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VARIATION IN SINGING ACTIVITY DURING THE BREEDING CYCLE OF THE EUROPEAN STARLING *STURNUS VULGARIS*

by

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SUMMARY

We examined the pattern of song output of male European starlings during different stages of the breeding cycle. Song activity dropped dramatically at pairing, suggesting that the song has an important mate-attraction function. Singing in the nest box occurred almost only when males were unpaired and when prospecting females were in the vicinity of the nest box. Pairing in starlings had several other effects on male behaviour : the occurrence of wing-waving (a visual display sometimes associated with singing) and of carrying green nest materials dropped significantly after pairing. Unpaired males sang significantly more close (≤ 1 m) to the nest box than paired males. After pair formation, an increase in singing activity was observed in the period coinciding with the presumed fertile period of the female. Evidence is presented that by singing males try to stimulate their females to solicit copulations during this period. Monogamous males almost completely stop singing after the egg laying period, whereas males attempting to become polygynous start/continue singing at another nest box at a level comparable to that of unpaired males.

Keywords : starling, *Sturnus vulgaris*, song, sexual selection, extra-pair copulations, mate guarding.

INTRODUCTION

Although the function of the song of the European starling *Sturnus vulgaris* has recently received much attention (EENS *et al.*, 1990, 1993 ; MOUNTJOY and LEMON, 1991 ; BÖHNER, 1993), the variation in male singing activity during the breeding season has so far not been quantified. Nevertheless, studying the pattern of song output during different stages of the breeding cycle may provide important information on the function(s) of song (CATCHPOLE, 1982 ; JOHNSON and KERMOTT, 1991). In a recent review, KROODSMA and BYERS (1991) even stressed that knowing exactly how a male uses his songs in natural situations, for instance during pair formation or during copulation, is a prerequisite for further work.

The aim of this paper is to document the variation in singing activity of male European starlings during the breeding season. As European starlings are facultatively polygynous (PINXTEN *et al.*, 1989 ; PINXTEN and EENS, 1990), we look at both monogamous and polygynous males. In particular, we pay attention to differences in singing activity and behaviour between unpaired and paired male starlings.

STUDY AREA AND METHODS

During the breeding seasons of 1988 and 1989, we obtained information on the pattern of song output during different stages of the breeding cycle from three starling males. Among these three males, two were monogamous and one became polygynous. The three males were watched almost daily during 30 minutes in the morning (between 0700 and 1100 hours) : during this period, we recorded every minute, at the signal from an electronic timer (Casio), whether they were singing or not. From another seven males, the singing activity and behaviour was recorded during similar observation periods of 30 minutes both when they were unpaired and immediately after they had obtained a female (*i.e.* the first day when they were observed with a female). From all 10 males, we also recorded whether they were (1) wing-waving (this is a visual display sometimes associated with singing : see FEARE, 1984 ; Eens *et al.*, 1990 ; BÖHNER and VEIT, 1993) ; (2) carrying green nest materials ; (3) sitting close ($\leq$1 m) to the nest box ; (4) singing in the nest box (small electret microphones implanted in the nest boxes and connected to a tape-recorder allowed us to verify this). All ten males were individually marked with colour-coded wing tags and/or colour rings. All observations were done in a nest box colony in Zoersel, near Antwerp, Belgium. Detailed information on the study area, the study population and the general methods employed in this study can be found elsewhere (PINXTEN *et al.*, 1989 ; PINXTEN and EENS, 1990 ; EENS *et al.*, 1991).

RESULTS

In Fig. 1 the percentage of time that male starlings spent singing in relation to the onset of egg-laying of their female, is shown for two monogamous males and one polygynous male. It can be seen that the singing activity decreased markedly at pairing. Considering all 10 males whose song activity was recorded before and immediately after pairing, a highly significant decrease in singing activity was observed (Table 1). Singing occurred significantly more close to the nest box when males were unpaired than when they had attracted a female (Table 1). Singing in the nest box also occurred significantly more when males were unpaired (Table 1). Unpaired males only sang in the nest box when a prospecting female was in the vicinity of their nest box. Finally, both wing-waving and carrying of green nest materials occurred significantly more in unpaired males (Table 1).

TABLE 1

A comparison of behavioural variables between unpaired and paired males (N = 10 males). Values given are means ± SE. Differences between unpaired and paired males were tested using Wilcoxon matched pairs signed ranks tests.

Behavioural variable	Unpaired	Paired	Wilcoxon test
% of time singing	58.3 ± 4.4	19.6 ± 2.8	$P < 0.01$
% of song produced close to the nest box	68.0 ± 4.0	9.0 ± 3.0	$P < 0.01$
% of time singing in the nest box	6.7 ± 1.7	0.7 ± 0.4	$P < 0.05$
% of time wing-waving	14.3 ± 3.5	2.7 ± 1.1	$P < 0.05$
% time carrying green nest materials	7.3 ± 2.5	0.7 ± 0.4	$P < 0.05$

In both monogamous males, an increase in singing activity after pair formation could be observed from about 2 to 4 days prior to laying; before the end of the laying period (which lasted 7 and 6 days, respectively), however, the singing activity decreased to zero or almost zero (Fig. 1a). After the egg-laying period, both monogamous males (almost) completely stopped singing.

When looking at the polygynous male (Fig. 1b), a similar increase in singing activity could be observed 2 to 3 days before the start of laying. At day 4 of the laying period of his female, however, this male temporarily deserted his female and he started singing at another nest box about 35 meters away from his first (between his first and second nest box there were 4 nest boxes occupied by another male). From this moment, he spent most of the time he was present in the colony singing in front of this nest box and he completely neglected his (first) female. The amount of time he spent singing from that moment, increased to a level that is comparable to that of unpaired males (Fig. 1b). Eight days later, the male succeeded in attracting a second female and again a dramatical decline in the singing activity was observed. The second female of this male never started laying and left the colony at day 20 (Fig. 1b) after which the male returned to his first female and started helping this female with the feeding of the nestlings. Later we never observed this male singing again.

DISCUSSION

Pairing in starlings had several major effects on the males' singing and general behaviour. First of all, the song activity of males decreased markedly at pairing. A similar decrease at pairing has been observed in other species (*e.g.* sedge warbler *Acrocephalus schoenobaenus* (CATCHPOLE, 1973), white-throated sparrow *Zonotrichia albicollis* (WASSERMAN, 1977); wood warbler *Phylloscopus sibilatrix* (TEMRIN, 1986), great tit *Parus major* (BJÖRKLUND *et al.*, 1989) and pied flycatcher *Ficedula hypoleuca* (ESPMARK and LAMPE, 1993)) and has been interpreted as

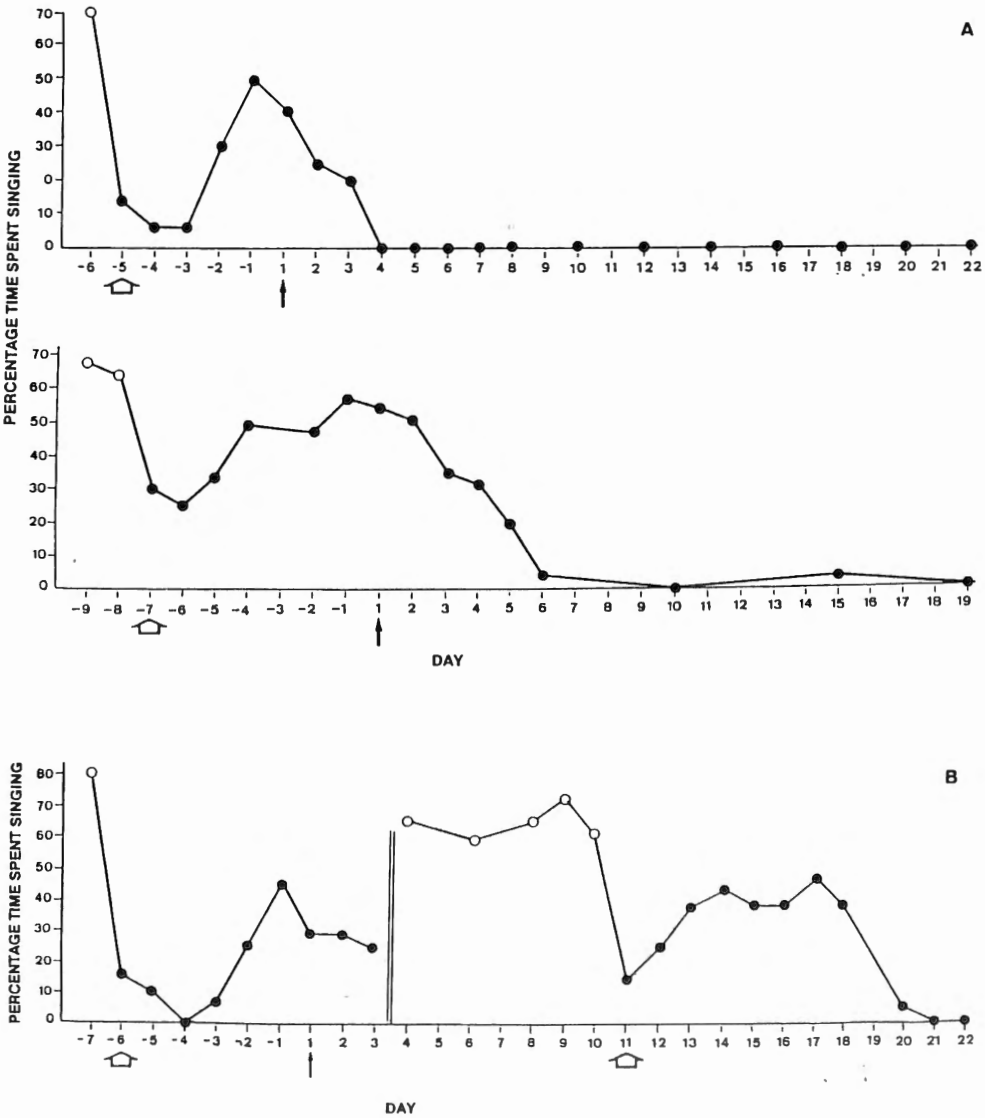

Fig. 1. — Percentage of time (based on the percentage of intervals) that males spent singing in relation to the onset of egg-laying by their female for (A) two monogamous males and (B) a polygynous male breeding in the nest box colony of Zoersel. Large arrows indicate the date of pair formation; small arrows indicate the onset of egg-laying of the females. Egg laying dates were 13 April 1988 (upper) and 9 April 1989 (lower) for the monogamous females, respectively, and 12 April 1988 for the primary female of the polygynous male. Open circles accentuate that the males were still unmated at that time. The vertical double line in Figure B indicates that this male started singing at a second nest box from this moment.

evidence that an important function of song is female attraction (SEARCY and ANDERSSON, 1986). The observed decrease in singing activity of male starlings after pairing is in agreement with earlier experimental work demonstrating that the starling song functions primarily in intersexual communication. CUTHILL and HINDMARSH (1985) showed that experimental removal of the female from pairs of starlings led to a dramatical increase in male singing activity. Accordingly, EENS *et al.* (1990, 1993) showed experimentally that unpaired captive male starlings strongly increased their singing activity when presented with a female.

The observation that unpaired male starlings sing in the nest box when a prospecting female comes in the neighbourhood of the nest box (or even in the nest box) indicates that males do not only sing to be rapidly detected by any potential female passing by (*i.e.* passive attraction : see SEARCY and ANDERSSON, 1986 and SLAGSVOLD *et al.*, 1988), but also suggests that females may actually use song as a cue for their mate choice. In agreement with this, it has been shown both in field and aviary conditions that female starlings prefer males singing more 'complex' songs (EENS *et al.*, 1991).

According to HINDMARSH (1984), male starlings almost completely stop singing as they get paired (see also CUTHILL and HINDMARSH, 1985). This is in strong contrast with our data which suggest that from two to four days prior to laying, the song activity of paired starlings increases again and stays at a similar (high) level until the end of the laying period when it decreases to zero or almost zero (at least in monogamous males). This was partly also noted by KLUYVER (1933 : p. 49) who mentioned that male starlings sing the most during the period of egg laying. The period of increased song activity after pair formation coincides with the 'presumed fertile period' of the females (see MØLLER, 1985 ; BIRKHEAD, 1987 ; BIRKHEAD *et al.*, 1987 for information on the fertile period). Previously, it was observed that most of the within-pair copulations occur between four days before egg-laying till the fourth day of the egg-laying period (EENS, 1992). This combined with the fact that all copulations are preceded by singing in the starling (EENS and PINXTEN, 1990 ; EENS, 1992) strongly suggests that an important function of the song after pairing might be to invite and stimulate the female to solicit copulations, as was also noted by HARTBY (1969). Indeed, it is interesting to mention that male starlings, in contrast to many other male songbirds (*e.g.* bunting species : BAKER and BAKER, 1988 ; redwinged blackbird *Agelaius phoeniceus* : SEARCY, 1989), do not have a copulation call or precopulatory vocalization. We suggest that by singing during the fertile period, male starlings try to stimulate their females to solicit copulations. We feel that it is not unlikely that female starlings at this moment assess the quality of their mate on the basis of his song (*e.g.* song rate and/or complexity) and adjust their copulation behaviour (both within- and extra-pair) accordingly. An alternative explanation for the high song activity during the fertile period might be that males sing at a high level during the fertile period of their mate in order to deter (neighbouring or other) males that want to obtain extra-pair copulations (MØLLER, 1988, 1991). We think, however, that in a (semi)-colonially breeding songbird that defends only a few meters around its nesthole, the presence of the male close to his female is more important to deter other males than his song. In agreement with

this, we never observed extra-pair courtship behaviour when the female's partner was nearby (EENS and PINXTEN, 1990 ; EENS, 1992).

The difference in the occurrence of wing-waving and the carrying of green nest materials before and after pairing confirms that both behaviours probably serve mainly a mate-attraction function (see EENS *et al.*, 1990, 1993). A final difference between unpaired and paired starlings concerned the position where males were singing : unpaired males sing most of their song close to the nest box, while paired males sing mostly from high in the tree (to which their nest box is attached). Unpaired males probably sing very close to their nest box to show it to prospecting females : in a hole-nesting species like the starling males can probably not obtain a pairbond with a female without having a nest box. A possible explanation why mated males sing high in the tree may be that in this way they can better mate guard their female. PINXTEN *et al.* (1987) showed that male starlings guard their females intensively during their fertile periods to avoid extra-pair copulations (EENS and PINXTEN, 1990 ; PINXTEN *et al.*, 1993). Another possibility might be that high in the tree, males can better observe eventual predators or that the distance over which the song is an effective signal is higher.

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