Stereotyped and plastic song in adult indigo buntings, *Passerina cyanea*

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Abstract. The vocal behaviour of indigo buntings was studied by monitoring individual males in sound isolation boxes with a computer-assisted system. Yearlings and older adults sang ‘adult plastic’ song as well as stereotyped song. Distinguishing features of adult plastic song include: a larger syllable repertoire; variable syllable order; emphasis of the syllables that appear in the terminal sequence of stereotyped song; a high-frequency ‘S-note’ of variable morphology; calls; occasional production of syllables poorly formed, of intermediate form, or in combination; and low amplitude of delivery. Stereotyped and adult plastic songs were delivered in distinct bouts. Adult plastic songs of indigo buntings share many of the characteristics of early plastic songs of young birds. Several other extended-age learners also exhibit a complex, variable, and low amplitude adult singing behaviour, sometimes described as subsong, in addition to loud stereotyped song. Indigo buntings, and other species that can learn new songs as adults, may retain into adulthood developmental processes that in most species largely terminate with the onset of stereotyped song.

A dramatic event during song development in passerine birds is the rapid transition from juvenile plastic singing to a stereotyped, adult pattern (reviewed in Marler & Peters 1982a). This transition has important behavioural implications, including the ability to compete for mates and territories (e.g. McDonald 1989), as well as profound physiological implications, especially emancipation from auditory feedback (Konishi 1965a). Much of the vocal material present in juvenile singing is no longer expressed after the emergence of crystallized song (Marler & Peters 1982b). Whether this material is completely lost remains unclear, however, because birds often exhibit abbreviated states of variable singing as they re-establish adult song in subsequent springs (Marler 1956, 1970; Mulligan 1966).

The description of song development has been largely derived from work with age-dependent learners, birds that usually do not change their songs as adults. In birds that modify song repertoires as adults, there is evidence that the plastic song stage is extended into adulthood so that two distinct types of song are maintained (Rice & Thompson 1968; Williams & MacRoberts 1977; Feekes 1982). Such birds may require auditory feedback to maintain their songs (Nottebohm 1980). The similarities between juvenile and adult plastic song, and the possible role of adult plastic song in adult song learning have not been extensively analysed. Because a bird with vocal experience has developed an internal representation between vocal gesture and produced sound, and has established a repertoire of sounds, this may effect both the rate and process of subsequent song learning.

To address these issues, we chose to study indigo buntings. This species has been the focus of extensive studies examining the basic singing behaviour, song learning, adaptive significance and cultural evolution of song (Thompson 1972; Emlen 1972; Payne et al. 1981, 1988). In particular, yearlings (birds in their second calendar year of life) and, to a lesser extent, older adult birds sometimes engage in ‘song matching’ (Thompson 1970; Payne et al. 1981, 1988). During song matching a bird can completely change his stereotyped song to closely mimic the song of a neighbouring adult (Payne 1981). This leads to groups of 2–22 birds sharing the same song (Payne et al. 1981, 1988).

The singing of male indigo buntings has been classified into three major types of song. Territorial
adults sing relatively simple stereotyped songs (also called the ‘advertising’ song; Thompson 1968) and occasionally sing more complex, longer songs. These longer songs often incorporate extra syllable types beyond those expressed in stereotyped song. Indigo buntings also sing low amplitude, long songs with ‘squeaky’ characteristics during staged territorial encounters (Emlen 1972; Thompson 1972). Squeaky songs are difficult to record in the field and have not been extensively studied. Here, we report that isolated indigo buntings in the laboratory commonly and spontaneously sing an apparently more variable form of squeaky song. Our analysis indicates that these songs have many features in common with early plastic songs of critical period learners, and we term it ‘adult plastic’ song. We note the similarity between this and various secondary singing behaviour described for other species and discuss the possible role adult plastic song may play in the modification of adult stereotyped songs.

METHODS

Bird Collection

Two groups of indigo buntings were collected by mist nets. Twenty birds were collected in Mississippi during the October 1987 southward migration, and are termed 1987 birds. We collected ‘immature’ birds (a few months old), ‘yearlings’ (birds in their second calendar year of life), and ‘older adults’ (birds in their third calendar year or later). These age groups are easily distinguished on the basis of plumage, with yearlings (and October immatures) but not older adults, exhibiting some brown feathers among the wing (primary) coverts (see Payne 1982). Because buntings isolated during their first year can develop abnormal songs (Rice & Thompson 1968; Payne 1981), the 1987 birds were housed throughout the autumn of 1987 in individual wire cages measuring 45 x 35 x 45 cm. The cages were kept in a general aviary where the birds could hear each other, and interact with neighbours in adjacent cages separated by 5 cm. The general aviary, which could hold up to 75 cages, also housed zebra finches, Taeniopygia guttata, and white-throated sparrows, Zonotrichia albicollis, and was maintained on a natural Chicago photoperiod. From January to August of 1988, small groups of these birds were moved into sound attenuation booths (IAC no. AC-1, with interior dimensions of 57.5 x 40 x 35 cm) and their vocal behaviour was monitored (see below). By this time, birds caught as immatures were in their second calendar year and so were called yearlings.

Six additional males, four yearlings and two older adults, were collected on 6–8 June 1989 near Niles, Michigan. The songs of all 1989 birds were recorded in the field with standard techniques prior to capture (see Payne 1982). These birds were immediately returned to the laboratory, housed in individual sound isolation boxes and monitored. For 1989 birds, the first songs were recorded within as little as 3 days of capture.

All birds in IAC boxes were housed in ‘standard’ wire cages measuring 45 x 35 x 25 cm and maintained on a 16:8 h light:dark cycle. Any residual acoustic cross-talk between booths during loud vocalizations was masked by wide-band noise (-80 dB) broadcast into the room. Some birds sang spontaneously, others came into full song only after receiving testosterone implants. The 1987 birds, moved from shorter days (in the general aviary) to longer days (in IAC boxes), were photosensitive and presumably maximally sensitive to the effects of testosterone on singing rate, while the 1989 birds, which had already experienced long days in the field, were presumably less sensitive (Nowicki & Ball 1989). We did not analyse any songs for 1987 birds until a bird had achieved full stereotyped song whereas we recorded all songs for 1989 birds immediately after capture. After recording individually isolated 1987 birds, 10 social pairings were established throughout the spring/summer of 1988 by housing pairs in half-cages (a standard cage divided in half by a hardware cloth partition with 1 x 1 cm mesh) within IAC boxes. One pair of birds interacted via an acoustic link but remained physically isolated in separate IAC boxes. Social pairings were maintained up to several months, after which birds were isolated and recorded again. Some individuals were socially paired two or three times. In this paper, we report on the singing behaviour of isolated birds. Changes in song during social pairings will be reported in a subsequent paper.

Song Recording and Display

Data collection

Vocalizations were recorded by microphones (Realistic no. 33-2011) inside the sound boxes, processed locally (AC coupling and gain), and driven differentially over 30-m cables to the laboratory. In the laboratory, the signal was processed with four-
pole lowpass and highpass filters, achieving a frequency response of the electronics of $\pm 0.5$ dB from 1–9.5 kHz, and $-24$ dB at 500 Hz and 20 kHz. The incomplete high-frequency filtering resulted in some artefacts when the signals were digitized (see below). Calibration was via a 1-inch (2.5-cm) Bruel & Kjaer microphone (no. 4145), a Hewlett-Packard wave analyser (no. 3581C), and computer analysis. The frequency response including microphones was relatively flat, however the small size of the IAC enclosures and interfering objects (water bottles, etc.) produced some acoustic clutter and resonances at the frequencies of song. Intensity calibration was with a Bruel & Kjaer sound level calibrator (no. 4230). For amplitude estimates, we assumed a distance of 30 cm between the bird and microphone.

Recording sessions lasted from a few hours to many days, during which all songs a bird sang were recorded. Songs were automatically recorded directly into a computer (DEC VAX 3200) by analogue-to-digital conversion at 20 kHz per channel, with 12-bit resolution in 1988 (Data Translation DT-2751) and with 15-bit resolution in 1989 (Preston GMAD-2A). The computer system we developed to collect the data (GATHER) continuously analysed the zero-crossings and amplitudes of vocalizations from several birds simultaneously. ‘Raw’ digitized songs were converted to an indexed file format to permit rapid random access of any song, and files were saved on 2-3 Gb tapes (Exabyte 8200).

Veridical song identification was achieved for each bird by adjusting frequency, amplitude and duration criteria for each channel. Typically, all the songs of a bird were recorded while much less than 1% of the file entries comprised calls, cage noises or spurious events. With this system, birds that sing more capture a greater amount of the computer's resources, and in general we found we could simultaneously monitor as many as four channels (Data Translation) and later 10 channels (Preston). Our use of this complex facility was developed over time. Early recordings were made while the stability of the system was being improved. There was also some tendency to truncate the beginnings and endings of low-amplitude recordings. This problem was solved with judicious choice of recording criteria.

**Digital spectrograms**

Songs were displayed as digital spectrograms on a graphics workstation (DEC Vaxstation 3200) coupled to a vector processor (CSPI Mini-Map XL). Spectrograms were generated with standard digital signal processing techniques (Oppenheim & Schafer 1975). Depending on choice of analysis parameters, it was possible to create a display similar in physical size and quality to that produced by a Kay analog Sonagraph, or to display spectrograms with up to the full dynamic range of the converter (90 dB). The latter capability permitted visualization of faint sounds in a loud song. The use of the vector processor allowed sonagrams to be displayed approximately in real-time, facilitating these investigations. For publication, the digital sonographs were transferred to a Macintosh computer and imaged with a digital camera (Genigraphics).

It should be noted that digital techniques can produce aliasing effects when signals with significant power at frequencies surpassing half the rate of sampling (the Nyquist frequency) are not completely suppressed by anti-aliasing filters. Such signals appear on the spectrogram reflected through a line representing the Nyquist frequency (10 kHz for this study). The very high frequency ‘S-note’ (see Results) often appeared this way, as did higher-frequency harmonics of some syllables. Such reflections have a sense of frequency modulation opposite that of the unreflected signal. In the case of harmonics, these can appear as a seemingly non-harmonically related signal (Fig. 1) or, if the harmonic passes through the Nyquist frequency, can have an apparent discontinuity where none actually exists. These signal artefacts are well understood within the context of digital sampling theory (Oppenheim & Schafer 1975). Digital techniques can produce spectrograms somewhat different in appearance from analogue spectrograms, nevertheless, with a little practice, reading digital spectrograms posed no problem.

**Analysis of syllable sequences**

We developed a variety of techniques to identify interesting portions of the large primary data base (approximately 300 000 songs) rapidly. Prior to visual inspection and coding of spectrograms, all file entries were automatically analysed for basic descriptive parameters, including amplitude, duration and number of segments. A simple graphics program permitted the rapid display of these data for many songs simultaneously. These procedures permitted rapid scanning of songs and
were useful in helping to identify putative bouts of plastic singing.

After extracting descriptive statistics from songs, spectrograms were manually analysed for their syllabic content by visual inspection. In this paper, we use ‘note’ to refer to a continuous trace on the spectrogram, ‘syllable’ to refer to a group of one or more notes, and ‘phrase’ to refer to a group of one or more syllables (Konishi 1985). ‘Syllable’ is synonymous with the term ‘figure’ used in the bunting catalogue (Thomson 1970), and has been described as the consensus term (Shiovitz 1975). Most of the analyses reported here concentrate on the syllabic material of song.

Prior to a detailed analysis of a bird, we first examined exemplars of stereotyped and adult plastic songs (see Results) to identify all common syllable types and common sequences of phrases, and to produce printed copies of all syllable exemplars. For comprehensive analysis, we entered the syllable sequences as a text file into the computer. As analysis proceeded, occasionally we found new syllable types. Clear exemplars of normal bunting syllables (e.g. represented in Thompson’s (1970) bunting catalogue) were immediately added to the syllable repertoire for that bird. We coded other sounds of indistinct quality or ‘spurious’ events as a ‘?’. In some cases a drawing was made for future reference to compare with other uncertain or putative syllable types. If the figure occurred frequently or with little variation from exemplar to exemplar, it was added to the syllable repertoire. At the end of an analysis, all exemplars of syllable types present at low frequency were re-sonographed to check for coding errors. All authors participated in the coding effort and there was a conscious effort to maintain a uniform coding standard. In general, we found agreement in our coding schemes, and resolved remaining uncertainties by discussion.

Canonical sequence

To define stereotyped song for quantitative analysis, we generally followed the procedure of Payne et al. (1981). The phrase sequences of all songs were determined (i.e. the sequence ignoring repetition of a syllable type). From this set, the most common initial sequence was determined. Starting with the most common sequence, one or more additional preferred phrases could typically be identified. The longest common phrase sequence was termed the canonical sequence. Some birds had two or three variations of their stereotyped song (see Thompson 1972; Payne et al. 1981). In these cases, a group of canonical sequences was defined. Finally, some recordings suffered from technical problems and did not include low-amplitude syllables. These cases could be clearly identified, as the initial syllables of these songs were truncated or missing. In these cases, a missing initial phrase was ignored.

Similarity of syllable sequences

As one measure of similarity between syllable sequences, we calculated the Levenshtein distance between songs, using a simple dynamic programming procedure (Kruskal 1983). This technique assigns a cost to each insertion or deletion (‘indel’), and substitution of elements of two sequences drawn from a common alphabet (the bird’s syllable repertoire). We assigned a cost of 1 for indels and 2 for a substitution for all syllable types in all Levenshtein distance calculations in this paper.

RESULTS

We recorded 13 of the males captured in 1987. During the initial observational phase of the project in 1988, several distinct types of songs were identified, including stereotyped songs, plastic songs and some intermediate forms. Subsequently, some 1987 yearlings and older adults were socially paired, and their songs were analysed again after separation. We also analysed the songs of all six 1989 birds, which were recorded shortly after capture to control for any effects of long-term housing in the 1987 birds.

For quantitative analysis, we categorized an individual’s types of songs on the basis of the criteria Payne et al. (1981) used in their study of song matching between individuals. Two sequences that matched in order \( m \) syllable types of the first \( m + i \) syllables of either sequence were termed an \( m - i \) match. As with the study by Payne et al., \( 3 - 1 \) matches respected the song categories we subjectively observed. Stereotyped songs and intermediate song forms were defined as sequences matching the canonical sequence using the \( 3 - 1 \) criterion. We distinguished intermediate forms from stereotyped songs by identifying those \( 3 - 1 \) matches that (1) were longer than the canonical sequence, or (2) were not longer than the canonical sequence, but incorporated syllables not drawn from the canonical
Table I. Numbers of phrases and syllable types in stereotyped, intermediate and plastic songs of indigo buntings*

<table>
<thead>
<tr>
<th>I.D.</th>
<th>Male</th>
<th>Stereotyped</th>
<th>Intermediate</th>
<th>Plastic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Age†</td>
<td>N‡ Phrases§</td>
<td>Syllables§</td>
<td>N Phrases</td>
</tr>
<tr>
<td>002</td>
<td>AD/87</td>
<td>131 4-11</td>
<td>9-11</td>
<td>10 8-50</td>
</tr>
<tr>
<td>005</td>
<td>YR/87</td>
<td>2556 5-58</td>
<td>8-82</td>
<td>100 10-03</td>
</tr>
<tr>
<td>007</td>
<td>YR/87</td>
<td>2040 3-45</td>
<td>7-02</td>
<td>157 8-21</td>
</tr>
<tr>
<td>008</td>
<td>AD/87</td>
<td>1318 5-38</td>
<td>9-55</td>
<td>50 9-76</td>
</tr>
<tr>
<td>017</td>
<td>YR/89</td>
<td>24 5-46</td>
<td>7-67</td>
<td>93 8-76</td>
</tr>
<tr>
<td>018</td>
<td>AD/89</td>
<td>57 6-39</td>
<td>11-30</td>
<td>29 8-59a</td>
</tr>
<tr>
<td>019</td>
<td>YR/89</td>
<td>27 3-85</td>
<td>6-63</td>
<td>33 8-88</td>
</tr>
<tr>
<td>020</td>
<td>AD/89</td>
<td>255 3-95</td>
<td>6-04</td>
<td>36 8-83a</td>
</tr>
<tr>
<td>021</td>
<td>YR/89</td>
<td>794 5-34</td>
<td>7-45</td>
<td>52 11-98</td>
</tr>
<tr>
<td>022</td>
<td>YR/89</td>
<td>750 5-02</td>
<td>8-46</td>
<td>78 6-76</td>
</tr>
</tbody>
</table>

*Note that the number of song components increase from stereotyped to plastic to intermediate songs (except where marked by 'a') but variance increases from stereotyped to intermediate to plastic songs (except where marked by 'b').
†YR: yearling; AD: older adult; 87: 1987 bird; 89: 1989 bird.
‡Number of songs coded per bird.
§Mean number per song (variance appears directly below the mean).

sequence. All songs not meeting the 3–1 matching criterion were termed plastic songs. Infrequently, some individuals sang one to three call notes prior to a stereotyped song. These 'churrs' (Thompson & Rice 1970) and other calls were ignored in applying the 3–1 matching criterion. Indistinct figures (see below) were also ignored in applying the 3–1 criterion. Finally, sequences shorter than three syllable types were defined either as stereotyped (matching exactly) or as plastic (not matching).

For eight birds, at least one long recording session (10–24 h) was analysed, to assess the distribution of stereotyped and plastic singing. We also coded shorter segments of singing recorded throughout the spring, summer and autumn. A total of 7952 stereotyped songs, 638 intermediate forms and 6915 plastic songs across 10 intensively studied, isolated birds were coded and entered into a computer data base (Table I). We listened to 4605 stereotyped songs and plastic songs ($\bar{x} \pm sd = 512 \pm 192$, range = 362–770) for the other five yearlings and four older adults, and analysed the spectrograms of a subset of these songs. The data from these birds were used to estimate the syllabic composition of stereotyped and plastic songs, and generally conformed to the results from the 10 extensively analysed birds.

### Stereotyped Song

Stereotyped song exhibited the characteristics of indigo bunting song that have been reported previously (Thompson 1968, 1972; Emlen 1972; Payne et al. 1981). The stereotyped songs of four birds are shown in Fig. 1. (In cases where stereotyped song changed during the spring/summer of 1988 by addition of syllables drawn from the plastic repertoire (unpublished data), we describe the final song.) Most of the syllables constituting these songs are described in the Thompson/Payne catalogue of bunting syllables (Thompson 1970; Payne & Payne, unpublished results), and are coded by their catalogue number. The few new syllable types we identified presumably result from the fact that the 1987 birds (caught in Mississippi during migration) probably represent population(s) not previously
studied (see Shiovitz & Thompson 1970; Emlen 1972). For 11 yearlings the canonical sequence had a mean (±se) of 6.6±0.5 (range 4–10) syllable types, while for eight older adults the canonical sequence had 7.8±0.4 (range 7–10) syllable types. The difference between the two groups is not significant (t = 1.711, df = 17, P > 0.1). These syllable counts are comparable to field observations (Thompson 1970; Emlen 1972). Indeed, the stereotyped songs we recorded in the laboratory closely matched in syllable and phrase sequence the songs 1989 birds delivered in the field, although we did note occasional extra terminal syllables identified as part of the canonical sequence, and occasional faint introductory whistles difficult to identify in the field recordings. It should be noted that one bird, IB017, sang only plastic song in the laboratory (see below). Although we identified a canonical sequence for this bird for purposes of analysis, he sang ‘stereotyped’ song 24 times while singing plastic song 577 times (Table I). The canonical sequence we identified was different from the stereotyped song recorded in the field, and for this and other reasons (see below) it is likely that we never recorded stereotyped song from this bird in the laboratory.

The phrase sequences of stereotyped songs were not entirely fixed (Thompson 1972). Two birds varied the terminal phrase, a third chose one of two introductory whistles, another occasionally inserted a second introductory whistle, and a fifth bird occasionally deleted two phrases from the middle of his song. Such variation did not significantly alter the rest of the motor pattern. For example, during a 10-h recording session, of 1164 songs starting with the sequence 1-E, yearling IB005 sang 988 songs with the sequence 1-E-46'-G-24-92-40 but only 79 songs with the sequence 1-E-46'-G-24-92-40-29. (The numbers refer to syllables in the bunting catalogue, letters refer to the syllables not in the catalogue; E was an isolate-like sound, see Payne 1981.) During the same period, of 243 songs starting with the sequence 1-46' (i.e. with the E phrase omitted), IB005 sang 231 1-46'-G-24-92-40 songs but only 10 1-46'-G-24-92-40-29 songs. That is, songs typically ending with syllable 40 but occasionally appending syllable 29 were noted for both the 1-E and 1-46' variants.

Stereotyped song was common in all 1987 birds, although some birds sang only sporadically and incompletely until receiving testosterone. In all cases, incomplete songs and plastic songs were recorded on days before birds came into full stereotyped song. All 1989 birds were singing stereotyped song when first recorded in the field. After being brought into the laboratory, some sang long bouts of stereotyped songs within a few days to 2 weeks, while others sang stereotyped songs less frequently. Nevertheless, all 1989 birds sang considerable plastic song within the first few days to a week after capture. Since most of the 1989 songs we analysed were delivered shortly after capture, relatively few stereotyped songs were coded for some 1989 birds (Table I). During a transition period of 2–8 weeks, the amount of stereotyped singing for some 1989 birds increased to normal levels. (In contrast, IB017 never sang bouts of stereotyped song in the laboratory, even when we recorded him 2 months after capture.) A peculiar aspect of the adjustment to the laboratory was that during the time birds normally sang stereotyped song (e.g. at daybreak), birds in transition sang very little. Thus, continuous recordings of these birds included periods of concentrated plastic singing in the afternoon, and striking gaps in the morning hours with few (<10) or no songs whatsoever. Nevertheless, the few songs sung during the morning hours were mostly stereotyped songs. Similar gaps in stereotyped singing occurred in several 1987 birds as testosterone implants were exhausted. In this sense, plastic and stereotyped singing were differentially labile.

Intermediate Forms of Song

As well as a clearly defined stereotyped song, birds occasionally sang intermediate forms (638 or 4.1% of all songs). None of these were common (Table I), but they were observed in all birds we analysed extensively. By definition, intermediate songs could either be shorter or longer than the canonical sequence. Shorter songs were sung occasionally (30.8% of intermediate songs), and did not occur in bouts. We defined a bout as comprising a consecutive series of songs where more than 75% are of one type. Most of the intermediate songs occurring within a bout of stereotyped singing were of the short form, however the majority of the short intermediate songs (74.1%) did not occur within a bout of stereotyped singing. Short intermediate songs within a bout of stereotyped songs could represent an occasional ‘random’ variation in choice of syllable type for stereotyped song.

Long intermediate songs were more common (69.1% of intermediate forms). Most long songs
Figure 1. Stereotyped songs of four indigo buntings. IB005 (yearling) and IB008 (older adult) are 1987 birds, IB020 (older adult) and IB021 (yearling) are 1989 birds. Syllables are numbered according to the bunting syllable catalogue. Prime symbol (e.g. 46') indicates a partial match with the catalogue. Letters (B, E) are syllables not found in the catalogue. Some of the 'background noise' on the spectrogram for IB020 is marked (arrowheads). These spurious signals result from aliasing due to incomplete filtering of high frequencies prior to digitization, and are not part of the actual vocal signal (see Methods).

(65.0% of intermediate forms) included syllable types not drawn from the canonical sequence (Emlen 1972; Thompson 1972). Long songs incorporated the introductory syllables only in the initial segment of the song. Often, the initial phrases were sung at high amplitude whereas the terminal syllables were sung at low amplitude (see Shiovitz 1975). The terminal syllables occasionally included an 'S-note' (see below) normally found in plastic song. Of 441 long intermediate songs, 53.7% (237) were delivered in bouts of two or more (maximum, 17). These bouts of long songs were most common at the boundary between bouts of stereotyped and plastic songs (see below), and may represent a transitional state.

**Adult Plastic Song**

In the following descriptions, the term 'adult plastic' song or 'plastic' song refers to the plastic sequences of both yearling and older males. Except where noted, we did not find differences between the two age groups. Plastic song sounds 'squeaky'
because it incorporates high frequency notes (Thompson 1972) that are louder than song syllables. We commonly observed these highly variable notes of 8–12 kHz in the plastic song of all birds, and term them S-notes. Field recordings of squeaky songs are relatively uncommon, in part because they are delivered at such low amplitude (Emlen 1972). Such songs have therefore only been described briefly and in qualitative terms.

In the laboratory, all birds sang adult plastic songs (Fig. 2). Many features of adult plastic song distinguish it from other types of song. One such characteristic is the common incorporation of S-notes: birds incorporated a total of 6329 S-notes in 43.6% (3014) of all adult plastic songs, whereas 280 S-notes were incorporated in 25.3% (185) of all intermediate songs. Excluding IB017, whose stereotyped song was never identified in the laboratory, S-notes were not part of the canonical sequences defined for any bird, and only 4 of 7928 stereotyped songs incorporated an S-note (as the initial note). By the 3–1 matching criterion, songs with S-notes in positions 1–4 could be classified as stereotyped even if S-notes were not part of the canonical sequence. (Curiously, by the 3–1 matching criterion, the single published spectrogram of a squeaky song (Thompson 1972, Fig. 5) shows a stereotyped song with S-notes; see Discussion.) Calls were also common to the plastic songs of all birds, including ‘adult cheets’, ‘churrs’, ‘adult chips’ and ‘teeps’ (Thompson & Rice 1970). Plastic songs also exhibit variability in the temporal pattern and duration. An example of this variability is seen in four consecutive plastic songs of IB007 (Fig. 3). Note that plastic sequences vary in duration and syllable order from song to song, and incorporate S-notes. Stereotyped songs often start with syllables comprising a collection of one to three short whistles (e.g. Fig. 1), thought to be a species-specific ‘sign-on’ (Shiovitz 1975). Plastic songs did not exhibit such a tendency.

When singing stereotyped song, birds often assumed an erect posture, tilted their heads back, and opened their bills wide. In contrast, when singing plastic song, birds typically assumed a crouch-fluff posture, and their bills appeared to be closed. These birds did not appear to be singing except for slight movement of the breast feathers.

**Phrase sequences**

Adult plastic songs tended to be intermediate between stereotyped songs and intermediate song forms in number of syllables and phrases, but plastic songs tended to have the greatest variability in these measures (Table 1). The variability in the phrase order of plastic song was exhibited on a song by song basis. We measured this variability by calculating the Levenshtein distance (see Methods), or dissimilarity, in phrase sequence between consecutive pairs of songs of the same type. We ignored S-notes in this calculation. (Inclusion of S-notes in the analysis would have increased the variability of plastic song relative to stereotyped song.) For the five recording sessions with both plastic and stereotyped song that we checked, most stereotyped songs had identical \( L = 0 \) or nearly identical \( L = 1 \) phrase sequences (Fig. 4). Indeed, as with field observations (R. B. Payne, personal communication) a more stringent matching criterion than the 3–1 criterion we used would have captured the majority of stereotyped songs. In contrast, the most common difference in phrase sequence of consecutive plastic songs was five insertions/deletions \( L = 5 \). For yearling IB005, for example, the average plastic song incorporated 10-09 phrases but there were an average of 9-0 insertions/deletions between consecutive plastic songs (Fig. 4). Thus, the sequence of phrases was variable on a song by song basis. This difference between stereotyped and plastic song was highly significant for IB005 \( \chi^2 = 1167, d.f. = 6, P < 0.001 \), and for four other birds tested at the same level of significance (Fig. 4).

One common feature of the sequence of syllables in plastic song was the incorporation of S-notes between phrases (Thompson 1972). There were a total of 21488 doublets (a sequence of two syllables of the same type) across all plastic songs, yet S-notes occurred between two syllables of the same type in only 43 cases. Furthermore, only 48 of 6329 S-notes were delivered as a doublet. Thus, single S-notes reliably served as an inter-phrase marker.

Individual birds exhibited different organizations of their plastic songs. In one striking example, the phrases in the plastic songs of older adult IB018 were more commonly delivered in reverse order to the canonical sequence than in any other sequence, 285 of 480 songs for one recording session. Other birds exhibited other idiosyncratic features of plastic song phrase sequences, although no other bird was so attracted to singing his song in reverse.

**Phrase transitions**

There was a clear preference for certain sequences of phrases in plastic song. We analysed
Figure 2. Plastic songs of the four buntings of Fig. 1. Comparing with Fig. 1, note the different sequential order of syllables, and high-frequency S-notes (S). Ts, tseep call; Ch, chip call. Combinations with S-notes are denoted by syllable number + S (e.g. 97+S).
Figure 3. Four consecutive plastic songs from one bird, year [BL07]. Note the duration and sequential order of syllable change from song to song.
Figure 4. Distribution of Levenshtein distances between consecutive stereotyped songs (left ordinate; ○) and plastic songs (right ordinate; ▲) for one bird (IB005, a), and summed for five birds (IB005, IB007, IB008, IB021, IB022, b). The Levenshtein distance, \( L \), a measure of the similarity between two sequences, was calculated based on the phrase sequence of the songs. Plastic and stereotyped songs were distinguished based on the \( 3 - I \) matching criterion (see text).

the frequency of transition between phrases in the stereotyped and plastic songs for 13 recording sessions (eight birds) that included substantial plastic and stereotyped singing. Four of these birds were older adults, three were yearlings and one (IB007) was recorded both as a yearling and as an older adult. The average (+SE) number of songs per recording session was 984 ± 180 (range = 248–2507). For stereotyped song, by definition, transitions early in the song were the most favoured. Transitions in stereotyped song not derived from the canonical sequence were delivered very infrequently (1.3%, 347/27 083). In 11 of 13 recording sessions, many favoured phrase transitions of plastic song also derived from the canonical sequence. (In the other two cases, most or all of the transitions of plastic song were non-canonical transitions.) For example, during one recording session a total of 10 canonical transitions occurred 419 times (Fig. 5a). Compared to 89.4 expected canonical transitions based on the distribution of phrases, this difference was highly significant (\( \chi^2 = 3011, df = 9, P < 0.001 \)).

Canonical transitions in plastic song were drawn primarily from the terminal parts of the canonical sequence. For example, during one recording session the most common canonical transition represented in the plastic song of IB005 was the sixth transition, syllables 92–40 (Fig. 5a). (Since this bird occasionally dropped the second syllable of the canonical sequence, occasionally this transition was
Figure 5. Number of phrase transitions for stereotyped song (□), and plastic song (■). (a) for IB005, each pair of letters and numbers indicates the phrase transition of the canonical sequence, either beginning with the phrase I-E and ending with 20-44, or beginning with the phrase I-46' and ending with 40-29 (omitting terminal phrases 29-20 and 20-44). Note the most common canonical transition of plastic song (92-40) occurs late in the canonical sequence. The canonical sequence is marked by a solid bar underneath the graph. Note also many phrase transitions favoured in plastic song are not derived from the canonical sequence. E: a syllable not found in the bunting catalogue; Ts: tseep call; Ch: chip call. (b) Sum of phrase transitions for seven birds (IB005, IB007, IB008, IB018, IB020, IB021, IB022), as a function of the position of the transition (i.e. 1: first transition; 2: second transition, etc.).

The fifth transition. For all birds, the most favoured canonical transition of plastic song occurred late in the canonical sequence (mean transition ± SE = 5.9 ± 0.5; Fig. 5b). We considered the possibility that this result was an artefact of low amplitude initial syllables of plastic song escaping detection by the computer. This is unlikely because (1) many syllables underrepresented in plastic song were syllables
normally delivered at the full amplitude of plastic song, and (2) there were relatively few spectrograms starting with partial notes. In this regard it is noteworthy that intermediate songs, which are louder than plastic songs, start with introductory notes but do not repeat them in subsequent segments of the song.

Many favoured transitions in plastic song were not drawn from the canonical sequence. For example, the most favoured transition of plastic song not derived from the canonical sequence was the most favoured overall in five recording sessions (three birds), and was the overall second or third most favoured transition in another seven recording sessions (six birds). Over all 13 recording sessions, there were 94 transitions drawn from the canonical sequence. Overall, the number of occurrences of the 94 most favoured transitions not in the canonical sequence (6369) was roughly the same as the number of occurrences of transitions drawn from the canonical sequence (6476). Of all non-canonical transitions of plastic song, 58% included at least one novel syllable not found in stereotyped song, whereas the rest were rearrangements of syllables from stereotyped song. Thus, the majority of transitions of plastic song included at least one syllable drawn from the stereotyped song (71%, 9142/12845). Finally, considering favoured transitions not represented in the canonical sequence, there was almost a complete dichotomy between plastic and stereotyped songs. The 347 occurrences of such transitions from stereotyped song comprised 54 different transition types. Only seven of these transition types were the same as one of the 94 most-favoured transition types of plastic song not drawn from the canonical sequence. In all these respects, plastic and stereotyped songs represent different motor patterns.

The analysis of transitions in plastic song can also serve as an independent test of whether the procedure for determining the canonical sequence identified the complete canonical sequence. For the most favoured transition of plastic song not drawn from the canonical sequence, this transition could logically be an extension of the canonical sequence in only two of the eight birds analysed. Even extending the analysis to the first four most-favoured transitions of plastic song not drawn from the canonical sequence for each bird, only five transitions (four birds) could logically be an extension of the canonical sequence. Two of these were mutually exclusive. Thus, the analysis of plastic song transitions provides support for the procedure used to identify the canonical sequence.

**Song amplitude**

Plastic songs were almost always delivered at low amplitude, whereas stereotyped songs were delivered both at low and high amplitude. Typically, high-amplitude stereotyped song was delivered in the morning hours and lower amplitude song throughout the day. For example, in 1005 stereotyped and plastic songs recorded for yearling IB022 in a 24-h period, almost all plastic songs were below 60 dB re. 20 μPa (Fig. 6). The mean amplitude of plastic song was approximately 40–50 dB lower than stereotyped song. These large differences between the amplitude of plastic and stereotyped songs were seen in all birds. Furthermore, S-notes were typically 10–20 dB louder than syllables of plastic song. Thus, the amplitude difference between syllables of plastic and stereotyped song is actually somewhat greater. Such soft sounds would be extremely difficult to record in the field.

**Song bouts**

Each individual tended to exhibit a given sort of singing behaviour at a predictable time of the day. Almost all birds began singing at first light with loud stereotyped songs, and sang plastic songs late in the day (12–16 h). Typically, plastic singing and stereotyped singing occurred in distinct bouts. We quantified singing in bouts by analysing the 13 long recording sessions that contained both plastic and stereotyped songs. In all cases, birds did not intersperse stereotyped and plastic songs (Fig. 7). For 665 plastic songs and 4298 stereotyped songs, a single plastic song was delivered between two stereotyped songs in only 32 cases. More commonly, songs of intermediate forms were interspersed with plastic songs at the boundaries between plastic and stereotyped singing. In the field, indigo buntings sing a series of stereotyped songs separated by several minutes of silence (about 24 songs per bout on average), although this depends on several factors (Thompson 1972). The highest rates of stereotyped singing in our isolated birds (151 songs/h, N = 5) is slightly lower than the highest rates observed in the field (179 songs/h, N = 3), which was for unmated birds (Thompson 1972). Birds sing essentially continuously at these highest rates.
The relative amounts and daily timing of bouts of stereotyped and plastic singing varied considerably between individuals and over long periods of time (see Thompson 1972). Most individuals, however, produced sustained stereotyped singing and established a clear pattern of singing in bouts over many days (Thompson 1972). To demonstrate this without manual analysis of thousands of songs, a 'variability' index was devised: the absolute value of the difference in duration between the current and previous song divided by the root-mean squared (RMS) amplitude of the current song. This ratio tends to be larger for bouts of plastic singing. On the basis of this measure we could identify a pattern of bouts of stable singing and bouts of variable singing over many days (Fig. 8). We confirmed that bouts of stable and variable singing corresponded to stereotyped and plastic singing, respectively, by visual analysis of randomly chosen songs. This pattern remained constant over at least 18 days (not shown).

Syllabic material

The core material of plastic song comprised normal bunting syllables found in the Thompson/Payne bunting syllable catalogue, as well as S-notes and calls. Not counting S-notes or calls, yearlings exhibited a mean (±se) of 11.9 ± 1.4 (range 7–21) syllables in plastic song while older adults exhibited 10.1 ± 0.7 (range 7–12) syllables in plastic song. The difference between the two groups is not significant (t = 0.597, df = 17, P > 0.2).

No syllable type was unique to stereotyped song or intermediate forms, but many syllable types were either unique or expressed much more frequently in plastic songs. For example, of 572 songs that older adult IB008 sang on 2 days in April 1988, a total of 4660 syllables and a canonical sequence of 10 syllable types were identified. On the basis of a 3 – 1 match, this material was separated into 459 stereotyped, 98 plastic and 15 intermediate songs. These accounted for 3685, 735 and 240 syllables, respectively. The 98 plastic songs expressed four extra syllable types beyond the canonical sequence, two calls and two normal bunting syllables. One of those syllables (no. 27, see Fig. 2) was the most common syllable in plastic song (sung 102 times), but was never sung in any stereotyped or intermediate song. We also coded a full 24 h of IB008's singing 18 months later and obtained similar results. At that time, 859 stereotyped songs were sung with only one no. 27 syllable, 35 intermediate songs incorporated 26 no. 27 syllables, while in 33 plastic songs 43 no. 27 syllables were produced. Thus, IB008 maintained syllable no. 27 in plastic and intermediate songs while expressing it very infrequently or not at all in his stereotyped song. Nevertheless, this was a
normal bunting syllable based on the bunting syllable catalogue, and was copied by a socially paired yearling (unpublished results).

Whereas some of the extra syllables of plastic song were expressed frequently, others were sung quite infrequently. These syllables met our criteria for an independent syllable type, including having a distinct morphology, occurring multiple times, and being represented in the bunting syllable catalogue. For example, two yearlings had unusually large syllable repertoires (23 syllable types). The complete repertoire for one, IB017, is shown in Fig. 9a, and the frequency of occurrence of the syllables in Fig. 9b. This repertoire derives from analysis of 32 h of recordings made 3 days after capturing the bird. Note that most of the repertoire comprises normal bunting syllables, most of which were not identified in the stereotyped songs recorded in the field or the few songs matching the canonical sequence recorded in the laboratory.

Variable syllables and indistinct figures

During plastic singing, syllables were often delivered with variable morphology. There was a clear difference in the variability of these syllables comparing yearlings and older adults, with yearlings' plastic songs exhibiting greater variation. As well as variation in morphology, yearlings' plastic syllables exhibited two-voice notes, as evidenced by non-harmonically related components (Greenewalt 1968). These were more common in plastic than stereotyped song, but also occurred in the latter. Older adults also exhibited some two-voiced notes, although it was our impression that these were less
Figure 8. Relative stability of singing in bouts. Each box represents 1 day’s recordings for older adult IB018 (14 March 1990 to 19 March 1990). In each box, the upper plot (■, left ordinate) is the number of songs per 30 min, and the lower plot (○, right ordinate) represents the average variability index over 30 min. Daybreak at 0830 hours (arrows on abscissa), lights off at 0030 hours. Note the variability index is low for songs early in the day, and is higher for songs later in the day. These songs were confirmed to be stereotyped and plastic songs, respectively (see text). Some spurious points occur when the variability index is averaged over only a few songs (arrows within boxes).

frequent. Elucidation of these differences awaits a quantitative analysis of the syllable morphology.

In many other cases, plastic song figures had indistinct and variable morphology, and could not
Figure 9. (a) Complete syllable repertoire for 1B017, an example of a large (23 syllable) plastic repertoire. The bird had only eight syllables in his canonical sequence (5-59'-20-40-24-T-92-12). The stereotyped song identified in field recordings was (5-66-59'-29; see text). Syllable 97 was sung independently, as part of syllable 92, and also in conjunction with S-notes (the conjunction labeled syllable T, not shown). Ts: tseep call; M, N, P: not found in bunting catalogue. (b) Frequency of occurrence of the syllables of (a). All syllables were produced multiple times.

be assigned to a known syllable type. We coded such figures as indistinct ("?"). Indistinct figures were produced by all birds during plastic singing, but were almost absent from stereotyped song. We coded a total of 4191 indistinct figures in plastic song across all birds, but only 28 indistinct figures for stereotyped songs. Because indistinct figures were ignored for the purpose of assigning song types, this distribution does not result from the definition of stereotyped song per se.

There was a weak tendency for indistinct figures to be more common in the plastic songs of yearlings.
than older birds. For the two 1989 older adults (IB018 and IB020) only 6.9 and 6.7% of their plastic songs contained at least one indistinct figure, whereas for the four 1989 yearlings this figure varied from 15.1 to 32.6%. During recordings made in February 1988, the yearling IB005 sang 811 indistinct figures in 1634 plastic songs; in July 1988, he sang 403 indistinct figures in 620 plastic songs and, in October 1988, he sang 18 indistinct figures in 180 plastic songs. A similar trend was seen in the yearling IB007, analysed from March 1988 to September 1989. Thus, there was a lower percentage of plastic songs incorporating indistinct figures as birds grew older.

We considered the possibility that indistinct figures were much more common in plastic songs because of limitations of Fourier techniques to resolve signals near to the noise floor of the data collection system. This explanation seems unlikely, because (1) for the Fourier components of the frequencies of interest, the signals were still 10-100 times higher than the noise level, and (2) the great majority of syllables of plastic song (94%, 66396/70587), were delivered at the same ranges of amplitudes but were easy to identify. Furthermore, if this result reflects biological limitations when producing low-amplitude sounds, one would expect similar variation with low-amplitude stereotyped songs, but such variation was not observed. Thus, the indistinct figures of plastic song represent a true variable component not represented in stereotyped song.

Syllable combinations

Infrequently, birds combined two syllable types into a novel form, sometimes truncating the leading syllable (e.g. Fig. 2). We coded a total of 162 occurrences of syllable combinations across all birds, 117 in plastic song, 23 in stereotyped song and 22 in songs of intermediate form. (We started to record this phenomenon late in our song coding effort, hence the frequency of occurrence reported here is possibly a significant underestimate.) S-notes were found commonly in combination with other syllables (95 times). Other combinations included but were not limited to syllables of the canonical sequence. Without exception, all combinations we identified were between syllables of different type. Combination of existing syllables may be a potent mechanism for generating novel syllables.

DISCUSSION

The Singing Behaviour of Indigo Buntings

Most attributes of the singing behaviour of indigo buntings described here are consistent with that which has been previously reported (Thompson 1968, 1972; Emlen 1972). For stereotyped song, these attributes include the number of syllables and phrases, the degree of stereotypy from song to song, the delivery of high-amplitude stereotyped song typically starting at daybreak, occasional bouts of stereotyped song delivered at lower amplitude, and variable numbers of terminal syllables. The similarity between our recordings and the field data demonstrate that stereotyped singing was not fundamentally affected by laboratory housing, although some differences in the variability of phrase sequences (Payne et al. 1981) and bout organization (Thompson 1972) may have occurred. There was considerable individual variation in the process of adjusting to the laboratory environment.

The relationship between our adult plastic song and Thompson's (1968, 1972) squeaky song or Emlen's (1972) soft and long songs is less clear. Emlen (1972, page 155) reported that compared to the advertisement song, soft song is 'the same song but at a much reduced volume', and that 'a bunting may add high frequency “squeak” notes to his normal song'. Thompson (1972, page 44) reported that indigo buntings sing 'a squeaky song in which squeaks of about 9 kHz are inserted between figure pairs of the usual song pattern', and shows the only previously published sonograph of a bunting song with S-notes. Thompson (1972) also gave a description of the syllable sequence of a squeak song. The descriptions of both authors are suggestive of our intermediate song, a song that starts with the complete (or almost complete) stereotyped pattern but is then extended by addition of extra syllables and/or modified by addition of S-notes. In contrast, the adult plastic song we commonly observed had very different characteristics from advertising song, especially the great variability in syllable pattern, and would not be described as the same song.

Previous studies indicate that long and squeaky songs are stimulated during territorial encounters
These songs are interpreted to represent a conflicting or ambivalent motivational state (Emlen 1972). The latter interpretation is consistent with our observation that acoustically isolated birds sing adult plastic song relatively frequently. Similarly, if stereotyped song is associated with a lack of conflicting drives or a predominance of aggression, this could explain why birds recently caged (and uncertain of their environment) sing plastic but not stereotyped songs. Although there are no published reports that, in the field, song with S-notes is delivered at times other than staged territorial encounters, several attributes of adult plastic song would make it difficult to detect in the field. Emlen (1972) reported that soft song cannot be heard in the field at distances of greater than approximately 8 m. The adult plastic songs we recorded were often delivered at very low amplitude, and could probably not be heard in the field without telemetry except under the best of circumstances. Furthermore, the normal song posture is not adopted when delivering plastic songs (see also Emlen 1972). If, as we hypothesize below, one role for low-amplitude plastic song is learning to sing, it may also be delivered while birds are not conspicuous.

Classification schemes such as stereotyped, intermediate and plastic songs should be approached with caution, because they may force categories where none exist. Indeed, intermediate song forms have characteristics of stereotyped song (starting with the canonical sequence delivered at high amplitude) and plastic song (additional phrases of lower amplitude and the inclusion of S-notes). Nevertheless, most stereotyped songs are largely invariant, repeated entities and are well separated in time, whereas plastic songs are variable entities with much more variable inter-song intervals. A simple criterion, such as a 3 – 1 match, split 95.9% of songs into plastic and stereotyped song categories. Although we separated song categories on the basis of the first four phrases and not by the presence of absence of S-notes, we found that S-notes were rarely included in stereotyped songs. Other analyses independent of the initial phrase sequence, such as the variability index that combined song duration and amplitude, could identify distinct groups of songs regularly sung at different times of the day, although whether these were completely isomorphic with the stereotyped/plastic song distinction was not assessed quantitatively. We did note some variability in the "stereotyped" songs of many individuals; this potentially important information was lost in our binary classification of these songs.

**Indigo Bunting Adult Plastic Songs Share Characteristics with Juvenile Plastic Songs of Other Species**

A comparison of adult plastic song of indigo buntings with the plastic song of young birds can give insight into the functional role of adult plastic song. Song development in juvenile birds is characterized by several distinct stages. The earliest stage (subsong) is thought to involve learning basic syringeal coordination, whereas subsequently learned material is rehearsed in plastic song (Marler 1976; Marler & Peters 1982a). Deafening experiments (Konishi 1964, 1965a, b; Nottebohm 1968) and quantitative analysis applied to syllable morphology (Clark et al. 1987) demonstrate distinct changes across developmental stages. In the earliest stage of plastic song in the swamp sparrow, *Melospiza georgiana*, syllables have variable morphology and are delivered in trills, while songs are long and have a variable pattern of syllable order (Marler & Peters 1982c). Earlier stages exhibit indistinct syllables and later stages exhibit greater order in songs.

The adult plastic song of indigo buntings shares characteristics with this early plastic song stage described by Marler & Peters (1982b), with occasional adult bunting songs exhibiting characteristics of the preceding subplastic phase. Indigo bunting adult plastic songs exhibit syllables with normal morphology, but also syllables with variable morphology, as well as other sounds either poorly formed and/or not conforming to a clear pattern. Presumably, these latter sounds are rudimentary syllables and/or notes. Many of the syllables of adult plastic song are not used in stereotyped song, and in an extended sense this is similar to juvenile plastic song. The syllables of indigo bunting adult plastic song are typically delivered in groups, while the overall songs are highly variable in temporal pattern, and are often very long. Occasionally, some bunting plastic songs would probably be classified as subplastic, especially when songs are laden with indistinct figures or two-voiced notes. We have rarely observed any adult singing that was suggestive of subsong, however. This is consistent with the hypothesis that adult song learning requires rehearsal of new material but not relearning of basic motor
coordination. When singing plastic song, indigo buntings assume a crouch-fluff posture with closed bills reminiscent of developmental subsong in juveniles of other species (Armstrong 1973). In indigo buntings this posture has yet to be quantitatively assessed. Young indigo buntings pass through subsong and plastic song stages (Rice & Thompson 1968; Payne 1981). A few days before the first stereotyped singing is recorded, birds sing plastic songs that incorporate S-notes, based on published figures (Rice & Thompson 1968; Payne 1981). Several aspects remain unclear, however. S-notes are not delivered as a call (Thompson & Rice 1970), and their ontogeny is uncertain. Furthermore, it is unclear whether the plastic songs Thompson & Rice (1970) recorded from immatures were maintained into adulthood. In the swamp sparrow, there is a dramatic cessation of plastic singing at the time of song crystallization (Marler & Peters 1982b). The functions of adult plastic song are poorly understood. In previous studies a communicative explanation for adult subsong has been suggested because it is often delivered in close proximity to another individual (e.g. Bertram 1970; Emlen 1972; Armstrong 1973; Feekes 1982; Adret-Hausberger 1989). One of the intriguing attributes of bunting plastic song is the use of S-notes. Similar high-frequency notes are incorporated into the secondary singing behaviour of other species (Marler et al. 1962; Bertram 1970; Mundinger 1975). These high-frequency notes probably serve a communicative function but it is also possible that they somehow facilitate or are a by-product of vocal plasticity. Although adult plastic song may have generally a communicative function, this does not preclude other functions, in particular vocal learning in adults. For species in which males make significant changes in their song repertoires from year to year, plastic song may play a role in these changes (e.g. Nottebohm et al. 1986).

Aspects of adult plastic song in indigo buntings suggest it as a mechanism for vocal modification. These include the variability of plastic song, both at the level of syllable sequence and morphology. In many species, including indigo buntings, birds most frequently modify their stereotyped songs within a song bout by deleting or adding terminal syllables. The emphasis in bunting plastic song on the terminal syllables of the canonical sequence appears a further expression of this plasticity. The existence of two-voiced notes in plastic song emphasizes that vocal plasticity requires the ability to modify lateral interactions. In the developmental
subsang of juveniles and immatures, vocal plasticity is normally expressed at low amplitude prior to loud stereotyped song (e.g. Armstrong 1973; Marler & Peters 1982a); the low amplitude of bunting adult plastic song and secondary singing in other species is therefore appropriate for plasticity. Indeed, in a few cases we have observed indigo buntings modify their stereotyped songs by modifying their plastic song syllable repertoire and by transferring plastic song syllables into stereotyped song (unpublished data). We suggest that the adult plastic song in indigo buntings, and by logical extension the secondary, low amplitude and apparently plastic singing behaviour in other extended-age and open-ended learners, may play a role in adult song modification.

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