EVALUATION OF THE SIZE AND COMPOSITION OF NONBREEDING SURPLUS IN A PIED FLYCATCHER *FICEDULA HYPOLEUCA* POPULATION: REMOVAL EXPERIMENTS IN GERMANY AND RUSSIA

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According to calculations, the annual proportion of non-breeding males in the Pied Flycatcher *Ficedula hypoleuca* in a study area in Lower Saxony (LS), Germany, was about 80% in yearlings (Sternberg, 1989). In order to detect non-breeders in populations and to determine their age and colour type, removal experiments were conducted in 1974 and 1976 on long-term used plots in LS and in 2000 on newly arranged plots in the Moscow Region (MR), Russia. The breeding populations of these study areas were similar in age structure but differed in recruitment rate (9% and <1%, respectively). During 2-3 weeks of the pre-breeding period, we removed all newly arrived males from the plot every day and kept them in an aviary. In LS, captive males were released in the same study area 3d before and 2 d after median onset of egg-laying in non-experimental plots in 1974 and 1976, respectively. In MR captive males were released 3 d before median onset of egg-laying in non-experimental plots. The number of removed males exceeded the number of males found on a control plot by about four times in both regions, indicating an equal ratio of non-breeders in the populations. The number of removed males was about four times higher in LS than in MR due to the lower occupation rate of the new plots in MR. After releasing the birds, similar proportions of birds bred in the plots during the same season in both regions. In LS, a further proportion of released males bred in three subsequent seasons. Assuming a mean annual mortality of adult birds of 50%, nearly all survivors out of the removed males bred in the LS study area in subsequent years. The proportion of subsequent breeders appears to be the same in MR. In both populations, the birds that were released and bred during the same season were older and more conspicuously coloured than non-breeders. The results suggest that high portions of non-breeders and a delay in the start of first breeding may occur both at high and low population densities.

Key-words: *Ficedula hypoleuca* - removal experiments - non-breeders - population surplus.

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INTRODUCTION

Most small passerine birds are known to be physiologically capable of breeding in their first year, but in quite some species some mature individuals do not breed in their first possible reproductive season. The proportion of non-breeders in various species ranges from 0 to 90%, and their age and number depend on both demographic and external factors (Payevsky 1985). In hole nesting species as Starling *Sturnus vulgaris* and Pied Flycatcher *Ficedula hypoleuca*, the proportion of one-year-old breeders decreased when suitable nest-holes were scarce (Polivanov 1957; Anorova 1976). Studying the age of first breeders among Pied Flycatcher males ringed as nestlings in Lower Saxony, Sternberg (1989) estimated the mean age of their first breeding to be 1.87 years. This age seems surprisingly old for a short-lived species. It was calculated assuming similarities of breeders and non-breeders in their annual survival rates and breeding site fidelity during their life. Sternberg hypothesised that about 60% of males stay as bachelors in the study area in any one year. Among one-year-old males, the proportion of non-breeders may be as high as 83%. Such a large number of non-breeding birds was believed to have resulted from competition for nest sites. Alternatively, it could be that some young birds do not leave their wintering quarters (Lundberg & Alatalo 1992) or breed for the first time in other areas due to dismigration (dispersal/spacing) (Berndt & Sternberg 1968; Sokolov 2000). These hypotheses suggest strong differences in proportion and life histories of non-breeders. In this study we aim to answer whether 1) a large number of non-breeders stay within the breeding area? and 2) if this is true, what the reproductive perspectives are of these non-breeders within the given breeding area in subsequent years? Therefore, the main goal of our research was to experimentally test Sternberg's (1989) assumption that a high number of Pied Flycatcher non-breeders actually is present in the breeding area, and that these birds will be breeding within the same area in future. Using temporary removal of all males just arrived in the breeding area, we attempted to determine the size and composition of the population surplus and to compare two geographically distant populations by these characteristics.

METHODS

We collected data in 1974 and 1976 at Drömling, near Wolfsburg (52°31'N, 10°54'E) in northern Germany (Lower Saxony, LS) and in 2000 at Zvenigorod Biological station of Moscow State University (55°44'N, 36°51'E), 70 km west of Moscow, Russia. In Germany, experiments were conducted on long-term studied plots where Pied Flycatchers have been breeding for at least five years in nest boxes. The experimental plot was located within the constant study area of 5x5 km (for more detailed information see Sternberg 1989). The study area in Russia (Moscow region, MR) was covered with mixed and coniferous forests. In 1987-90, seven plots of about 60 ha in mature forest were supplied with 300 nest boxes. Main characteristics of the breeding populations in LS and MR are shown in Table 1. In both populations, the colour type of male changed on average one unit on Drost's (1936) scale between first and second year of life, and remained the same subsequently. In LS, the mean colour type of one-year-old birds was 6.7 (n = 221) and 5.7 (n = 860) in males between two to eight years of age. In MR, it was 4.7 (n = 109) in one-year-old birds and 3.9 (n = 137) in older males. The analysis of age structure in LS was based on known-age individuals ringed as nestlings. Age of males in MR was estimated as one-year-old or older according to the shape of their central tail feathers (Vysotsky 1989). All newly captured males in the study areas were ringed.

Design of the removal experiments

The experimental work could be divided into two parts. The first part corresponds to the proper removal experiment, in which all newly arriving males that inspected nest boxes were removed from the studied population. This manipulation

Table 1. Main characteristics of the breeding populations of the Pied Flycatcher in Lower Saxony and Moscow Region in old plots. Occupation rates in MR plots (30-100 boxes/5-10 ha plots) were recalculated per 100 nest boxes per plot for twelve years period (1989-2000). Occupation rate in LS was calculated per 100 boxes per 10 ha plots for eight years period (1970-1973, 1975, 1977-1979).

Characteristics	Study area	
	Lower Saxony	Moscow Region
Proportion of one-year-old males, % (sample size)	21.4 (1681)	31.0 (303)
Mean colour type by Drost's scale (sample size)	5.9 (1583)	4.2 (675)
Nestbox occupation rate, %	50.1*	57.0*
Population density, pair/ha (sample size)	5.0 (8)	4.5 (19)
Recruitment rate of nestlings, %	9	< 1
Nest predation rate, %	< 20	51

provided information on the number of potential settlers in the study area. The second part was the study of life histories of experimental birds after their simultaneous release. It lasted some years including the year of the removal experiment. During this period, all breeding attempts of released birds in the study area were recorded. Subsequent breeding of a bird was considered a reliable sign of its local population membership. We recorded breeding attempts of experimental males during 1974–79 in LS and during 2000 – 2001 in MR.

Experimental work in LS was carried out in a 10-ha plot supplied by 100 nest-boxes. The experimental area was surveyed daily during 27 Apr-12 May 1974 and 1 May-16 May 1976 . The date of the experiments' start in both years was determined by arrival of the first male in the area. Each nest box was supplied with a wire automatic trap set inside it from 06.00-12.00 a.m. We checked the nest boxes once every hour to remove all captured males. The removed males were kept in an aviary up to 16 d and released in the study area on 12 May in 1974 and 16 May in 1976. Median onset of egg-laying in non-experimental plots in these years was respectively 15 May (n = 164) and 14 May (n = 156). Following the released of males from the aviary, all nest boxes in the study area were checked weekly during the breeding period. Besides the released males, only few new males were caught as breeders in the experimental plot (one male in 1974 and three males in 1976). Hence, nearly all potential male breeders were temporarily removed from the experimental plot in these years. Occasionally, some females were trapped and removed from the experimental plot in the aviary, but contrary to males, the method of capturing birds did not allow to reliably assess the number of females that visited the plot. The long-term average number of male breeders occupying the same old plot in the non-experimental years was used as a control value.

In April 2000, two new (experimental and control) plots were arranged in the same habitat nearby the old plots. There were 100 nest-boxes set out in each 10-ha plot just before arrival of the Pied Flycatchers. From 22 Apr 2000 to 19 May 2000, all nest boxes in the experimental plot were daily supplied with traps and checked hourly between 5:30 a.m. and 13:30 p.m. All males trapped in the experimental plot were removed and placed in an aviary until the end of the experiment on 19 May. The only exception was made for one male who already had his nest in the adjacent old plot and for this reason was released just after capturing. During the time of the removal experiment, the control plot was checked daily at the same time as the experimental plot and all males trapped in nest boxes were individually marked and released just after capture. The number of males captured in nest boxes on the control plot during the time of removal experiment was used as a control value.

Adjacent old plots were also monitored daily and newly arriving males were captured by traps selectively set in nest boxes situated near males' singing sites. After the release of males in the study area, all plots were monitored at least once every three days for detecting breeders. The median laying date of the first egg in the non-experimental plots corresponded to 22 May (n = 195). Thus, the design of the removal experiments was different in two regions. First, we removed birds from a long-term studied plot in LS, and from a new plot in Russia. Second, the method of estimation of control occupation rate differed between MR and LS.

Aviaries

The size of the aviary was 2x4x2 m in both regions. Each aviary was supplied with perches. The plastic netted ceiling and plastic translucent walls of the aviary prevented birds from injuries. The birds were supplied with fresh water and meal worms *ad libitum*. In MR, the mass of the removed males increased on average one gram during their stay in the aviary.

RESULTS

Size of population surplus

The number of removed males exceeded the number of males captured in the control plot nearly four times in both regions. The two regions did not differ statistically in the proportion of removed males (χ^2_1 = 0.37, P = 0.5). Furthermore, the number of removed males was about four times higher in LS than in MR (fig. 1), reflecting the higher density in the control plots in LS. Among the males captured in the MR experimental plot, only five birds (11.4%) were captured previously in neighbouring old plots during the same season. Of all the males previously captured in the nearby

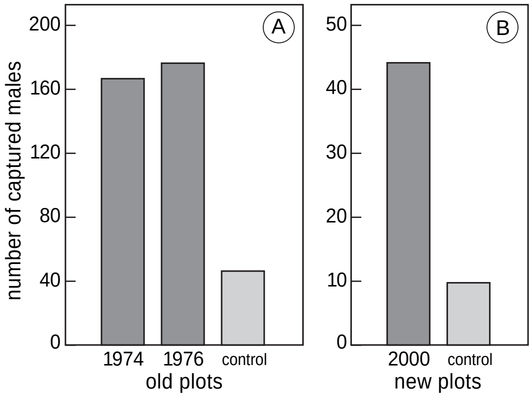

Fig. 1. The number of Pied Flycatcher males captured by traps in empty nest boxes in the experimental and the control plots in the German, Lower Saxony (A), and Russian, Moscow Region (B), study areas. The dark grey bars show the values for the experimental plots, and the light grey bars show the values for the control plots. Long term average number of male breeders occupying the same old plot in non-experimental years was considered as a control value for German data.

old plots within the study area, only 7.8% (n = 54) were recaptured in the experimental plot during the period of the removal experiment. None of the males captured for the first time in the control plot was found later in the experimental plot.

Structure of population surplus

The proportion of yearlings was different among males removed in 1974 and 1976 from the LS experimental plots (56.6%, n = 113 and 36.6%, n =101, respectively, χ^2_1 = 8.6, P < 0.005). Among the removed birds, the proportion of males born in the study area was 66.9% in 1974 and 56.7% in 1976. The average proportion (61.7%) was similar to that in the breeding males before conducting the removal experiments in LS. In MR, the proportion of yearlings among removed males was 52.3%. None of the removed males was born in the study area, what corresponded to the very low recruitment rate in this population (Table 1). The changes of colour type and age structure of the removed males in order of their arrival in LS are shown in figure 2. It is known

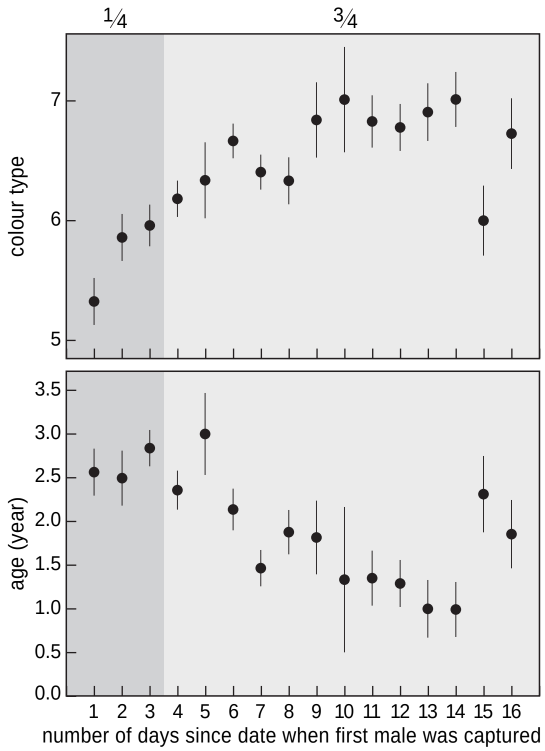

Fig. 2. Mean colour type and age (± SD) of Pied Flycatcher males captured in the experimental plot according to their arrival order in Lower Saxony. The data collected in 1974 and 1976 are combined (n = r347 and n = r 214 for colour type and exact age, respectively). The vertical dotted line shows the day when one-fourth out of all captured males was removed. It was assumed that these males had the highest probability of breeding on the experimental plot during the current season (see the text for explanation).

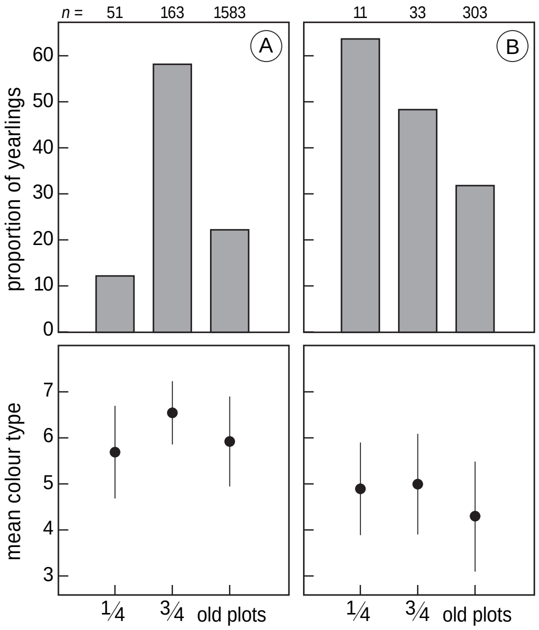

Fig. 3. The proportion of yearlings and the mean colour type (± SD) of Pied Flycatcher males from the first quarter and subsequent three quarters out of the removed birds. The quarters were selected according to the arrival order of the males on the experimental plot in Lower Saxony (see also Fig. 2). Left panels (A) present the data from Lower Saxony, and right panels (B) present the data from Moscow Region. The digits show the sample size.

that males occupying nest boxes earlier have better chances for breeding in a given area than males arriving later. In a comparison between the most likely settlers and the non-breeding individuals we designated the first quarter of the arriving birds as the would-be breeders, and the 75% as the non-breeding surplus. In LS, the proportion of yearlings from the non-breeding surplus markedly exceeded that from the early arrived males (χ^2_1 = 33.7, P < 0.001) and the ratio of yearlings in the breeding males (χ^2_1 = 107, P < 0.001) estimated during the long term population study in this area (see Sternberg 1989) (fig. 3). Plumage of the early arrived birds was more conspicuous than that of later arrived males (Mann-Whitney U Test: $Z_{51, 163}$ = -5.28, P < 0.001). This tendency holds if only the old males were considered (mean (± SD) colour types 5.56 ± 0.97 (n = 45) versus 6.19 ± 0.78 (n = 68); Mann-Whitney U-test: $Z_{45, 68}$ = -3.39, P < 0.001). At the same time, the males belonged to the first quarter of the removed birds did not significantly differ from the males bred in the intact old plots by their age and colour type (Fig. 3). In MR, age and colour type of removed males were not related to their arrival dates. Males captured on the control plot and males

Table 2. The features of the released Pied Flycatcher males of the different reproductive status in Moscow Region.

Features	Subsequent reproductive status of released males		
	Disappeared (*n* = 21)	Stayed in the study area but did not breed (*n* = 11)	Bred (*n* = 12)
Mean (±SD) body mass	12.0 ± 0.5	12.0 ± 0.3	12.1 ± 0.6
Mean (±SD) arrival date (21 April = 1^{st})	19.9 ± 5.4	20.6 ± 6.0	22.8 ± 4.8
Mean (±SD) colour type	5.3 ± 1.1	5.0 ± 1.2	4.3 ± 0.9
Number of yearlings (number of old males)	13 (8)	8 (3)	2 (10)

removed from the experimental plot had a relatively pale plumage and had a high proportion of yearlings in comparison with males settling and breeding in the old plots (t = 4.2, $P < 0.001$ for mean colour type and $\chi^2_1 = 12.4$, $P < 0.001$ for differences in age structure).

Territorial status of released males

After release, a minority of males occupied nest boxes and bred in the experimental and nearby plots in the same season. The proportion of these males was 37.7% out of 162 released males in 1974 and 18.9% (*n* = 175) in 1976 in LS. This difference between the two experimental years was significant ($\chi^2_1 = 14.8$, $P < 0.0001$). Some other released males were found firstly breeding in the study area in subsequent years. Assuming a mean annual mortality of adult birds of 50%, nearly all survivors out of the released males bred in the LS study area in subsequent years. It means that a great majority of males removed in LS study area (on average, 87.2%) must be considered as potential local breeders (fig. 4). In MR, twelve released males (28.6%, *n* = 42) bred in the experimental and neighbouring plots during the season when the removal experiment was conducted (2000). Six more males were found breeding here during the next year (2001). Using the calculations presented in figure 4, we revealed that first-year and second-year breeders must represent 57% (24/42) of released males. The latter proportion is lower than that calculated for the LS group (about 70% of released males during the first two years after the removal experiment, see figure 4). However, this difference between populations seems to be non-considerable because detection of breeders in MR study area was less successful due to the high nest predation (table 1).

Features of released males of different reproductive status

Special attention was paid to the features of the males that bred after their release during the experimental (current) season. In LS, the males which managed to breed in the same season after their release in 1974 were significantly older (2.5 ± 1.4 yr (±SD) versus 1.4 ± 0.9 yr, Mann-Whitney U Test: $Z_{44,64} = -4.1$; $P < 0.0001$) and conspicuously coloured (mean (±SD) colour types 6.0 ± 1. 0 versus 6.4 ± 0.8; Mann-Whitney U Test: $Z_{61, 101} = -2.3$, $P < 0.05$) than non-breeders. The effect of colour type was pronounced independently of age (Mann-Whitney U Test: $Z_{19, 30} = -2.5$, $P < 0.05$ for the sub-samples of old males with stabilised plumage coloration). At the same time, the males that firstly bred during subsequent years did not differ in age and colour type (estimated in 1974) from those that were never found again in the study area because they probably died (average (±SD) values were 1.3 ± 0.68 for age (*n* = 24) and 6.5 ± 0.79 (*n* = 34) for colour type in breeding males versus 1.5 ± 0.96 for age (*n* = 40) and 6.4 ±

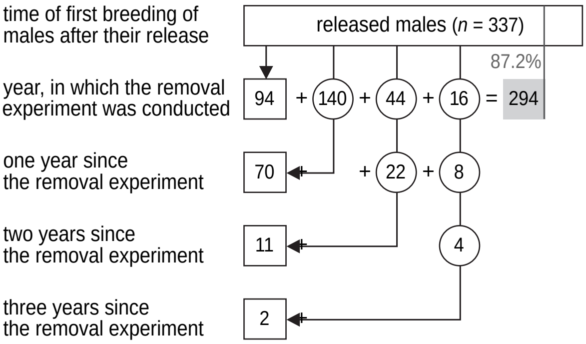

Fig. 4. Flow graph showing the fate of the released Pied Flycatcher males in the year of the experiment and the subsequent years in the Lower Saxony study area. The digits in the rectangles show the number of the released males, which bred in the study area in Lower Saxony (the data of two experiments were combined). The digits in the circles denote the expected number of the released males, which must survive by a given season to produce the corresponding number of breeders in future if the annual mortality is 50% . The digits in the dotted rectangles show the expected proportion of potential local breeders.

0.85 (n = 67) for colour type in disappeared males). However, age and colour type differences between current season breeders and non-breeders were negligible in males released after the removal experiment in 1976 (2.3 yr versus 2.1 yr for age and 6.4 versus 6.4 for colour types, correspondingly).

In MR, three states of the future histories of the released males were distinguished: the males which were not detected after their release in the current season (n = 21); the males which were found in the current season but were not recorded as breeders (n = 11); the males which started to breed in the current season (n = 12). Body mass on the day of capture and arrival dates estimated by dates of first captures were not related to subsequent reproductive status of males during the current season (Mann-Whitney U Test: $Z_{12, 21} = -0.39$, $P = 0.69$ and $Z_{12, 21} = -1,53$, $P = 0.12$ for body mass and arrival date, respectively). The males which were found breeding were older than the disappeared males (Fisher exact two-tailed test: $P < 0.05$) and those males which were thought to be bachelors (Fisher exact two-tailed test: $P < 0.05$). The males which were found breeding had more conspicuous plumage than the disappeared males (Mann-Whitney U Test: $Z_{12, 21} = -2.3$, $P < 0.05$) while non-breeders settled in the study area were coloured intermediately. This difference held in the sub-sample of old males acquiring stable plumage coloration mean ± SD 4.2 ± 0.9 versus 5.4 ± 1.1; Mann-Whitney U Test: $Z_{8,10} = -2.1$; $P < 0.05$).

DISCUSSION

The results show that the two studied Pied Flycatcher populations were similar in the ratios of the number of removed birds and the number of birds settled in the control plots, but differed markedly in their abundance. Two main questions arise from this study. First, do these experiments allow us to detect the actual surplus of non-breeders? If this is true, the second question is: what is the nature of inter-population differences in the surplus size? One can propose that transient migrants, which are not potential local breeders, could be captured in the removal experiment. We consider this unlikely, because the males were trapped in nest boxes. It was shown that inspecting of nest holes was not typical for transient migrants in this species (Sokolov & Vysotsky 1990). According to the data on the subsequent history of released males in LS, nearly all of them sooner or later bred in the study area. This suggests that the sample of removed males must have consisted mainly of potential local breeders.

Alternatively, the replacement of removed males may be explained by the short distance movements of birds primarily settled in neighbouring plots. However, these movements could hardly be considered as a main source of replenishment of the number of the removed males. As shown, a few males that had previously settled in other parts of the MR study area visited the experimental plot later. Thus, the consistent portion of the removed males could be considered as potential competitors for breeding resources within the experimental plot. The number of removed males in relation to the control value may be used as an estimate of non-breeding surplus. The latter ratio equalled to 3.5:1 in LS suggesting that proportion of non-breeding surplus could be calculated as (3.5-1)/3.5. According to the calculation the surplus was about 70% of males staying in this breeding area. Taking into account the small portion of males which could arrive from neighbouring plots, this proportion is rather similar to the value of 60% of males predicted earlier for this local population (Sternberg 1989). Among one-year-old males, the proportion of non-breeders was about 80% (this proportion was calculated using the control value and arrival order in LS experiments). This estimate consists with long-term ratio of non-breeding males in yearlings (83%) calculated on the basis of demographic structure of breeders.

One can propose that those released males which were able to breed during the current season could be regarded as better competitors for breeding resources. These birds tended to be older and more conspicuously coloured than current non-breeders in both study areas. By these features, the successful males were similar to breeders settled in intact plots in both regions. Improvement of competition abilities with age seems to be a general phenomenon in many bird species. It has been shown that conspicuous males arrive earlier on the breeding areas (Jarvi *et al.* 1987), and are more effective in female attraction (Lifjeld & Slagsvold 1988; Sætre *et al.* 1994; Ivankina *et al*. 1995; Ilyina & Ivankina 2001, but see Alatalo *et al.* 1990), more aggressive (Slagsvold & Sætre 1991), and invest more efforts while breeding for the first time (Grinkov 2000; Ivankina *et al.* 2001a) than pale males. It is important to note that even without the advantage of early arrival (-through simultaneous release) both conspicuous and old males were more effective in breeding attempts than pale and young ones.

Substantial differences between the two study areas existed in the surplus size and arrival pattern of removed males in relation to their age and colour type. However, these differences are most likely not to be influenced by regional characteristics of the populations, but by the differences in experimental design. As mentioned above, the experiments in Russia were conducted on a newly arranged plot, while an old plot was used in Germany. In both study areas, lowered breeding densities and high proportion of one-year-old individuals were characteristic of populations formed in new areas in comparison with those existing in older areas (Sternberg 1972; Ivankina *et al.* 2001b). Hence, the small sample size of males removed in the Russian population could be affected by plot novelty in this study area. Both populations were similar in their age dependent pattern of arrival order in males settled in intact old plots. In both regions, new plots were occupied by younger and more pale males than old ones. Therefore, the absence of arrival asymmetry in age and colour type of males removed from MR plot as well as their resemblance to those captured in control plot could be explained by distinctive features of males colonising new areas.

It is of interest to note that similar proportions of proposed non-breeders were found in situations of high and low occupation rates of plots. The results of our removal experiments suggest that the effect of displacement of potential breeders due to competition may occur even in non-saturated areas. The results also suggest that a high portions of non-breeders and as a consequence a delay in the start of first breeding may occur both at high and low population densities. The mechanisms which refrained birds from breeding in case of low population densities are not quite clear. Clarification of these mechanisms requires further investigations including experiments carried out in plots with the same occupation rate or/and with the same history.

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REFERENCES

Alatalo R.V., A. Lundberg & J. Sundberg 1990. Can female preference explain sexual dichromatism in the Pied Flycatcher, *Ficedula hypoleuca*. Anim. Behav. 39: 244-252

Anorova N.S. 1976. Breeding of Pied Flycatcher depending on age of birds. Ornitologiya 12: 77-86. (In Russian).

Berndt R. & H. Sternberg 1968. Terms, studies and experiments on the problems of bird dispersion. Ibis 110: 256-269.

Drost R. 1936. Über das Brutkleid männlicher Trauerfliegenfänger, *Muscicapa hypoleuca*. Vogelzug 6: 179-186.

Grinkov V.G. 2000. The conditions of maintenance of stable phenotypic population structure: with reference to variation of male plumage colour in Pied Flycatcher (*Ficedula hypoleuca Pall*.). Author's abstract of the dissertation on competition for an academic degree of a Candidate of biological sciences. M.: Moscow State University. [In Russian].

Ilyina T.A. & E.V. Ivankina 2001. Seasonal variation of singing activity and relative effect of advertising behavior of males with different plumage color in the Pied Flycatcher (*Ficedula hypoleuca*). Acta Ornith. 36: 85-89.

Ivankina E. V., T. A. Ilyina & A. B. Kerimov 1995. The male plumage variability and the strategy of attracting a female: the estimation of the advertising behaviour's spatial organisation in bright and cryptically coloured Pied Flycatcher males (*Ficedula hypoleuca, Passeriformes, Aves*). Zhurnal Obshchey Biollogii 56: 762-775. [In Russian].

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

Ivankina E.V., H. Sternberg, A.B. Kerimov, T.A. Ilyina, V.G. Grinkov & A. Schwarz 2001b. Features of new populations of the Pied Flycatcher in Russia and Germany. The avian calendar: exploring biological hurdles in the annual cycle. Third Conference of the European Ornithologists' Union. Programme and Abstracts. Haren/Groningen, The Netherlands

Järvi T., R. Røskaft, M. Bakken & B. Zumsteg 1987. Evolution of variation in male secondary sexual characteristics. A test of eight hypotheses applied to Pied Flycatcher. Behav. Ecol. Sociobiol. 20: 161-169.

Lifjeld J.T. & T. Slagsvold 1988. Female Pied Flycatcher *Ficedula hypoleuca* choose male characteristics in homogeneous habitats. Behav. Ecol. Sociobiol. 22: 27-36.

Lundberg A. & R.V.Alatalo 1992. The Pied Flycatcher - T. and A.D. Poyser, London.

Payevsky V.A. 1985. Demography of birds. Proc. of Zoology Institution of USSR Acad. of Sci., 125. Leningrad, Nauka. [In Russian].

Polivanov V.M. 1957. Local populations in birds and their stability. In Proc. of Darwinian State Reserve. Vologda 4: 79-155. [In Russian].

Sætre G-P., S. Dale & T. Slagsvold 1994. Female Pied Flycatchers prefer brightly coloured males. Anim. Behav. 48: 1407-1416.

Slagsvold T. & G-P. Saetre 1991. Evolution of plumage color in male Pied Flycatchers (*Ficedula hypoleuca*): evidence for female mimicry. Evolution 45: 910-917.

Sokolov L. 2000. Philopatry, dispersal and population structure of passerines on the Courish Spit of the Baltic Sea. Vogelwarte 40: 302-314.

Sokolov L.V. & V.G. Vysotsky 1990. The accuracy of the spring migratory navigation in the adult and subadult Pied Flycatchers (*Ficedula hypoleuca*) and Chaffinches (*Fringilla coelebs*) at the Courish Spit of Baltic Sea. Ecology, migration and protection of baltic birds. Proc. of the Fifth Conf. on the Study and Conservation of Migratory Birds of the Baltic Basin ('Baltic Birds-5', Riga, 5-10 October, 1987), (2): 163-167. Zinatne, Riga.

Sternberg H., 1972. The origin and age composition of newly formed populations of Pied Flycatcher *Ficedula hypoleuca*. Proc. Int. Orn. Congr. 15: 690-691.

Sternberg H. 1989. Pied Flycatcher. In: Newton I. (ed.) Lifetime reproduction in birds: 55-74. : Academic Press, London.

Vysotsky V.G. 1989. Ageing of Pied Flycatcher (*Ficedula hypoleuca*) during breeding period. In Proc. Zool. Inst. of USSR Science Academy 'Fauna and Ecology of Eurasian birds', 197: 49-52. [In Russian].

SAMENVATTING

In Nedersaksen, Duitsland, komt ongeveer 80% van de eerstejaars mannetjes van de Bonte Vliegenvanger *Ficedula hypoleuca* niet tot broeden. In 1974 en 1976 zijn hier in een onderzoeksgebied (LS) waar al langere tijd nestkasten werden gebruikt, gedurende 2-3 weken voorafgaande aan de broedperiode alle mannetjes die aankwamen, dagelijks weggevangen en tijdelijk in een volière bewaard. In 2000 is dat ook gebeurd in een gebied rond Moskou (MR), waar dat jaar voor het eerst nestkasten waren opgehangen De vogels werden twee tot drie dagen voor de mediane eilegdatum in nabijgelegen controle plots weer losgelaten. De twee onderzochte populaties bleken een gelijke leeftijdsopbouw te hebben, maar verschilden in het aandeel ter plekke geboren jongen dat in de populatie als broedvogel terugkeerde (9% tegen <1%). In beide onderzoeksgebieden was het aantal weggevangen mannetjes in de experimentele plots vier keer groter dan het aantal mannetjes dat zich als broedvogel in controle plots vestigde. Hoewel de verhouding tussen het aantal broeders en niet-broeders in beide gebieden gelijk was, werden in LS vier keer zoveel mannetjes verwijderd in vergelijking tot MR. Waarschijnlijk komt het kleine aantal in MR door de veel lagere nestkastbezetting in dit gebied. Na het vrijlaten broedde een deel van de mannetjes alsnog in het onderzoeksgebied. Het percentage was voor LS en MR gelijk. In LS keerde een extra deel van de vrijgelaten vogels in de volgende jaren terug als broedvogel. Als verondersteld wordt dat de jaarlijkse overleving van adulte vogels 50% is, dan kan berekend worden dat bijna alle overlevende individuen van de verwijderde vogels uiteindelijk in het studiegebied in LS tot broeden kwamen. Hoewel voor MR er minder jaren verstreken zijn na het wegvangexperiment, lijkt hier het percentage vogels dat als broedvogel terugkeerde, gelijk te zijn aan LS. In beide populaties waren de weggevangen vogels die na loslating in hetzelfde jaar toch nog tot broeden kwamen, ouder en donkerder gekleurd dan de niet-broeders. Deze resultaten laten zien dat zowel bij een hoge (LS) als bij een lage (MR) dichtheid aan Bonte Vliegenvangers een hoog percentage mannetjes niet tot broeden komt en het broedproces bij vogels die hieraan voor de eerste keer deelnemen, op een later tijdstip kan beginnen.. (CB)