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Factors responsible for the long-term dynamics of the Pied Flycatcher *Ficedula hypoleuca* populations in the taiga of Karelia, Russia

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Abstract. A Pied Flycatcher population breeding in nest-boxes in a Karelia forest was studied from 1981 to 2007. Breeding density varied between 47.3 and 94.6 pairs/km^2. The density of the breeding population was influenced by three demographic factors: maximum summer population density in the previous season, male return rate and immigration rate. Three relatively independent processes play a significant part in the population dynamics of the study area: 1) initial abundance and reproductive intensity, 2) survival rate between breeding seasons, and 3) redistribution of birds across their range. The weather in spring, when the birds arrive and settle, was found to be equally important. The population density, nest site fidelity of adults and yearlings, and immigration rate were related to temperature patterns in May. It may be assumed that the spring weather influences the birds' survival and their distribution across the northern part of their range, as well as the participation of one-year old birds in breeding.

Key words: Pied Flycatcher, *Ficedula hypoleuca*, abundance, dynamics, demography, weather, ambient temperature

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INTRODUCTION

The problem of dynamics of avian numbers has been discussed in many general and specialised publications (Lack 1966, Haartman 1971, Stenning et al. 1988, Winkel 1989, Newton 1998, Sokolov 2000, Thingstad et al. 2006). However, many questions still remain unanswered, as relative importance of different factors that shape population dynamics may vary due to regional and local conditions in different parts of the species range. It is commonly assumed that in peripheral populations, bird numbers are more strongly dependent on extrinsic factors than in the core part of the range (e.g. Mayr 1970, Järvinen 1989).

The Pied Flycatcher has a large breeding range. It extends from Tunisia (35°N) to northern Scandinavia (70°N) and from the Atlantic coast to the valley of the Yenisey (Cramp & Perrins 1993, Glutz von Blotzheim & Bauer 1993). Detailed studies of the population dynamics of this species were performed in Central Europe, Britain and in Fennoscandia (e.g. Lack 1966, Stenning et al. 1988, Järvinen, 1989, Winkel 1989, Thingstad et al. 2006, Nilsson 2008). In relation to the region and parameters analysed, factors that significantly influenced the dynamics of different populations varied. For example, in southern England the most important factors governing breeding density were population the density during the preceding summer season and immigration rate (Stenning et al. 1988). In Finnish Lapland such factors were the weather and breeding performance (Järvinen 1983, 1989), in Brunswick (Germany) breeding performance and droughts in the Sahel (Winkel 1989). Population dynamics of Pied Flycatchers in northern Scandinavia was governed by immigration rate from more southern areas (Thingstad et al. 2006).

Karelia lies in the northern part of the Pied Flycatcher range. Living conditions here are less optimal than in central Europe, but are less severe than in northern Scandinavia. Therefore, a detailed analysis of fluctuations of breeding density in this region is of certain interest.

The aim of this study was to isolate the main factors that influence the dynamics of the local population and to estimate contribution of each factor to the fluctuations of the breeding density. To do this, I analysed parameters that characterize population density and reproduction rate in the preceding season, the composition of the breeding population (proportions of immigrants, residents, and autochthons), return rate to the site of birth or previous breeding, weather conditions of the current breeding season. Some of these factors had been included into analyses by other authors, but no analysis has been performed that would include all of them.

MATERIALS AND METHODS

The paper is based on the results of monitoring the Pied Flycatcher population in taiga forests of Karelia (Mayachino field station, 60°46´N, 32°48´E) in 1979–2007. My study was carried out in forest types typical of the Lake Ladoga area. Nest-boxes were provided in mature pine and spruce stands with small admixture of birches (pines 120–130, spruces 80–100 years old), in pine and deciduous mixed forests (70–80 years old), deciduous and spruce mixed forests, black alder stands (70–80 years old), and in young and submature pine and deciduous forests (20–50 years old, with pines, birches, spruces and aspens). A detailed description of the study area and methods has been published elsewhere (Artemyev 1998, 2002).

In a forest plot of the total area of ca. 10 km^2, nest boxes were provided. Some 40–50 pairs breed in these 10 km^2 in natural cavities, whereas on average 100 pairs/year bred in nest-boxes. In the nest boxes, all nests were checked, most adults were captured and 98% of nestlings were ringed (Table 1). A pair was considered as a breeding pair if the female laid at least one egg. Some "pairs" were incomplete, as 6% of males were polygynic. A foraging area of a Pied Flycatcher is usually an area within 50 m from its nest. Therefore, to calculate the population density were only included the area of the nearest vicinity of nest boxes: forest belt with the width of 100 m along the nest-box lines (50 m from the each side). In northern Europe, hole or nest-box availability is an important factor limiting numbers of hole breeders (Haartman 1971, Lundberg & Alatalo 1992). In my study area, Pied Flycatchers occupied 23–42% of nest boxes, occupancy by other species did not exceed 12%. Therefore, at least one-half of nest boxes remained vacant each year, so that population growth was not limited by nest-box availability.

Following other studies of the Pied Flycatcher demography (Stenning et al. 1988, Sokolov 1991), breeding individuals were classified into three categories in relation to their residence status: immigrants, residents, and autochthons. Immigrants are all birds not born in the study area and breeding there for the first time. Residents are all birds that have bred in the study area previously but were not born there. Autochthons are all breeding birds that were born in the study area.

Male (female) return rate was calculated as the percentage of breeders that had been marked in the previous season as adults and returned to the study area, corrected for the capture probability. On average 79% of males and 91% of females

Table 1. Main parameters of the study plot and the population studied in 1981–2007.

Parameter	Mean ± SE	Min.	Max.
Number of nest boxes	323 ± 7.9	267	401
Area occupied by nest boxes (ha)	145 ± 3.1	119.7	169.4
Number of breeding females	103 ± 5	60	158
Breeding population density (pairs/km^2)	70.6 ± 2.6	47.3	94.6
Summer density (fledglings + adults/km^2)	462.1 ± 18.9	319.1	669.5
Breeding success (No of fledglings/No of eggs)(%)	75.4 ± 1.3	59.9	88.9
Proportion of successful nests (%)	82.1 ± 1.5	64.3	93.9
No of fledglings raised per one female	4.6 ± 0.1	3.29	5.8
Captured males (%)	79.7 ± 2.3	64.2	98.7
Captured females (%)	90.7 ± 1.2	82.4	100
Male return rate (%)	41.4 ± 1.7	23.87	61.1
Female return rate (%)	16.7 ± 0.9	5.63	26.5
First-year recruits rate (%)	1.0 ± 0.1	0	2
Onset of the first clutch (1–1 May)	20 ± 0.8	10	27
Mean monthly air temperature in May (°C)	9.3 ± 0.3	5.7	11.9
Mean daily temperature in 11–20 May (°C)	9.0 ± 0.5	4	14.9

were controlled in nest-boxes. Correction factor depended on the annual percentage of breeders captured. (If among 80 birds trapped, 40 carried rings of the previous year, and 80% of breeding birds were captured, I assumed that among the 20 individuals that escaped capture, 10 had been ringed. Therefore I assumed that the number of Pied Flycatchers ringed in the previous year and returned was in fact 50. This figure was used to calculate return rate).

First-year recruitment rate was calculated as the percentage of breeding autochthonous yearlings of the fledglings' number recorded in the previous year. Summer population density (after Stenning et al. 1988) is the sum of adult breeders and fledglings per unit area.

The data for 27 years, 1981–2007, were included in the analysis. All parameters were lumped into four relatively independent groups, parameters that: 1) characterised population density and reproductive performance in the previous year (number of fledglings per breeding pair and per 1 ha, percentage of successful nests, number of fledglings per egg laid); 2) characterised the breeding population composition in the current year (number of immigrants, residents, and autochthons); 3) are related to site fidelity and local survival rate (return rate of adults and nestlings); 4) characterised weather conditions and included mean monthly and 10-day average air temperatures in April and May. In each group, the most significant factors were identified, and then their contribution to the population dynamics was estimated.

Correlation (Spearman's rank correlation) and regression analyses were used as implemented in the Statgraphics statistical package. In multiple regression analysis, standardised deviations from the parameters analysed were used as the function and variables. Deviations were standardised following the formula $(X_i–M)/S$, where X_i was the parameter value, M was its mean, and S was standard deviation.

RESULTS

Impact of demographic parameters on population dynamics

Reproduction rate and population density in the preceding season. Reproduction rate parameters, such as the number of fledglings raised per breeding pair per season and the breeding success rate (number of fledglings per number of eggs laid), varied strongly on the annual basis. However, these factors did not help explain population density in the subsequent year (Table 2). Breeding density in a current year was related only to such parameters of the previous breeding season as the breeding density and population density after fledging (Fig. 1). Stepwise regression analysis of these factors showed that the most significant

Table 2. Correlations between the breeding population density and some population and weather parameters in 1981–2007. * factors that enter to stepwise regression analysis.

Parameter	r_s	p
Year	-0.26	0.1
Previous season		
breeding population density (pairs/km^2)	0.53	< 0.01
breeding success (No of fledglings/No of eggs)	-0.11	0.29
proportion of successful nests (%)	0.03	0.44
no of fledglings raised per one female	0.01	0.49
density of fledglings (fledglings/km^2)	0.52	< 0.01
summer density (fledglings + adults/km^2)*	0.57	< 0.001
Structure of population		
no of immigrants *	0.87	< 0.0001
no of residents	0.62	< 0.001
no of autochthons	0.59	< 0.001
Recruitment and survival		
male return rate *	0.61	< 0.001
female return rate	0.12	0.27
first-year recruits rate*	0.37	< 0.05
Weather conditions		
mean ambient temperature in May	0.3	0.06
mean daily temperature in 11–20 May *	0.39	< 0.05

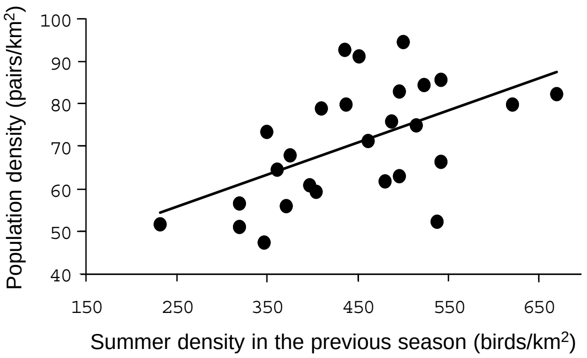

Fig. 1. Breeding density of Pied Flycatchers in Karelia in relation to the summer population density in the previous season.

effect on the population density was produced by summer population density in the previous season ($y = 0.001 + 0.54x$; $R^2 = 28.9$, $p = 0.004$).

Structure of the breeding population. The local population annually recruited a significant number of immigrants that had hatched outside the study plot. In the study plot, immigrants comprised ca. 70% of the local population (Fig. 2). Population density was directly related to the numbers of birds of all three categories: immigrants, residents, and autochthons (Table 2). Stepwise regression analysis showed that the only significant factor contributing to variation of population density was the number of immigrants ($y = -0.001 + 0.86x$, $R^2 = 73.1$, $p = 0.0001$).

Site fidelity and survival rate. Site fidelity is related to the immigration rate and survival rate outside the breeding season. In Karelia, return rate of adults and yearlings was positively related to breeding density (Table 2). Stepwise regression

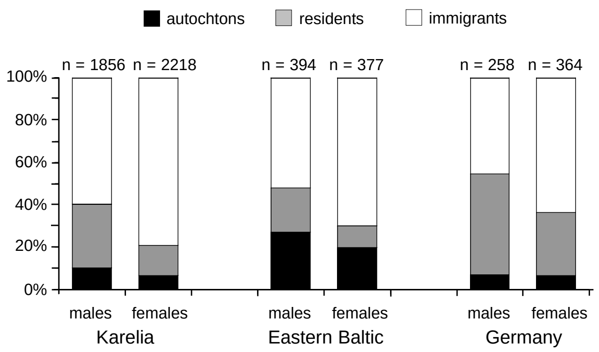

Fig. 2. Proportions of autochthons, residents, and immigrants in the breeding Pied Flycatcher populations in Karelia (1981–2004, this study), on the Courish Spit, Eastern Baltic (1983–1988, Sokolov 1991) and in NW Germany (1976–1981, Winkel 1982).

analysis yielded the equation that showed the relationship between population density and site fidelity of birds of different sex and age ($y = 0.001 + 0.49$male return rate $+ 0.31$recruiting index of yearlings, $R^2 = 42.5$, $p = 0.0013$). Most surviving adult males return to their breeding areas, therefore male return rate is actually an index of their survival rate. This parameter is positively related to the overall number of resident birds of both sexes in the breeding population ($r_s = 0.43$, $p < 0.01$), and to the number of immigrants ($r_s = 0.51$, $p < 0.01$). It is probably a proxy to the overall survival rate of adults between the breeding seasons.

Autochthonous birds play a limited role in the breeding population dynamics. However, yearling recruiting rate was positively related to the number of immigrants ($r_s = 0.59$, $p < 0.001$). This parameter apparently reflects survival rate of birds during their first winter. Therefore, the relative number of recruits not only characterises the contribution of autochthonous yearlings to the local population dynamics, but is a proxy to the intensity of immigration of yearlings. The equation obtained actually shows the relationship between population density and survival rate of different age groups outside the breeding season.

Analysis of combined impact of the main demographic parameters on the numbers of Pied Flycatchers revealed that that summer density (x_1) was responsible for 15.7% of variation, male return rate (x_2) for 18.7%, and the number of immigrants (x_3) for 49.7%. It yielded regression equation that most completely characterised population dynamics in my study area H: $y = -0.001 + 0.23x_1 + 0.31x_2 + 0.62x_3$; ($R^2 = 84.1$, $p = 0.0001$).

Impact of the spring weather on population dynamics

In Karelia, breeding density was related to air temperature in the second 10-day period of May. This is the period when the bulk of birds arrives and settles in the area (Fig. 3). To estimate the combined contribution of the demography and weather factors to variations in the density of the local bird population, we performed a two-factor regression analysis with the summer population density in the previous season (x_1) (the main variable that characterises reproduction effort) and mean ambient temperature in the second 10-day period of May (x_5) as variables. The equation has the form of $y = 0.001 + 0.42\,x_1 + 0.26\,x_5$ ($R^2 = 34.4$, $p = 0.009$). ANOVA analysis showed that the first

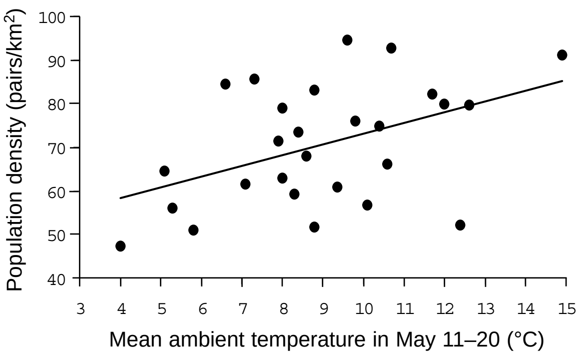

Fig. 3. Population density of Pied Flycatchers in Karelia in relation to the mean ambient temperature in the second 10-day period of May.

factor was responsible for 21.6% of variation, and the second one for 12.8%.

These calculations show that the weather has a weaker impact on bird numbers than reproduction rate. However, in my calculations I did not take into account the fact that May air temperatures also influenced the main demographic parameters that govern population dynamics. Summer population density (x_1) included into the equation was itself dependent on the weather in the current season, as it was positively related to the mean air temperature on 11–20 May ($r_s = 0.46$, $p < 0.01$). Air temperature in this period was also positively correlated with other demographic variables: number of immigrants ($r_s = 0.52$, $p < 0.01$), number of residents ($r_s = 0.43$, $p < 0.01$) and autochthons ($r_s = 0.45$, $p < 0.01$), and the yearling recruiting index ($r_s = 0.31$, $p = 0.06$).

DISCUSSION

A high breeding success rate is characteristic of the studied local Pied Flycatcher population breeding in nest-boxes (Table 1). Failed nests make up just ca. 18%, and only one-half of losses may be attributed to predation. Unlike other parts of the breeding range where cavity nesters suffer large losses to predation (Walankiewicz 2002, Czeszczewik 2004, Czeszczewik et al. 2008), diversity and numbers of predatory animals in the study region are small. Therefore, they do not play a significant role in the population dynamics of Pied Flycatchers.

The analysis of different parameters characterising reproduction rate in the population the study showed that the main factor affecting Pied Flycatcher numbers in the subsequent breeding season in Karelia was population density in the end of the breeding season. This is probably one of the main components of dynamics of Pied Flycatcher numbers within the whole of its range. The same parameter was the most important one for population dynamics in southern England (Stenning et al. 1988). Relationships between Pied Flycatcher numbers and other parameters that characterise population density at the end of the preceding breeding season have been reported from different regions. In Finnish Lapland it was the overall number of fledglings produced (Järvinen 1989), in the Brunswick region (Germany) the number of successful nests in the study plot (Winkel 1989), on the Courish Spit in western Russia the number of juveniles captured during the postfledging period (Sokolov 2000).

The bulk of the Pied Flycatcher breeding population in Karelia consisted of immigrants, and this cohort played the lead role in the fluctuations of numbers. In different parts of the range Pied Flycatcher breeding populations include 50–70% of immigrants (Fig. 2). In more southern parts of the range the proportion of immigrants was smaller, but their impact on the numbers was still apparent. In the Dean forest in southern England immigrants comprised ca. 49% of breeders, but their contribution to population dynamics was not smaller than that of the reproduction rate (Stenning et. al. 1988).

Significant contributions to the fluctuation of numbers in the population under study were also made by parameters that reflected survival rate of adults and juveniles, i.e. by male return rate and first-year recruits rate.

The results of multivariate analyses of the various demographic parameters showed that the dynamics of the local population could be described following the classic pattern. Three comparatively independent processes play the main role in the population dynamics: initial numbers and reproduction rate; survival rate between the breeding seasons and spatial movements (immigration and emigration). My calculations made it possible to estimate the contribution of each factor to the dynamics of the local population. In Karelia the main input is made by immigration rate. Smaller and similar inputs are made by the factors related to reproduction rate and survival rate.

Spring weather in Karelia influences the process of reproduction (Artemyev 2002) and the breeding density. A direct influence of the spring weather on the Pied Flycatcher breeding density has been found in other parts of the range. In particular, in Finnish Lapland bird numbers were correlated with the mean daily temperatures in late May-early June and across June, with the weather being the main factor governing population dynamics (Järvinen 1983, 1989). On the Courish Spit (Eastern Baltic) the numbers of breeders at the study plot were related to April temperatures (Sokolov 2000). A comparison of the original and literature data reveals that the strongest influence on the dynamics of avian numbers has the weather in spring and early summer. In Karelia the most important period is 11–20 May when Pied Flycatchers arrive and settle. Unlike Finnish Lapland, in Karelia the spring weather is not the key factor of population dynamics. However, it is not less important than demographic variables that play the decisive role for population dynamics, as they themselves are related to spring temperatures.

In spite of numerous reports that spring weather influences breeding density in many avian species, the mechanism underlying this process still remain obscure. It is commonly assumed that the weather conditions influence the survival rate in spring. In some migratory birds the mortality rate of yearlings was shown to increase strongly during spring arrival and settlement, leading to elimination of the 'population surplus' (Payevsky 1985, 1999).

In Karelia, breeding density of Pied Flycatchers drops after cold springs. Recruiting rate of yearlings and immigration rate declines. However, this decline might be due not only to the increased mortality rate of yearling birds, but also due to the increased proportion of non-breeding second-year birds. In the Pied Flycatcher a proportion of birds each year do not breed and form population reserve. In the Brunswick region in Germany ca. 60% of Pied Flycatcher males and 40% of females, mainly yearlings, do not breed (Sternberg 1989). It cannot be ruled out that apart from other factors, the spring weather is important for the decision of juveniles to take part in reproduction. Temperature regimen of spring is known to influence the rate of physiological processes related to breeding (Silverin 1995, Meijer et. al. 1999). Therefore, the spring weather may influence not only survival rate, but also the physiology of yearlings. They might stimulate or inhibit reproduction in birds and thus shift the balance between breeders and non-breeders.

The impact of the spring weather on population numbers may also work through the redistribution of the birds across the breeding range. It has been shown in various avian species that in cold springs, migrants do not reach the northernmost parts of the range and breed further south (Danilov 1966, Ryabitsev 1993). It cannot be ruled out that a similar process takes place in the northern part of the Pied Flycatcher range.

The aforementioned data are just some of the possible mechanisms of spring weather impact on the birds. They are not mutually exclusive and it cannot be ruled out that the weather influences mortality rate, the proportion of non-breeders, and the distribution of the breeders across the range. The relative importance of different factors most probably varies between the populations. However, further studies, including experimental physiological work, are needed to decipher the mechanisms of the spring weather influence on the birds.

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STRESZCZENIE

[Czynniki wpływające na dynamikę liczebności muchołówki żałobnej w tajdze Karelii]

Karelia znajduje się na północnym skraju zasięgu muchołówki żałobnej. Warunki tu panujące są mniej optymalne niż w Europie Środkowej, ale łagodniejsze niż w Skandynawii. Możliwe więc, że znaczenie poszczególnych czynników wpływających na liczebność tutejszej populacji może różnić się w porównaniu do innych terenów. Na terenie ok. 10 km^2 rozwieszono ponad 250 skrzynek lęgowych (Tab. 1). Populacja ptaków je zasiedlających badana była w latach 1981–2007. Skrzynki były kontrolowane, aby zebrać podstawowe dane o biologii lęgów, znaczna większość piskląt była obrączkowana, chwytano także ptaki dorosłe. Pozwoliło to dość dobrze scharakteryzować badaną populację (Tab. 1).

W pracy analizowano wpływ na dynamikę liczebności czterech grup czynników: zagęszczenia i wyników lęgów w poprzednim roku, charakterystyki demograficznej populacji w danym roku, przeżywania i przywiązania do terenu oraz pogody.

Stwierdzono, że zagęszczenie populacji zależne było od maksymalnej liczebności muchołówek na koniec poprzedniego sezonu lęgowego (łącznie liczone ptaki dorosłe oraz podloty) (Fig. 1), powracalności samców oraz udziału imigrantów (Tab. 2). Imigranci — osobniki, które nie gniazdowały wcześniej lub nie wykluły się na danej powierzchni stanowiły ok. 70% populacji lęgowej, co jest jednym z najwyższych wyników stwierdzanych w Europie (Fig. 2). Istotny wpływ na liczebność populacji miała temperatura drugiej dekady maja, w okresie przylotu ptaków z zimowisk i zajmowania terytoriów (Fig. 3). Autor wskazuje, że pogoda (temperatura) ma wpływ na przeżywanie ptaków, udział ptaków dwuletnich w rozrodzie oraz przywiązanie do terenu i rozmieszczenie osobników.

Tak wiec na liczebność populacji muchołówki w Karelii najważniejszy wpływ ma liczebność i wyniki lęgów w poprzednim sezonie, przeżywalność oraz przemieszczenia ptaków w obrębie areału.