



Cultural influences on female mate choice: an experimental test in cowbirds, *Molothrus ater*

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Previous studies of brown-headed cowbirds, *Molothrus ater*, have shown that social learning and cultural transmission can influence courtship and mating patterns. These earlier studies did not test whether cultural background influenced mate choice in females and therefore whether culture could potentially play a role in sexual selection in this species, as has been suggested by recent theory. Here, we tested whether culture influences female mate choice in brown-headed cowbirds. Female cowbirds from a South Dakota population were housed with adult cowbirds from the same South Dakota population or with adult cowbirds from a behaviourally distinct population from Indiana. We tested the mating preferences of females of the South Dakota culture and females of the Indiana culture in sequential mate-choice trials with males, controlling for intrasexual interactions. The males were South Dakota cowbirds that had also been housed either in the South Dakota culture or in the Indiana culture. Females showed mating preferences for males from their own culture. These results suggest that mate choice in female cowbirds can be influenced by cultural background. We briefly discuss the effect that culture may have on sexual selection and on the evolution of female mating preferences.

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This study tested the hypothesis that culture influences the mating preferences of female brown-headed cowbirds, *Molothrus ater*. Here we define culture as a system of functional behaviour that is socially learned and transmitted across generations (see Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). We use culture broadly to describe behavioural traditions in nonhuman animals and not as a process homologous to human culture (see Galef 1992). The potential for culture and social learning to shape female mating preferences, and thus to influence sexual selection, may be under-appreciated. Numerous hypotheses have been proposed to explain females' preferences for phenotypes of males, including the genetic coupling of phenotype and preference through the process of Fisherian sexual selection (Fisher 1958), pre-existing biases (Burley et al. 1982; Basolo 1990), selection for phenotypic indicators of good genes (Hamilton & Zuk 1982), and selection directly on female preference for characters that confer fitness benefits from males (Kirkpatrick & Ryan 1991; Kirkpatrick 1996). However, none of these hypotheses explicitly addresses the roles

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of experiential factors in the ontogeny of mating preferences in individual females and the effect of developmental processes on sexual selection.

Traditionally, the mating preferences of females have been thought to be largely closed to the influences of learning or other environmental factors (Fisher 1958; O'Donald 1980). Recent theoretical and empirical studies indicate, however, that mating preferences of females can be influenced by experience (Payne 1973; Real 1990; Dugatkin 1992; Dugatkin & Godin 1992; Payne et al. 1992; Pruett-Jones 1992; Rosenqvist & Houde 1997; Galef & White 1998). Furthermore, recent models suggest that learned preferences in female animals, acquired through sexual imprinting or cultural transmission, may affect the evolutionary dynamics of populations. Some models suggest that learned preferences in females will tend to reduce the probability of novel traits evolving in males (Kirkpatrick & Dugatkin 1994; Laland 1994a). Because learned preferences will result in homogeneous behavioural repertoires, social transmission of mating preferences will promote consistent selection pressures within populations. Furthermore, with any regular dispersal or migration between populations, the cultural transmission of mating preferences will facilitate gene flow between

those populations (Laland 1994a, b). Alternatively, culture in some instances may enhance the process of reproductive isolation, and potentially speciation through sexual selection, by facilitating rapid nongenetic changes in female mating preferences.

We addressed the question of cultural influences on female mate choice with cowbirds for a number of reasons. Cowbirds are obligate brood parasites; female cowbirds lay their eggs in the nests of other species and young cowbird nestlings are therefore always raised to independence by heterospecifics (Friedmann 1929). The brood parasitic nature of cowbirds has led to a traditional view of the species as being an exemplar for innate or genetically closed systems of behavioural development, particularly for behaviours related to species and mate recognition (see Mayr 1974; Bonner 1980). Thus, cowbirds offer a powerful test of the effects of social learning and cultural transmission on mating decisions.

Earlier experimental work with captive populations of cowbirds indicated that patterns of assortative mating and courtship in individuals are influenced by experience with different cultural backgrounds (Freeberg 1996). Young female and male cowbirds from a South Dakota population were housed over the winter either with adult social models (or 'demonstrators,' see Galef & Allen 1995), from the same population or with adult social models from an Indiana population. The Indiana population was chosen as one set of social models because it is behaviourally distinct from the South Dakota population. South Dakota males possess vocal repertoires that are measurably different from those of Indiana males; for example, while the majority of songs of South Dakota males consist of three note clusters and a concluding whistle, songs of Indiana males almost never contain more than two note clusters followed by a concluding whistle (T. M. Freeberg, A. P. King & M. J. West, unpublished data). More importantly, females of both populations prefer the songs of males of their own population, as assayed by the number of copulatory postures given to playbacks of male songs (West et al. 1998).

Freeberg (1996) tested whether the social environments of cowbirds could influence patterns of assortative mating at a population level. In this earlier study, male–male and female–female interactions could not be controlled for because females and males were tested in large groups in a multiple-choice design; thus, the effect of differential social experience on female mate choice was not explicitly tested. The question of female mate choice is an important one in cowbirds, because both field and captive studies indicate that female choice is an important determinant in the mating patterns of this species (West et al. 1981, 1983; Yokel & Rothstein 1991; O'Loughlen & Rothstein 1995). Furthermore, the earlier experimental work with the South Dakota population (Freeberg 1996, 1998) as well as a study with wild West Coast populations of cowbirds (O'Loughlen & Rothstein 1995) strongly suggest that female mating decisions are influenced by social experience. In the present study, we tested for cultural influences on the mating preferences of females, using a sequential mate-choice design that controlled for intrasexual interactions (e.g. Wagner 1998).

MATERIALS AND METHODS

Subjects

Subjects were 3-year-old female and male brown-headed cowbirds, *M. ater artemisiae*, that had been captured as juveniles in the summer of 1993 in Fall River and Custer Counties, South Dakota. These birds were a subset of young South Dakota birds that were housed over the winter (1993–1994 and 1994–1995) either with South Dakota adults or with Indiana adults, in large outdoor aviaries in Bloomington, Indiana (for details, see Freeberg 1996). Thus, while all the young cowbirds shared the genotypes and early experiences characteristic of the South Dakota population, one set was provided with further experience in the South Dakota culture (hereafter, SDC birds) and one set was provided with experience in the Indiana culture (INC birds). Following their second breeding season, after 2 years of housing with either adult South Dakota cowbirds or adult Indiana cowbirds, the SDC and INC birds were placed in separate aviaries where they were housed with sets of juvenile South Dakota cowbirds, as part of a different study (Freeberg 1998).

All SDC and INC birds were marked with uniquely coloured leg bands 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. Birds also had access to live food in the aviaries and testing cages in the summer months when insects and other invertebrates were abundant.

Mate-choice Trials

We used a sequential mate-choice design to test female preferences. Over a 6-day testing period, we allowed each female to interact with a male of one culture for the first 3 days, then with a male of the other culture for the second 3 days. We chose a sequential design because, although both sequential and simultaneous choice designs can control for male–male interactions, only sequential tests permit free physical and behavioural interactions between the female and male, and these interactions have been shown to be important to pairing in both captive and field studies of cowbirds (e.g. West et al. 1981; Eastzer et al. 1985; Yokel 1986).

The SDC and INC birds were tested in outdoor cages (2 × 3 × 2 m) at the Laboratory of Avian Behavior in Bloomington, Indiana. Each cage was separated by at least 2 m and was visually isolated from the other cages. On the afternoon before the first day of testing for a given female, we introduced the female and a male of either the same or different cultural background into the testing cage. The female and male were kept in the cage for three consecutive mornings and behavioural data were collected on each of these mornings. On the afternoon after the third morning of testing, we replaced the first male with a male of the other cultural background, and monitored the female and this second male for three consecutive mornings. Thus, if an INC female was presented with an INC male for the first 3 days of testing, she was

presented with a SDC male for the second 3 days of testing. At all times, females were tested with males with which they were not individually familiar; females were never from the same overwintering housing aviary as the males with which they were tested. Replicate South Dakota culture and Indiana culture aviaries allowed the testing of females of one set of aviaries with males of the other set of aviaries (see Freeberg 1996).

Nine SDC females and nine INC females were tested in this study. There were two rounds of testing for each female: one in the first half of the breeding season, from 22 May to 10 June 1996, and the other in the second half of the breeding season, from 11 June to 29 June 1996. Within each round of testing, there were three testing periods. In each testing period, three SDC females and three INC females were tested in different cages. Presentation of SDC and INC males was systematically balanced across females within their testing periods and for each female over the two rounds (for example, if a female was presented first with an INC male and then with a SDC male during the first half of the breeding season, she was presented first with a SDC male and then with an INC male during the second half of the breeding season). Within each cultural background, individual males were randomly chosen. Eleven different SDC males and 12 different INC males were used in the mate-choice tests. The SDC males were used an average of 3.3 times each (range 2–4) and the INC males were used an average of 3.0 times each (range 2–4).

Female mate choice was determined by a hierarchy of a priori criteria known to influence the establishment of mated pairs in cowbirds: (1) the number of copulations with SDC and INC males; (2) the number of copulatory postures given by the female to SDC and INC males; and (3) the number of directed vocalizations heard by the female from SDC and INC males during each testing period (see West et al. 1981; Eastzer et al. 1985; Rothstein et al. 1986, 1988; Dufty & McChrystal 1992; Freeberg et al. 1995; Freeberg 1996). Directed vocalizations were defined as vocalizations given by a male to a female from within a distance of 0.5 m, with orientation and/or body movements of the male towards the female, and often accompanied by the male's song spread or bowing display (Friedmann 1929; Lowther 1993). A female was assumed to prefer the male with which she copulated the most. If a female did not copulate with either male or if the female copulated with each male an equal number of times, we relied on the second criterion, copulatory postures. We assumed copulatory postures were indicative of intent to copulate and, therefore, preference. Finally, if both copulations and copulatory postures were equivocal, we assumed that females preferred the male that was permitted the largest number of directed vocalizations. We used directed vocalizations as our final criterion of mate choice because female cowbirds actively control the proximity of males. Females do this by lunging at or flying away from some males and by remaining to hear more vocalizations from other males (Freeberg 1998). Females that do not actively avoid a male (and therefore may be assessing the male's vocalizations), will hear more directed vocalizations from that male (West et al. 1981). Because the cages

used in the mate-choice trials were relatively small, we did not consider actual physical proximity or time spent within a certain distance of the male to be reliable indicators of preference.

Data Collection and Statistical Analyses

Data were collected by two of the authors (S.D.D. and T.L.K.). Prior to the onset of data collection, observer reliability was measured by having each observer independently and simultaneously collect data on two different female and male pairs, neither of which was later used in the mate-choice tests. For the first pair observed, interobserver reliability was 85% (34 of 40 behaviours observed matched); for the second pair, reliability was 100% (22 of 22 behaviours observed matched). During the mate-choice tests, the observers were blind to the cultural backgrounds of the birds being tested. We obtained 60 min of behavioural data for each female and male pair on a given morning (each data collector observed each pair of birds for three 10-min periods during a morning).

We used nonparametric tests to analyse the data (Siegel & Castellan 1988). We used two-tailed sign tests to determine whether females preferred males of the same cultural background. We used Fisher's exact tests to determine whether the pairing pattern of INC females differed from that of SDC females. In other words, the Fisher's exact test determined whether the INC females preferred SDC males less (and INC males more) than did the SDC females.

RESULTS

In the first round of testing, 15 of the 18 females (83.3%) preferred males of the same cultural background (Table 1; two-tailed sign test: $P=0.008$). Seven of the nine SDC females preferred SDC males, while eight of the nine INC females preferred INC males (Fisher's exact test: $P=0.008$). In the second round of testing, female preferences were in the same direction as in the first round, but were not statistically significant. Twelve of the 18 females (66.7%) preferred males of the same cultural background (two-tailed sign test: $P=0.238$). Six of the nine females (66.7%) in each culture preferred males of their own culture (Fisher's exact test: $P=0.145$).

Comparing both rounds of testing for each female, 11 females showed consistent preferences across testing rounds, and 10 (90.9%) of these females preferred males of the same cultural background (two-tailed sign test: $P=0.012$). Additionally, of these 11 females, the preferences of INC and SDC females differed significantly (Table 1; Fisher's exact test: $P=0.015$). Nine of the 11 females that showed consistent preferences for males over the two rounds of testing either copulated more with and/or gave more copulatory postures to the male in at least one of the testing rounds. Of these nine females, eight (88.9%) copulated more with and/or gave more copulatory postures to males of the same cultural background (two-tailed sign test: $P=0.04$).

Table 1. Mate preferences of females of the South Dakota culture (SDC) and females of the Indiana culture (INC) for SDC and INC males over the two rounds of testing

Female	First round		Second round		Overall
SDC					
1	SDC	P, V	SDC	V	SDC
2	INC	C, P, V	SDC	C, P, V	0
3	SDC	V	INC	V	0
4	SDC	V	INC	V	0
5	SDC	V	SDC	C, P, V	SDC
6	SDC	V	SDC	V	SDC
7	SDC	P	SDC	V	SDC
8	SDC	V	INC	V	0
9	INC	C	SDC	V	0
INC					
10	INC	C	INC	V	INC
11	INC	V	INC	C, P, V	INC
12	INC	C, P, V	INC	V	INC
13	INC	V	INC	V	INC
14	INC	V	SDC	C, P, V	0
15	SDC	C, P, V	SDC	C, P, V	SDC
16	INC	C, P	INC	C, P	INC
17	INC	C	INC	V	INC
18	INC	C	SDC	C, V	0

We determined female preference using the following hierarchy of factors known to be determinants of stable mating pairs in cowbirds: (1) copulations between the female and male (C), (2) copulatory postures given to the male by the female without copulation following (P), or (3) the number of directed vocalizations from the male that were heard by the female (V). A combination of C, P and/or V indicates the criteria for which the female displayed a mate preference. Presence of V alone indicates that both C and P were equivocal (see text).

DISCUSSION

Females preferred males of the same cultural background in the mate-choice tests, indicating a cultural influence on female mate choice. Females showed significant preferences for males of the same cultural background during the first half of the breeding season (first round of testing) and across the breeding season (female preferences from the first and second rounds of testing combined). More importantly, the preferences displayed by INC females (for INC males over SDC males) differed significantly from those of SDC females (for SDC males over INC males). It is important to reiterate here that all of the SDC and INC females we tested were cowbirds captured as independent juveniles from the same population (South Dakota). The only difference between the two groups was that over the winter one was housed in a South Dakota cultural background and the other was housed in an Indiana cultural background.

Patterns of courtship that result in assortative mating in cowbirds can be socially learned by one generation of birds (Freeberg 1996) and culturally transmitted to another generation of birds (Freeberg 1998). The present data extend these earlier findings, indicating a significant role for social learning and cultural transmission in the mating preferences of female (and male) cowbirds. Moreover, these data lend support to recent theoretical work suggesting that experiential factors may substantially influence the reproductive outcomes of individuals, and thus have evolutionary consequences for populations (Laland 1994a, b).

Although mating preferences were in the predicted direction in the second round of testing for SDC and INC females, they did not differ significantly from random choice. Females may simply become less choosy as the breeding season progresses. Theory suggests that the costs of being choosy may increase as the season progresses (Real 1990). Supporting this idea, and consistent with our results, are studies with red junglefowl, *Gallus gallus*, indicating that females show less repeatability in their mating preferences in the second half of the breeding season than in the first half of the breeding season (Johnsen & Zuk 1996). In addition to the potentially increasing costs of choosiness, there could also be changes in the proximate factors influencing female choice over the course of the breeding season, such as in male behaviour or in the hormonal conditions of males and females (Enstrom et al. 1997).

Our results indicate that the social and cultural environment females inherit can strongly influence their courtship behaviours and mating preferences. Consistent with our results, O'Loughlen & Rothstein (1995) found that recently captured female cowbirds preferred prerecorded vocalizations of males from their own versus a different dialect population. It is likely that these dialect preferences are learned by the females, given the very close geographic proximity between the two dialect populations, and that females disperse from their natal grounds as juveniles and breed in non-natal areas (Fleischer & Rothstein 1988; Fleischer et al. 1991).

Female mating preferences may drive sexual selection and here we have demonstrated that these preferences can be shaped by culture. Influences of social learning and cultural transmission on courtship behaviour suggest the possibility of genetic divergence and perhaps rapid speciation through sexual selection, driven by non-genetic changes in female mating preferences. Work by Payne and colleagues with brood-parasitic *Vidua* finches has provided behavioural, morphological and genetic evidence in support of a 'cultural speciation' possibility (Payne et al. 1992; Klein et al. 1993; Payne & Payne 1994).

Alternatively, the behavioural plasticity that is a result of social learning and cultural transmission can also lead to genetic cohesion of different populations (Wright 1931), if dispersal or migration occurs between populations. Further work is necessary to determine the extent to which cultural changes can limit or facilitate gene flow among populations. Recent analytical models predict that social transmission of mating preferences cannot lead to speciation in populations with regular migration (Laland 1994a). Furthermore, patterns of assortative mating (whether culturally transmitted or not) will likely only lead to a speciation event if the divergent or diverging populations are also ecologically isolated (Littlejohn 1993). In the present case of cultural influences on female mate choice in cowbirds, then, there would need to exist strong selection against mating with an individual of a different cultural background, in addition to strongly positive assortative mating, for populations to become reproductively isolated. Thus, it seems likely in cowbirds that culturally transmitted courtship behaviours and mating preferences may facilitate, rather than prevent or limit, gene flow between populations. The present study provides experimental evidence that factors directly related to gene flow (courtship behaviours and mating preferences) can be attributable to culture and social transmission. Our results therefore lead us to argue that social factors should be considered in explanations of intersexual mate choice in animals that learn socially.

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