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The Cowbird: Reflections on Development from an Unlikely Source

Learning plays a critical role throughout the life of this brood parasite, interacting with genetic factors to influence song and identification of species and mate

Avian brood parasites have fascinated students of animal behavior since the time of Aristotle (*1*). Because they do not rear their own young, they represent exceptions to the traditional pattern of vertebrate parental behavior. The cowbird, *Molothrus ater* (Fig. 1), is a particularly intriguing example because it parasitizes so many different species. Its behavior raises many questions, such as how the parasitic habit evolved, how the female executes the exchange of eggs, how young cowbirds elicit care from so many different hosts, and how cowbirds identify one another given their atypical upbringing (*2*).

The cowbird's "exceptional" status as brood parasite has led to certain assumptions about the role of species-typical stimulation in its development. It has often been proposed, for example, that cowbirds may lack sensitivity to certain forms of early experience, thus reducing the risk of incorrect mate identification (*3*). The potential for incorrect identification seems substantial, given the fact that cowbird young are raised by over 100 different species and 200 different subspecies (*4*). A "closed" system of species recognition—that is, a genetically determined system in which environmental influences play a minimal role—has in fact been described or assumed on many occasions, perhaps most clearly by Mayr (*5*):

> When a female cowbird lays her eggs into the nest of a song sparrow and the song sparrow parents raise the young cowbird, the young cowbird has never seen another cowbird. Yet two or three weeks after it has left the nest, having been fed by the song sparrow during the entire time, the young cowbird suddenly leaves the song sparrows and goes off in search of other cowbirds. It joins one of their flocks, stays with them throughout the fall and winter and finally, in spring, mates with another cowbird. Here we have what I call an entirely closed genetic program. As far as mate selection is concerned, at least as far as the nature of the species of the mate is concerned, there is no input through experience [pp. 11–12].

A similar assumption has been made by Lehrman, who cites the cowbird as an example of a species in which mating preferences are not affected by learning, and by Wallace (*6*), who states that "there may be great advantages to closed genetic programs especially for species that do not tend to learn much or do not tend to learn certain things" (p. 79).

What features of the cowbird's behavior might qualify as part of a closed system of species recognition? Clearly, communicative behaviors would be of primary significance. As Mayr (*7*) comments: "Since much of the behavior directed toward other conspecific individuals consists of formal signals and of appropriate responses to such signals, and since there is much selective premium for these signals to be unmistakable, the essential components of the phenotype of such signals must show low variability and must be largely controlled genetically" (p. 657).

A likely candidate for such an identifying signal in cowbirds is the male's song, which occurs in the context of mating as well as during other intraspecific interactions. Certainly, visual displays such as the cowbird's preening solicitation or the spread posture that accompanies song (*8*) could also function as mechanisms of species identification, but because of its clear relationship to mating, song might be of crucial importance. On the basis of the preceding description of a closed developmental system one might also expect that cowbird communication would develop normally without species-typical stimulation: females without previous contact with their own species would recognize males by their song and males would sing recognizable cowbird song without the need for adult models.

We now know that these expectations

Figure 1. Like most icterids, the brown-headed cowbird, *Molothrus ater*, is sexually dimorphic in both plumage and size, the male (*right*) more distinctly marked and slightly larger than the female (*left*). The female's dull coloration and stealthy behavior help to conceal her from potential hosts while she searches for nests. The Latin species name means "black vagabond," undoubtedly referring to the cowbird's parasitic habit. The English name derives from the common association of cowbird flocks with herds of cattle, primarily for insects and grain. (Drawing by J. Fenwick Lansdowne, by permission of M. T. Feheley Arts Company Limited.)

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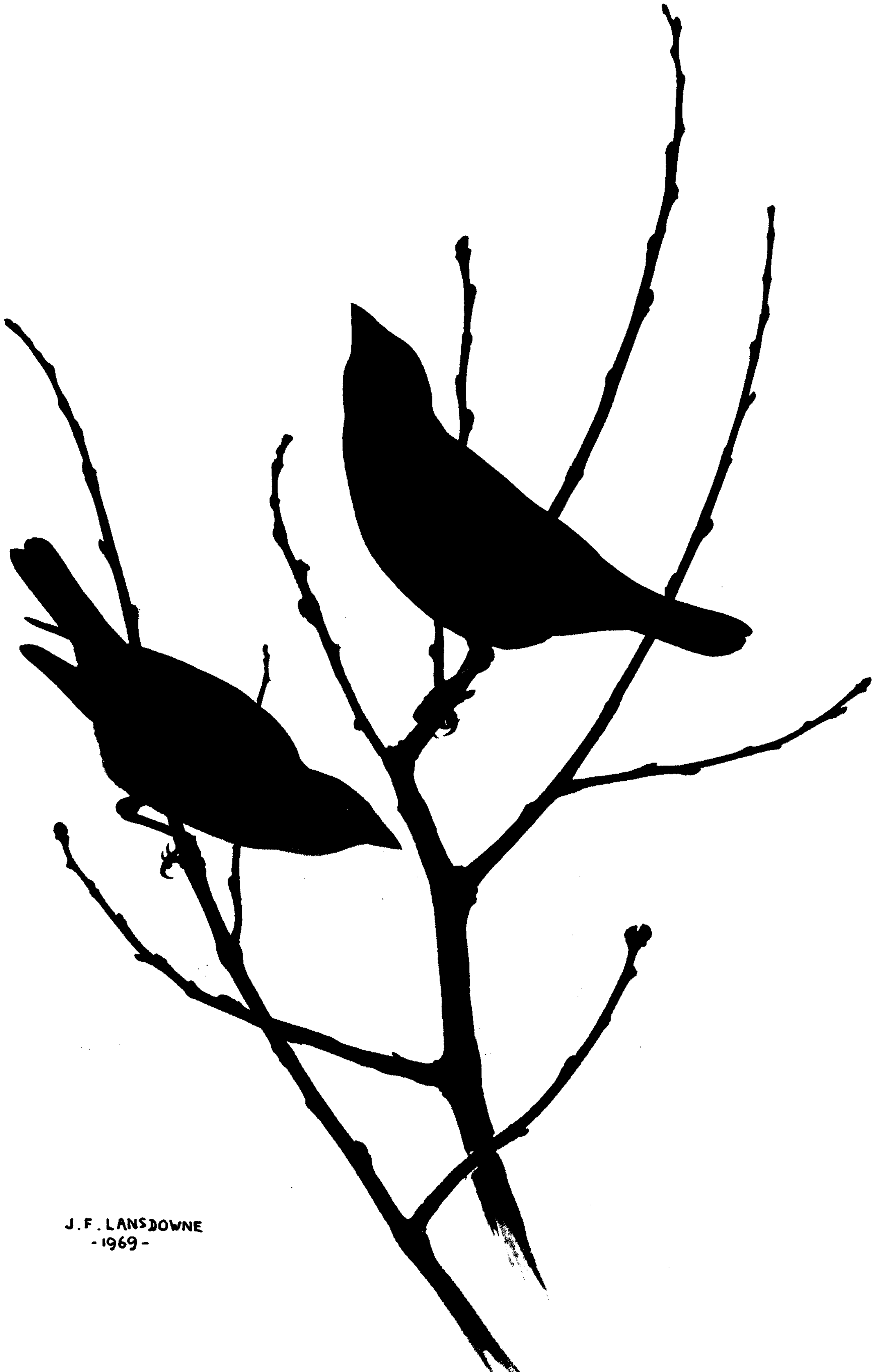
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Figure 2. The copulatory posture of the female cowbird—neck and back arched, wings lowered, feathers around the cloacal region spread—offers an easily recorded response by which the relative effectiveness of male song can be measured. (Photo by A. P. King.)

are essentially correct: naive females do respond appropriately to male song and naïve males produce effective songs (*9*). We established these facts by rearing male and female cowbirds in isolation from two days after hatching until their first breeding season. At that time, the songs of isolated and normally reared males were played back to the isolated females. The females readily adopted copulatory postures in response to cowbird song but not to the songs of other species. This effect has been replicated with many individuals and two cowbird subspecies (*10*).

The first experiment not only indicated that female cowbirds could identify males by their song without experience, it also demonstrated that female cowbirds, unlike many female song birds, possess an easily perceived response to male song (Fig. 2). Several features of the copulatory response make it especially suited to studies of song function. First, it is a rapid and unambiguous reflex: upon hearing a given song, the female either immediately adopted the full posture (i.e. arched her neck and back, lowered her wings, and spread the feathers around the cloacal region) or, conversely, continued whatever behavior she had been engaged in before the song began, with no apparent change. The response often began before the song ended and frequently lasted for up to seven seconds after a song's termination. Thus, recording the response was a simple matter and the result highly reliable.

Second, by maintaining females apart from males and hence lowering their threshold for song, the response could be elicited for up to six weeks, i.e. for the length of the female's reproductive period as indicated by egg-laying. It was therefore possible to test the female's response to a number of different songs over an extended period of time. Third, wild-caught and sexually experienced females also showed the response, thereby confirming its generality and allowing us to include in the tests females who had had experience with song in more natural contexts. Fourth, the response was selective: the females did not respond to the songs of other species and did not respond equally often to all cowbird songs. There was, however, substantial consistency across females in the songs that did or did not evoke copulatory responses. Quantitative estimates of the relative effectiveness of different males' songs were thus possible (*10*). In summary, the female's response offered the opportunity to make an empirical bioassay of cowbird song.

The isolate song effect

By studying this response we have learned a great deal about song function. Perhaps the most striking finding is that the songs of male cowbirds reared in isolation from male conspecifics are twice as effective in releasing the copulatory response as are the songs of normally reared males. This preference for isolate song also held true for wild-caught females: even though they had interacted with and presumably mated with normal males, they consistently responded more often to the songs of isolate males in the laboratory (*10*).

Although this finding is certainly not irreconcilable with the mechanism of innate recognition described earlier, it does suggest that the structure of cowbird song is susceptible to environmental modification and that female cowbirds perceive such changes. Most puzzling, of course, is the fact that isolate song is *better* than normal song in releasing the female's response.

For many who read of our findings, and even for ourselves, the question kept arising: Why would isolate song be more effective? Some of the comments we received reflected this paradox: "anomalous, not worth pursuing," cautioned a developmental psychobiologist; "I don't understand it, it violates Darwinian principles," complained an evolutionary biologist; "intriguing but puzzling," communicated an ethologist. What everyone seemed to be saying was that it might make developmental or evolutionary sense if isolate song were equivalent to normal song in effectiveness, and it would certainly have been all right if it had been less potent, but isolation should not produce a more effective song! The finding did not seem to fit existing schemata of song development, nor did it mesh with the assumptions underlying deprivation and enrichment paradigms. Perhaps it could be explained if it could be shown that cowbirds make use of this mechanism in nature by being solitary or nomadic. Unfortunately, all the available field data confirm that cowbirds live in large flocks during the winter and spring, the presumed period of song learning (*11*). What, then, did the finding signify?

Our goal here is to explain this "isolate song effect." We hope to show that (1) although the finding was anomalous, pursuit of its explanation has led to discoveries about the integral role of learning and early experience in the development of cowbird song; (2) not only do these data not violate ideas of Darwinian selection, they confirm them; (3) the apparently puzzling nature of this effect may stem more from our biases about isolation and the role of learning than from the curious developmental circumstances of the cowbird.

Our investigation of isolate song included three lines of research. The first consisted of analyses of the acoustic structures of normal and isolate song. The second involved bioassays of the relative effectiveness of songs of males reared in different degrees of social and sensory deprivation. The third focused on the relationship between the effectiveness of a male's song as measured by the female bioassay and the male's mating success. In all three inquiries, the aim was to understand why isolate song would be more effective and, more importantly, what acoustic, developmental, and social mechanisms contributed to this effectiveness.

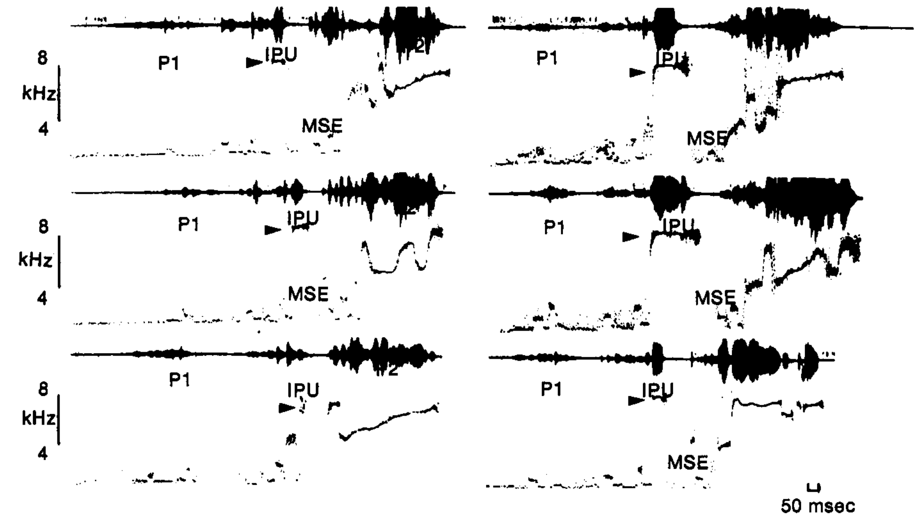

Figure 3. In these six examples of song from the Southern subspecies, *Molothrus a. obscurus*, the three songs at the left were recorded from normally reared captive males, the three at the right from males reared in isolation from 150 days of age. Note the greater amplitude of the inter-phrase unit (IPU, *marked by arrow*) relative to the first phrase (P1) in the songs of the three isolate males. Songs of the Eastern subspecies, *Molothrus a. ater*, show the same contrast in IPU amplitude between normally reared and isolate males (*10*). Other features of the distinctive cowbird song are the midsong element (MSE), found only in the *Molothrus a. obscurus* song, and the final phrase (P2). (No MSE is present in the song at the lower left.) All songs were recorded during the breeding season. The displays, made on a zero-crossings analyzer, are taken from a photograph of the face of a dual-beam oscilloscope. The upper beam shows amplitude variation, the lower indicates inter-zero-crossings times, i.e. instantaneous frequencies (*26*).

Cowbird acoustics

Greenewalt has identified several characteristics that distinguish normal cowbird song from the songs of other birds he has studied (*12*). Among the features that impressed him were the following: (1) the frequency range and maximum frequency of the song were the greatest of any species studied; (2) the frequency spread of the two voices—two full octaves—was exceeded in only one other species; (3) the modulating frequency in parts of the song was substantially higher than in any other species; and (4) the second phrase began with one of the shortest notes (about 2 msec) and contained one of the most rapid glissandos he had encountered.

Knowledge of these features guided our initial exploration of the functional basis of the enhanced potency of isolate song. In particular, we focused our attention upon the "interphrase unit" (IPU), which is defined as the first high-frequency note following the low-frequency tone bursts of the first phrase (Fig. 3). We chose it because, on the average, isolate songs consistently exhibited greater amplitude in the IPU relative to the rest of the song than did normal song, although isolate and normal song differed in several other respects as well (*10*). By playing back experimentally altered songs to captive females, we determined that songs containing an IPU were twice as effective in releasing the copulatory response as were songs lacking it. Furthermore, the absence of an IPU produced a greater response decrement than did deletion of the entire first or second phrase, although these two phrases are substantially longer and superficially more complex.

By manipulating amplitude relationships, we also learned that the amplitude of the IPU relative to the rest of the song was important: females responded most often to songs in which the relative amplitude of the IPU was equal to the peak amplitude of the song. Not only could the rate of response be lowered by decreasing the relative amplitude, it could also be raised by increasing it. These data thus suggested, albeit inconclusively, that the enhanced effectiveness of isolate over normal song rested heavily on acoustic differences in the IPU of isolate song.

Further investigations confirm this but suggest that other features are also important, and that male cowbirds manipulate several features to modulate the potency of their song. As we study more individuals and more songs from each bird, we have become increasingly impressed by individual variation in song. For this reason, we have devoted most of our empirical attention to studies of song development and function. Our interest was also diverted because we knew that even if we could pinpoint the acoustic reason for the isolate song effect (which we cannot as yet), we still would not know why it occurred.

Social and sensory factors

When male cowbirds are reared in isolation, what are they deprived of? Among the most obvious deficits are social and sensory experiences: isolate males cannot interact with or hear conspecific companions. To separate these effects, we designed an experiment which would allow us to analyze the role of social and sensory stimulation in cowbird potency. We maintained a total of 24 male cowbirds, juvenile and adult, in four different conditions of social, auditory, and visual deprivation from October to June (Table 1). Males in condition 1 were maintained in auditory and visual isolation, males in condition 2 in visual isolation, and males in condition 3 in social isolation; males in condition 4 were housed as a group, experiencing no isolation.

We chose to include adults for two reasons: first, to test the flexibility of song learning in the wild-caught adult, and second, to test the reversibility of early species-typical or atypical experiences by manipulating the laboratory environment of birds whose developmental histories were known. Thus, we altered the environments of several isolate males by housing them for the first time with male companions, and we isolated several other adults who until that point had always lived with male cowbirds. To test all these effects, we used the bioassay described earlier: during the breeding season we played back the songs of the males to eleven captive females who had been housed in sound-attenuation chambers from October to June; we then measured the number of copulatory postures evoked by each song. Potency was thus operationally defined as effectiveness in releasing the female's copulatory posture.

Table 1. The effects of different types of social and sensory deprivation on song potency

Deprivation condition	*Description of condition*	*Mean % and range of copulatory responses to resulting songs**
1. Auditory and visual isolation from male conspecifics (*N* = 7).	Individually housed, each with 3 females. Six condition-1 males were housed in sound-attenuation chambers,† a seventh in a flight cage (1 × 1.5 × 0.5 m) with a male starling (*Sturnus vulgaris*).	60% (31–89%)
2. Visual isolation from male conspecifics (*N* = 4).	Housed in adjacent identical flight cages (1.8 × 1.8 × 2.4 m), with visual access to other cages blocked.‡ Could hear condition-4 males.	55% (27–96%)
3. Social isolation from male conspecifics (*N* = 3).	Housed as in condition 2, but each could see into a group cage containing 3 males and 3 females.	23% (0–56%)
4. No isolation; group maintenance (*N* = 10).	Seven males and 3 females were housed in an indoor-outdoor aviary in which the indoor section measured 4.8 × 9.6 × 10.5 m, the outdoor section 3 × 10.5 × 14.4 m. The remaining 3 males were housed in a single flight cage with 3 females.	28% (0–79%)

* The songs were played back to 11 wild-caught experimentally naïve females housed in sound-attenuation chambers. Numbers represent the mean percentage of all the females' responses to the males in each condition. There was an average of 100 playbacks to each condition. Differences among the conditions were tested by a Friedman one-way analysis variance yielding a reliable effect, $X_r^2 = 40.1$, $p < .001$. Differences were also tested by the Wilcoxon signed ranks test for matched pairs with the following comparisons yielding significant differences: condition 1 vs. conditions 3 and 4; condition 2 vs. conditions 3 and 4.

† The sound-attenuation 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 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 could not see them.

Two songs from each of the males, recorded within 5 days of one another, were selected as playback songs on the basis of quality of recording. Several songs recorded and tested in previous years from the three males formerly isolate but now living together were also included. Each day for about six weeks—the length of the breeding season, which occurs in May and June—the females heard seven different songs, one approximately every 90 minutes. The order and content of the songs varied each day but were the same for all the females. The response measure was the presence or absence of each female's copulatory posture.

The males also participated in additional manipulations in the second part of the experiment. After all the males had come into reproductive condition and their songs had been recorded, four of the males housed in condition 1 (two first-year males and two adults) were placed together without females and further recordings of their songs were made after 2½ weeks. The purpose here was to see if a short-term change in the social environment would affect song potency. We also observed the behavior of some of the isolate (conditions 2 and 3) and group (condition 4) males upon introduction into an aviary housing an established colony of cowbirds. They were placed in the indoor section of the aviary for a 4-hour period from dawn to 10 A.M., during the time when the residents were actively engaged in mating and egg-laying. Two behaviors of particular interest were song and aggression. Would the introduced isolate males sing? To whom would they sing? Would they be attacked by the resident males?

We had previously speculated that isolate male cowbirds might develop more effective song because of their different auditory environments; i.e. given the fact that they had never heard adult males sing, they might not include all possible types of information in their song. This in turn might have resulted in a song containing an overemphasized or "purer" courtship message (*9*). The data show that this is not the case. Males deprived of visual contact with other males but exposed naturally to the songs of adult and juvenile males (condition 2) also developed highly effective songs (Table 1). These songs are in fact indistinguishable in potency from those of males housed in auditory and visual isolation (condition 1). Likewise, although the amount and kind of sounds available to complete isolate and visual isolate males differed greatly, males housed in these two conditions produced songs of equivalent potency. The effect of social feedback was also clear from the songs of condition-3 males: males physically isolated from other males but allowed to witness the social interactions of the groups sang songs that were no more effective than those of the communally housed males who sang the least effective songs.

Effects of social change

Equally impressive, however, were the data on the adults whose song histories were known. In the case of four of the five birds, manipulation of social environment significantly affected song potency. The two condition-1 males who had earlier been reared in a group showed significant increases in potency: from 27% to 51% for male LB and from 29% to 71% for male Z. Conversely, the two condition-4 males who had originally been reared in isolation showed significant decreases in song effectiveness when they became part of a group. The average effectiveness of male P's song after group living was 30%, as compared to 60% for his isolate songs. A similar decrease took place in the case of male R, whose group and isolate songs averaged 36% and 65%, respectively. The third male did not, however, show this effect; male Y's group songs were as effective as his isolate songs—an average of 64% in both cases. The latter part of the experiment, in which males alone were used, also demonstrated the importance of social context. When the four males were placed together, the two adults dropped their song potency by half (from 51% to 29% and from 71% to 31%) within 2½ weeks. This reduction did not occur in the first-year males. Few obvious social interactions occurred among the four besides perch displacements, probably because no females were present. Thus, these data provide evidence that males, at least adults, can modify the effectiveness of their song. It did not, however, tell us much about how isolates behave when confronted with other males. The second manipulation, in which males were placed in an aviary with an established colony, was designed to provide us with this information.

Six males (2 visual isolates, 1 social isolate, and 3 group males) were individually introduced into the aviary for two 4-hour sessions one week apart. The results for the group males were quite straightforward: none sang in the presence of 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 visits. During the second visits a week later only one of the group males sang—again, only when alone. The isolates' behavior, by contrast, was quite different. All three of the isolates sang repeatedly to resident males and females on their first visits. 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 the reintroduction of the six males a week later, one visual isolate did not sing at all and was not attacked. The other two isolates sang, although much less frequently than during their first visits, and both were attacked. (The only attack *by* an introduced bird occurred during 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 their first sessions, the group males only twice; the isolates were attacked 8 times, the group males once. During the second visits, the isolates sang 11 times to the residents, and the group males did not sing at all. There were two attacks during the second sessions, both on isolate males.

It is imperative to note that the group males sang both during the visits and in their home cages. The difference was that whereas the isolate males sang to resident males during the visits, the group males sang only when the resident males were in another part of the aviary. In their home cages, both sets of males sang equally often, but the group males sang songs of much lower potency. Thus, the effect we observed does not rest on isolate males singing more in quantitative terms but on the fact that they sing potent songs in different contexts.

We examined the possible relationship between frequency and potency by monitoring frequency of song in isolate and group males during the winter and spring. To do this, we recorded all songs sung by 10 individuals, including both isolate and group males, in a series of forty 3-hour sessions beginning in January and ending in April, documenting an average of 67 hours of song for each individual. No relationship was found between frequency and potency as tested by the female bioassay; the two factors did not correlate significantly (r_s = .29; N = 10). For example, the two isolate males that sang the most effective songs ranked first and last with respect to frequency of song.

Do male cowbirds use different song types—stereotyped song patterns, for instance—to communicate potency or lack of potency? Other passerines have been shown to use different song types in different contexts (*13*), but we find no evidence for such a mechanism in cowbirds. Individual males do have different song types, but thus far there is no evidence that they use them systematically in different contexts.

We have one final source of information regarding the consequences of singing high-potency songs. In the course of our experimentation over the past five years, we have transferred a total of 68 males from one aviary to another during the breeding season. For each male, information on song potency as tested by the female bioassay has been available. Of these 68 males, 21 sang high-potency songs

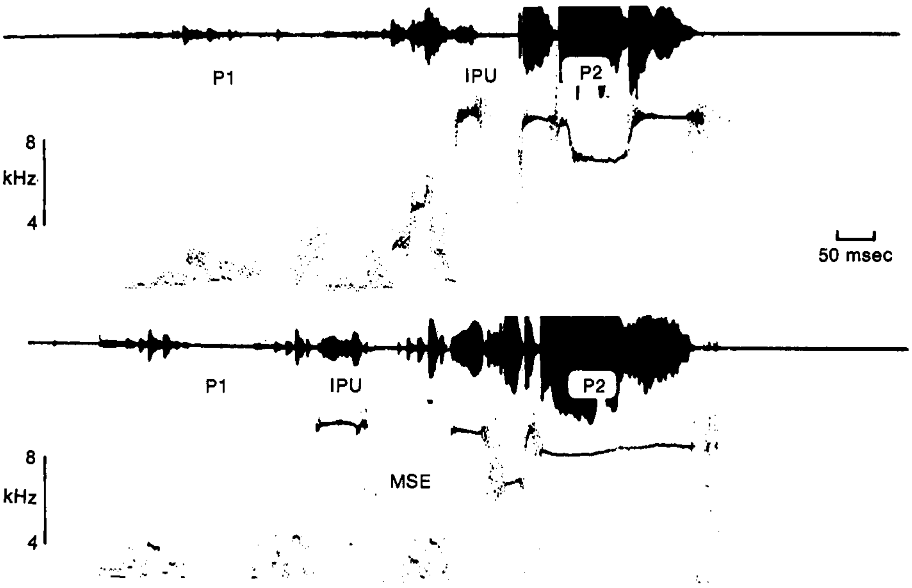

Figure 4. These examples of the song of the Eastern subspecies, *Molothrus a. ater* (*above*), and the Southern subspecies, *Molothrus a. obscurus* (*below*), show an important structural difference: the Southern song contains a mid-song element (MSE) not present in the Eastern song. Whereas Eastern males isolated as nestlings later produced songs containing an MSE, those captured as juveniles never included this element, suggesting that this structural unit results from conspecific stimulation and hence is learned.

(defined as having an average potency level above 50%) and 47 sang low-potency songs (defined as having an average potency below 50%). The mean potency for the high group was 65% (range: 50% to 95%), that for the low group 28% (range: 7% to 48%).

Of the 21 high-potency males introduced into new aviaries, 9 were killed by the resident males within a week and one was severely attacked and was removed by us. Of the 47 low-potency males, none was injured or killed. Thus high-potency males run a much higher risk of attack unless they begin to sing less potent songs. That males will do this is shown by the result just reported. Of the three formerly isolate males placed in condition 4, two lowered their potencies, while one did not. That third male, however, was killed during the course of the breeding season. Evidence thus exists on several levels of the disadvantages of very effective songs.

The data indicate, then, that the critical feature of isolation is the absence of male conspecifics with whom to interact. More particularly, they suggest an inverse relationship between song potency and the degree of interaction with males: the more removed a male is from male companions, the more likely he is to sing a potent song. Thus males living in a group (as in nature) may learn to modify the potency of their song, thereby avoiding attack. The role of learning is evident in each of the four conditions but is perhaps most dramatically demonstrated in the significant alteration of the song potency of adult cowbirds whose song histories are known.

Although having a potent song might be an advantage in attracting females, it appears to have adverse effects in dealing with other males. Part of the isolate song effect is therefore properly interpretable only with the addition of more criteria by which to measure outcome. That is, isolate song can be considered to be superior only if the single outcome of female response to song is the measure. The data thus emphasize the inadequacy of terms such as "isolation," "deprivation," and "enrichment" in characterizing the behavioral changes we have outlined. In the case of the cowbird, what would intuitively have been thought of as appropriate and inappropriate circumstances—group living and isolation, respectively—clearly resulted in a counterintuitive outcome, in that isolation produced the more effective song.

Auditory experience

The experiment just described appears to minimize the role of species-typical auditory stimulation, although social stimulation is shown to be very important. Again, this might seem appropriate in a brood parasite. However, other work in our laboratory on geographic variation in song demonstrates that conspecific auditory stimulation also plays a part in the development of cowbird song. We established this fact by studying the songs of two geographically separated populations of cowbirds, Eastern *Molothrus a. ater* males collected in Maryland and Southern *Molothrus a. obscurus* males collected in Texas. We discovered that the Southern males' songs contained an additional element not found in the songs of the Eastern males (Fig. 4).

This element, termed the "mid-song element" (MSE), occurs after the IPU and before the final whistle phrase. The MSE was found in the songs of all the Southern males tested but two (N = 22 males; 225 songs) and in none of the songs of adult Eastern males tested (N = 32 males; 1,300 songs). We also tested females collected at the same time from the same respective areas and found that they consistently responded more often to songs from their own geographic area. Thus it was clear that structural differences in the songs could be used by the females as a means of intraspecific identification.

To learn more about the development of these structural differences, we studied the songs of two groups of Eastern *Molothrus a. ater* males, one group isolated as 2-day-old nestlings, the other as 100-day-old juveniles. We found that whereas the Eastern males isolated as nestlings later produced songs containing the MSE, those captured as juveniles never sang songs with this element. Hence conspecific stimulation during the first 100 days produced a modification in song structure such that an element was eliminated. The fact that this element normally occurs in the songs of Southern males suggests that in the case of the Eastern males experience serves to shape their song more toward the Eastern version, thereby facilitating intraspecific identification. That this shaping procedure can be accomplished by environmental input during the first 100 days is another example of the part that learning plays in the development of cowbird song.

Song potency and mating

The data thus indicate that cowbird song can be modified by a male's social or auditory experiences or both. An attribute that seems to be especially affected is song potency, i.e. the properties of the song that elicit the female's copulatory posture. Moreover, the data suggest that differences in song potency might represent an important factor in the female's choice of a mate. The data discussed thus far, however, provide no direct evidence of a relationship between song potency and mating success. To examine this possibility, we designed an experiment that would enable us to look at the role of song potency in the context of mating.

We chose not to work with wild populations for two reasons. First, cowbirds can be very mobile during the breeding season because of their parasitic habit and emancipation from parental care; second, the properties of the song that release the female's response are perceptible only at short distances, and thus accurately recording or playing back song in the field is very difficult. This is primarily a consequence of the rapid attenuation of song content in the higher frequencies, including the IPU. We also knew that the female's response could be depressed by even small changes in the signal-to-noise ratio. This presents a problem under any recording conditions but particularly in the field (*12*).

We set up breeding colonies of cowbirds in two large indoor-outdoor aviaries and observed the colonies from late winter through the breeding season. The aim was to look for parallels to the isolate song effect—that is, to see which males, in terms of song potency and certain social features, obtained copulations with females. In addition to tallying the number of copulations for each male, we also played back their songs to a separate group of captive females to provide an independent measure of potency.

For our purposes, the most important findings concern the male dominance hierarchy, the number of copulations obtained by each male, and the results of the song bioassay (Table 2). In both aviaries, linear dominance hierarchies were formed and maintained throughout the late winter and early spring. The male's dominance status as determined by number of perch displacements was in turn an important predictor of behavior during the breeding season, in that for both aviaries the males with the highest status accounted for the majority of copulations and had songs of the highest effectiveness.

Because of the correlational nature of this finding, a question remained concerning causation: Do males become dominant because they have a potent song, or do they sing more potent songs because they are dominant? Other data suggest the latter interpretation. During the time the dominance hierarchies were being formed, all the males sang, but they sang ineffective song as measured by the female bioassay (*14*). The songs produced at this time appeared to be acoustically degraded, perhaps making information about potency harder to detect (*15*). Some males, particularly dominant males, sang songs that were more degraded than those of other males, suggesting that this behavior could be a mechanism to mask potency in the early spring.

We also had data indicating that dominance must be "earned" before potent songs could be sung with impunity. At one point we removed the dominant male from aviary B and placed him with a new group of males; we then observed the behavior of the remaining males in the old context and the dominant male in the new context. Two noteworthy events occurred. First, within a day other males in aviary B began to court and sing to females, some for the first time all spring. Second, the dominant male was killed by his companions two days after being introduced into the new group. The first event suggests that the dominant male was able to prevent other males from obtaining access to females, the second that he may have tried to do the same thing with the new males and failed or—

Table 2. The relationship between dominance, mating success, and effectiveness of song

Males in aviary A*	♂1	♂2	♂3	♂4	♂5
Number of copulation attempts	14	8	5	1	0
Number of females copulated with	4/7†	1/7	1/7	1/7	0
Effectiveness of song‡	58%	43%	32%	20%	29%

Males in aviary B	♂1	♂2	♂3	♂4**	♂5	♂6	♂7	♂8	♂9
Number of copulation attempts	21	0	0	0	0	0	0	0	0
Number of females copulated with	3/4								
Effectiveness of song	62%	45%	7%	—	24%	20%	—	—	—

* Males are listed in order of dominance rank as determined by number of perch displacements, which was sampled periodically during March and April. A rank of 1 indicates that this male was displaced least often and displaced the other males most often.

† 4 of 7 available females.

‡ The songs were played back to 15 females in sound-attenuation chambers. Numbers represent the mean percentages of the females' responses to each male's song. There was an average of 150 playbacks of each song. Differences in song effectiveness were significant as tested by Friedman one-way analyses of variance ($X_r2 = 20.9$, $p < .001$ for aviary A; $X_r2 = 12.04$, $p < .02$ for aviary B).

** The songs of males 4, 7, 8, and 9 were not tested because they sang so infrequently.

more likely—that he may have continued to behave as a dominant male when he no longer was one. To put this another way, he behaved the same way the isolates did in the previous experiment and suffered the same consequences.

Taken as a whole, these data suggest that intense competition occurs among male cowbirds during the spring and the breeding season, and that only the winners extensively court females and produce potent songs. In absolute terms the songs they produce are not as potent as the ones produced by isolates. This could be due to the constraints of captivity, familiarity with the females, or the continued presence of other males.

Dominance and isolation

To relate these findings to the two previous experiments and to the question of the isolate song effect, we suggest that what we see as dominance in the third experiment may represent the same functional process as isolation in the first. A dominant male may "isolate" himself from the other males by eliminating (perhaps emasculating?) them as sexual competitors. In aviary B, one male accounted for all the copulations and the vast bulk of the courtship activity. In aviary A, the dominant male accounted for half of the copulations, but the other males obtained copulations in the latter half of the breeding season, when the dominant male had begun to court less. The second and third highest number of copulations obtained then were, however, by the second- and third-ranked males respectively (*16*).

Thus far we have not considered the possibility that a truly isolate male could obtain copulations. Our data suggest that this could not happen in nature. First, other males would intervene to attack and drive off the potential competitor. Second, and most importantly, our data show that females do not copulate with males until they have been courted for at least a week (*16*). Familiarity with an individual male appears to be necessary. Consequently, nomadic and perhaps solitary males such as isolates would probably not be successful in obtaining mates.

These data add a new dimension to our explanation of the isolate song effect, suggesting that isolate males sing potent songs because they are dominant males and that, among cowbirds, only males with high dominance status sing potent songs in a variety of contexts. This is not to say that any male cowbird is incapable of singing a potent song; on the contrary, we know that most have this capability. Rather, we suggest that they may not sing potent songs in mixed-sex colonies without the advantage of dominance, which may provide protection from attack by other males.

Thus the inverse relationship between exposure to males and song potency which we have proposed to explain the results of the first experiment finds support here. The development of a potent song appears to hinge on a test of male fitness which determines who will be allowed to sing potent songs. This pattern, relying upon intense male competition and female choice, closely resembles that of another brood parasite, the indigo bird, as well as those of many nonparasitic species (*17*).

Because we worked with captive birds, the task of relating these findings to the behavior of cowbirds in the field remains to be carried out. This will be difficult, not only because of the problems mentioned earlier but also because other investigators have uncovered a diverse array of cowbird social arrangements, ranging from strict monogamy and territoriality to promiscuity to a lek system in which birds have a common site where courting takes place (*18*). The brood parasitic habit may require such social flexibility where the limiting resource is suitable host nests for the female's eggs: different populations would display different social systems depending on whether suitable nests were abundant or scarce. Ecological constraints would thus predict flexibility (*19*). Differences in song potency would clearly be important in polygamous populations, and because males outnumber females three to two even in monogamous groups (*20*), competition is likely. We therefore suspect that song will be shown to be an important index of male fitness in a variety of social groupings.

Exception or rule?

We would now like to discuss more generally some of the developmental and evolutionary implications of the findings presented here. Are they indeed anomalous, and do they in fact violate principles of natural selection, as some of the comments quoted earlier suggested? What is their relevance for other birds or other vertebrates?

Current trends in the study of early development suggest that although these particular findings regarding the cowbird might not have been predicted, they should not come as a surprise (*21*). Other writers have for some time questioned the interpretation of deprivation and enrichment studies, and still others have reported sometimes counterintuitive results (*22*). It should be clear by now that deprivation and enrichment are not unitary experiences and that their effects cannot be measured by single outcomes. Moreover, the organism undergoing these experiential alterations is neither unchanging nor inactive during either treatment or assessment. The contribution of this study to developmental literature is thus significant not because it illustrates new principles but because it extends accepted principles so readily to so improbable a model.

Just as the data outlined here can be easily assimilated into theories of behavioral development, so also they present no problem for modern views of selection. The data show that male cowbirds undergo intense competition that should result in the fittest male inseminating the greatest number of females. Furthermore, the female's requirement of familiarity prior to copulation provides another important constraint assuring copulation with the fittest male.

The evidence shows that male cowbirds exhibit vocal learning from an early age and continue to demonstrate it as adults. Rather than being idiosyncratic or exceptional by virtue of their parasitism, cowbirds fall well within the range of nonparasitic passerines with regard to patterns of song acquisition (*23*). What the data suggest is that the normal development of cowbird song derives from both genetic and experiential sources. Neither is sufficient in and of itself to produce a male that can sing the appropriate song in the appropriate contexts.

What are the implications of these data for the conception of the cowbird as exhibiting a closed system of species recognition? At one level—that of "nature of the species" identification—they require no change at all, in that cowbirds associate with one another early in ontogeny, long before differences in song performance could be a factor. Whether this identification rests on visual signals, auditory signals, or both has yet to be determined. Our data do, however, contradict the generalization that learning plays no role in *mate selection* or *preferences,* a view implied or actually stated by some of the researchers quoted earlier, as well as by others (*24*).

The last point might be made clearer by considering the fact that the identification of species or of potential mate is not a single event occurring at a single moment in ontogeny, but a series of interactions among individual birds at different times of the year under different circumstances, involving maturing organisms whose own developmental histories are constantly changing. The goal, then, is not to pinpoint precisely when a female can recognize a male or vice versa but to capture the multiple social, perceptual, and maturational processes that lead to *changes* in how one member of a species interacts with another.

To assume that the processes responsible for the initial event—the first encounter among conspecifics, for instance—also account for the subsequent differentiated system of interaction among species members would be to take a very narrow view. And yet this is the assumption one has to make to equate species recognition with mate selection. A conceptually related example of this danger can be seen in the literature on imprinting, where the debates surrounding the criteria of imprinting and its potential long-term effects turn on whether one considers only the preferences established by the young chick or that same animal's later sexual preferences. It seems clear that for many species the prior attachments of the young chick are not sufficient to explain later mate choice (*25*). In the same way, even if the juvenile cowbird's ability to recognize a conspecific during its first summer or to produce a cowbird-like song in the absence of conspecifics is present at hatching, this does not preclude the possibility of extensive and necessary learning about mate choice and song later on.

It might be tempting to dismiss these qualifications as minor or as based on a semantic quarrel. The data from the three experiments described here, particularly the last one, should explain why we do not agree with such contentions. The first experiment demonstrates that male song can be modified by altering the male's social environment and that such modifications are reversible—clear evidence of learning capacity. The second experiment details the role of auditory experience, while the third supplies the ecological context for these experiences, emphasizing moreover the importance of song for mate selection. Thus, the essential role of species-typical social and sensory stimulation in affecting the female's choice of mate by virtue of its effects upon the attribute of male song cannot be overlooked.

While it could be argued that initial species identification need not require species-typical stimulation, the same argument cannot be made about mate choice, which is, of course, a fundamental variable in the evolutionary process of speciation. To explain the latter, one is led by the evidence to recognize the integrative function of learning throughout the reproductive life of the cowbird. To call such a system "closed" is both inappropriate and imprecise. That cowbirds can afford to depend upon the environment for so critical a function is elegant, if unlikely, testimony to the powerful role of learning in development and evolution.

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"I stopped taking the medicine because I prefer the original disease to the side effects."