A Bioassay of Isolate Cowbird Song

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Captive female cowbirds, both isolation reared and wild caught, were exposed during the breeding season to experimentally manipulated versions of isolate male song. The data show that a single song element, a brief note between the song phrases, plays a pivotal role in eliciting the female's copulatory response to song. The data also demonstrate that relative amplitude variation and the fine structure within the interphrase unit affect the potency of a given song. These results suggest that the acoustic properties of this unit may account for the enhanced effectiveness of isolate song over normal cowbird song as a sexual releaser.

In a series of experiments on species identification, King and West (1977) established that naive female cowbirds (Molothrus ater) maintained in isolation possess a rapid and distinctive response to male cowbird song which is termed the "copulatory posture." Moreover, this response was specific to cowbird song. An additional finding of equal interest was that the females responded preferentially to the atypical songs of males reared in isolation. The isolate songs in fact elicited over twice as many copulatory postures as did normal songs. Taken together, these two findings indicate a mechanism of species identification for cowbirds that is eminently suited to a parasitic species, as neither males nor females require experience with adult cowbirds for the mechanism to operate. We now report data that describe some of the functional and acoustic properties of isolate song. The results indicate the differential contributions of several elements within isolate song to its effectiveness and point to one particular feature as especially critical to eliciting the female's copulatory response.

Male Cowbird Song: Structure and Development

The song of the normally reared male cowbird is brief and simple in structure in comparison with the songs of other passerines. The initial phrase (P1) consists of a series of low-frequency tone bursts delivered in an unmistakably "liquid" manner. These notes are transcribed by Greenewalt (1968) and Peterson (1947) as "glug glug" sounds. The second phrase, termed the interphrase unit (IPU), consists of a very brief frequency modulation and tone, which typically lasts only 50 msec. The final phrase (P2) is a whistle consisting of several frequency sweeps, ending in an almost pure tone. Greenewalt and Peterson both refer to this whistle as a "glee" sound and the entire song as "glug glug glee."

Several quite unusual features of cowbird song are revealed when comparisons with the songs of other species are made. Greenewalt, who analyzed the songs of over 200 species in great detail, declared that the cowbird "is the undisputed winner in the decathlon of avian vocalizations" (1968, p. 119). Among the cowbird's achievements, as cited by Greenewalt, are the following: (a) The frequency range and maximum frequency of the song were the widest of any
species studied, (b) the frequency spread of the two voices, two full octaves, was exceeded by only one other species, (c) the glee phrase began with the shortest notes (about 2 msec) and contained one of the most rapid "glissandos" Greenewalt encountered, and (d) the modulating frequency in parts of the song was higher by a substantial margin than any other.

As several of these features seem to be unique to the cowbird, they represent plausible candidates for species-identifying elements. Further description and analysis of cowbird song has strengthened and extended Greenewalt's findings (Eastzer, Note 1). Eastzer spectrographically analyzed 522 songs collected over a period of several months from winter to early spring from six males which were housed in an indoor-outdoor aviary with a number of females. Several of his findings are of relevance here. First, he reported substantial variability within and across males with respect to several song features. In the first phrase, for example, the time interval between the notes ranged from 180 to 290 msec, and the number of notes ranged from one to four. Thirty-three percent of the first phrases ended with a rapid glissando covering a frequency range of 1-4 kHz in 5-20 msec. The glee phrase was even more variable. Eastzer identified several whistle types: 60% of the songs had frequency modulations that were W-shaped, beginning with the initial sound at 8-10 kHz and dropping to two low points of around 6.5 kHz; 27% of the songs had square-shaped whistles beginning at 8-10 kHz and dropping to lows of 5.5 kHz; and 14% had U-shaped whistles, again with the average low point being around 5.5 kHz. There were, in addition, several timing and frequency range differences within these categories for individual males.

The most stable feature of male song was the IPU, which occurred between the two phrases in 100% of the songs analyzed. It followed the first phrase within 10 msec and was always between 8 and 10 kHz. This unit also always marked the highest frequency found anywhere in the song. Although Greenewalt did not refer to this unit as a discrete element (it is present in his zero-crossings displays), all but one of his statements about the properties of cowbird song relate directly to it. Specifically, the IPU marks the highest frequency in cowbird song, and frequently begins with the very brief note (actually the first element in the sweep of the IPU) that Greenewalt encountered. Furthermore, analyses of songs in our laboratory reveal that very rapid glissandos and unusually high modulating frequencies are also typically associated with IPUs. Thus, not only does cowbird song contain a number of unique features but most of these features are associated with the IPU. These findings point to the IPU as a unit of potentially critical importance for understanding how the information for species and mate identification have been coded into the male's courtship signal.

Although based on limited data, information regarding the development of male song also suggests the importance of the IPU. King and West (1977) raised several males from the egg in isolation from one another and from adult males. They also raised a small number which had contact with young males but not adults. The songs of both these groups were recorded periodically until the birds came into breeding condition the following spring. The songs of the males reared as a peer group did not differ in any obvious way from those of normally reared males. The songs of the isolate males, however, were different in several ways, although there also were many similarities (Figures 1 and 2). The most obvious differences were the following: (a) The extent of the frequency modulation of the IPU was greater in isolate song (5.7-7 kHz) than in normal song (0-5.8 kHz); (b) the amplitude of the IPU in isolate song was greater relative to the rest of the song, often reaching the peak amplitude, whereas the IPU in normal song most often was up to 10 dB below the peak; and (c) the glee phrase in isolate song contained more frequency modulations and more extensive ones than did the same phrase in normal song. These...
Figure 1. Zero-crossings analyzer display of the isolate song used in this experiment. (The display is from a photograph of the face of a Tektronix Model 5103 dual-beam oscilloscope. The upper beam shows amplitude variations throughout the song. The lower beam shows inter-zero-crossings times [measured from the top of the display downwards], i.e., instantaneous frequencies, shown on the ordinate in kilohertz. The song divides into three phrases: an initial low-amplitude, low frequency "glug glug," here repeated twice [P1]; the interphrase unit [IPU]; and a terminal phrase beginning with three up-and-down frequency sweeps and ending with a 3-kHz intense almost-pure tone ["tsee"; P2]. The fuzzy display at the end of the tone is not noise but results from the tone continued at very low amplitude.)

One obvious question raised by these findings is the basis for the enhanced effectiveness of isolate song. The playback experiments described here are addressed to one part of this question, namely, to identify the acoustic basis for the effectiveness of isolate song.

The purpose of the first series of playbacks was to determine the contribution of several isolate song components to the song's effectiveness in eliciting the copulation posture. The choice of components to be manipulated was based on the descriptive analyses of normal song by Greenewalt (1968) and Eastzer (Note 1) as well as our own analyses of isolate song stemming from the earlier experiments on species identification (King & West, 1977). Specifically, the experiments measured the differential effectiveness of each of the two phrases of isolate song and of the IPU. Obviously, other features could also have been manipulated, such as timing or syntax. Timing was considered of lesser importance because of its variability within isolate and normal song, and syntax was considered only peripherally, partly for practical reasons of having to limit the number of conditions and partly because investigators of other species had not found it to be a critical factor (Emlen, 1972; Shiovitz, 1975).

ÉXperiment 1: First Playback Series

Method

Subjects. The subjects were five female cowbirds tested during their second breeding season. All had been hand reared in the laboratory out of contact with adult cowbirds. The eggs had been obtained from a captive colony of cowbirds and had been incubated out of contact with cowbirds. A day or two prior to hatching, the eggs had been transferred to the nests of barn swallows (Hirundo rustica), where they had remained until the cowbird nestlings were 2-3 days of age, at which time the nestlings had been transferred to the laboratory and raised in auditory isolation from adult cowbirds. They had been placed in sound-attenuating chambers when they were between 35 and 60 days of age. The birds were housed in pairs. Their companion was either a female cowbird or a female red-winged blackbird (Agelaius phoeniceus). The females' re-
sponses to cowbird song (normal and isolate) had first been tested during the prior breeding season. At that time, the females were exposed daily to five playbacks of male song for a period of 6 wk. Following this period, the females were maintained as before until their second breeding season. Thus, although the females were no longer naive with respect to cowbird song at the time of these experiments, their experience had been restricted to recorded song during one breeding season. The birds were fed a modified form of the Bronx Zoo diet for omnivorous birds.

Housing conditions. The sound-attenuating chambers each consisted of two concentric boxes constructed of plywood and Sheetrock. Wood and acoustic tile baffles between the boxes were designed to be most effective between 2 and 16 kHz. Suppression was greater than 39 dB at 1000 Hz, and it increased with higher frequencies to greater than 50 dB between 8 and 16 kHz. The interior box was a 1.1-m cube, fabric-lined to reduce sound reflection, lighted by two 40-W Vita Lite tubes and continuously ventilated. White noise was broadcast in the room housing the chambers when the doors to the chambers were opened.

Playback procedure. There were six playbacks each day, separated in time by approximately 90 min over a period of 4 wk. Only one song was presented during each playback trial. The order of songs presented each day varied but was the same for each bird. The response measure was the presence or absence of the copulatory posture.

All songs were played back through a JBL 2420 driver and 2340 horn, with a Uher 4000L recorder. All the songs had been recorded with the same Uher recorder and a Uher 517 dynamic microphone. Playback levels were measured with a General Radio 1933 sound pressure meter. The same sound pressure level was used for all songs: At 35 m from the speaker, the SPL was 86 ± 1.5 dB slow reading. The A-weighted SPL inside the chamber was 50 dB slow reading.

Playback songs. Playback songs were constructed through splicing and rerecording. Sound spectrograms and zero-crossings plots of the songs were made to assist in this procedure (Figures 1–3). The zero-crossings

Note that the purpose was not to compare the effectiveness of these elements relative to the comparable elements in normal song. The decision to concentrate primarily upon isolate song rested on the belief that it was necessary to understand what made isolate song effective at all before attempting to explain what made it more effective. Obviously, the same reasoning could be used to argue for beginning with an examination of normal song. This was rejected because it was thought that the higher level of responding by the females to isolate song allowed for more degrees of freedom in manipulating the song content and thus might be more productive to formulating hypotheses about the acoustic bases for the differential effectiveness of the two signals.
plots (see Figures 1 and 2) were obtained by displaying on the face of a storage oscilloscope a dot corresponding to each positive going zero-axis crossing of the sound wave. The horizontal position of the dot was determined by the time-base circuits of the oscilloscope and its vertical position by an external time base reset by each axis crossing. This method of recording is highly sensitive to rapid changes in frequency, and it works exceptionally well with passerine song (Staddon, McGeorge, Bruce, & Klein, 1978). The songs tested were isolate song with and without the IPU; the first phrase (P1) of the same isolate song with and without the IPU; the second phrase (P2) of isolate song with and without the IPU preceding it; reversed isolate song (IPU P2 P1); full normal song of a wild-caught adult male; and the songs of several other passerines: meadowlarks (Sturnella magna), red-winged blackbirds, and Baltimore orioles (Icterus galbula). The IPU was not presented alone because prior testing had established its ineffectiveness under these conditions.

Results and Discussion

The results indicate the differential effectiveness of certain components of isolate song (Table 1). The females responded more often to songs containing an IPU than to the same songs without it, and they responded more frequently to P1 song than P2 song. Reordering of the elements of the song produced only a moderate response decrement. Moreover, isolate songs were more effective than either normal song or the songs of other species (grouped here as “control” songs).

Table 1

<table>
<thead>
<tr>
<th>Song condition</th>
<th>M% response</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isolate song + IPU</td>
<td>75</td>
<td>54–88</td>
</tr>
<tr>
<td>Isolate song - IPU</td>
<td>38</td>
<td>8–58</td>
</tr>
<tr>
<td>Phrase 1 + IPU</td>
<td>62</td>
<td>50–64</td>
</tr>
<tr>
<td>Phrase 1 – IPU</td>
<td>27</td>
<td>21–36</td>
</tr>
<tr>
<td>Phrase 2 + IPU</td>
<td>46</td>
<td>29–69</td>
</tr>
<tr>
<td>Phrase 2 – IPU</td>
<td>19</td>
<td>0–48</td>
</tr>
<tr>
<td>Reversed song</td>
<td>60</td>
<td>41–73</td>
</tr>
<tr>
<td>Full normal song</td>
<td>35</td>
<td>28–48</td>
</tr>
<tr>
<td>Control songs</td>
<td>3</td>
<td>0–14</td>
</tr>
</tbody>
</table>

Note. There were 120 ± 10 playbacks of each song condition with the exception of the control song for which there were 72 playbacks. IPU = interphrase unit.
The overall difference in the order of the effectiveness of the songs was tested by a Friedman two-way analysis of variance. The differences among the song conditions were reliable ($X^2 = 31.92, p < .001$). Differences between certain song types were tested by the Walsh test (Siegel, 1956). Differences between full isolate song with and without the IPU and P1 song with and without the IPU were reliable at $p < .062$. The difference between P1 song with the IPU and P2 song with the IPU and that between full isolate song and reversed isolate song were not reliable ($p < .125$).

The results indicate that different elements within isolate song make different contributions to the effectiveness of the song. Although removal of either phrase reduced responding, removal of P1 produced a greater decrement than did removal of P2. This suggests that P1 contains more information directly related to breeding than does P2, whose more variable structure across males indicates that it might be more adapted to messages of individual identity or status, territorial information, and so forth. It might be argued that the P1 songs were more effective than P2 songs because they were less novel, i.e., the females' responding to P2 might have been suppressed because they were unaccustomed to hearing songs that began with the IPU or P2, i.e., an order effect was violated. This explanation seems unlikely, however, because of the fact that reversed song, which also violates an order "rule," worked as well as P1 song and almost as well as full song.

The data on manipulation of the IPU, however, are of most interest. The females responded less often to songs missing only an IPU than to songs missing an entire phrase despite the fact that removal of either phrase deleted substantially more sound from the song than did removal of the IPU alone. Again, as with the phrase differences, the importance of the IPU does not appear to be its position but its content. If position were the key, then the reversed song condition should have reduced responding to a greater degree, which it did not. The data suggest then that the IPU may play a critical role in transmitting the male's reproductive message. Its role is undoubtedly an interactive one, as P1 and P2 are also important, but the striking reduction in response obtained when the IPU was deleted suggests that it may contribute pivotal information not present in either P1 or P2.

**Experiment 2: Second Playback Series**

This series was designed to answer the following questions:
1. How do wild-caught female cowbirds respond to isolate song as compared with females reared with isolation?
2. How do internal amplitude relations among the elements of the isolate song affect the female's response?
3. Are the two main features of the IPU, the sweep and the tone, differentially effective?

A possible limitation of the results discussed thus far is their generality across female cowbirds. Because the original concern in much of the work had been the development of species identification, the females tested had necessarily had very limited contact with male song and no contact with males themselves. Here, however, where the purpose was to explore the functional significance of isolate song components, this lack of experience might represent a limitation on the generality of the results. For this reason, a second wild-caught group of females was added: These females had had behavioral as well as auditory contact with males. Our purpose was to test the generality of the original finding of the superior effectiveness of isolate song and to investigate further the role of the individual song components.

Our previous descriptive studies of normal and isolate song pointed to the probable role of amplitude relations. Although a given isolate or normal male appeared to modify the frequency pattern of a particular song type very little over time, relative amplitude variation was quite common. This was especially noticeable with respect to the IPU; for example, a given song might at one point be sung with the IPU at 70 dB and the peak amplitude of the song at 90 dB and on another occasion be sung with the IPU at 90 dB and the peak amplitude of the rest of the
song at 90 dB. Moreover, the IPU in isolate song typically occurred at a higher relative amplitude than did the IPU in normal song. To test the significance of these observations, we designed a series of playbacks that systematically varied the amplitude relation between the IPU and the peak amplitude of the other song components. Absolute amplitude of the song was also varied. The aim was to investigate the communicative significance of relative amplitude of the IPU with respect to other parts of the song. The fact that the males naturally manipulated amplitude made this an especially interesting series.

Finally, several playbacks were included to refine further the previous results by contrasting the effectiveness of certain elements with the IPU. The features chosen for manipulation were the sweep and tone burst elements of the IPU (see Figures 1 and 2). These were chosen because they represented obvious divisions within the interphrase interval and because of their contrast with the IPU in normal song which has a less pronounced sweep. The purpose here was to determine whether the females were differentially sensitive to one or the other of these elements within the isolate IPU.

Method

Subjects. Two groups of females were used. The first group consisted of the five females originally reared in isolation, now in their third breeding season. The second group consisted of eight females captured in the wild in late fall and maintained in a fashion identical to that of the other females until the following spring.

Playback procedure. The same procedure and apparatus were used with the exception that there were seven playbacks each day. The songs tested were as follows: full isolate song (another song from the same male used in the first playback series); the same isolate song minus only the IPU note; the song minus only the IPU 15-msec sweep; the song at each of three different peak amplitudes, 70, 80, or 90 dB; the 90-dB peak amplitude song with the IPU at 90, 70, or 60 dB; the 90-dB peak amplitude song with the IPU at 90, 80, or 70 dB. The control songs used in the first playback series were also included as well as several samples of normal song. Unless as noted above, the SPL of the playback songs was 81 ± 1.5 dB fast reading.

The playback songs for the amplitude series were made by rerecording the test songs at different amplitude levels and then splicing together the final test songs from these recordings. The amplitude relations of the final songs were confirmed by examining amplitude plots of zero-crossings analyzer displays. The overall playback levels for all songs were determined with a General Radio 1565A sound pressure meter.

Results and Discussion

There were no reliable differences between the two groups of females on any of the playback conditions, and therefore the data for the two groups were pooled.

The mean percentage of responses across the 13 females to normal cowbird song was between 25 and 35 (depending on the particular song). Because the focus of the present experiment was on a dissection of isolate song, these data are not considered further. They were included only as reference points to document the enhanced effectiveness of isolate song in yet another group of females in another breeding season. The mean percentage of response to the songs of other species was 2.3. These data also are not discussed further.

The females responded differently to the same song when the relation between the amplitude of IPU and that of the rest of the song was varied (Table 2). The three playback conditions most frequently responded to were 70/70, 80/80, and 90/90 dB, i.e., the three conditions in which the IPU was at the same level as the rest of the song. Lowering the relative amplitude of the IPU substantially reduced the number of responses: Songs in which the IPU was 10 or 20 dB below that of the song showed almost a linear decline in effectiveness.

The differences among the song conditions were tested with the Friedman analyses of variance. The overall order of song effectiveness for the seven conditions were reliable across the 13 females ($X^2 = 40.9, p < .001$), as were the differences among the three song conditions at the 80 and 90 dB levels (at 80 dB, $X^2 = 11, p < .01$; at 90 dB, $X^2 = 17.23, p < .001$). By using the Walsh test to test between conditions, reliable differences were obtained between (a) 80/80 and 90/70 dB, (b) 80/70 and 90/60 dB, (c) 90/90 and 90/80 dB, and (d) 90/90 and 90/70 dB ($p < .005$).

The females also were sensitive to changes in the acoustic content of the IPU. The mean percentage of responses to full isolate song was 70 (range, 50%-100%) compared
BIOASSAY OF ISOLATE SONG IN COWBIRDS

Table 2
Mean Percentage and Range of Copulatory Responses to the Same Song Played Back at Different Peak and Relative Amplitudes

<table>
<thead>
<tr>
<th>Amplitude level of IPU</th>
<th>% of Peak 70</th>
<th>Range</th>
<th>% of Peak 80</th>
<th>Range</th>
<th>% of Peak 90</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Same as peak</td>
<td>76</td>
<td>33-100</td>
<td>70</td>
<td>50-100</td>
<td>60</td>
<td>38-71</td>
</tr>
<tr>
<td>10 dB below peak</td>
<td>57</td>
<td>17-90</td>
<td>31</td>
<td>0-70</td>
<td>24</td>
<td>0-64</td>
</tr>
<tr>
<td>20 dB below peak</td>
<td>32</td>
<td>0-70</td>
<td>24</td>
<td>0-64</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. There were 125 ± 5 playbacks of each condition. IPU = interphrase unit.

The results of the second playback series complement those of the first in several ways. First, they demonstrate that wild-caught female cowbirds also respond preferentially to the isolate song, thereby ruling out the restricted upbringing of the hand-reared females as a critical factor. Second, they reveal another facet of female cowbirds' sensitivity to male song, i.e., their responsiveness to internal amplitude relations. Note also that the results cannot be explained in terms of absolute amplitude differences in the IPU. Inspection of Table 2 reveals that in the three conditions in which the amplitude of the IPU was 70 dB, the females responded quite differently: Their response rate was 24% to the 70-dB IPU when the peak song amplitude was 90 dB, 57% when the peak was 80 dB, and 76% when the peak was 70 dB. Third, the results indicate another dimension to the effectiveness of IPU, namely, its amplitude relation with the other song elements. Fourth, they suggest the need to look at even smaller and finer units of song, as the data show a differentiation of function even within the 50 msec of the interphrase interval, with the frequency sweep contributing more heavily to the effectiveness of the unit than did the accompanying tone bursts.

A possible confounding in the data from the first playback series concerned the explanation of the finding that removal of the IPU substantially decreased responding. Was this due to the absence of this presumably important acoustic structure (i.e., the absence of the information contained with the IPU), or was it because the song had been rendered unfamiliar or less recognizable because the song now differed in terms of timing and length? In this case, when the IPU was removed from the test song, no additional tape was added to replace the 50 msec of sound attributable to the IPU. Perhaps the females had responded less because the song was shorter and possessed a novel timing element between the two phrases rather than because the key content ingredient was missing. One obvious way to test these hypotheses would be to test a song that had blank tape inserted where the IPU had been removed. This procedure was attempted but with uninterpretable results. Although the females rarely responded to this song type, it could not be concluded that it was only because the IPU had been removed. The blank tape added to the song introduced a novel sound or space distinctly audible to the experimenters and thus obviously perceptible to the birds. Thus, it seemed possible that the females' lack of response could have been due to the introduction of the novel element (the blank tape sound) rather than due to absence of the IPU. The amplitude series, however, offered another means of addressing this question. When the amplitude of the IPU was decreased 20 dB (the 80/60 dB condition in Table 2), many of the amplitude minima within the IPU were below the SPL of the chamber. Thus, while parts of the IPU were...
presumably undetectable to the females, the rest of the song was audible, which thereby created a song in which the IPU was partially absent but neither timing nor song length was distorted. The females showed a sharp reduction in response to this condition. The effect was comparable with the result in the first series in which the IPU was removed altogether. This finding suggests then that the females in the first series were responding to the absence of the IPU rather than to a change in song timing, length, or both.

General Discussion

The results permit some conclusions about isolate song on both a general and a specific level. With respect to the overall structure of the song, the data suggest a redundancy of information among the song's elements. Either P1 or P2 presented alone elicited far greater responding than did other species' songs, which demonstrates that either is sufficient to identify the singer as a male cowbird. At the same time, the data also suggest the presence of nonoverlapping information among the elements of the song, as P1 alone produced more responding than P2 alone and as removal of the IPU produced a substantially greater response decrement than did removal of P1 or P2. Finally, the data suggest a dependency among the elements of the song, as the IPU is effective only when accompanied by another song element and when its amplitude is comparable with that of the other song elements.

This characterization of isolate song, involving redundancy, distinctiveness, and interaction among the song's elements, is consistent with descriptions of other passerine song (e.g., Emlen, 1972; Falls, 1969; Marler, 1960; Shiovitz, 1975) and probably reflects the fact that passerine song contains several types of information, each perhaps encoded in a different acoustic dimension. Thus, the redundancy among the elements might reflect the song's primary goal of at all times signaling the species of the singer, whereas the distinctive properties of the two phrases might indicate the encoding in only one phrase of information, identifying the singer on an individual basis. The dependency among the elements might represent a means to vary the intensity of a particular message and thus to reflect the immediate motivational state of the singer. A similar partitioning of structure/function relations has been suggested for several other species (Emlen, 1972; Falls, 1969; Shiovitz, 1975), although in these studies the bioassay was the male's response to the songs of other males.

On a more specific level, the data draw attention to the possible role of fine acoustic elements within song. The results suggest that the effectiveness of isolate song is especially determined by the structure of the IPU, a brief 50-msec unit, that represents less than 5% of the song's total duration. Furthermore, the data indicate a further differentiation within this unit such that a disproportionately large amount of its effect depends on the 15-msec sweep that begins the interval. Although others have discussed the role of fine structural units (Emlen, 1972; Shiovitz, 1975), the cowbird data represent one of the first direct demonstrations in passerine song of the role of such a small unit.

Besides indicating something about the nature of isolate song, the data also suggest, albeit indirectly, that the basis for the enhanced effectiveness of isolate song over normal song rests on acoustic differences in isolate and normal IPUs. The normal IPU typically has less of a sweep associated with it (i.e., the sweep covers less of a frequency range), and it is typically sung at a lower relative amplitude. If, as suggested earlier, the IPU affects the intensity of a song, it may be then that isolate song simply represents a stronger or more emphatic version of the male's advertisement for a mate.

These last statements are still speculative. The present experiments need to be extended in several ways before firmer statements can be made. First, other manipulations within isolate song need to be considered. The amplitude of the IPU, for example, has been lowered relative to the rest of the song; perhaps, if it were at a higher relative amplitude, its effect could be increased. Also, it will be necessary to manipulate the content of P1 and P2 in detail. Second, a bioassay of normal song must be
carried out perhaps focusing on the features identified by Greenewalt (1968). Third, a direct comparison of normal and isolate song will have to be made, perhaps by interposing elements of the two songs in order to pinpoint the role of elements such as the IPU. Fourth, the analysis must be extended to more males in order to establish the generality of these findings, because considerable variability in song is present in both normal and isolate male cowbirds. Finally, detailed observations of the male’s use of song and the female’s response to it in different contexts is needed.

Very little is known about cowbird social behavior under natural conditions (Darley, 1968). What information does exist, however, suggests that cowbirds exhibit extremely flexible patterns of social behavior at least with respect to mating systems and territoriality (Darley, 1968; Friedmann, 1929; Laskey, 1950; Nice, 1937; Gochfeld, Note 2). This may be due to their parasitic habit which frees both the male and female from any parental care. This flexibility may also be reflected in the male’s song. It may be, for instance, that the male’s manipulation of the amplitude of the IPU is a further example of the cowbird’s social plasticity.

Isolate song has been used here primarily as a convenient starting point for the functional analysis of cowbird song. However, the fact that in this species isolation rearing can lead to a signal of enhanced effectiveness deserves some mention. The idea that isolation, an “unnatural” condition, can lead to enhancement of a species-specific signal may at first seem theoretically unpalatable. It has long been known, however, that certain naturally occurring animal signals could be manipulated to become “supernormal” in effectiveness. One difference here is that the manipulation used to alter the signal, isolation rearing, is typically thought of as neutral or negative in its effects and not as a complex alteration of the stimulation available to the developing organism. These results with the cowbird then should serve as a striking reminder of the potentially constructive properties of isolation and of the active participation of the organism in its own development. These facts might remain more salient if we abandoned the term “isolation” in favor of the more accurate conceptualization of isolation as a particular kind of “biased rearing” (Gibson, 1969, p. 235).

Reference Notes


References


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