

Inter-Specific Aggression between the Collared Flycatcher and the Pied Flycatcher: The Selective Agent for the Evolution of Light-Coloured Male Pied Flycatcher Populations?

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# Inter-specific aggression between the Collared Flycatcher and the Pied Flycatcher: the selective agent for the evolution of light-coloured male Pied Flycatcher populations?

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The average plumage colour of the head and back of male Pied Flycatchers varies geographically. Light-coloured males live in sympatry, dark-coloured males in allopatry with the Collared Flycatcher. Because the two species of flycatcher compete for nesting holes, inter-specific aggression may have been a selective agent behind the evolution of light-coloured male Pied Flycatchers. Experiments with stuffed dummies of male Pied Flycatchers showed that male Collared Flycatchers were more aggressive towards a black dummy than towards a light-coloured one. Light-coloured male Pied Flycatchers may avoid attacks by male Collared Flycatchers either because they appear less threatening to the Collared Flycatcher in the competition for nest-holes (i.e. inter-specific status signalling) or because they closely resemble female Collared Flycatchers (i.e. inter-specific female mimicry).

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## Introduction

The plumage colour of the head and back of male Pied Flycatchers *Ficedula hypoleuca* varies from female-like brown to pure black (e.g. Drost 1936). Average plumage colour varies geographically, with darker-coloured populations in Fennoscandia and England and lighter-coloured ones in Central Europe and Russia (Drost 1936, van Haartman 1949, Anorova 1977, E. Røskaft and T. Järvi, unpubl.). In both dark and light populations, males breeding for the first time are light-coloured and their plumage becomes increasingly darker with age (Røskaft et al. 1986). In dark populations dark males are significantly larger than brown males, while in light populations there is no significant differences in size (Røskaft et al. 1986). In the dark populations, black males seem to be dominant over brown-coloured males.

The coloration of the head and back is therefore considered to act as a status signal (Järvi 1983, Järvi et al. 1987).

The Pied Flycatcher is sympatric with the Collared Flycatcher *Ficedula albicollis* over less than 50% of its breeding range, whereas the Collared Flycatcher is sympatric with the Pied Flycatcher over more than 80% of its range. In fact, light-coloured Pied Flycatcher populations have been found to be either wholly sympatric, or nearly so, with those of the Collared Flycatcher (Røskaft et al, 1986). In these populations all male Collared Flycatchers are very dark compared with the male Pied Flycatchers.

In their areas of sympatry, the Pied and the Collared Flycatchers compete for nest cavities, the Collared Flycatcher nearly always winning inter-specific aggressive encounters (Löhrl 1955).

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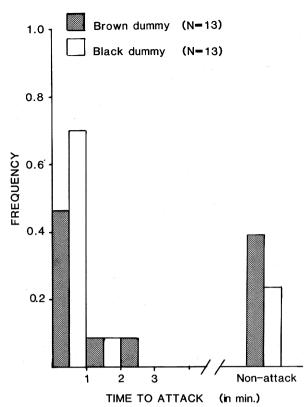


Fig. 1. The time to attack by male Collared Flycatchers on brown and black male Pied Flycatcher dummies placed on their nest-box. The distribution of the two categories of time-lags was significantly different (Kolmogorov-Smirnov Two-sample Test;  $DN=0.54\ P<0.05$ ), suggesting that Collared Flycatchers attacked black males more promptly than they attacked brown ones.

Taken together, the overlap between the light-coloured Pied Flycatcher and the Collared Flycatcher populations, the fact that the male Collared Flycatchers dominate male Pied Flycatchers, and the presumed status signalling function of the coloration of male Pied Flycatchers, suggest that aggressive interaction between the two species has been the selective mechanism leading to the evolution of the observed geographic variation in secondary sexual characteristics of Pied Flycatchers. If aggression by the male Collared Flycatcher is the mechanism, then one would expect that male Collared Flycatchers should attack black male Pied Flycatchers more frequently and aggressively than they attack brown-coloured ones. The aim of this study was to experimentally test this prediction.

### Material and methods

In 1986, a series of experiments were conducted in the Sovinec – Dlouhá Loucka area in northern Moravia, CSSR (49°50′N, 17°15′E). The experimental area is sit-

uated at an altitude of 300–480 m a.s.l. and both Pied and Collared Flycatcher populations were present. The dominant tree species were oak *Quercus petraea* and beech *Fagus silvatica*, with less than 1% coniferous trees.

To investigate whether male Collared Flycatchers attack black male Pied Flycatchers more frequently and vigorously than they attack brown-coloured ones we designed the following experiment. A stuffed dummy of either a brown (16 trials) or, alternatively, a black (17 trials) Pied Flycatcher male was placed on the nestbox of a male Collared Flycatcher, in the same posture as that normally adopted by a singing male. At the same time, a tape of a male Pied Flycatcher song was played back (2 to 3 phrases min<sup>-1</sup>). The behaviour of the Collared Flycatcher males was then observed and, when an attack on the dummy was made, the time-lag between the return of the Collared male and the attack was noted. The following types of behaviour were noted: (1) physical attack, (2) sham-attack, and (3) absence of attack. Since seven Collared Flycatcher males did not respond and approach the dummy during the experiment only 13 trials for each dummy type are reported. The sequence of dummy colour-morphs tested was randomly constructed and each male was only tested in one trial. Each trial was conducted during the period before egg-laying had started in the respective nest.

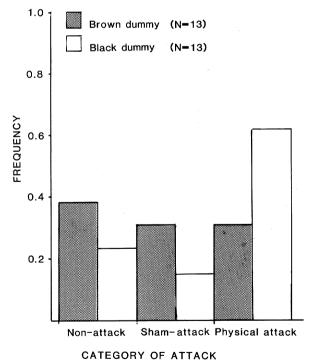


Fig. 2. The frequencies of two types of attack, and non-attack, after response by male Collared Flycatchers on a brown and a black dummy male Pied Flycatcher. The difference in response towards brown and black dummies was highly statistically significant (Kolmogorov-Smirnov Two-Sample Test; DN=1.07; P<0.0001.

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### Results and discussion

Male Collared Flycatchers attacked a black dummy more promptly and also more strongly than they attacked a brown one (Figs 1 and 2). Both these results support the hypothesis that the selective mechanism leading to the evolution of light-coloured male Pied Flycatcher populations in areas of sympatry has been inter-specific aggression from Collared males.

Two hypotheses can be proposed to explain why brown male Pied Flycatchers are less strongly attacked by male Collared Flycatchers than black-coloured ones (Røskaft et al. 1986).

- (1). Status signalling. In dark-coloured Pied Flycatcher populations, black males attacked black dummies more strongly than brown-coloured ones. They were therefore thought to behave more aggressively in nature towards black than towards brown males (Järvi et al. 1987). The reason for this difference in aggression may be that brown males represent less of a threat than black ones, an assumption that was supported by an experiment in Red-winged Blackbirds (Røskaft and Rohwer 1987). This assumption is also supported by the individual variation in plumage among male Pied Flycatchers which is assumed to function as a cue to fighting ability (i.e. status signalling). To some small extent the back and head plumage coloration of the male Collared Flycatcher varies like that of the male Pied Flycatcher (Røskaft and Järvi, unpublished material from the British Museum, Tring). If the plumage coloration of male Collared Flycatchers provides a means of intraspecific signalling of fighting ability and social status, then one would also expect them to attack brown Pied Flycatcher males less frequently and less strongly than they attack black ones, because black male Pied Flycatchers more closely resemble dominant Collared Flycatcher males. In areas where Collared Flycatchers are common, light-coloured male Pied Flycatchers would have higher Darwinian fitness than black ones, i.e. natural selection favouring a light plumage colour.
- (2). Inter-specific female mimicry. Rohwer et al. (1980) suggested that subdominant males may mimic females in order to avoid attacks from dominant males. The head and back plumage of female Collared Flycatchers

is light brown. The reason why male Collared Flycatchers attack brown-coloured male Pied Flycatchers less than they attack dark ones could therefore be that the former resemble female Collared Flycatchers and so gain in Darwinian fitness.

From the results of the present experiment we are unable to decide in favour of either of these two hypotheses, because the same outcome would be predicted by both. Our data suggest, however, that the selective agent behind the evolution of light-coloured populations of male Pied Flycatchers has been interspecific aggression from Collared Flycatcher males.

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