

Assortative mating in captive cowbirds is predicted by social experience

TODD M. FREEBERG

Department of Biology, Indiana University

(Received 27 November 1995; initial acceptance 16 February 1996;
final acceptance 12 April; MS. number: A7463)

Abstract. Experimental evidence has shown that brown-headed cowbirds, *Molothrus ater*, display pairing preferences for their native population. Here, the question of whether social experience affects such preferences was tested. Four groups of juvenile female and male cowbirds from a South Dakota population were housed either with adult birds from the same population or with adult birds from an Indiana population. The Indiana population is from a different subspecies from the South Dakota population, and adult Indiana cowbirds display communicative behaviours that are different from adult South Dakota cowbirds; the communicative cultures of the two populations thus are distinct. The pairing and mating patterns of the juvenile females and males were assessed during their first two breeding seasons. In the first year, 71.4% of the pairings that occurred in a testing aviary were between unfamiliar birds of the same cultural background. In the second year of testing, after another winter of social experience with adults of their respective cultures, 86.2% of the pairings, and 77.3% of the copulations, that occurred were between birds of the same cultural background. These data demonstrate the learning of population-specific courtship and mating patterns in cowbirds, and are among the strongest experimental data to date indicating assortative mating in birds based upon social experience.

© 1996 The Association for the Study of Animal Behaviour

Captive adult cowbirds from geographically distant populations mate assortatively. Birds from a North Carolina population, *Molothrus ater ater*, and from a Texas population, *M. a. obscurus*, paired assortatively at approximately a 2:1 ratio (Eastzer et al. 1985). The aim of the present study was to determine experimentally whether social experience predicts patterns of assortment in cowbirds in semi-natural, captive environments, i.e. whether populational pairing patterns such as those documented by Eastzer et al. (1985) could be learned.

Brown-headed cowbirds are obligate brood parasites; female cowbirds lay their eggs in the nests of other species (Friedmann 1929; Friedmann et al. 1977). Its parasitic nature has led many to view it as a species for which developmentally closed, or innate, systems of behaviour should prevail, particularly for those behaviour patterns involved in species recognition or mate recognition (Mayr 1963, 1974; Lehrman 1970;

Bonner 1980; Todd & Miller 1993). Elements of male cowbirds' courtship systems, primarily the ontogeny of whistles and songs, however, are influenced by social experience (Rothstein et al. 1986; West & King 1986, 1988; Rothstein & Fleischer 1987; O'Loughlen & Rothstein 1993). Recent evidence indicates learning with respect to the effective use of vocal signals in males. Social experience with different species affected mate recognition in young male cowbirds (Freeberg et al. 1995), and social experience with adult males and females affected young male cowbirds' abilities to acquire mates (Freeberg et al. 1995; West et al. 1996).

Traditionally, the mating behaviours of female animals have been assumed to be determined innately (Fisher 1958; O'Donald 1983). Recent work in a variety of organisms implicates a role for social experience, however (Sonnemann & Sjolander 1977; Miller 1979; Clayton 1990; Gibson et al. 1991; Dugatkin 1992; Dugatkin & Godin 1992; Collins 1995). Although experimental evidence indicates that male cowbirds possess flexible, open systems of behavioural ontogeny, it thus far indicates a general lack of developmental

Correspondence: T. M. Freeberg, Department of Biology, Indiana University, Jordan Hall, Bloomington, IN 47405, U.S.A. (email: tfreeber@bio.indiana.edu).

flexibility in females' preferences for the songs of males (King & West 1983, 1987). These studies involved housing female cowbirds in pairs with a male tutor in sound-attenuation chambers; the environments of the female subjects thus were socially limited. In the present study, I tested whether housing groups of young cowbirds with groups of adult models in more socially complex and interactive contexts might provide more optimal conditions to influence the pairing patterns of females as well as males. Recent work with California populations of *M. a. artemisiae* suggests that wild females may learn their preferences for male flight whistles (O'Loughlen & Rothstein 1995). These questions of whether female preferences can be affected by social experience are important, because both captive and field studies have indicated a role for female choice in the mating patterns of cowbirds (West et al. 1981, 1983; Yokel & Rothstein 1991, O'Loughlen & Rothstein 1995).

In the present study, I tested whether the pairing and mating patterns of cowbirds could be affected by experience with different conspecific populations. I did not seek to determine the extent to which female choice alone (or, for that matter, male choice alone) was influenced by social experience. Throughout the study, including the overwintering social housing conditions as well as the breeding season testing conditions, groups of females and males were always housed together. Young South Dakota cowbirds, *M. a. artemisiae*, were housed in large social groups either with adult females and males from their South Dakota population or with adult females and males from a southern Indiana, *M. a. ater* population. The young South Dakota birds housed with South Dakota adults hereafter will be denoted as the 'Cheyenne River' groups, and the young South Dakota birds housed with Indiana adults will be denoted as 'Griffy' groups, after geographical landmarks near the capture sites of the respective populations.

I used South Dakota adults as one set of cultural models, or demonstrators (sensu Galef 1994; Galef & Allen 1995), for young South Dakota birds, to expose the Cheyenne River birds to population-typical behaviour patterns. I chose Indiana adults as cultural models for the Griffy females and males, because several lines of evidence suggest that the Indiana and South Dakota populations are behaviourally, and perhaps

genetically, distinct (Freeberg et al. 1995; West et al. 1996, in press). The two populations are from two of the three recognized subspecies of cowbirds (Friedman 1929; Lowther 1993). Juvenile Indiana males housed with canaries or with Indiana female conspecifics developed their vocal repertoires at a more rapid rate than juvenile South Dakota males housed with canaries or with South Dakota female conspecifics, respectively (King et al. 1996). Captive adult South Dakota females responded with more copulatory postures to playbacks of songs of South Dakota males than to playbacks of songs of Indiana males, and adult Indiana females responded more to songs of Indiana males than to songs of South Dakota males. Finally, there appear to be structural differences in the vocalizations of adult South Dakota and Indiana males (A. P. King, M. J. West & T. M. Freeberg, unpublished data).

In the present experiment, I tested whether the patterns of assortative mating seen in the adult cowbirds in the Eastzer et al. (1985) study could be influenced by social experience in the Cheyenne River and Griffy birds. I predicted that such an influence of culture would occur; i.e. that young South Dakota females and males housed over the winter in either the Cheyenne River (with South Dakota adults) or the Griffy (with Indiana adults) cultural groups would preferentially court and pair with other young South Dakota birds from the same cultural background. I tested the same birds over two breeding seasons, using more extensive measures of the relations between pairing and copulation patterns in the second year.

YEAR 1 SOCIAL EXPERIENCE AND PAIRING PATTERNS

Methods

Subjects

I captured 65 juvenile brown-headed cowbirds in Fall River and Custer Counties of South Dakota in early August 1993. Birds were captured in a portable funnel trap (1.3 × 1.3 × 2.6 m) or in potter traps. The birds were judged to be juveniles based upon plumage. Thirty-three of the juveniles were females and 32 were males. I determined sex of the birds based upon differences in wing chord

measures. The birds were housed in small wire mesh cages together during transport to Bloomington, Indiana.

The adult birds serving as social models in this study were captured in Fall River and Custer Counties, South Dakota ($N=18$ females, 17 males), and in Monroe County, Indiana ($N=18$ females, 14 males). Five South Dakota females and eight South Dakota males were caught in the wild as adults in July 1991 and May 1992. The remaining 13 females and nine males were caught in the wild as juveniles in August 1991. All of the Indiana females and males were captured in the wild as adults from June to July 1992, or March to July 1993. All of the adult birds had been housed socially with other cowbirds at the Laboratory of Avian Behavior, Bloomington, Indiana, until used in this study.

All birds were banded with uniquely coloured leg rings to permit individual identification. Birds were maintained on a modified Bronx Zoo diet for blackbirds and received white and red millet, canary seed, cracked corn and fresh vitamin-treated water daily. All birds remain in captivity and are subjects in ongoing behavioural studies.

Winter social housing

Upon their arrival in Bloomington, on 11 August 1993, I placed 62 of the 65 South Dakota juvenile cowbird subjects into two indoor/outdoor holding cages ($3.1 \times 10.9 \times 3.4$ m). On the same day, I separated Indiana and South Dakota adult cowbirds into two groups each and placed them in four identical indoor/outdoor aviaries (outdoor = $9.1 \times 18.3 \times 3.4$ m; indoor = $9.1 \times 3.1 \times 2.4$ m). On 25 August 1993, I divided the juvenile birds between these four large aviaries (Fig. 1). South Dakota juveniles placed into aviaries with Indiana adults constituted the 'Griffy A' and 'Griffy B' groups, and South Dakota juveniles housed with South Dakota adults comprised the 'Cheyenne River A' and 'Cheyenne River B' groups. The 'A' and 'B' designations are arbitrary markers to indicate birds that come from the same source population (South Dakota) and that are from the same cultural background but that have no direct experience with one another. Griffy and Cheyenne River birds were separated by at least 80 m, and each aviary was visually isolated from the others. The last three juvenile cowbirds, all males, were originally part of a different experiment, and were

added to their respective social housing aviaries as yearlings (one to each of the Griffy aviaries, and the third to one of the Cheyenne River aviaries) in early March 1994. Prior to the first breeding season, each aviary housed 7–10 yearling females, 8 yearling males, 8–9 adult females, and 7–9 adult males.

Breeding season housing and testing environments

On 16 May 1994, I removed the Griffy and Cheyenne River females and males from the overwintering housing aviaries and placed them into four indoor/outdoor holding cages ($3.1 \times 10.9 \times 3.4$ m), with each cage housing a Griffy or a Cheyenne River group (the A and B groups were not mixed). Each holding cage was visually isolated from the others. From 16 to 22 May, each holding cage also contained one adult female and one adult male from the Griffy or Cheyenne River birds' respective overwintering aviaries to stimulate courtship in the yearling birds. The Griffy and Cheyenne River birds, when not being tested in the pairing assessment aviary (described below), remained in these holding cages throughout the 1994 breeding season.

On 17 May 1994, I placed four Griffy A and four Cheyenne River A yearling females into a multiple-choice pairing-assessment aviary with four Griffy B and four Cheyenne River B yearling males. The pairing assessment aviary was new to all of the birds and its dimensions were identical to the birds' winter housing aviaries. It was visually isolated from the Griffy B and Cheyenne River B holding cages, and was separated by at least 19 m from the Griffy A and Cheyenne River A holding cages.

Data collection

From 18 May to 2 July 1994, I documented courtship interactions and pairing behaviours of the Griffy and Cheyenne River birds. To expose birds to unfamiliar Griffy and Cheyenne River birds of the opposite sex, I ran two testing rounds (Fig. 1). In the first round (18 May–4 June), I placed sets of four Griffy A and four Cheyenne River A females into the pairing assessment aviary with sets of four Griffy B and four Cheyenne River B males. In the second round (5 June–2 July), I tested Griffy B and Cheyenne River B females in the pairing assessment aviary with Griffy A and Cheyenne River A males.

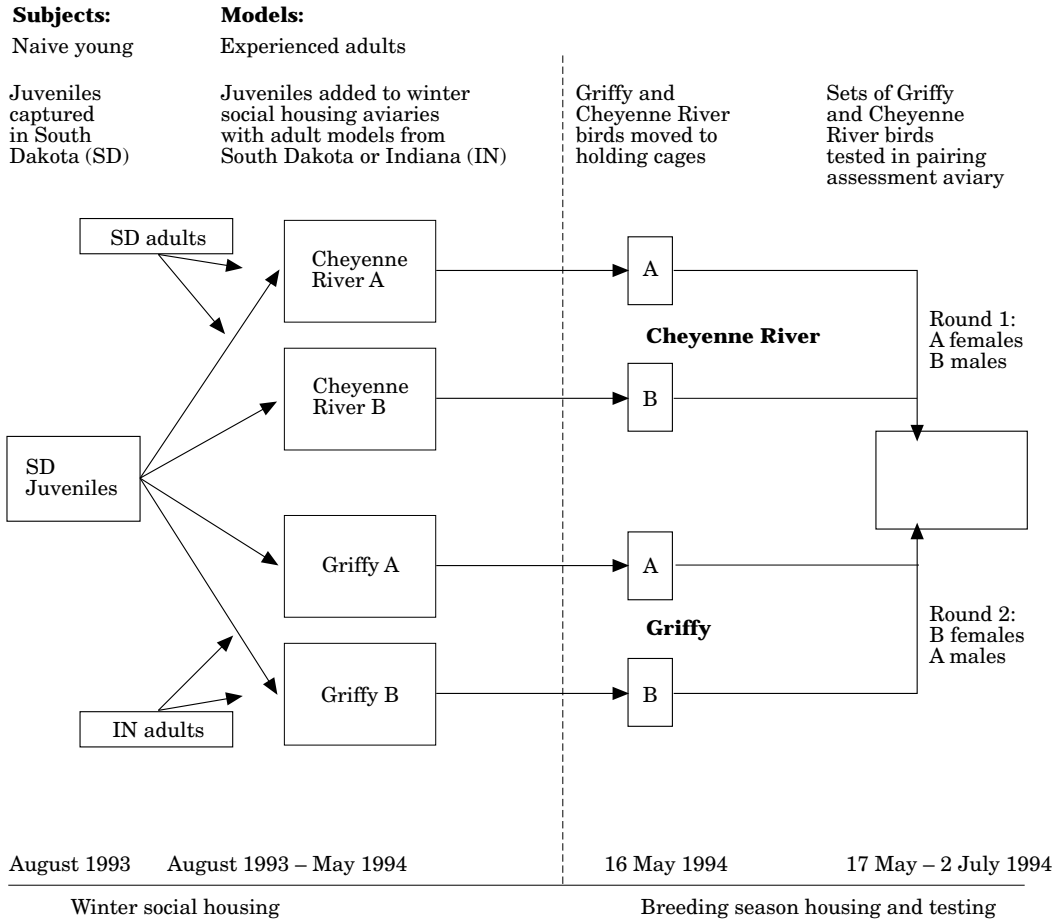


Figure 1. Protocol for testing effects of social experience on pairing patterns in brown-headed cowbirds in the year 1 study (see text).

Each morning, between approximately 0600 and 1030 hours, I observed the birds, taking two 10-min focal samples of each male (Altmann 1974). I sampled by focal males using a methodology successfully used in earlier studies (Eastzer et al. 1985; Freeberg et al. 1995; West et al. 1996). I collected data on the following.

(1) Total vocalizations of males. These included songs and whistles of males, whether directed or undirected, whether perched or on the ground (West et al. 1981; Rothstein et al. 1986, 1988; Dufty & McChrystal 1992).

(2) Directed vocalizations of males. These are a subset of the total vocalizations of males, and included only songs and whistles oriented towards a female from a distance of less than 0.5 m, with

the head and body movements of the male in the direction of the female.

The major dependent measures were pairings between females and males. The pairing measure requires persistent courtship activity by a female and male over a period of days. I used the following criteria which were reliable at predicting stable mating pairs in earlier studies (Eastzer et al. 1985).

(1) Consort day. Two criteria had to be met to determine whether a female A and male B had established a consort day. First, of all the directed vocalizations that female A heard from all males through the duration of the morning, the highest number had to be from male B. Second, male B had to direct at least 10 vocalizations to females

during the two 10-min focal samples, or at least 20 songs to females during the entire morning (this includes 'incidental' vocalizations documented outside the focal sampling period for a particular male), at least a third of which had to be directed to female A.

(2) Pairing. For a pairing to be established, the female and the male had to obtain 3 consecutive consort days, or 2 consecutive days, if on the second day a copulation occurred. On six occasions, the female and male in an ongoing consortship did not quite meet the criteria for a consort day on the second or third consecutive day, so I observed the birds' behaviour on a fourth day. On three of these six occasions, a pairing was established; two involved Cheyenne River males and Cheyenne River females, and one involved a Griffy male and Cheyenne River female. Of the three occasions that did not result in pairings, two were between Cheyenne River males and Cheyenne River females and one was between a Griffy male and Griffy female.

(3) Copulation. Copulations were scored when a female gave a copulatory posture in response to directed male vocalizations, and the male mounted the female.

Once a pairing occurred, I removed both the female and the male, returned them to their respective holding cages, and replaced them with a female and male of the same condition (a Griffy A female with another Griffy A female, and so on). If a bird did not court for 4–5 consecutive days, it was removed and replaced with another bird of the same sex and in the same condition. All of the birds entered the pairing assessment aviary at least once, and most entered twice. Towards the ends of the first and second rounds, females and males that paired previously in the round were placed into the pairing assessment aviary only with birds with which they had not paired earlier. Thus, although some females and males paired twice, every pairing that occurred was unique and was between unfamiliar birds; none of the pairings was between birds of the same winter social housing aviary, such as two Griffy A birds.

To measure observer reliability, on two occasions during the pairing assessment I collected data with two different observers who were familiar with the birds and with the types of data I was collecting, but not with whether the individual birds were from the Cheyenne River or Griffy cultural groups. The reliability scores with both

observers were 100% for determining whether birds met the criteria for a consort day.

Data analyses and statistical tests

Because of the distributions in the data for the two groups of birds, non-parametric tests were used in the analyses. All statistical tests are two-tailed.

Results

Pairings

Females and males of the same cultural background tended to pair more often with each other than with birds of different cultural backgrounds, although the difference was statistically non-significant. Fifteen of 21 pairings (71.4%) were in the predicted direction: Griffy–Griffy or Cheyenne River–Cheyenne River (Fig. 2; sign test for females, $P > 0.05$). Eight of 10 pairings involving Griffy females were with Griffy males, and seven of 11 pairings involving Cheyenne River females were with Cheyenne River males.

The 21 pairings involved roughly half the birds: eight of the 16 Griffy females, nine of the 17 Cheyenne River females, seven of the 16 Griffy males, and seven of the 16 Cheyenne River males. Seven of the 21 pairings involved a bird that had paired once earlier in the test. If only the first pairing for each bird that paired is analysed, 12 of 17 (70.6%) females paired with a male of the same experiential background, and 10 of 14 (71.4%) males paired with a female of the same experiential background.

Pairings between females and males of the same cultural background were based on an average of 98.1 directed vocalizations (range 20–201; focal sampling plus 'incidental' data) from the male to the female. Pairings between Griffy and Cheyenne River birds resulted from an average of 71.2 directed vocalizations (range 30–117; focal sampling plus 'incidental' data) from the male to the female.

Copulations

At least one copulation was observed in nine of the 21 pairings; no copulations were found to occur outside established pairings. Four of the nine copulations were between birds of the same

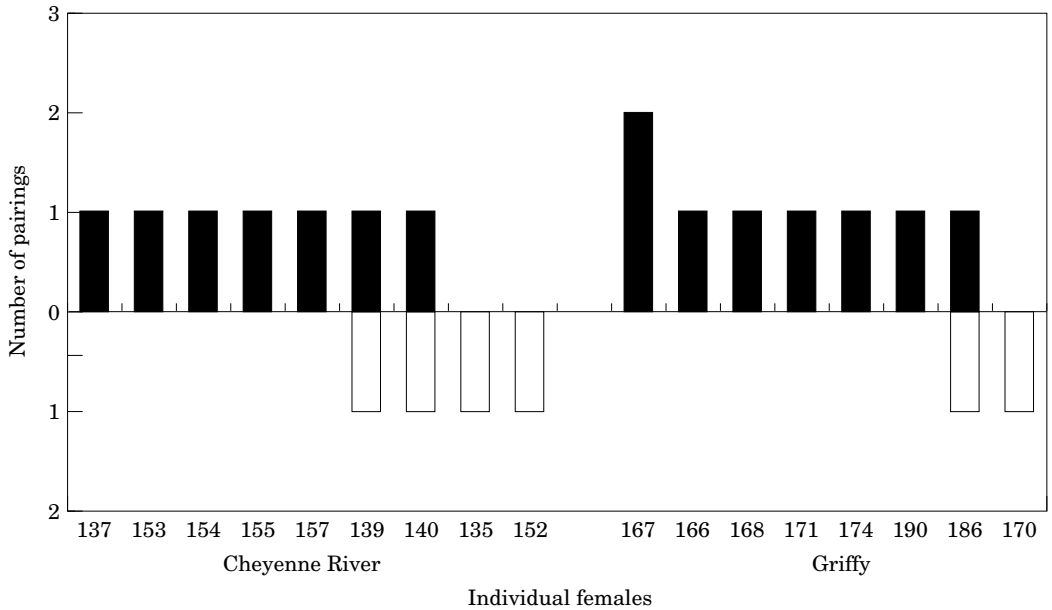


Figure 2. Number of pairings by Cheyenne River and Griffy females in the year 1 study. ■: Pairings with males of the same cultural background. □: Pairings with males of the different cultural background.

cultural background (sign test for females, $P > 0.05$).

Consort days

Ten of 14 (71.4%) Griffy females that obtained at least one consort day with males consorted more with Griffy males than with Cheyenne River males, with one Griffy female consorting equally with both types of male. Ten of 14 (71.4%) Cheyenne River females that obtained at least one consort day with males consorted more with Cheyenne River males than with Griffy males. I did not perform statistical tests on these consort day data, because consort days were used in the criteria for the establishment of pairings.

For the females that obtained more than one consort day, I compared their first consort day with the remainder of their consort days, in terms of whether they consorted more with males of the same cultural background. Of the 11 females that obtained their first consort day with a male of the same cultural background, only one (9.1%) consorted more with males of the different cultural background for the remainder of her consort days. Of the nine females that obtained their first consort day with a male of the different cultural background, however, five (55.6%) consorted

more with males of the same cultural background for the remainder of their consort days (Fisher's exact test, $P < 0.05$).

Discussion

Cowbirds from a South Dakota population, housed over the winter with adults from either an Indiana population or the same South Dakota population, tended to pair more with unfamiliar South Dakota birds that shared a similar cultural, or experiential, background. Data on copulations, however, were limited and did not support my prediction. Five of the nine observed copulation sets (where a female and male copulated at least once) were between Cheyenne River and Griffy birds. The process of continuously removing and adding new birds to obtain the maximum information on pairing preferences, however, affects normal patterns of copulating, because the majority of copulations occur after the third day among established pairs in such captive settings (Eastzer et al. 1985). Thus, in the next year, I used a different procedure to measure the pairing behaviours of these same birds (now coming into their second year), to assess more sensitively the relationship between pairing and copulation patterns.

YEAR 2 SOCIAL EXPERIENCE AND PAIRING PATTERNS

In year 2 of the experiment, I used the same general methodology to measure the effects of cultural background on pairing and mating patterns. Changes in methods involved rotating birds in and out of the pairing assessment aviary at a lower rate than in year 1 to allow for more typical copulatory behaviour. Furthermore, I added hand-reared juvenile females and males (Indiana, South Dakota and hybrid birds from a different experiment) to the four aviaries, and tested them in the pairing assessment aviary (in their first year) with the two-year old Cheyenne River and Griffy birds.

Methods

Subjects

Subjects in year 2 were all of the Cheyenne River and Griffy birds from year 1, as well as the adult South Dakota and Indiana birds with which they were housed. Except for one adult South Dakota female and the addition of a few new Indiana adults, I maintained the individual make up of each of the cultural groups from the year 1 study: the young and adult South Dakota birds of the Cheyenne River A aviary were again housed in that aviary, and so on for the other three cultural groups. The one adult South Dakota female mentioned above was moved from the Cheyenne River B group to the Cheyenne River A group in an attempt to balance losses of adult females from the latter aviary. Three adult Indiana females and males were added to each of the Griffy aviaries to replace adult Indiana birds that died or that became part of another study. These adults were caught from May to June 1994, and had not been in contact with any of the Griffy birds before becoming part of the present study. From May 1994 to May 1995, five Cheyenne River females, two Cheyenne River males and one Griffy male died.

Crosses of South Dakota–South Dakota, Indiana–Indiana, and South Dakota–Indiana adults during the 1994 breeding season produced nine hand-reared juvenile females and 10 hand-reared juvenile males that were added into the Cheyenne River and Griffy cultural groups. These hand-reared cowbirds were not offspring of any

of the Cheyenne River or Griffy birds. The hand-reared birds in their first breeding season were simultaneously tested with the Griffy and Cheyenne River birds in their second breeding season, during the year 2 pairing assessment test (see below).

Winter social housing

Housing and care of birds was identical to that described for year 1. Prior to the second breeding season, each aviary housed 2–3 yearling hand-reared females, 1–3 yearling hand-reared males, 6–10 second-year females, 7–8 second-year males, 6–8 adult females and 7–9 adult males.

Breeding season housing and testing

Adult South Dakota and Indiana males were removed from the winter housing aviaries in early May 1995, to attempt to keep the Cheyenne River and Griffy groups as stable as possible while decreasing the potential aggression in the four aviaries. Thus, all Cheyenne River and Griffy females and males were housed during the breeding season in their same winter housing aviaries, except for when they were tested in the pairing assessment aviaries. Furthermore, adult South Dakota females remained housed with the Cheyenne River cultural groups and adult Indiana females remained housed with the Griffy cultural groups for the duration of the breeding season.

On 12 May 1995, I placed four Cheyenne River A females and four Griffy A females into a pairing assessment aviary (the same aviary in which they had been tested in the year 1 study) with four Cheyenne River B males and four Griffy B males. Because of the change in the breeding season housing from year 1 to year 2, the pairing assessment aviary was visually isolated from the four aviaries housing the Cheyenne River and Griffy birds.

Data collection

From 13 May to 6 July 1995, I documented courtship interactions and pairing and mating behaviour of the Cheyenne River and Griffy birds with methods similar to those of the year 1 study. The first round of testing (A females with B males) lasted from 13 May to 12 June, and the second round of testing (B females with A males) lasted from 13 June to 6 July. From 1 to 12 June, three

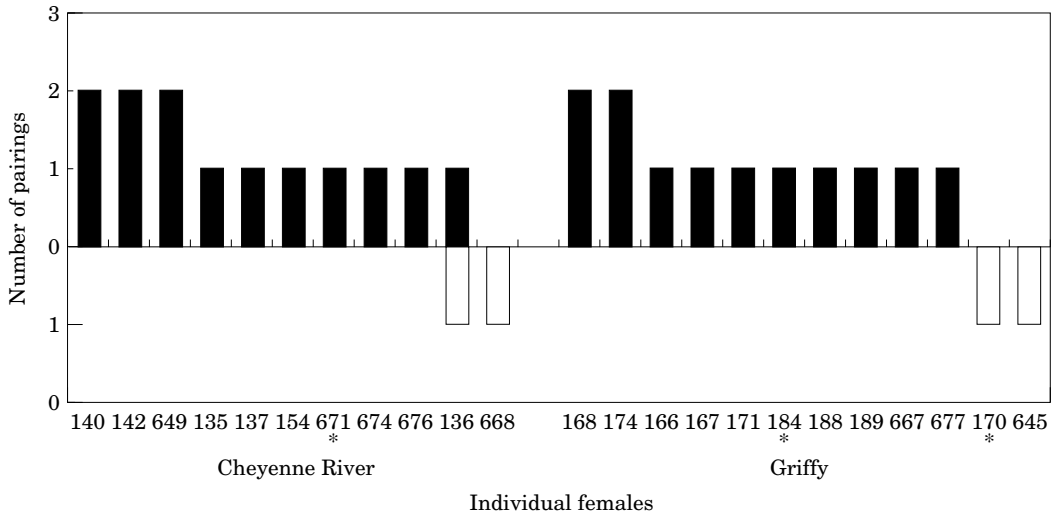


Figure 3. Number of pairings by Cheyenne River and Griffy females in the year 2 study. Females with identification numbers in the 600s were hand-reared (see text). * = Female copulated with a male outside an established pairing. ■: Pairings with males of the same cultural background. □: Pairings with males of the different cultural background.

Cheyenne River females and three Griffy females were tested with three Cheyenne River males and three Griffy males; at all other times, four of each cultural group and sex were tested. Data were not collected on 13 May and 2 June owing to heavy rain.

The major difference between year 1 and year 2 pairing assessment methodologies was in pairing criteria. In the year 2 study, females and males had to engage in 4 consecutive consort days (versus 3 days in year 1) for a consortship to be established, unless the birds copulated on the second or third day of an ongoing consortship. Furthermore, I only removed females and males that were not courting if they did not court for 5–9 consecutive days, rather than 4–5 days of the year 1 study. Thus, birds were rotated in and out of the testing aviary at a lower rate in year 2 relative to year 1.

To measure observer reliability, on six different occasions during the pairing assessment, I collected data with two different observers who were familiar with the birds and with the methods of data collection but not with whether the individual birds were from the Cheyenne River or Griffy cultural groups. For the four scores with one observer, the range in reliability measures was 83.3% to 100% for determining whether birds met the criteria for a consort day. The two measures with the other observer were both 87.5%. Data

analyses and statistical tests were identical to those used in year 1.

Results

Pairings

Females and males of the same cultural background paired more with each other than with birds of the different cultural background. Of 29 pairings, 25 (86.2%) were in the predicted direction: Griffy–Griffy or Cheyenne River–Cheyenne River (Fig. 3). Twelve of the 14 pairings involving Griffy females were with Griffy males, and 13 of the 15 pairings involving Cheyenne River females were with Cheyenne River males (sign test for females, $P < 0.001$). Excluding hand-reared females from the analysis, six Cheyenne River females and nine Griffy females from the year 1 study paired with males in year 2 for a total of 20 pairings. Eighteen (90.0%) of these pairings were with males of the same cultural background (sign test for females, $P < 0.01$).

The 29 pairings involved 58.1% of the birds: 12 of 21 Griffy females, 11 of 16 Cheyenne River females, nine of 19 Griffy males and 11 of 18 Cheyenne River males. Twelve of the 29 pairings involved a bird that had paired once earlier in the year 2 testing. If only the first pairing for each bird

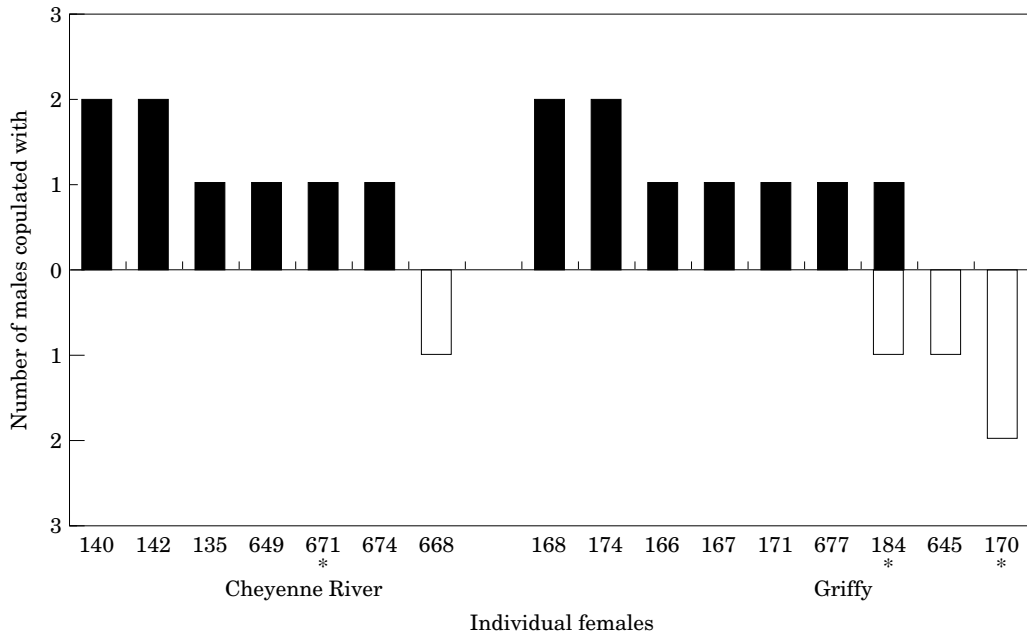


Figure 4. Number of different males mated with by Cheyenne River and Griffy females in the year 2 study. Females with identification numbers in the 600s were hand-reared (see text). * = Female copulated with a male outside of an established pairing. ■: Matings with males of the same cultural background. □: Matings with males of the different cultural background.

that paired is analysed, 20 of 23 (87.0%) females paired with a male of the same cultural background, and 17 of 20 (85.0%) males paired with a female of the same cultural background. Two of the pairings in the year 2 study involved birds that had paired with one another in year 1: one pairing was between a Griffy female and Griffy male, and the other pairing between a Cheyenne River female and Cheyenne River male.

Pairings between females and males of the same cultural background were based on an average of 43.9 directed vocalizations (range 13–88; focal sampling data only) from the male to the female. Pairings between Griffy and Cheyenne River birds resulted from an average of 36.8 directed vocalizations (range 24–67; focal sampling data only) from the male to the female. Data from incidental, non-focal, observations were not collected in year 2.

Of the 29 pairings in the year 2 study, 10 involved at least one of the hand-reared birds. Eight hand-reared females paired (three Griffy and five Cheyenne River). Six of these hand-reared females (75.0%) paired with males of the

same cultural background more than with males of the different cultural background (sign test for females, $P > 0.05$). Four hand-reared males paired (one Griffy and three Cheyenne River); three of these males (75.0%) paired with females of the same cultural background more than with females of the different cultural background.

Copulations

Copulations in the year 2 study showed the predicted effects of social experience on courtship patterns. I observed 22 unique sets of females and males to copulate at least once. Of these, 17 (77.3%) were between birds of the same cultural background (Fig. 4). Of the 16 females to copulate with at least one male (seven Cheyenne River and nine Griffy females), 12 (75.0%) copulated with a male (or two) of the same cultural background, and one female copulated with a male of each cultural background (sign test for females, $P < 0.05$). Excluding hand-reared females from the analysis, three Cheyenne River females and seven Griffy females from the year 1 study copulated

with males in year 2, for a total of 16 matings. Thirteen (81.3%) of these copulations were with males of the same cultural background (sign test for females, $P < 0.05$).

Of the 22 instances where a female copulated at least once with a male, 19 (86.4%) occurred within an ongoing pairing between the female and male. Thus, only three copulation sets occurred outside the operationally defined pairing measure. Two were between Griffy females and Cheyenne River males, and the third was between a Cheyenne River female and Cheyenne River male.

I documented the vocal sequence that immediately preceded a copulation for 25 of the total copulations that occurred (some female-male pairs copulated more than once). The copulations were immediately preceded by an average of 3.0 (range=1-6) vocalizations. All 25 (100%) of these copulations were preceded by songs (range=1-6). Six (24%) of the copulations were preceded by both songs and flight whistles. The female began to adopt the copulatory posture during a male's song in 22 (88%) of the copulations and during a male's flight whistle in three (12%) of the copulations. Flight whistles occurred after the female had gone into the copulatory posture in 14 (56%) of the copulations, and songs occurred after the female had gone into the posture in nine (36%) of the copulations.

Consort days

Twelve of 18 (66.7%) Griffy females that obtained at least 1 consort day with males consorted more with Griffy males than with Cheyenne River males, two (11.1%) Griffy females consorted equally with both types of male, and four (22.2%) consorted more with Cheyenne River males. All 16 of the Cheyenne River females obtained at least 1 consort day with males; 11 (68.8%) consorted more with Cheyenne River males than with Griffy males, and five (31.2%) consorted more with Griffy males. Of the 34 females to obtain at least 1 consort day with males, eight were hand-reared (three Griffy and five Cheyenne River females). Five of these eight hand-reared females (62.5%) consorted more with males of the same cultural background, and one consorted equally with Cheyenne River and Griffy males. I did not perform statistical tests on these consort day data, because consort days were used in the criteria for the establishment of pairings.

For the females that obtained more than 1 consort day, I compared their first consort day with the remainder of their consort days in terms of whether they consorted more with males of the same cultural background. Of the 19 females that obtained their first consort day with a male of the same cultural background, only two (10.5%) 'switched' to consort more with males of the different cultural background. Of the 12 females that first consorted with a male of the different cultural background, however, six (50%) 'switched' to consort more with males of the same background (Fisher's exact test, $P < 0.05$).

Discussion

Similar to the results from year 1, data from year 2 further indicate that social experience predicts assortative pairing and mating. South Dakota birds housed in the Griffy cultural group (with Indiana adults) paired more often with birds from the other Griffy cultural group than with birds housed in the Cheyenne River cultural group (with South Dakota adults). Similarly, the Cheyenne River cultural groups paired more often with one another than with the Griffy cultural groups. The data show positive assortative pairing based upon cultural background at roughly a 5:1 ratio. Copulation data indicate a strong pattern of positive assortative mating based upon cultural background, at approximately a 3:1 ratio. These are among the strongest data to date in the class Aves showing that social experience can drive patterns of assortative mating.

GENERAL DISCUSSION

Earlier work in cowbirds indicated that geographically distant populations court and mate assortatively (Eastzer et al. 1985). The present study indicates that the behaviour patterns that underlie these patterns of assortative pairing and mating can be profoundly influenced by conspecific social experience. All of the Griffy and Cheyenne River birds shared both a common genetic and natal experiential background, because all were caught in the wild in large flocks of juvenile cowbirds. What differed was the birds' social experience with adult cowbirds in the autumn, winter and spring months prior to the breeding season.

The pairing and mating patterns of the Griffy and Cheyenne River birds were predicted based upon knowledge of the differences in the birds' respective cultural backgrounds. Without knowledge of the birds' social experience or population, one would probably have explained the data as resulting from different phylogenetic backgrounds in the birds (Mayr 1963; Lott 1991). Differences in the cultural environments experienced by the young South Dakota birds and the ontogenetic effects these environments had on the birds' communicative development, however, would not have been likely explanations. The present study, therefore, indicates the importance of analyses of the social environments of animals in our efforts to understand population-level patterns of social and mating assortment.

Few studies have linked individual social experience directly to patterns of assortative mating in populations. Although a great deal of work on sexual imprinting is suggestive of this link, these studies typically provide evidence only for homotypic preferences in one sex, the imprinted sex (Immelmann 1972; Kruijt 1985; ten Cate 1989). Evidence for homotypic pairing preferences does not constitute evidence for positive assortative mating, however (Burley 1983). Recent work with *Drosophila paulistorum* is beginning to provide direct experimental evidence for this 'experience-assortative mating' link (Kim et al. 1996). Pre-adult flies experimentally secluded at various stages of development mated more often with partners having similar seclusion experience.

Patterns of positive assortative pairing, and especially mating, were stronger in the year 2 study. These differences could have arisen for a number of reasons. First, first-year male cowbirds in western populations are not as successful at obtaining mates as older males (Rothstein et al. 1986). Thus, the males (and, perhaps, females) in the year 2 study may have been more behaviourally competent simply as a result of their being older. Second, many of the birds of the year 2 study also had had another year of experience with their respective cultural conditions. This additional year of social experience may have resulted in the second-year birds being behaviourally more competent. Further work with first- and second-year birds will be able to address the extent to which these two possibilities might account for the data. Finally, in year 2, birds being tested during the breeding season were

added to and removed from the pairing assessment aviary at a lower rate than in year 1. Thus, the social contexts during the breeding season of Cheyenne River and Griffy birds were more constant in year 2, which may have led to more stable and reliable behavioural patterns in the pairing assessment test.

In the Eastzer et al. (1985) study, winter experience with different conspecific populations had a negligible effect on subsequent pairing and mating patterns. These earlier results may seem to contradict the results of the present study, but differences in methodologies probably account for the different results. First, in the earlier study, only a small subset of the experimental birds was housed in an aviary with birds from a different population prior to testing; most were housed only with members of their own subspecies (Eastzer et al. 1985). Second, all of the males housed in the aviary containing birds of both subspecies were adults that had had at least one year of normal experience with their own population in the wild. Finally, all of the birds caught as juveniles in the experiment were captured in November or January. Thus, each juvenile had had roughly 5–7 months of experience with its own population prior to inclusion in the study. In the present study, the birds had been captured in the wild as juveniles in early August. The several months of natal-population experience in the Eastzer et al. (1985) study might have made the pairing preferences of the juvenile birds largely unalterable by later social experience.

Pairing and reproductive success in animals is determined not only by the qualities of the individual female and male, but by their behavioural compatibility as well (Halliday 1983). An individual, by choosing to pair with a familiar individual, can reduce the time and opportunity costs involved in searching for and assessing mates (Real 1990). My results indicate that direct familiarity with an individual does not have to be a necessary component of the pairing decisions of a bird, as has been found in barnacle geese, *Branta leucopsis* (Choudhury & Black 1994); familiarity with cultural background can be sufficient to affect choices of mates. Evidence for cultural familiarity as a factor in the mating decisions of the Cheyenne River and Griffy birds is also indicated by comparing the courtship behaviour of a female on the first day she courts relative to the rest of the days she courts in the pairing

assessment test. Females that first consorted with males of the different cultural background were more likely to switch and later consort more with males of the same cultural background than were females that first consorted with males of their own culture. These results suggest that the decisions cowbirds make regarding potential mates may take days of social interaction and courtship to develop; this sort of mate assessment period has been found in other captive studies of eastern populations of cowbirds (West et al. 1981, 1983).

As noted before, female preferences for males' songs have appeared difficult to alter experimentally in earlier studies of cowbirds (King & West 1983, 1987). Data from the present study suggest that these earlier results may, in part, be a product of the methodology used. Much of the work in song learning and sexual imprinting in birds involves housing a male or female individually with a tutor (i.e. a conspecific, heterospecific or taped playback of song). Rarely are test subjects housed in large, socially complex groups with their respective models (Johnston 1985; Miller 1985; Gibbons et al. 1994). Experience and learning in a social group can produce greater developmental flexibility in foraging preferences (Zentall & Galef 1988; Laland et al. 1993; Galef & Allen 1995), vocalizations (Nowicki 1989; Payne & Payne 1993; Elowson & Snowdon 1994) and species recognition (Gottlieb 1993) than learning in an individual context. The present study extends these findings, demonstrating that the development of mating patterns of male and female cowbirds is open to the influence of experience when the social context is complex and interactive, not unlike the social dynamic of birds in the wild.

The questions that must now be addressed are how, when and in what contexts these pairing and mating preferences were socially transmitted from the adults to the young. Young Griffy and Cheyenne River females and males may have learned from observing the interactions of the Indiana and South Dakota adults, respectively, with which they were housed, as well as from interacting with the adults themselves. Future studies are needed to address the extent to which social and/or individual learning influences the development of pairing and mating patterns in cowbirds and whether young females and young males are differentially influenced.

ACKNOWLEDGMENTS

The study was supported by grants from the Center for the Integrative Study of Animal Behavior at Indiana University, the College of Arts and Sciences at Indiana University and the Animal Behavior Society. I thank Meredith West and Andrew King for assistance with the study. Thanks to Meredith West, Elaina Tuttle, Stephen Rothstein, Adrian O'Loughlen, Andrew King, David Enstrom, Daniela Corbetta, Kris Bruner and three anonymous referees for helpful comments on the manuscript. Thanks to Laura Twardy, V. Anne Smith, Mark Ochsner and Mary Brooke McEachern for help in obtaining measures of observer reliability. I thank the personnel of Custer State Park, South Dakota, and the Fall River Feedlots, South Dakota, for assistance in capturing birds under federal permit No. PRT 767881.

REFERENCES

- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–265.
- Bonner, J. T. 1980. *The Evolution of Culture in Animals*. Princeton, New Jersey: Princeton University Press.
- Burley, N. 1983. The meaning of assortative nesting. *Ethol. Sociobiol.*, **4**, 191–203.
- ten Cate, C. 1989. Behavioural development: towards understanding processes. In: *Perspectives in Ethology*, Vol. 8 (Ed. P. P. G. Bateson & P. H. Klopfer), pp. 243–269. New York: Plenum Press.
- Choudhury, S. & Black, J. M. 1994. Barnacle geese preferentially pair with familiar associates from early life. *Anim. Behav.*, **48**, 81–88.
- Clayton, N. S. 1990. Subspecies recognition and song learning in zebra finches. *Anim. Behav.*, **40**, 1009–1017.
- Collins, S. A. 1995. The effect of recent experience on female choice in zebra finches. *Anim. Behav.*, **49**, 479–486.
- Dufty, A. M., Jr & McChrystal, R. 1992. Vocalizations and copulatory attempts in free-living brown-headed cowbirds. *J. Field Ornithol.*, **63**, 16–25.
- Dugatkin, L. A. 1992. Sexual selection and imitation: females copy the mate choice of others. *Am. Nat.*, **139**, 1384–1389.
- Dugatkin, L. A. & Godin, J.-G. J. 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proc. R. Soc. Lond. Ser. B.*, **249**, 179–184.

- Eastzer, D. H., King, A. P. & West, M. J. 1985. Patterns of courtship between cowbird subspecies: evidence for positive assortment. *Anim. Behav.*, **33**, 30–39.
- Elowson, A. M. & Snowdon, C. T. 1994. Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Anim. Behav.*, **47**, 1267–1277.
- Fisher, R. A. 1958. *The Genetical Theory of Natural Selection*. 2nd edn. New York: Dover.
- 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. *J. comp. Psychol.* **109**, 357–367.
- Friedmann, H. 1929. *The Cowbirds: A Study in the Biology of Social Parasitism*. Springfield, Illinois: C. C. Thomas.
- Friedmann, H., Kiff, L. F. & Rothstein, S. I. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. *Smithson. Contrib. Zool.*, **235**, 1–75.
- Galef, B. G., Jr. 1994. Olfactory communications about foods among rats: a review of recent findings. In: *Behavioural Aspects of Feeding: Basic and Applied Research in Mammals* (Ed. B. G. Galef, Jr, M. Mainardi & P. Valsecchi), pp. 83–101. Reading, Pennsylvania: Harwood Academic.
- Galef, B. G., Jr & Allen, C. 1995. A new model system for studying behavioural traditions in animals. *Anim. Behav.*, **50**, 705–717.
- Gibbons, E. F., Jr, Wyers, E. J., Waters, E. & Menzel, E. W., Jr. 1994. *Naturalistic Environments in Captivity for Animal Behavior Research*. Albany, New York: State University of New York Press.
- Gibson, R. M., Bradbury, J. W. & Vehrencamp, S. L. 1991. Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behav. Ecol.*, **2**, 165–180.
- Gottlieb, G. 1993. Social induction of malleability in ducklings: sensory bases and psychological mechanisms. *Anim. Behav.*, **45**, 707–719.
- Halliday, T. R. 1983. The study of mate choice. In: *Mate Choice* (Ed. P. Bateson), pp. 3–32. Cambridge: Cambridge University Press.
- Immelmann, K. 1972. Sexual and other long-term aspects of imprinting in birds and other species. *Adv. Study Behav.*, **4**, 147–174.
- Johnston, T. D. 1985. Introduction: conceptual issues in the ecological study of learning. In: *Issues in the Ecological Study of Learning* (Ed. T. D. Johnston & A. T. Pietrewicz), pp. 1–24. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Kim, Y.-K., Ehrman, L. & Koepfer, H. R. 1996. Developmental isolation and subsequent adult behavior of *Drosophila paulistorum*. II. Prior Experience. *Behav. Genet.*, **26**, 15–25.
- King, A. P. & West, M. J. 1983. Female perception of cowbird song: a closed developmental program. *Devl Psychobiol.*, **16**, 335–342.
- King, A. P. & West, M. J. 1987. Different outcomes of synergy between song production and song perception in the same subspecies (*Molothrus ater ater*). *Devl Psychobiol.*, **20**, 177–187.
- King, A. P., Freeberg, T. M. & West, M. J. 1996. Social experience affects the process and outcome of vocal ontogeny in two populations of cowbirds (*Molothrus ater*). *J. comp. Psychol.*, **110**, 276–286.
- Kruijt, J. P. 1985. On the development of social attachments in birds. *Neth. J. Zool.*, **35**, 45–62.
- Laland, K. N., Richerson, P. J. & Boyd, D. 1993. Animal social learning: toward a new theoretical approach. In: *Perspectives in Ethology*, Vol. 10 (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 249–277. New York: Plenum Press.
- Lehrman, D. S. 1970. Semantic and conceptual issues in the nature–nurture problem. In: *Development and Evolution of Behavior: Essays in Memory of T. C. Schneirla* (Ed. by L. R. Aronson, E. Tobach, D. S. Lehrman & J. S. Rosenblatt), pp. 17–52. San Francisco: W. H. Freeman.
- Lott, D. F. 1991. *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge: Cambridge University Press.
- Lowther, P. E. 1993. Brown-headed cowbird (*Molothrus ater*). In: *The Birds of North America*, No. 47 (Ed. by A. Poole & F. Gill), pp. 1–24. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, Massachusetts: Belknap Press of Harvard University Press.
- Mayr, E. 1974. Behavioral programs and evolutionary strategies. *Am. Scientist.*, **62**, 650–659.
- Miller, D. B. 1979. Longterm recognition of father's songs by female zebra finches. *Nature, Lond.*, **280**, 389–391.
- Miller, D. B. 1985. Methodological issues in the ecological study of learning. In: *Issues in the Ecological Study of Learning* (Ed. T. D. Johnston & A. T. Pietrewicz), pp. 73–95. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Nowicki, S. 1989. Vocal plasticity in captive black-capped chickadees: the acoustic basis and rate of call convergence. *Anim. Behav.*, **37**, 64–73.
- O'Donald, P. 1983. Sexual selection by female choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 53–66. Cambridge: Cambridge University Press.
- O'Loughlen, A. L. & Rothstein, S. I. 1993. An extreme example of delayed vocal development: song learning in a population of wild brown-headed cowbirds. *Anim. Behav.*, **46**, 293–304.
- O'Loughlen, A. L. & Rothstein, S. I. 1995. Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. *Behav. Ecol. Sociobiol.*, **36**, 251–259.
- Payne, R. B. & Payne, L. L. 1993. Song copying and cultural transmission in indigo buntings. *Anim. Behav.*, **46**, 1045–1065.
- Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *Am. Nat.*, **136**, 376–405.
- Rothstein, S. I. & Fleischer, R. C. 1987. Brown-headed cowbirds learn flight whistles after the juvenile period. *Auk*, **104**, 512–516.
- Rothstein, S. I., Yokel, D. A. & Fleischer, R. C. 1986. Social dominance, mating and spacing systems,

- female fecundity, and vocal dialects in captive and free-ranging brown-headed cowbirds. In: *Current Ornithology*, Vol. 3 (Ed. R. F. Johnston), pp. 127–185. New York: Plenum Press.
- Rothstein, S. I., Yokel, D. A. & Fleischer, R. C. 1988. The agonistic and sexual functions of vocalizations of male brown-headed cowbirds, *Molothrus ater*. *Anim. Behav.*, **36**, 73–86.
- Sonnemann, P. & Sjolander, S. 1977. Effects of cross-fostering on the sexual imprinting of the female zebra finch *Taeniopygia guttata*. *Z. Tierpsychol.*, **45**, 337–348.
- Todd, P. M. & Miller, G. F. 1993. Parental guidance suggested: how parental imprinting evolves through sexual selection as an adaptive learning mechanism. *Adapt. Behav.*, **2**, 5–47.
- West, M. J. & King, A. P. 1986. Repertoire development in male cowbirds (*Molothrus ater*): its relation to female assessment of song. *J. comp. Psychol.*, **100**, 296–303.
- West, M. J. & King, A. P. 1988. Female visual displays affect the development of male song in the cowbird. *Nature, Lond.*, **334**, 244–246.
- West, M. J., King, A. P. & Eastzer, D. H. 1981. Validating the female bioassay of cowbird song: relating differences in song potency to mating success. *Anim. Behav.*, **29**, 490–501.
- 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 ater*). *J. comp. Psychol.*, **110**, 15–26.
- West, M. J., King, A. P. & Freeberg, T. M. In press. Building a social agenda for bird song. In: *Social Influences on Vocal Development* (Ed. by C. T. Snowdon & M. Hausberger). Cambridge: Cambridge University Press.
- West, M. J., King, A. P. & Harrocks, T. J. 1983. Cultural transmission of cowbird song (*Molothrus ater*): measuring its development and outcome. *J. comp. Psychol.*, **97**, 327–337.
- Yokel, D. A. & Rothstein, S. I. 1991. The basis for female choice in an avian brood parasite. *Behav. Ecol. Sociobiol.*, **29**, 39–45.
- Zentall, T. R. & Galef, B. G., Jr. 1988. *Social Learning: Psychological and Biological Perspectives*. Hillsdale, New Jersey: Lawrence Erlbaum Associates.