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# Male colour type and lifetime breeding success in the Pied Flycatcher *Ficedula hypoleuca*

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**Ivankina E. V., Grinkov V. G., Kerimov A. B. 2001. Male colour type and lifetime breeding success in the Pied Flycatcher *Ficedula hypoleuca*. Acta Ornithol. 36: 91–96.**

**Abstract.** The lifetime breeding success of male Pied Flycatchers was evaluated over a period of nine years (1991–99). The breeding success of males recorded in at least two breeding seasons, and nesting at least once in the study area, was analysed. The lifespan number of offspring was positively and significantly correlated with longevity. The reproductive investment in the first year of life did not correspond with longevity, and hence non-breeding males in the first year did not compensate for the losses in fecundity. There were no differences in longevity between dark, intermediate and female-like coloured males. Darker males were less successful in their breeding attempts in the first year than paler birds. Breeding in the first year of life positively influenced the future number of fledglings, and the greater investment in reproduction in this year positively affected future brood size in dark males. Among males successfully breeding in the study area from their first season, dark males reared significantly more offspring during their lifetime, and in the first year of life, than paler ones. Nevertheless, in the total sample, lifetime brood size did not vary between differently coloured males, perhaps because dark males are more vulnerable to predators. The general difference between differently coloured males lay in how breeding efforts were distributed during life. Dark males can maximise reproductive investment from the first breeding year, while paler males increased average brood size in the following years of life only.

**Key words:** Pied Flycatcher, *Ficedula hypoleuca*, lifetime reproductive success, breeding strategies,

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## INTRODUCTION

The history of studies on the variability of the Pied Flycatcher male breeding plumage covers a period of more than twenty years and has resulted in some important findings. Coloration of male breeding plumage, as a whole, becomes darker with age (Anorova 1977, Roskaft et al. 1986, Lundberg & Alatalo 1992, Vysotsky 1995). A two-component nature of coloration heredity is proved experimentally i.e. not only genotype (Anorova 1981, Lundberg & Alatalo 1992), but also environmental conditions influence the content of melanin in a feather (Slagsvold & Lifjeld 1992). Also, the geographical trends in frequencies of colour morphs in populations have been described in general terms; in northern populations of the species bright coloured males prevail (Roskaft et al. 1986).

Nevertheless, mechanisms for the maintenance of this variability still have not been solved; it is unclear how the variability is maintained in populations (Grinkov & Kerimov 1998). In spite of the fact that the adaptive value of many phenotypic traits in the Pied Flycatcher males, including coloration of the breeding plumage, repeatedly has been estimated (Roskaft et al. 1986, Jarvi et al. 1987, Slagsvold & Lifjeld 1988, Potti & Montalvo 1991, Slagsvold & Saetre 1991, Lundberg & Alatalo 1992, Saetre 1993, Grinkov & Kerimov 1998), there

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is still a shortage of long-term studies. In this study we intended to bridge a gap between studies on lifespan success and phenotypic characteristics relations in the Pied Flycatcher.

## STUDY AREA AND METHODS

The paper is based on a nine-year period (1991–1999) of research on the Pied Flycatcher at the Zvenigorod Biological Station near Moscow. Nest boxes were used to study breeding success of Pied Flycatcher males. In early spring, during the arrival of the Pied Flycatcher, we caught single males engaged in female attraction. We used automatic valve traps. Not all males were possible to catch before pair formation. The composition of local breeders was confirmed during the nestling period. Males that we could not catch in spring, as well as previously trapped males, were caught while feeding their fledglings. However, the local population suffered greatly from nest predation, which reached its maximum rate during egg laying and incubation (Kerimov et al. 1995). Therefore, males which lost their clutches, could not be separated from non-breeders and transients. We analysed the breeding success of males that were registered at least in two breeding seasons and nested at least once in the study area to avoid the effect of spring transients to be included in the sample.

We controlled boxes with a frequency sufficient to define exactly the first egg laying date, clutch size and number of fledglings. All captured birds were ringed as well as their nestlings.

We assigned age „x" to the birds which were captured for the first time in the study area, and age x + n (where n = 1, 2, 3, etc) for those of them which were recaptured in subsequent years. As a rule, the exact ageing was not possible due to the low recruitment rate (less than 1%) in the study population.

Based on Drost's (1936) seven point score, we used a simplified scale of colour types taking in to account the age dependency of male's breeding plumage colour. In the Moscow region, the mean lifespan change of colour type was limited to one step on Drost's scale, which is similar to plumage change in other parts of the species range (Anorova 1977, Roskaft et al. 1986, Vysotsky 1995). We calculated the average colour type of each male for its lifespan, and if it was smaller than three, the male was included into the group of „bright" males (the „bright" male is the most blackish one). The group of „intermediate" males contained individuals having an average colour type for lifespan equal to four. Males with an average colour type for lifespan five or more were combined in to the set of „dim" males.

## RESULTS

The interaction between components of breeding success in males was analysed for a whole population of the Pied Flycatcher (Table 1).

Table 1. Relationship between fitness parameters of males estimated for their lifetime. $r_s$ — Spearman Rank Correlation, * — $p < 0.05$, ** — $p < 0.01$, **** — $p < 0.0001$, N — sample size.

| Pairs of correlated parameters | $r_s$ | p | N |
|---|---|---|---|
| Longevity: lifetime number of fledglings | 0.49 | **** | 132 |
| Longevity: non breeding years before first reproduction | 0.14 | ns. | 132 |
| Number of fledglings in the first reproductive year: longevity | -0.14 | ns. | 133 |
| Number of fledglings in the first reproductive year: future number of fledglings | 0.25 | ** | 130 |
| Non breeding years before first reproduction: lifetime number of fledglings | -0.46 | **** | 137 |
| Non breeding years before first reproduction: future number of fledglings | -0.18 | * | 132 |

Surprisingly, there was no future compensation of losses in fledgling numbers due to missed out reproduction in the first year of life. Though, there was a gradual increase in the average brood size during life in birds not breeding in their first year (Fig. 1). The failure to breed in the first year of life did not lead to increased longevity.

The analysis of lifetime breeding success of males showed that the breeding in first year of life positively influenced the future number of fledglings in „bright" males (Table 2). Also, the greater investment in reproduction in first year did not reduce, but on the contrary, positively affected future brood size in „bright" birds (Table 2). These relationships between current breeding effort and future reproductive value clearly separated „bright" males from paler individuals, in which no such interactions were observed.

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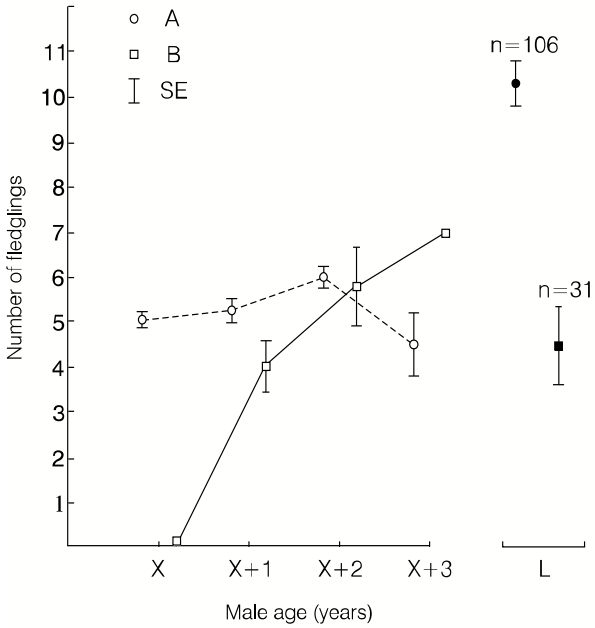



Fig. 1. Average number of fledglings reared by males in different years of life. A — mean brood size of males which started breeding from the first year, B — mean brood size of males which did not breed in the first year, L — mean number of fledglings reared by males for their lifetime.

fered nest predation. Therefore, we divided the further analysis of the data in two ways. In the first case, we analysed the influence of breeding plumage colour on lifetime reproductive success without the control for whether the bird was breeding in the first year of life or not. This analysis enabled us to estimate the ratio of „realized" fitness in various phenotypes in the population. In the second case, we analyzed reproductive traits of individuals breeding in the first year of life. Such way of processing enabled us to reveal a breeding strategy for intrapopulation groups.

In the first case, the average lifetime number of fledglings did not differ between „bright", „intermediate" and „dim" males. In addition, we did not identify any significant deviations in average brood size between differently coloured males in any age classes. Thus, there was a balance in fitness as estimated by brood size differences between colour groups in Pied Flycatcher males as in our study population. Also, the average brood size did not change during life in „bright" males. The age of males exerted influence on the average number of fledglings in „intermediate" (ANOVA: $F = 4.47$, $p < 0.05$) as well as „dim"

Table 2. Relationship between lifetime fitness components of differently coloured males. Symbols — see Table 1.

| Pairs of correlated features | „bright" | | | „intermediate" | | | „dim" | | |
|---|---|---|---|---|---|---|---|---|---|
| | $r_s$ | N | p | $r_s$ | N | p | $r_s$ | N | p |
| Longevity: Lifetime number of fledglings | 0.57 | 28 | ** | 0.44 | 54 | *** | 0.48 | 52 | *** |
| Longevity: Non breeding years before first reproduction | -0.24 | 28 | ns | 0.12 | 55 | ns | -0.14 | 52 | ns |
| Number of fledglings in the first reproductive year: Longevity | 0.23 | 28 | ns | 0.15 | 54 | ns | 0.14 | 51 | ns |
| Number of fledglings in the first reproductive year: Future number of fledglings | 0.52 | 28 | ** | 0.05 | 53 | ns | 0.16 | 51 | ns |
| Non breeding years before first reproduction: Lifetime number of fledglings | -0.73 | 28 | **** | -0.31 | 54 | * | -0.46 | 52 | *** |
| Non breeding years before first reproduction: Future number of fledglings | -0.44 | 28 | * | 0.04 | 54 | ns | -0.19 | 52 | ns |

The special importance of first year reproductive success on lifetime breeding success in „bright" males inclined us to carefully consider the ratio of breeding to non-breeding males in their first year of life, in differently coloured males. „Bright" males were clearly overrepresentated in the group of males with unsuccessful attempts to breed in the first year in comparison with the two other colour groups (Table 3, $\chi^2 = 6.0$, $p < 0.05$). We could not, by certainty, distinguish non-breeding birds from those unmarked birds which suf-

Table 3. Distribution of non breeders in the first year of life among differently coloured males.

| Colour type | N | Observed | Expected |
|---|---|---|---|
| „bright" | 28 | 10 | 5 |
| „intermediate" | 55 | 11 | 13 |
| „dim" | 52 | 10 | 13 |

($F = 4.67$, $p < 0.05$) males. These individuals increased the average brood size with age. We

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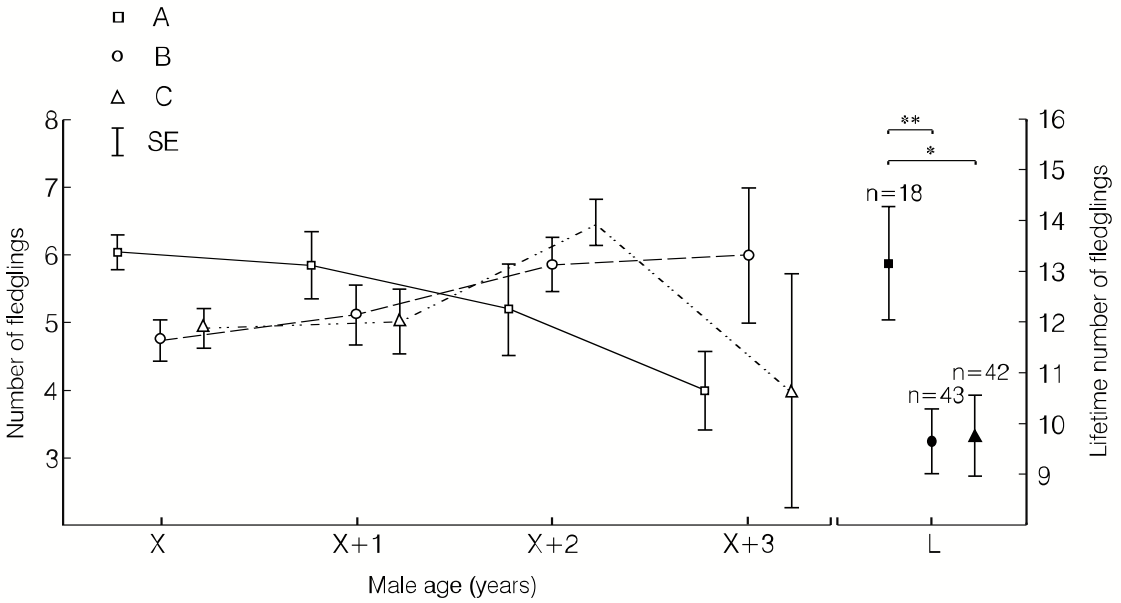



Fig. 2. Average number of fledglings reared by males in different years of life in view of their plumage colour type. A — mean brood size of the „bright" males, B — „intermediate" males, C — „dim" males, L — mean lifetime number of fledglings reared by males with different plumage, * — $p < 0.05$, ** — $p < 0.01$ (Student's test).

considered these distinctions between „intermediate" and „dim" males in more detail below where the analysis was conducted on the sample of all males breeding in the first year of life.

The second way of data processing resulted in significant differences between „bright" males and individuals belonging to two other colour groups with respect to average lifetime number of fledglings and to average brood size in the first breeding year (Fig. 2). In our opinion, the differences in the trends of change of an average brood size with age were most interesting. The brightest birds had a slow decrease in brood size ($g = -0.33$, $p < 0.05$; Gamma correlation), whereas, on the contrary, mean brood size gradually increased in „intermediate" and „dim" males ($g = 0.23$, $p < 0.05$ and $g = 0.28$, $p < 0.05$, respectively) with age.

## DISCUSSION

On the one hand, we estimated the ratio of fitness of existing phenotypes in the population, and on the other, we describe the breeding strategy of Pied Flycatcher males, taking into account only the most important components of breeding success. We summarize the latter material aiming at describing differences in a qualitative manner. We can not give a direct answer supported by an appropriate statistical analysis to the question why significantly more individuals did not reach breeding status in „bright" males. It does not seem probable that the cause was female rejection for „bright" males. These males are very likely to be the most successful in attracting females and having an advantage in a competition for the mate (Alatalo et al. 1984, Lifjeld & Slagsvold 1988, Saetre et al. 1994, Saetre et al. 1995, Ivankina et al. 1995). A probable reason for „bright" males to not to be breeding is predation pressure. „Bright" males are known to differ from female-like males by their advertising behaviour and by using more open nest boxes for female attraction (Ivankina et al. 1995). The strategy of „self-advertising" may make „bright" males more vulnerable to predators. Nevertheless, the fact is that the breeding success in the first year is a key part of lifetime breeding success for „bright" males. In our opinion, the decrease in breeding efforts throughout life in „bright" males can be considered as an ageing process of an organism, aimed at the maximal realisation of the reproductive potential. On the contrary, the successful reproduction of „intermediate" and „dim" males is connected to an increase in individual experience in the course of life. The results obtained are in good agreement with earlier published material (Grinkov & Kerimov 1998). On the basis of the correlation analysis of reproductive traits in the species, we suggest that bright males' breeding behaviour

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conforms to a strategy as „now or never", whereas lighter males keep a strategy such as „if not now, then later". The data presented in this article is the first direct confirmation of this our own hypothesis.

Also, data from this study makes the patterns of geographical variation in colour type frequencies in populations of the Pied Flycatcher more clear. „Bright" males will inevitably obtain an advantage in less predictable environments with higher risks to fail in reproduction because of negative climatic fluctuations and under conditions of time stress, such as breeding at northern latitudes. „Bright" males are capable of making a maximal reproductive work at the first opportunity. Nevertheless, it is still not yet clear at which cost levels „intermediate" and „dim" males start to prevail in zones with a milder climate. There are data on „bright" males showing higher basal metabolic rates than „dim" ones (Gavrilov et al. 1993), and nestlings of such parents also have increased resting metabolic rate (Kerimov & Ivankina 1999). Such energetics of individuals correspond to a potential opportunity to develop a large work output, including investment for breeding (Gavrilov 1997). However, the maintenance of such high level of energy expenditure is more expensive in comparison with individuals having low basal metabolic rates. Most likely, the more expensive way of life of „bright" males makes them capable to justify themselves only in extreme environments for the Pied Flycatcher.

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STRESZCZENIE

**[Typ ubarwienia a sukces lęgowy u samców muchołówki żałobnej]**

Badania prowadzono w latach 1991–1999 w oparciu o skalę Drosta (1936) wyodrębnioniającą siedem typów ubarwienia samców muchołówek. Jeżeli średni typ ubarwienia samca odpowiadał typom od 1 do 3 — zaliczano go do grupy „kontrastowych". „Pośrednimi" samcami były osobniki charakteryzujące się ubarwieniem odpowiadającym typowi czwartemu, „szarymi" — przynajmniej piątemu.

Do badań nad sukcesem lęgowym wykorzystano dane dla samców stwierdzanych przynajmniej w czasie dwóch sezonów lęgowych i przynajmniej raz gniazdujących na terenie objętym badaniami.

Stwierdzono, że liczba piskląt byla istotnie skorelowana z długością życia samców (Tab. 1). Przystępowanie do lęgów w pierwszym roku nie było związane z długością życia i stąd dla samców nie gniazdujących w pierwszym roku nie stwierdzono zwiększania liczby piskląt w kolejnych latach (Tab. 1, Fig. 1). Nie stwierdzono różnic w długości życia u samców kontrastowo, pośrednio i słabo wybarwionych. Kontrastowo ubarwionym samcom rzadziej niż pozostałym udawało się przystąpić do lęgów w pierwszym roku (Tab. 3, $\chi^2 = 6.0$, $p < 0.05$). Gniazdowanie w pierwszym roku życia pozytywnie wpływały na przyszłą liczbę wychowanych piskląt i większe zaangażowanie rodzicielskie w tym roku korzystnie wpływało na przyszłą wielkość lęgu u kontrastowo ubarwionych samców (Tab. 2). Wśród samców wyprowadzających lęgi od pierwszego sezonu, kontrastowo ubarwione wyprowadzały więcej młodych niż pozostałe (Fig. 2). Mimo to wielkość lęgów generalnie nie różniła się u samców o różnym ubarwieniu, być może dlatego, że kontrastowo ubarwione samce są najbardziej narażone na atak drapieżników.

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