

Searching for the functional origins of song in eastern brown-headed cowbirds, *Molothrus ater ater*

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Abstract. Three experiments were conducted to examine the functional properties of vocal precursors to stereotyped song in socially housed captive cowbirds. Previous studies had shown that eastern male cowbirds developed different song repertoires when housed in different social contexts. This paper reports on the acoustic origins of the different vocal outcomes. In addition, a winter roost of cowbirds was studied to investigate the setting in which males naturally develop song. Analyses of the vocalizations of laboratory-housed subjects revealed acoustic differences from the earliest stages of song ontogeny. The field data indicated that free-living and laboratory-housed males shared the same structural categories of song and that the winter roost provided males with opportunities to interact with females. Taken as a whole, the studies suggest that song ontogeny is a dynamic process involving social and vocal interactions between singers and listeners.

Structurally distinctive and functionally significant differences occur in the songs of acoustically naive eastern *Molothrus ater ater* males housed with either conspecific *M. a. ater* or heterosubspecific *M. a. obscurus* females (King & West 1983a; West & King 1985). The specific features of the songs affected by such social housing in these studies included acoustic elements that females have been shown to use to discriminate the two subspecies' song variants (King & West 1983b). The vocal differences were present in early spring prior to the initiation of courtship when the males were 270 days of age. Because female cowbirds do not sing, they could not have acted as tutors, ruling out vocal imitation as the underlying mechanism. Instead, the findings suggest that males may be able to modify their songs on the basis of social stimulation.

In this paper, we report three experiments on the acoustic nature of vocal precursors to stereotyped cowbird song as a first step in determining when in ontogeny the behaviour of listeners begins to elicit vocal modifications by singers. The vocalizations analysed in the first two experiments were recorded as part of the earlier investigations establishing differential vocal outcomes under different conditions of social housing (King & West 1983a). In the first experiment, we examined how early in development we could detect the influence of externally provided acoustic stimulation in the songs of tutored, socially housed males. In the second

experiment, we investigated how early in development we could find differences in the vocal precursors of males that were acoustically deprived, but socially housed. Finally, we observed a winter flock of cowbirds to see if a natural context exists for social learning between males and females and to compare the structure and rate of song development of captive and free-living males.

Although mature bird song has always been considered a complex form of vocal communication, the ontogenetically prior forms, termed sub-song and plastic song, have typically not been considered as communicative (Thorpe 1961). They have been studied most thoroughly with respect to their role as motor activity preceding the 'perfection of the new skill of guiding the voice by ear rather than by proprioception or by endogenous motor programming' (Marler & Peters 1982a, page 45). Such a role in no way rules out a communicative function, but such a function has not been the focus of experimental inquiry.

There are several probable reasons why the communicative potential of the early stages of song production has not been explored. First, young birds in many species deliver immature song in soft soliloquies with little apparent attention to the actions of potential listeners, in stark contrast to their behaviour when singing as adults. Second, the content of such singing is so variable and inarticulate that it would seem suited only to the advertisement of the bird's youthful status. Third, songbirds

differ widely in how much singing occurs outside of the breeding season. These three phenomena may have supported the implicit idea that such vocalizations are not communicative in and of themselves but are prerequisite stages that lead to the achievement of the adequate level of sensory-motor competence necessary in order for communication to occur.

Laboratory studies of immature songs are also rare, making those of Marler & Peters (1982a, b, c) especially significant for the degree of experimental control and focus on explanatory principles. The use of a classificatory system to capture transitions in vocal development and the findings of developmental over-production and selective attrition represent major advances. Although the ontogenetic role of social stimulation was not directly studied, its potential importance was explicitly recognized.

The accumulating evidence indicating the widespread role of social stimulation in vocal learning in songbirds also underscores the need to consider the function of vocal precursors from a social perspective (Baptista & Petrinovich 1984, 1986; King & West 1984; Eales 1985; Pepperberg 1985). These studies call into question the premise that songbirds use only auditory information to 'modify or enhance vocal development' (Kroodsma 1982, page 1). Social interactions involving visual displays by listeners could, for example, stimulate vocal improvisation. In many songbirds the correlated nature of vocal and social influence among male singers and tutors has precluded the investigation of mechanisms specifically related to social, as opposed to vocal, learning. We chose to focus on the effects of female companions during development because, in species where females do not sing, vocal and social effects could potentially be segregated.

EXPERIMENT 1

The purpose of the first study was to look at the developmental course of the male's incorporation of tutored song when housed with either female cowbirds of a second subspecies, *M. a. obscurus*, or canaries, *Serinus canaria*. The focus was not on the final outcome which was already known: males housed with the heterosubspecific females sang less of the tutor song and developed more original song than did the males housed with canaries (King & West 1983a; West & King 1985). The question was

at what point in ontogeny did the two groups of males begin to diverge in terms of their patterns of singing? In other words how far back into development could we detect the influence of differential social housing?

The structural categories used in the present experiments generally correspond to those used in other species. Using differences in the morphology and order of syllables as major criteria, Marler & Peters (1982a) defined four major stages of song development for several sparrow species: subsong, subplastic song, plastic song (three categories) and crystallized song. In relation to the present work, Marler & Peters' stage of crystallized song corresponds to stereotyped song and their stages 2 and 3 within plastic song correspond to formatted song.

Methods

Subjects

Molothrus ater ater males were hand-reared from 4–5 days after hatching in acoustic isolation from adults. The eggs had been obtained from locally caught *M. a. ater* females breeding in aviaries in Orange County, North Carolina. They had been incubated by canaries until several days before hatching and then placed in the nests of barn swallows, *Hirundo rustica*, until 4–5 days of age (all age figures are averages for the 18 birds comprising experiments 1 and 2). The males were housed together in acoustic isolation until they were placed into their experimental groups. The males were assigned randomly to two experimental conditions at 50 days of age. In the first group, three males were housed individually with pairs of *M. a. obscurus* females and in the second, three were housed with pairs of male and female canaries.

The *M. a. obscurus* female companions were adults obtained in Starr County, Texas the previous winter and housed with *M. a. obscurus* males until the onset of the experiment. Wing-length measurements of the females fell within the ranges published by Oberholser & Kincaid (1974) for Texas populations.

All birds were housed in sound-attenuating chambers, maintained on a normal photoperiod for 35° latitude, and fed a modified version of the Bronx Zoo diet for omnivorous birds (see King & West 1977).

Tutoring procedure

The song of a locally caught adult *M. a. ater* male residing in an aviary was used for tutoring. The

song had previously been played back and found to be a potent stimulus for eliciting copulatory postures from *M. a. ater* but not *M. a. obscurus* females. The young males heard the tutor song daily from the beginning of September until the end of November (60–150 days of age). Each day, at about the same time in the morning, the males were exposed to 240 repetitions of the song over a period of 3 h. The tutor tape was played back with a Technics RS 1500 recorder, a Urei 537 1/3 octave equalizer and Crown D75 power amplifier through JBL 2105 speakers. The tutoring level was adjusted to 83 dB impulse at 0.5 m on axis from the speaker as measured with a Brüel & Kjaer 2105 sound-level meter.

Recording procedure

The males were recorded in 11 sessions beginning 30 November (150 days of age) and ending 7 June (300 days of age). Recording was not attempted earlier because the males vocalized too erratically and infrequently to make comparisons possible. Two days were generally required to record each male, with the exception of the November and December sessions in which it took up to 5 days to record several of the more infrequent singers. The songs of the tutored males were recorded with a Uher 4000 at 19 cps until 40 min of singing per session had been obtained. The average number of songs recorded for each male was 240; the minimum was 65 and the maximum was 592. Less than 70 songs were recorded in only five sessions and less than 150 in only 13. A total of 16 440 vocalizations was recorded and analysed (\bar{X} = 2737, range 2281–3277 per male).

Scoring of songs

To establish the reference template against which the vocal precursors could be compared, the original tutor song was displayed on the face of an oscilloscope using a zero-crossings-analyser which provides a frequency-by-time picture of the song (West et al. 1979). Clear acetate was then placed over the oscilloscope and a hand-tracing was made of the tutor song. The developmental songs were then displayed on the oscilloscope and compared with the acetate tracing of the tutor song. A vocalization was considered a match if there was 75% or more overlap in the acetate tracings.

Developmental song classification

The vocalizations were first divided into four

categories to mark structural shifts during development in cowbird song, i.e. the transition from subsong to plastic song to formatted to stereotyped song (Figs 1 and 2). The definitions were as follows.

Subsong. Unstructured, highly variable vocalizations of generally low amplitude containing elements not identifiable to the human ear as 'cowbird-like'. Subsong contains no discrete high voice notes or high-frequency whistles and is characterized by broad band noise.

Plastic song. Vocalizations containing low- and high-frequency notes and whistles characteristic of the species but with the elements often poorly articulated and variably ordered across bouts. The vocalizations last from 200 ms to 4–5 s.

Formatted song. Vocalizations possessing definite timing and syntactic ordering to the acoustic elements. The songs last between 800 and 1200 ms with variable content across renditions in terms of the specific elements included. Such songs begin with low-frequency tone bursts grouped into note clusters and terminate with a high-frequency whistle.

Stereotyped song. Vocalizations possessing the same form and elements on each rendition and lasting approximately 1 s. Stereotyped songs were further categorized in terms of the geographical content (Fig. 2).

Inter-phrase-unit song. Vocalizations containing the prototypical structure of eastern *M. a. ater* males consisting of two–three clusters of tone bursts followed by an inter-phrase unit, which is the first high-frequency note in the song (greater than 5 kHz) and the element that almost always marks the highest frequency of the song. The inter-phrase unit is typically, but not always, followed by a high-frequency whistle.

Mid-song-element song. Vocalizations containing additional notes (300–5500 Hz) after the inter-phrase unit and before the whistle. Mid-song-element songs occur in the songs of *M. a. obscurus* males but not in the songs of wild *M. a. ater* males.

No inter-phrase-unit song. Vocalizations consisting of tone bursts and whistles but lacking inter-phrase units or mid-song-elements making them unclassifiable with respect to subspecies identity as they lack prototypical markers.

Whistle. Vocalizations consisting of one or two high-frequency (greater than 2.5 and less than 13 kHz) tones with a duration of greater than 200 ms and usually lasting 300–500 ms.

Formatted and stereotyped songs were also

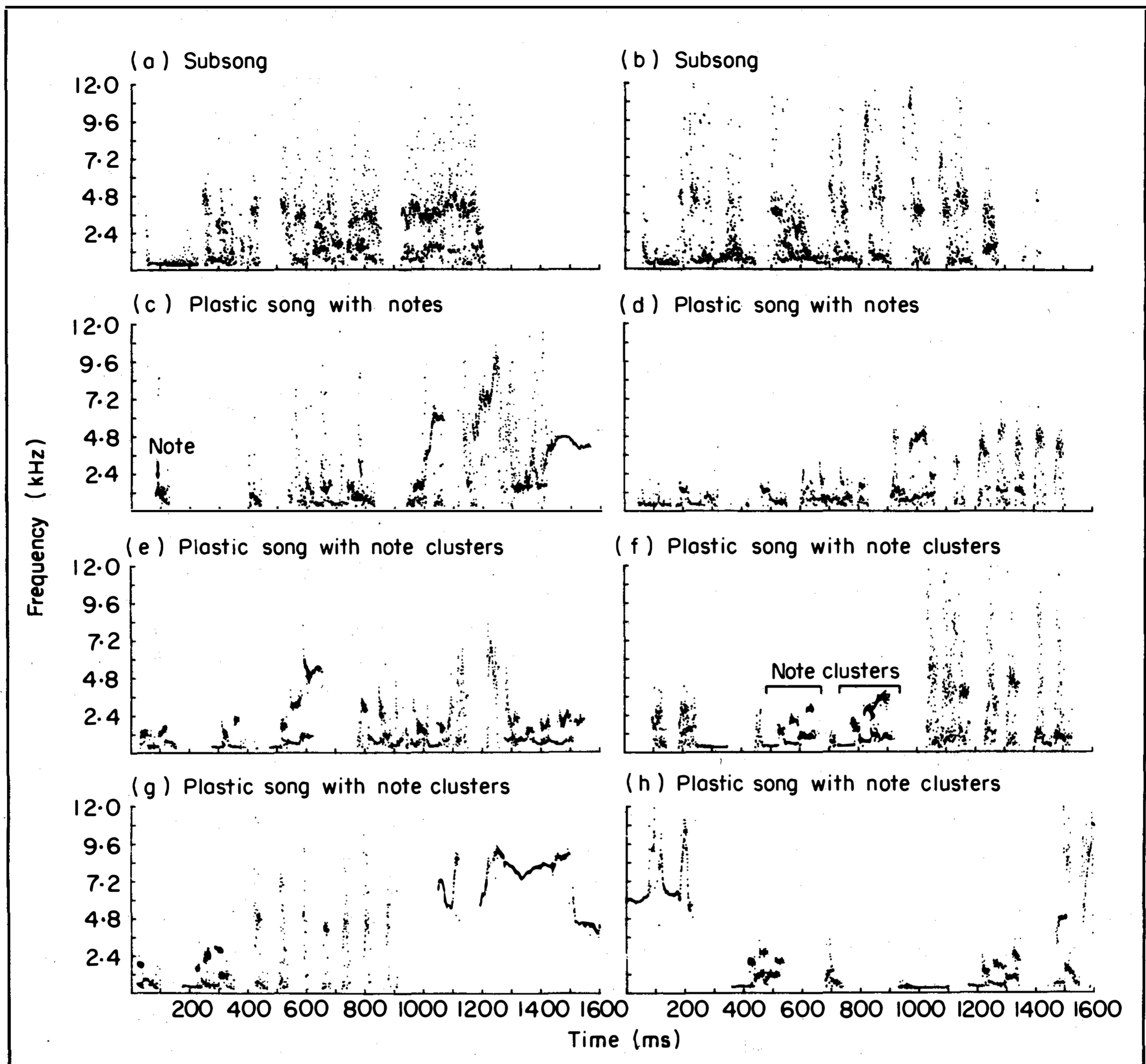


Figure 1. Zero-crossings-analyser displays of subsong and plastic song. See text for definitions. An example of a note is shown in c and note clusters are marked in f.

classified in terms of originality, or lack thereof, with respect to the tutor song. A song was scored as a copied full song if there was a 75% correspondence between it and the tutor song. If only part of the tutored song was reproduced, the song was scored as a copied phrase if there was a 75% correspondence to either the introductory notes or the whistle phrase of the tutor song. Songs not meeting either of these criteria were termed original songs.

Results

The effects of differential social housing were evident early in ontogeny. The males housed with

M. a. obscurus females sang more original song throughout development and the males housed with canaries more often copied the tutor song, either as full or partial renditions (Fig. 3).

Across all ages, the repertoires of the males housed with *M. a. obscurus* females averaged 76% (range 0–96) original song in contrast to 20% (range 0–31) for the males housed with canaries. Copying of the tutor song also differentiated the two groups: the repertoires of the males housed with *M. a. obscurus* females averaged only 24% (range 4–41), in contrast to the males with canaries which averaged 79% (range 69–100) copied song or phrases.

To determine at what age the differences between

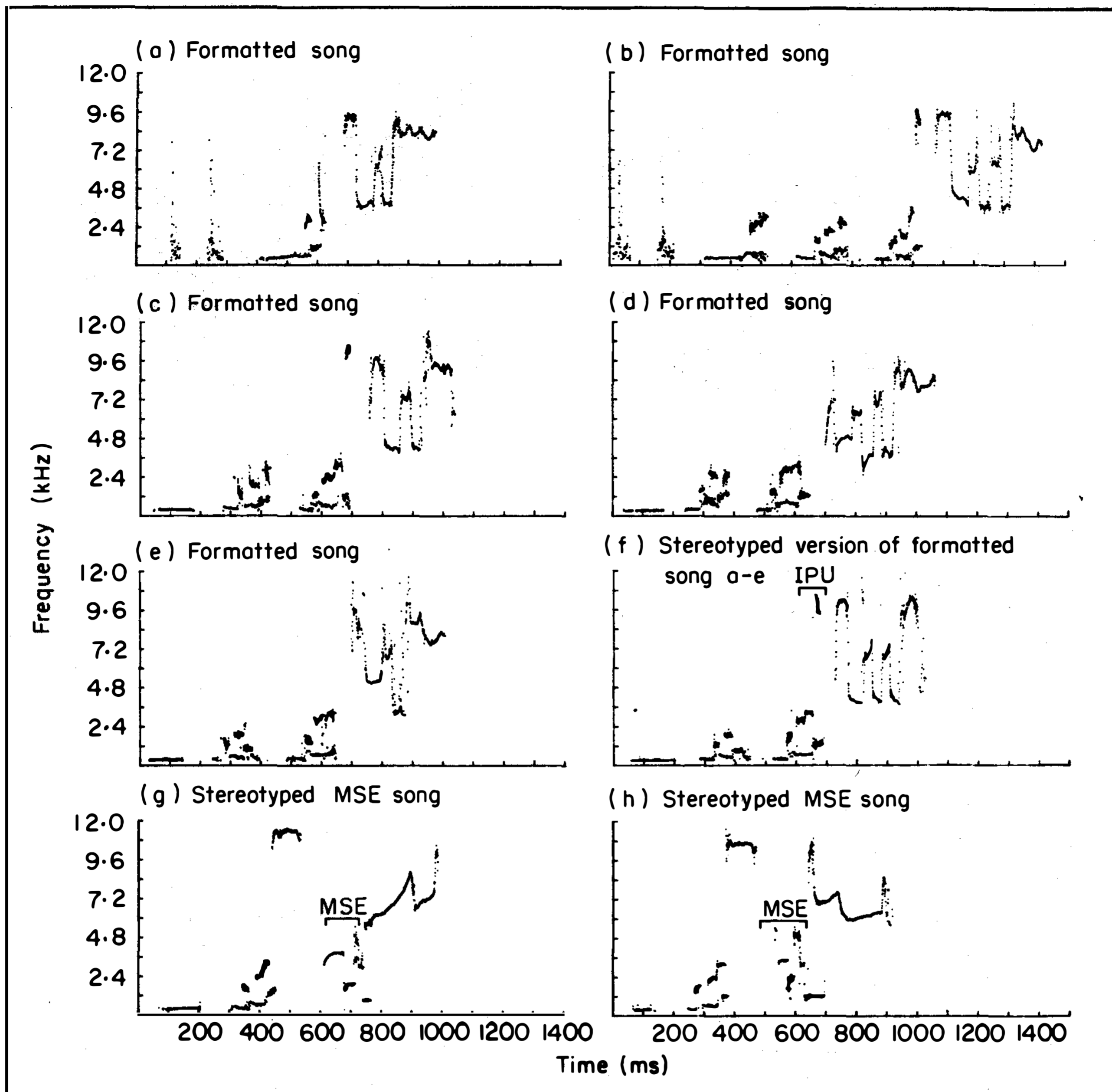


Figure 2. Zero-crossings-analyser displays of formatted and stereotyped song. The vocalizations shown in a–e were produced by the male which ultimately sang the stereotyped rendition of an inter-phrase-unit song (IPU) shown in f. g and h are examples of two different songs with mid-song elements (MSE).

the two groups began to emerge, the frequency of occurrence of subsong, plastic song, copied full song, copied phrases and original song was examined for each recording session. Due to the small number of subjects, there could be a significant difference only if there was no overlap in the measures for the two groups (Mann–Whitney U -test, $U=0$, $P<0.05$). Hence, all references to significant differences are based on a U -value of 0.

For subsong, no differences occurred at any point. The frequency of plastic song differed slightly between the two groups, with the males housed with *M. a. obscurus* females continuing to sing more plastic song until a later age (Fig. 3). For

the categories of original and copied songs, the groups began to diverge when the males were 240 days of age (session 5). For original song, the males housed with *M. a. obscurus* females sang more original song in seven of the 11 sessions, singing significantly more in five sessions (sessions 3, 8, 9, 10 and 11).

For the combined category of copied full song and copied phrases, the divergence between the groups began around 270 days of age (session 6), with significant differences occurring for sessions 6, 8, 9 and 11, and corresponding trends for sessions 7 and 10. For the category of copied phrases alone, the groups differed even earlier in development,

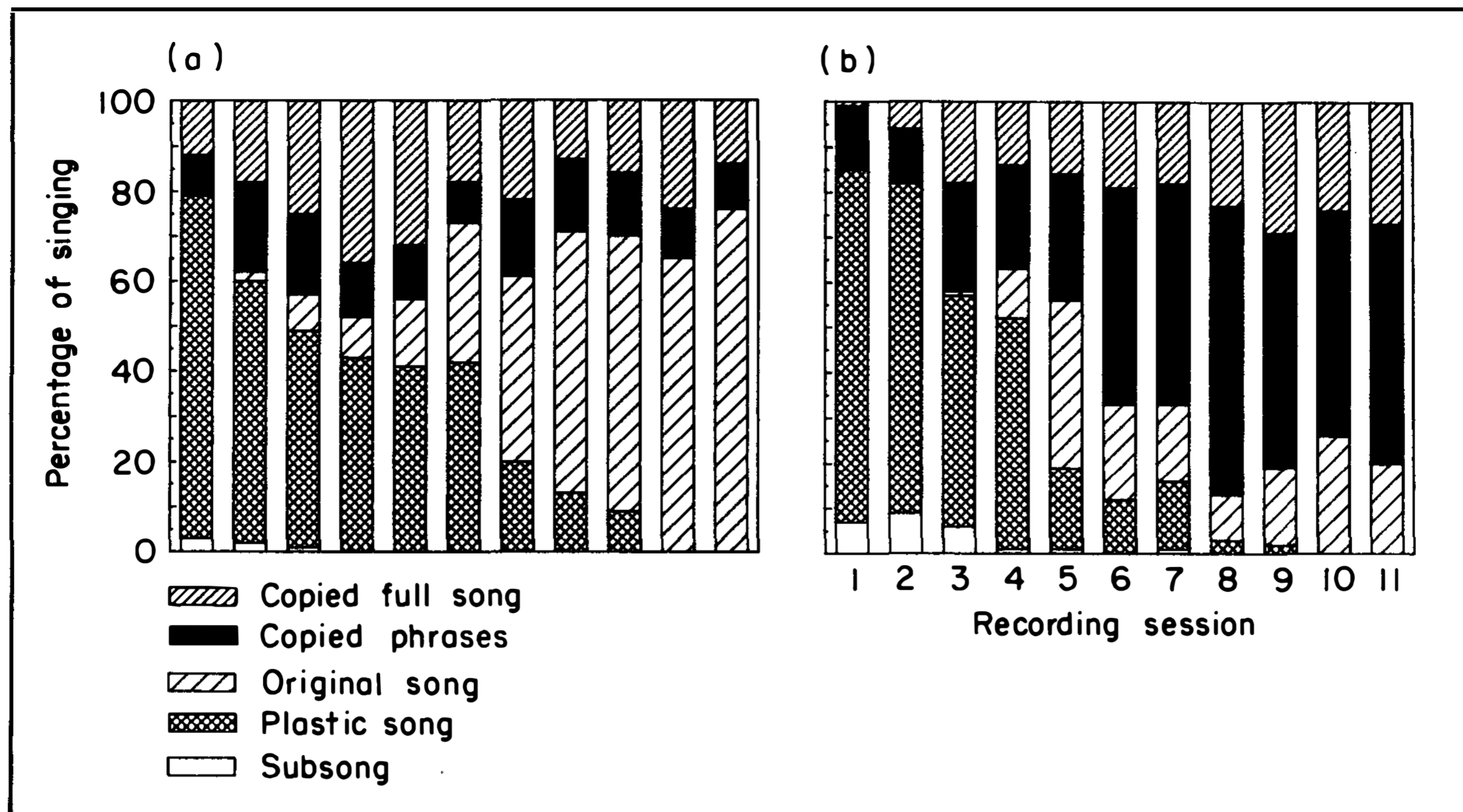


Figure 3. Mean percentage of vocalizations falling into each of five categories for the two groups of males in experiment 1: a shows the averaged data for males housed with *M. a. obscurus* females and b shows the data for males housed with canaries. See text for definitions of categories. The actual dates for the 11 recording sessions for experiments 1 and 2 were: 1 (30 November–12 December); 2 (27 December–2 January); 3 (18–30 January); 4 (10–17 February); 5 (28 February–2 March); 6 (13 March); 7 (30 March–1 April); 8 (13 April); 9 (30 April); 10 (10–17 May); 11 (25 May–7 June).

beginning with significantly more copied phrases being sung by the males housed with other species at 210 days of age in session 4 and continuing throughout. The differences between the groups were significant for all subsequent sessions except 5 and 10.

The category of copied full song showed fewer differences. For the first five sessions, males housed with *M. a. obscurus* females tended to sing more complete renditions, but for the remaining sessions, no clear pattern was evident.

Inventive singing

As a final attempt to look for divergence, the categories of plastic and original song were combined as a measure of song invention (sensu Marler & Peters 1982a). By this measure, the groups diverged in March, around 240 days of age, with the males housed with *M. a. obscurus* females singing a significantly higher proportion of plastic and original song for sessions 6, 8, 9 and 11 and showing the same trend for sessions 7 and 10.

Discussion

Males tutored with the same *M. a. ater* song but in the presence of different social companions displayed different vocal ontogenies. Differences

between the two groups' repertoires appeared at least 2 months prior to the time when males court females and were apparent even earlier in development. Given the sample size, caution must be exercised in interpreting the data, but they do suggest that males may be stimulated by the behaviour of their audience well before song vocalizations attain stereotyped form.

Song development in passerines has long been thought of as a time for vocal experimentation. The present data are consistent with this view. In addition to their longer retention of plastic song renditions, the males housed with *M. a. obscurus* females developed more original song types suggesting they were stimulated to innovate late into development. Conversely, the males housed with canaries (which presumably displayed less stimulating behaviour) persisted in singing the one song type with which they were tutored. Marler et al. (1972) found a similar effect in red-winged blackbirds, *Agelaius phoeniceus*, where males tutored with heterospecific songs copied less when housed with female conspecifics than when they were housed alone. Marler & Peters (1982c) also reported significant amounts of song invention in tutored swamp sparrows, *Melospiza georgiana*.

All the males exhibited the capacity to sing clear

copies of the tutor song as early as 150 days of age. Thus, the capacity to sing in an articulate manner existed early in development. But all the males continued to produce plastic song for months after the point at which the motor apparatus was sufficiently developed to produce structurally articulate song, a phenomenon also reported by Marler & Peters (1982c). The co-occurrence of plastic and stereotyped songs suggests that motoric proficiency is only one possible function of a protracted period of song development. Among other possible objectives are the development of a variety of song material to provide males with rich song reservoirs to aid in the development of functional proficiency, i.e. learning about the behavioural consequences of singing structurally different precursors in social interactions.

EXPERIMENT 2

The purpose of the second experiment was to chart the course of vocal development in *M. a. ater* males deprived of species-typical auditory contact with males but exposed to social stimulation from *M. a. ater* or *M. a. obscurus* females or non-conspecifics. Again, as in experiment 1, the final outcome was known: males developed significantly different repertoires biased toward the subspecific preferences of their female companions. Given the match between the males' final repertoires and the subspecific song preferences of females from these populations, the data suggested that males did not need external song models in order for song differentiation to occur. But, at what point did differentiation occur and which vocal features were most susceptible?

In the first experiment, the differences in the repertoires of the two groups were most apparent in early spring, at which time the males were producing songs that were sufficiently articulate for the majority to be classified as copied or original song types. Perhaps the males began to pay more attention to social consequences when they achieved the ability to sing different renditions of formatted or stereotyped song, or perhaps females begin to produce more social signals at this time. But the higher incidence of plastic song among the males housed with *M. a. obscurus* females in experiment 1 suggests that males may also experiment with the more rudimentary vocal patterns and that trial-and-error learning may pertain to plastic song as well as stereotyped song.

In experiment 2, we were able to test whether subsong and plastic song were affected by social influence because acoustically deprived male cowbirds develop their song repertoires more slowly than do tutored males. Although the more gradual emergence of song allowed us to probe for earlier evidence of differentiation, it necessitated different analyses of song structure because the early vocalizations were too primitive and syntactically variable to be compared with any final standard: no match was possible given the fundamentally different nature of the sounds (Figs 1 and 2).

We chose to study five characteristics of individual notes in vocal precursors. The measures were chosen on the basis of previous research in which we had established which elements within song were most critical to eliciting the female's copulatory posture, as well as on the basis of the acoustic differences found in the final repertoires of the males (King & West 1983a; Figs 1 and 2).

In addition to the analyses of notes, we examined group differences in stages of song development and categories of stereotyped song. In particular, we looked for differences in the males' incorporation and retention of the mid-song element (Fig. 2), a note cluster that occurs in songs of *M. a. obscurus* populations but not *M. a. ater* populations. Playback studies had confirmed the importance of the mid-song element to copulatory responding by *M. a. obscurus*, but not *M. a. ater*, females (King et al. 1980; King & West 1983b). In addition, we looked for the presence of the inter-phrase unit (Fig. 2) in the males housed with *M. a. ater* females because responsiveness to song playback by *M. a. ater* (but not *M. a. obscurus*) females is significantly reduced when this brief element is omitted (West et al. 1979; King & West 1983b).

Methods

Subjects

Twelve *M. a. ater* males served as subjects and were reared and housed using the procedures detailed in experiment 1. At 50 days of age, the males were assigned randomly to three groups. Three males were housed individually with non-conspecifics (two with pairs of canaries and one with a starling, *Sturnus vulgaris*), four were housed with adult *M. a. obscurus* females obtained from the same site as in experiment 1, and five were housed with adult *M. a. ater* females captured in Orange County, North Carolina. One of the males

housed with *M. a. obscurus* females died in April, reducing the number of subjects to three for the final three recording sessions for that group.

Recording procedure

The males were recorded following the same procedures and using the same equipment described for experiment 1.

Song analysis

Beginning with session 5 when the males were 210 days of age, a total of 13 367 vocalizations were recorded that fell into the plastic or formatted categories. For the males with other species, 3425 vocalizations were analysed ($\bar{X}=189$, range 103–272 per male), for males with *M. a. ater* females, 6159 vocalizations were analysed ($\bar{X}=212$, range 98–330 per male), and for males with *M. a. obscurus* females, 3783 vocalizations were analysed ($\bar{X}=177$, range 88–285 per male).

Prior to session 7, 96 s of vocalizing or 100–112 discrete songs were analysed for each session for each male. Taken together, these criteria produced a comparable sample across males. These vocalization units were chosen on the basis of recording quality from the much larger set of recorded vocalizations. Vocalizations were excluded if extraneous noise (such as wing or foot movements) was present or if the vocalization's signal-to-noise ratio was below 25 dB when measured peak to peak.

Across all sessions, we analysed 50 345 high voice notes (13 927 for males with other species, 22 034 for males with *M. a. ater* females, and 14 384 for males with *M. a. obscurus* females) and 65 477 low notes (17 875 for males with other species, 26 990 for males with *M. a. ater* females, and 20 612 for males with *M. a. obscurus* females).

Note feature analysis

The note measures were collected by a Brüel & Kjaer 2033 spectrum analyser controlled by a Hewlett Packard 86 B computer. The computer also controlled an Otari 5050MX audio recorder and a custom-designed gating system to feed vocalizations into the Brüel & Kjaer 2033 spectrum analyser. The note measures were defined as follows.

High voice notes. Tones between approximately 1500 and 12 000 Hz lasting between 5 and 1000 ms. Tone bursts between 1500 and 5000 Hz and of short

duration (10–50 ms) are frequently followed by low voice notes arranged in note clusters (Fig. 1).

Low voice notes. Tones produced between 300 and 1500 Hz. These notes show independent amplitude and frequency modulations from high voice notes.

Note synchrony. The frequency of low voice note amplitude peaks occurring within a 40 ms epoch after a high voice note peak amplitude. The epoch was sub-divided into 10 4-ms units.

Scan procedure

The vocalizations were scrolled through the spectrum analyser in 3-ms steps which created a topographical map of the vocalization. The map is equivalent to a narrow-band sonagram featuring 25-Hz frequency resolution. During the generation of the map, the operator moved a cursor to separate the high and low voices and to indicate to the computer when to edit extraneous noises from the map. After the map was completed, it was stored on magnetic disc.

After the maps were created, they were recalled to the Hewlett Packard 86 B computer and each note was measured to extract the following information: frequency, time and level of the peak amplitude of each note. In addition, the frequency bandwidth or modulation of the note were measured to determine the degree of modulation and whether it ascended or descended. As part of this measurement, the minimum and maximum frequency of each modulation and its amplitude level were collected. Finally, the onset time and duration of each note were measured relative to the beginning of the entire vocalization.

Of the machine measurements of the onset and offset of notes, 25% were compared with human judgements of the same parameters from zero-crossings-analyser plots; there was better than 90% agreement. The purpose was to adjust the computer program's definition of note onset and offset to correspond to the way a human observer would see onset or offset in a zero-crossings-analyser plot. For measurement of actual frequency, time and amplitude of the notes, the Brüel & Kjaer 2033 spectrum analyser provides a precise measurement.

Classification of songs

Songs were classified into stages according to the same definitions used in experiment 1.

Results

The three groups of males differed in the nature and rate of song development from the earliest point at which measures could be obtained. Significant differences occurred between the groups before the vocalizations could be classified into song types: the males differed with respect to the number and kind of high voice notes they produced and with respect to the timing of high and low voice notes. From the earliest point at which the vocalizations could be typed into stable syntactic orderings, the males differed in their inclusion of the *M. a. obscurus* marker, the mid-song element, and in their production of whistles.

High voice notes

The males housed with *M. a. obscurus* females sang the fewest high voice notes in every recording session, with the males in the other two groups singing about the same proportion (Fig. 4). Kruskal-Wallis analyses of variance were calculated for each recording session and revealed that males with *M. a. obscurus* females sang significantly fewer high voice notes in sessions 1, 3, 5 and 6 ($P < 0.05$ for 1 and 6 and $P < 0.01$ for 3 and 5), and averaged the fewest notes in sessions 2, 4 and 7, although the means were not significantly different.

Differences between the two groups housed with females were also examined, revealing no overlap between the scores of individual males with *M. a. ater* versus *M. a. obscurus* females for sessions 1, 3, 5, 6 and 7. The pattern for the males with other species was less clear; there was greater variability among the three males.

High voice notes under 5 kHz

A similar effect was obtained for the subset of high voice notes sung at frequencies under 5 kHz: the males with *M. a. obscurus* females sang the fewest such notes in all seven sessions, with reliable effects occurring for sessions 5 and 7 ($P < 0.05$) and with the males with *M. a. obscurus* females averaging the fewest notes under 5 kHz in all remaining sessions (Fig. 4).

High notes under 5 kHz modulated more than 2 kHz

A different effect occurred for this measure: the males housed with *M. a. obscurus* females consistently sang the most modulated notes with reliable differences occurring for sessions 3–11 ($P < 0.05$ for 3–7 and $P < 0.01$ for 8–11). The same trend was also apparent in the earlier sessions (Fig. 4).

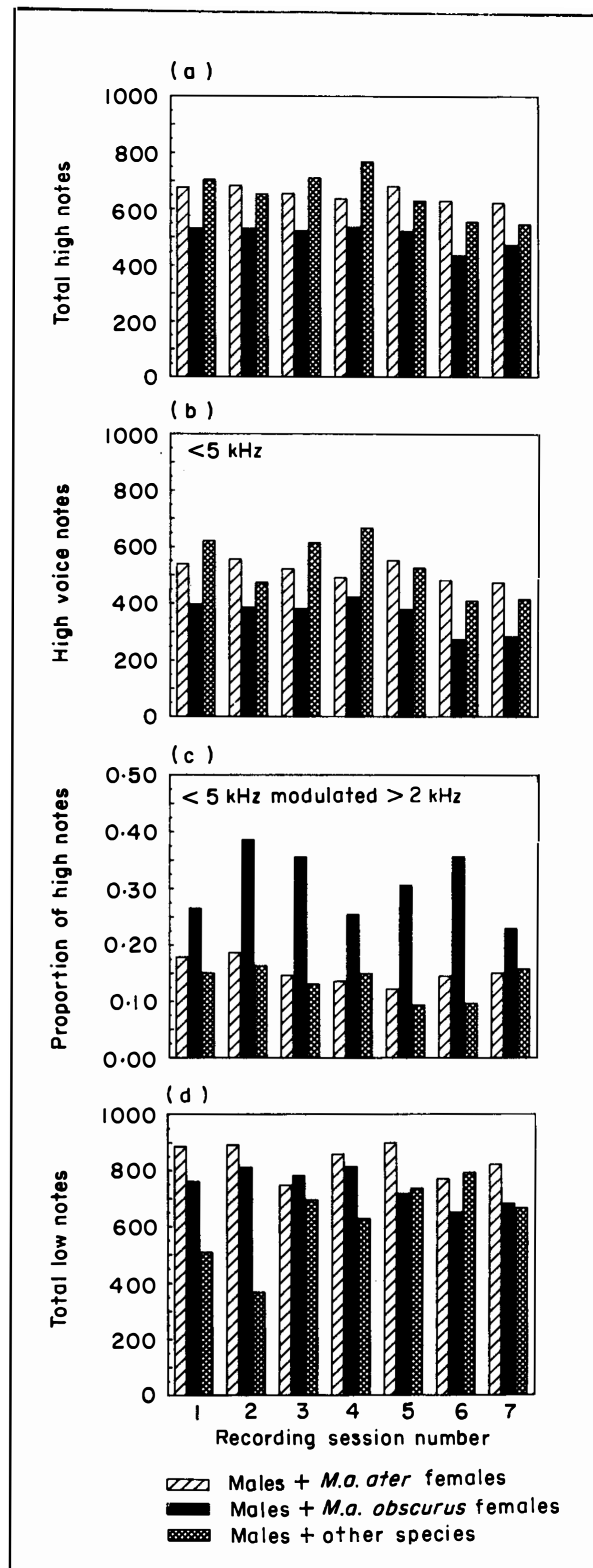


Figure 4. Acoustic characteristics of the notes for the males from experiment 2 housed with *M. a. ater* females, *M. a. obscurus* females or other species. b and c are measures derived from a: b shows the number of high notes less than 5 kHz and c shows the proportion of these notes that were modulated more than 2 kHz.

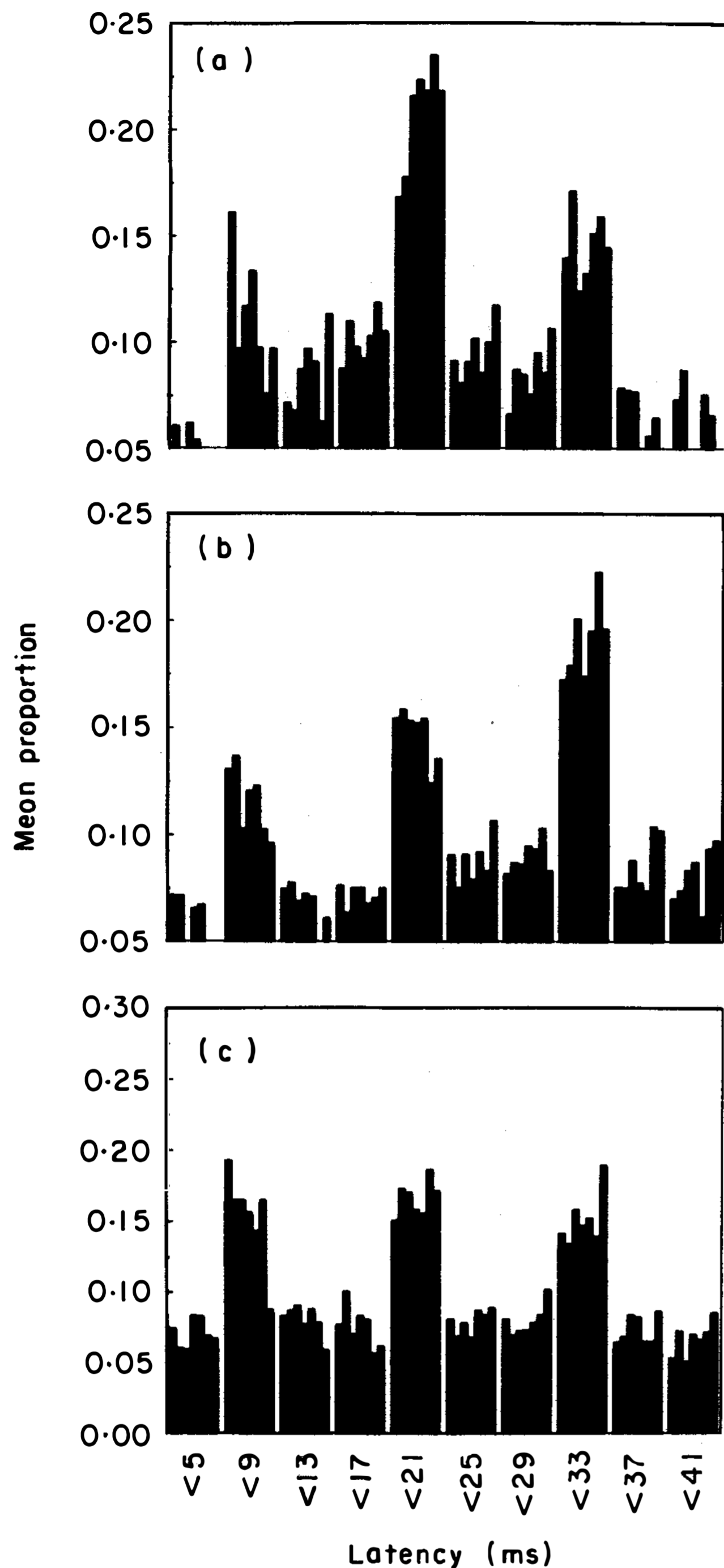


Figure 5. The mean proportions of low voice amplitude peaks that followed each high voice amplitude peak as a function of time are shown for males housed with other species (a), males with *M. a. ater* females (b), and males with *M. a. obscurus* females (c). The individual bars within each cluster represent recording sessions 1–7 to show session-to-session changes. The time epochs displayed on the abscissa are 4-ms divisions of the first 41 ms following every high voice peak.

No overlap or minimal overlap (one male in either group falling within the range of the opposite group's scores) occurred in individual scores between males housed with *M. a. ater* or *M. a. obscurus* females in the first seven sessions.

Proportion of low notes

No consistent pattern occurred with respect to the proportion of low notes produced as a function of social companion.

Note synchrony

All three groups displayed the greatest proportion of low voice notes in relation to high voice notes at the same three temporal locations in the vocalization: during the second (5–9 ms after the first note), the fifth (22–25 ms after) and the eighth time interval (33–37 ms after). But the groups differed in how the notes were apportioned within these three intervals (Fig. 5).

Friedman analyses of variance of ranks were used to test within-group consistency in synchrony. The time interval containing the most and greatest amplitude peaks of high and low voice notes was ranked 1, and the time interval displaying the least was ranked 10.

For the males housed with other species, the fifth time interval contained the highest proportion of low and high voice note synchrony. This time interval was favoured for five sessions, yielding statistically significant values for sessions 3–6 ($P < 0.01$) and for session 7 ($P < 0.01$).

For the males housed with *M. a. ater* females, the eighth time interval was strongly favoured in sessions 2–7, yielding significant Friedman scores for sessions 2, 3, 5 and 7 ($P < 0.02$ – 0.001). For sessions 4 and 6, the fifth and eighth intervals were ranked first or second by four of the five males.

For the males with *M. a. obscurus* females, the fifth time interval showed the highest average rank in sessions 2–6, producing significant Friedman scores ($P < 0.02$ for two sessions and $P < 0.001$ for the other sessions).

Song classification

Although no group differences occurred with respect to plastic song, the males with *M. a. obscurus* females averaged the most plastic song and sang it later in the year. Formatted song waned first among the males with other species and last among the males with *M. a. obscurus* females. These males sang significantly more formatted song than either group in sessions 7 and 8 ($P < 0.01$).

The major difference with respect to the categories of stereotyped song (Table I) was the complete absence of mid-song elements in the repertoires of the *M. a. ater* males in any of the recording sessions

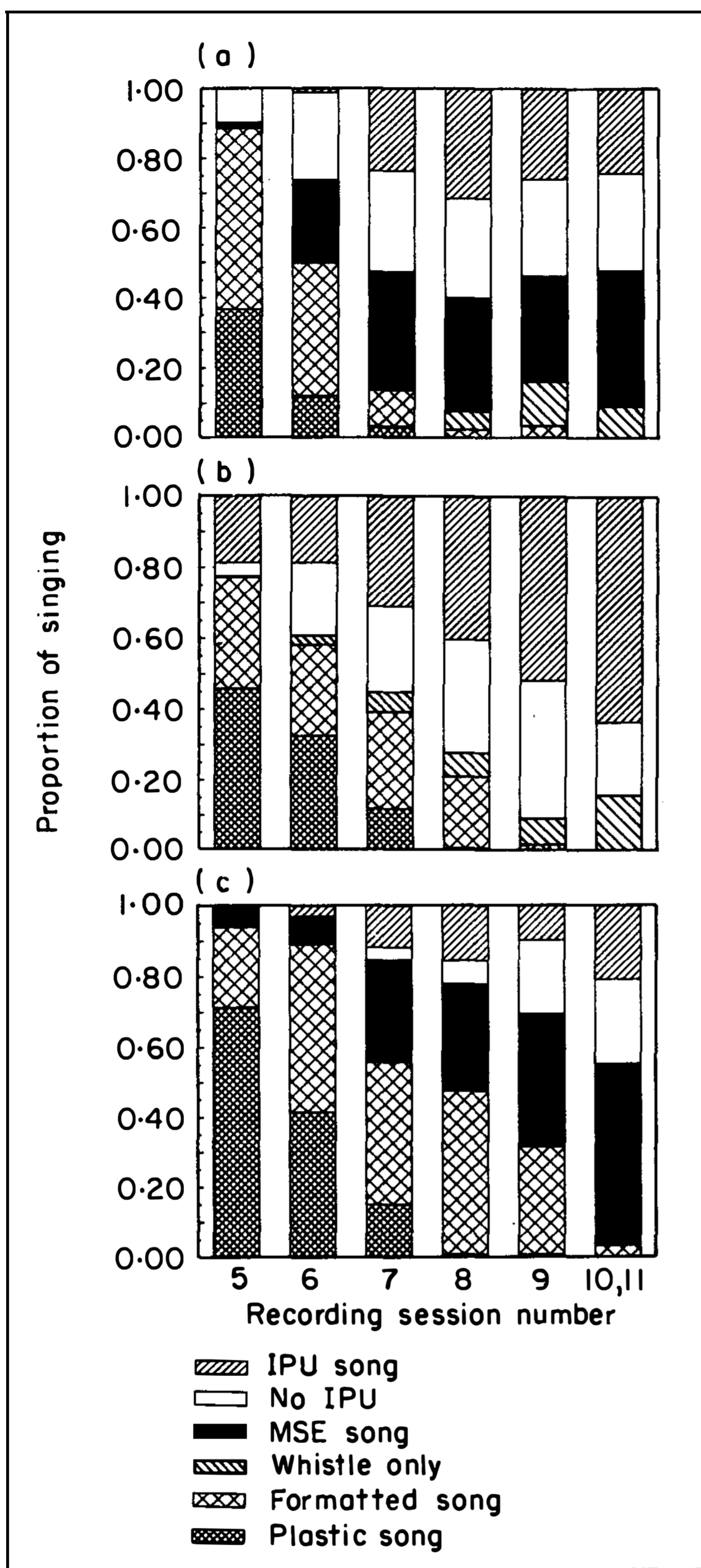


Figure 6. The mean differences in proportion of singing between the three groups in experiment 2 in terms of stages of song development and categories of stereotyped song for sessions 5–11. (a) Males housed with other species; (b) males with *M. a. ater* females; (c) males with *M. a. obscurus* females.

and the virtually complete absence of whistles by males with *M. a. obscurus* females (Fig. 6).

The males housed with *M. a. ater* females averaged the most eastern or inter-phrase unit song. The major differences between the groups were in the numbers of males producing this category and the developmental pattern associated with its production. Four of the five males with *M. a. ater* females consistently sang inter-phrase-unit

song, whereas only two of the four males with *M. a. obscurus* females ever sang it. All three males housed with other species also sang it consistently. Songs classed without inter-phrase unit song showed no consistent pattern of differentiation between the three groups.

Songs composed of only whistles were infrequent for all three groups, never averaging more than 16% of singing in any session for any group. Males with *M. a. ater* females and other species sang the most whistles, especially in the last three sessions (range 0–40%). Males with *M. a. obscurus* females sang virtually no whistles; only one male produced any whistles (1% of his singing in sessions 10 and 11).

Discussion

The results indicated effects of social housing in the absence of external song stimulation and demonstrated that the vocal differences between the groups could be predicted from a priori knowledge of the parts of cowbird song most critical to eliciting copulatory responding from female companions. The data thus support further exploration of vocal precursors to determine how social stimulation mediates vocal modifications.

In other studies, we have found populational differences in the perceptual modifiability of the *M. a. ater* female cowbird's responses to song: *M. a. ater* females from Oklahoma, for example, appear to have more modifiable preferences than females in the east (King et al. 1986; King & West 1987). Although both populations show evidence of social influence, the direction of effects appears to differ, and thus it is important to note that the inferred direction of social influence of females on males in eastern *M. a. ater* cannot as yet be extended to other populations within the subspecies or across cowbird subspecies.

EXPERIMENT 3

Do males in nature have opportunities during ontogeny to be stimulated by companions and is the course of vocal development similar to that of males housed in the laboratory? We chose to explore these questions by conducting a field study to learn if the categories of vocal precursors that characterized the singing of the laboratory-housed males also described the vocalizations males normally sing and females normally hear.

Table I. Proportion of vocalizations in each of three song categories for free-living males during the winter

Session	No. of songs	Song categories		
		Plastic	Formatted	Stereotyped
November–December				
Flock males*	182	0.53	0.21	0.27
Nine banded yearlings	72	0.85	0.04	0.11
January				
Flock males	41	0.51	0.24	0.24
Ten banded yearlings	249	0.52	0.44	0.04
February				
Flock males	62	0.31	0.32	0.37
Four banded yearlings	149	0.20	0.32	0.47

* Flock males were of unknown age and were recorded at the baited area.

In addition to identifying categories of vocalizations, we were interested in the nature of transitions from more-variable to more-stereotyped song. In experiment 1, we had found that males did not delete plastic songs from their repertoire once they were capable of singing stereotyped songs. As seen in Fig. 3, plastic song and stereotyped songs co-occurred in roughly equal proportions until March, at which point plastic song waned. Was the gradual disappearance of the immature vocal forms a result of the relatively impoverished auditory environment? If wild males, which naturally have more auditory and social stimulation, also showed overlap in the classes of vocal precursors sung at the same point in time, a stronger argument could be made that the retention of variable vocal material was an ecologically relevant phenomenon.

Methods

Subjects and setting

Cowbirds were observed and recorded at the Dorothea Dix Farm in Wake County, North Carolina during the months of November, December, January and February, corresponding to sessions 1–5 in experiments 1 and 2. Birds were trapped and banded with coloured leg streamers and coloured plastic rings. Males were aged by plumage: yearling males retain brown juvenile feathers in the under wing coverts, adults do not. Females could not be aged.

Banding and recording were conducted in eight sessions, beginning in early December 1983 and ending in early March 1984. A site at the roost was

baited with seed, as well as with decoy cages housing female cowbirds. Multiple microphones were placed around the site on trees and microphone stands. The microphones were connected via 8- and 12-m cables to a switching box allowing the observer to select the microphone closest to singing males. The observer dictated notes about the identity of the singers into the second channel of a Uher recorder. In January, 10 yearlings were caged together to obtain more-extensive vocal samples. Vocalizations were analysed using the equipment and procedures described in experiment 1.

Flock composition was sampled by counting the number of males and females in the groups at the baited site and surrounding trees and telephone wires.

Results

We colour-banded 197 birds, with an overall banding ratio of 118 males (67 yearlings, 51 adults) to 79 females = 1.49. The sex ratios in the groups at the baited site varied across sessions from ratios of 2.3 to 0.50, averaging 1.83 males to females. Of the birds banded, 14% were sighted again and, of these, 75% were yearling males. More females than adult males were captured during the banding sessions, yielding a ratio of 0.97 adult males to females. Juvenile males were captured with females during every banding session, yielding a sex ratio of 1.27 yearling males to adult females.

The three vocal categories that emerged from the analysis of 755 field vocalizations corresponded well with those in experiments 1 and 2 (Table I). No

new categories were needed to account for the wild males' vocal behaviour. Moreover, the seasonal shifts toward more-stereotyped song paralleled those obtained in the first two experiments.

For the 10 caged yearlings recorded in January, each individual male's inclusion of the three categories was computed to determine the co-occurrence of the three categories. The males each sang all three categories, yielding mean proportions of 0.47 (range 0.20–0.71) for plastic song, 0.37 (range 0.08–0.80) for formatted song and 0.16 (range 0–0.50) for stereotyped song.

Discussion

Young males in the winter flock were not segregated from females during the period of song development. Yearling males appeared to retain variable vocal material well beyond the point at which they were capable of singing stereotyped song, a finding in accord with the results of experiment 1.

Looked at from the perspective of the female, the field data also show that females in the field and laboratory were exposed to comparably diverse stages of song production at the same time of year.

The structural categories used in the present experiments generally agree with the distinctions made for other species. Given the extreme structural diversity across songbird species and differences in life histories, the parallels in vocal development suggest that early over-production of material and later attrition may be mechanisms that are quite general (see West & King 1986 for a demonstration of over-production and attrition at the level of the song repertoire).

In the present study, individual cowbirds studied in the laboratory and in the field intermixed vocalizations of strikingly different levels of articulation, even in February and March. Although Marler & Peters (1982c) reported little intermingling of vocal categories once crystallized song occurred in the swamp sparrows, they reported some intermingling during the stages of plastic song. In song sparrows, even more intermingling occurs (Marler, personal communication). The life histories of cowbirds and sparrows differ in many ways. Perhaps the most relevant difference with respect to song ontogeny is that singing does not cease during the winter for cowbirds, but does so in the sparrows. Despite this difference, parallels in

vocal development are apparent, holding forth promise for identifying broad comparative principles of vocal learning (Pepperberg 1985).

GENERAL DISCUSSION

Vocal precursors to stereotyped song in eastern cowbirds possessed different acoustic characteristics when males were housed with different social companions. Males housed with *M. a. obscurus* females produced significantly more mid-song elements than males housed with other species, and males housed with *M. a. ater* females completely omitted this element. Such a convergence of male production and female preference strongly suggests that vocal precursors have functional properties capable of evoking different reactions from listeners. The presence of acoustic differences between the group very early on also suggests that social stimulation from listeners is of noticeable consequence throughout development. Opportunities for social interactions between the sexes seem to be naturally available, as shown by the field observations of young males associating with adult females in winter flocks.

Although the present work contrasted possible effects of female influence, the effects of social and vocal interactions with males are undoubtedly of considerable importance (West & King 1986). In this regard, Dufty (1985, 1986) has demonstrated that song is a critical behaviour for the establishment of male dominance in captivity, and thus some of the male's vocal modifications in nature are surely in response to intrasexual interactions.

In summary, the data add further incentives to the task of specifying the diverse ways in which social stimulation can affect vocal development. In addition to the well-documented influence of vocal tutors, the data suggest that social companions lacking the ability to sing can also affect vocal development. The present data suggest that one role of social stimulation during development may be to sensitize singers to the functional properties of particular vocal elements contained within the reservoir of vocal material available to them. The behavioural course of possible sensitization is now under study: such social experiences may serve to transmit to singers not the sounds, but the sense, of species-typical vocal signals.

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