IBIS 138: 172–176

Different singing styles in mated and unmated Reed Buntings *Emberiza schoeniclus*

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Ewin described two singing styles, "rapid" and "slow", in the Reed Bunting *Emberiza schoeniclus*. My research has demonstrated that the prevalence of song styles is related to male mating status. Songs of mated and unmated males differed in the interval structure, number of syllables per song, number of frequency modulations per syllable and number of introductory syllables. Since both singing styles are uttered at the same intensity, it is not likely that they are parts of a continuous range and it is justified to treat them as two different song categories. After losing their mate, males sang like unpaired males and therefore a learning effect can be excluded. Both singing styles were directed to females, the slow one probably only to the mate. The use of these singing styles as a means of territory or mate defence cannot be excluded, but, if so used, it would seem to be of minor significance.

Many songbirds use different songs in different situations. Mate attraction and territory defence are seen as the main functions of song (e.g. Thorpe 1961) and also as the origin of different singing categories, e.g. in the Great Reed Warbler *Acrocephalus arundinaceus* (Catchpole 1983) or in many species of North American warblers of the subfamily Parulinae (Spector 1992).

In 1976 J.P. Ewin (unpubl. PhD thesis, University of London) described two different singing styles in the Reed Bunting *Emberiza schoeniclus*. Because of the different lengths of the intervals within the songs, he distinguished "rapid" and "slow" singers. Rapid refers to short and slow to long intrasong intervals. These differences appeared stable over time and therefore excluded change in motivation as a satisfactory explanation. Ewin suggested that this dichotomy originated in a learning mistake by birds reared near a Chaffinch *Fringilla coelobs* population at his study site.

During my research I was also confronted with these strikingly different songs. Since I was monitoring the breeding success of individual birds, I soon recognized a connection between the breeding stage and the song. In three cases, paired males switched from a slow to a rapid singing style after they lost their mates, thereby discrediting the explanation of a learning effect for the two categories.

The aims of this paper are to justify the differentiation of the two singing styles and to examine if it is possible to distinguish paired and unpaired males by song. I discuss the functional significance of this singing dichotomy in the context of the breeding behaviour of the Reed Bunting. Here a recent discovery by Dixon *et al.* (1994) deserves special attention: 55% of the young in a group of Reed Buntings studied in England were the result of extra-pair copulations. Because of the importance of sperm competition I tested two hypotheses proposed by Møller (1988) to explain song function after pairing in the Yellowhammer *Emberiza citrinella*. The first, the male deterrence hypothesis, suggests that song is used to deter potential intruders during the fertile period of the females to prohibit extra-pair copulations. It predicts that song activity peaks during the fertile period (see also Birkhead & Møller 1992). The second, the female attraction hypothesis, considers that song is used to attract females of neighbouring pairs; here males should sing more outside the fertile period of their mates.

Females of the Reed Bunting can recognize their mates by song alone (Nemeth 1994). The relevance of this finding is also discussed.

STUDY AREA AND METHODS

The study was carried out during 1990 and 1991 on 3 ha at the dry edge of the reed belt of Lake Neusiedl near Illmitz (47°46′N, 16°46′E) in eastern Austria.

Colour rings and individually distinct song features were used to distinguish individual Reed Buntings. Pairing date was defined as the first observation of a female in a territory which was followed by "mate guarding" by the resident male. Mate guarding means that the male normally stays a short distance from the female and both birds make contact calls (Ghiot 1976). A male was treated as unpaired if no female was seen in his territory on at least three consecutive days. Since I observed the territories throughout the breed-

Figure 1. Spectrograms of song type I (upper) and song type II (lower) in Reed Buntings. Both songs are from the same individual, when unpaired (upper) and paired (lower). Note the same introductory syllables at the beginning of the songs.

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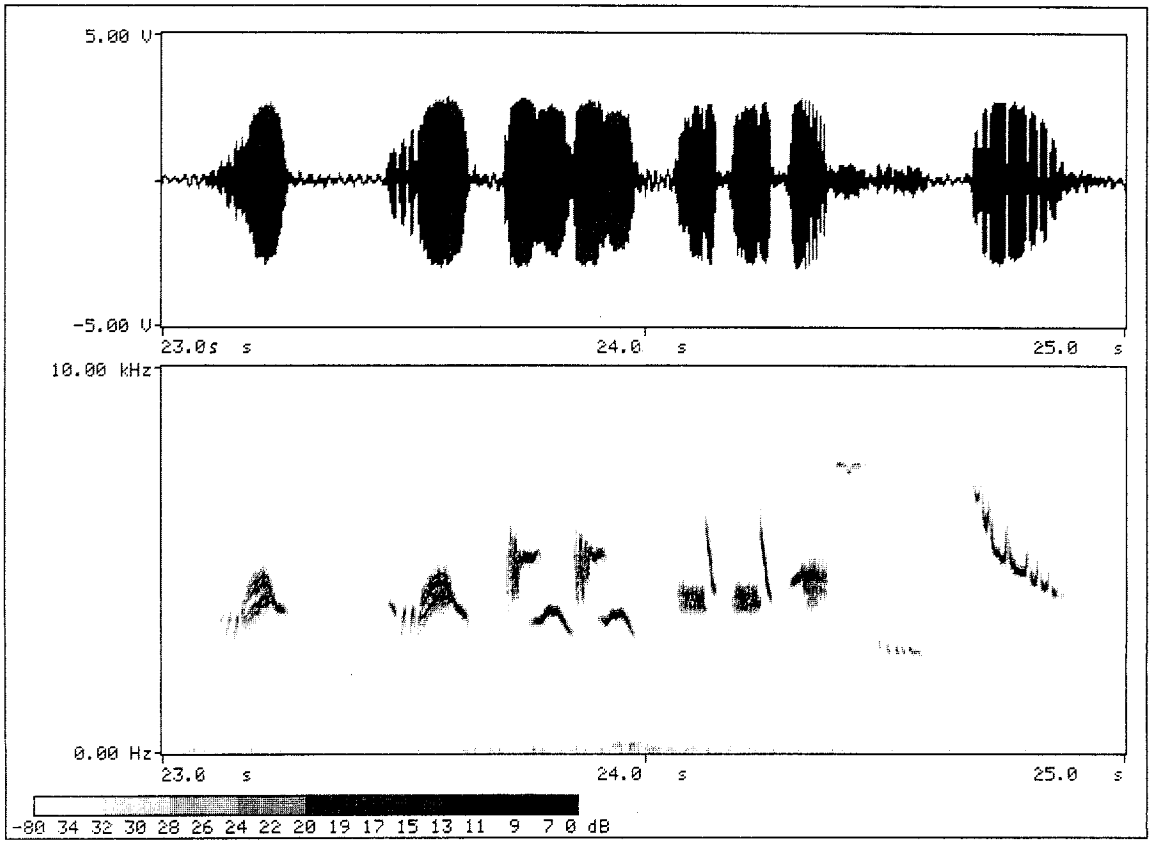
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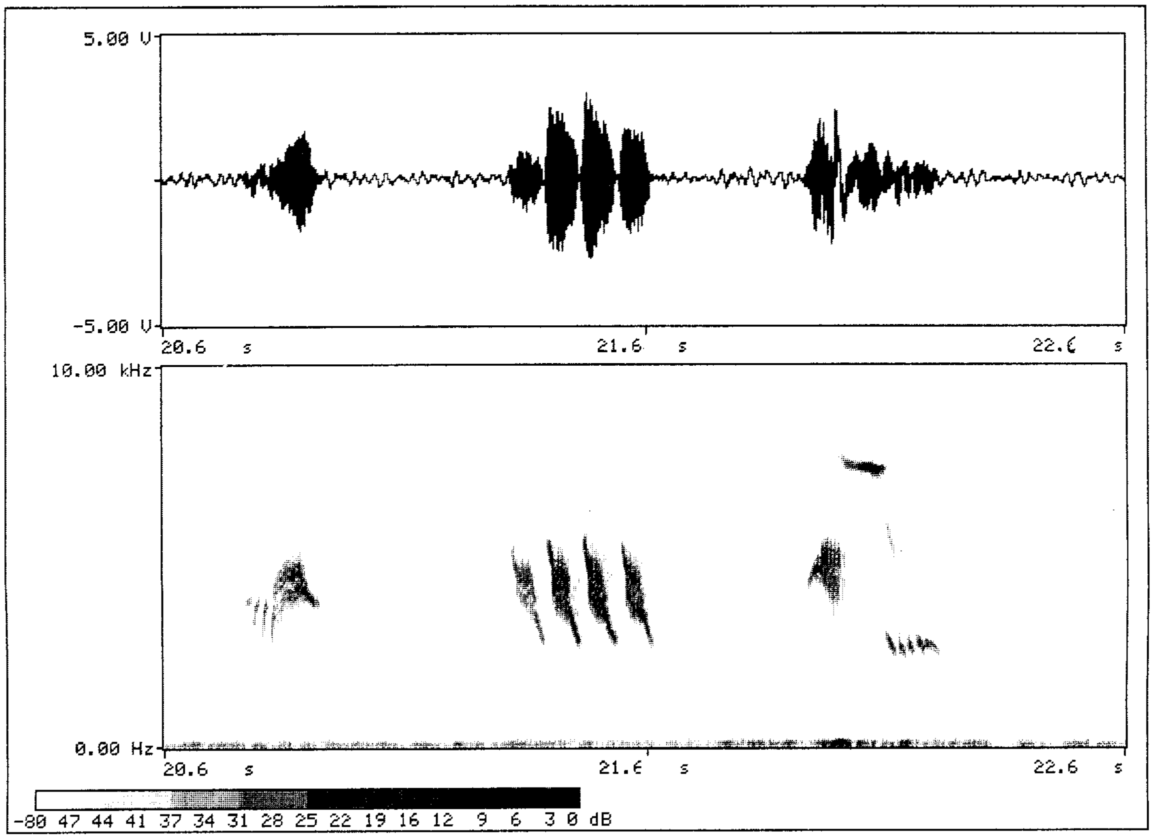
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ing season, it is very unlikely that I mistook a paired male as being unpaired.

The basic unit of song is the syllable. A syllable can consist of one or more elements. An element is defined as a continuous trace on the spectrogram. If elements are separated by more than 10 milliseconds (ms) they are treated as syllables. In the rapid singing style, single songs are separated by longer intersong intervals. The slow singing style sometimes sounds continuous, with no possibility of separating single songs according to different interval distribution within and between songs. Fortunately, the birds use specific introductory syllables (one or two per male) so it is possible to use this syntactical feature for defining each song. Every occurrence of an introductory syllable after another syllable marked the beginning of a new song. In rare cases when the intervals between two introductory syllables were longer than 1.5 s, I counted them as intersong intervals. In this paper I use rapid singing style (introduced by J.P. Ewin, unpubl. PhD thesis, University of London) synonymous with singing type I or first song type and slow singing style synonymous with singing type II or second song type.

I recorded the songs of 21 male birds during the first 6 h after sunrise for a total of 80 h. All of these recordings were scanned visually on a real time frequency analyser. Since single syllables have stable structures during the whole season and even in consecutive years (E. Nemeth, unpubl.), all different syllable types for each bird were recorded, digitized and stored on a computer. I measured the following variables for all syllables (n = 474): (1) total length in milliseconds, (2) number of elements, (3) maximum and minimum frequencies in kHz, (4) frequency range, (5) number of frequency modulations (FMs), (6) modulation frequencies of these FMs and (7) percentage FM, defined as the mean frequency deviation from the carrier frequency expressed as a percentage of carrier frequency (Greenwalt 1968).

To discriminate the songs of paired and unpaired males, I measured 11 recordings in each case. Since six birds were identical in both groups, a total of 15 different birds was investigated. I did not exclude the occurrence of the same birds in the two groups because a change in singing style by the same individual is additional information. Because of the effort involved, I restricted the analysis per bird to a 3-min recording extracted from one song bout. Subsong, which is characterized by a great variability in syllable structure at the beginning of the season, was excluded. All songs by the paired males were recorded either during the nest building period or when eggs were being incubated. The syllables in the selected recordings were measured and the following variables, in combination with the already measured syllable structure variables, were calculated: (1) number of songs per minute, (2) number of syllables per song, (3) number of syllables per minute, (4) number of syllable types per minute, (5) percentage of introductory syllables, (6) average number of FMs per syllable, (7) intervals within and between songs, (8) average frequency range per syllable, (9) average frequency maximum and minimum per syllable, (10) average modulation rate per syllable, (11) average modulation frequency per syllable and (12) total length of all syllables per 1 min.

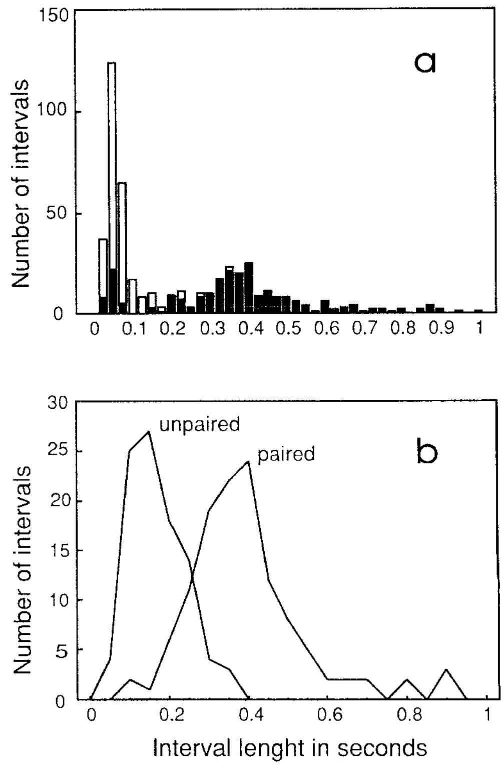

Figure 2. Interval distributions of the song of Reed Buntings. (a) All intrasong intervals; (b) The first interval. The filled part of the bars in (a) represents the paired singers (n = 11 mated and 11 unmated males).

The recordings of the songs were made with a Sony WM-D6C Walkman Professional connected to an AKG C535 microphone and a Grampian parabola (60 cm diameter). I used a UNISCAN II Real Time Frequency Analyzer and the Modular Signal Processing System Spektro produced by MEDAV for measurements. The accuracy of time and frequency measurements depended on the different window sizes and time settings of the spectrograms. Maximums of 0.4 ms time and of 25 Hz frequency resolution were achieved.

RESULTS

The sonagrams of songs of mated and unmated males showed differences in intrasong interval length (Fig. 1). A double peaked distribution was evident when the lengths of all intrasong intervals of both groups were plotted against their frequencies (Fig. 2a). Most of the longer intervals (greater than 200 ms) belonged to paired males, but there were also some smaller intervals within their songs. This was because some syllables were arranged in groups within the songs and these had shorter intervals. The length of the first syllable was clearly different between the two groups (Fig. 2b). In

Table 1. *Correlation of characters with the canonical discriminant axis, univariate F-values and group averages of paired and unpaired male Reed Buntings. Each group contains 11 different males*

Variable	Correlation coefficient	$F_{1,21}$	P	Group averages: Paired males	Group averages: Unpaired males
Length of first interval (ms)	−0.95	67.9	<0.0001	384	126
Syllables per song	0.90	45.9	<0.0001	3.1	7.4
Number of songs per minute	−0.76	19.7	<0.0003	15.3	7.0
Frequency modulations per syllable	−0.75	19.1	<0.0003	1.5	0.9
Length of song interval (ms)	0.70	14.8	<0.001	3441	7518
Percentage of introductory syllables	0.49	5.2	<0.03	44.3	29.9

the subsequent multivariate analyses, it was possible to utilize this normally distributed measure as representative of the intrasong intervals.

For the canonical discriminant analyses, I used all variables with univariate F-values smaller than 0.05 (Table 1). No significant differences in the number of syllables per minute or total length of all syllables were found. Since both variables are an adequate measure of song output, this implies that both singing styles can be uttered at the same intensity and that the two song categories cannot be considered as parts of a continuous range. No difference in repertoire size was found ($F_{1,21}$ = 0.32, n.s). Surprisingly, FMs and introductory syllables per song and FMs per syllable were significantly different between the groups (Table 1). It can be argued that introductory syllables have more FMs and that both variables are measuring the same thing. However, this is refuted by the weak correlation between them (r_9 = 0.21, n.s.). The canonical discriminant function analysis correctly attributed all of the song styles, a more accurate classification than expected by chance alone (50%; Table 1). Because of the high intercorrelations of most variables, it is not easy to interpret single correlations of the variables with the first discriminant axis. Even when the variable with the highest F-value (first song interval) was excluded and a new discriminant function was calculated, the discrimination remained correct in all cases.

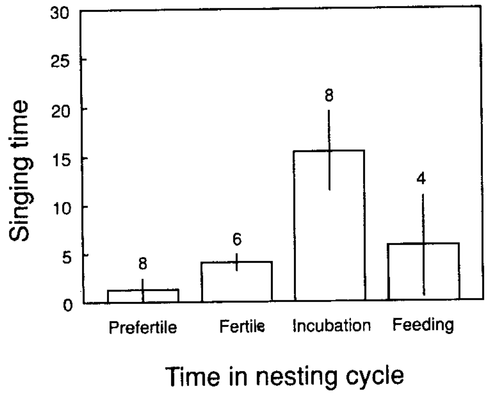

Figure 3. Time spent singing by paired male Reed Buntings in different periods of the breeding cycle of their mates (min/h, mean ± s.d.). Numbers above bars denote the number of individuals observed.

The singing activity of the paired males reached a peak when their females were incubating (Fig. 3) and was significantly higher than during the fertile period (Mann-Whitney $z_{8,6} = 3.09$, $P < 0.01$).

DISCUSSION

The discriminant analysis revealed that paired and unpaired Reed Bunting males can invariably be distinguished by song. The differences in interval distribution confirmed the subjective impression, but surprisingly there were also differences in the FMs and introductory syllables between the two groups. A closer examination of the breeding biology of the Reed Bunting is necessary to interpret the function of these characteristics.

A first cue is supplied by the singing activity before and after pairing. After arrival in their territories, the males sang the type I song intensively. Sometime later, pairs formed and the mated males sang, only on rare occasions, the song type II (Nemeth 1994). Several weeks passed until the the females laid eggs and the males sang more often, but only in the slow type II singing style. This time pattern seems to be the same throughout Europe (Okulewicz 1989). The song cessation after pairing implies that mate attraction is the main function of song type I (Catchpole 1982).

Song type II increased during the breeding cycle and peaked during incubation by the female (Fig. 3), which contradicts the male deterrence hypothesis but meets the predictions of the mate attraction hypothesis. Furthermore, there was a negative relation between mate guarding and singing activity (Nemeth 1994), which is also an argument in favour of mate attraction as the main function for song activity after pairing (Møller 1988).

Why do Reed Buntings use different song types? This may be related to the identity of the singer. Field experiments demonstrated that female Reed Buntings recognized their males individually by their songs. During the fertile period, they moved towards the songs of their mates and took up copulation postures (Nemeth 1994). The males help in the feeding of the young, so a female should select only a resident male. As in the Dunnock *Prunella modularis* (Wiley *et al.* 1991), this should increase the breeding success. This conclusion seems to contradict the implications of the high extra-pair fertilization rates found by Dixon *et al.* (1994). But as Birkhead and Møller (1992) pointed out, if parental care is important for reproductive success, it cannot be argued that it occurs simply because there are few opportunities for extra-pair copulation.

I believe it is necessary to extend the female attraction hypothesis for song type II in the Reed Bunting: the song is used not only to attract females of neighbouring pairs but also to retain the male's own female. Reed Buntings are able to rear two or three broods per year (Ghiot 1976, Okulewicz 1989), and, because of predation, they start even more clutches; so it should be important for males to keep their mates for the next clutch. Since the females discriminate the songs of different males, during incubation they are able to assess the location, identity and singing activity of the males. This information could be used to choose the next copulatory partner. A paired male that does not sing risks losing his mate to a neighbour in the next fertile period. Maintaining the pair pond as well as attracting a mate can be seen as the reasons for song type II.

Singing during the incubation period could also serve a territorial function, but the weak responses of paired males to playback discredit this interpretation (E. Nemeth, pers. obs.). Other hypotheses, such as stimulation of the female to incubate, cannot be excluded.

The results indicate that both singing styles seem to be directed to females: the rapid singing style of song type I to unpaired females and the slow singing style to a paired one, either the mate or another female in the neighbourhood. The physical structure of the singing styles could reflect the different intended receivers. Singing type I, with short intrasong and longer intersong intervals, is directed to approaching, unmated females and could be more easily localized than the more continuous song type II. According to sperm competition theory, the more continuous song of the paired males may be addressed to surrounding females and therefore, perhaps, stresses individual features. The larger usage of FMs (Beecher *et al.* 1989) and/or the higher proportion of introductory syllables could be the result of this individuality, but more research is needed to answer these questions.

I thank H. Winkler for advice during the study and H. Winkler and H. Hoi for comments on the manuscript. I am grateful to A. Herzig and A. Grüll for their hospitality at the Biologische Station, Illmitz. This study was part of my PhD thesis and was supported by the Konrad Lorenz Institute of Comparative Ethology of the Austrian Academy of Sciences.

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Submitted 17 June 1994; revision accepted 24 December 1994