

Aggressive responses of two hole-nesting passerines, *Parus major* and *Ficedula hypoleuca*, to the play-back of sympatric species song

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JÄRVI, T., T. RADESÄTER & S. JAKOBSSON: *Aggressive responses of two hole-nesting passerines, Parus major and Ficedula hypoleuca, to the play-back of sympatric species song.* — *Ornis Fennica* 55:154–157.

The songs of Great Tits, Pied Flycatchers, Marsh Tits and Willow Warblers were played in the territories of six male Great Tits and six male Pied Flycatchers. Not only were strong aggressive responses elicited by conspecific song, but there were also significantly more aggressive responses to songs from another hole-nesting species than to song from a species that does not compete for nesting holes.

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Introduction

A number of studies have shown that bird songs convey species-specific information and that birds do not generally respond to the songs of other species (e.g. THIELCKE 1969, EMLEN 1972, SHIOVITZ 1975). It seems reasonable to assume, however, that under special circumstances evolution may favour, not only reactions to conspecific song, but also adequate responses to individuals of another species. This would be the case if the members of the species were competing for a resource in short supply.

Interspecific territorialism based on aggressive behaviour has often been reported in the literature (ORIAN & WILLSON 1964, MURRAY 1971, MOORE 1978), but there are only a few obser-

vations of aggressive behaviour elicited by recordings of another species' song. CATCHPOLE (1977) found that the Sedge Warbler *Acrocephalus schoenobaenus* responded with aggressive behaviour to the song of the sympatric Reed Warbler *A. scirpaceus* but not to the Blackbird *Turdus merula*, which was also a common inhabitant of the experimental area. FALLS & SZIJJ (1959) reported that the Eastern Meadowlark *Sturnella magna* showed an aggressive reaction to the song of the Western Meadowlark *S. neglecta* when the two species inhabited adjacent territories but not otherwise.

An experimental field study was conducted to investigate whether two hole-nesting species, the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*, which compete for

a single resource — the nesting box — show any response to each other's song or to the song of two other sympatric passerines, the Marsh Tit *Parus palustris* and the Willow Warbler *Phylloscopus trochilus*.

Methods

To determine whether males of the Great Tit and the Pied Flycatcher respond with aggressive behaviour to each other's song and to the song of the two other species a series of play-back trials were conducted. Before each test the territory of a male bird was mapped and the experimental equipment (Uher Cassette Recorder CR 240 and a Peerless MC 225 HFC loudspeaker) was set up at a distance of 10 m from the nest box.

During each test, recordings of the songs of a Great Tit, Pied Flycatcher, Marsh Tit and Willow Warbler were played in the territory and the reactions of the territorial male recorded. Willow Warbler song was selected as a control sound. This species is a common inhabitant of the research area but does not compete for nest boxes. At each trial a sequence of songs of the four species (each 60 s long, with silent intervals of 15 s) was played to the territorial male. The order of the songs was changed at random.

Six Great Tit and six Pied Flycatcher males were tested. The reactions of the tested bird were recorded as follows:

- a. attack on loudspeaker
- b. visual threat displays
- c. approaching within 2 m of loudspeaker
- d. aggressive calls
- e. territorial song

The reaction was labelled "aggressive" when at least two of these criteria were fulfilled.

The experiments were carried out in the early mornings during the third week of May 1978 at Tovetorp Zoological Research Station, 100 km south of Stockholm.

Results and discussion

The behavioural reactions of each of the tested males are summarized in Table 1. The song of competing hole-nesting species elicited significantly more aggressive reactions, as defined above, than did the song of the Willow Warbler ($P < 0.05$, Fisher's Exact Probability Test). Territorial Great Tit males responded with aggressive reactions on all six occasions when song from another Great Tit was played, on five occasions when they heard the song of a Marsh Tit but not at all to songs from Pied Flycatchers or Willow Warblers. On certain occasions males appeared to flee in response to

FIG. 1. Spectrograms of song phrases used in the play-back experiments: A=Willow Warbler, B=Pied Flycatcher, C=Great Tit and D=Marsh Tit.

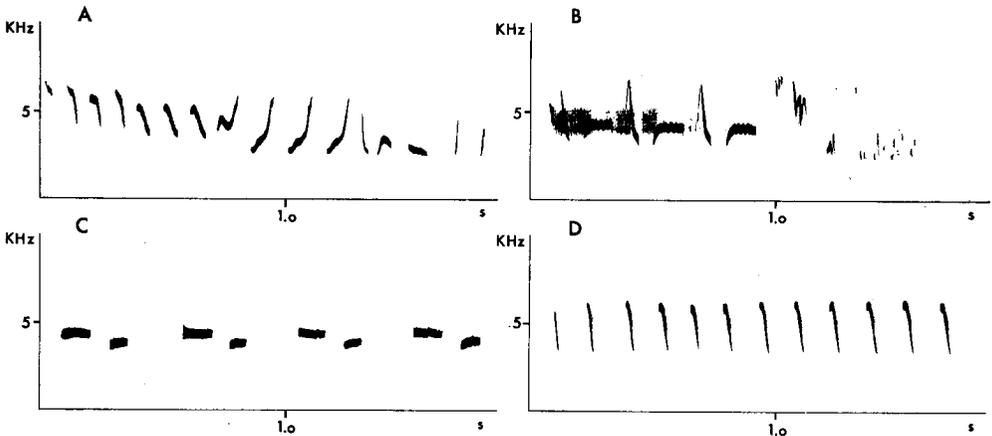


TABLE 1. Responses of territorial males of the Great Tit and Pied Flycatcher to play-back of Great Tit, Pied Flycatcher, Marsh Tit and Willow Warbler song. += "aggressive" response, -= no observed or defensive response.

Song of:	Tested males											
	Great Tit				Pied Flycatcher							
	♂1	♂2	♂3	♂4	♂5	♂6	♂1	♂2	♂3	♂4	♂5	♂6
Great Tit	+	+	+	+	+	+	+	-	+	+	-	+
Pied Flycatcher	-	-	-	-	-	-	+	+	+	+	+	+
Marsh Tit	+	+	-	+	+	+	+	-	+	+	-	-
Willow Warbler	-	-	-	-	-	-	-	-	-	-	-	-

recorded song. In two trials, when the Great Tit heard a Flycatcher he flew away from his territory. Territorial Pied Flycatchers showed aggressive responses on four occasions to Great Tit song, five times to Flycatcher song, three times to Marsh Tit song and not at all to the song of a Willow Warbler.

An important question is whether the birds were in fact responding to the song of the other species or whether they were confused by similarities to the song of their own species. During earlier play-back experiments with Willow Warblers and Chiffchaffs *Phylloscopus collybita*, THIELCKE & LINSENMAYER (1963) found an interspecific response, but SCHUBERT (1971) pointed out that Willow Warbler songs sometimes contain Chiffchaff syllables and concluded that this was the reason for Chiffchaff responses to Willow Warbler songs. As none of the songs used in this study (Fig. 1) contains syllables also sung by one of the other species, our results are probably not due to this kind of confusion.

The literature contains numerous descriptions of competition between Great Tits and Pied Flycatchers (see SLAGSVOLD 1975, 1978 for further references). Overt aggression between the two may be considerable, also leading to vicious fighting and killing.

Most authors state that the flycatcher is the more aggressive of the two species and that generally dominates the tit in encounters outside the nesting box. When the tits have started incubating the dominance-relation is reversed and only a very few flycatchers are able to take over nests occupied by tits. In an experimental study by SLAGSVOLD (1978) every nest box except those already containing a tit nest was made uninhabitable ($N=40$) but, despite increased efforts, only two flycatchers succeeded in taking over a nest box.

Both the Great Tits and the Pied Flycatchers responded to the song of the Marsh Tit and advanced towards the loudspeaker in an aggressive manner. There are no reports of intensive competition between the Marsh Tit and either of the other species, and both GIBB (1965) and NILSSON (1975) claim that the Marsh Tit prefers nest boxes with a smaller bottom area than that in the boxes chosen by Great Tits and Pied Flycatchers. However, there is also some evidence that Marsh Tits have better reproductive success in boxes with a larger bottom area than they "prefer" (LUDESCHER 1973). An explanation of this contradiction may be that this "preference" for a sub-optimal bottom area is a result of competition between the Marsh Tit and other hole-nesting passerines, most

probably Great Tits and Pied Flycatchers. According to our observations both these species seem to dominate Marsh Tits.

SLAGSVOLD (1978) suggests that severe competition between hole-nesting birds may be of comparatively recent origin, arising when modern forestry management practices cause a grave scarcity of suitable nest holes. This raises the question whether the responses to the song of other species demonstrated in this study are innate or learned. As mutual territorialism is not exclusive and considering the short amount of time since competition started we suggest that individual learning seems the most probable explanation.

Acknowledgements. We would like to thank Birgitta Järvi and Birgitta Lång for their most helpful assistance during the field work and to Dr. Al Sosiak for improving the English text. The study was supported by grants from the Bank of Sweden Tercentenary Foundation and from the Swedish Natural Science Research Council.

Selostus: Talitiaisen ja kirjosiepon aggressiivinen reaktio eräiden sympatristen lajiin lauluun

Kokeessa soitettiin nauhalta kuuden talitiaisen ja kuuden kirjosieppokoiraan reviiressä talitiaisen, kirjosiepon, viitatieisen ja pajulinnun laulua. Koiraan reaktio luokiteltiin aggressiiviseksi, mikäli se suoritti vähintään kaksi seuraavista toiminnoista: a) lähestyi vähintään 2 m:n päähän kovaäänisestä, b) hyökkäsi sitä kohti, esitti c) uhkauseleitä, d) aggressiivista ääntelyä tai e) reviiirilaulua.

Koeyksilöt reagoivat aggressiivisesti muiden pöntössä pesivien lajiin (kirjosieppo, talitiainen, viitatieainen) lauluun, mutta eivät pajulinnun lauluun (taul. 1). Talitiaiskoiraat eivät kuitenkaan käyttäytyneet aggressiivisesti kuultuaan kirjosiepon laulua, vaan usein pakenevat. Kilpailussa pesäpaikoista oletetaan kirjosiepon yleensä voittavan.

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Received November 1978.