SEX-RELATED NATAL DISPERSAL OF PIED FLYCATCHERS: HOW FAR AWAY FROM HOME?

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Abstract. Over four years, nestling Pied Flycatchers (*Ficedula hypoleuca*) were banded and recaptured in nest boxes at a 44 km long and 1–1.5 km wide study area along the Courish Spit on the southeast Baltic coast. The return rate for males was nearly twice as high as for females. Males settled significantly closer to their natal sites than predicted by the null model, which assumed that any nest box in the study area was selected at random. For females, the frequency distribution of natal dispersal distances was not significantly different from that predicted by the null model. The difference in average dispersal distance between the sexes was highly significant. Although some individuals settled within tens of kilometers, most male Pied Flycatchers settled within several kilometers of their natal sites. We suggest that even if females settle on average farther from their natal sites than males do, both sexes imprint on a relatively small (several kilometers in diameter) area during postfledging exploration, to which they return each spring.

Key words: natal dispersal, Pied Flycatcher, return rate, sex bias.

Dispersión Natal Relacionada con el Sexo en *Ficedula hypoleuca*: ¿Qué tan Lejos del Hogar?

Resumen. A lo largo de cuatro años, se anillaron y recapturaron pichones de *Ficedula hypoleuca* en cajas de nidificación ubicadas en un área de estudio de 44 km de largo y 1–1.5 km de ancho a lo largo del Courish Spit, en la costa sureste del Báltico. La tasa de retorno de los machos fue casi el doble que la de las hembras. Los machos se establecieron significativamente más cerca de sus sitios natales en comparación con lo predicho por un modelo nulo que suponía que las cajas de nidificación eran escogidas al azar. Para las hembras, la distribución de frecuencias de las distancias de dispersión no fue significativamente diferente de la predicha por el modelo nulo. La diferencia en la distancia promedio de dispersión entre los sexos fue altamente significativa. Aunque algunos individuos se establecieron a decenas de kilómetros de sus sitios natales, la mayoría lo hicieron a unos pocos kilómetros de éstos. Sugerimos que aún si las hembras se establecen en promedio más lejos de sus sitios natales que los machos, ambos sexos se fijan mediante impronta a un área relativamente pequeña (de varios kilómetros de diámetro) durante sus exploraciones posteriores al abandono del nido, y regresan a estas áreas cada primavera.

Dispersal behavior is fundamental to all organisms and a major determinant of many basic patterns and processes (Walter 2000). Natal dispersal is the movement between the places of birth and first breeding, which to a large extent governs the dynamics and genetic structure of populations (Johnson and Gaines 1990, Whitlock 2001). Natal dispersal patterns may have serious microevolutionary implications for avian populations (Garant et al. 2005, Postma and van Noordwijk 2005). Even though a great number of studies have dealt with natal dispersal distances (Swingland 1983, Clobert et al. 2001), many were performed in study plots too small to detect individuals that disperse longer distances (Hanski and Gilpin 1997, Clobert et al. 2001).

The Pied Flycatcher (*Ficedula hypoleuca*) has been the subject of many population studies in Europe (Lundberg and Alatalo 1992). Most estimates of the mean natal dispersal distance of Pied Flycatchers do not exceed several kilometers. However, observed return frequencies never exceed 14% (Lundberg and Alatalo 1992), which means that many birds might breed away from their natal areas. If the breeding population remains stable, this emigration has to be compensated for by immigration, thus actual natal dispersal distances must be much larger than hundreds of meters or several kilometers.

Artemyev (1994) argued that anecdotal cases of long-distance dispersal reported for the Pied Flycatcher in fact represent a frequent phenomenon. This author suggested that second-year birds settle within hundreds of kilometers of their natal site, not just several kilometers as suggested by most studies (reviewed by Lundberg and Alatalo 1992). Vysotsky

(1994) argued against this viewpoint and suggested that long-distance dispersal was an exception, rather than the rule, in European Pied Flycatcher populations.

However, Vysotsky (2000, 2001) subsequently reanalyzed the data on natal dispersal of Pied Flycatchers collected in the southeastern Baltic in 1982–1995 and accepted the hypothesis of frequent long-distance dispersal. Vysotsky (2000) showed that the frequency distribution of natal dispersal distances in his 9 km long study plot on the narrow Courish Spit did not differ significantly from the distribution expected if Pied Flycatchers were randomly distributed in relation to their natal sites. The author thus suggested that, in contrast to earlier beliefs (Löhrl 1959, Berndt and Winkel 1979, Sokolov et al. 1994), juveniles of both sexes do not imprint on any small area during the postfledging period, but are rather distributed randomly across an area some 50–100 km in length.

It is well established that size of the survey area is crucial when estimating dispersal distances, and that estimates based on data from areas that are too small may be seriously biased (Hanski and Gilpin 1997, Clobert et al. 2001). We believe that most controversy concerning the scale of natal dispersal in birds and other animals is due to small study plots in most studies and detection probabilities dropping sharply from the center to the periphery of these plots. A method has been suggested to correct for the underestimate of dispersal on the basis of detection probability (Baker et al. 1995, Koenig et al. 2000). However, this useful approach is limited by the assumption that no significant dispersal occurs at distances farther than the largest dimension of the study area. To circumvent this problem, we used a comparatively large study plot and compared the actual distribution of dispersal distances with a null model that assumed random settlement within our study area.

The aim of this study was to test whether Pied Flycatchers which returned to breed in our study plot were randomly distributed across it, or whether they tended to settle closer to their natal sites than predicted by the null model. We also tried to estimate the effective natal dispersal distance in our Pied Flycatcher population to answer the question: how large is the area occupied by a local population? Is it measured by dozens, hundreds, or tens of thousands of square kilometers?

METHODS

STUDY AREA

The Courish Spit is a long and narrow strip of land stretching 100 km along the southeastern Baltic Coast. It is 1–1.5 km wide in most areas (max. = 3.8 km). The spit separates the Courish Lagoon from the Baltic Sea, with its northern half belonging to Lithuania and the southern half to the Kaliningrad region of Russia. The Courish Spit is forested, containing both deciduous and coniferous forests, mainly Scots pine (*Pinus sylvestris*) and mountain pine (*P. montanus*). For a detailed description of the study area, see Payevsky
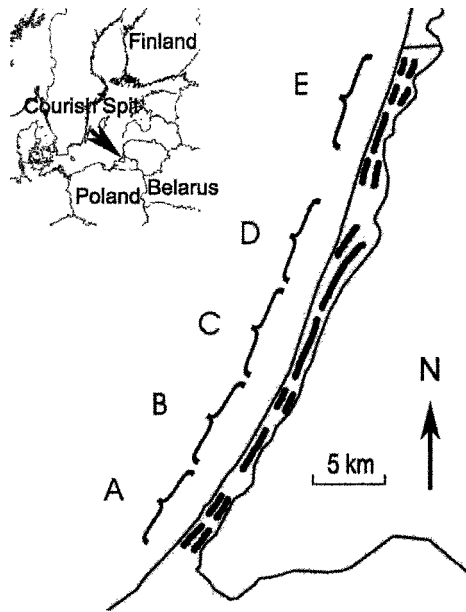

FIGURE 1. Location of the Courish Spit on the southeast Baltic Coast and the position of study plots where Pied Flycatchers were banded (1999–2003) and recaptured (2000–2003). Shaded areas are the lines of nest boxes. There were 200 nest boxes in study plots A, C, and D, 300 in plot C, and 440 in plot E.

(1999). Due to the physical features of the spit, our study site was practically linear (Fig. 1). It is thus more appropriate to speak of its length than of its area.

In 2000, 1040 nest boxes were provided in study plots A, B, D, and E. In addition, 300 nest boxes had been available to the birds since 1981 in the 9 km long plot C (Vysotsky 2000). Thus, the new, enlarged study area included nearly the whole Russian-owned portion of the Courish Spit, was 44 km long, and included 1340 nest boxes. GPS-based coordinates of each nest box were available, which made it possible to calculate the exact distance between any pair of nest boxes.

FIELD METHODS

We tried to capture all male and female Pied Flycatchers breeding in nest boxes in our study area, and to band all nestlings shortly before fledging. Nest fate (fledging success) was assessed after chicks fledged. Capture efficiency for males and females varied in the different plots. Females were usually captured during incubation or when feeding young. Males were often captured when they visited empty nest boxes before the onset of nest construction. This increased the proportion of males captured by 25%, compared with solely trapping males when they were feeding nestlings (Sokolov et al. 1990). In the core of

TABLE 1. Returns of Pied Flycatcher nestlings banded (1999–2002) and recaptured (2000–2003) in nest boxes in different study plots (A–E) along the Courish Spit on the southeast Baltic coast. There were 200 nest boxes in plots A, B, and D, 300 in plot C, and 440 in plot E. Percentages of recaptured birds are given in parentheses. Lower return frequency in study plot A, situated in mature deciduous forest, could be due to many birds nesting in natural holes. Also, less effort was spent capturing adults in peripheral plots, especially males during the prebreeding season. M = male, F = female.

Study plot	Nestlings banded	Sex	Birds recaptured					
			A	B	C	D	E	A–E
A	498	M	3 (1.2)	2 (0.8)	0	0	1 (0.4)	6 (2.4)
		F	0	0	1 (0.4)	1 (0.4)	0	2 (0.8)
B	527	M	1 (0.4)	14 (5.3)	4 (1.1)	1 (0.4)	2 (0.8)	22 (8.3)
		F	1 (0.4)	8 (3.0)	2 (0.8)	2 (0.8)	0	13 (4.9)
C	641	M	1 (0.3)	12 (3.8)	15 (4.7)	1 (0.3)	1 (0.3)	30 (9.4)
		F	1 (0.3)	5 (1.6)	6 (1.9)	3 (0.9)	1 (0.3)	16 (5.0)
D	528	M	1 (0.4)	0	6 (2.3)	10 (3.8)	2 (0.8)	19 (7.2)
		F	1 (0.4)	1 (0.4)	4 (1.5)	1 (0.4)	2 (0.8)	9 (3.4)
E	172	M	0	0	1 (1.2)	1 (1.2)	4 (4.7)	6 (7.0)
		F	0	0	1 (1.2)	1 (1.2)	1 (1.2)	3 (3.5)
Total	2366	M	6 (0.5)	28 (2.4)	26 (2.2)	13 (1.1)	10 (0.8)	83 (7.0)
		F	3 (0.3)	14 (1.2)	14 (1.2)	8 (0.7)	4 (0.3)	43 (3.6)

the study area (plots B, C, and D), ca. 85% of males were banded, but in peripheral areas this proportion was lower. Capture efficiency for females breeding in nest boxes was close to 100%. A proportion of the Pied Flycatcher population bred in natural cavities, mainly in areas of mature deciduous forest (plots B and D). These birds were not included in the study. The overall occupancy of available nest boxes by Pied Flycatchers, Great Tits (*Parus major*), Blue Tits (*P. caeruleus*), Coal Tits (*P. ater*), and Marsh Tits (*P. palustris*) did not exceed 30%–40%; therefore, nest boxes were always available in excess. Thus, vacant nest boxes were always available to flycatchers at a distance not exceeding 200–300 m, and physical exclusion of Pied Flycatchers by larger, more aggressive, and earlier-breeding titmice should not have influenced the spatial distribution of Pied Flycatchers to any considerable extent. If a Pied Flycatcher was captured several times in different nest boxes (which was sometimes the case with males), only the capture in the nest box where the bird bred was included in analyses.

STATISTICAL ANALYSIS

To ascertain whether Pied Flycatchers that returned to the Courish Spit to breed were randomly distributed across the study area, we compared the frequency distribution of natal dispersal distances with a null model, which assumed that distribution of breeding birds was random. To construct this model, we calculated the distances between all possible pairs of nest boxes from which Pied Flycatcher chicks successfully fledged in year i and all nest boxes where a male or a female was captured in the year $i + 1$. This yielded a frequency distribution of predicted natal dispersal distances if Pied Flycatchers returned randomly to any site in our study area. The predicted distribution was already corrected for recapture effort, as only nest boxes where at least one parent was captured were included in the analyses.

Simulations were run separately for males and females, because: (i) natal dispersal distances differ between the sexes (Sokolov 1997), and (ii) techniques used to capture males and females differed and had varying efficiency. To avoid possible biases, only birds recaptured the year following fledging were included. The data on birds not found until subsequent years were excluded from the main analysis, but used for discussion of the possible reasons for sex-related difference in site fidelity. Values reported are means ± SE.

RESULTS

RETURN FREQUENCIES IN DIFFERENT PLOTS

A total of 8821 Pied Flycatcher nestlings were banded in 1981–2002, of which 561 (6.4%) were recaptured in the study area in subsequent years, most (70%) of them in the first year after banding (i.e., as yearlings).

We analyzed the data from the birds banded in 1999–2002 and recaptured in the enlarged study area in 2000–2003. In these years, 2366 Pied Flycatchers were banded and 126 were recaptured. Breeding male Pied Flycatchers were most often found in the study plot where they had been banded as nestlings (Table 1, 2). In females, this tendency was significant only in plot B (Table 2).

DISTANCE AND DIRECTION OF NATAL DISPERSAL

Male Pied Flycatchers ($n = 83$) dispersed on average 4.3 ± 0.6 km from their natal nest box (range = 0.04–28.6 km, median = 2.8 km); females ($n = 43$) dispersed 6.6 ± 0.8 km (range = 0.5–24.6 km, median = 4.8 km). The difference in natal dispersal distance between the sexes was highly significant (Mann-Whitney U-test, $z = 3.1$, $P < 0.01$).

An approximately equal number of males and females moved to the northeast and southwest: 40 males to the NE, 43 to the SW; 21 females to the NE,

TABLE 2.   Returns of Pied Flycatcher nestlings banded (1999–2002) and recaptured (2000–2003) in nest boxes in the same study plots and in different study plots (A–E) from where they were banded along the Courish Spit on the southeast Baltic coast. The total number of nestlings banded and percentage recaptured are given in parentheses. We assumed an equal sex ratio among Pied Flycatchers banded as nestlings. M = male, F = female.

Plot of recapture	Sex	Number recaptured (total n, %)		Significance of difference (Yates-corrected χ^2)
		Banded in the same plot	Banded in a different plot	
A	M	3 (n = 249, 1.2%)	3 (n = 934, 0.3%)	χ^2_1 = 1.54, P = 0.21
	F	0 (n = 249, 0%)	2 (n = 934, 0.2%)	χ^2_1 = 0.02, P = 0.89
B	M	14 (n = 263, 5.3%)	8 (n = 919, 0.9%)	χ^2_1 = 19.20, P < 0.001
	F	8 (n = 263, 3.0%)	5 (n = 919, 0.5%)	χ^2_1 = 9.54, P < 0.01
C	M	15 (n = 320, 4.7%)	15 (n = 862, 1.7%)	χ^2_1 = 7.05, P < 0.01
	F	6 (n = 320, 1.9%)	10 (n = 862, 1.2%)	χ^2_1 = 0.44, P = 0.51
D	M	10 (n = 264, 3.8%)	9 (n = 919, 1.0%)	χ^2_1 = 8.54, P < 0.01
	F	1 (n = 264, 0.4%)	8 (n = 919, 0.9%)	χ^2_1 = 0.17, P = 0.68
E	M	4 (n = 86, 4.7%)	2 (n = 1097, 0.2%)	χ^2_1 = 23.30, P < 0.001
	F	1 (n = 86, 1.2%)	2 (n = 1097, 0.2%)	χ^2_1 = 0.39, P = 0.53

22 to the SW. Thus, natal dispersal was not directional.

OBSERVED VS. PREDICTED NATAL DISPERSAL DISTANCES

The frequency distribution of male natal dispersal distances was significantly different from the prediction of the null model (Wilcoxon matched pairs test: z = 2.4, P < 0.02; Fig. 2a). Male Pied Flycatchers were found significantly closer to their natal nest boxes than would be predicted by random dispersal, breeding within 6 km of their natal site with a higher probability than would be predicted by chance. The difference between the observed frequency distribution of natal dispersal distances and the prediction of the null model was not significant for females (Wilcoxon matched pairs test: z = 1.6, P = 0.10; Fig. 2b).

We also calculated the predicted frequency distribution of natal dispersal distances (under the assumption of random distribution) for each nest box from which Pied Flycatchers later found as yearlings fledged. Of 83 males for which natal dispersal distance was known, 69 (83%) were found closer to their natal site than the median of the frequency distribution predicted by the null model for their natal nest box (ratio significantly different from being equal: two-tailed sign test, z = 5.9, P < 0.001). Of 43 females, 29 (67%) bred closer to their natal nest box than the median of the predicted frequency distribution (ratio significantly different from being equal: two-tailed sign test, z = 2.1, P = 0.03). This analysis showed that both males and females settled significantly closer to their natal site than if they were distributed randomly.

RETURN OF FLEDGLINGS IN SUBSEQUENT YEARS

In 1999–2000, 797 unsexed nestling Pied Flycatchers were banded in our study area. Thirty-nine females were recaptured in subsequent years in the same area,

of which 16 (41%) were first recaptured older than yearlings. In the same time period, 64 males banded as nestlings in 1999–2000 were recaptured; 23% (15 individuals) were first recaptured aged >1 year. The difference between the sexes is marginally significant: χ^2_1 = 3.6, P = 0.06. This analysis was restricted to the birds hatched in 1999–2000 because Pied Flycatchers have a maximum lifespan of four years; therefore, at the time of analysis the birds of this cohort were unlikely to be recaptured again.

DISCUSSION

Our data show that male Pied Flycatchers generally returned to an area smaller than the whole study area: they settled within 6 km of their natal site with a greater probability than predicted by chance. The hypothesis of random return to an area much greater than several kilometers in diameter is not supported by our data for males. During the postfledging period, juvenile Pied Flycatchers explore the vicinity of their natal area. The mean distance of these movements in the Courish population has been estimated at 1.4 ± 1.9 (SD) km (n = 481, greatest distance = 13.4 km; Vysotsky et al. 1990). In spring, yearling Pied Flycatchers likely aim to return not to their natal site, but rather to the site they imprinted on during postfledging exploration. Certainly, some Pied Flycatchers do settle father than 6 km from their natal nest box: the longest dispersal distance we recorded for a male was 29 km. Undoubtedly, some birds settle even farther from their natal area, up to several hundred kilometers away (Vysotsky 1994). However, these events occur more rarely than what would be expected by random probability and likely do not contribute much to the spatial structure of Pied Flycatcher populations.

The frequency distribution of female natal dispersal distances did not show a significant difference from the pattern expected if they returned randomly. In spite of a higher capture efficiency for females, male
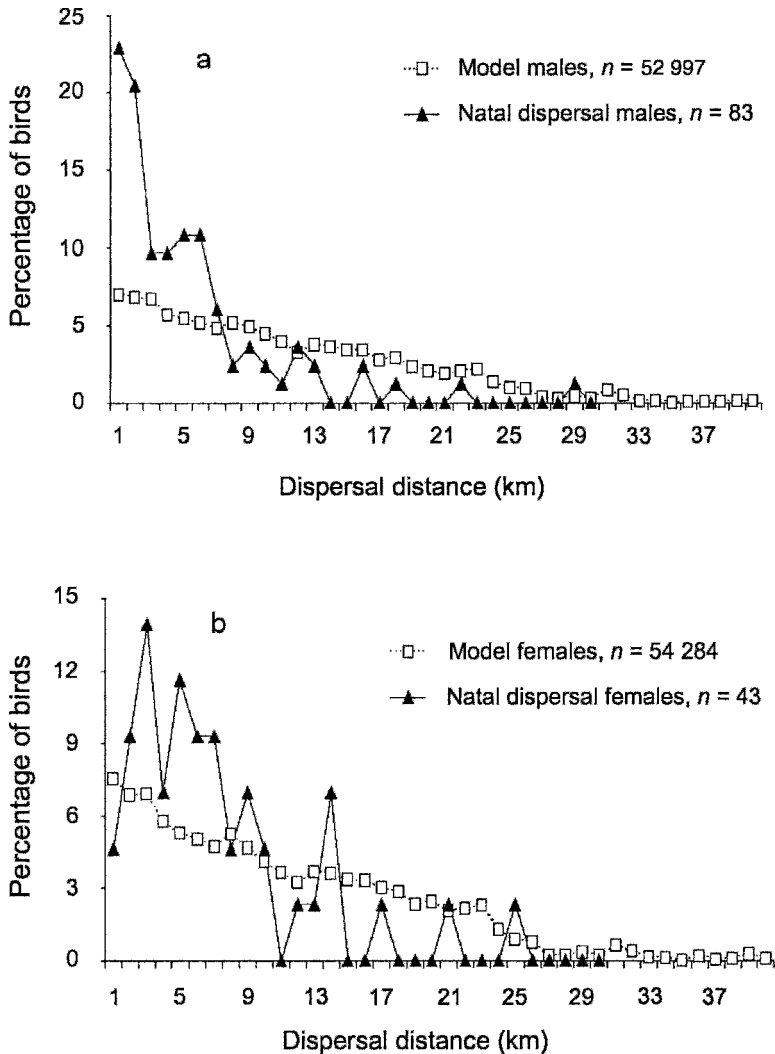
FIGURE 2.   Frequency distributions of natal dispersal distances of Pied Flycatchers on the Courish Spit on the southeast Baltic Coast. The distributions of observed dispersal distances of banded males (a) and females (b) are compared with predicted frequencies generated by a null model which assumes that any nest box within the study area is selected at random.

returns were nearly twice as high as female returns (7.0% and 3.6%, respectively). Assuming that sex ratio at fledging is close to being equal and that the true survival rate of both sexes from fledging until first breeding does not differ greatly, we are forced to conclude that twice as many females as males emigrate from the study area. However, females are more likely than males to be recaptured for the first time at an age >1 year. As a result, sex-related differences in returns are smaller if all birds ever recaptured in the study area are considered, than if only the ones recaptured as yearlings are included. This indicates that emigration from the study area

may not be permanent. It is possible that migrating females may be diverted by prospecting males during the last stages of spring migration (Greenwood 1980, Vysotsky 1994). Some of them may return in subsequent years to the area on which they imprinted in their first summer of life (usually not far from the natal site), especially after a failed breeding attempt in the novel area.

Our results (sex-biased natal dispersal) are at variance with results obtained from the same species in central Europe (Winkel 1982, Glutz von Blotzheim and Bauer 1993). Natal dispersal distances were not sex-biased in a large German study area (2250 km^2),

with sample sizes of 1363 one-year-old males and 3717 one-year-old females (Glutz von Blotzheim and Bauer 1993). As the German study was based on a large sample and probably did not suffer from a small study plot, we attribute this discrepancy to interpopulation variation. However, in many birds females tend to disperse greater distances than males (Greenwood 1980). Female Pied Flycatchers may settle up to 600 km from their natal sites (Berndt and Sternberg 1969, Vysotsky 1994). Nonetheless, females generally do not disperse randomly across an area several dozens of kilometers or more in diameter. As shown by Vysotsky and Valkiunas (1992), most Pied Flycatchers of both sexes breeding on the Courish Spit are hatched on the spit and are not immigrants from the mainland. This is indicated by the lack of *Leucocytozoon* spp. blood parasites (Haemosporidia) in local breeding adults. *Leucocytozoon* cannot infect passerines on the Courish Spit, because their vectors (sand flies, Simuliidae) do not occur here (Valkiunas 2004). Thus, all infected birds are immigrants from the mainland (Vysotsky and Valkiunas 1992), and the absence of infected individuals in the breeding Pied Flycatcher population suggests that the proportion of immigrants is lower than 5% (Vysotsky and Valkiunas 1992, Vysotsky 2000). Therefore, female Pied Flycatchers probably do not routinely settle farther than 30–40 km from their natal sites.

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