighbour points and 7502 song points during 1576 data blocks, for a total of 262.7 h of data (577 data blocks in autumn, 464 in winter and 535 in spring). Of the 163

days spanned by the three sampling periods, we collected data on 136 days. We took data on a median of 6 days a week (range 3–7 days). On days when we collected data, we took a median of 11 data blocks (range 1–38 data blocks; representing 1.8 h of data, range 0.2–6.3 h).

#### **Housing During the Breeding Season**

For the breeding season assessment, we separated the birds into individual testing aviaries. We wished to measure the courtship abilities of juvenile males relative to each other. Because juvenile males tend to do poorly when in competition with adult males and it is more difficult to determine relative ranks of the poorer courters (O'Loughlen & Rothstein 1993), we tested the juveniles separately from the adults. Furthermore, because only a few top males tend to emerge in each social group in captivity (West et al. 1981), we used small groups of five to seven males to minimize the number of

poorer courters. Although the aviary complex was quite spacious, we felt that had we left the birds together, the number of males competing could have produced high levels of aggression, endangering the birds. Therefore, we chose to divide the birds into five or six separate large aviaries, lowering both the number of males in direct competition with one another and the density of birds. In addition, the multiple aviaries allowed the possibility of removing males that became the target of excessive aggression from their aggressor without losing the ability to collect data on their courtship behaviour.

On 13 May, we removed approximately half of the birds (33 of 65 that remained at this date) from the experimental complex. We confined the remaining 32 birds to sections 1–3 of the complex (see Fig. 1). We housed the removed birds in three separate outdoor aviaries in groups of 11 (section 4 of Fig. 1 and two similar aviaries). On 18 May, we confined the other 32 birds to single aviaries in groups of 10–12 (sections 1, 2 and 3; Fig. 1). On this date, we also removed one juvenile male from his aviary and placed him in section 1 (Fig. 1) due to excessive aggression directed towards him by another male in his original aviary; he was the only bird moved for such a cause.

All six aviaries housed either adult males and adult and juvenile females or juvenile males and adult and juvenile females. In all aviaries, there were at least as many females as males and never more than one more female than males. To provide multiple assessments of each male in competition with different social groups, we rearranged the birds into five aviaries twice, on 27 May and 6 June, always keeping with the above age and sex restrictions and having 11–15 birds per aviary. We collected data from all five aviaries except for one aviary after the 27 May move and two aviaries after the 6 June move.

### Breeding Season Assessment

We collected data on each male while the males were housed with a single social group for 9 days (except for one group, where we collected only 6 days of data due to inclement weather). See Table 1 for definitions used. We began data collection on the day we placed the birds in the aviaries (13, 18, 27 May and 6 June). We collected data for each adult male while the males were housed with one to three different social groups, and for each juvenile male while the males were housed with three social groups. On each day, we observed all males for two 10-min periods between 0630 and 1130 hours to make a 20-min focal sample. We observed males in different orders each day and balanced times of observations across males.

### Analysis and Statistics

We analysed two features of social proximity: the patterns of association forming the proximal networks of individuals and the relative strength of assortment between classes. We measured patterns of association by

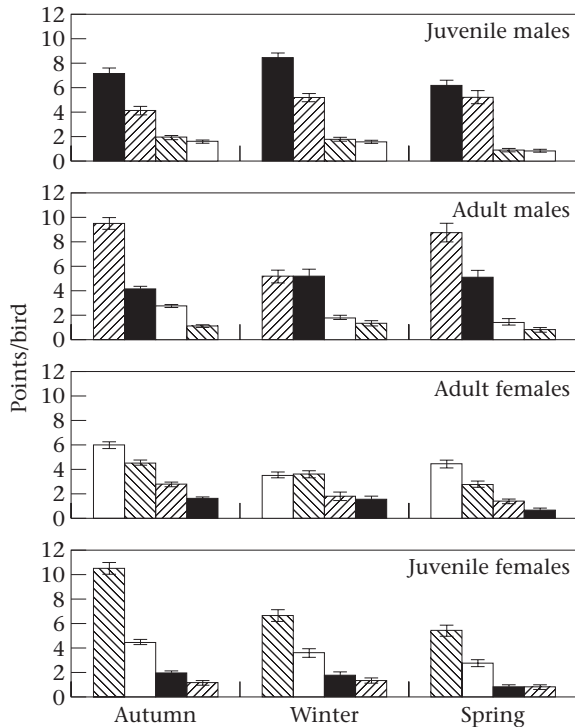
the number of near-neighbour points consisting of an age and sex class, calculated as points per bird. We did this by summing the total near-neighbour points scored for an individual for all birds in a class and dividing by the number of birds with which it was possible to associate in the class. We determined the relative strength of assortment by comparing the proportion of points per bird, calculated as above, from each age-sex class that contributed to an individual's sum of all class points per bird. For example, if a significantly higher proportion of points per bird from the opposite age and sex class contributed to the sum of all class' points per bird for individuals in one class than those in a different class had from their opposite class, the first class was said to assort more with its opposite class. We compared the strength of assortment only for associations of adult males and females with juvenile males.

We treated the autumn, winter and spring samples as separate experiments for the purpose of statistical analysis. Variances of the data in analyses were not homogeneous, so we used nonparametric tests throughout. When comparing the amount of association with the four classes or the strength of assortment of the four classes, we performed multiple comparisons only when a nonparametric analysis of variance (ANOVA) was significant. If more than one nonparametric ANOVA was performed, we only considered it significant if the significance value was less than a corrected *P* value determined by dividing by the number of tests (in text as 'significant at  $P < [\text{corrected value}]$ '; Bonferroni correction, Sokal & Rohlf 1995, page 240). We treated multiple comparisons within one ANOVA similarly. We used Friedman ANOVAs with Wilcoxon matched-pairs signed-ranks tests and Kruskal–Wallis ANOVAs with Mann–Whitney *U* tests where appropriate. We divided each sampling period into four divisions of approximately 2 weeks for comparison of adult versus juvenile singing rate, and corrected for multiple tests in each sampling period. All tests were two-tailed. The adult male that had been in captivity for 4 years was excluded from courtship analysis due to the fact that he had been housed alone with the previously captive female in the year previous to the experiment.

We performed Spearman rank correlations using the data from the three sampling periods combined because we were interested in examining correlations of the entire experience of the birds. We used the proportion of points per bird for correlations because the number of points per bird was confounded with the total number of near-neighbour points scored by individuals. In correlations of singing behaviour, we included only birds that remained throughout the entire overwinter period of data collection.

## RESULTS

Nonrandom patterns of association emerged in the group of freely assorting birds. Individual differences in juvenile males' navigation of the social environment was correlated with developmental variables. The courtship success of juvenile males was correlated with their association



**Figure 2.** Proximal sets. Average ( $\pm$ SE) points per bird (see Methods for definition) with the age and sex classes in all three sampling periods are shown in separate graphs for each class. ■: Points per bird with juvenile males; ▨: points per bird with adult males; ▩: points per bird with juvenile females; □: points per bird with adult females. Bars for each graph are ordered such that the class with which the individuals associated most appears farthest left, and least, farthest right. This results in a different order of bars for each class. Nonoverlapping error bars correspond generally to significant differences (see Table 2 for actual comparisons).

with adult males. The singing behaviour of juvenile males was correlated with their association with females.

### Association Patterns

A general pattern of age-by-sex association emerged across all four age and sex classes. Individuals had the highest number of near-neighbour points per bird with others of their own age and sex, the next highest with birds of the same sex but different age, fewer points per bird with those of different sex but the same age and the least near-neighbour points per bird with birds of the opposite age and sex class (Fig. 2). The birds rapidly developed differential association with one another; significant assortment was evident within 6 days of beginning data collection.

This pattern was present in all sampling periods, although differential association between ages was not as strong in winter and spring. In winter, adult males and adult and juvenile females associated similarly with both ages of males, and adult females and juvenile males associated similarly with both ages of females. In spring, juvenile males and females associated similarly with both ages of males, and adult and juvenile males associated

similarly with both ages of females (Fig. 2; see Table 2 for statistics).

### Strength of Assortment

In the autumn, adult males assorted less with juvenile males than did adult females with juvenile females. In winter, adult males showed more association with juvenile males than did any juveniles with the adults of their sex. Most strikingly, in autumn and winter, adult females associated more with juvenile males than did other classes with their opposite age-sex class (see Table 3).

### Developmental Measures of Juvenile Males

Courtship success of juvenile males was correlated with individual differences in association with adult males over the year. Juvenile males that associated more with adult males had lower latencies to form a consortship (Spearman rank correlation:  $r_s = -0.712$ ,  $N=14$ ,  $P<0.01$ ; Fig. 3).

The juvenile males developed appropriate social behaviour in the group setting and courted successfully during the breeding season. They did not differ from adult males in latency to form consortships, copulations and songs to females (see Table 4). Latency to form consortships was correlated with both copulations and songs to females (Spearman rank correlation: copulations:  $r_s = -0.650$ ,  $N=29$ ,  $P=0.0001$ ; songs to females:  $r_s = -0.706$ ,  $N=29$ ,  $P<0.0001$ ).

Juvenile males increased singing rate for most of the autumn sample, then sang at a high rate through to the end of the year (see Fig. 4). Juvenile males that associated less with females sang more over the year (Spearman rank correlation: adult females:  $r_s = -0.604$ ,  $N=14$ ,  $P<0.05$ ; juvenile females:  $r_s = -0.578$ ,  $N=14$ ,  $P<0.05$ ; Fig. 5, data in Table 4).

### Singing Behaviour of Adult Males

Adult males sang significantly less than juveniles for all of the winter sample (Mann-Whitney  $U$  test: 2-week periods beginning 17 December, 31 December and 14 January:  $U \leq 25$ ,  $N_1=20$ ,  $N_2=14$ ,  $P<0.0125$ ; 19-day period beginning 28 January:  $U=35.5$ ,  $N_1=19$ ,  $N_2=14$ ,  $P<0.0125$ ; see Fig. 4). Adult males that sang more over the entire year showed a nonsignificant tendency to associate more with juvenile males (Spearman rank correlation:  $r_s=0.435$ ,  $N=16$ ,  $P<0.10$ ).

## DISCUSSION

The aims of this study were to characterize the social context that forms the environment surrounding social learning experiences for juvenile males and to determine whether individual differences in association patterns are correlated with differences in developmental variables of juvenile males. The group of freely assorting birds displayed a highly organized pattern of social association based on similarity in age and sex. For juvenile males,

**Table 2.** Statistical comparisons for association in proximal networks

Sampling period	Class	Friedman $\chi^2_3$	N	Multiple comparisons Wilcoxon matched-pairs signed-ranks test					
				AM-JM	AM-AF	AM-JF	JM-AF	JM-JF	AF-JF
Autumn	JM	35.8*	14	**	**	**	**	**	**
	AM	58.9*	20	**	**	**	**	**	**
	JF	49.9*	17	**	**	**	**	**	**
	AF	61.1*	23	**	**	**	**	**	**
Winter	JM	38.1*	14	**	**	**	**	**	T=27, NS
	AM	51.8*	20	Z=-0.04, NS	**	**	**	**	**
	JF	45.9*	17	Z=-2.53, NS	**	**	**	**	**
	AF	40.3*	22	Z=-1.27, NS	**	**	**	**	Z=-0.24, NS
Spring	JM	33.9*	14	T=30, NS	**	**	**	**	T=48, NS
	AM	49.5*	19	**	**	**	**	**	Z=-2.46, NS
	JF	40.3*	16	Z=-0.21, NS	**	**	**	**	**
	AF	52.0*	21	**	**	**	**	**	**

JM: Juvenile males, AM: adult males, JF: juvenile females, AF: adult females.

\* $P < 0.0125$ ; \*\* $P < 0.0083$ ;  $T \leq 6$  for JM,  $Z \leq -3.40$  for AM,  $Z \leq -3.36$  for JF,  $Z \leq -2.69$  for AF.

**Table 3.** Strength of assortment comparisons of adult males' and adult females' association with juvenile males to other classes' association with the equivalent class

Association	Autumn		Winter	
	$H_3$	$U$	$H_3$	$U$
<b>Same sex, different age†</b>	21.1*		23.7*	
AM-JM versus				
AF-JF		76**		NS
JM-AM		NS		45**
JF-AF		NS		36**
<b>Opposite age/sex class‡</b>	35.5*		15.6*	
AF-JM versus				
AM-JF		53.5**		96**
JM-AF		NS		52**
JF-AM		48**		92**

AM: Adult males ( $N=20$ ), JM: juvenile males ( $N=14$ ), AF: adult females ( $N=23$  autumn, 22 winter), JF: juvenile females ( $N=17$ ).

†We determined the strength of associating with the same sex and different age class by comparing the associations between adult males and juvenile males with associations between adult females and juvenile females, juvenile males and adult males, and juvenile females and adult females.

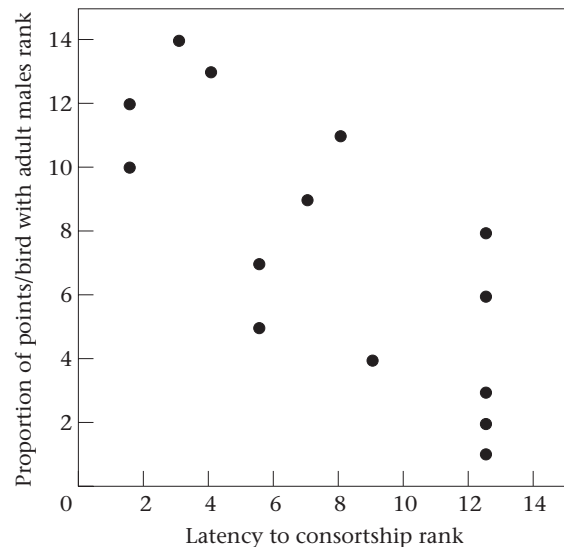
‡We determined the strength of associating with the opposite age/sex class by comparing the associations between adult females and juvenile males with those between adult males and juvenile females, juvenile males and adult females, and juvenile females and adult males.

\* $P < 0.025$  (Kruskal-Wallis test); \*\* $P < 0.0083$  (Mann-Whitney  $U$  test).

differences in association with adult males correlated with courtship success and differences in association with females correlated with singing behaviour.

### Proximal Networks and the Social Backdrop

A general pattern of associating with others based on similarity in age and sex emerged rapidly and was relatively stable over the three sampling periods. A



**Figure 3.** Correlation between courtship success of juvenile males and their association with adult males. The ranks for latency to form a consortship (see Table 1 for definition) and the proportion of points per bird with adult males are plotted against each other. A higher rank denotes a higher number; therefore, rank 1 for latency to consortship represents the bird with the shortest latency (i.e. the highest courtship success), and rank 14 for the proportion of points per bird with adult males represents the bird with the highest proportion (i.e. the most association with adult males).

captive flock of cowbirds of mixed age and sex self-organized to produce for its members proximal networks, wherein the relative amount of association an individual experienced with other birds was predictable based on age and sex class. These proximal networks provided the backdrop of social organization in which the behavioural development of young males occurred.

Previous work has shown that social companions can affect the development of important courtship behaviour in cowbirds, like singing and mate choice (West et al.

**Table 4.** Breeding season assessment for adult and juvenile males, and singing and association data for juvenile males

	Latency to consortship*	Copulations/day	Songs to females/min	Proportion of points/bird with adult males	Song points	Proportion of points/bird with adult females	Proportion of points/bird with juvenile females
<b>Juvenile males</b>							
MNyb	0.37	0.56	0.82	0.330	429	0.098	0.095
MWyl	0.37	0.30	0.54	0.331	233	0.122	0.143
MYby	0.56	0.15	0.34	0.411	308	0.078	0.084
MRyl	0.63	0.11	0.32	0.408	322	0.076	0.111
MGrd	0.74	0.19	0.38	0.318	296	0.082	0.111
MDrd	0.74	0.07	0.29	0.326	237	0.080	0.098
MOby	0.78	0.00	0.26	0.328	342	0.082	0.093
MLrd	0.81	0.19	0.40	0.331	174	0.100	0.096
MOdr	0.96	0.04	0.25	0.311	231	0.090	0.071
MRby	1.00	0.22	0.20	0.301	324	0.075	0.080
MMyI	1.00	0.07	0.16	0.318	138	0.103	0.144
MByI	1.00	0.00	0.12	0.285	227	0.096	0.128
M2by	1.00	0.00	0.06	0.277	147	0.105	0.148
MYrd	1.00	0.00	0.04	0.327	243	0.107	0.125
<b>Adult males</b>							
MNO	0.33	0.11	0.68				
MRD	0.33	0.00	0.58				
MML	0.46	0.21	0.83				
MWO	0.50	0.13	0.73				
MRW	0.56	0.22	0.44				
MDR	0.58	0.08	0.56				
MLO	1.00	0.13	0.18				
MRO	1.00	0.08	0.06				
MMN	1.00	0.00	0.23				
MMG	1.00	0.00	0.18				
MYM	1.00	0.00	0.04				
MRB	1.00	0.00	0.04				
MWD	1.00	0.00	0.02				
MRN	1.00	0.00	0.01				
MLM	1.00	0.00	0.00				

Comparison between adult and juvenile males in latency to consortship, copulations/day, and songs to females/min: Mann-Whitney  $U$  test:  $U \geq 105$ ,  $N_1=15$ ,  $N_2=14$ , NS for all comparisons.

\*A latency proportion of 1.00 indicates the male never achieved a consortship.

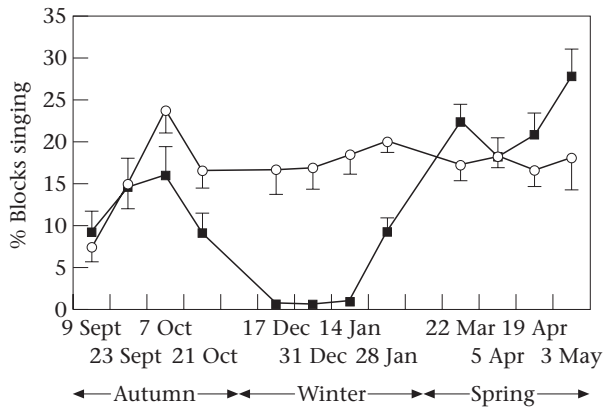
1983, 1996; Freeberg et al. 1995, 1999; Freeberg 1996, 1998). The results of the current study show that for birds in a large group, social associations were not random pairings with all other birds in the group, but were unevenly distributed through different subsets. The proximal networks of an individual cannot be assumed to consist of equal association with all other birds in a group. Noting the composition of groups is a useful first step for examining possible social associates but is not sufficient to characterize the makeup of an individual's proximal network (e.g. King & West 1988).

### Behavioural Development of Juvenile Males

While proximal networks may be similar on a broad scale within a single age and sex class, it was individual differences in how juvenile males navigated the social environment that correlated with developmental variables. Even though juvenile males as a group associated most with other juvenile males, it was the amount of association with adult males that correlated with courtship success and the amount of association with females,

which formed the smallest part of their proximal networks, that correlated with singing behaviour. Each individual apportioned their associations differently. Juvenile males that associated more with adult males did not necessarily associate less with females; some associated relatively less with their own class and relatively more with females. While in the same social group, individual juvenile males experienced different proximal networks.

Juvenile males that had a higher proportion of near neighbour points with adult males achieved consortships faster. Juvenile males that had a higher proportion of near-neighbour points with females sang less over the year. However, it is impossible to determine whether these differences in development were the result of social learning in different social contexts or the result of individual propensities that were correlated with these variables influencing social associates. It is possible that association with adult males lead to learning skills that improved courtship ability and that association with females suppressed singing. However, it is also possible that adult males associated more with those juveniles that

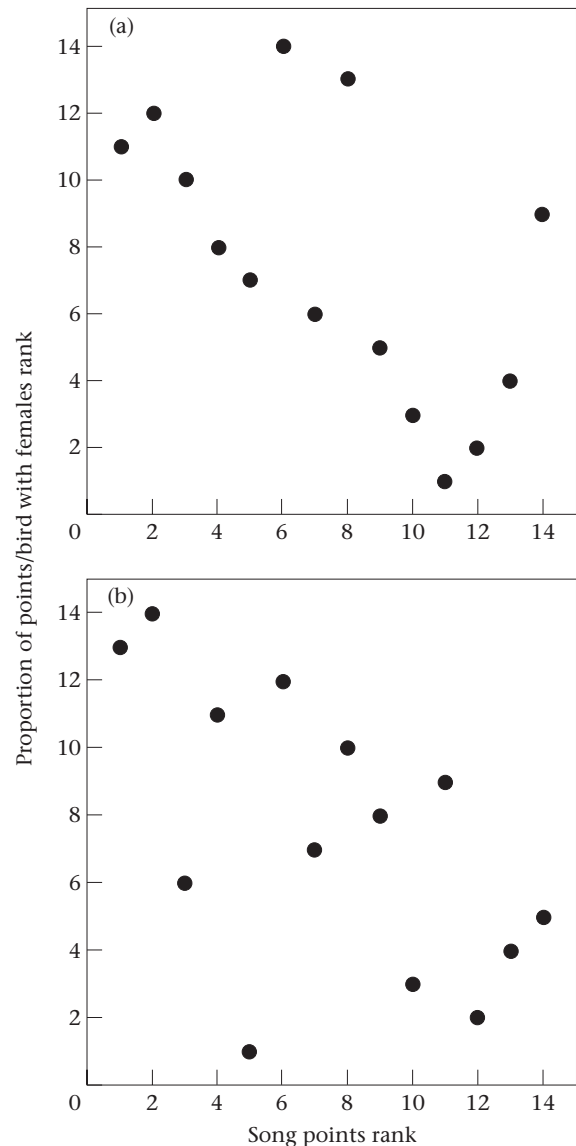


**Figure 4.** Amount of singing. The average percentage of 10-min data blocks during which adult and juvenile males were recorded as singing for each of four subsampling periods in autumn, winter and spring. Dates on the X axis represent the first day of each subsampling period. The first three subsampling periods spanned 2 weeks each, the last subsampling periods were 10 days (autumn), 19 days (winter) and 8 days (spring). Error bars represent the standard error of the mean; for points with no visible bar the standard error was less than the width of the point. ■: adult males; ○: juvenile males.

were inherently more competent and that females preferred to associate with quieter juveniles. The truth is probably a self-referential combination of both these possibilities: with individual differences driving the composition of proximal networks, which then leads to differential social learning.

Freeberg (1999) also found a positive correlation between juvenile males' courtship success and association with adult males in one condition, but not another, where transmission of mating preferences was weaker. The condition in which the correlation was absent was the novel culture condition, where the adult demonstrators had developed assortative mating by exposure as juveniles to adults of a different subspecies. The condition where the correlation was present was the more natural condition, where the adult demonstrators had developed assortative mating by exposure as juveniles to adults from their own population, and is similar to the configuration of the current study. The fact that the correlation was only present in the condition with stronger evidence for social learning from adults, as shown by the high fidelity of transmission of mating preference, hints that association of juveniles with adult males may have been a mechanism of social learning in this condition. These results, combined with the tendency in the current study for a positive correlation between adult males' association with juvenile males and amount of singing, indicates juvenile males may be learning from their adult male companions and choosing as companions those adults that sing more.

In the rich social environment of over 70 interacting cowbirds, the juvenile males developed successful social behaviour as evidenced by their competency in mating. The juveniles did not compete directly with adult males for mates but were similar to them in all measures of



**Figure 5.** Correlation between the amount of singing by juvenile males and their association with females. The ranks for amount of singing and the proportion of points per bird with adult (a) and juvenile (b) females are plotted against each other. A higher rank denotes a higher number; therefore, rank 14 for singing represents the bird with the most song points (i.e. the most singing over the year), and rank 14 for proportion of points per bird represents the bird with the highest proportion (i.e. the most association with adult or juvenile females).

courtship success. In contrast, in a previous study, juvenile males housed with only females in a sound-attenuation chamber before the breeding season did not court successfully when competing against only other juveniles (Freeberg et al. 1995).

### Opportunities for Social Learning from Adult Males

As mentioned above, juvenile males that associated more with adult males had higher courtship success

suggesting that associations with adult males probably include social learning interactions. In previous studies, experience with older males led to reliably greater levels of courtship competency in previously socially deprived first-year males (Freeberg et al. 1995; West et al. 1996).

Juvenile males sing at a fairly steady rate over the year, while adults show a near cessation of singing in winter. In the wild, juvenile males are known to sing a great deal in winter roosts (Friedman 1929; King & West 1988). The period during which juveniles sing, but adults do not, may allow juvenile males to learn about social interactions involving song without the inhibition of hearing song from older, and probably more dominant, individuals. During the winter, the adult males in the present study associated as much with younger males as they did with their peers, even though the juvenile males were singing while the adults were generally silent. Also, adult males associated with juvenile males relatively more than both sexes of juveniles associated with same-sex adults. The implications of these results are unclear, but it is indicative that adult males were available to juvenile males for social interactions at this time. By the spring, the adults were singing again, and juvenile males associated as much with adult males as they did with males of their own age class. Here, the juveniles may be learning specifically about singing interactions with older males as well as with each other.

### Opportunities for Social Learning from Adult Females

Research has implicated adult females in modification of juvenile males' vocal development, affecting geographic specificity, amount of copying versus improvisation, rate of development and quality of song (King & West 1983, 1989; Smith et al. 2000). The results of the present study indicate that adult females were available to juvenile males as social companions in a seminatural situation. While juvenile males formed the smallest part of adult females' proximal networks, adult females associated more with juvenile males than did other classes with their opposite class. This relative abundance of association with the smallest portion of their proximal network indicates that adult females could have been engaged in behaviour that modified the juvenile males' development.

Juvenile males that associated more with adult females over the year sang less. We know that the amount of feedback from females can have an effect on vocal production, leading to less singing once songs reach later developmental stages (Smith et al. 2000). In the current study, all juvenile males sang at a high rate over the year, but those juvenile males that spent more time with females, and therefore had more opportunity to receive feedback from females, sang less in total. It is possible that those males did not need to practice as much because they received more feedback from females. As mentioned earlier, it is also possible that females chose to remain near quieter males. In close quarters, females often fly away from a juvenile male's song overture and only very rarely or in extraordinary circumstances approach him

(Smith et al. 2000). However, these two possibilities are not mutually exclusive and probably both are operating. Those juvenile males that inherently sang less may have initially interacted with females more, received female feedback on their song and hence needed to practice less, while those that sang more received less female feedback, driving their need for more individual practice. Thus, each juvenile developed song in an environment tailored by his own interactions to be complementary to his individual propensities.

### Implications for Social Learning

The current study has both encouraging and discouraging implications for investigations into social learning in a group context. On the negative side, it shows that we cannot assume two individuals in the same group share similar experiences. This means that as studies move towards using groups of demonstrators and observers instead of individuals, we must remain aware that it is not necessarily true that all observers, for example, experience equivalent social stimulation from demonstrators. The idea that individuals in a single social group may have divergent experiences has been noted by researchers of social learning and social foraging (Giraldeau & Lefebvre 1986, 1987; Giraldeau & Templeton 1991; Galef & Allen 1995; Drea & Wallen 1999). In the current study, social companions making up a bird's proximal network were affected both by the age and sex of the individual (other factors may be more important in different species) and by individual differences. On the positive side, our study shows that it is possible to measure these proximal networks, the first step towards examining their influence on social learning.

Researchers have recognized that patterns of social learning are dependent not only on the proximal mechanisms of transferring information from one animal to another, but also on the social context in which learning occurs (Laland et al. 1993; Coussi-Korbel & Fragaszy 1995; Galef & Allen 1995). The perception that large social groups are highly complex, too complex from which to draw useful information, may be the reason why so many studies concentrated on examining mechanisms of learning between two or a few individuals.

Our study does not contradict this perception; the social organization of a flock of captive birds is complex, with differences in proximal networks based on age and sex and individual propensities. A wild flock would be even more complex, where individuals are capable of joining or abandoning the group. The increasing difficulty of studying such complex systems calls for new methods of data collection and analysis. Computer-aided data collection, using systems such as voice recognition to transcribe information into formats parsed and read automatically by databases, will enable the handling of the large volumes of data necessary to measure greater detail of the social environments (White et al., *in press*). Computer simulation, using methods such as individual-based modelling of social interaction and evolutionary algorithms to evolve models to fit real data, opens up entirely new techniques of analysis by providing an arena

for virtual manipulation of the system and producing nonintuitive results for the forces driving behaviour of individuals that may not be accessible in any other manner (Schank & Alberts 1997; Schank 2001).

We were able to measure the proximal networks of birds in a complex social environment and connect them with developmental variables known to be affected by social learning. Large captive groups such as in the current study, an approximation of the sometimes overwhelmingly complex natural situation, are a reasonable starting point for investigation. Combined with computer-aided methods of data collection and analysis, such studies can give us a better understanding of how social context affects social learning and development.

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