

Developmental Origins of Sociality in Brown-Headed Cowbirds (*Molothrus ater*)

Jennifer L. Miller and S. Grace Freed-Brown
Indiana University

David J. White
University of Pennsylvania

Andrew P. King and Meredith J. West
Indiana University

Five variables were studied relating to the emergence of sociality in hand-reared cowbirds (*Molothrus ater*): proximity, sex assortment, reactions to adults, head-down displays, and vocalizations. The authors were especially interested in female sociality because adult female birds influence male courtship, song content, and use through proximity, attention, and displays. The authors found that young female birds failed to show same-sex affiliation typical of the species at any point in the study. Brief introduction of adults did not affect social patterns. Adults used more head-down displays than juveniles, who used more displays with familiar peers. Directed and undirected singing emerged concurrently; directed singing was positively correlated with earlier hatching. This is the first demonstration of the need for early learning in the development of female sociality.

Keywords: social behaviors, development, female sociality, brown-headed cowbird

For the study of development to be inclusive, investigators must attend to co-occurring behaviors from different domains that emerge at roughly the same time (W. J. Smith, 1977). A young animal must find food while avoiding predators, communicating with conspecifics, and changing social roles during events such as weaning, dispersal, and resource competition. Textbooks in animal behavior compartmentalize the functional categories that often develop concurrently: species recognition, communication, predation, foraging, navigation, and social systems (Alcock, 2001). Texts on human development also tend to compartmentalize the child into separate systems, including motor, perception, cognition, language, and socialization development (Spelke & Newport, 1998). Obviously, authors must adhere to some form of sequential presentation of knowledge. However, these accounts may de-emphasize the co-occurring and interactive nature of developmental events (L. B. Smith & Thelen, 1993).

Behaviors may also be organized into nondevelopmental systems such as the motivational and ecological accounts of Hogan (1994) and Timberlake (1993) or the social analysis of infant

interactions by Carpenter, Pennington, and Rogers (2002). However, these approaches run the risk of misinterpreting the functions of behavior as the context changes (West, King, & White, 2003). If function is misinterpreted, then we may misunderstand the basis of selection.

In the present study, we carried out concurrent analyses of the origins of behaviors that contribute to early sociality in brown-headed cowbirds (*Molothrus ater*). Brown-headed cowbirds are intriguing subjects for a developmental analysis because their broods' parasitic habits emphasize the need for acquiring conspecific social behavior after they leave the care of foster species. Within a matter of days or weeks after fledging, young cowbirds are found in juvenile flocks, although little is known about their early flock organization (Friedmann, 1929). During these first two months, cowbirds become independent from their host species, start to find food on their own, and join or form flocks with conspecifics (Woodward, 1983). As flocks of juveniles and adults form, social organization is characterized by robust sex and age assortment (V. A. Smith, King, & West, 2002). During this same time frame, male birds begin to produce primitive sounds representing the first traces of song development.

Our subjects were studied during the first two months of life. We hand reared birds from the egg to give them comparable social experiences to observe how they behaved during the period from dependence to independence and to examine the transition to more socially diverse settings. Hand rearing from the egg permitted us to control postnatal variation in ambient temperature, diet, and feeding times. We could also obtain day-accurate physical and social measures for birds of both sexes to categorize and measure the timing of changes in sociality.

Our efforts included examining both the origins and modifiability of early behavior, leaving open the possibility of environmental influence from the onset of a behavior's history, a point empha-

Jennifer L. Miller, S. Grace Freed-Brown, Andrew P. King, and Meredith J. West, Department of Psychological and Brain Sciences, Indiana University; David J. White, Department of Psychology, University of Pennsylvania.

The work was supported by grants from the National Science Foundation and the Explorer's Club. Research was approved by the Institutional Care and Use Committee of Indiana University (01-085). We thank Lucy Ho for her help. We also thank Erin Ables and Julie Gros-Louis for providing helpful comments on drafts of this article.

Correspondence concerning this article should be addressed to Meredith J. West, Department of Psychological and Brain Sciences, Indiana University, 1101 East Tenth Street, Bloomington, IN 47405. E-mail: mewest@indiana.edu

sized by Burghardt (1977). Our goals were to demarcate the emergence and change of five target behaviors and look for evidence of behavioral interdependence, possibly leading to different developmental trajectories. First, we recorded the nature of affiliations from the time at which the young birds could locomote and choose social partners. Second, we derived sex assortment from the affiliation data. Third, we documented the young birds' first reactions to adult cowbirds. Fourth, we measured the use of a species-typical behavior, the head-down (HD) display, which is used by adults and juveniles and sometimes thought to be associated with species recognition (Göth & Hauber, 2004). Fifth, we recorded song development in male birds, including whether their songs were directed to another individual or undirected. We know that sex assortment and singing skills interact. Adult female birds show strong assortment apart from young male birds by metering their social distances while showing strong affiliation with female birds (V. A. Smith et al., 2002). However, some female birds show more affiliation with male birds than do others, and rate of affiliation affects rate of song ontogeny and development of countersinging (King, White, & West, 2003). For example, male birds with more female interactions develop stereotyped song earlier than male birds with fewer social interactions with female birds. Thus, variation in the ontogeny of sex segregation may interact with the ontogeny of song content and use.

We were especially interested in studying the emergence of sex assortment in flocks. The flocks we have previously studied have varied in size from 7 to 80 birds that live and feed together. Sex and age assortment are fundamental characteristics of cowbird flocks, and variation in flock assortment is highly predictive of reproductive success (King et al., 2003; V. A. Smith et al., 2002). For example, low sex assortment increases reproductive output (King et al., 2003), and high male age assortment is associated with increased reproductive success (Gros-Louis, White, King, & West, 2006). Flock structure defines opportunities for young male and female birds to learn about one another and acquire social skills necessary for successful courtship (King et al., 2003; West et al., 2003; White, King, & West, 2002). A consequence of sex and age assortment is the creation of *social gateways* controlling the flow of stimulation throughout the group (West et al., 2003; White, King, Cole, & West, 2002). For example, low sex assortment allows male birds to approach and learn about female birds and vice versa, whereas high sex assortment creates few such learning opportunities (King et al., 2003).

The use of flock housing and the concept of the social gateway grew out of the discovery that both male and female birds learn new skills that are not seen when birds are housed in highly restricted settings such as social isolation in pairs (King, West, & White, 2002; Nordby, Campbell, Burt, & Beecher, 2000). We have found that female birds modify their own mate and song preferences when they live in flocks but not when living in pairs in conventional laboratory housing (Freeberg, 1996; King et al., 2003; West, King, White, Gros-Louis, & Freed-Brown, in press).

Why would flock housing foster learning not seen in other settings? In a flock, birds can meter their distance from conspecifics, negotiate proximity with flockmates, and form stable bonds with members of different age or sex classes. Individuals can also deny other birds access to them and therefore to the opportunities that emerge from interacting with them. We believe these options stimulate the birds' attention to one another and modulate their

chances to learn from conspecifics (Beecher, 1996). Flock attributes, like sex attributes, define what is to be learned.

In this study, we had three hypotheses. First, on the basis of the strong same-sex affiliation of adult female birds across many experiments and settings, we expected that young female birds would show same-sex affiliation earlier than young male birds (V. A. Smith, King, & West, 2000). Second, we thought that undirected song would emerge prior to directed song on the basis of our findings of earlier use of directed song in male birds housed with responsive adult female or older male birds (V. A. Smith et al., 2002; White, King, & West, 2002). Finally, we expected evidence of social organization soon after independence.

General Methods

Hand Rearing Methods

Subjects. We hand reared from the egg a total of 68 nestlings, 36 female birds and 32 male birds. The eggs came from six captive flocks of local cowbirds (*Molothrus ater*) that had between 7 and 8 male birds and 8 and 10 female birds from Monroe County, Indiana. All eggs were incubated in a Petersime (Gettysburg, OH) Model 1 incubator until hatched on Days 11 or 12. After hatching, all nestlings were taken from the incubator and housed in nestcups in pairs or triads in a Hovabator (Model 1692N; GQF Manufacturing, Savannah, GA).

Housing. Around postnatal Day 10, birds were taken out of the Hovabator, placed in age-matched flocks, and housed in small indoor cages (0.6 m × 0.9 m × 0.73 m) until Day 20 (Experiment 1). Across the experiment, seven flocks were formed. Around Day 20, flocks were moved to outdoor aviaries (20 m × 10 m × 8 m) until Day 55 (Experiment 2). Birds remained in these aviaries with the same flock except for a 5-day social assessment test (Experiment 3) with a 36-m × 10-m × 12-m aviary. Ecological conditions were similar in all aviaries and comprised a grass-covered ground, perches, and sheltered areas. Birds were exposed to sights and sounds of the area, which included wild conspecifics and the sight and attention of predators.

Feeding schedule. From the time of hatching until postnatal Day 10, birds were hand fed a meatglop diet through 1-mL syringes every 15 min from 0600 to 2200 (Searcy, Peters, & Nowicki, 2004). From Day 10 to Day 20, birds were hand fed eggfood or meatglop in rotation every 30 min. After postnatal Day 20, birds were hand fed eggfood until they were able to feed independently, which occurred around Day 25. Beginning on Day 11, birds were provided with white and red millet, canary seed, vitamin-treated water (Aqua-Vite; Nutritional Research Associates, South Whitley, IN), and a modified Bronx zoo diet for blackbirds, which included Avia (Nutra-Vet Research Corporation, Poughkeepsie, NY). The birds wore colored leg bands to permit individual identification.

Data Collection

In addition to taking data by hand, we used voice recognition (White, King, & Duncan, 2002). Observers spoke leg band acronyms into wireless microphones (Telex WT 150; Telex Communications, Burnsville, MN). We used IBM (White Plains, NY) ViaVoice Millennium Pro Edition voice recognition software operating on a Pentium III, 500-MHz IBM compatible computer, running Microsoft Windows 98 and Microsoft Word 2000 to receive the voice signal and transcribe speech into text. We exported the text into a database (4th Dimension, Version 6.8; ACI Inc., Reno, NV).

Statistical Analysis

Because of low sample size and nonheterogeneity of variance, we used nonparametric tests with two-tailed *p* values set at .05 for the analysis. All

statistical analyses were done with SPSS Version 10 (SPSS, 2005). We used relative differences in number and proportion of female–female (FF), female–male (FM), male–male (MM), and male–female (MF) points. The calculation of proportion for FM is 1 FF and for MF is 1 MM. Tests were conducted between FF and FM to determine whether sex assortment was present. Identical tests were conducted between MM and MF. There were no differences in the amount of activity between female and male birds, thus rates and 95% confidence intervals (CIs) are reported for descriptive purposes. Individual birds could not be reliably sexed until the end of the experiment. Thus, with regard to sex assortment, most of the data were collected blind. Interobserver reliability measures were not tested during the first and second experiment because only during the third experiment did individuals take comparable amounts of data during same time frames. Interrater reliability during Experiment 3 between Miller and Freed-Brown was .91 (intra-class correlation coefficient).

Experiment 1: First Measure of Sex Assortment

The purpose of the first experiment was to measure sex assortment in birds 10–23 days of age in three flocks, each consisting of 9–10 individuals, totaling 29 hand-reared birds.

Method

Three observers recorded the social assortment of 29 birds in three flocks throughout the day. Social assortment was measured by a scan procedure, which recorded near-neighbor (NN) points in the small indoor cages. A NN point was scored when an individual bird was within 6.4 cm of another bird. The birds on perches were sampled by scanning horizontally across the cage. Birds were not recorded as NNs when they were on the bottom of the cage because it was likely that they were near one another because of attraction to food or water rather than to each other. We opportunistically took 3–9 scans between feedings per flock per day. NN scans were recorded by hand, typed into Microsoft Word 2000, and imported into a database (4th Dimension, Version 6.8; ACI Inc., Reno, NV).

Results

During 70 NN scans, we recorded a total of 566 NN points for three flocks. Across the three flocks, the rate of MM NN points was higher than FF NN points (male birds: $x = 2.30$, CI = 0.18–4.12; female birds: $x = 1.70$, CI = 0.48–2.92). There was no difference between the average proportion of NN points for MM and MF affiliations (MM: $x = 0.53$, CI = 0.49–0.57; MF: $x = 0.46$, CI = 0.42–0.50). In addition, there were no differences between the average proportion of NN points for FF and FM affiliations (FF: $x = 0.47$, CI = 0.27–0.67; FM: $x = 0.53$, CI = 0.33–0.73; see Figure 1).

Experiment 2: Second Measure of Sex Assortment

The purpose of the second experiment was to measure sex assortment in 65 birds 26–56 days of age in seven flocks, each consisting of 6–12 individuals. After Experiment 1, all birds were moved to large outdoor aviaries (see the *Subjects and Housing* section for details).

Method

Three observers recorded social assortment for each flock between 0700 and 1000. Social assortment was measured in 7-min NN blocks with a scan procedure. A NN point was scored when two birds were within 15 cm of each other. A bird had to leave the vicinity and rejoin to be counted as another NN point. Because the birds moved infrequently, it was possible to record all NN points.

A total of 52 birds in five flocks were included in the analysis because of skewed sex ratios in the remaining two flocks, discovered at the end of the experiment. The sex of individuals could not be reliably determined until the end of the experiment. For the flocks not included, one flock had 7 female birds and 2 male birds, and the other flock comprised all female birds.

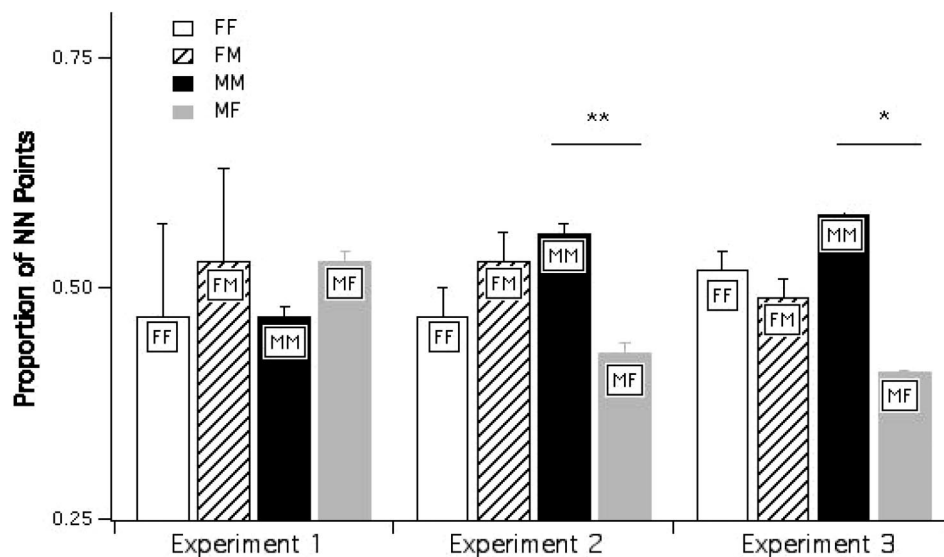


Figure 1. Average proportion of female–female (FF), female–male (FM), male–male (MM), and male–female (MF) near-neighbor (NN) points during Experiments 1–3. Data are displayed as means and standard errors. * $p < .05$ (statistically significant difference). ** $p = .084$ (trend).

Results

During 168 NN blocks, we scored a total of 6,838 NN points for the five flocks. Across the five flocks, the rate of MM NN points was higher than FF NN points (male birds: $x = 17.80$, $CI = 10.96-24.64$; female birds: $x = 13.16$, $CI = 5.19-21.13$). There was a trend for the average proportion of NN points to be higher for MM than MF affiliations (Wilcoxon's Signed Ranks Test: $T = 0$, $N = 5$, $p = .084$). However, there were no differences between the average proportion of NN points for FF and FM affiliations (Wilcoxon's Signed Ranks Test: $T = 4$, $N = 5$, $p = .345$; see Figure 1). Figure 2 shows that the male birds (see bottom panel) showed more consistent same-sex assortment than did female birds

(see upper panel) who assorted more with male birds on approximately the same number of days as with female birds.

Experiment 3: Third Measure of Sex Assortment and Adult Introduction

The purpose of the third experiment was to measure patterns of affiliation during the hand-reared birds' first cohabitation with adult conspecifics. The flocks were placed in a new aviary for a 5-day assessment with adults and then returned to the conditions of Experiment 2. We used an A-B-A-B-A design in which each A involved 1 day of measuring baseline juvenile behaviors, and each

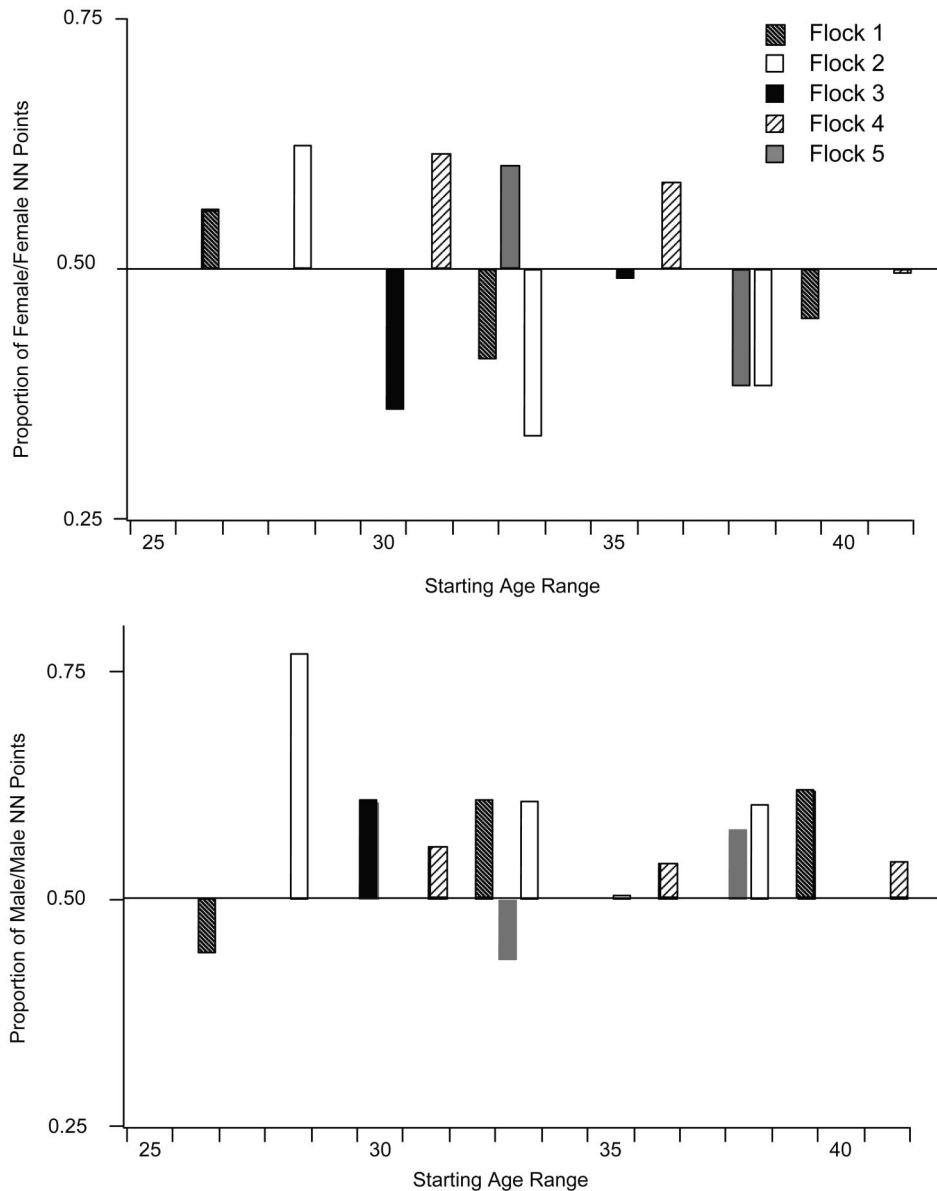


Figure 2. Average proportion of female–female (top panel) and male–male (bottom panel) near-neighbor (NN) points during Experiment 2. Data are broken into two 3–5-day periods. The youngest bird in the flock determines the starting age range. Data are displayed as means.

B represented 1 day of measuring juvenile behaviors when adults were introduced. The entire experiment spanned 5 days for each of six flocks, with three 1-day baseline periods separated by 1 day of interacting with adult male birds and 1 day of interacting with adult female birds. Previous research has suggested that the HD displays of cowbirds are associated with species recognition (Hauber & Sherman, 2003). Thus, we took the opportunity to measure HD displays and NN data during the 5-day experiments.

Method

We created six new flocks of birds between the ages of 31–54 days by recomposing the flocks from Experiment 2: For four of the flocks, we took half of one flock and paired it with half of another flock, and two flocks were composed from three Experiment 2 flocks. We divided the flocks such that the sex ratios were approximately equal, and the flock sizes were of equal number. Because of age differences, we collected data on two flocks at a time in two different aviaries that were visually separated from one another. The first 5-day test round began with the earliest hatching birds and the last round concluded with the later hatched birds so that all birds were run within the same age range.

During Days 1, 3, and 5 of each of the assessments for each of the six flocks, when adult birds were not present, two observers took six (three between 0800 and 1000, and three between 1400 and 1500) 7-min NN scan blocks in each aviary for a total of twelve 7-min blocks of observations in each aviary (see Figure 3). We measured the social assortment by using similar NN procedures as above, except the area between the target bird and its NN was expanded to an area of 30 cm because of the increase in size of the aviary (36 m × 10 m × 12 m). During Days 2 and 4, we put three adult female birds or three adult male birds into an aviary with juveniles 15 min before data collection began in the morning and removed them around 1600. On Day 4, the location of the adults was switched so that the aviary with female birds had male birds, and the aviary with male birds had female birds. A total of 18 adult female and male birds were used, with 3 different male and female birds used during each round. Twelve NN blocks were taken each day except for 1 day in Round 1, which had 9 and 10 blocks because of weather.

A HD was scored when one bird would lower its head (also known as soliciting or initiating a HD) to another individual (recipient). The recipient may or may not HD back to the individual soliciting the HD.

Results

Spatial proximity and sex patterns. We collected a total of 354 NN scans across Experiment 3; a total of 19,094 NN points were taken for the six flocks between 31 and 54 days of age. Each flock was considered an independent data point. Across the six flocks, the average number of MM NN points per block was higher than the average number of FF NN points (male birds: $x = 6.01$, CI = 4.59–7.43; female birds: $x = 4.30$, CI = 3.08–5.52). There was a significant difference between the average proportion of NN points for MM and MF affiliations (Wilcoxon's Signed Ranks Test: $T = 0$, $N = 6$, $p = .026$). However, there were no differences between the average proportion of NN points for FF and FM affiliations (Wilcoxon's Signed Ranks Test: $T = 4.50$, $N = 6$, $p = .207$; see Figure 1).

Reaction to adults. There were no significant differences in the average proportion of NN points across the 3 baseline days for each of the following: MF, FM, MM, or FF (four Friedman Tests, all $\chi^2 > 1.333$, $p = .260$). Because there were no differences between the baselines, we used a mean average proportion to determine whether there were differences when adult male birds or adult female birds were introduced. During adult introduction days, statistical tests were done on adult–juvenile data. There were no significant differences between the average mean proportions on baseline days compared with days when adult male birds or adult female birds were introduced (Wilcoxon's Signed Ranks Test: all $T_s > 4$, $N = 6$, all $ps > .34$). Further inspection of NN assortment revealed no developmental changes in same-sex assortment across Experiment 3 (see Figure 4).

Use of HD displays. We recorded a total of 48 HDs; 23 were recorded for juveniles, and 25 were recorded for adults.



Figure 3. Photograph illustrates a female adult introduction to a flock of juvenile cowbirds in Experiment 3. In the photograph, 3 adult female birds and 8 juvenile birds are present. The similarity of plumage demonstrates the difficulty in determining the sex of juvenile female and male birds as well as differentiating the age of the adult female birds from the juvenile birds. The photograph also illustrates typical spacing and range of behaviors that characterize a flock of birds this age and size.

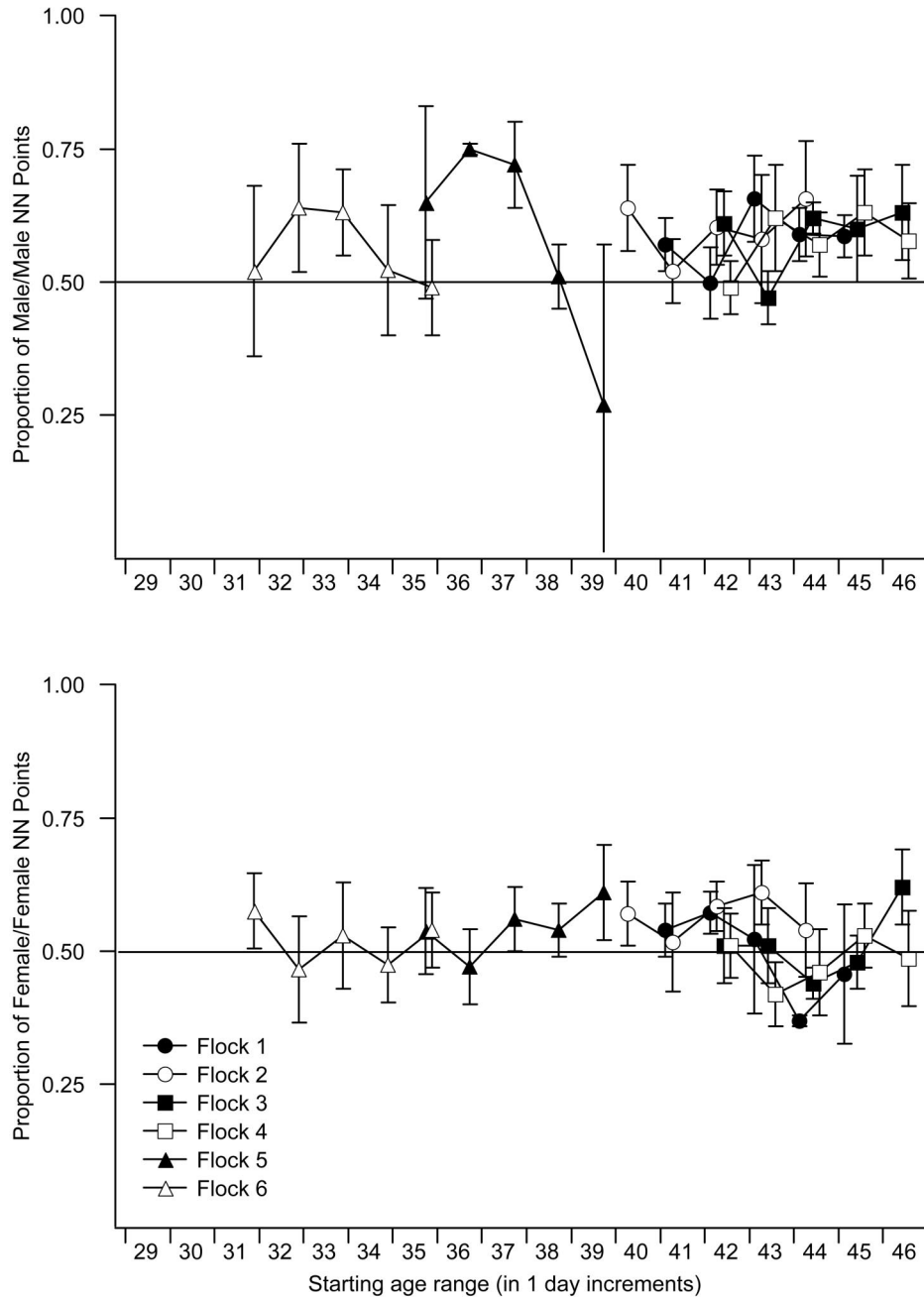


Figure 4. Average proportion of male–male (top panel) and female–female (bottom panel) near-neighbor (NN) points during Experiment 3, which included the recomposition of juvenile birds and the introduction to adult birds. Data are displayed during each day, and the youngest bird in the flock determines the starting age range. Data are displayed as means and 95% confidence intervals.

During adult introduction days, adults initiated more HDs with juveniles than they did with adults (Wilcoxon's Signed Ranks Test: $T = 0$, $N = 6$, $p < .05$). Adults were also more likely to initiate HDs with juveniles than juveniles were to initiate HDs with adults ($T = 0$, $N = 6$, $p < .05$). Adult male birds were more likely to solicit HDs to juveniles than adult female birds ($T = 0$, $N = 6$, $p < .05$). Across Experiment 3, juvenile HDs were more likely to occur between two juveniles who had

previous social experience with one another than between juveniles who had never encountered one another ($T = 0$, $N = 6$, $p < .05$).

Experiment 4: Origins of Song

The purpose of Experiment 4 was to record the emergence and use of subsong, plastic song, and wing spread displays on Days

42–63 (during Experiments 2 and 3). We observed all juvenile male cowbirds (JMs); however, only 9 vocalized.

Method

One observer took 7-min focal samples of JMs between 0700 and 1000. Male birds were chosen for observation on the basis of when they were vocalizing as it is an infrequent activity at this age. The vocalizations consisted of subsong and plastic song, which are characterized as containing primitive and variable sounds (V. A. Smith et al., 2000). Flight whistles did not occur at this age.

In each sample, we recorded NN points, undirected vocalizations, directed vocalizations, display behaviors, and reactions to directed vocalizations. An undirected vocalization was measured when an individual was more than 7.6 cm from another bird, whereas a directed vocalization was scored when an individual was oriented toward and less than 7.6 cm from another individual on the same perch. Precursors to the male bird's wing spread display were also recorded if the bird's feathers were raised and the wings were at least partially fanned (Cooper & Goller, 2004). Reactions received from directed vocalizations were recorded. Reactions to song included pecks and leaves by male and female birds. We scored a leave when an individual departed either during or within 1 s of the offset of a vocalization.

Results

We took a total of 22 focal samples on 9 male birds. JMs produced more undirected than directed vocalizations (Wilcoxon's Signed Ranks Test: $T = 2$, $N = 9$, $p = .015$). For the 8 male birds that had directed vocalizations, more were directed toward male than female birds ($T = 0$, $N = 8$, $p = .018$). Because of small sample sizes, pecks and leaves were combined as responses to JM vocalizations. Between JMs and juvenile female cowbirds (JFs), responses to JM vocalizations were not different (JMs: $T = 6$, $N = 5$, $p < .686$; JFs: $T = 5.50$, $N = 8$, $p = .067$). JMs produced significantly more directed displays than undirected displays ($T = 0$, $N = 8$, $p = .012$). JMs also produced more displays during vocalizations than displays without vocalizations ($T = 0$, $N = 9$, $p = .007$). NN analysis revealed JM social affiliation did not differ between JMs and JFs (Mann-Whitney U Test: $U = 22$, $n_1 = 9$, $n_2 = 9$, $p = .113$). Hatching order was positively correlated with number of directed songs (Spearman rank correlation: $r_s = .693$, $N = 9$, $p = .039$), and singing rate per minute was positively correlated with the amount of NN points and approaches from other JMs ($r_s = .740$, $N = 9$, $p < .025$).

General Discussion

The study of later development informs the study of earlier development by providing direction while exploring a time of much variability. A specific set of findings on adult female song perception led to the present study. The finding that JFs—living in captive outdoor flocks with only adult female birds—showed no preferences for local song in playback tests suggests that female birds require social contact with male birds to acquire stable local preferences (West et al., in press). To find the origins of sociality in cowbirds, we took a parallel approach to early development: We assumed that young animals show multifaceted behavior very early in ontogeny and that new behaviors can emerge from the use of familiar actions in new contexts. We approached the question of eventual local song preference by first looking for a logical pre-

cursor, that is, female cowbirds recognize gender as evidenced by same-sex assortment. We also adopted the approach of studying developmentally coincidental behaviors because the retrospective method runs the risk of overlooking ontogenetic adaptations or youthful behaviors rarely seen in adulthood such as juvenile play (West & King, 1987; West et al., 2003).

Proximity and Sex Assortment

These data show that hand-reared female cowbirds do not assort by sex at an age when male cowbirds do. We were surprised by the female bird's lack of sex assortment because a wealth of studies had led us to assume that social proximity between the sexes would not require maturation or learning. We have found that same-sex assortment varies over a wide range but is a consistent and stable characteristic of all cowbird flocks we have studied. We have also found that once a pattern of same-sex assortment is established, it is likely to persist until spring when breeding commences (V. A. Smith et al., 2002; White, King, & West, 2002), unless the flock is perturbed by the introduction of female birds that are indiscriminate in their interactions with male birds (King et al., 2003). Even a few female birds that do not exhibit same-sex assortment can change the social dynamic of an entire flock (King et al., 2003). Although such indiscriminate female birds are not common, we have thought that such behavior represents natural variation in female preferences for male song. In decades of copulation solicitation studies, we have routinely found that about 10% of the female birds were highly responsive and indiscriminate to male song. The results from this study, when added to other findings, suggest that same-sex assortment and responsivity may initially be indiscriminate but is then shaped by social experience.

Three recent studies recorded same-sex assortment in very young cowbirds housed with and without adult female birds and are especially relevant to the present findings. In the first, we looked at same-sex assortment in 18 hand-reared female birds housed with 12 hand-reared male birds and 8 adult female birds. We hand reared these baby birds using procedures identical to those in the present study with the exception that on about Day 20 they were housed with adult female birds. By around Day 90, all the female birds showed strong same-sex assortment (88:12 [FF:FM]; unpublished data, King, 2004). In a second study of four flocks of wild-caught JMs collected at around 30 days of age and housed with adult female birds, we again found strong same-sex assortment, averaging across the four flocks 85:15 (FF:FM; King et al., 2003). In the third study, two flocks of wild-caught JFs were housed with JMs, but no adult female birds were present. These female birds were collected by around Day 30. However, as the local adults were still present and courting, the young would have had some limited exposure to adult male and female stimulation prior to collection. By around Day 60, we found that these two flocks showed female same-sex assortment but only at a 67:33 (FF:FM) level. This pattern persisted throughout the fall and into the spring (Freed-Brown, King, Miller, & West, submitted manuscript for publication). Thus, in the two experiments in which JFs were housed with JMs and adult female birds, female same-sex assortment was substantially higher than when the JFs were not housed with adult female birds.

Finally, as part of this third study, two additional flocks housed adult female birds with JMs. The adult female same-sex assort-

ment in these two flocks averaged 87:13 (FF:FM). We measured same-sex assortment from August through December in the two adult female flocks and the two juvenile flocks and found non-overlapping distributions of sex assortment, with the JFs consistently interacting more with JMs than did the adult female birds with their JMs (Freed-Brown et al., submitted manuscript for publication, Miller, 2005). However, what if adult male birds are present? During the late summer and fall, we also recorded same-sex assortment in two flocks comprising only adult male birds and female birds, some of whom had mated in the previous breeding season. In these flocks, we found an average of 51:49 (FF:FM) sex assortment (unpublished data). Thus, adult female birds interact with familiar adult male birds far more than they interact with JMs, which is not surprising in that the JMs lack competent social and vocal skills. Taken as a whole, it seems that adult female birds severely limit their interactions with juvenile, but not adult, male birds; furthermore, if JFs are present, JFs conform to the behavior of the adult female birds. Thus, the indiscriminate sociality of the female birds in the present study would seem to prepare them to be sensitive to the social patterns exhibited by local adult female birds, thereby facilitating transmission of adult female preferences from one generation to the next.

Reactions to Adults

We exposed the young cowbirds to adults for relatively brief periods of time in Experiment 4. The presence of adults did not appear to affect juveniles or adults. In White, King, Cole, and West's (2002) study, we found that comparably aged wild-caught cowbirds reacted to the presence of adults by associating more with other juveniles than they did with adults and by singing less than the juveniles housed without adults. The adults showed no interest in the juveniles as we found in this study. Many attempts have been made to uncover a recognition signal between young and adult cowbirds (Göth & Hauber, 2004; Hauber, Russo, & Sherman, 2001). This study thus joins with others in finding no privileged recognition mechanism (see King & West, 1977) and adds weight to Hauber, Sherman, and Parprika's (2000) account of cowbird recognition as being multifaceted.

HD Displays

A possible creator of adult-young relationships could be HD displays. Contrary to our hypotheses, however, we found that adults initiated the display more often with juveniles than juveniles did with adults. Familiar peers were the most frequent targets of HDs by other juveniles. Both observations provide evidence that the display may not function as a species recognition mechanism but instead may serve to facilitate cohesiveness in flocks (Scott & Grumstrup-Scott, 1983).

Ontogeny of Vocal Skills

Directed and undirected singing began synchronously. We had expected undirected singing to develop earlier than directed singing because the latter appears to involve clear learning from adults (West, King, & Freeberg, 1996; White, King, & West, 2002). Directed singing is an important predictor of reproductive success (Hamilton, King, Sengelaub, & West, 1998; White, King, & West,

2002). Its frequency also correlates with volumetric measures of area X in the anterior song pathway and nucleus rotundus in the thalamic area. These neural data do not reveal the direction of effects. However, in V. A. Smith et al.'s (2002) study, wild-caught JMs were randomly assigned to chambers with two female birds from either local or distant populations. The song structure diverged in the two groups, and the male birds with local female birds sang much more potent song than the male birds with the distant population female birds. In addition, at 1 year of age, nucleus rotundus was larger ($p < .053$) in the male birds that were housed with local female birds than those with distant female birds (Freeberg, West, King, Duncan, & Sengelaub, 2002). As female cowbirds do not sing, the neural differences appear to be a consequence of female social behavior. Video analysis of the female reactions to the male birds in V. A. Smith et al.'s (2002) study revealed that local female birds used wing strokes and gapes as reactions to male-directed song much more frequently than did the female birds from a distant population (King, West, & Goldstein, 2004). Thus, female reaction to directed song appears to shape both neural structure and vocal content in this species (Freeberg, King, & West, 1995; King & West, 1983; King et al., 2004; West & King, 1988). Miller (unpublished data, 2006) has found highly divergent vocal patterns as early as 140 days if young male birds are housed in aviaries with adults as opposed to JFs: Male birds housed with adult female birds produce more note clusters than male birds housed with JFs. Thus, the early appearance of directed song and lack of same-sex assortment by female birds appear to maximize the opportunity for early female influence on male neural and communicative development as well as to maximize young female exposure to male song and associated social behaviors.

Taken as a whole, these findings demonstrate that female spatial assortment operates as a social gateway to regulate the flow of stimulation about song and adult behavior. This gating process appears to operate as early as it can be measured. It is the proximate social group of different individuals and/or classes that gate, channel, or give meaning to proximity within the flock. The filtering or transmission of stimulation may be direct or inadvertent. For example, older female birds may channel the song stimulation available to younger female birds. First, they may direct the younger female birds' attention to adult male birds, as shown by their flocking responses when a male bird or his song is introduced, but may gate subsequent contact by repeatedly landing in between a perched male bird and a JF, advertising her presence and drawing the male bird's attention to her. They may also produce wing stroke displays noticed by male and female birds (Gros-Louis, White, King, & West, 2003).

Thus, access to potential stimulation is context and activity dependent. This applies to many social species: Basic knowledge resources come through older organisms or peers who facilitate or constrain sensory exposure, timing, and duration. Therefore, in arguing for a multibehavior and multitasking approach, we are also arguing for a change in our perception of an animal's environment. Although we need to sensitize ourselves to the different natures of animals' worlds, we need to be alert as to how information gets from one Umwelt to another (King et al., 2003).

The ubiquity and robustness of same-sex assortment across different contexts in cowbirds suggested to us for many years that female sociality fit one of the classic assumptions for establishing

a behavior as innate (Marler & Hamilton, 1966), that is, the same pattern of behavior, occurring in diverse contexts, is not easily perturbed out of the attractor state of same-sex and same-age affiliation. However, as is often the case in the study of the development of behavior, inattention to seemingly incidental social sources of influence often reveal nonobvious forms of experience (Gottlieb, 1980). For example, in a study of the development of communication in human infants, we have shown that mother's nonvocal responses like touching or smiling were sufficient to advance phonological development (Goldstein, King, & West, 2003). Previous studies have only focused on maternal imitative vocalizations, even though touching and smiling occurred. However, here was a form of effective enhancement of speech that often was considered ground, not figure (Goldstein et al., 2003). Imitation was once considered the motor behind avian and human vocal development; however, our new data show that we need to know with whom and how young learners associate before we ask what they learn.

References

- Alcock, J. (2001). *Animal behavior: An evolutionary approach* (7th ed.). Sunderland, MA: Sinauer Associates.
- Beecher, M. D. (1996). Bird song learning in the laboratory and the field. In D. E. Kroodsma & E. L. Miller (Eds.), *Ecology and evolution of acoustic communication* (pp. 61–78). Ithaca, NY: Cornell.
- Burghardt, G. M. (1977). Ontogeny of communication. In T. Sebeok (Ed.), *How animals communicate* (pp. 67–93). Bloomington, IN: University of Indiana Press.
- Carpenter, M., Pennington, B. F., & Rogers, S. J. (2002). Interrelations among social-cognitive skills in young children with autism. *Journal of Autism and Developmental Disorders*, *32*, 95–106.
- Cooper, B. G., & Goller, F. (2004, January 23). Multimodal signals: Enhancement and constraint of song motor patterns by visual display. *Science*, *303*, 544–546.
- Freeberg, T. M. (1996). Assortative mating in captive cowbirds is predicted by social experience. *Animal Behaviour*, *52*, 1129–1142.
- Freeberg, T. M., King, A. P., & West, M. J. (1995). Social malleability in cowbirds (*Molothrus ater artemisiae*): Species and mate recognition in the first 2 years of life. *Journal of Comparative Psychology*, *109*, 357–367.
- Freeberg, T. M., West, M. J., King, A. P., Duncan, S. D., & Sengelaub, D. R. (2002). Cultures, genes, and neurons in the development of song and singing in brown-headed cowbirds (*Molothrus ater*). *Journal of Comparative Physiology A*, *188*, 993–1002.
- Freed-Brown, S. G., King, A. P., Miller, J. L., & West, M. J. (submitted manuscript for publication). *Uncovering sources of variation in the sociality of female cowbirds (Molothrus ater)*.
- Friedmann, H. (1929). *The cowbirds: A study in the biology of social parasitism*. Springfield, IL: Charles C Thomas.
- Goldstein, M. H., King, A. P., & West, M. J. (2003). Social interaction shapes babbling: Testing parallels between birdsong and speech. *Proceedings of the National Academy of Sciences, USA*, *100*, 8030–8035.
- Göth, A., & Hauber, M. E. (2004). Ecological approaches to species recognition in birds through studies of model and non-model species. *Annales Zoologici Fennici*, *41*, 823–842.
- Gottlieb, G. (1980). Development of species identification in ducklings: VI. Specific embryonic experience required to maintain species-typical perception in ducklings. *Journal of Comparative Physiological Psychology*, *94*, 579–587.
- Gros-Louis, J., White, D. J., King, A. P., & West, M. J. (2003). Female brown-headed cowbirds social assortment in response to male song: A potential source of public information. *Behavioral Ecology and Sociobiology*, *53*, 163–173.
- Gros-Louis, J., White, D. J., King, A. P., & West, M. J. (2006). Do juvenile males affect adult males' reproductive success in brown-headed cowbirds (*Molothrus ater*)? *Behaviour*, *143*, 219–237.
- Hamilton, K. S., King, A. P., Sengelaub, D. R., & West, M. J. (1998). Visual and song nuclei correlate with courtship skills in brown-headed cowbirds. *Animal Behaviour*, *56*, 973–982.
- Hauber, M. E., Russo, S. A., & Sherman, P. W. (2001). A password for species recognition in a brood parasitic bird. *Proceedings of the Royal Society London B*, *268*, 1041–1048.
- Hauber, M. E., & Sherman, P. W. (2003). Designing and interpreting experimental tests of self-referent phenotype matching. *Animal Cognition*, *6*, 69–71.
- Hauber, M. E., Sherman, P. W., & Parprika, D. (2000). Self-referent phenotype matching in a brood parasite: The armpit effect in brown-headed cowbirds (*Molothrus ater*). *Animal Cognition*, *3*, 113–117.
- Hogan, J. A. (1994). Structure and development of behavior systems. *Psychonomic Bulletin and Review*, *1*, 439–450.
- King, A. P. (2004). [Adult females affect juvenile sex assortment]. Unpublished raw data.
- King, A. P., & West, M. J. (1977, March 11). Species identification in the North American cowbird: Appropriate responses to abnormal song. *Science*, *195*, 1002–1004.
- King, A. P., & West, M. J. (1983, October 20). Epigenesis of cowbird song—A joint endeavor of males and females. *Nature*, *305*, 704–706.
- King, A. P., West, M. J., & Goldstein, M. (2004). Nonvocal shaping of avian song development: Parallels to human speech development. *Ethology*, *111*, 101–117.
- King, A. P., West, M. J., & White, D. J. (2002). The presumption of sociality: Social learning in diverse contexts in brown-headed cowbirds (*Molothrus ater*). *Journal of Comparative Psychology*, *116*, 173–188.
- King, A. P., White, D. J., & West, M. J. (2003). Female proximity stimulates development of male competition in juvenile brown-headed cowbirds (*Molothrus ater*). *Animal Behaviour*, *66*, 817–828.
- Marler, P., & Hamilton, W. J. (1966). *Mechanisms of animal behavior*. New York: Wiley.
- Miller, J. L. (2005). [Fall sex assortment in adult cowbird flocks]. Unpublished raw data.
- Miller, J. L. (2006). [Repertoire size of juvenile males housed with adult or juvenile females]. Unpublished raw data.
- Nordby, J. C., Campbell, S. E., Burt, J. M., & Beecher, M. D. (2000). Social influences during song development in the song sparrow: A laboratory experiment stimulating field conditions. *Animal Behaviour*, *59*, 1187–1197.
- Scott, T. W., & Grumstrup-Scott, J. M. (1983). Why do brown-headed cowbirds perform the head-down display? *Auk*, *100*, 139–148.
- Searcy, W. A., Peters, S., & Nowicki, S. (2004). Effects of early nutrition on growth rate and adult size in song sparrows (*Melospiza melodia*). *Journal of Avian Biology*, *35*, 269–279.
- Smith, L. B., & Thelen, E. (1993). *A dynamic systems approach to development: Applications*. Cambridge, MA: MIT Press.
- Smith, V. A., King, A. P., & West, M. J. (2000). A role of her own: Female cowbird influences on vocal development. *Animal Behaviour*, *60*, 599–609.
- Smith, V. A., King, A. P., & West, M. J. (2002). Learning in a social context: Affiliation patterns in a captive flock of brown-headed cowbirds (*Molothrus ater*). *Animal Behaviour*, *63*, 23–35.
- Smith, W. J. (1977). *The behavior of communicating*. Cambridge, MA: Harvard University Press.
- Spelke, E. S., & Newport, E. L. (1998). Nativism, empiricism, and the development of knowledge. In W. Damon & R. M. Lerner (Eds.), *Handbook of child psychology: Theoretical models of human development* (Vol. 1, 5th ed., pp. 275–340). New York: Wiley.

- SPSS. (2005). SPSS (Version 10) [Computer software]. Chicago: Author.
- Timberlake, W. (1993). Behavior systems and reinforcement: An integrative approach. *Journal of the Experimental Analysis of Behavior*, *60*, 105–128.
- West, M. J., & King, A. P. (1987). Settling nature and nurture into an ontogenetic niche. *Developmental Psychobiology*, *20*, 549–562.
- West, M. J., & King, A. P. (1988, July 21). Female visual-displays affect the development of male song in the cowbird. *Nature*, *334*, 244–246.
- West, M. J., King, A. P., & Freeberg, T. M. (1996). Social malleability in cowbirds: New measures reveal new evidence of plasticity in the eastern subspecies (*Molothrus ater*). *Journal of Comparative Psychology*, *110*, 15–26.
- West, M. J., King, A. P., & White, D. J. (2003). The case for developmental ecology. *Animal Behaviour*, *66*, 617–622.
- West, M. J., King, A. P., White, D. J., Gros-Louis, J., & Freed-Brown, S. G. (in press). The development of local song preferences in female cowbirds (*Molothrus ater*): Flock living stimulates learning. *Ethology*.
- White, D. J., King, A. P., Cole, A., & West, M. J. (2002). Opening the social gateway: Early vocal and social sensitivities in brown-headed cowbirds (*Molothrus ater*). *Ethology*, *108*, 23–37.
- White, D. J., King, A. P., & Duncan, S. D. (2002). Voice recognition technology as a tool for behavioral research. *Behaviour Research Methods, Instruments & Computers*, *34*, 1–5.
- White, D. J., King, A. P., & West, M. J. (2002). Facultative development of courtship and communication in juvenile male cowbirds (*Molothrus ater*). *Behavioral Ecology*, *13*, 487–496.
- Woodward, P. W. (1983). Behavioral ecology of fledging brown-headed cowbirds and their hosts. *Condor*, *85*, 151–163.

Received January 9, 2006

Revision received April 5, 2006

Accepted April 10, 2006 ■

E-Mail Notification of Your Latest Issue Online!

Would you like to know when the next issue of your favorite APA journal will be available online? This service is now available to you. Sign up at <http://watson.apa.org/notify/> and you will be notified by e-mail when issues of interest to you become available!