



ARTICLES

The cultural transmission of courtship patterns in cowbirds, *Molothrus ater*

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ABSTRACT

In this study, I tested whether the courtship behaviours that facilitate patterns of assortative pairing and mating could be culturally transmitted across generations of brown-headed cowbirds. In an earlier study, I housed a first generation of young South Dakota cowbirds in one of two cultural backgrounds: (1) with adult social models from the same population; or, (2) with adult social models from a behaviourally distinct Indiana population. During the breeding season, the first cultural generation of South Dakota cowbirds paired and mated assortatively based upon their cultural backgrounds. In the present study, I tested whether these courtship patterns could be culturally transmitted to a second generation of young South Dakota cowbirds. Serving as adult social models for birds of the second cultural generation were the first cultural generation of South Dakota birds from the previous study. During their first breeding season, the birds of the second cultural generation paired assortatively by cultural background at roughly a 3:1 ratio. In addition to the pairing data, the behavioural responses of females to the vocalizations of males indicated the influence of cultural backgrounds. This experimental demonstration of the cultural transmission of courtship patterns points to the importance of social environments as mechanisms whereby behavioural systems are inherited from one generation of animals to the next.

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The aim of this study was to test experimentally whether courtship behaviours resulting in patterns of assortative courtship and mating could be culturally transmitted in captive populations of brown-headed cowbirds. By culturally transmitted, I refer to behaviours that are socially learned by naive individuals from experienced individuals, or social models (see Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Laland et al. 1993; Galef 1995; Heyes & Galef 1996). To demonstrate experimentally the cultural transmission of behavioural variants in populations of animals, three questions need to be addressed (see Galef 1990; Galef & Allen 1995). First, can the behavioural variants be learned in a social context? Second, can the behavioural variants learned by one generation be transmitted socially to another generation? Finally, what learning mechanisms are involved in the transmission of the behavioural variants? In answer to the first question, results of a previous study showed that

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the courtship behaviours that facilitate assortative mating in cowbirds could be socially learned (Freeberg 1996); the second question is addressed by the present study.

Understanding the cultural transmission of behavioural systems is fundamental to understanding the evolutionary processes affecting animal populations that learn socially. Behaviours that are learned socially can spread rapidly through populations. The rapid diffusion of socially learned behaviours can allow populations to exploit and modify their physical and social environments quickly, which may in turn affect the course of their subsequent evolution (Johnston 1982; Lewontin 1983; Bateson 1988; Plotkin 1988; Wcislo 1989; Gottlieb 1992; Laland 1992; Smillie 1993). Recent theoretical work further indicates that cultures themselves can be viewed as evolutionary agents; socially learned traits in a population are culturally generated, selected and transmitted (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Laland et al. 1993). Increased efforts by researchers focusing on the transmission of courtship behaviours would significantly extend these ideas. Not only do courtship

behaviours represent variants that can potentially arise and spread through populations, they also serve as strong selective agents because they directly influence reproductive success (see Laland 1994a, b).

Broadly defined, behaviours that are culturally transmitted involve social learning between members of the same generation, or by one generation from an older generation. Transmission that involves learning the behaviours of other individuals of the same generation is termed 'horizontal', transmission that involves learning the behaviours of parents by young animals is termed 'vertical', and transmission that involves learning the behaviours of unrelated older individuals by young animals is termed 'oblique' (Cavalli-Sforza & Feldman 1981). Although considerable theoretical work has been devoted to these three types of cultural transmission, experimental studies have largely focused on horizontal transmission. Work with Norway rats, *Rattus norvegicus*, and with pigeons, *Columba livia*, has shown that foraging preferences can be learned by one set of individuals and transmitted to another set of individuals, and that these preferences can persist for several learning generations before they are lost (for reviews see Lefebvre & Palameta 1988; Laland et al. 1993; Galef 1995, 1996; Terkel 1996).

Cultural transmission between generations (from old to young) will act as a very different evolutionary process than will cultural transmission within generations, because the former results in behavioural systems that typically are more stable across generational time than the latter (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981). Relatively few empirical studies, however, have focused on the transmission of behaviours from older generations to younger generations (and even fewer on the transmission of behaviours affecting courtship and mating patterns, the topic of the present study). Studies of bird song learning have indicated that elements of courtship systems can be transmitted across generations. Work on indigo buntings, *Passerina cyanea*, and on Darwin's finches, *Geospiza fortis* and *G. scandens*, has provided the best empirical evidence to date for the transmission of cultural variants influencing mating patterns. Adult male buntings arriving to breeding territories earliest tend to have song variants that are copied the most by younger males (Payne & Payne 1993). These song variants are stable over a number of generations and social learning processes appear to play the major role in the maintenance of song variants (Payne et al. 1981; Payne & Payne 1993; Payne 1996). Finally, the song variants that male indigo buntings use during the breeding season can influence their mating success (Payne 1982), although more recent studies indicate that song variants alone are not always sufficient to explain patterns of mating (Payne & Payne 1993). Work on two species of Darwin's finches has indicated that songs of males most closely resemble those of their father and their paternal grandfather (and not their maternal grandfather, thus indicating cultural inheritance), and female mating decisions are influenced by the songs of males (Grant & Grant 1996).

In an earlier study, I tested whether the courtship behaviours that give rise to patterns of assortative mating

could be influenced by social experience (Freeberg 1996). To test this question, I captured young female and male cowbirds, *M. a. artemisiae*, in late summer as juveniles (50–100 days of age), from a South Dakota population. I split these young cowbirds into four groups, two of which were housed with adult birds from the same population (South Dakota culture birds) and two of which were housed with adult *M. a. ater* birds from an Indiana population (Indiana culture birds). South Dakota and Indiana adult males possess acoustically distinct variants of vocal signals and females of the two populations prefer the songs of males of their own population (West et al. 1998). For example, while the majority of the songs of South Dakota males consist of three note clusters followed by a whistle, virtually none of the songs of Indiana males contains more than two note clusters followed by a whistle (T. M. Freeberg, A. P. King & M. J. West, unpublished data). I tested the courtship patterns of the four groups of young South Dakota birds during their first two breeding seasons, and found that birds paired and mated significantly more with birds that shared a similar experiential, or cultural, background. At the level of male song, most of the songs sung by males from the South Dakota culture contained three note clusters, while virtually all of the songs sung by males from the Indiana culture contained two note clusters. Furthermore, I was able to predict the cultural background for most of the males from the South Dakota culture and the Indiana culture by their flight whistles (along with songs, the other major class of male cowbird vocalization), which were similar to those of males from South Dakota and Indiana populations, respectively. Taken together, these data experimentally demonstrated the social learning of populationally distinct courtship behaviours, and indicate that cultural factors can powerfully influence patterns of assortative pairing and mating in cowbirds.

The present study tested whether the Indiana and South Dakota cultural variants learned by an older generation of South Dakota cowbirds could be transmitted to cohorts of a 'second cultural generation' of young cowbirds from the South Dakota population. Serving as the social models for the second cultural generation of young South Dakota birds were the first cultural generation of birds that had been exposed to Indiana and South Dakota models in the earlier study (Freeberg 1996). Because none of the adult birds from the original South Dakota and Indiana populations were used as social models in the present study, I could test the cultural transmission of courtship systems directly. My assays for this question were the courtship interactions and pairing preferences of the second cultural generation of South Dakota birds during their first breeding season.

METHODS

Subjects

I collected 56 juvenile brown-headed cowbirds in Fall River and Custer Counties of South Dakota in early August, 1995. The birds were captured in a portable funnel trap or in potter traps. I judged the birds to be

juveniles based upon their plumage; given the breeding and egg-laying season in South Dakota, these juveniles were probably between 50 and 100 days of age (South Dakota Ornithologists' Union 1991). I determined at the time of capture that 29 of the juveniles were females and 27 were males, based upon differences in wing chord measures (these sex-determinations were verified when the birds moulted and began to attain their adult-like plumage later in the autumn). The birds were housed together in small wire-mesh cages during transport to Bloomington, Indiana.

The adult birds serving as social models in this study were either captured as juveniles in Fall River and Custer Counties, South Dakota, in early August 1993, or were hand-reared from eggs collected in aviaries from May to July 1994. These adult females and males had been housed either as young birds with adult birds from a south-central Indiana population or with adult birds from the same South Dakota population. Thus, the adult social models used in the present study were all from the same South Dakota population; one group had been housed in a South Dakota cultural background (SDC birds) and the other in an Indiana cultural background (INC birds). In total, from August 1995 to May 1996, 20 adult females and 19 adult males of the Indiana culture and 16 adult females and 15 adult males of the South Dakota culture served as social models for sets of the young birds of the second cultural generation.

All birds were banded with uniquely coloured plastic leg rings to permit individual identification. Birds were maintained on a modified Bronx Zoo diet for blackbirds and provided with white and red millet, canary seed, cracked corn and fresh vitamin-treated water daily. Birds also had access to live food in the aviaries in the autumn, spring and summer months when insects and other invertebrates were abundant.

Housing

Winter social aviaries

The adult SDC and INC social models were housed in four identical large indoor/outdoor aviaries (9.1 × 21.4 × 3.4 m). They had been housed in the same aviaries for the previous 2 years (for details, see Freeberg 1996). The 56 juvenile South Dakota birds were evenly distributed across two indoor/outdoor holding cages (3.1 × 10.9 × 3.4 m) for a brief quarantine period upon arrival in Bloomington, Indiana, on 6 August 1995. On 27 August 1995, I divided the juvenile birds across the four large aviaries containing the adult INC birds (two aviaries) and the adult SDC birds (two aviaries). Replicates of each culture were used so that during the breeding season I could test females with males with which they were unfamiliar individually, but that either shared a similar cultural background or did not (see below). Prior to the 1996 breeding season (all the juvenile South Dakota birds, hereafter referred to as yearling SD birds), each aviary housed 7–8 yearling females, 6–7 yearling males, 8–11 adult females, and 7–11 adult males.

Breeding season aviaries

I removed adult male social models from the winter social housing aviaries immediately prior to the breeding season, in mid-May 1996, to decrease the potential for male–male aggression in the four aviaries, while keeping the SDC and INC groups as stable as possible. All yearling females and males remained in their respective social housing aviaries during the breeding season, except when they were being tested in the pairing-assessment aviaries (see below). Adult female social models of both cultures also remained with the yearlings in their respective aviaries for the duration of the breeding season, except for periods when subsets of the adult females were removed briefly to be used in a separate experiment.

Pairing-assessment aviaries

Two pairing-assessment aviaries were used to test the pairing and mating behaviours of yearling birds from the South Dakota and Indiana cultures during the 1996 breeding season. Both aviaries were identical in dimensions to those used for winter social housing, but were unfamiliar to the birds being tested. Both aviaries were visually isolated from the four winter social housing aviaries containing the yearling SDC and INC birds and the adult female social models of their respective cultures. The two pairing-assessment aviaries were adjoining. Birds of one pairing-assessment aviary could hear birds in the other aviary, but were largely visually isolated due to the presence of trees and a four-panel plywood wall separating the two pairing-assessment aviaries. Very little social interaction was documented between birds of the separate pairing-assessment aviaries during the breeding season.

On 21 May 1996, I placed into one of the pairing-assessment aviaries, eight yearling females (four from one of the INC aviaries and four from one of the SDC aviaries) and eight yearling males (four from the second INC aviary and four from the second SDC aviary). In the other pairing-assessment aviary, I placed yearling SDC and INC males from the first set of aviaries with yearling SDC and INC females from the second set of aviaries. Thus, at all times, females were never tested with males with which they had individual experience prior to the breeding season. Furthermore, birds were tested in a multiple-choice design in social groups; each individual therefore had several potential mates from which to choose. Finally, none of the adult social models was ever present in the pairing-assessment aviaries; the INC and SDC birds tested here were all yearling birds of the second cultural generation. This design, as with the earlier study (Freeberg 1996), thus ensured that if any differences in courtship or pairing patterns were found between SDC and INC birds during testing in the pairing-assessment aviaries, the only variable that could give rise to those courtship differences was the cultural background of the birds.

Data Collection

I documented courtship interactions and pairing and mating patterns of the yearling INC and SDC birds in the

pairing-assessment aviaries from 22 May to 30 June 1996, using methods similar to those detailed in the earlier study (Freeberg 1996). Each morning, between approximately 0630 and 1030 hours, two trained assistants (S. McGann & J. Schilling) and I observed the birds during two 10-min focal samples of each male (Altmann 1974). Neither of the trained assistants knew the cultural background of the individual birds they were observing. Focal males were sampled following a methodology successfully used in earlier studies with the South Dakota population and with other populations of captive cowbirds (Eastzer et al. 1985; Freeberg et al. 1995; Freeberg 1996; West et al. 1996).

I collected data on directed vocalizations of males, which included only songs and flight whistles oriented towards the 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 (West et al. 1981; Rothstein et al. 1986, 1988; Dufty & McChrystal 1992). These body movements are often associated with the song-spread or bowing display of male cowbirds (see Friedmann 1929; Lowther 1993). In response to a male's first directed vocalization within a vocal bout to a female, where one or more directed vocalizations is uninterrupted by flight or by vocalizations to or from other birds, I documented whether females flew away from the male within 1 s after hearing the vocalization, or remained within 0.5 m to hear at least one more directed vocalization from the male. 'Remaining' and 'flying away', as defined here, do not constitute 100% of a female's behavioural responses to the directed vocalizations of males. For example, females can lunge at or attack males, vocalize themselves with a chatter or rattle vocalization, or adopt a copulation solicitation display (Friedmann 1929; Rothstein et al. 1986; Lowther 1993).

The major dependent variables were pairings and copulations between females and males. The pairing measure requires persistent courtship activity by a female and male over a period of days, and has been found to be a reliable predictor of stable mating pairs in other populations of cowbirds (Eastzer et al. 1985). I determined pairings based on observations of female and male cowbirds engaging in consecutive consort days with one another. 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 female A heard from all males throughout the morning's observations, the highest number had to be from male B. Second, male B had to direct at least 10 vocalizations to females during his two 10-min focal samples, at least a third of which had to be directed to female A. For a pairing to be established, the female and male had to engage in 4 consecutive consort days. Copulations, the other major dependent variable, typically occur after successive days of consorting between a female and male (Yokel 1986; in the present study, however, some copulations occurred after only a day of documented consorting). Copulations were scored when a female gave a solicitation display (copulatory posture) in response to a male's directed vocalizations, and the male mounted the female. If a female and male copu-

lated, I determined that they had paired, whether or not they met the criteria for establishment of a consort day or a pairing.

After a female and male had paired by consorting for 4 consecutive days, I left them in the pairing-assessment aviary for 1 additional day to increase the possibilities of observing copulations. After this additional day, I removed the pair from the pairing-assessment aviary, returned them to their respective social housing aviaries, and replaced them with a female and male of the same culture and aviary (an INC female with another INC female of the same INC aviary, and so on). If a female and male copulated, they were also removed and replaced with birds of the same culture and aviary. If a bird did not court at all for several days, it was removed and replaced with a bird of the same culture and aviary. Ten of the females entered the pairing-assessment aviary once, 18 entered twice and one entered three times. Six of the males entered the pairing assessment aviary once, 17 entered twice and four entered three times. Towards the middle and end of the breeding season, I placed females and males that paired previously into the pairing-assessment aviaries only with birds with which they had not paired earlier (the exceptions are described below). Thus, although some females paired twice (none paired more than twice), every pairing that occurred was unique.

Testing the Stability of the Pairing Measure

To determine whether the pairing criteria could reliably predict stable, long-term mating pairs, I reintroduced 12 female-male pairs that had paired earlier in the season into the pairing-assessment aviary. In each of these 12 cases, I introduced one member of the pair into the pairing-assessment aviary several days before the other member. Starting on the day I reintroduced the second member of the pair, I collected the same data for the pair as detailed above (number of directed vocalizations, flying away or remaining responses of females to directed vocalizations of males, whether the female and male met the criteria for a consort day, and whether the female and male copulated). If the reintroduced pair did not meet the criteria for a consort day but the male directed at least two vocalizations to the female during that morning's observations, I determined that the male and female courted on that day.

Observer-reliability Measures and Data Analyses

To measure observer reliability, a male from one of the pairing-assessment aviaries was randomly chosen and observed for 10 min, simultaneously and independently by me and one of the two trained assistants. Observer-reliability measures were taken at the end of a morning's observations. After each 10-min reliability sample, I determined interobserver agreement on whether the focal male had obtained a consort day with a female (and, if so, which female), and the extent of agreement in total behavioural data collected. I measured reliability with

Table 1. Number of pairings between females and males from the South Dakota culture (SDC) and the Indiana culture (INC)*

Female ID	Paired with	
	First male	Second male
SDC 91	<i>INC</i>	SDC
92	<i>SDC</i>	
93	<i>SDC</i>	<i>INC</i>
98	<i>SDC</i>	
99	<i>SDC</i>	
106	<i>SDC</i>	
108	<i>SDC</i>	<i>INC</i>
110	<i>SDC</i>	<i>SDC</i>
111	<i>SDC</i>	
113	<i>SDC</i>	<i>SDC</i>
116	<i>SDC</i>	
INC 95	<i>INC</i>	<i>INC</i>
96	<i>SDC</i>	<i>INC</i>
97	<i>INC</i>	
103	<i>INC</i>	
105	<i>SDC</i>	<i>INC</i>
107	<i>SDC</i>	
112	<i>SDC</i>	
114	<i>INC</i>	
115	<i>INC</i>	<i>SDC</i>
118	<i>SDC</i>	
119	<i>INC</i>	

*Culture designations in italics indicate males that copulated with the female at least once.

one assistant 18 times, and with the other assistant 17 times. Agreement scores with the two assistants on whether the randomly chosen males had obtained a consort day were 89 and 82%, and agreement scores on total behavioural data collected were 84 and 81%, respectively.

I used nonparametric tests to analyse the data (Siegel & Castellan 1988). I analysed data on pairings between females and males of the two cultures in two ways. First, I used two-tailed sign tests to determine whether females paired more with males of the same culture. Second, I used Fisher's exact tests to determine whether the pairing patterns of INC females differed from those of SDC females. In analyses of the data on female responses to the directed vocalizations of males, I included only females that heard at least five directed vocalizations from males of both cultures. I used two-tailed Wilcoxon signed-ranks tests to determine whether the females responded differently to the directed vocalizations of males of the same or different cultural background, and Fisher's exact tests to determine whether responses of INC females differed from those of SDC females.

RESULTS

Pairings

Females and males from the same cultural background paired more with each other than with birds from the different cultural background (Table 1; two-tailed sign test: $k=3$, $N=16$, $P<0.05$). Of the 56 birds tested, 38

(67.9%) were involved in at least one pairing, representing 31 unique pairs. Twenty-two of the 31 pairs (71.0%) were in the predicted direction. Thirteen of the 16 pairings involving SDC females were with SDC males, and nine of the 15 pairings involving INC females were with INC males. In the pairings, focal males directed an average (\pm SD) of 10.8 ± 6.3 and 10.2 ± 5.7 vocalizations per 20-min observation per morning to SDC and INC females, respectively.

The pairing pattern of INC females differed from that of SDC females (Table 1; Fisher's exact test: $P<0.05$). Of the 11 SDC females that paired with at least one male, eight (72.7%) paired more often with SDC males, and three (27.3%) paired with a male from each cultural background. Of the 11 INC females that paired with at least one male, five (45.5%) paired more often with INC males, three (27.3%) paired more often with SDC males, and three (27.3%) paired with a male from each cultural background.

Nine of the 31 pairings involved a female that had paired earlier in the pairing-assessment testing (no female paired more than twice). If only the first pairing for each female that paired is analysed, 16 of 22 (72.7%) females paired with a male of the same cultural background, a nonsignificant result (Table 1; two-tailed sign test: $k=6$, $N=22$, NS). Analysing only the first pairing for each female, however, indicated that the pairing preferences of INC females differed from those of SDC females (Fisher's exact test: $P<0.05$).

Copulations

Patterns of copulations were in the predicted direction for the effects of social experience on courtship and mating patterns, but the sample sizes were small and the differences observed were not statistically significant. Of the 18 unique pairs of females and males that copulated at least once, 12 (66.7%) were between birds of the same cultural background (Table 1). Of the 14 females that copulated with at least one male (nine SDC females and five INC females), eight copulated with one to two males of the same cultural background, three copulated with a male of the different cultural background, and three copulated with both a male of the same and of the different cultural background (two-tailed sign test for females: $k=3$, $N=11$, NS).

Directed Vocalizations of Males and Female Responses

Females heard more directed vocalizations from males of the same culture than from males of the different culture (two-tailed Wilcoxon signed-ranks test: $T^+=330$, $z=2.432$, $N=29$, $P<0.05$). Fourteen of the 14 SDC females heard more directed vocalizations from SDC males, and seven of the 15 INC females heard more directed vocalizations from INC males (Fig. 1; Fisher's exact test: $P<0.01$).

In response to a male's first directed vocalization within a bout, females flew away more often when the male was

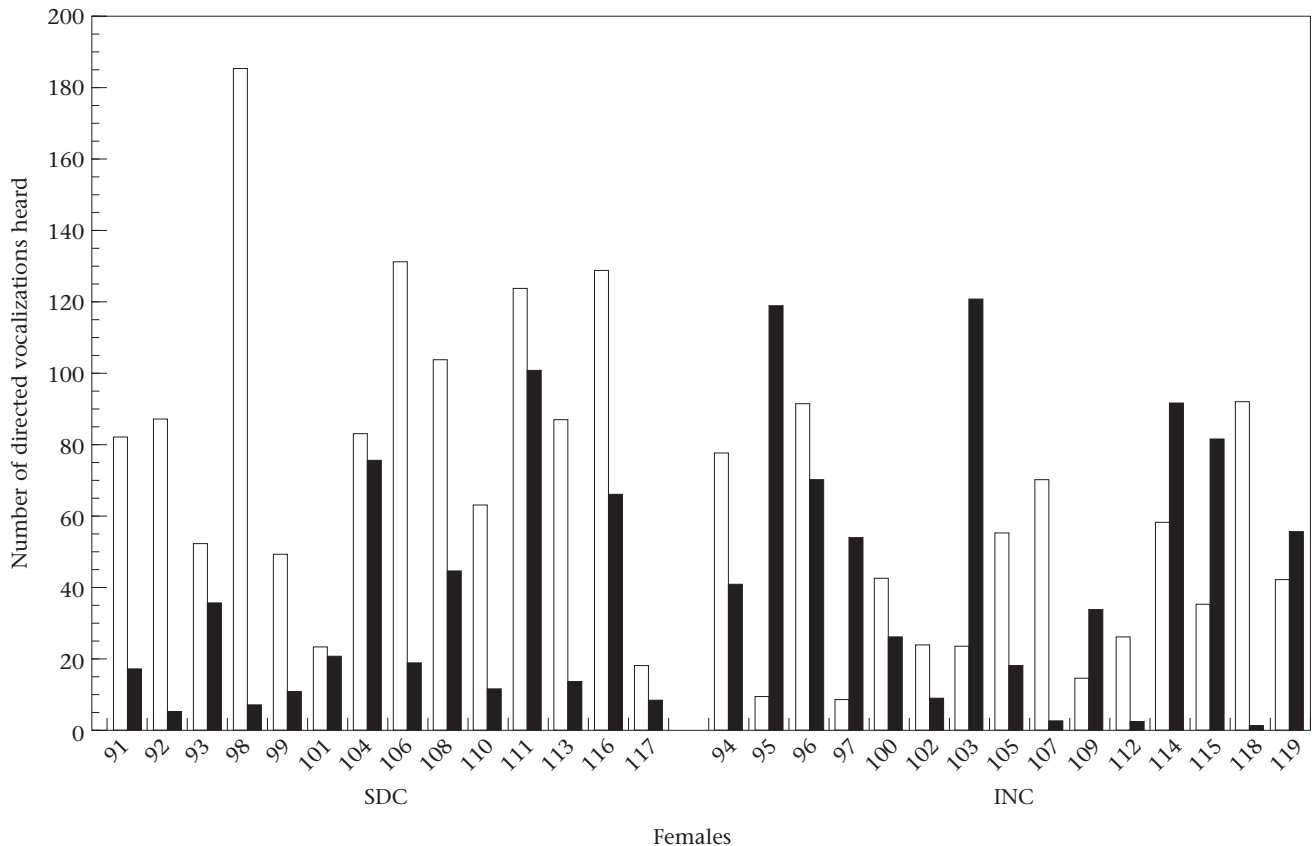


Figure 1. Number of directed vocalizations that South Dakota females from the South Dakota culture (SDC) and the Indiana culture (INC) heard from SDC (□) and INC (■) males.

from the different culture (two-tailed Wilcoxon signed-ranks test: $T^+ = 269$, $z = 2.865$, $N = 25$, $P < 0.01$). Nine of 13 (69.2%) SDC females flew away from vocalizing INC males more often than they did from vocalizing SDC males, and 10 of 12 (83.3%) INC females flew away from vocalizing SDC males more often than they did from vocalizing INC males (Fig. 2; Fisher's exact test: $P < 0.05$).

Females remained within 0.5 m to hear at least one more directed vocalization from a male, following an initial directed vocalization from that male, more often if that male was from the same culture (two-tailed Wilcoxon signed-ranks test: $T^+ = 233.5$, $z = 2.386$, $N = 24$, $P < 0.05$). Unlike the pattern for flying away from vocalizing males, the pattern displayed by INC females for remaining near a vocalizing male did not differ significantly from the pattern displayed by SDC females. Ten of 13 (76.9%) SDC females and 6 of 11 (54.5%) INC females remained to hear at least one more vocalization from a male, following an initial directed vocalization, more often when that male was from the same culture than if the male was from the different culture, and one INC female remained equally for males of both cultures (Fig. 2; Fisher's exact test: NS).

Reliability of the Pairing Measure

Twelve pairs of females and males that paired early in the pairing-assessment testing were reintroduced later in

the breeding season (Table 2). In five of the cases, the pair copulated by the fifth day of their reintroduction. In another five cases, the pair met the criteria for consort days or courted one another on most or all of the 4–5 days they were together in the pairing-assessment aviary. The final two pairs of females and males that were reintroduced did not court one another for the 5 days they were together in the pairing-assessment aviary. However, in one of these pairs, the male was injured on his reintroduction, and did not seem to interact socially with any of the birds on the days he was in the pairing-assessment aviary. Discounting the pair with the injured male, of the 11 pairs of females and males that paired earlier in the pairing-assessment aviary, 10 (90.9%) were found to copulate, consort with, and/or court one another upon reintroduction (Table 2; two-tailed sign test: $k = 1$, $N = 11$, $P < 0.05$).

DISCUSSION

Female cowbirds paired more with males sharing the same cultural background than they did with males possessing a different cultural background. Females tended to copulate more with males of the same experiential background, although the proportion did not differ statistically from chance. Assortative pairing by experiential background occurred at nearly a 3:1 ratio, and assortative mating by experiential background occurred at a

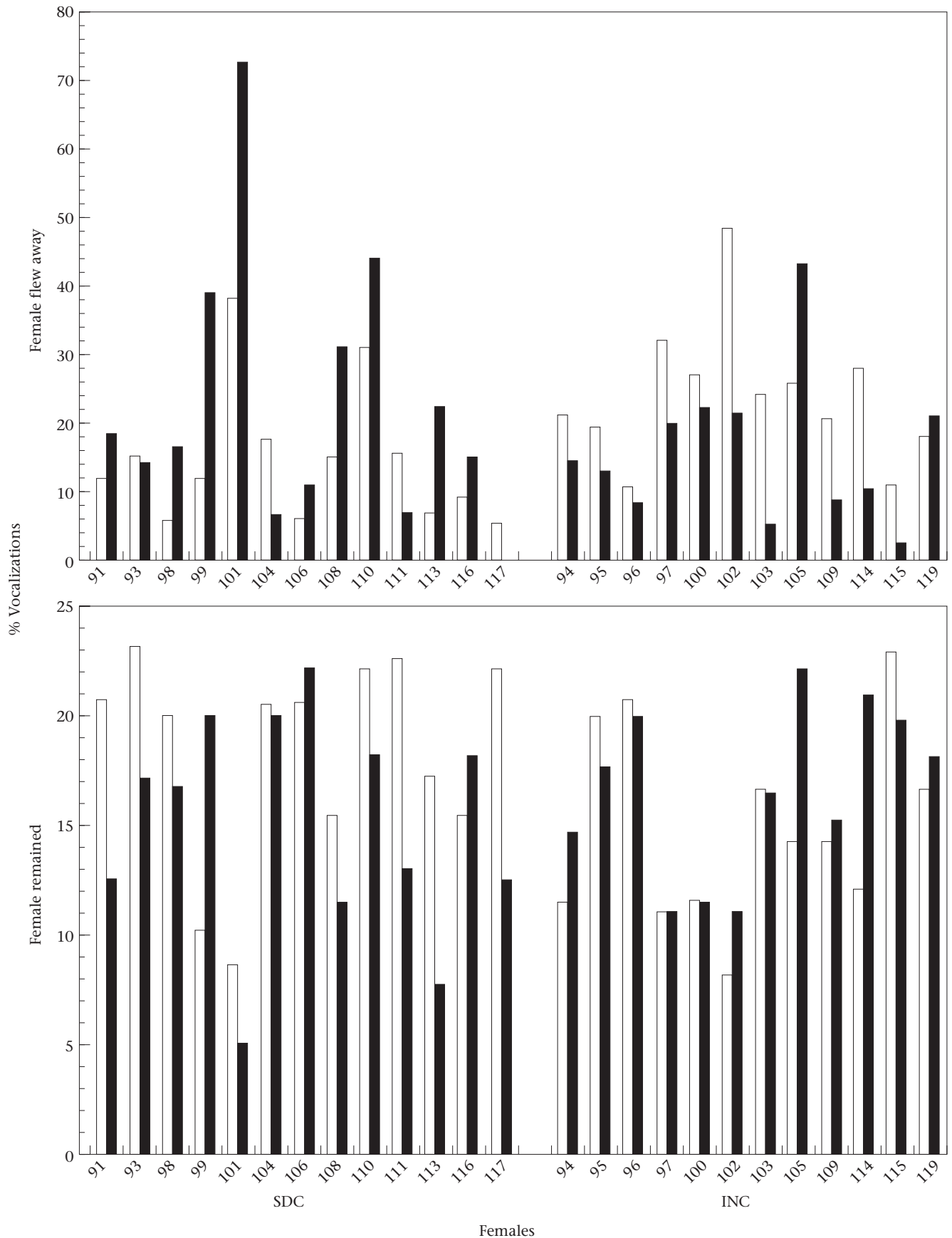


Figure 2. Female responses to the directed vocalizations of SDC (□) and INC (■) males. The percentage of directed vocalizations after which SDC and INC females (a) immediately flew away, and (b) remained within 0.5 m to hear at least one more directed vocalization.

Table 2. Outcomes of reintroductions of previously paired females and males from the South Dakota culture (SDC) and the Indiana culture (INC)

Female ID	Male	Reintroduction				
		Day 1	Day 2	Day 3	Day 4	Day 5
SDC 91	INC	0	0	0	0	0
SDC 92	SDC	0	0	Copulate	X	X
SDC 98	SDC	Court	Court	Court	Consort	0
SDC 106	SDC	Court	Court	Consort	Court	X
SDC 108	SDC	0	Consort	Copulate	X	X
SDC 110	SDC	Copulate	X	X	X	X
SDC 110	SDC	Consort	Consort	Consort	0	X
SDC 116	SDC	Consort	Court	0	Court	0
INC 96	SDC	Court	Consort	Consort	Court	X
INC 103	INC	0	Court	Court	Copulate	X
INC 105	SDC	0	Court	0	0	Copulate
INC 112	SDC*	0	0	0	0	0

X: One or both of the birds were removed from the pairing-assessment aviary following the previous morning's observations; 0: no courtship behaviour was observed.

*This male was injured during reintroduction into the pairing-assessment aviary.

2:1 ratio. These ratios of assortative pairing and mating are comparable to those found in earlier studies with the South Dakota population and with other populations of cowbirds (Eastzer et al. 1985; Freeberg 1996). It is important to reiterate here that all of the birds used in this study (the adult social models and the yearling subjects) were from the same South Dakota population. The only difference between the yearling South Dakota cowbirds tested in this study was that one set was housed with South Dakota adults that had been housed earlier as young with South Dakota adults, while the other set was housed with South Dakota adults that had been housed earlier as young with Indiana adults.

Further evidence for cultural transmission comes from the data on females' responses to the directed vocalizations of males. Females flew away from vocalizing males more often if those males were from the different culture. By immediately flying away from a vocalizing male, a female actively distances herself from the male, and therefore decreases the number of vocalizations the male can direct to her. Furthermore, flying away from a male during or immediately after a male's vocalization may decrease the potency of the male's vocalization by decreasing the signal-to-noise ratio of the vocalization (King et al. 1981). In response to a male's directed vocalization, females remained within 0.5 m to hear at least one more directed vocalization more often if that male was from the same culture. By remaining near a vocalizing male, a female actively builds a vocal history with that male, perhaps allowing her to better assess his qualities as a potential mate (see West et al. 1981; Yokel 1986; Yokel & Rothstein 1991).

Data suggest that SDC males directed more vocalizations to females in general than did INC males (see Fig. 1). Thus, females might simply have preferred males that sang the most, and therefore the cultural background of the birds may have played a relatively minor role in their courtship patterns. This interpretation can be discounted for three reasons. First, the pattern of hearing

directed vocalizations shown by the INC females differed significantly from that of SDC females (Fig. 1). Second, the pattern of flying away in response to the directed vocalization of a male shown by the INC females differed significantly from that of the SDC females (Fig. 2). Regardless of the number of directed vocalizations from INC and SDC males, females flew away more often from males of the different culture. Third, it is possible that differences in singing rate, as well as in the songs themselves, may have been due to cultural background. More work is needed to address this latter possibility.

The extent to which the courtship behaviours of INC birds were similar to those of adult Indiana birds, and the courtship behaviours of SDC birds were similar to those of adult South Dakota birds remains to be tested directly. Preliminary evidence suggests that significant differences in the vocalizations (both songs and flight whistles) of the males of the South Dakota and Indiana cultures exist. South Dakota females display significantly more copulatory responses to playbacks of the songs of adult South Dakota males of the South Dakota culture than to playbacks of the songs of adult South Dakota males of the Indiana culture (T. M. Freeberg, A. P. King & M. J. West, unpublished data). South Dakota females also prefer the songs of normal (captured in the wild as adults) South Dakota males relative to the songs of normal Indiana males (West et al. 1998).

Pairing and mating preferences for males of the same cultural background appeared to be stronger in SDC females than in INC females (Table 1). Numerous possibilities might account for this difference; three of the most likely are discussed here. First, the transmission fidelity of a more novel culture in cowbirds (or in animals in general) may not be high enough to ensure that transmission occurs without a significant amount of alteration from one generation to the next. In the present study, the South Dakota system of courtship behaviours, being the typical system for South Dakota birds, might have been easier for the young South Dakota birds to

learn and maintain. In contrast, the Indiana system of courtship behaviour, being atypical for South Dakota birds, might have been transmitted with more errors in learning (for discussions of biases in cultural transmission, see Lumsden & Wilson 1981; Boyd & Richerson 1985).

Second, there may have been cohort differences between the juvenile birds collected in 1993 for the earlier study (Freeberg 1996) and the juvenile birds collected in 1995 for the present study. It is possible that the breeding season in South Dakota in 1995 began earlier than the breeding season in 1993. If this occurred, when these young birds were captured in South Dakota in early August of 1995, they may have had several days to a few weeks more exposure to adult cowbirds than did the young birds captured in August 1993. This should have led to stronger preferences for the South Dakota culture in the SDC birds, and more equivocal preferences in the INC birds, which were the results obtained. Thus, the amount of exposure as juveniles to adult vocalizations and potentially to courtship behaviour could have differed between the juvenile cowbirds of this study and the juvenile cowbirds of the earlier study (Freeberg 1996). For example, studies with both white-crowned sparrows, *Zonotrichia leucophrys*, and indigo buntings indicate that young males can learn their breeding season vocalizations either shortly after their own independence in the early autumn months or in the weeks just prior to the onset of the breeding season the following year, depending upon the population and the social context (Payne 1981; Nelson et al. 1995). Further work is needed with South Dakota cowbirds to determine when males in the wild learn their vocalizations. Data from captive studies thus far suggest that vocal learning can occur in both the autumn and in the spring (unpublished data).

Third, the INC birds were housed in their winter social housing aviaries with slightly more adult male social models than were the SDC birds. The presence of more adult males in the INC aviaries prior to the breeding season may have diminished the general courtship activity of the INC males during the breeding season. This could have resulted in INC females being courted relatively less by INC males, which might have affected the general pairing patterns of those females. Interestingly, this possibility is supported by the earlier study (Freeberg 1996). In the first year of the earlier study, the birds housed with South Dakota adults were housed over the winter with slightly higher numbers of adult males than were the birds housed with Indiana adults. During their first breeding season, the pairing patterns of the birds housed with South Dakota adults were not as strongly assortative as those of the birds housed with Indiana adults.

The within-season stability of the pairing patterns of the SDC and INC birds is supported by the results of the reintroductions to the pairing-assessment aviary of birds that had paired earlier in the breeding season. Discounting the pair in which the male was injured during the move into the pairing-assessment aviary, 91% of the reintroductions resulted in further courting, the establishment of consort days, and/or copulations. The fact that

these pairings were resumed after separation for up to 3 weeks is relevant to this species in that the breeding season for cowbirds lasts roughly 8 weeks (Friedmann 1929; South Dakota Ornithologists' Union 1991; Lowther 1993). The pairs, operationally determined by the pairing criteria used in this study and in the previous study of social learning and courtship systems (Freeberg 1996), thus appear to represent relatively long-term pairing associations between female and male cowbirds.

The results reported here constitute some of the first experimental evidence for the cultural transmission of courtship patterns in animals. The experiential backgrounds of the young South Dakota cowbirds consisted of social interactions with only adult South Dakota birds: adult cowbirds that had developed in an Indiana culture or in a South Dakota culture. The South Dakota and Indiana systems of courtship behaviour that were socially learned by the first cultural generation of birds (Freeberg 1996) were transmitted to the second cultural generation of birds in the present study. Our knowledge of transmission fidelity across generations of animals and the extent to which social learning can lead to adaptive behaviour patterns in populations has been greatly increased by recent work on foraging behaviour in a number of taxa (see Laland et al. 1993; Galef 1995; Galef & Allen 1995). The present study extends these lines of research, by demonstrating experimentally that the courtship patterns of animals can also be transmitted across generations. Further work on the transmission of systems of courtship behaviour would prove beneficial in that courtship systems themselves represent selective agents and thus have direct evolutionary implications for animal populations. Different patterns of reproduction could arise as a result of social learning and cultural transmission, and could result in genetic changes in the interacting populations.

Positive assortative mating has been documented in captive studies with cowbirds at the level of subspecies (Eastzer et al. 1985) and of social or cultural background (Freeberg 1996, and the present study). Positive assortative mating occurs in a wide variety of taxa, and it can occur for a number of reasons: it may be advantageous in that it ensures that local adaptations of the population are transmitted to progeny, it may be a by-product of mechanisms for species recognition, or it may be a direct result of selection for behavioural complementarity (see Mayr 1963; Burley 1983; Cooke & Davies 1983; Partridge 1983). The present study with cowbirds suggests a proximate reason for assortative mating, related to the behavioural complementarity hypothesis: young cowbirds develop a courtship system characteristic of the culture they inhabit. This courtship system is composed of communicative behaviours, preferences for those behaviours and the social competence to use those behaviours effectively (see West et al. 1997). Individuals selectively pair and mate with individuals that share a similar culturally transmitted courtship system over individuals with different courtship systems.

Social learning and cultural transmission represent important mechanisms for the inheritance of acquired characters among animal populations. Whether the

behaviours are maintained across generations and whether the behaviours have direct fitness consequences on the animals that acquire those systems will determine the evolutionary implications for animal populations (for historical discussions of this see Baldwin 1902; Schmalhausen 1949; Gottlieb 1992). South Dakota cowbirds exposed to an atypical social environment (housing with Indiana adults) developed courtship patterns that differed from South Dakota cowbirds exposed to a more typical environment (housing with South Dakota adults). Different social environments resulted in patterns of assortative courtship and mating (Freeberg 1996). In the present study, the different cultural lines were maintained sufficiently intact that a new generation of birds displayed assortative courtship patterns based on those inherited social environments. These results point to the need for determining the nature of the inherited environments of animals that learn socially (Oyama 1985; Schleidt 1985; West & King 1987; Alberts & Cramer 1988; West et al. 1988; Gottlieb 1992; Stephens 1993). Finally, to determine how learned behaviour may influence the evolutionary processes affecting animal species, studies of the social or cultural transmission of behavioural systems must focus on behaviours of adaptive significance (see Scott 1989; Laland et al. 1993; Galef 1995; Lefebvre & Giraldeau 1996). Testing the extent to which culturally transmitted behavioural systems influence actual reproductive success among individuals in a population is crucial. This can be addressed by captive studies, but the real significance of these lines of research to the evolutionary dynamics of animal populations will most strongly be borne out by studying wild populations.

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