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Seasonal variation of singing activity and relative effect of the advertising behaviour of males with different plumage colour in the Pied Flycatcher *Ficedula hypoleuca*

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Abstract. From late April to the second 10-day period of June 1994–1999, in 76 unmated males the time-budget was measured during 304 hours in a 6.6 km² area of mature mixed and coniferous forests near Moscow. In 1999, territorial males were counted at least once per pentade throughout the breeding season in a 35 ha plot with 180 nest-boxes. Dark (grades 2–3 on Drost's scale) and pale (grades 5–7) males had similar levels of singing activity, but in cold weather the former had higher song rates than the latter. The singing activity of all the males was relatively low at the beginning of the season (by the mid-May). Dark males sang mainly from open perches (67.6% of songs, compared with 23.2% for pale males). In dark males visual stimulation compensated for the relatively low acoustic activity in early spring when trees were still lacking leaves. The immediate vicinities of nest-boxes occupied by dark males were visited by females significantly more frequently than those of pale ones.

Key words: Pied Flycatcher, *Ficedula hypoleuca*, singing activity, mating behaviour

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INTRODUCTION

In many bird species, mates are chosen by females and this can be explained by the higher cost of reproduction for the latter sex (Trivers 1972, Dale & Slagsvold 1994). A female's choice can be determined by the quality of a male itself and/or the quality of resources protected by it. Sometimes, these characteristics are closely related. For example, in some cases best territories appear to be occupied by best males (Kerimov et al. 1994), and good feeding conditions are known to favour the increase in a male's advertising activity which promotes mating success (Gottlander 1987, Alatalo et al. 1990). Relative role of a male quality per se in attraction of a female can vary even in one species. In Pied Flycatcher a female's choice is based on the qualities of both a territory and a hole rather than on the quality of a male advertising them (Alatalo et al. 1986). However, in uniform habitats having no distinct gradients of living conditions the quality of a male affects a female's choice (Lifjeld & Slagsvold 1988).

Järvi et al. (1987) and Lifjeld & Slagsvold (1988) showed that male's mating success correlates positively with its reproductive experience, body size, weight, and brightness of nuptial plumage. In this species, male nuptial plumage coloration in a particular population can vary from bright black-and-white to light brown female-like. This variation is not related directly with the age although first-year males are generally more brownish than older ones (Drost 1936, Järvi et al. 1987). All characteristics mentioned above as well as some peculiarities of male acoustic repertoire positively correlated with the brightness of plumage coloration. Darker males have larger song figure repertoires and more versatile song samples than brown ones (Lampe & Espmark 1994). Thus, plumage coloration together with song repertoire may be considered indicators

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of male quality. Brightly coloured males are also assumed to be more attractive for females as a result of their conspicuousness (Lifjeld & Slagsvold 1988). Bright males are more conspicuous also due to their peculiar behaviour: visual displays are more common for them than for pale individuals (Ivankina et al. 1995). This must enhance the chances not only for „active", but also „passive" choice of bright males by females, particularly in early spring when leaves are not developed and, as a result, visibility is high.

Since mating success is higher in actively singing males, acoustic activity should expected to be higher in dark individuals than in pale ones. However, the authors who compared singing activity in differently coloured males never reported higher song rate in dark birds (Gottlander 1987, Lampe & Espmark 1994). Two explanations of this are possible:

1) differences in song rate between dark and pale males are really absent. Dark males are attractive for females exclusively due to their coloration, body size and song repertoire quality;

2) such differences exist but overlooked since they become obvious in some specific conditions only.

The aim of this paper was to try to decide between these alternatives by comparing advertising behaviour, especially singing activity, of dark and pale unmated males in different periods of a breeding season and at different ambient temperatures. The latter two factors (together with food abundance on a territory) are known to have a strongest influence on a song rate (Gottlander 1987).

STUDY AREA AND METHODS

The material was collected in Zvenigorod Biological Station, 70 km west of Moscow (55°44′N, 36°51′E). The study area (6.57 km^2 in size) is covered with mature mixed and coniferous forests. In 1987–1990, in a 35-ha plot within this area in mixed forest 180 nestboxes were placed.

In different years average colour grade of males plumage in the local population of Pied Flycatcher varied from 4.1 to 4.4 by Drost's (1936) scale. Males belonging to grade 1 (darkest) were never recorded. Advertising behaviour of 76 unpaired males was investigated in 1994–1999 from the last decade of April to the second decade of June (the 12th and the 17th decades from the beginning of the year, respectively).

Total duration of observations were 131 hours for 34 dark males (2nd–3rd grades by Drost's scale) and 173 hours for 42 pale ones (5th–7th grades by Drost's scale). In this paper we did not use data on the behaviour of males belonging to grade 4 by Drost's scale. Most males were aged as either first-year (sb ad) or older (ad) birds on the basis of the shape of their central tail-feathers (Visotskiy 1989). Among the dark males of known age, 22 were adults and 1 was subadult. The respective figures for the pale males were 16 and 17. Other males were not aged.

Usually, each male was time-budgeted 4 times a day, during an hour in every time interval: 6:00–10:00 a.m., 10:00 a.m.–2:00 p.m., 2:00–5:00 p.m. and 5:00–9:00 p.m. In few males time-budget was measured 3 or 5 times a day. Song output was measured as a number of songs produced in a one-hour period. Timing of the behaviour lasted for an hour even if a male remained silent. Such cases were observed several times in cool afternoons. For each male, one-hour song outputs were then averaged.

During a day or in two subsequent days, differently coloured males were observed by turns. Thus, observations of individuals belonging to different colour types were distributed uniformly over the season. In the days of these observations, daily air temperatures averaged 12.8°C for the pale males and 13.1°C for the dark ones.

Song posts were divided into 3 types: „open" (perches located in marginal parts of trees), „partly open" and „concealed" (perches sheltered by foliage and branches). Numbers of songs produced while sitting on each of them were counted separately.

Females visiting nestboxes or their vicinities were recorded within a distance of 5 m. The latter restriction allowed us to compare numbers of females' visits to males' territories having different camouflage properties. Number of females' visits per hour was used as a characteristic of a male's attractiveness. Surprisingly, most females, which visited males' territories during our observations, disappeared in a few minutes. We suppose that to be the effect of human presence rather than the consequence of unattractiveness of a male or its territory.

In 1999, singing males were regularly censused in the 35-ha nestbox plot at least once a pentad throughout the breeding season. Most males were captured and banded with individual combinations of colour rings and marked with paint (colour makeup).

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The dates of arrival were estimated on the basis of individual recoveries of 228 males in 1996–1999.

RESULTS

Spring arrival and breeding stages

Usually, local males return to the Moscow region in the 3rd decade of April (the 12th decade from the beginning of the year). The data for the period 1996–1999 showed no significant differences between arrival dates of males with different plumage coloration.

No correlation between plumage coloration and dates of arrival was found neither for the combined data of the years 1996–1999 (the data was corrected to remove the effect of the differences in arrival dates in different years) (Spearman rank correlation, $r_s = 0.11$, n = 228, ns) nor for each year separately (1996: $r_s = 0.04$, n = 79, ns, 1997: $r_s = 0.15$, n = 66, ns, 1998: $r_s = 0.06$, n = 52, ns, 1999: $r_s = 0.12$, n = 31, ns).

The number of singing and displaying males within the plot increased up to mid-May (Fig.1) and began to decline immediately after the peak of pair formations. Some males continued to behave as if they would be unpaired, though they had already formed pairs and their mates were laying eggs or incubated. The latest unpaired male displaying advertising behaviour was recorded on 25 June.

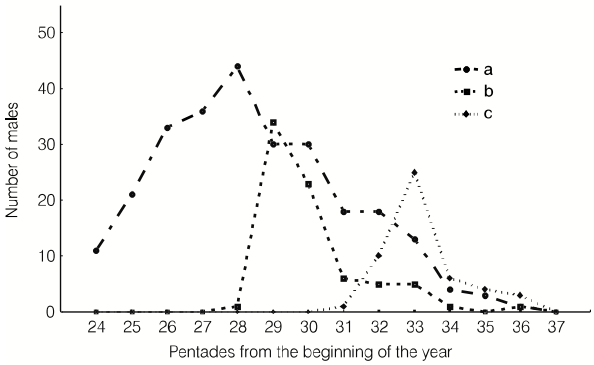


Fig. 1. Number of males displaying advertising behaviour (a), paired ones during egg-laying period (b), and during the period of hatching the young (c).

Seasonal changes in singing activity

In the beginning of the season, when the number of males was lowest, both dark and pale males had relatively low singing activity (Fig. 2). Singing activity increased considerably by mid-May: song rate correlated positively with calendar dates ($r_s = 0.69$, n = 14, p = 0.006, and $r_s = 0.74$, n = 24, p = 0.00004, respectively).

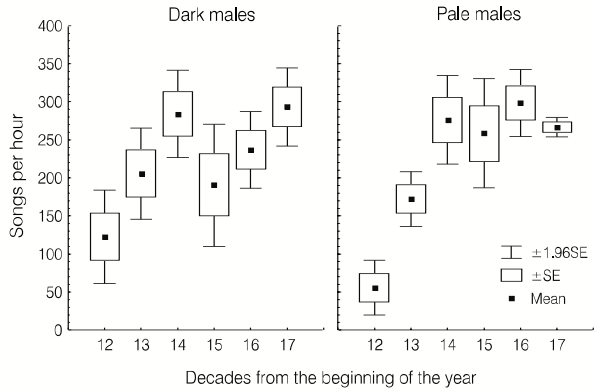


Fig. 2. Song rates in males of the two colour types during the breeding seasonr.

By mid-May, song rate positively correlated with calendar date both in subadults ($r_s = 0.72$, n = 10, p = 0.018) and adults ($r_s = 0.84$, n = 20, p < 0.001).

Since mid-May (the 14th decade from the beginning of the year), singing activity remained fairly stable during the whole subsequent period (for dark males $r_s = 0.35$, n = 20, ns; for pale males $r_s = 0.12$, n = 18, ns). In June, when most of the males were already mated and the number of unpaired males decreased considerably, singing activity of the latter ones did not reduce.

No relationship between the type of male coloration and its song rate was revealed for the whole study period, i.e. singing activities of differently coloured males were similar (ANOVA, F = 0.02, df = 74, ns). The effect of age was not significant either (ANOVA, F = 2.01, df = 54, ns).

Effect of air temperatures on singing activity

In the years 1996-1999, the average level of singing activity of pale males significantly correlated with average daily temperature ($r_s = 0.54$, n = 42, p < 0.001). The same correlation for dark males was weaker and insignificant ($r_s = 0.23$, n = 34, ns).

In 1999, the first half of May was extremely cold: maximum air temperatures never exceeded +10°C and daily temperatures averaged +3.7°C. In these unusual conditions, the pale males kept silence significantly more often than dark ones. Censuses conducted in the 35-ha nestbox plot revealed 16 singing vs. 6 non-singing individuals among the dark territorial males. Respective figures for the pale territorial males were 10 and 13. The difference in the proportions of singing vs.

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non-singing individuals between the colour types was significant ($\chi^2 = 3.94$, df = 1, $p < 0.05$).

An analysis of observations conducted in days with average temperatures below +12.5°C revealed higher song rates in dark than in pale adult males (mean = 202.0 ± 102.0, n = 11 and mean = 96.8 ± 66.2, n = 6, respectively; Mann-Whitney U-test: U = 13.0, z = -2.01, $p < 0.05$). The same but insignificant patterns were found when the data for both ages were pooled (mean = 204.5 ± 109.1, n = 17 and mean = 161.6 ± 99.3, n = 14, respectively, Mann-Whitney U-test: U = 92.0, z = -1.07, ns).

Male coloration and song post concealment

Dark males were observed singing mainly in open perches. By contrast, number of songs produced by pale males were evenly distributed over the song post types. This was typical for both adults and subadults. No clear differences between ages were found in the pale males (Fig. 3).

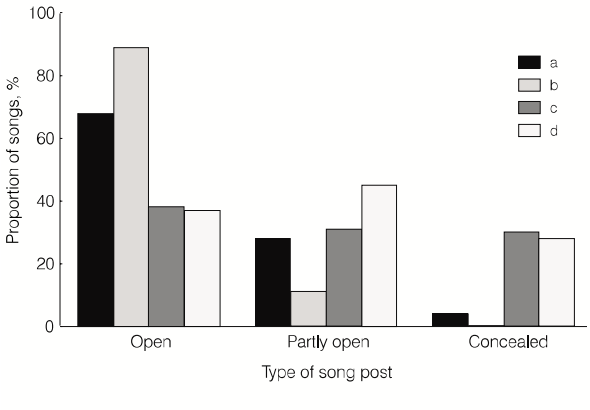


Fig. 3. Proportion of songs produced by males of the two colour types at different song posts. a — dark adults, (8 males, number of songs = 2941), b — dark subadults, (1 male, number = 1306), c — pale adults, 3 males, (number = 498), d — pale subadults, (6 males, number = 2384).

Male coloration and efficiency of advertising behaviour

The proportion of the observation hours during which females visited vicinities of nestboxes at least once was significantly higher in the dark males than in the pale ones (Kruskal-Wallis test: $H_{(1,n = 262)} = 8.32$, $p = 0.039$).

The number of females' visits to nestboxes of the dark and pale males averaged 0.63 (SD = 0.58, n = 31) and 0.28 (SD = 0.31, n = 38), respectively. The difference was significant (Mann-Whitney U-test, U = 336, z = -3.05, p = 0.002).

We analysed age effect only for the pale males and the effect of plumage coloration only for adult males because of lack of data on the dark yearlings.

The number of females' visits to vicinities of nestboxes seemed to be independent from both coloration and age of males when the data for the whole breeding season was analysed together (Kruskal-Wallis test: $H_{(1,n = 30)} = 1.84$, ns, and $H_{(1,n = 34)} = 2.48$, ns). However, in the first half of the season (by mid-May) the attractiveness of the dark males was found to be higher than that of the pale ones. This was true for the males of both ages taken together ($H_{(1,n = 43)} = 6.57$, $p = 0.01$) as well as for adult males analysed separately ($H_{(1,n = 19)} = 3.81$, $p = 0.05$). For the second half of the breeding season, the differences in attractiveness between the two colour types were insignificant ($H_{(1,n = 26)} = 2.43$, ns, and $H_{(1,n = 15)} = 0.01$, ns, respectively).

DISCUSSION

In this study, Pied Flycatcher males with different colorations were found to differ in several characteristics of their advertising behaviour. Although no differences in singing activity between dark and pale males were found in the pooled data, in cold weather the former ones were much more active than the latter. We suggest that dark males are more resistant to low temperatures thanks to higher level of their basal metabolism (Gavrilov et al. 1993). It appears to be advantageous in northern parts of the species' range as well as in its other parts in the beginning of the reproductive season when the probability of cold weather is high. Relatively warm conditions „equalize" the chances of differently coloured males to display advertising behaviour. Our results match the suggestion (Grinkov 1998, Grinkov & Kerimov 1998) that in dark males reproductive behaviour is less dependent from environmental fluctuations than in pale ones.

High level of singing activity is known to promote pairing success in Pied Flycatchers (Eriksson & Wallin 1986, Gottlander 1987, Alatalo et al. 1990). In the beginning of the breeding season the song rate was relatively low in both dark and pale males. In this period, the role of „passive" attraction of a female (e.g., due to qualities of a repertoire and visual demonstrations) is relatively high. Trees are still lacking leaves at this time and singing males are most conspicuous, especially dark males preferring open song posts.

Variety of the repertoire is associated not only with plumage coloration but also with arrival

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dates: early arriving males have larger song figure repertoires and song versatility than those arriving later (Lampe & Espmark 1994).

It is reasonable to expect that in the beginning of a breeding season more conspicuous dark males having higher levels of basal metabolism are more successful in both „active" and „passive" advertising than the pale ones. Judging from the numbers of females' visits, dark males are more attractive than pale ones especially in this period.

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STRESZCZENIE

[Zmienność intensywności śpiewu i efektywność zachowań godowych samców muchołówki żałobnej o różnym kolorze upierzenia]

Badania prowadzono w lasach iglastych i mieszanych pod Moskwą, na powierzchni 6.6 km^2. Zależnie od kolorów ubarwienia wyróżniono dwie grupy samców — dobrze wybarwione czarno-białe (stopień 2–3 wg skali Drosta 1936) i podobne upierzeniem do samic szaro-białe (stopień 5–7).

W latach 1994–99, od końca kwietnia do drugiej dekady czerwca, u 76 nie będących w parach samców muchołówki żałobnej mierzono budżet czasowy (304 godziny obserwacji). W 1999 r. terytorialne samce były liczone przynajmniej raz na 5 dni przez cały sezon lęgowy na powierzchni 35 ha z rozwieszonymi 180 skrzynkami lęgowymi (Fig. 1).

Samce obu grup miały podobną intensywność śpiewu, ale przy niższych temperaturach samce szare śpiewały rzadziej, niż samce ciemne. Wszystkie samce śpiewały mniej intensywnie na początku sezonu lęgowego, do ok. połowy maja (Fig. 2). Ciemne samce śpiewały siedząc głównie na miejscach odsłoniętych — 67.6% śpiewów, w porównaniu z 23.2% śpiewów samców szarych (Fig. 3). Prawdopodobnie w ten sposób bodźce wzrokowe (widok wyraźnego czarno-białego samca) kompensowały niską aktywność głosową na początku sezonu lęgowego, gdy drzewa są jeszcze mało ulistnione. Najbliższe okolice skrzynek lęgowych zajętych przez ciemne samce były odwiedzane przez samice znacznie częściej niż okolice miejsc gniazdowych samców szarych.

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