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Social Guidance of Vocal Learning by Female Cowbirds: Validating its Functional Significance

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With one figure

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Abstract

Juvenile male *M. a. ater* cowbirds, who have never heard other male cowbirds sing, develop distinctively different repertoires when housed with *M. a. ater* females from their own area versus *M. a. obscurus* females from a distant population. Because female cowbirds do not sing, the differences in the males' songs do not arise through vocal imitation. Here we provide data demonstrating that the songs of female-housed males are functionally, as well as acoustically, distinctive. The songs of 8 groups of males were tested where the groups differed by age of singer, acoustic experience, and identity of social companion. The playback results demonstrate that non-singing female cowbirds not only stimulate the male to modify song content, but song potency. As such, they demonstrate the critical role female cowbirds may assume in the proximate and ultimate regulation of vocal development.

Introduction

Here we report new data on the male cowbird's sensitivity to his social environment, in particular, his capacity to change his song on the basis of social stimulation from non-singing female cowbirds (WEST et al. 1983; KING & WEST 1983 a). Playback tests of song potency are used to assess the relevance of the acoustic modifications males make in their songs when they are deprived of auditory, but not social, stimulation from companions.

Vocal learning is widely established among the songbird species although different methods and criteria have been used to estimate species' vocal capacities. KROODSMA & BAYLIS (1982), in a world survey of vocal learning by birds, accepted four lines of evidence as indicative of vocal learning: first, vocal imitation of avian or human sounds under conditions of controlled

rearing; second, interspecific imitation among wild birds; third, intraspecific imitation in the form of geographic variation or dialects among free-living populations; and fourth, abnormal vocal development under laboratory conditions of acoustic deprivation.

Cowbirds (*Molothrus ater*) qualify as vocal learners by the first, second, and fourth criteria (KING & WEST 1977; KING et al. 1980). They also display evidence of vocal learning not captured by KROODSMA and BAYLIS's criteria or by KROODSMA's definition of vocal learning as "the ability to use auditory information (including feedback) to modify or enhance vocal development" (KROODSMA 1982, p. 1). Cowbird males can also modify the acoustic and functional nature of their songs on the basis of *non-auditory* information (WEST et al. 1981, 1983; WEST & KING 1980; KING & WEST 1983 a).

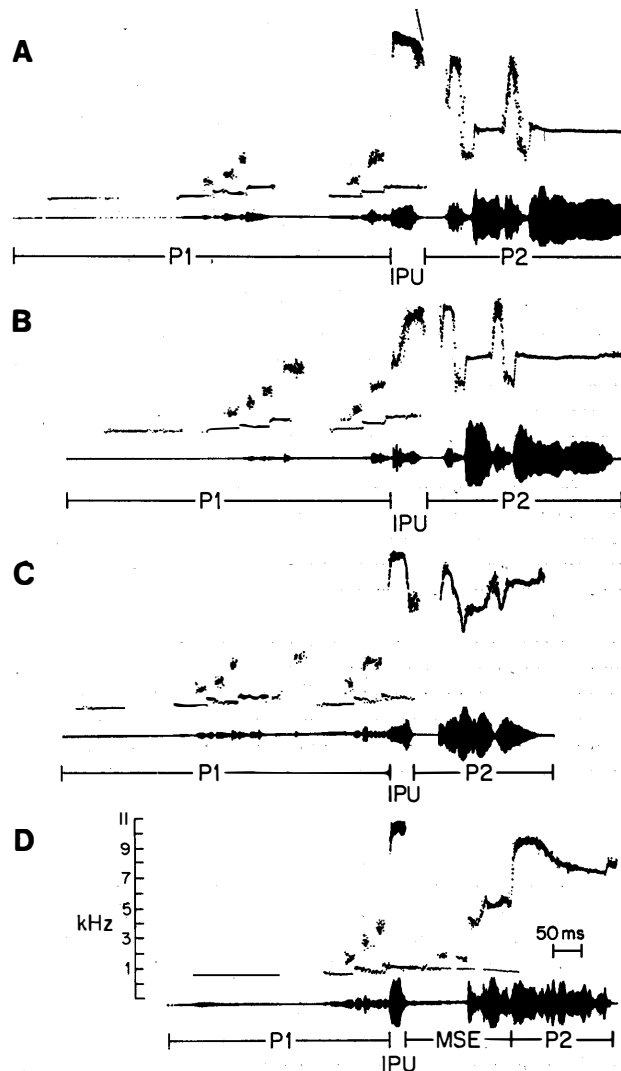
The role of non-auditory experience was studied by measuring the effects of female companions on male song development (KING & WEST 1983 a, 1984). To this end, we housed naive eastern *M. a. ater* males with other species or female *M. a. ater* or *M. a. obscurus* females for one year (KING & WEST 1983 a). The males with other species developed heterogeneous repertoires composed of *M. a. ater* and *M. a. obscurus* song elements as well as other species-atypical sounds. Males housed with *M. a. ater* females had homogeneous repertoires composed entirely of *M. a. ater* song. Males housed with *M. a. obscurus* females, however, sang a substantial proportion of their songs with *M. a. obscurus* elements, yielding statistically significant differences among and between the groups. The groups also differed reliably on several other acoustic measures including the number of notes and maximum frequency bandwidth of the first phrase (Fig. 1). Thus, males developed reliably different vocal phenotypes solely on the basis of differential social stimulation.

The effects of external tutoring in conjunction with female stimulation was also tested by housing naive eastern *M. a. ater* males with other species or *M. a. obscurus* females and tutoring them daily for three months with the same eastern *M. a. ater* adult song. Again, the groups differed despite the standardized auditory tutoring: males housed with other species developed repertoires composed primarily of copies of the tutor song whereas males with *obscurus* females sang significantly less of the tutor song developing original song types instead (KING & WEST 1983 a).

Although the social environment of songbirds has long been recognized to mediate vocal perception and production, the possibility of non-imitative influences has traditionally not been considered as a separate source of influence (e.g., BAPTISTA & PETRINOVICH 1984; IMMELMANN 1969; PAYNE 1981; PRICE 1979; TODT et al. 1979). Such social learning has typically not been studied in songbirds because of the difficulties of separating the correlated effects of social and vocal stimulation from male tutors, a difficulty overcome here by using non-singing female "tutors" (GALEF 1976).

We propose that the evidence presented earlier signifies that cowbirds may qualify as vocal *and* social learners: they can learn directly from sounds they and other males make and indirectly by observing the effects of their

Fig. 1: Zero-crossing-analyzer displays photographed from the face of a dual beam oscilloscope. For each song, the upper trace displays instantaneous frequency measured in kHz; the lower trace displays simultaneously changes in amplitude. Song A is the tutor song. It was recorded from a wild-caught acoustically isolated adult *M. a. ater* male originally captured in Orange County, North Carolina. Song B shows a rendition of the tutor song by one of the tutored males housed with other species. Song C is a song by a tutored male housed with *M. a. obscurus* females and represents the best rendition of the tutored song by any male with a *M. a. obscurus* female. Song D is another original song by the same male who sang Song C. Songs A—C are categorized as *M. a. ater* songs; Song D as a *M. a. obscurus* song because it contains the MSE. P1 = first phrase, IPU = interphrase unit, P2 = final phrase, MSE = mid-song element which normally only occurs in *M. a. obscurus* song



songs on listeners. But thus far only acoustic descriptions of the vocal phenotypes have been used to document the presence of social learning in cowbirds. Now we present the more critical data on the functional properties of songs produced by males whose environments differed in the nature of the social stimulation available to them.

We tested the songs of the males from KING & WEST (1983 a) and from a third experiment in which we recorded the song development of wild-caught juvenile and adult *M. a. ater* housed with *M. a. obscurus* females. We played back all the songs to *M. a. ater* females in two playback seasons where the female's only exposure to the males was their tape-recorded song. We asked

if songs that we judged to be acoustically distinct would be differentially effective elicitors of the female cowbird's copulatory response. In addition, we asked whether social learning would be evident in the song development of wild-caught and therefore more experienced males.

General Methods

Subjects

Playback females. Playback tests were carried out in two separate breeding seasons. In the first season, 10 females, the Test 1 group, heard the songs of the 18 juvenile *M. a. ater* males from the two experiments summarized in the introduction (KING & WEST 1983a). In the other season, a different set of 10 females, the Test 2 group, heard the songs of 3 juvenile *M. a. ater* males housed individually with *M. a. ater*; 3 adult *M. a. ater* males housed individually with the *M. a. ater* females; and 2 *M. a. ater* adults housed singly with *M. a. obscurus* females.

All the playback females were captured as juveniles at our laboratory in Orange County, North Carolina, and housed in pairs or triads of females from early fall through April. Eight of the Test 1 females were housed individually for the duration of the playback tests (May—June), the others were housed socially. The Test 2 females had *M. a. ater* male companions until April and then were housed in pairs of females for the playback period.

Female companions. All females used as social companions for the males whose songs were tested had been wild-caught as adults: the *M. a. obscurus* females were obtained in Starr County, Texas, the *M. a. ater* females in Orange County, North Carolina. Wing cord measurements were used to select *M. a. obscurus* females in order to ensure that they were not overwintering *M. a. ater* females. The females had an average wing length of 92.9 (range 89.5 to 94.5) thus falling within the ranges published by OBERHOLSER (1974) for Texas populations. Details of housing and care can be found in KING & WEST (1983a, b, c).

Procedures

Playback tests. The females were tested in their sound attenuation chambers. There were 6 playbacks each day, separated in time by approximately 90 min, over a 6-week period. Only one song was presented in each playback trial. The order of songs presented each day varied but was the same for all females.

A positive response was scored for an individual female if she adopted a copulatory posture within 1 s of song's onset. A copulatory posture was defined as follows: the female lowers and spreads her wings, her neck and body are arched, and the feathers around the cloacal region are separated. The onset of the posture typically occurs approximately 400—500 ms after the onset of the playback song. After adopting the posture, the female may stay in the posture between 1 and 7 s. A negative response was scored for no response. As partial components of copulatory reflex sequence do not occur, the reflex sequence either does or does not occur eliminating the need for any categories of "partial" responses.

Playback Songs

For both series of playbacks, the best rendition of each of the male's song types was played back (cowbirds have 1—6 song types). In the Test 1 series, 16 songs were tested from the 6 tutored males and 31 from the 12 untutored males. The males had 2—5 song-types. The females heard the 16 songs of the tutored males for the first half of the breeding season and the 31 songs of the 12 untutored males for the second half. In the Test 2 series, 14 playback songs from the 8 males were used. Details of the recording procedures can be found in KING & WEST (1983a, b, c).

Results

The Wilcoxon test for matched pairs and the Friedman one way analysis of variance were used to test the significance of differences in potency between conditions (MARASCUILO & MCSWEENEY 1977). In the Test 1 series, potency differences were tested between the songs of the tutored males housed with other species or *M. a. obscurus* females and among the untutored males housed with other species or *M. a. ater* or *M. a. obscurus* females. Because the playback females did not hear the songs of the tutored and untutored males in the same playback set, but in sequential sets, potency differences were not compared between tutored and untutored males. In the Test 2 series, differences in potency were tested between *M. a. ater* males housed with *M. a. ater* versus *M. a. obscurus* females. Potency differences across playback series (e.g., Test 1 juveniles and Test 2 juveniles housed with *M. a. ater*) were not investigated because the different playback females were exposed to the different companion sets of songs.

Song Potency of Males with Different Companions

Females responded differentially to the songs of males tutored with the same song but housed with different social companions. They responded reliably less to the songs of the males tutored with *M. a. ater* song and housed with *M. a. obscurus* females, $T = 3$, $p < .01$ than to those of males tutored with the same song but housed with other species (Table 1).

Table 1: Mean percentage (and ranges in parentheses) of song potency

Source of playback songs	% copulatory responses
<i>Test 1 Series</i>	
Tutored juvenile <i>M. a. ater</i> with other species	50 (32—78)
Tutored juvenile <i>M. a. ater</i> with <i>M. a. obscurus</i> females	41 (30—51)
Naive juvenile <i>M. a. ater</i> with other species	50 (15—61)
Naive juvenile <i>M. a. ater</i> with <i>M. a. ater</i> females	54 (21—92)
Naive juvenile <i>M. a. ater</i> with <i>M. a. obscurus</i> females	23 (2—42)
<i>Test 2 Series</i>	
Adult <i>M. a. ater</i> with <i>M. a. ater</i> females	55 (49—61)
Juvenile <i>M. a. ater</i> with <i>M. a. ater</i> females	59 (50—68)
Adult <i>M. a. ater</i> with <i>M. a. obscurus</i> females	19 (14—31)

The females also displayed significantly fewer copulatory postures to the songs of the untutored males housed with *M. a. obscurus* females and displayed the most to those of males housed with *M. a. ater* females or other species, yielding a reliable difference among the songs for the three groups $\chi_r^2 = 12.6$, $df = 2$, $p < .01$. The songs of the males housed with *M. a. obscurus* females were significantly less potent than those of males housed with either *M. a. ater* females ($T = 0$, $p < .01$) or other species ($T = 1$, $p < .01$). All the females responded less to the songs of the *M. a. obscurus* versus *M. a. ater* housed males and all but one responded less to the songs of males with *M. a. obscurus* females versus other species. The potency of the songs of the males housed with other species was not reliably different from that of the songs of males housed with *M. a. ater* females with five females each responding most to songs of the two groups ($T = 20.5$, $p > .05$).

Differences in song potency also occurred for the songs of adult *M. a. ater* housed with *M. a. obscurus* and juvenile or adult *M. a. ater* housed with *M. a. ater* females, the Test 2 series (Table 1). *M. a. ater* males, here wild-caught adults, housed with *M. a. obscurus* females sang significantly less potent songs than did *M. a. ater* males with *M. a. ater* females. Because inspection revealed no differences in the potency of juvenile or adult *M. a. ater* housed with *M. a. ater* females, these conditions were collapsed for statistical purposes. The Wilcoxon test for matched pairs revealed a reliable effect of housing: all females responded least often to the songs of the *M. a. obscurus*-housed adults $T = 0$, $p < .01$.

Effects of Playback Housing on Female Responding

To test for social effects of housing on the playback females, we examined the responses of the solitary versus group housed females in the Test 1 series. Averaged across conditions, solitary females responded to 44 % of all playback songs (range 22 to 59) and females in pairs to 43 % (range 24 to 53). Inspection revealed no systematic difference by condition with a mean difference of 4.5 % between the responses of females tested alone or in pairs.

For the females housed in pairs in Test 2, two other measures were used to check for social facilitation or inhibition. First, Spearman rank order correlations were computed between the responses of all pairs of females residing in the same chambers for all playback songs to the Test 2 females. No excitatory or inhibitory effects occurred; the correlations for each pair averaged $-.05$ and ranged from $+.59$ to $-.59$. Second, the mean responsiveness of each female to the playback songs was computed and within- and across-chamber difference scores were calculated. Thus, each female's responsiveness was compared to her chambermate and also to a randomly selected female housed in another chamber. If the females were influencing each other, the difference scores should have been lower for females in the same chamber than across chambers. No effect occurred: the mean difference scores for females in the same chamber was 24 % (range 14—33) and was 21 % (range 13—29)

across chambers. No facilitatory or inhibitory effects have ever occurred for any set of playback subjects (KING & WEST 1983 a, c).

Monitoring of Females

Female cowbirds have never been reported to sing in the wild or in the laboratory (FRIEDMANN 1929; PAYNE pers. comm.; ROTHSTEIN pers. comm.), but the possibility of song was however carefully monitored in this investigation. Over 23,000 vocalizations were recorded and scored, the vast majority of which were recorded with an observer present who narrated accompanying social behavior: all 23,000 songs were sung by males. Attempts in our laboratory to induce singing in females through injection of testosterone also corroborate our 10 years of laboratory observation of females. Even with repeated doses of testosterone (during which time the birds were monitored for any sounds for long periods each day), no recognizable full songs occurred although the females did increase the rate of call vocalizations (calls males also make).

Female and male cowbirds do share one call, a "Kek" vocalization, but the call does not occur in response to song and is an infrequent event among small groups of birds in the laboratory (KING & WEST 1983 a).

Discussion

The data demonstrate the potential reproductive significance of social learning for the transmission of bird song. Male cowbirds modified the structure and potency of their songs in response to nonimitative feedback from female companions. The specific acoustic modifications made involved properties of the song known to affect female discrimination of song and female selection of mates. The data thus call for the need to broaden concepts of song development to include both vocal and social learning.

The Form of Female Guidance

How do females communicate their perceptions of songs? Females appear to inherit macrogeographic song preferences that are highly resistant to post-natal modification (KING & WEST 1983 c). Ongoing investigations of female hybrids (*M. a. ater* female \times *M. a. obscurus* male) also implicate primarily genetic control as the F1 daughters prefer *M. a. ater* song as strongly as their mothers (KING & WEST, unpubl. data). The possibility of environmental influences on microgeographic preferences must however be explored as it is at this local level of song discrimination that females actually compare songs (MILLER 1979).

Observations of the courtship and mating behavior of *M. a. ater* and *M. a. obscurus* females suggest possible forms of female feedback but as the effects obtained here all occurred before any breeding behavior was observed, we offer them with caution. Just as the females did not communicate by singing, they did not do so by adopting copulatory postures. In observation of

four captive colonies across two breeding seasons, consistent differences occurred in the responses of *M. a. ater* and *M. a. obscurus* females to songs and song overtures by *M. a. ater* or *M. a. obscurus* males (WIENER 1982). Differences occurred in the duration of male-female interactions, the frequency of rattle vocalizations and lunges by females, and the frequency of male chases of females. For example, during periods of active courtship, 80% of the songs directed to an *M. a. obscurus* female were when the male was within 15 cm of her but 80% of the songs directed to *M. a. ater* females occurred when the male was 30 cm or more away. Moreover, a male typically sang two or more songs during each interaction with a *M. a. obscurus* female but only one when singing to a *M. a. ater* female. These differences in the behavior of the *M. a. ater* and *M. a. obscurus* females suggest potentially quite conspicuous social signals for males to use.

A likely social signal displayed by females during the fall, winter, and spring is modification of male-female distance. Females may "shape" song development, i.e., indicate preferred and non-preferred song renditions, by increasing or decreasing distance between themselves and the singing male. Proximity between males and females during song delivery is ecologically quite relevant as the song elements coding potency degrade over extremely short distances (KING et al. 1981). Males appear to attempt to sing as close as possible to the female, often using other social behaviors such as head-down displays to decrease distance before singing (KENNEDY 1982). Females also responded to winter songs by changing their posture and head position. Thus, males may attend to kinesic and proxemic information.

Trial and Error Song Learning

The results from the males housed with heterospecific companions suggest a trial and error process of vocal modification and social learning. Trial and error learning also occurs in other avian species. Selection of song types in birds with overlapping repertoires, for example, can be influenced by a male's perception of that song's consequences when sung by another male (PAYNE 1982). But such learning still rests on song imitation or song matching. Male cowbirds, however, cannot match or model the behavior of their female companion but must extract from her behavior information about song consequences.

Although the songs of the males with other species were acoustically distinct from those of males with *M. a. ater* or *M. a. obscurus* females, they were only slightly less potent than those of males with *M. a. ater* females and they contained both *M. a. ater* and *M. a. obscurus* geographic markers. Young males may then initially possess a repertoire that normally includes diverse variants of potent song that are shaped by subsequent social experience with males and females.

Observations of captive colonies reveal that males deprived of contact with other males, even if they possess potent songs, must also learn how to compete for the opportunity to sing to them and to learn when not to sing

to them or risk attack, injury, or death (WEST et al. 1981). Thus, postnatal social stimulation from males and/or females may normally modify song content and potency (WEST & KING 1980). As BURGHARDT (1977) has argued, the processes responsible for the predictable origins of a behavior have often been confused with those responsible for its equally predictable modification by species-typical experience. The data presented here suggest that females as well as males may provide continuing postnatal experience.

Interpreting "Positive Effects" from the Laboratory

Here we isolated for experimental purposes a form of stimulation, feedback from females, that in nature would normally interact with feedback from males. How singers integrate the two forms of stimulation (and undoubtedly self-stimulation as well) is not known. Our studies of captive colonies, especially those containing "bilingual" males, suggest that males may selectively imitate other males on the basis of social information including dominance status and mating success (WEST et al. 1983). They may also do so on the basis of observing other males', as well as their own, "success" when singing to females. But *M. a. ater* adults become bilingual only when in the presence of *M. a. obscurus* males and females, not *M. a. obscurus* males alone, indicating the potential importance of observing the social consequences of singing and of recognizing potent songs.

Males' sensitivity to female preferences may be especially important for *M. a. ater* populations as the young males often overwinter in mixed *M. a. ater* and *M. a. obscurus* flocks (COON & ARNOLD 1977). The opportunity to learn *M. a. obscurus* song thus exists. As *M. a. ater* females appear insensitive to *M. a. obscurus* influence, *M. a. ater* males who learn *M. a. obscurus* song may be at a reproductive disadvantage when they return to breeding areas. If, however, males in nature attend to homosubspecific female feedback during the winter, they may avoid mis-learning and its consequences for lowered reproductive success. The laboratory effects described here then possess potential ecological relevance as feedback from females as well as males may serve as joint "fail-safe" mechanisms facilitating the adaptive transmission of song (KROODSMA 1983).

Conclusions

We have argued that social, as well as vocal, learning can mediate song ontogeny. The challenge for social theories of song learning is now to develop the vocabulary and behavioral variables to capture the means by which animals communicate about communicating. What is most visible about the vocal endeavors of male cowbirds is the behavioral effort males expend as they repeatedly approach and sing and attend to the actions of their companions. As such, the data highlight an often neglected property of the development of behavior, the energy and activity associated with "learning what comes naturally" (KAUFMAN 1975, p. 129).

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Literature Cited

- BAPTISTA, L. F. & L. PETRINOVICH (1984): Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. *Anim. Behav.* **32**, 172—181 •
- BURGHARDT, G. M. (1977): Ontogeny of communication. In: *How Animals Communicate*. (SEBEOK, T. E., ed.) Indiana Univ. Press, Bloomington, pp. 71—97.
- COON, D. W. & K. A. ARNOLD (1977): Origins of brown-headed cowbird populations wintering in Central Texas. *North Am. Bird Banding* **2**, 7—11.
- FRIEDMANN, H. (1929): *The Cowbirds*. Charles C. Thomas Press, Springfield, IL.
- GALEF, B. G. (1976): Social transmission of acquired behavior: A discussion of tradition and social learning in vertebrates. *Adv. Study Behav.* **6**, 77—100.
- IMMELMANN, K. (1969): Song development in the zebra finch and other estrildine finches. In: *Bird Vocalizations*. (HINDE, R. A., ed.) Cambridge Univ. Press, Cambridge, pp. 61—74.
- KAUFMAN, I. C. (1975): Learning what comes naturally: The role of life experience in the establishment of species-typical behavior. *Ethos* **3**, 129—142 •
- KENNEDY, J. M. (1982): Winter behavior of cowbirds. Unpubl. ms., Univ. of North Carolina •
- KING, A. P. & M. J. WEST (1977): Species identification in the N. A. cowbird: Appropriate responses to abnormal song. *Science* **192**, 1002—1004 •
- KING, A. P. & M. J. WEST (1983a): Epigenesis of cowbird song: A joint endeavor of males and females. *Devel. Psychobiol.* **305**, 704—706 •
- KING, A. P. & M. J. WEST (1983b): Dissecting cowbird song potency: Assessing a song's geographic identity and relative appeal. *Z. Tierpsychol.* **63**, 37—50 •
- KING, A. P. & M. J. WEST (1983c): Female perception of cowbird song: A closed developmental program. *Dev. Psychobiol.* **16**, 335—342 •
- KING, A. P. & M. J. WEST (1984): Social metrics of song learning. *Learn. Motiv.*, in press •
- KING, A. P., M. J. WEST & D. H. EASTZER (1980): Song structure and song development as potential contributors to reproductive isolation in cowbirds (*Molothrus ater*). *J. Comp. Physiol. Psychol.* **94**, 1028—1036 •
- KING, A. P., M. J. WEST, D. H. EASTZER & J. E. R. STADDON (1981): An experimental investigation of the bioacoustics of cowbird song. *Behav. Ecol. Sociobiol.* **9**, 211—217 •
- KROODSMA, D. E. (1982): Learning and the ontogeny of sound signals in birds. In: *Acoustic Communication in Birds*. (KROODSMA, D. E. & E. H. MILLER, eds.) Acad. Press, New York, pp. 1—33 •
- KROODSMA, D. E. (1983): The ecology of vocal learning. *BioScience* **33**, 165—171 •
- KROODSMA, D. E. & J. R. BAYLIS (1982): Appendix A: A world survey of vocal learning. In: *Acoustic Communication in Birds*. (KROODSMA, D. E. & E. H. MILLER, eds.) Acad. Press, New York, pp. 311—337.
- MARASCUILO, L. & M. MCSWEENEY (1977): *Non-parametric and Distribution-free Methods for the Social Sciences*. Brooks-Cole, Monterey, CA. •
- MILLER, D. B. (1979): Long term recognition of father's song by female zebra finches. *Nature* **280**, 389—391.
- OBERHOLSER, H. C. (1974): *The Bird Life of Texas*. Univ. of Texas Press, Austin.
- PAYNE, R. B. (1981): Song learning and social interaction in indigo buntings. *Anim. Behav.* **29**, 688—697 •
- PAYNE, R. B. (1982): Ecological consequences of song matching: Breeding success and intraspecific song mimicry in indigo buntings. *Ecology* **63**, 401—411 •
- PRICE, P. H. (1979): Developmental determinants of structure in zebra finch song. *J. Comp. Physiol. Psychol.* **93**, 260—277.
- TODT, D., H. HULTSCH & D. HEIKE (1979): Conditions affecting song learning in nightingales (*Luscinia megarhynchos*). *Z. Tierpsychol.* **51**, 23—25.

Nature

WEST, M. J. & A. P. KING (1980): Enriching cowbird song by social deprivation. *J. Comp. Physiol. Psychol.* **94**, 263—270 • WEST, M. J., A. P. KING & D. H. EASTZER (1981): Validating the female bioassay of cowbird song: Relating differences in song potency to mating success. *Anim. Behav.* **29**, 490—501 • WEST, M. J., A. P. KING & T. H. HARROCKS (1983): Cultural transmission of cowbird song: Measuring its development and outcome. *J. Comp. Psychol.* **97**, 327—337 • WIENER, L. (1982): Courtship behavior in *M. a. ater* and *M. a. obscurus* females. Ms., Duke Univ.

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