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Enriching Cowbird Song by Social Deprivation

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Male cowbirds, juveniles and adults, were maintained in one of four conditions: (a) visual and auditory deprivation from males, (b) visual but not auditory deprivation, (c) social isolation, and (d) full contact with males. Their songs in the breeding season were tested with captive female cowbirds. The females responded with copulation postures most often to the songs of the males reared in conditions a and b. Female cowbirds showed no preferences for the songs of males they had been housed with. Comparisons of the behaviors of isolate and group-maintained birds when introduced into an established cowbird colony revealed that isolate males sang more and received more attacks. These results indicate the critical importance of the male cowbird's social environment for song potency. Comparisons of the song potency among the adults also showed the reversibility of early species-typical or species-atypical experience with regard to song performance.

Male cowbirds, reared in isolation from adult male conspecifics, develop atypical but highly effective courtship songs (King & West, 1977). Contrary to expectation, these isolate songs are twice as effective as normal songs in eliciting the female's copulatory posture (West, King, Eastzer, & Staddon, 1979). This is a puzzling finding in at least two respects. First, rearing an animal in isolation typically does not have a more positive outcome than rearing in the normal environment. Because the cowbird is a brood parasite, one might predict that song would develop appropriately with only self-stimulation (Gottlieb, 1973), but one would not predict such a substantial difference in the effectiveness of isolate over normal song. Second, this finding raises questions about the evolution and development of song in this species. If living alone enhances song effectiveness, why is it that male cowbirds live in large flocks during this presumably important period for song acquisition? The purpose here was to examine this question by investigating the effect of visual, auditory, and social stimulation on cowbird song potency for both juvenile and adult males.

Our interest in the adult was stimulated by two factors. First, we had observed that adult male cowbirds, like some other song birds, go through a period of winter song in which their songs appear to "redevelop," i.e., their songs go from being soft and poorly articulated in later winter to loud and clearly articulated in early spring (Thielcke, 1976). This suggested to us that the same types of processes that might affect initial song acquisition might also operate in subsequent years. Second, we had in our laboratory several males that had been reared and maintained in isolation and had developed highly effective songs for three consecutive breeding seasons, as well as several wild-caught group-maintained males that had for several seasons consistently sung songs of only moderate effectiveness. We decided, therefore, to test the flexibility of adult song by manipulating the environments of these males. Could the isolate males be induced to sing less effective songs, and could males with relatively ineffective songs develop more potent ones?

To answer these questions, we carried out

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two experiments. The first experiment was composed of three separate but interrelated phases. The first consisted of housing juvenile and adult males in varying degrees of visual and/or auditory stimulation from late fall until the breeding season; the second phase was a short-term manipulation of the social environment of a small group of males; the third was a playback experiment in which the recorded songs of the males were tested for their effectiveness as elicitors of the female's copulatory response. The second experiment had two parts. The first consisted of raising adult males in either visual or social isolation from other males; the second involved observation of the behavior of these males when introduced into a captive colony of cowbirds.

Experiment 1

Method

Subjects. Both juvenile and adult males were used in the rearing experiment. Age of the birds was determined by examination of the wing feathers (Selander & Giller, 1960). Some of the males had been hand-reared in our laboratory (see King & West, 1977, for details), but the majority had been obtained from the Patuxent Wildlife Station, Laurel, Maryland, in late fall. Eleven adult female cowbirds were used in the playback series.

Procedure. The three housing conditions for the males were as follows: complete isolation from adult male cowbirds (n = 7; 4 juveniles and 3 adults), visual but not auditory isolation from males (n = 4; 2 juveniles and 2 adults), and group living (n = 6; 4 adults and 2 juveniles). Three of the complete-isolation males were housed in sound-attenuating chambers, each with several female cowbirds; the fourth, in a flight cage (1 × 1.5 × .5 m) with a male starling (*Sturnus vulgaris*). The sound-attenuating chambers consisted of two concentric boxes constructed of plywood and Sheetrock with wood and acoustic baffles between the two boxes. Suppression was greater than 39 dB at 1 kHz and increased with the higher frequencies to greater than 50 dB between 8 and 16 kHz. The interior box was a 1.1-m cube, fabric-lined, lighted by two Vita-lite tubes and continuously ventilated.

The males reared in visual but not auditory isolation were individually housed in flight cages (1.8 × 1.8 × 2.4 m), each with several females. The cages were all located in the same room, but black plastic covered the adjacent cage walls so that the birds could hear other males and females but not see them.

The males living in a group were housed in an indoor-outdoor aviary located next to the area housing the visual isolates. The indoor section was 4.8 × 9.6 × 10.5 m, and the outdoor section was 3 × 10.5 × 14.4 m. Female cowbirds were also present in the aviary. Thus the males in the latter two groups shared an overlapping auditory environment.

Three of the adult males housed together in the aviary had originally been hand-reared and maintained in isolation from conspecific males. Two of the males housed in complete isolation had previously been reared and maintained in a group of cowbirds.

Four males participated in the second part of the experiment. After all the males had come into breeding condition and their songs had been recorded, four of the males housed in complete isolation (two juveniles and two adults) were placed together in one attenuation chamber, and further recordings of their songs were made. The females were removed. The purpose here was to ascertain whether a short-term change in the social environment would affect song potency.

Eleven females were tested in the playback experiment. All were housed in pairs or triads in the sound-attenuating chambers. For eight of the females, a male cowbird was present in the chamber until just prior to the breeding season. There were seven playbacks each day, separated by 90 min. The order of song presentation varied each day but was the same for all females. The response measure was presence or absence of the female's copulatory posture.

Two songs from each male, recorded within 5 days of each other, were selected as playback songs on the basis of quality of recording. In addition, another song from each of the four males placed in a group was included. These were recorded after the birds has been together for 2.5 wk. Finally, several songs recorded and tested in previous years from the three former isolate males now living together were included.

The playback songs were recorded with either a Uher 517 dynamic microphone or a Sennheiser 435 microphone and a Uher 4000 IC recorder. The Uher microphone was used only for males housed in the attenuation chambers. The males were recorded at less than 3 m, and most recordings occurred at distances of less than 1 m. The songs were played back through a JBL 2420 driver and 2340 horn. The sound pressure level was 80 dB fast reading on axis, .4 m from the speaker, as measured by a Brüel and Kjaer 2209 sound pressure meter.

Results and Discussion

The females responded most often to the songs of the complete and visual isolates and least often to the socially housed males (Table 1). The songs of the juveniles in each condition were slightly more effective, although not reliably so, than those of the adults. The differences among the conditions were tested by a Friedman analysis of variance, which yielded a reliable effect, χ_r^2 (6) = 40.1, $p < .001$. The differences between conditions were tested by the Wilcoxon signed-ranks test for matched pairs. The following comparisons were reliable at $p < .01$: total isolation versus group living

(T = 0 for juveniles and adults) and visual isolation versus group living (T = 1 for juveniles and T = 2 for adults).

The data on the adults with known song histories provided further evidence for the effect of social environment on song. The two males that were individually isolated after group rearing showed significant increases in potency: For Male LB, the increase was from 27% to 51%; for Male Z, from 29% to 71%. Conversely, the two group males that had originally been reared in isolation from cowbirds showed significant decreases in song effectiveness. For Male P, the average effectiveness of his songs after group living was 30% compared with an average of 60% for his isolate songs. For Male R, the decrease was similar; the effectiveness of his group songs averaged 36%; of his isolate songs, 65%. The third male, Male Y, did not, however, show this effect: His group songs were as effective as his isolate songs, an average of 64% in both cases.

The potency of the songs of the four males placed together was adversely affected for the two adults and unchanged for the juveniles (Table 2).

Although the primary focus of this experiment was on male song performance, the housing conditions used might also have affected the females' responses because many of the females used in the playback experiment had been housed with either a complete or a visual isolate. This factor may have confounded the results. To determine whether any of the females had "preferences" for the songs of the males they had lived with during the winter and early spring, we compared each female's responses to her resident male's song with her responses to the songs of the other males in the same housing condition (either complete or visual isolation). The results indicate that familiarity with the males did not affect the females' responses. The mean percentage of copulatory responses of the females to their resident males did not differ reliably from that of the females' responses to the other males reared under similar conditions (Table 3).

Table 1
Mean Percentage and Range of Copulatory Responses to Each Song Condition

	% Copulatory responses			
	Experiment 1		Experiment 2	
Song condition	*M* %	Range	*M* %	Range
Total isolation				
Adults	55	31–89	—	—
Juveniles	65	42–89	—	—
Visual isolation				
Adults	52	29–89	48	20–90
Juveniles	60	27–96	—	—
Social isolation				
Adults	—	—	23	0–56
Juveniles	—	—	—	—
Group rearing				
Adults	27	0–79	29	8–60
Juveniles	26	8–60	—	—

Note. Each number represents the average of the females' responses to all of the songs of the males in a given condition. In Experiment 1, there was an average of 110 playbacks in each condition; in Experiment 2, there was an average of 80 playbacks in each condition.

Table 2
Mean Percentage and Range of Copulatory Responses to Songs of Four Males Before and After Confinement as a Group

	Song potency as isolate		Song potency as group member	
Subject	*M* %	Range	*M* %	Range
Juvenile 2H	78	57–100	65	43–100
Juvenile LBDB	63	36–100	70	31–91
Adult LB	51	29–75	29	6–67
Adult Z	71	25–90	31	0–80

Note. There were 75 playbacks of each song.

The data indicate a major role for social experience and context in affecting cowbird song potency. Such experience, in fact, appears to be even more important than species-specific auditory stimulation. Previously, we had speculated that isolate male cowbirds developed more effective songs because of their different auditory experiences, i.e., as they had never heard adult males sing, they might not have included all possible types of information in their song. Information regarding territorial status or individual identity, for example, might have been omitted. This in turn might have resulted in a song containing a "purer" or "overemphasized" courtship message (King & West, 1977). We can now

Table 3
Mean Percentage of Females' Copulatory Responses to Songs of Males They Were Housed With and to Songs of Other Males in the Same Housing Condition

Female	*M* % Responses	
	To own male	To other males in same condition
BW	53	59
LG	87	87
20	44	39
Y	40	55
YB	44	52
CB	100	88
B	93	88
2R	91	84
Grand *M*	69	69

rule out this suggestion. Males deprived only of visual contact with other males, but exposed naturally to the songs of adult and juvenile males, also developed highly effective songs. The potency of these songs was in fact indistinguishable from that of males reared in visual and auditory isolation. Likewise, although the complete isolate and visual isolate males differed greatly in amount and kind of sounds available to them, they produced songs equivalent in effectiveness.

The data also show that the impact of the social environment does not diminish in adulthood: Adult and juvenile male cowbirds were both affected. When the four isolate males were placed together, only the adults' songs were affected, which suggests the social environment might affect adults even more.

Perhaps the most impressive demonstration, however, of the importance of social stimulation comes from the adults whose song histories were known: For four of the five birds, manipulation of their social environment produced either substantial increases or decreases in song potency. This fact also indicates the highly reversible effects of early species-typical or species-atypical experience in cowbirds.

Experiment 2

The second experiment addressed two questions that followed directly from the first: (a) Would males that could see but not participate in the social interactions of other males sing potent songs? (b) How would isolate and group-maintained males behave when they were introduced into an established breeding colony of cowbirds? We knew from the first experiment that males deprived of seeing other males, even if they could hear them, sang very effective songs. To learn more about the basis of this effect, we maintained males in one of three conditions: visual but not auditory isolation from males (as in the first experiment), social but not visual isolation, and group living. How would the potency of these three groups compare as tested by playbacks to females?

The second question represented an attempt to learn more about the consequences of isolation and group maintenance beyond the single measure of song potency as measured by the female's response. As a first step in extending our analysis of the consequences of our experimental conditions, we chose to observe the behavior of the isolate and group-maintained males upon introduction into an aviary housing an established colony of cowbirds. The males were introduced during a time period when the residents were observed to be engaged actively in mating and egg laying. Two behaviors of particular interest were song and aggression: Would the introduced males sing, to which birds would they sing, and would they be attacked by the resident males?

This design was intended to yield multiple assessments of the experimental conditions. The playback results would give an estimate of song effectiveness based on female response. The introduction series would determine the male response to the song and behavior of the experimental males. Observation of the behavior of the introduced birds would provide the critical link between the two assays, i.e., how varying degrees of social and visual deprivation affected the ongoing behavior of males during actual interactions with conspecifics.

Method

Subjects. Eight adult males were used as subjects.

Ten female cowbirds were tested in the playback experiment. The females, none of which were used in the first experiment, had not been exposed to any of the males.

Procedure. The flight cages for the males in this experiment were located in the same room so that all the birds shared a common auditory environment. All the cages were identical in size (2 × 2.5 × 3.5 m). Five cages were arranged in a row so that the first and last in the row contained one male cowbird each along with several females. These cages had black plastic on the walls to keep the birds in visual isolation from all the other birds. The cages next to these each held one male cowbird along with several females. The cage in the center contained three male cowbirds and three females. Thus, the males in the middle three cages were in visual contact with one another. A sixth cage, housing one male and several females, was located in the same room in visual isolation from the rest of the cages. In summary, three males were housed in visual isolation, two in social isolation, and three as a group.

The males were maintained in these cages from late fall through the breeding season. Playback songs were recorded when the birds had come into breeding condition, by using the same procedure outlined for the first experiment.

The playback experiment itself also followed exactly the procedure outlined earlier.

The introduction experiment was conducted over a 2-wk period during the breeding season. Our method was to remove a male from his cage and to place him in another identical cage in the same room. This cage was the indoor section of a large outdoor aviary (3 × 10.5 × 14.4 m) housing five male and six female cowbirds. Observation of the introduced male began at 6–6:30 a.m. and continued until 10:00 a.m. All songs sung by him and to him were noted as well as any attacks, chases, or other socially directed behaviors. The male was removed after the morning observation session. Each male was introduced a second time 1 wk later.

Results and Discussion

Playback responses. The songs of the visual isolates were substantially more effective than the songs of either the social isolates or the group-maintained males (Table 1). The songs of the social isolates and group males received approximately equal responses from the females. The differences between the visual isolate and the social isolate songs and between the visual isolate and the group songs were tested with the Wilcoxon matched-pairs test, which yielded reliable results ($T = 1$, $p < .01$ for both comparisons).

Introduction series. Six of the males (two visual isolates, one social isolate, and three group males) completed the series of two 4-hr sessions in the aviary. The results for the group males were quite straightforward: They almost never sang when in the presence of one of the resident males, and only one was attacked, and then only once. Two of them did sing, however, when alone in the indoor section during their first introduction. On the second introduction, only one of the group males sang and, again, only when alone. The isolates' behavior, however, was quite different: All three of the isolates sang repeatedly to resident males and females on their first visit. Two of them (a social isolate and a visual isolate) were also attacked several times by the resident males. The third isolate was not attacked but was displaced from perches and chased around the aviary by the resident males. Upon their reintroductions 1 wk later, one visual isolate did not sing at all and was not attacked. The other two sang, although much less frequently than during their first introduction, and both were attacked. The only attack *by* an introduced bird occurred on a first visit: The social isolate initiated an attack on one of the resident males within several minutes of the start of the session. In summary, the isolates sang 52 times to resident birds during the first session, and the group males sang only twice; the isolates were attacked 8 times, and the group males once. During the second session, the isolates sang 11 times to the residents, and the group males sang not at all. There were two attacks during the second session, both on isolate males.

The data provide further confirmation of the importance of social feedback to cowbird song performance. Males physically isolated from other males but allowed to witness the social interactions of the group sang songs that were no more effective than those of the communally housed males. Other males, exposed to the auditory components of the same interactions but without visual access, sang significantly more potent songs.

The results of the introduction series indicate other important differences between isolate and group-maintained males. The isolate birds sang much more often to the new males and received more attacks than did the group-maintained males. As almost all the attacks occurred within seconds after an introduced male had sung, it seems ap-

parent that the resident males were attending in particular to this feature of the introduced bird's behavior. That the isolates sang much less upon their second session suggests that they were learning to attend to this dimension of their own behavior. As all the birds were adults, it can be assumed that they had had experience with males the previous year. How juveniles would respond in this setting remains to be explored. Because only one social isolate was tested in the introduction series, it is difficult to interpret the finding that despite having low-potency songs, the social isolate was repeatedly attacked. This was the only male, however, that initiated an attack. Perhaps, social isolation leads to an intermediate effect in which song potency resembles that of the group males but other behavior, such as social responses to males, is more like that of other isolates. This would make sense, given that the social isolates had no actual interaction with other males.

Finally, it is important to note that the group-maintained males did sing, both during the introduction series and in their home cages. The differences were that during the introduction series they sang only when no other males were present and that in their home environment, they sang ineffective songs. Thus, being in a group does not mean that singing does not occur but that what songs and to which birds they are directed differ.

General Discussion

Briefly stated, the data suggest that living in isolation from males enhances song effectiveness and that living in or observing a group of males depresses it. What about the presence of males produces this effect? The introduction series and the observation of our resident colonies over the past several years provide some of the answers. Over the past 3 yr, five males living in our group aviary have been killed or badly injured as a result of attacks by other male cowbirds. In each case, the victim had a song with an overall effectiveness above 60%. In the first experiment, three males were killed: Male Y, the former isolate that continued to sing a potent song, and two visual isolates that were killed when all the visual isolates were subsequently housed together. Conversely, males with ineffective songs have not shown evidence of having been attacked. Data from the introduction series complement the above observations: Isolate males directed more songs to colony members and were attacked more often than males from the group.

It may be, then, that what attracts the female listener in cowbird song offends the male. As a result, males living in a group of males and females may modify the content of their song and thus avoid attack. Or they may learn to use only certain types of songs in particular contexts, as has been reported for some other passerines (Lein, 1978). The mechanism underlying this modification is unclear. It might be that males can recognize the sensitive passages in their own song as well as in others and learn that by deleting these structures or singing them only under certain circumstances, they avoid conflict with other males. Darley (1978), for example, also working with captive cowbirds, reported that adult males will chase, block, threaten, or displace juvenile males that are attempting to court females. The data from the second phase of the first experiment and from the introduction series highlight the importance of experience with males. When the four males were placed together, only the two adults, both of which had been group-reared, showed a reduction in song potency. During their confinement together, these four males did not injure one another and few attacks were observed, probably because no females were present. Thus, the adults may have modified their song because they had learned in previous breeding seasons to do so when in close contact with other males. The findings from the introduction series suggest this to be the case. The juveniles, however, having had no such experience and in the absence of attack by the adults, continued to sing potent songs as did the isolates when first exposed to the new colony.

It is not clear at this point how long and at what point in song development males have to encounter other males for song modification to occur. Thus far, we know that song potency can be diminished in a short time,

but we do not know how much time is required to develop a highly effective song. Moreover, it is unclear whether learning (i.e., the development of song or songs), performance (i.e., the motivation to sing a certain song or songs), or both are affected by the altered housing conditions.

Thus far, we have talked exclusively about the effects of the environmental manipulations on the males. What about the females from the first experiment that were housed with some of the males and then subsequently used as playback subjects? It might be argued that because the females are housed with the complete isolate males, they were biased to respond more often to isolate song. Bateson (1978), for example, suggested that early exposure to conspecifics might result in sexual preferences for mates with characteristics similar to the animal they were reared with, although not a preference for that particular individual that would be regarded as a sibling. Several facts argue against this interpretation of the results reported here. First, the females did not respond more to their own male's song, a finding that rules out any preferences based solely on familiarity. Nor did they respond less often to their own male, which thereby rules out a phenomenon similar to that described by Bateson. On the basis of our findings, the females would have mated just as often with their "sibling" male as with any other male in that group. Second, we know from our previous work that females reared without males at all, or reared in the wild, show the same "preference" for isolate over normal song (King & West, 1977; West et al., 1979). We also know that females of another subspecies of cowbirds show the same preference for both their own and this subspecies' isolate songs (King, West, & Eastzer, Note 1). In over 5 yr of testing, the data have been extremely consistent: Every female ($N = 45$) has responded, on average, twice as often to the song of any male reared in isolation from adult males as to that of males reared normally.

Our acoustic analyses of cowbird song have shown that the first two phrases of the song, and especially the second phrase, are pivotal to determining the song's potency and are different in normal and isolate song (West et al., 1979). The first phrase consists of low-frequency tone bursts; the second, of a very brief frequency modulation and tone in the range of 8–12 kHz. Evidence exists that such high-frequency information is seriously degraded in the atmosphere except at very short distances (Morton, 1975; Wiley & Richards, 1978). Thus, wild cowbird males may avoid alerting other males by singing their more potent courtship songs only at very close distances to the female. What is known about cowbird mating suggests this to be the case: The male pursues the female until she lands and then repeatedly sings and bows to her while very close to her (Payne, 1973). In captivity, where it is more difficult for males to remain unobserved by other males, this system cannot operate and serious conflict results.[1]

In summary, these findings support and extend our earlier work in several ways. First, they demonstrate the reversibility of the effects of early species-typical or species-atypical stimulation with regard to song potency. Second, they indicate the special importance of the cowbird's social environment for the learning and/or performance of song. Although social factors have been identified in other species as important early determinants of song structure (Immelman, 1972; Jenkins, 1978; Kroodsma, 1974), our work with the cowbird suggests an even broader role such that throughout a male cowbird's life, social feedback from companions may affect the functional properties of his song. Finally, the data indicate the inadequacy of terms such as "isolation," "deprivation," and "enrichment" to describe and/or explain behavioral changes. In the case of the cowbird, what would intuitively be thought of as appropriate or inappropriate experiences had counterintuitive outcomes. Multiple assays of outcome were necessary even to begin to

[1] The indoor-outdoor aviary housing the birds was quite large (see Method), and although a large physical space cannot compensate for the critical feature of confinement, it is important to keep in mind that the birds were not crowded. The males could stay out of contact with one another and still have food, water, perching trees, and female cowbirds available to them.

understand what is "enriching" or "depriving" in the development of cowbird song.

Reference Note

1. King, A. P., West, M. J., & Eastzer, D. H. *Song structure and song development as potential mechanisms of reproductive isolation in cowbirds.* Unpublished manuscript, 1979.

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