SONG IN SWEDISH GREAT TITS: INTRA- OR INTERSEXUAL COMMUNICATION?

by

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(With 1 Figure)

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Introduction

For centuries it has been accepted that bird song can be used in two different ways. WHITE (1789) suggested that its main function was competition for space, whereas DARWIN (1871) argued that it was female attraction. The two ways of using song do not need to be mutually exclusive (TINBERGEN, 1939). Since then, a number of examples of both functions have been given (for reviews see CATCHPOLE, 1982; PAYNE, 1983; SEARCY & ANDERSSON, 1986). In a given species, the way males use song depends on the ecology and life history of the species (CATCHPOLE, 1982).

The great tit (Parus major) has often been cited as an example of a species in which the main use of song is for territorial defense. KREBS (1977a), in an experiment in England, showed that great tit song has a repulsive effect on settling great tit males. In England, great tits are mainly sedentary, and good breeding habitat is a limiting resource, i.e. there are more pairs than there are available breeding sites (KREBS, 1971; PERRINS, 1979; CLOBERT et al., 1988). Pairing precedes both territory establishment and the peak period of singing (HINDE, 1952; KREBS, 1971). In contrast, Swedish great tits are migratory to a large extent (ULFSTRAND et al., 1979; KÄLLANDER, 1983), and pairing generally occurs after territory establishment since males return to the breeding area earlier than females (Table 1). Every year one or several unpaired males have been observed in the population that we have been studying
TABLE 1. The number of males and females in the study area in relation to date in 1983 (in 10-day periods)

<table>
<thead>
<tr>
<th></th>
<th>February</th>
<th>March</th>
<th>April</th>
</tr>
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<tbody>
<tr>
<td>Date</td>
<td>26 5 15 25</td>
<td>7 17 27</td>
<td>6 16 26</td>
</tr>
<tr>
<td>No males</td>
<td>4 9 10 13</td>
<td>13 13 14</td>
<td>15 15 16</td>
</tr>
<tr>
<td>No females</td>
<td>0 7 7 7</td>
<td>7 8 9</td>
<td>12 12 13</td>
</tr>
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(Björklund et al., unpubl.). These movements make the probability of remating very low, and each spring most birds have to find a new mate. Furthermore, the population density is low in relation to abundance of breeding sites, so most birds are able to find a place to breed (Björklund & Westman, 1986a). Given this difference in ecology, the question naturally arises: do Swedish great tits use song in the same manner as males in the English populations?

The conclusion that song in British great tits is mainly used for intrasexual communication was based on a number of observations and experiments. In this paper we will use these results as predictions; if song is used in the same way in the two populations, our observations should match those in the British population. The main predictions, if song is used mainly in intrasexual communication, are: i) neighbouring males countersing, i.e. have song duels (Krebs et al., 1981a). ii) Neighbours exchange strong song responses; in particular, they match their song types during countersinging (Krebs et al., 1981a), and iii) as a consequence neighbouring males share a larger part of their repertoires than do more distant males (McGregor & Krebs, 1982). Finally, iv) according to the “Beau Geste” hypothesis (Krebs, 1977b), which argues that repertoires have evolved to give potential immigrants a false impression of a high density of birds, males will tend to switch song types when they change song perches (Krebs et al., 1978; Dawson & Jenkins, 1984).

In this paper we will also examine the possible importance of song as an intersexual signal, either as a means for unpaired males to attract females or as communication within established pairs. If males direct their song to females rather than to other males we would expect that v) males should decrease singing after pairing (Falls, 1978; Catchpole, 1982), and that vi) singing should depend on female presence: if song is used as a contact call between the pair members, the male should increase his rate of singing when the female is temporarily absent (Krebs et al., 1981b; Johnson, 1983; Cuthill & Hindmarsh, 1985). Obviously,