

Social Malleability in Cowbirds (*Molothrus ater artemisiae*): Species and Mate Recognition in the First 2 Years of Life

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In a longitudinal study, the authors housed wild-caught juvenile male cowbirds (*Molothrus ater artemisiae*) with female cowbirds or canaries (*Serinus canaria*) from August until May. The males were then exposed to 3 social contexts. Males housed with canaries directed more vocalizations to canaries than to female cowbirds. Males housed with female cowbirds vocalized most to other males. The data revealed plasticity at a rudimentary level of reproductive behavior, selective responding to members of one's own species. Song potency, as assayed by playback, did not predict vocal use. To test adult malleability, the authors studied the males for a 2nd year. Half were housed with conspecific females and experienced males and half with only females. The manipulation eradicated any signs of the males' 1st-year experiences. The data suggest malleability in species and mate recognition in cowbirds.

Considerable evidence indicates that male cowbirds' vocal repertoires are socially malleable. The timing and extent of exposure to adult male models affects the content of two vocal signals, the song and the flight whistle (Dufty, 1985; King & West, 1990; King, West, & Eastzer, 1980; O'Loughlen & Rothstein, 1993). Moreover, in some parts of the species' range, female cowbirds, which do not sing, can shape the content of the males' vocal repertoires through visual responses (West & King, 1988). In this report, we pose a broader question about male cowbirds' vocal capacities: How does a juvenile male's access to social stimulation affect his ability to use vocal signals effectively during the breeding season? To this end, we housed young males either with conspecific females or with canaries during their 1st year and then measured patterns of vocal behavior in the context of mate assortment during the breeding season. We followed this experiment with a second one in which we looked for evidence of plasticity in vocal and courtship skills in the same males' 2nd year.

Although abundant evidence exists on the role of learning in songbirds' acquisition of vocal signals, few such studies include assessments of how males actually use their vocalizations in species-typical circumstances. Studies of blue-

winged warblers (*Vermivora pinus*) and yellow warblers (*Dendroica petechia*), however, indicate that vocal use, in addition to vocal content, is affected by learning (Kroodsma, 1988; Spector, McKim, & Kroodsma, 1989). Few methodologies exist, however, to assess song use in relation to other reproductive skills. The constraints of captive housing often preclude establishing the conditions appropriate to elicit breeding behavior, even in normally reared individuals. Cowbirds do readily breed in captivity, however, displaying patterns of consortship formation and copulation quite similar to those observed in the field (Lowther, 1993; Rothstein, Yokel, & Fleischer, 1986). We exploited this capability to look for evidence of the role of learning in males' use of vocal signals over the first 2 years of life.

The protocol for Experiment 1 included three assessments during the species' normal breeding season. We increased the complexity of the males' social surroundings in three phases to allow us to observe several critical components involved in typical cowbird courtship: (a) attending to appropriate recipients (i.e., females from the same species), (b) vocalizing persistently to such recipients over a period of several days, and (c) competing with other males for mates. In Phase I, we exposed the males individually to new female cowbirds and canaries. In Phase II, we observed the males in an aviary in which other naive males were always present, thus allowing us to assess how males interacted with potential mates in the presence of possible competitors for the females' attention. We included female cowbirds from the males' local South Dakota (SD) population as well as female cowbirds from a distant population, North Carolina (NC), to explore how selective the male's attention would be toward potential mates. Females from NC represent a second subspecies, *M. a. ater*, allowing us to measure the breadth of the males' preference. Canaries and starlings were also present. The starlings were included to provide a species equally unfamiliar to the males but closer in size to cowbirds than canaries. In Phase III, we added adult NC and

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SD males to the aviaries to assess how the younger males responded in the presence of experienced males and to assess whether the SD and NC females would be responsive to normally housed males. The latter two phases used a modified form of a protocol developed previously to document positive assortment at the subspecies level in captive cowbirds in other populations (Eastzer, King, & West, 1985).

The primary measure, in all three phases, was the males' use of songs or flight whistles while in close proximity (less than 0.3 m) to female cowbirds. This measure has been used to define consortships between males and females in wild and captive populations (Dufty & McChrystal, 1992; Rothstein et al., 1986; West, King, & Eastzer, 1981; Yokel & Rothstein, 1991). Although differences occur in parts of the species range in which vocalization (song or whistle) is used just before copulation, all reports agree that males sing repeatedly over several days to females during the period of consort formation (West et al., 1981; Rothstein et al., 1986; Yokel & Rothstein, 1991).

The study focused on cowbirds of the *M. a. artemisiae* subspecies, collected in the southern Black Hills of SD, within the ancestral range for the species (Friedmann, 1929). Evidence exists of geographic differences in ontogenetic patterns of vocal development, with some of the ancestral populations showing greater dependence on learning (King & West, 1987; King & West, 1990). Studies of the *M. a. artemisiae* subspecies in California also indicate vocal plasticity after a male's 1st year in the formation of whistle dialects and the size of song repertoires (O'Loughlen & Rothstein, 1993). These findings suggested that the juvenile males from SD might also show malleability beyond the 1st year, and thus we studied the same males for a 2nd year, under social conditions designed to look more closely at the role of stimulation from experienced, wild-caught adult males. During the males' second breeding season, tests of vocal use and courtship behavior were carried out again, as well as playback tests.

Experiment 1

The wild juveniles that served as subjects were captured from cowbird flocks in late summer; thus, the males had interacted with conspecifics, as well as with their host species. We assumed that such species-typical experience with conspecifics would allow us to focus the inquiry on mate, rather than species, identification. We manipulated the social stimulation available to the juvenile male cowbirds by individual housing either with canaries or female conspecifics from the same capture site. Before initiating the three phases described above, we recorded the males' vocal repertoires. We played back their vocalizations to SD females to obtain a measure of potency, that is, the frequency of copulatory postures elicited by each vocalization.

Method

Juvenile males. Ten juvenile male cowbirds, determined by plumage and date of capture to be between 50 and 100 days of age,

served as primary subjects. They were collected in August 1991 in Fall River and Custer Counties in SD and were returned to the laboratory in Bloomington, Indiana where they were divided into two experimental groups of 5 birds. The female-housed (FH) males were housed individually with pairs of juvenile female cowbirds collected from the same site. The canary-housed (CH) males were housed with pairs of adult male and female canaries (*Serinus canaria*). All resided in sound-attenuating chambers (King & West, 1977) until the following May.

Adults. Other groups of SD cowbirds, captured from the same counties, participated at points in the study. Seven adult males and 15 females were housed in an indoor-outdoor home aviary (9.1 m × 18.3 m × 3.4 m) from August 15, 1991 (10 of the females and 5 of the males), or from May 5, 1992 (5 females and 2 of the males). The females served as potential recipients of vocal use in Phases I–III. The males served as potential competitors during Phase III. Vocalizations recorded from some of these adult males while in their home aviary were also used for playback tests.

Six male and 13 female cowbirds originally captured in Orange County, NC also served as potential competitors or recipients in Phases II and III. All of the NC birds were housed in an indoor-outdoor home aviary (9.1 m × 18.3 m × 3.4 m) from March 15, 1990, until July 1992. The birds were adults and had been in the laboratory since 1989.

Two canaries, 1 male and 1 female, were used in Phase I. Each test aviary also contained 5 canaries at all times during Phases II and III to serve as potential recipients of social behavior. Altogether, 17 canaries (10 males and 7 females) were rotated through the aviaries. Ten starlings (*Sturnus vulgaris*), 5 in each of the two test aviaries, also served as potential recipients of social behavior during Phases II and III. The starlings had resided in each of the test aviaries since March 15, 1992. One aviary contained 3 adult and 2 fledgling starlings and the second contained 2 adults and 3 fledglings.

Playback subjects. Six yearling SD females, captured from the same sites, served as subjects for the playback of the yearling and adult SD males' vocalizations in May and June of 1992. Five of the 6 females had been housed with the FH males from August 15, 1991, until May 11, 1992. The remaining female was housed with SD males and females in an aviary before playback tests. During the playback tests, 2 females were housed together and the remainder were housed alone in sound-attenuating chambers (see West & King, 1986).

All birds used in the study were banded with colored leg rings to permit individual identification. All were maintained on a modified version of the Bronx Zoo diet for omnivorous birds and were given millet, canary seed, and vitamin-treated water daily.

Testing environments. The 10 juvenile males resided in sound-attenuating chambers with their respective companions until May 11, 1992. On that date, the 10 males (hereinafter called yearlings) were moved into two flight cages (1.8 m × 2.4 m × 1.8 m), one housing the 5 FH males and the other housing the 5 CH males. They remained so housed until May 21, 1992, when they were moved either into a testing or holding aviary, except for the Phase I sessions. While in the cages, both groups could see and hear each other as well as the canaries housed in adjoining cages.

The Phase II and III testing aviaries were unfamiliar to all the males. The aviaries measured 9.1 m × 18.3 m × 3.4 m, and the holding aviaries measured 3.1 m × 10.9 m × 3.4 m. All aviaries had indoor sections; food, vitamin-enriched water, and perches were available inside and outside the inner sections. When not being observed in a testing aviary during Phases II or III, the yearling males were housed in separate holding aviaries. The adult

SD and NC males and females and canaries were returned to home aviaries when not being observed in a test aviary.

Phase I: Responses to unfamiliar individuals. To observe the CH and FH males' behavior toward new representatives of the two classes of companions, we housed 2 canaries and 2 SD females in an indoor 1.8 m × 2.4 m × 1.8 m flight cage for 10 days beginning May 15, 1992. None had been housed with the FH or CH males. Twice daily, we introduced 1 of the CH or FH males for 20 min, with each male participating in one morning and one afternoon session (on different days) in a random order. We videotaped the sessions; two coders also observed each session, noting each vocalization and whether it was directed to an individual. To direct a vocalization (song or whistle), a male had to move to within 0.3 m of a recipient and turn his head and body toward the bird. All other vocalizations were scored as undirected.

Phase II: Behavior in the presence of other CH and FH males. To assess the males' responsiveness to conspecific females and canaries while also in the presence of similarly experienced yearling males, we placed the birds in one of the two testing aviaries beginning on May 21, 1992, and ending June 16, 1992. At all times, we observed 5 of the yearling males (2 or 3 from each group) in an aviary. Each aviary also contained 5 SD and 5 NC females, 5 canaries, and 5 starlings. We removed the male and replaced him with another male after repeated singing and chasing of the same bird for 3 days or after approximately 7 days. We removed and reintroduced each male three times, in units of 3 to 9 days, with males averaging 15.8 days in the aviaries (range = 13–20 for both groups) in Phase II. We exchanged all females between the two testing aviaries on May 30, 1992, in an attempt to stimulate the males' courtship behavior. We removed and added canaries more frequently, approximately every 5 days, because they were less hardy and we were concerned about their health. We did not remove the starlings, because they were breeding in the aviaries as part of another study.

Two observers scored vocal behavior and copulations from 6:45 a.m. to 10:00 a.m., 7 days a week, using 20-min units of focal sampling per male. To be scored as directing vocalizations on a given day to a class of individuals, a male had to produce a minimum of two or more directed songs or whistles while facing and moving within 0.3 m of the individual, and he had to follow the vocalization with a chase if the recipient departed. We defined chasing as two or more consecutive flights following the departure of the bird being pursued. Males potentially could interact with more than one class per day. We measured the males' latency in days to vocalize toward each class. We scored a copulation if the female adopted a copulatory posture and the male mounted her.

We calculated the number of days on which a male displayed directed vocal behavior to each of the classes of potential recipients. We chose to report data by day to capture the persistence of males in allocating behavior to the different classes over the breeding season (Eastzer et al., 1985). Thus, a male that vocalized 9 times to a female on 1 day and 6 times on the next day was scored as having directed social behavior on 2 days, whereas a male that vocalized 15 times on only 1 day was scored as having directed social behavior on 1 day.

Phase III: Behavior in the presence of adult male cowbirds. To assess responsiveness when experienced males from both cowbird populations were also present, we used methods identical to those of Phase II except that we introduced the FH and CH males only two times, and only one test aviary was used. Phase III began June 17, 1992, and ended July 2, 1992. At all times, the aviary contained 3 yearling males (2 FH or 1 CH or vice versa), 3 adult NC males, and 3 SD adult males. In addition, the aviary contained 6 NC and 6 SD females, 6 canaries, and 5 starlings. The CH and FH males

averaged 5.4 days in residence (range = 3–8 for both groups), and the adult SD and NC males averaged 6.2 days (range = 3–14). We used the same criterion for removing and replacing males as in Phase II. We removed 3 of the original 6 SD and NC females and replaced them with new females from the same populations on June 26, 1992, to stimulate the males' interest.

Recording and playback procedures. The males were recorded in their home chambers in early May when their vocalizations had crystallized. We used a Nagra IVS operating at 19.05 cm/s with Sennheiser RF condenser microphones. We played back songs using an Otari MX5050 recorder, a Urei 537 1/3-octave equalizer, and a Crown D75 power amplifier through JBL 2105 speakers located in each female's chamber.

We chose vocalizations on the basis of recording quality from a total of 1,487 songs and whistles (average/male = 148.7 vocalizations, range = 85–181) for the CH and FH males and 1,987 recordings of the SD adults (average/male = 283.9 vocalizations, range = 141–450). The yearling males had repertoires of 2 or 3 vocalizations each, yielding 12 test vocalizations for CH males and 14 for FH males. We tested 12 vocalizations (1–3/male) from 6 of the 7 SD adult males used in Phase III. For CH, FH, and adult SD males, both songs and flight whistles were included. The SD adults were recorded in their home aviary.

We played six vocalizations per day to the SD females, with one vocalization per trial, separated in time by 90 min. The females heard the vocalizations in varying orders each day, but each vocalization was presented an equal number of times at different times of day. We played back each vocalization eight times to each female over the course of the experiment. We scored a positive response if a female adopted a copulatory posture within 1 s from onset of the sound, that is, if she arched her neck and back and separated the feathers around the cloacal area.

Results

Phase I: Responses to unfamiliar individuals. In the cage setting, the CH males directed significantly more vocalizations to canaries, and the FH males directed significantly more vocalizations to female cowbirds. The CH males directed a median of 27 vocalizations (range = 3–74) to canaries and 5 vocalizations (range = 1–22) to female conspecifics. The FH males directed a median of 27 (range = 22–111) of their vocalizations to female cowbirds and 0 to canaries. Mann-Whitney tests yielded reliable differences between the groups ($U = 1$, $p < .004$ for both comparisons). The groups did not differ in the frequency of undirected vocalizations ($Mdn = 3$, range = 0–142 for FH males; $Mdn = 10$, range = 3–65 for CH males).

Phase II: Behavior in the presence of other CH and FH males. Four of the 5 CH males directed the most vocalizations on the most days to canaries; none of the FH males vocalized to canaries (see Table 1). The FH males vocalized most persistently to males. Neither group of males directed vocalizations toward the starlings. Vocalizing to NC and SD females did not differ reliably by group (Table 1). One male in each group consistently vocalized toward an NC female and 3 males (1 CH and 2 FH) directed vocal behavior to SD females. Differences in behavior within the CH and FH groups toward the potential recipients were tested using Friedman analyses of variance (excluding the class of starlings for both groups and canaries for the FH males),

Table 1
Median Percentage (and Range) of Days Vocalizing to Each Class of Recipient for Phases II and III

Class	Recipients			
	Canaries	SD females	NC females	Males
Phase II				
CH yearlings	50 (43-87)	17 (0-65)	20 (0-100)	36 (12-40)
FH yearlings	0 (0)	21 (0-100)	21 (0-100)	43 (43-94)
Phase III				
CH yearlings	34 (0-63)	25 (0-57)	0 (0)	50 (0-67)
FH yearlings	0 (0)	20 (0-100)	0 (0-100)	100 (80-100)
SD adults	0 (0)	100 (50-100)	0 (0-20)	72 (3-100)
NC adults	0 (0)	21 (0-27)	100 (50-100)	47 (23-100)

Note. SD = South Dakota; NC = North Carolina; CH = canary-housed male; FH = female-housed male.

yielding significant differences ($\chi^2 = 10.5, p < .02$ for CH males; $\chi^2 = 11.8, p < .01$ for FH males).

The FH and CH males differed in how quickly they began to vocalize to the different classes (see Table 2). The CH males interacted with the canaries within a day of being introduced to the aviary. The FH males interacted first with other males, a reliable difference (Mann-Whitney test, $U = 0, p < .01$). Interactions with NC and SD females varied by individual but were not significantly different by group.

Phase III: Behavior in the presence of adult male cowbirds. Of the vocalizations the adult NC and SD males directed to conspecific females, almost all were directed toward females from their respective natal population (Table 1). The latency to approach conspecific females was also significantly shorter than that of the FH or CH males when they had been introduced in Phase II (Table 2). Differences in latency to vocalize to SD and to NC females were significantly different among the four groups of males as tested by a Kruskal-Wallis analysis of variance (SD: $H = 12.2, p < .01$; NC: $H = 11.9, p < .01$).

In Phase III, the CH and FH males generally did not change their behavior from Phase II: Four of the CH males continued to vocalize to canaries, and the FH males continued to vocalize most to other yearling males. The same CH male and 2 different FH males vocalized to the new SD females. Differences in directed vocal behavior among the four groups of males were tested by separate Kruskal-Wallis analyses of variance for the classes of NC and SD females. For NC females, the males differed significantly among themselves ($H = 19.2, p < .001$), with the major difference being the greater courtship of NC females by NC males compared with SD males (Mann-Whitney test, $U = 0, p < .001$), but with significant differences between NC males and CH or FH males as well (Mann-Whitney tests, $U = 1, p < .004$; and $U = 2, p < .009$, respectively). For SD females, the males also differed ($H = 12.7, p < .01$), with

significant differences between SD and NC adults (Mann-Whitney test, $U = 1, p < .001$) and SD adults and FH and CH males (Mann-Whitney tests, both groups, $U = 1, p < .003$). The males did not differ significantly in the mean percentage of days vocalizing to conspecific males, but there were nonoverlapping ranges for CH and FH males, with the latter group vocalizing more to males.

The overall rate of vocalizing (to conspecific females or males, or undirected) did not differ between groups in either test: 16.2/focal sample (range = 9-40) for CH males and 18.5 (range = 8-26) for FH in Phase II and 14.6 (range = 10-214) for FH and 11.6 (range = 2-141) for CH males in Phase III. The rates for the adults in Phase III were 14.3 (range = 1-26) for SD and 18.0 (range = 16-32) for NC.

One CH and 1 FH male copulated during Phase I. Two CH males and 1 FH male copulated during Phase II, over a period of 21 days in the aviaries. Three copulations were with 3 different SD females (involving 2 CH males), and 9 copulations were with 4 different NC females (involving 1 FH male and 1 CH male). No copulations occurred for the CH males or FH males in Phase III, although 1 FH male and 1 CH male had females adopt copulatory postures without the males mounting them. The SD and NC adults copulated often and always with conspecific females (27 copulations by 9 males and 10 different females in 16 days). All copulations were preceded by at least one song or whistle, with a range of 1-4 vocalizations immediately before the female's copulatory posture.

Measure of song potency. The SD playback females responded as much to the songs of the SD adults as to the FH males, yielding a median of 30% (range = 6-58) and 31% (range = 17-81), respectively. In contrast, the median percentage of responses to CH song was 7% (range = 0-63). The females showed significant agreement with respect to the relative effectiveness of the three classes of vocalizations (Friedman analysis of variance, $\chi^2 = 68.4, p < .001$). The females responded significantly more often to the songs of the FH as opposed to the CH males (Wil-

Table 2
Median Number (and Range) of Days for Males to Vocalize to Each Class of Recipient After Introduction to Testing Aviary

Class	Recipients			
	Canaries	SD females	NC females	Males
Phase II				
CH yearlings	1 (1)	7 (3-13)	3 (1-13)	4 (3-6)
FH yearlings		9 (7-14)	8 (2-8)	1 (1-2)
Phase III				
SD adults		1 (1-6)	5 (1-9)	2 (1-6)
NC adults		4 (3-11)	1 (1)	1 (1-4)

Note. SD = South Dakota; NC = North Carolina; CH = canary-housed male; FH = female-housed male.

coxon signed rank test, $T = 0$, $p < .05$). Females showed no systematic preferences for the songs of males with whom they had been housed. The median percentage of responses to familiar FH males relative to the median percentage for the other males were as follows for the 5 females so housed: 16/34, 41/29, 32/50, 8/25, and 67/17. Of the five whistles played back, the most responses were to a whistle from an SD adult, 8%; the other values were 6%, 3%, 3%, and 0%.

Discussion

Although the CH and FH males as juveniles had interacted with other cowbirds in SD before capture, they displayed considerable malleability with respect to species and mate recognition. The behaviors observed qualify as neophenotypic, ones usually not seen in a species but within the norm of reaction (Gottlieb, 1992; Kuo, 1967). The abilities of both groups of males to use vocalizations effectively with female cowbirds were clearly deficient. The CH males allocated more than 50% of their singing to canaries in Phase II while in the aviaries with unpaired female cowbirds. The measures taken underestimated the time the CH males devoted to the canaries and the amount of time they ignored conspecific females. The canaries (which were courting one another) rarely stayed still during a male's vocal overture or remained in close proximity when approached. It was, therefore, difficult to measure the CH males' persistence. On some days, males repeatedly pursued canaries but did not get close enough to sing a directed song and, therefore, received no positive score for that day. On many days, males chased canaries without vocalizing, sometimes plucking tail feathers. Cowbirds are not known to engage in forced copulations, and, thus, the lack of copulation attempts most likely reflects the canaries' failure to adopt copulatory postures. We should also note that the males attempted to interact with any canary. Some canaries had bright yellow plumage, whereas some were tan and brown striped: The males pursued either type. No evidence of possible optimal outbreeding was evident, that is, CH males housed with yellow canaries did not preferentially pursue the tan ones or vice versa (Bateson, 1978). The influence of the canaries also extended to the males' vocalizations. Three of the CH males produced canary-type song elements, especially in their whistles.

The present data add support to earlier findings showing that playback potency is a necessary but not sufficient explanation for reproductive success in cowbirds (West et al., 1981). Though the FH males' vocalizations were as potent to playback females as those of the adults, the FH males used them differently. Further experimental work is needed to explain these data, but we offer two possible explanations for the failure of the FH males to succeed on the basis of the potency of their songs. In previous work, we have found that males attend more to males with effective rather than ineffective songs and imitate effective songs more frequently than ineffective songs (West & King, 1980; West & King, 1986). Thus, the potencies of the FH males' songs may have diverted their attention from the female cowbirds and toward other FH males.

The second explanation (and it is not independent from the first) concerns the potential conspecific female recipients. It was striking to observe how rarely the SD females remained anywhere near, and hence available to, the yearling males in Phase II. Their absence was all the more notable in light of their conspicuous presence when the SD and NC adults were added in Phase III. Perhaps the females perceived immature qualities in the yearlings. In previous aviary contexts and in field studies, it is apparent that females assess persistent vocal and social behavior before forming a consortship (Rothstein et al., 1986; West et al., 1981). The FH males showed few efforts to pursue female cowbirds even after they had vocalized or copulated. Wild male cowbirds perching, vocalizing, and following females from outside the aviary were able to induce copulatory posture in 4 different females (3 SD and 1 NC female) inside the aviary in Phase II, suggesting that the females could be stimulated if they experienced the appropriate signals. The female cowbirds' considerable levels of interest when adults were added in Phase III also provided confirmation of the females' reproductive state.

In addition to the failure of the CH or FH males to persist in their vocal efforts toward conspecific females, they displayed atypical behavior toward one another. Lowther (1993) has noted, for wild cowbirds, that "if two males are together . . . for even a few seconds, one invariably starts directing song toward the other who more often than not also starts directed songs" (p. 6). We find that such counter-singing is just as frequent in our captive aviaries containing normally reared males. However, no instances of counter-singing were recorded until June 10, 1992, a month after all the males had been in contact with one another. Thus, even though the males frequently vocalized to one another, they did so in a nonreciprocal manner. During Phase II, only 5 instances of counter-singing occurred over 23 days, out of 636 instances of male-directed vocalizing. The 5 instances involved the 2 males who courted conspecific females most persistently. In contrast, 15 instances of counter-singing involving adults occurred within the 1st hr after their introduction in Phase III and remained frequent throughout Phase III. Thus, the female cowbirds may have used the absence of counter-singing as an obvious indicator of the novel quality of the FH and CH males.

One might argue that the deficiencies in the males were a result of general immaturity; perhaps male cowbirds are not reproductively competent at the end of their 1st year. In some California populations, 1st-year male cowbirds are not as successful in pairing as adults (probably because of the male-biased sex ratio), but in many other populations, yearlings are at no disadvantage (Lowther, 1993; Yokel & Rothstein, 1991). We should also note that during Phases I and II, 6 of the males copulated at least once. Finally, in another study in our laboratory, more normally reared yearling SD males formed consortships and copulated in their first breeding season (Freeberg, 1995). The importance of the capability to breed in the 1st year is reinforced by demographic data, indicating a 50% mortality rate between the 1st and 2nd year for cowbirds in many areas (Lowther, 1993). Thus, the misallocation of vocal signals toward other

species or primarily toward males, as opposed to courting conspecific females, would be potentially very costly. What experiences facilitate acquisition of the necessary skills to be successful in courting females? We examine this question in the next experiment.

Experiment 2

Taken as a whole, the data from Experiment 1 suggest that yearling males, although able to develop potentially effective vocal signals through interactions with female cowbirds, need other kinds of experience to shape vocal use. To explore this suggestion, we carried out a second experiment in which we exposed the same yearling males to different conditions of social housing during their 2nd year. Half of the males were housed in an aviary with adult SD females and experienced adult SD males. The other half were housed together in an aviary with only adult SD females. Thus, although all males had the opportunity to interact with one another and with adult SD females, only one group could interact with males more experienced than themselves. We predicted that the males housed with adult males would be more successful in obtaining consortships and copulations in the following breeding season. We measured their behavior during the breeding season following the general procedures of Phase II of Experiment 1, except that females from an Indiana population were used as a comparison to SD females. In addition, the generally higher level of competent courtship allowed us to use measures of consort formation, in addition to measures of directed vocal behavior.

Method

Yearling males. The 10 males used in Experiment 1, now coming into their 2nd year, served as subjects. These birds were divided into two experimental groups of 5 males each in August 1992. Both groups were housed with sets of SD adult females; one group was provided (PRO) social contact with experienced, adult males, and the other group was deprived (DEP) of such contact. The birds were split randomly. As we could not split the 5 CH and 5 FH males evenly across the two groups, however, we chose to place 3 CH males in the PRO group. Such placement biased the experiment against our prediction that the PRO yearlings would be more socially competent in their second breeding season than the DEP males. One of the DEP males died in April 1993.

Adult males. Five adult males were housed with PRO yearlings during the same time period. All of these birds had been captured at the same SD sites in July or August 1991 or in May 1992 and housed in indoor-outdoor aviaries in Bloomington, Indiana from time of capture to their being used in Experiment 2. All had been observed to show typical courtship in May and June 1992.

Females. The PRO males were housed with 8 females, and the DEP males were housed with 4 females to keep equal sex ratios in each group. The females (from the same SD capture sites) were added at the same time as the adult males.

Housing. The two groups resided in large indoor-outdoor aviaries (see Experiment 1 for dimensions) that were visually isolated from one another. All other details of care were the same as in Experiment 1. The testing and holding aviaries were the same dimensions as those used in Experiment 1.

Playback subjects. Eleven SD females served as subjects for the playback of PRO and DEP males' vocalizations recorded during the subsequent, 1993, breeding season. Six of the females had been the playback subjects of Experiment 1. Four of the remaining females had been caught in the wild as adults, either in July 1991 or May 1992 and housed in indoor-outdoor aviaries in Bloomington, Indiana with other cowbirds from time of capture until July 2, 1992. The 11th female had been captured in the wild as a juvenile in August 1991 and had been housed in indoor-outdoor aviaries in Bloomington with other cowbirds from time of capture until August 1993. All females were from the same capture sites as the other SD birds. They were housed together in a flight cage from July 1992 until May 1993. At that time, they were placed in sound-attenuating chambers. Ten females were housed in pairs, and 1 was by herself.

Aviary participants. During the aviary tests, 18 SD females served as recipients of male vocal and courtship behavior. Ten of these females were housed over the winter with the PRO or DEP groups. The remaining 8 SD females were housed in a separate aviary with adult males from SD and Indiana over the winter. In addition to females of the SD population serving as recipients of male behavior, 21 females from a southern Indiana population were used. They were captured in Monroe County, Indiana between February and July 1992. Indiana females were chosen to test a geographically closer population, one perhaps phenotypically more similar to the SD birds than were the NC birds. Before the aviary test, the Indiana females had been housed in an identical large indoor-outdoor aviary with other Indiana cowbirds.

Four starlings and 15 canaries also served as possible recipients. The starlings had resided in the aviary or in other indoor-outdoor aviaries since March 15, 1992. The canaries had been housed in indoor holding cages before their use in the aviary.

Aviary test of PRO and DEP males' abilities to pair with conspecific females. From May 28, 1993, to July 6, 1993, we observed the courtship behaviors of PRO and DEP males. At all times in the aviary, there were 6 PRO and DEP males (typically 3 from each group but sometimes 2 and 4), 6 SD females, 6 Indiana females, 5 canaries, and 4 starlings. From 6:30 a.m. to 10:30 a.m. every morning, we observed each male twice in 15-min focal sampling sessions. We documented males' number of vocalizations directed to the various classes of birds, chases of conspecific females, fights with males, and copulations according to the definitions listed for Experiment 1.

Our primary dependent measure was the number of consortships the PRO and DEP males obtained with different female cowbirds. We also measured copulations but relied on them as a secondary measure because our procedure of removing individuals after 3 days affected typical copulation patterns (Eastzer et al., 1985). A consortship was based on previously established definitions (see Eastzer et al., 1985) but was modified to a stricter criterion as follows: If a male sang at least 10 songs to conspecific females in a morning, of which at least a third were to a particular female, we scored it as a consort day for the male and that particular female. For a consortship to be established, 3 consecutive consort days with the same female had to occur. If a copulation occurred on the 2nd day of a developing consortship, we judged that the pair of birds formed a consortship. Once a consortship was established, we removed either the male or the female from the aviary and replaced it with a bird of the same class (i.e., a male with another male, an SD female with another SD female). We removed males that did not court female cowbirds after 4 consecutive days and replaced them with other males. In this manner, we cycled each PRO and DEP male through the aviary at least three times (three

to four times for PRO males and three to five times for DEP males).

The PRO males were in the testing aviary an average of 26.2 days (range = 24–28) and the DEP males an average of 27.5 days (range = 23–31). The PRO males averaged 7.7 days for every block of time they were in the aviary (range = 3–16), and the DEP males averaged 7.3 days for every block of time (range = 3–14).

Recording and playback procedures. We used the same procedures and equipment as in Experiment 1, except that we used a Sony TCD-D10 PRO digital audio tape recorder for recording. We then dubbed the recordings chosen for playback to an Otari MK III half-track recorder at 15 inches per second. We obtained vocalizations of the PRO and DEP males, while in their respective social housing aviaries, immediately before their second breeding season in May 1993. We could not obtain sufficient vocal recordings from 2 of the PRO males in the social housing aviary. We placed the 2 males into a smaller holding cage with 2 SD females, recorded them, and then returned them to their social housing aviary. We recorded both songs and whistles from the PRO males (average/male = 94.4, range = 70–150) and DEP males (average/male = 79.8, range = 55–125). The PRO males had three to five songs in their repertoires, and the DEP males each had four. The two most stereotyped and highest quality vocalizations of the DEP male that died in April 1993 were tested.

Finally, we examined two measures of vocal structure and vocal use most comparable to the measures obtained in Experiment 1. First, we compared the effectiveness of the vocalizations as elicitors of playback copulatory responses. We tested 2 songs from each of the males for a total of 20 songs. We tested four whistles, one each from 2 PRO males and two from a DEP male. We obtained measures of copulatory responsiveness to playback from 11 SD females according to the procedures listed for Experiment 1. Second, we compared the males' rate of directing vocalizations to SD females in the aviary test, as this measure was judged to be the most sensitive assay of selective song use.

Results

Aviary test. The PRO males obtained reliably more consortships with SD females than did the DEP males (see Table 3; Mann-Whitney Test, $U = 1, p < .02$). They also obtained more copulations with different females, although the difference was not significant (Mann-Whitney Test, $U = 4, p < .095$). All copulations were immediately preceded by a mean of 3.8 (range = 1–7) songs or whistles. Consortships and copulations were positively correlated (Spearman rank order correlation coefficient, $r_s = .77, p < .03$). These data include pairings with females with whom the males had over-wintered. If only unfamiliar females are included, the PRO males still obtained reliably more consortships (Table 3; Mann-Whitney test, $U = 2, p < .033$). Over the test days, the PRO males tended to vocalize to females more often than did the DEP males (see Table 4). In addition, the PRO males tended to vocalize more to other males. Vocal behavior toward starlings and canaries was very rarely observed for PRO or DEP males.

Both groups of males obtained consortships and copulations with Indiana females (no Indiana males were present). The numbers of consortships did not differ reliably by group: The PRO males obtained 0, 0, 1, 3, and 6 consortships compared with 0, 1, 3, and 4 for the DEP males.

Table 3
Number of Consortships With Different SD Females and Number of Different SD Females Copulated With by the PRO and DEP Males in Experiment 2

Male	1992 class	No. consortships with SD females	No. consortships with unfamiliar SD females	No. different SD females copulated with
PRO 1	CH	7	4	6
PRO 2	CH	5	4	2
PRO 3	FH	3	3	1
PRO 4	FH	3	1	2
PRO 5	CH	2	1	1
DEP 1	FH	2	1	2
DEP 2	CH	2	0	0
DEP 3	CH	1	1	1
DEP 4	FH	1	0	0

Note. The males' social housing in their 1st year is given in the second column. SD = South Dakota; PRO = group was provided social contact with experienced adult males; DEP = group was deprived of social contact with experienced adult males; CH = canary-housed male; FH = female-housed male.

Measure of song potency. All 11 SD females responded more often to songs of DEP males than to those of PRO males, averaging 69% (range = 52–93) responses to the former and 49% (range = 10–66) to the latter (Wilcoxon signed ranks test, $T = 0, p < .001$). The response rates to the four whistles were 0%, 2%, 3%, and 17%. Only 1 of the 20 songs played back was responded to less often than the whistle responded to most often.

Table 4
Mean Number of Vocalizations per Day to Females From PRO and DEP Males in Experiment 1 Relative to Experiment 2

Male	1992 class	Year 1 to SD and NC females (Phase II)	Year 2 to SD females
PRO 1	CH	3.5	51.3
PRO 2	CH	10.5	23.6
PRO 3	FH	3.9	16.2
PRO 4	FH	6.5	15.4
PRO 5	CH	9.5	6.8
DEP 1	FH	33.1	16.0
DEP 2	CH	3.8	13.0
DEP 3	CH	26.5	6.6
DEP 4	FH	0.4	5.2

Note. The vocalizations per focal sampling in Experiment 1 (20 min/male) were multiplied by 1.5 to standardize data for comparison with Experiment 2 data, where the focal sampling was 30 min/male. PRO = group was provided social contact with experienced adult males; DEP = group was deprived of social contact with experienced adult males; SD = South Dakota; NC = North Carolina; CH = canary-housed male; FH = female-housed male.

Comparisons to 1st year. We ranked the males on the basis of the average percentages of copulatory responses from Experiments 1 and 2 and found a correlation of $r_s = -.1758$, $p > .50$, between years. The male with the songs of lowest potency in 1992 had the songs with the highest potency in 1993, whereas the male with the highest potency songs in 1992 had the fourth highest rank in 1993. We also ranked the males on the basis of their mean rate of vocalizations per day to females for both years (Table 4). The rates were not significantly correlated ($r_s = -.01$, $p > .50$). Song potency, as measured in the males' 2nd year, and number of copulations in the second breeding season were negatively correlated (Spearman rank order correlation coefficient, $r_s = -.7417$, $p < .025$).

Discussion

The results indicate that social malleability is evident in male cowbirds after their 1st year, at least in some populations. The results also provide new experimental evidence indicating the role of experience with other males in the ontogeny of avian reproductive skills (see also Groothuis, 1989). The experiences acquired by the yearlings during their 2nd year appeared to override the developmental perturbations evident in the 1st year. The males originally housed with canaries directed virtually no vocal behavior toward canaries in their 2nd year. Of the 16,022 vocalizations scored in Experiment 2, 13 were directed to canaries and 42 to starlings, yielding rates of 0.08% and 0.26%, respectively. Moreover, all of the CH males obtained at least one consortship with an SD female (Table 3). Indeed, the male that had pursued canaries most frequently in all tests in Experiment 1 (a PRO male in the 2nd year) obtained the most consortships and copulations with SD females in Experiment 2. The PRO males' housing differed in two ways from that of the DEP males. They could interact with experienced adult males and they could interact with more individual cowbirds. At this point, we cannot separate these influences. Both of these social differences, however, suggest that the PRO males were more successful because of the greater social complexity of their over-wintering experience.

The measures of playback potency also indicated evidence of vocal modifiability. The potencies of songs sung by males in their 2nd year could not be predicted from potencies in their 1st year. Acoustic examinations of the males' 2nd-year songs demonstrated vocal modification. Only two of the males' song types from 1992 survived into 1993. The males as a whole developed 32 new songs. Song sharing was relatively low in both groups. The DEP males shared one song type; the PRO males shared two types. One PRO male shared a song type with one of the experienced adults. Too few whistles were recorded before the breeding season to calculate sharing precisely, but among the DEP males, one whistle type was shared by 3 males and another type was produced by only 1 male. Among the PRO males, there was one whistle type shared by 2 males out of the six whistle types recorded.

As in Experiment 1, song potency did not predict success in courting or copulating, adding further credence to the view that song potency is not sufficient to predict mating success (West et al., 1981). Some of the differences between the PRO and DEP males indicate the other behaviors they needed to be successful: The PRO males tended to vocalize more to appropriate consubspecific females than did the DEP males. In other work with captive cowbirds, we have found that females tend not to copulate until they have been courted for several days by the same male (West et al., 1981). This finding is consistent with field reports (Rothstein et al., 1986). Thus, females may be assessing the persistence and timing of suites of behaviors, such as singing and chasing or singing and guarding (Yokel, 1986; Yokel & Rothstein, 1991). Some of the females were familiar to the males. These females were not favored by either group (Table 3). If familiarity were a factor, we would assume it would be more of an advantage for the DEP males as their attention might have been more focused on females during their social housing. This did not occur. We have yet to find evidence of familiarity affecting playback responsiveness in this or any previous study (King & West, 1983; West & King, 1980) or in studies of mate assortment (Eastzer et al., 1985).

General Discussion

Because of its parasitic nature, the cowbird has been and continues to be described as a paradigmatic species for which a "genetically closed" system of behavioral development should be useful, particularly for those behaviors comprising the systems of species or mate recognition (Lehrman, 1970; Mayr, 1974; Todd & Miller, 1993). Many previous studies have indicated that cowbirds, like some other brood parasites (Payne, 1973), rely on vocal learning (King & West, 1990). The present data, however, are the first to indicate modifiability related to species or mate recognition in cowbirds. At the same time, the data suggest that such malleability would typically lead to correct recognition because the "average expectable" environment (sensu Eisenberg, 1971) would contain reliable and redundant sources of information to guide learning about male and female conspecifics. Although evidence exists linking vocal content to eventual mate assortment in birds (see Searcy & Andersson, 1986), fewer data are available on the antecedent condition of learning from whom to acquire relevant vocal experience. Thus, by studying these intermediate phases, we are attempting to explore an ontogenetically prior stage in the development of competent reproductive skills.

The results from Experiment 2 indicate, however, that such learning can take place later in development as well. The patterns of vocal use displayed by the CH males in their 1st year were reversible. The CH males did not retain any persistent patterns of vocalizing or orienting toward canaries. The PRO group, which was more successful at obtaining consortships and copulations, contained 3 of the original 5 CH males.

The data from Experiment 2 point to the need to consider more carefully the role of males in the transmission of skills associated with vocal use, in addition to the information they offer regarding vocal form. In their 1st year, the CH or FH males showed courtship skills too variable to permit us to rely on measures of consortships in the way we and others have done previously with populations both in captivity and in the field (Dufty & McChrystal, 1992; Eastzer et al., 1985; Yokel & Rothstein, 1991). Moreover, not only were typical signs of pairing absent, behaviors between males in Experiment 1 were also atypical, especially the absence of counter-singing. Virtually all male-directed singing in Experiment 2 was counter-singing, in contrast to Experiment 1. Although previous studies of other populations of cowbirds have suggested that female cowbirds can impart vocally relevant skills to males (West & King, 1988), the present data suggest an important role of social transmission from older to younger males. Field studies of cowbirds in California, focusing on this subspecies and on *M. a. obscurus*, indicate that young males learn whistle dialects from older males. Such dialect learning often may not occur until after a male's first breeding season (O'Loughlen & Rothstein, 1993). Thus, the present data are consistent with the view that vocal competence may develop quite gradually in some populations of this parasitic species.

We were not able to predict males' courtship effectiveness from their song potencies in either experiment, nor were we able to predict either song potencies or courtship effectiveness across years of the study. In the past, we, like many others, have looked for concordance between song potency, as measured by female responsiveness to song playback, and reproductive success. We had also examined the question experimentally, demonstrating positive correlations between song potency and copulatory success in several studies of captive, eastern cowbirds (West et al., 1981; West, King, & Harrocks, 1983). However, those males had been housed, recorded, and tested in resident aviaries containing conspecific males and females. Thus, their social and vocal experience had been closer to natural conditions, and they had learned their songs and used their songs in the same context (West et al., 1981, 1983). These studies, along with Eastzer et al. (1985), are the strongest experimental evidence to date in captive birds relating song cues to copulatory success (Searcy & Andersson, 1986). The present work, however, suggests caution in the interpretation of playback tests for birds with atypical developmental histories.

Most of our previous work on vocal development has been on eastern *M. a. ater* populations. In previous studies of eastern males housed with canaries, we had observed heterospecific imitations of canary vocalizations, but only during the stage of plastic song (King & West, 1988). These elements were not retained in the eastern males' final repertoires. We did not, however, test the birds in a situation in which they were given an opportunity to interact with females or canaries. Thus, we need to test other cowbird populations to determine whether the plasticity found in the *M. a. artemisiae* population is characteristic of other populations and the species in general.

All of the males came into the experiment with conspecific experience: They were associating with members of their species at the time of collection. Such early experience would not rule out subsequent sexual imprinting, and some of the data from both years suggest the need to consider what possible role sexual imprinting might play in this species. As outlined by Gallagher (1978), "only persistent mate choice of specific morph or species is an appropriate basis to infer sexual imprinting" (p. 482). Both traditional and more recent formulations of sexual imprinting rely on the premise that knowledge of an animal's early social environment should allow one to predict the animal's future mate choices (see Bischof, 1985; Bolhuis, 1991; Immelmann, 1972, 1975; Kruijt, 1985; ten Cate, 1989; ten Cate, Vos, & Mann, 1993).

The differences between the CH and FH males' behavior suggest that such concepts of sexual imprinting are not consistent with the present data. If the basis of the CH males' behavior toward canaries was sexual imprinting, then the FH males should have shown heightened responsiveness to SD females. They did not. Moreover, by some accounts, the CH males in Experiment 2 might have been expected to broaden their choices to include females but not to eliminate a previously chosen class (ten Cate et al., 1993). They did not. If optimal outbreeding were at work for the FH males, it would seem most plausible that they would have directed the most songs to the NC females or, possibly, to the juvenile starlings, whose plumage was similar to that of female cowbirds. However, the FH males vocalized on most days to other males; male and female cowbirds are distinctly sexually dimorphic in color and size. To fit the FH males' behavior into the construct of sexual imprinting would then require that the optimal courtship "choice" for FH males was not females at all but other SD males. Such a broadening of the concept of imprinting would appear only to weaken its explanatory power. More detailed investigations with more birds are, however, clearly needed to evaluate the various criteria now offered as possible evidence for sexual imprinting (Baptista, Bell, & Trail, 1993; ten Cate et al., 1993).

We used a more extensive assessment of males' social and vocal development than is often the case in the study of songbird vocal ontogeny. Many studies end with acoustic assessments of vocal structure. Others conclude with brief tests of choice under highly constrained conditions of testing, similar to the conditions we used in Phase I of Experiment 1, where males were placed in a small test cage with unfamiliar individuals. Such choice or approach tests may be inadequate to assess courtship skills or potential success, although they have frequently been used as indirect evidence of mating preferences (see Searcy, 1992, for a review). If we had terminated this study at either of these two points, we would have come to quite different conclusions about interrelationships between social experience and vocal use. On the basis of vocal potency, we would have assumed that male cowbirds housed with only female cowbirds would fare as well as adult, socially experienced males. On the basis of Phase I, we would also have con-

cluded that males housed only with conspecific females would sing frequently to them and thus enjoy the "advantage" of their potent songs. The observations in the aviaries revealed the limits of these measures to expose the extent to which the manipulation of social environments affected subsequent behavior. By virtue of the experimental manipulations used here, we undoubtedly separated processes that occur simultaneously in nature. Access to appropriate stimulation, however, appears to vary across the cowbird's extensive geographical range, allowing future inquiries to focus on the relative contributions of the nature and timing of social experience to the development of species and mate recognition.

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