

Epigenesis of cowbird song—A joint endeavour of males and females

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The role of social stimulation from female cowbirds (*Molothrus ater*) on male song learning was tested. In this species the females do not sing. However, we have found that both male and female cowbirds contribute to the maintenance of geographic variation in the songs of the two subspecies, *Molothrus ater ater* (AT) and *Molothrus ater obscurus* (OB)^{1,2}. We therefore performed two studies using males of the eastern subspecies (AT) reared in complete isolation from male conspecifics. In the first study, AT males, tutored with AT song, were individually housed with other species or with females of the southern *M. a. obscurus* subspecies (OB). In the second study, naive AT males were housed, without tutoring, with other species or AT or OB females. In both studies the males developed significantly different song repertoires that were biased towards the preferences of their non-singing female companions. These data establish a new, non-auditory, source of vocal instruction: social stimulation from the song's intended recipient.

Our earlier results revealed reciprocal contributions by male and female cowbirds to the maintenance of geographical variation in the songs of the two subspecies, AT and OB (Fig. 1). Juvenile AT males became bilingual (singing clear renditions of both AT and OB variants) when exposed to OB males¹. Adult AT males did not learn OB song when housed with OB males, but they did do so when housed with OB males and females². Moreover, adult AT and OB males substantially altered their songs when housed only with non-singing females of other subspecies (A. P. K. and M. J. W., unpublished results). The preferences of females for their native geographic variant were found to be highly resistant to postnatal modification^{3,4}. Song biases were also evident in choice of mates in that captive females copulated most often with males who sang the highest proportion of the female-appropriate song variant².

In this study we searched for ontogenetically prior instances of mutual adaptation. Could the female affect song outcome

Table 1 Effects of housing on song development of males tutored with AT song

	Males housed with other species			Males housed with OB females		
	RDB	2B	DBW	RLB	RW	P
Song content						
% Full tutored song	24	34	21	0*	58	0
% Partial tutored song	48	66	38	30	0	0
Original song	28	0	41	70	42	100
No. of original song types	2	0	1	3	3	3

A song was defined as copied if it possessed the same sequence of frequency contours of the same frequency duration and with the same minimum and maximum frequency (see Fig. 1). Full tutored song constituted copies of the tutored AT song; partial songs were copies of the AT song that consisted of only the first song phrase; original songs were any non-copied song; and song types were stereotyped variations of original themes which could be AT or OB. The group differences for full and partial tutored song and the number of song types were significant as tested by the Mann-Whitney test ($U=0$, $P<0.05$ for all comparisons).

* Male RLB sang the tutored song during the winter but deleted it from his repertoire in April.

not only by her choice of mates but also by her presence during development itself?

The AT males were hand-reared from 4–5 days after hatching in acoustic isolation until, at 50 days old, they were placed in their respective conditions using previously described procedures³. All females were adults: the AT birds were caught in the wild in Orange County, North Carolina and the OB birds in Starr County, Texas. Non-conspecific companions were male and female canaries (*Serinus canaria*) for all males except one which was housed with a female starling (*Sturnus vulgaris*). Methods of housing and recording followed techniques described elsewhere¹.

In the first study, six naive AT males were tutored daily (240 repetitions of the same AT song over 3 h) for 3 months (September to November). Three males were separately housed with one or two birds of other species and the remaining three were housed individually each with two OB females. In the second study, 12 naive AT males were housed separately: three with one or two individuals of other species, five with 2–4 AT and four with two or three OB females.

During both experiments, singing behaviour was monitored from November to June. In all, 23,000 songs were recorded from males and none from females. The only vocalization made

Fig. 1 Zero-crossings analyser display of typical *M.a. ater* (AT, upper panel) and *M.a. obscurus* song (OB, lower panel). P1 represents the first phrase; IPU, the inter-phrase unit; MSE, the mid-song element; and P2, the whistle phrase. The MSE is found only in OB song¹. Playbacks of songs where the presence or absence of the MSE was manipulated demonstrated the sensitivity of OB, but not AT, females to this element: when the MSE was removed, OB, but not AT, females showed a significant decrease in the copulation response to OB song⁷. Thus, the operational definition of AT song is P1 IPU P2 and that of OB song is P1 IPU MSE P2. Cowbird song typically ranges from 500 to 12,000 Hz.

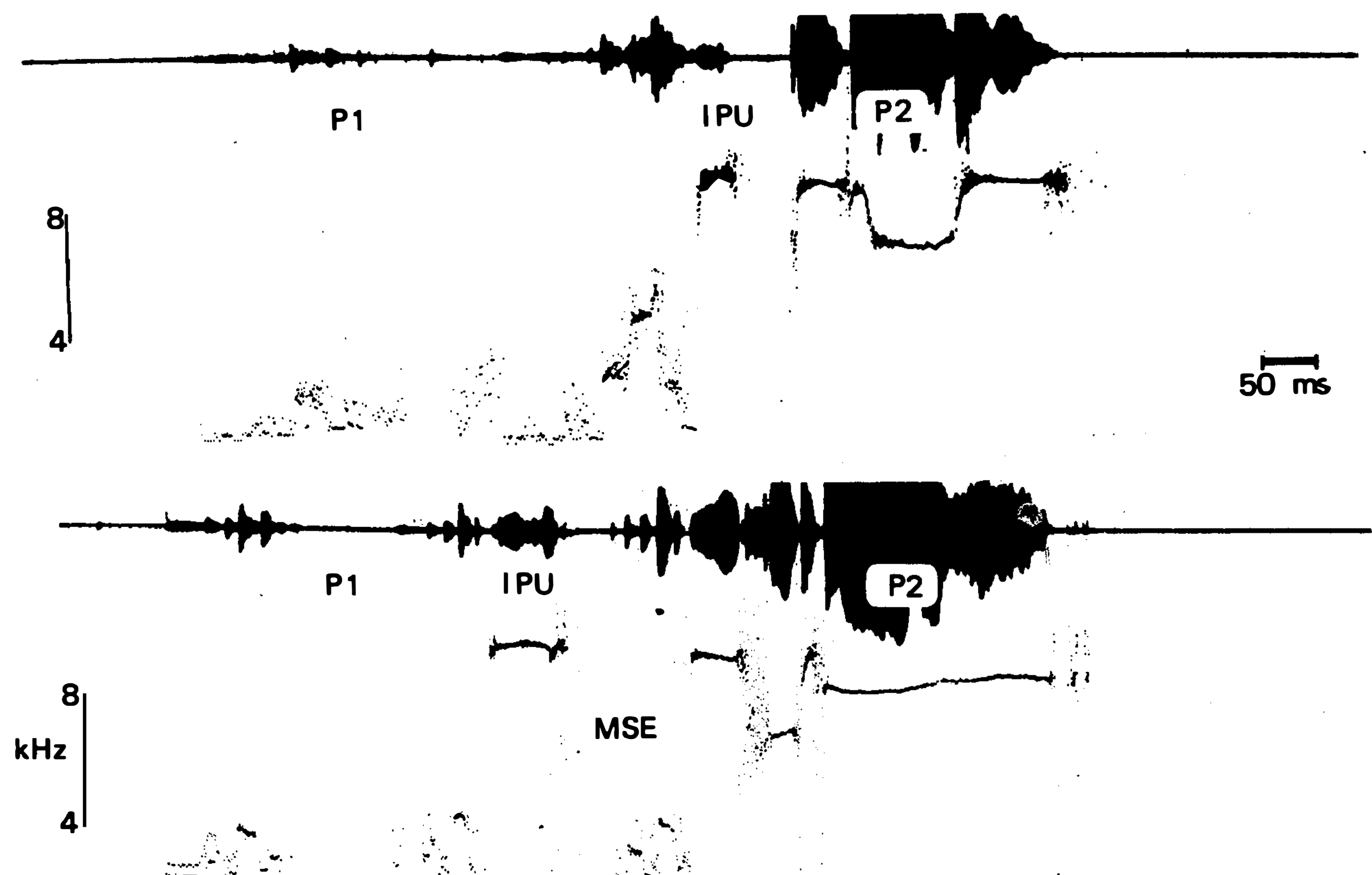


Table 2 Effects of housing on non-tutored males

	Males housed with:		
	Other species	AT females	OB females
Mean value			
Frequency width of phrase 1 (Hz)	3,517 (1,033–5,903)	3,091 (2,100–4,591)	5,912 (5,210–6,800)
No. of notes in phrase 1	5.2 (3–13)	4.8 (2–7)	2.6 (1–4)
% AT song	26 (16–37)	51 (18–93)	15 (0–38)
% OB song	36 (0–63)	0 (0)	64 (2–100)
% Partial song	38 (0–84)	49 (0–98)	21 (0–50)

Frequency range refers to the bandwidth (in Hz) of the maximum frequency modulation of the notes in phrase 1; no. of notes is the number of discrete frequency modulations of phrase 1; % AT or OB refers to the percentage of songs classified as AT and OB on the basis of the presence or absence of the MSE (see Fig. 1); partial song refers to songs sung without an inter-phrase unit or composed only of whistles. Values in parentheses are the range. Kruskal Wallis' one-way analyses of variance were significant at d.f. = 2 and $P < 0.049$ for: frequency range ($H = 5.9$), no. of notes ($H = 6.8$), % AT ($H = 6.5$) and % OB ($H = 6.7$). Mann-Whitney U -tests were used to compare the mean differences of males reared with AT versus OB females and all were significant: frequency range ($U = 0$, $P < 0.008$), no. of notes ($U = 0$, $P < 0.008$), % AT ($U = 1$, $P < 0.016$), and % OB ($U = 0$, $P < 0.008$).

frequently by the females was a call given during feeding, usually transcribed as a 'chuck' or 'kek' sound. This call is made equally frequently by the males. In addition, females produced 'rattle' vocalizations in May and June. These calls were acoustically the same in AT and OB females. Female cowbirds have never been reported to sing in the wild nor have we observed it in 10 years of laboratory recording⁵.

The data reported here are based only on songs recorded when the males were in full breeding condition as determined by courtship activity. The songs of each male were recorded during two separate sessions on at least 3 days for a minimum of 7 recording hours; 1,036 songs were analysed in the first experiment and 2,191 in the second. The mean numbers of songs sampled for males in each condition were comparable. In the first experiment, a mean of 165 songs (range 133–213) was obtained for the males housed with other species and 180 (range 114–226) for the males housed with OB females; in the second experiment, an average of 175 songs (range 115–252) was analysed for the males housed with AT females, 188 (range 95–247) for the males housed with OB females and 188 (range 165–205) for males housed with other species. We based our sampling criteria on other data comparing the daily song samples of 14 males recorded for a 7-week period, with over 500 songs from each male. These data indicated that 95% of a male's song types (males have 1–6 song types) are represented in 87% of daily samples of 11–20 songs, 98% are represented in samples of 21–40 songs, and 99% in samples of 41–85 songs (D. H. Eastzer, unpublished observations).

The standardized auditory experience provided for the males in the first study produced significantly different outcomes (Table 1). Copied song (clear renditions of the tutor song) constituted 77% of songs of males housed with other species and only 29% of the songs of males housed with OB females. Conversely, the males housed with other species sang an average of 23% original songs while the males with OB companions sang a mean of 71% original songs. Males housed with other species also produced fewer stereotyped versions (song types) of original song while males housed with OB females produced

more original song types. Finally, one of the AT males housed with OB females developed an OB song type. This finding contrasts with previous data from nine juvenile AT males caught in the wild and housed individually with AT females: in that case, no males produced an OB song although they too were limited in their early exposure to AT song².

The second study afforded another view of the potential influence of the female because auditory stimulation was not provided; the impact of the female was even more conspicuous. Due to the absence of a standardized song input, song development was measured differently. Based on previous data showing that the first half of cowbird song accounted for over 90% of song potency, acoustic differences in it were compared across the three groups^{6,7}. In addition, the proportion of each male's songs that was prototypically AT or OB was computed (Table 2). Significant differences occurred on all measures, most notably between males housed with AT versus OB females. The performance of the males housed with other species was almost uniformly intermediate, highlighting the 'biasing' effect of female presence.

Thus, the presence of females affected the male's tendency to incorporate auditory input and his organization of auditory output. As such, these data go beyond investigations of other species in which the social properties of vocal transmission have been identified⁸. In that case, the social transfer of information was vocal, that is, the 'tutor' sang and the 'pupil' listened and copied what he heard. In the present study, as the female cowbirds never sang, the transmission of information did not rely on modelling or imitation.

Although cowbirds are brood parasites, and hence restricted in their access to early species-typical stimulation, they seem to rely on learning as much as other non-parasitic species⁹. As the males reared with other species appeared to possess geographically nonspecific repertoires, the role of the female may be to guide the male through trial and error learning towards an adaptive repertoire.

There have been sufficient observations of potential social influences in other species to suggest that the processes described here are of broad significance^{10–15}. The concept of the social mediation of song learning is not inconsistent with present formulations on the nature of the acoustic controls¹⁴. Rather it points to a new and socially derived origin for some of the constraints on vocal learning. As such, the data also address the parallels between song and speech: songbirds, like humans, may need to experience not only the sounds but the consequences of their vocal endeavours.

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