

Facultative development of courtship and communication in juvenile male cowbirds (*Molothrus ater*)

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We investigated effects of naturally occurring variation in experience with adult males on development of song and courtship competence in captive juvenile cowbirds. We studied birds in groups housed in large outdoor aviaries that allowed birds to regulate access to social stimulation. In two aviaries, we housed juvenile males and females either with or without adult males. Birds remained in these conditions from September 1999 through their breeding season. We documented social and vocal development of juvenile males in the two aviaries by measuring social assortment and patterns and frequencies of their song interactions. We then brought the juveniles from the two aviaries together to compete against each other for access to females. In addition, we recorded juveniles' songs four times over the study and played back their breeding season songs to females in sound-attenuating chambers to measure the effectiveness of songs in eliciting copulatory responses from the females. Compared to juvenile males housed with adult males, juvenile males housed without adult males developed atypical behavior patterns. They (1) displayed little intrasexual aggression or near-neighbor associations and (2) exhibited different patterns of courtship and copulation, but (3) were as successful at competing for copulations. Furthermore, they developed stereotyped songs sooner and developed more potent breeding season songs. These different outcomes could not be traced to one variable but to a cascade of effects involving diverging patterns of song acquisition and social interaction. The patterns of social skills that emerged indicate considerable plasticity in the mechanisms underlying acquisition of courtship competence. *Key words:* cowbirds, developmental ecology, facultative development, *Molothrus ater*, social behavior, social learning. [*Behav Ecol* 13:487–496 (2002)]

The social environment is a component of an animal's ecology that can have extensive effects on development. For many animals, interactions with conspecifics are predictable and stable sources of information and selection throughout life (Heyes and Galef, 1996; Mousseau and Fox, 1998; West-Eberhard, 1983). The social world in which an animal develops can provide opportunities for learning about food, habitat, mates, and communication (Doligez et al., 1999; Freeberg, 1998; Galef, 1996; Nordby et al., 2000; Stamps and Krishnan, 1999; ten Cate and Bateson, 1988; West and King, 1988).

Within a social environment, variation in densities and assortments of peers, mates, and relatives can change the environmental landscape dramatically, and with it the costs and benefits of interacting with others. Social environments are created from a number of individuals with differing interests, strategies, and experience where information may flow through only subsections of populations or at different rates (Dolman et al., 1996; Mottley and Giraldeau, 2000; Reader and Laland, 2000).

The brown-headed cowbird (*Molothrus ater*) is an excellent model to explore how social environments can organize and control behavioral development because the species experiences such a wide variation in social ecology. Being brood parasites, cowbirds spend their early life unexposed to species-typical behavior, but once they fledge, they join cowbird flocks that can vary extensively in age and sex composition (Friedmann, 1929). Because cowbirds have been so successful in expanding their range, they can now be found in a variety of

different physical and social ecologies. Cowbirds inhabit most parts of North America (Smith et al., 2000), and they have been reported to parasitize many different species (more than 200 different host species; Rothstein and Robinson, 1998) in almost any type of habitat (Morrison et al., 1999). Across their range, cowbirds can experience differences in population density (Johnsgard, 1997), climate (Ortega, 1998), sex ratio (Rothstein et al., 1986; Woolfenden et al., 2001), and timing of the breeding season (Ortega, 1998). Different groups show regional differences in song dialects and whistles (King and West, 1988; Rothstein et al., 1988); some populations migrate, and some do not (Ortega, 1998). Adults and juveniles may migrate different distances (Cristol et al., 1999). Variation also exists in their mating systems, which can range from promiscuity with no pair bonds to polygyny, polyandry, and monogamy, which seems to be the most prevalent (Barnard, 1998; Rothstein et al., 1986).

Thus, cowbirds can experience myriad different social environments. In some locations, throughout their first year juveniles may never interact with adults, whereas in other locations juveniles join flocks of other cowbirds while adults are still in the final days of breeding and remain with them for the entire year (Friedmann, 1929; O'Loughlen and Rothstein, 1993; Rothstein et al., 1980). Flocks composed of all females, all juveniles, and all classes have been reported in the field (Friedmann, 1929). Such diversity in ecology and behavior provided us the impetus to study how young cowbirds come to behave in ways appropriate to their group. We focused on what can be learned within these social groups by juvenile males in their first year; a time in which they must learn to sing, interact with others in their group, and court and mate in the breeding season.

Past work has shown that social learning is important for juvenile cowbirds to develop normally. For example, male song is influenced by interactions with females and other males (O'Loughlen and Rothstein, 1993; West and King, 1988).

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Furthermore, development of courtship competence and even mate preferences are influenced by exposure to conspecifics (Freeberg, 1998; Freeberg et al., 1995; West et al., 1996). These studies, however, have not directly focused on what young males can learn from adult males. In many other species of songbirds, adult males are the important source of learning for young males. For example, song sparrows (*Melospiza melodia*) learn songs from hearing adult males in the vicinity (Beecher, 1996). In cowbirds, however, at least regarding learning about song, it is not clear what role adult males play. Juvenile male cowbirds have the ability to copy songs from adult males (King and West, 1989), but they can also develop species-typical song without exposure to adults (King and West, 1977).

Some research provides evidence that juvenile male cowbirds do indeed acquire information important for successful reproduction from adult males. In a recent study, Smith et al. (2002) placed a group of 75 cowbirds composed of both sexes and of juvenile and adult age classes in a large aviary system and observed their social interactions for a year. Throughout the year, birds assorted based on similarity in age and sex. However, juvenile males that associated more with adult males were more successful in courting females than were juvenile males that associated less with adult males. Because these effects were found in one group, however, the causative nature of these associations could not be determined.

The current study was undertaken to investigate the importance of the presence or absence of adult males in the social environment on juvenile male development. In large aviaries, we housed groups of juvenile males with females and either with or without adult males. Therefore, for half of the juvenile males, the social group contained both age classes of males and for the other half, adult males were absent. We wanted to study not only how juveniles learn song, but also how they learn to use song to negotiate their social environment (West et al., in press). We thus observed juveniles' social behavior within the groups over the course of their first year, focusing on the development of singing interactions. For cowbirds, song is the critical component of the communication system. It is used in male-male counter-singing bouts to establish dominance hierarchies in a group (Dufty, 1986) and singing persistently to females is required to mate successfully.

A main goal of our work was to study social learning and development in a group setting that provided the animals opportunities to self-select information to be learned. An animal must acquire species-typical behavior while dealing with the social pressures of group living and possible competition for informational resources. Although laboratory studies have amply documented the potential interaction between social interaction and vocal learning, many such studies provide animals with information in largely compartmentalized settings where the information for learning is restricted by choices made by the experimenter. In such contexts, the learner may not be able to regulate access to information (e.g., when caged tutors or tape recordings are used). In addition, the animal may be spared knowledge of the natural efficacy of using newly acquired vocal or social skills because the relevant social contingencies do not exist in the captive setting. Studies of song learning in birds that are sensitive to the self-regulated nature of social contexts have begun to produce novel insights into how social experience can affect opportunities for learning and development (Beecher et al., 1994; Bell et al., 1998; Kroodsma et al., 2000; Nordby et al., 1999, 2000; Payne and Payne, 1993; Petrinovich, 1988).

For these reasons we studied juvenile male development in large aviaries where we attempted to remove experimenter-imposed barriers between social and vocal learning by maintaining an environment with species-typical sources of infor-

mation and species-typical feedback. Although the aviaries were large, they obviously cannot be considered directly analogous to natural conditions. The social compositions of the groups, however (i.e., social groups with adult males present or social groups with adult males absent) do occur naturally and are comparably stable in the wild (King and West, 1988).

We were interested in both the breeding season outcomes of the effect of adult males on juveniles and the processes that led to these outcomes. We thus observed birds throughout the experiment and measured social behavior in each condition to track the developmental trajectories of communicative and courtship abilities of the juveniles. Over the fall, winter, and spring before the breeding season, we recorded near-neighbor associations of all the birds to provide a measure of the overall social environment and to determine where opportunities for learning existed. We also measured social interactions by conducting a census of song production and song use for all the males in the conditions. For outcome measures we observed males' courtship success in the breeding season in both their home aviary and then in a new aviary where juveniles from the two conditions could compete against each other for copulations with new females. We also recorded songs of males in each season and analyzed song structure. Finally, we played males' breeding season songs to females in sound-attenuating chambers to measure the effectiveness of the songs in eliciting females' copulatory postures.

METHODS

Subjects

We collected 20 juvenile male, 10 juvenile female, 5 adult male, and 14 adult female brown-headed cowbirds in Monroe County, Indiana, USA, to serve as subjects throughout the experiment. We determined juveniles to be between 50 and 70 days of age by plumage and date of capture. Adult birds were at least 1 year old at the beginning of the experiment. We trapped birds in July and August of 1999 in three areas; two areas were on the laboratory property within 0.25 km of each other and one was located on a horse farm approximately 15 km southwest of the laboratory. Because it was impossible to know much about the prior experiences of the birds being trapped, we randomly assigned birds to conditions ensuring that location and date of capture of the individuals was randomized. We found no systematic differences in behavioral outcomes of individuals based on trapping location or date of capture. We marked all birds with uniquely colored leg bands to permit individual identification. We housed birds in two large 9.1 × 21.4 × 3.4 m outdoor aviaries, where we provided them daily with vitamin-treated water and white millet, red millet, and canary seed plus a modified Bronx zoo diet for blackbirds. The two aviaries were visually and acoustically isolated from each other. Ecological conditions in the two aviaries were similar, with each containing trees, perches, feeding stations, and a grass-covered ground surface and shelters. Being outdoors, birds were exposed to weather conditions, wild local cowbirds that would occasionally land on the aviaries, and the attention of predators.

The only difference between the two aviaries was the presence or absence of adult males. We randomly assigned birds to the two aviaries in the following numbers. In both aviaries, we housed seven adult and five juvenile females. In one aviary, referred to as the juvenile male-adult male condition (JA), we housed eight juvenile males and five adult males. In the second aviary, referred to as the juvenile male condition (J), we housed 12 juvenile males and no adult males. Density and sex ratio were the same between conditions. All birds remained in their home aviaries from September 1999 through

June 2000. Across the entire year, two juvenile males, one adult male, and one adult female died in the JA condition and one juvenile female and one adult female died in the J condition.

Procedure

For 404 total observation hours from September through June, two observers recorded birds' vocal behavior (using song censuses; see below) and social assortment behavior (using near-neighbor associations; see below) for 0.5 to 1.5 h per aviary, starting between 0600 h and 0800 h, depending on seasonal variation in sunrise, and ranging from 5 to 7 days per week. We divided observations into two phases: prebreeding season (22 September through 27 April) and breeding season (28 April through 1 June). At the end of the breeding season phase, we removed birds from their home aviaries and conducted a mating competency tournament, combining subsets of juvenile males from the two conditions in a new aviary with a new group of females.

Song censuses consisted of 15-min blocks in which observers occasion-sampled aviaries, noting any male that vocalized. For each vocalization, we recorded whether it was directed toward another bird or was undirected. To be scored as a directed vocalization, the bird had to vocalize toward a recipient, oriented on axis between approximately 0° and 45°. The distance between vocalizing bird and recipient could not exceed 60 cm. We considered vocalizations produced that were not oriented to another bird as undirected. We recorded a soliloquy from any bird that made 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.

Using 7-min sampling blocks, we recorded near-neighbor associations by sampling each bird (referred to as the "target") in an aviary and noting any other bird (referred to as the "near neighbor") that was within 30 cm. Once we recorded a pair as near neighbors, they could not be recounted as another near-neighbor association unless the pair moved apart and then reassociated. Inter-observer reliability for the prebreeding season was high for song census measures of songs per male and for near neighbor associations per bird (both $r = .89$, both $p < .001$).

For the first 8 months, we manually recorded measures on data sheets. During the breeding season, we developed and began using a system for automated data collection using voice recognition (White et al., 2002). We used IBM ViaVoice Millennium Pro Edition voice recognition software operating on a Pentium III, 500 MHz IBM-compatible computer (Compaq Deskpro EP), running Microsoft Windows 98. We used a solid-state, wireless, omni-directional lapel microphone (Telex WT 150; Telex Communications Ltd.) and receiver system (Telex FMR 150). Microsoft Word 2000 word processing software transcribed speech into text. We then exported text into a database (4th Dimension v. 6.5.1; ACI Inc.) that we programmed to match incoming text to a list of possible codes to detect and correct errors automatically. Interobserver reliability was high using voice recognition for song censuses (songs per male; $r = .98$, $p < .001$) and for near-neighbor associations (near-neighbor associations per bird; $r = .87$, $p < .005$).

Prebreeding season

We divided the prebreeding season into three samples: fall (22 September through 27 November), winter (10 January through 1 March), and spring (2 March through 27 April). The amount of observation time in each sample was equal at 37.5 h per condition for song censuses and 9.33 h for near-

neighbor measures. At the end of each sample, we calculated for each juvenile the number of soliloquies sung and the number of vocalizations directed to males (male-directed song) and females (female-directed song). Also, to measure the length of singing interactions, defined as any instance where a male sang at least one directed song to an individual recipient, we calculated mean songs per interaction as the average number of vocalizations a male directed to an individual recipient within a song census block.

Breeding season

The breeding-season phase commenced on the day of the first observed copulation and continued until we began removing birds from home aviaries for the mating competency tournament. We observed birds between 0600 and 1000 h, the time when virtually all copulations occur (Rothstein et al., 1986). We continued to measure near-neighbor associations as we did in the prebreeding season for a total of 35 observation hours. The implementation of voice recognition for song censuses allowed us to record new behaviors in addition to singing. We recorded a "leave" when the recipient of a directed vocalization flew away within 1 s of the end of the vocalization. We recorded a "depart" when a bird that made a directed vocalization flew away from the recipient within 1 s of the end of the vocalization. Leaves and departs were thus measures of disruptions of singing interactions. We recorded all "copulations," defined as a male mounting a female that had assumed a copulatory posture. We defined a "copulatory posture" as a female arching her back in response to a directed vocalization. We recorded "usurps," occurring when males attempted to copulate with females that had gone into a posture as a result of another male's vocalization. Finally, we scored "fights" when males came into physical contact with one another. We conducted 75.75 observation hours of song censuses in the breeding season.

Mating competency

To compare courtship abilities of juveniles from the two conditions, we conducted a mating competency tournament. We combined a random selection of three juveniles from each condition in a new test aviary, identical to their home aviaries, and observed their courtship success with a group of three juvenile and four adult females that had formerly been housed in an aviary with adult males. We observed birds each morning from 0600 h to 1000 h for a total of 42.25 observation hours. We used song censuses procedurally identical to the breeding season censuses. To test the possibility that scan sampling vocalizing males was systematically biasing our observations, we also took 15-min focal samples on each male in the competition each day, recording the same measures as in song censuses. During these focal samples, we continued to scan for and record any copulations that occurred in the aviary. Focal and scan sampling measures produced similar patterns of results for singing ($r = .72$, $p < .001$). We collected 3.16 times more data in scan samples than we did in focal samples.

We considered a male a success in the tournament if he copulated more than three times or consorted with the same female for 3 days in a row. We considered a male to have obtained a consort day with a female if he either copulated with her or sang the majority of his female-directed songs to her. The consort persistence measure (3 consecutive consort days with the same female) has been shown in the past to be a predictor of copulatory success (Freeberg et al., 1995). We considered males failures if they sang less than one female-directed song per day over a 4-day period. When males reached criterion for success or failure, we replaced them with

males from their original conditions. The test continued until all males from one condition competed in the tournament.

Song recordings

We recorded juvenile males' vocalizations in fall (October 1999), winter (December 1999), spring (April 2000), and finally when their vocalizations had crystallized in the breeding season (May 2000). We made the recordings in their home aviaries using Sennheiser RF condenser microphones recorded into a Sony TCD-D10 PRO digital audiotape recorder. To measure the rate of development and quality of the songs of juvenile males, we (1) documented the emergence of mature song elements in each bird's vocal repertoire from the recording sessions before the breeding season and (2) played the breeding season recordings to females in sound attenuating chambers, measuring each song's efficacy in eliciting a copulatory response from the females.

Song development

We measured the rate of development of song for each juvenile in the two conditions by tracking the emergence of note clusters within their vocalizations. Note clusters are typical features of mature crystallized cowbird song. We plotted songs on a zero-crossing oscilloscope and printed them to paper. Samples averaged approximately 30 vocalizations per male from the fall recording, 20 vocalizations per male in winter, 20 vocalizations per male in spring, and 50 vocalizations per male in the breeding season. For any vocalization to be regarded as a note cluster, we had to be able to detect at least two notes ranging from 300 Hz to 1400 Hz (low-voice notes) and two notes ranging from 1500 Hz to 13000 Hz (high-voice notes). Low- and high-voice notes had to alternate within the note cluster, and all four had to be represented within approximately 200 ms. For each recording session, we then determined the proportion of each male's vocalizations that could be classified as note clusters.

Playbacks

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 1/2-octave equalizer, and a Crown D75 power amplifier through JBL 2105 speakers located in each sound-attenuating chamber. The sound pressure levels of the songs were 85 ± 2 dB (a weighted impulse reading at 0.8 m from the speaker as recorded by a B&K 2209 sound pressure meter). We selected one song from each male in the two conditions based on recording quality from a selection of approximately 50 songs per male. Signal-to-noise ratios, measuring peak noise to peak signal, did not differ between songs from the JA and J conditions (means 48.84 and 48.87, respectively, Student's *t* test, $t_{44} = 0.028$, ns).

Starting on 15 May 2000, we played the songs to a group of females composed of eight adults and six juveniles that had previously been housed in an outdoor aviary from September 1999. The females had been housed without males in the aviary, but they could see, hear, and interact through the aviary wire with resident cowbirds. On 27 April 2000, we brought the females into the lab and housed them in pairs in 1.3-m³ chambers. Housing females in pairs reduced potential stress from being housed in chambers and has been shown to have no influence on females' responses to played back song (Smith et al., 2000; West et al., 1996). 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

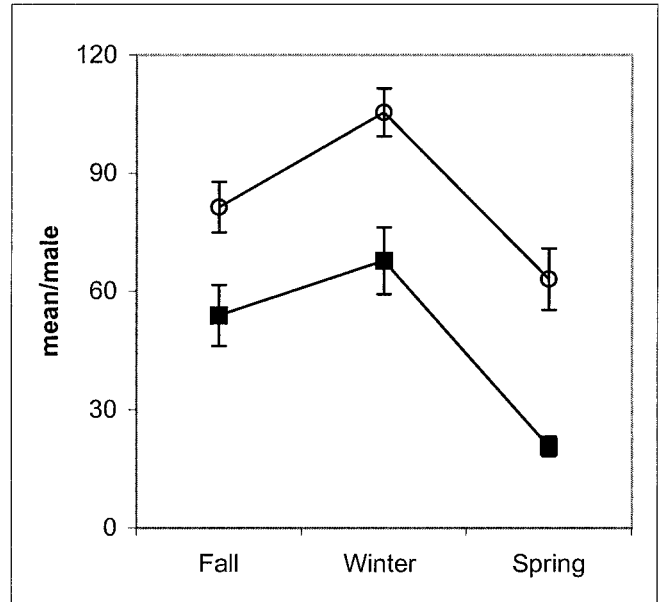


Figure 1 Mean soliloquies per male for juvenile males in the J (circles) and JA (squares) conditions for the three samples of the prebreeding season.

potencies, we computed mean number of responses per female for each song and averaged over all males in each condition. We removed one adult female from the experiment who never responded to any playbacks.

Statistical analysis

We considered the fall, winter, and spring phases of the prebreeding season as three separate experiments for statistical purposes. Due to small sample sizes and heterogeneity of variance between conditions, we used nonparametric statistical analyses throughout. For illustrative purposes, however, we depict means, standard errors, and ranges in results.

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

RESULTS

Prebreeding season

Singing

Juvenile males in the two conditions displayed different vocal and social patterns throughout the months before the breeding season. Figures 1 through 4 depict male singing (mean songs per male) for the three seasons. J-condition juvenile males sang significantly more soliloquies (Figure 1) in the fall (Mann-Whitney *U* test, $U_{5,12} = 14$, $p < .05$), winter ($U = 8$, $p < .01$), and spring ($U = 3$, $p < .001$) than did JA-condition juvenile males. J juveniles sang fewer female-directed songs (Figure 3) than did JA juveniles in winter ($U = 4$, $p < .005$) and had similar trends in the fall ($U = 17.5$, $p > .08$) and spring ($U = 15$, $p > .052$). J juveniles also sang significantly fewer male-directed songs than did JA juveniles during each season (all $U < 13$, all $p < .05$; Figure 2). JA juveniles sang 64% (± 0.09) of their male-directed songs to juvenile males (juvenile male-directed song) during the fall, 49% (± 0.06) during the winter, and 37% (± 0.07) during the spring. There

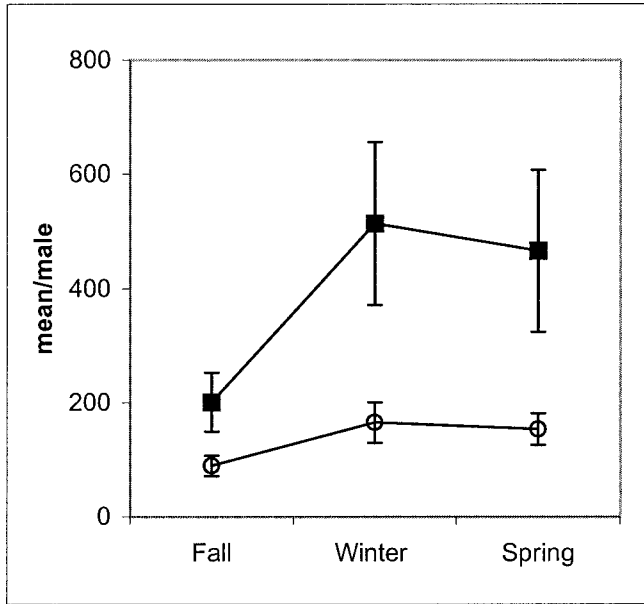


Figure 2
Mean male-directed songs per male for juvenile males in the J (circles) and JA (squares) conditions for the three samples of the prebreeding season.

was no significant difference between conditions comparing juvenile male-directed song (all $U > 20$). J juveniles had fewer songs per interaction across all seasons (all $U < 1.5$, all $p < .001$; Figure 4), even when only comparing songs per interaction for juvenile male-directed song (all $U < 5$, all $p < .005$). Within the JA condition, juvenile males sang significantly more songs per interaction with adult males than with juvenile males in winter (3.26 ± 0.45 songs per interaction vs. 2.40 ± 0.20 , respectively; Wilcoxon T test, $T_6 = 0$, $p < .05$) and spring (2.84 ± 0.45 vs. 1.99 ± 0.26 ; $T_6 = 0$, $p < .05$) but not fall (2.24 ± 0.27 vs. 2.11 ± 0.25 ; $T_6 = 9$, ns).

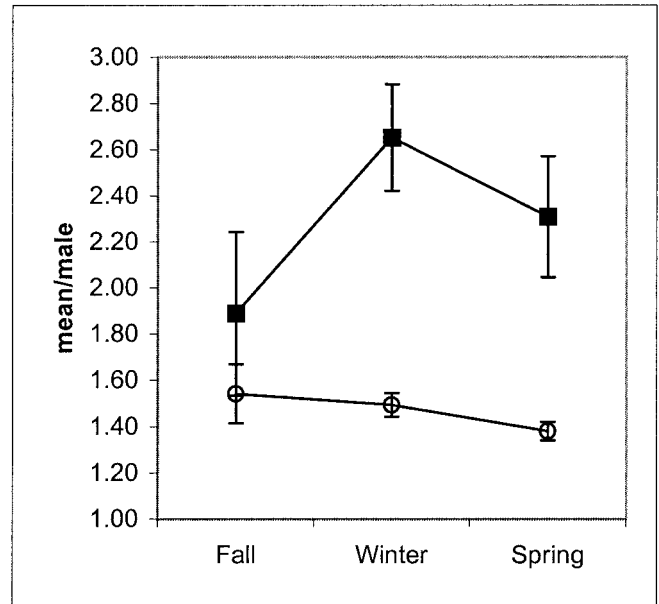


Figure 4
Mean songs per interaction per male for juvenile males in the J (circles) and JA (squares) conditions for the three samples of the prebreeding season.

Near neighbor

Between the two conditions, there were large, significant differences in juvenile male near-neighbor associations. Compared to J juvenile males, JA juvenile males had significantly more near-neighbor associations with other juvenile males in the fall ($U_{7,12} = 0$, $p < .001$), winter ($U_{6,12} = 0$, $p < .001$), and spring ($U_{6,12} = 0$, $p < .001$; Figure 5). JA juveniles also had significantly more near-neighbor associations with females in the fall ($U_{7,12} = 0$, $p < .001$) and winter ($U_{6,12} = 0$, $p < .001$) but not spring ($U_{6,12} = 20$, ns; Figure 6) than did J juveniles.

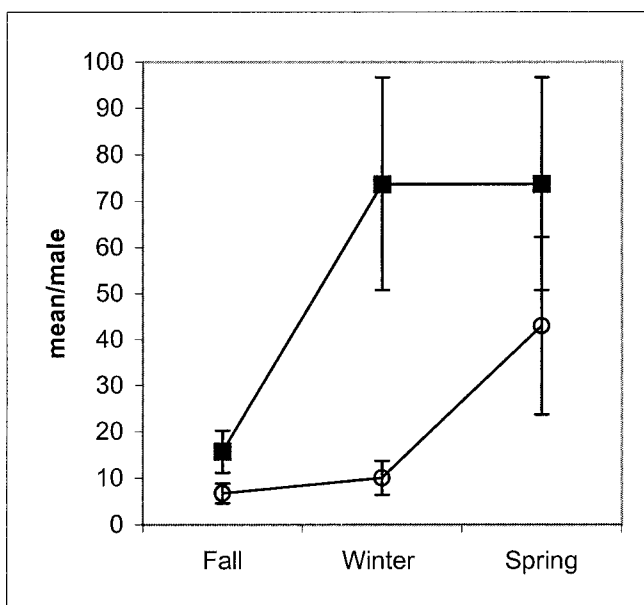


Figure 3
Mean female-directed songs per male for juvenile males in the J (circles) and JA (squares) conditions for the three samples of the prebreeding season.

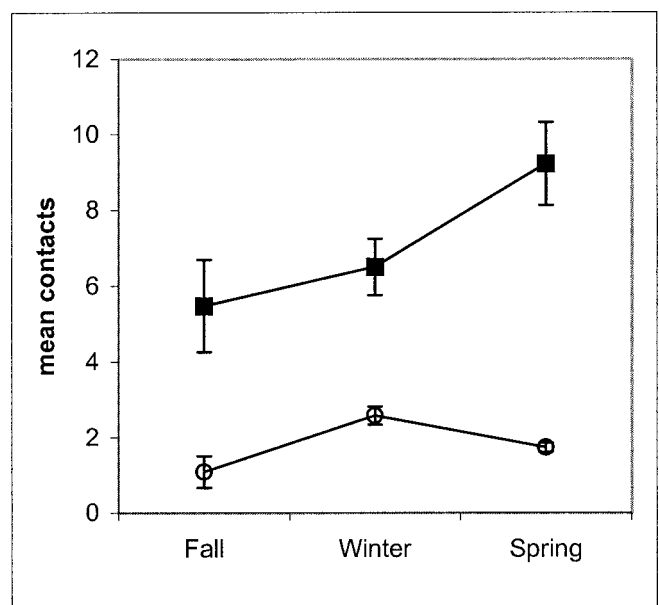


Figure 5
Mean neighbor associations among juvenile males in the J (circles) and JA (squares) conditions for the three samples of the prebreeding season.

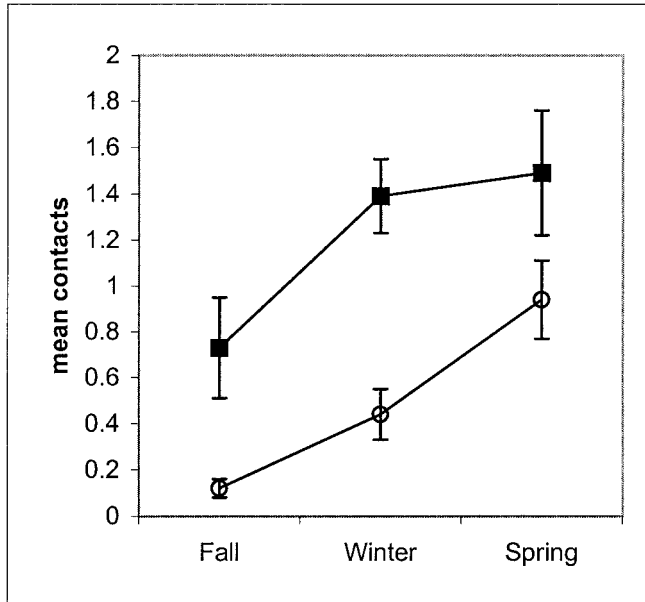


Figure 6
Mean neighbor associations among juvenile males and females in the J (circles) and JA (squares) conditions for the three samples of the prebreeding season.

Adult males

Singing patterns of adult males in the JA condition were variable among males and across seasons before the breeding season. In fall, adult males sang (mean songs per adult male) 17.5 (± 4.11) soliloquies, 113.25 (± 34.87) male-directed songs (31% [± 0.05] of which were juvenile male-directed), 19.25 (± 11.45) female-directed songs, and 1.95 (± 0.22) songs per interaction. In winter, adult males sang 24 (± 9.74) soliloquies, 163 (± 99.23) male-directed songs (65% [± 0.10] of which were juvenile male-directed), 16.75 (± 11.67) female-directed songs, and 2.31 (± 0.57) songs per interaction. In spring, adult males increased singing to 21 (± 3.54) soliloquies, 964.5 (± 105.79) male-directed songs (41% [± 0.20] of which were juvenile male-directed), 185.75 (± 55.17) female-directed songs, and 2.43 (± 0.22) songs per interaction.

Summary

Juvenile males differing only in exposure to adult males displayed dramatically different patterns of singing and social assortment from early in fall to late spring. J juvenile males engaged in more noninteractive, undirected singing and engaged in less interactive, directed singing. When they did sing to other birds, J juveniles sang fewer songs per interaction than did JA juvenile males. Furthermore, as measured by near-neighbor associations, J juveniles spent less time in close association with other birds. We continued observing juveniles in their home aviaries into the breeding season to determine whether these patterns of behavior from the prebreeding season revealed differences that were important to development of courtship behavior.

Breeding season

A summary of singing performance is depicted in Table 1. There were no significant differences in amount of song produced by juveniles between conditions. Differences in how the birds used their song, however, did exist. As a proportion of the number of directed songs sung, J juvenile males had more leaves in response to directed song ($U = 1$, $p < .01$) and more

Table 1
Breeding season singing patterns

	Undirected	Male-directed	Female-directed
JA juveniles			
Mean	76.33	453.50	208.00
Range	2–154	33–876	2–598
J juveniles			
Mean	213.08	331.50	272.17
Range	27–540	61–600	10–840
JA adults			
Mean	70.25	756.50	603.50
Range	14–150	278–1335	16–1059

Mean number of songs per male and range for each condition for undirected song, directed song to males (male-directed), and directed song to females (female-directed) in the breeding season. J, juvenile male condition; JA, juvenile male–adult male condition.

departs ($U = 10$, $p < .02$). There was also a significant difference in how juveniles in the two conditions distributed female-directed song. JA juveniles sang 82.7% of their female-directed songs to their consort female (the female to whom the male sang the most of his female-directed song), whereas J juveniles distributed more female-directed song to other females, singing a significantly smaller proportion to their consort (54.8%; $U = 4$, $p < .005$).

A summary of courtship performance is depicted in Table 2. There were no significant differences in courtship abilities between the two conditions as measured by copulations and postures ($U = 33$, ns). There were, however, significant differences in other breeding-related measures. Only J juveniles ever engaged in usurps ($U = 3$, $p < .001$). J juveniles were less aggressive than JA juveniles as measured by total fights ($U = 0.5$, $p < .001$) and by fights among juvenile males only ($U = 11.5$, $p < .01$). The majority of females that copulated in the J condition copulated with more than one partner (6/9 females, mean of 2.11 partners), whereas no females in the JA condition ever copulated with any male other than their consort (Fisher's Exact test, $p < .01$).

Figure 7 depicts near-neighbor associations for the breeding season. JA juveniles engaged in more near-neighbor associations with other juvenile males than did J juveniles ($U_{6,12} = 2$, $p < .001$). There was no difference in associations among

Table 2
Breeding season behaviors

	Copulations	Leaves	Departs	Usurps	Fights
JA juveniles					
Mean	1.33	66.33	2	0	7.33
Range	0–6	4–143	0–6	0.00	3–10
J juveniles					
Mean	1.58	256.42	17	0.75	1.25
Range	0–7	20–653	1–30	0–2	0–3
JA adults					
Mean	9.75	136.25	5	0	8.50
Range	0–26	53–254	2–9	0.00	1–17

Mean number of breeding season behaviors scored per male and range for each condition. J, juvenile male condition; JA, juvenile male–adult male condition.

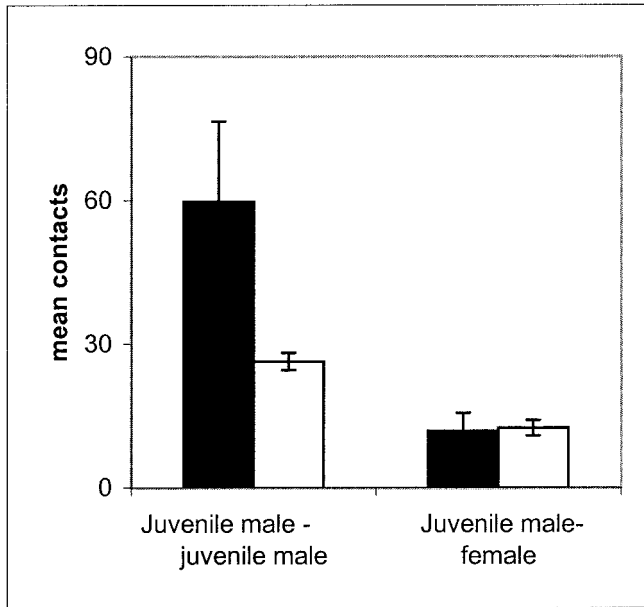


Figure 7
Mean near-neighbor associations among juvenile males and among juvenile males and females in the J (open bars) and JA (filled bars) conditions in the breeding season.

juvenile males and females between the two conditions ($U_{6,12} = 27$, ns).

Summary

Juvenile males housed with adults displayed singing and courtship patterns typical of juvenile males raised in an environment with all classes of birds (Smith et al., 2002) and typical of behavior reported in the field (Rothstein et al., 1986). Juvenile males housed without adult males, however, exhibited a pattern of courtship behavior heretofore undescribed for cowbirds in Indiana. These males engaged in few extended bouts of singing, displayed little intrasexual aggression, did not consort consistently with individual females, and copulated with several females. Differences also existed across conditions in the behavior of females. Females in the J condition copulated with several partners, whereas females in the JA condition each copulated with one male.

Although we suggested here that both groups of juveniles were equally successful at getting copulations, it could be argued that the comparison of courtship abilities across conditions was not appropriate because JA juveniles were competing against adult males. We therefore conducted the mating-competence tournament to compare the courtship abilities of the two classes of juveniles.

Mating competency

Table 3 presents a summary of juvenile male singing and courtship for both conditions. Three of the six JA juvenile males tested reached criterion for success and six out of eight J juvenile males tested reached criterion for success (Fisher's Exact test, ns). Of those who sang to females, J juveniles sang fewer directed songs to females but received significantly more copulations per female-directed song than did the JA juveniles ($U_{6,6} = 5$, $p < .05$).

Summary

J juvenile males were successful in courting a new group of females when placed in direct competition with JA juveniles.

Table 3
Mating competency patterns

	Undirected	Male-directed	Female-directed	Days	Copulations	Consorts
JA juveniles						
Mean	18.50	83.17	190.50	7.83	0.67	2.81
Range	0–46	5–275	4–433	4–13	0–3	0–8
J juveniles						
Mean	15.50	42.88	156.00	5.63	2.63	3.00
Range	1–43	2–145	1–352	4–7	0–8	0–6

Mean number per juvenile male and range for each condition for undirected song, male-directed song, female-directed song, number of days in tournament (days), number of copulations in tournament, and number of consorts in the mating competency tournament. J, juvenile male condition; JA, juvenile male–adult male condition.

In fact, the significant difference in number of copulations received per female-directed song and the trends in number of birds reaching success, number of days to reach success, number of copulations, and number of consort days all suggest that the J juveniles were more successful in the competition than the JA juveniles.

Song analysis

Song development

Over the entire set of recordings, we documented 11 note clusters that were sung repeatedly between J juvenile males and 13 repeatable note clusters for JA juveniles. Compared to JA juveniles, J juvenile males had a significantly greater proportion of vocalizations that were classified as note clusters in fall (0.22 of JA juvenile vocalizations and 0.70 of J juvenile vocalizations; $U_{12,5} = 2$, $p < .002$) and in spring (0.96 and 0.99, respectively; $U_{12,6} = 11.5$, $p < .02$) and had a similar trend in winter (0.59 and 0.76, respectively; $U_{12,5} = 12$, $p > .058$). For reference, 93% of vocalizations of adult males in the JA aviary were classified as note clusters in fall, and 100% in spring. Adults did not vocalize enough in winter to record a representative sample. In addition, J juveniles had a significantly higher proportion of their spring songs match exactly their song types sung in the breeding season than did JA juveniles (0.45 of spring vocalizations compared to 0.19, respectively, $U_{12,6} = 6$, $p < .005$). There was also a difference in the structure of the songs. A cowbird song is typically sung with two note clusters but can be sung with three. Significantly more J juveniles (11/12) had three-note cluster songs in their breeding season song repertoires than did JA juveniles (0/6; Fisher's Exact test, $p < .001$). We recorded no three-note cluster songs from adult males in the JA condition.

Playbacks

Females responded with a copulatory response significantly more often to the songs of J juveniles than they did to songs of JA juveniles (Wilcoxon T test, $T_{13} = 91$, $p < .001$; Figure 8).

DISCUSSION

The presence of adult males in the juvenile males' social environment had significant influences on the development of juveniles' vocal and courtship behaviors. Compared with juvenile males housed without adults, juvenile males that had experience interacting with adult males (1) engaged in more

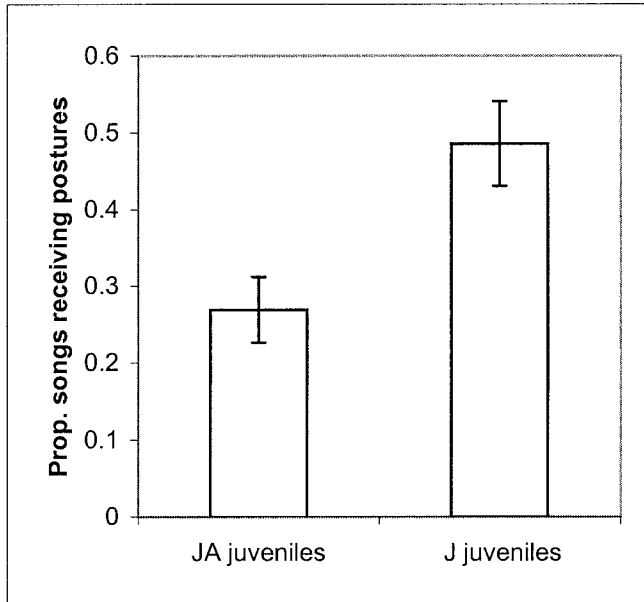


Figure 8
Mean proportion of playbacks for each song from JA and J conditions to which females responded with a copulatory posture.

and longer duration singing bouts with other males, (2) displayed patterns of courting and copulating within the breeding season more typical of wild local cowbirds, and (3) developed song more slowly and of lower potency.

Cowbird song serves two functions in social interactions. It is sung to females as part of courtship, and it is sung to males to establish intrasexual social relationships within the flock (Dufty, 1986). Thus, to breed successfully, males must develop song effective at eliciting copulatory postures from females and, just as important, must sing the song. Similar to females, males can distinguish a high-potency from low-potency song (West and King, 1986). Singing a high-potency song can result in aggression from other males. Thus, song develops as a compromise between intersexual and intrasexual pressures. In the present study, without adult male influence, the J males assorted less with other males, interacted less with song with other males, and sang more undirected song. This relative lack of male social interactions cascaded into lack of aggressive interactions and lack of competition. In comparison, juvenile males in the JA condition were more frequently interrupted in attempts at soliloquies by the arrival or nearby presence of other males. These juveniles engaged in more male singing interactions and produced less undirected song. These differences served to launch juveniles in the two conditions down very different vocal and social developmental trajectories, influencing song potency and even mating behavior.

Possibly, the observed difference in song potency between JA and J juvenile males was an artifact of JA males being in a confined area with adults. On this hypothesis, JA juveniles sang less mature song while in the adults' presence to allow them to escape negative consequences of aggression by adults (see Casey and Baker, 1993; Payne, 1981; West and King, 1980). Throughout the extensive observations we made across the study, however, we found no evidence that adult males conspicuously or continuously dominated or threatened young males that directed songs to them (although it may not take extensive feedback for aggression to have an effect). Contrary to an aggression hypothesis, J juveniles' song was more developed as early as the fall and winter; times at which adult

males in the JA condition rarely interacted at all with the juveniles.

We suggest that the different learning environments that emerged in the two conditions provided juveniles with different types of reinforcement for their actions, thus influencing their behavioral and vocal development. Adult males behaved and interacted in different ways from juveniles, and when juvenile males interacted with adults, different patterns of singing and social associations by adults provided JA juveniles with different response contingencies to their actions. For example, song practice appears to be related to song potency and song stereotypy, and opportunities for song practice may depend on the contingencies present in the social group.

Additionally, responses to song differed in the two conditions. Adult males in the JA aviary often responded to song by not moving away from song overtures. In past work, we have shown that when singing to females, young male cowbirds appear to be able to modulate song content in a facultative manner; specifically, young males appear to be sensitive to how often females stay and how often they respond when males direct a song to them, and males modify vocal content in response to such behavior (Smith et al., 2000; West and King, 1988). In the present case, it is possible that a similar facultative ability when singing to males may have led to opposing effects on song development.

It is possible that the effects revealed in this study could be epiphenomena of the unnatural aviary setting or that some other unmeasured variable in the aviaries could be responsible for the observed findings. Past work, however, has replicated some of the main effects observed here. For example, patterns of near-neighbor associations, singing interactions, and courtship behavior of the birds in the JA condition were similar to the findings of Smith et al. (2002), where birds were housed in the same social composition in an aviary complex four times the size of the ones used in the current study. Also, the patterns of behavior from the JA condition are representative of observations made in the field (King and West, 1988). And past work replicates the finding that juvenile males with no adult male feedback do not learn rudiments of countersinging and display, important components of intrasexual singing interactions (Freeberg et al., 1995; West et al., 1996, 1997). We have also recently replicated the early effects of adults on juvenile social assortment and singing patterns in groups of young juveniles that were within weeks of independence from their hosts (White et al., 2002). Even in these young birds, the effects of adding or removing adults from their social group on their behavior were similar to the effects shown in the present study. For example, juveniles who were housed without adults had fewer near-neighbor associations and began singing earlier and more frequently than juveniles housed with adults.

Finally, because we used naturally occurring variation in social groups, some of the patterns of behavior seen here can be tested in free-living groups in nature (see Freeberg et al., 2001, for a comparative study of song structure between two cowbird populations that also differ in social ecology). The effects seen in captivity in this study can be used to make testable predictions about spacing behavior, song potency, and patterns of mating behavior for groups of cowbirds in the wild, and such a social approach to looking at behavioral development may be able to explain some of the observed variation in demographics and behavior reported in the field (Rothstein and Robinson, 1998). Also, investigations of how variation in social experience affects development in other species can begin to shed light on general rules of social organization (see, e.g., Adkins-Regan and Krakauer, 2000; Korpela and Sandnabba, 1994; Moore et al., 1995; Price et al., 1994).

Developmental ecology

Regardless of the causes of the differences across conditions, the outcome was clear: developmental reaction norms (Schlichting and Pigliucci, 1998) for juvenile male social behavior were large and variable. Such variability is especially striking for a species classically considered as having a closed developmental system (Lehrman, 1974; Mayr, 1974). A benefit of such a facultative system of development that allows for patterns of behavior to be organized in response to recurring patterns of social stimulation could be to permit young cowbirds to enter and conform to the variety of social environments they may encounter. This research program is in its infancy and will require more study of how individuals of different ages and sex fit together in a group to make up a social system. The next phase of this study will be to see how these different patterns of behavior displayed by the two groups of juveniles persist into adulthood and to examine the stability of social groups as new generations of juveniles are introduced. Determining the mechanisms of cross-generational transmission of information important in developing typical breeding season behavior, as well as determining the duration and stability of these behavior patterns, will provide insight into how selection acts on social behavior over ontogeny.

This paradigm, studying how social factors present in a large social group can influence development, provides a new means for understanding and predicting mating behavior. Ecological conditions have traditionally been considered critical in the evolution of mating behavior (Emlen and Oring, 1977). Additionally, ecological conditions experienced throughout development can influence phenotypic expression. Here, integrating social ecology with an ontogenetic perspective revealed facultative properties of mating and vocal behavior that potentially have important evolutionary consequences. These properties can only be understood by taking into account the social ecology the birds experienced across development.

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