

# Philopatry, dispersal and population structure of passerines on the Courish Spit of the Baltic Sea

By Leonid Sokolov

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Philopatry, especially natal philopatry, can vary noticeably even in related species. Ringing of nestlings and native juveniles on the Courish Spit revealed that in some species (Barred Warbler *Sylvia nisoria*, Willow Warbler *Phylloscopus trochilus*, Chaffinch *Fringilla coelebs*) the bulk of yearlings returns to breed at their natal site, whereas in other species (Lesser Whitethroat *Sylvia curruca*, Scarlet Rosefinch *Carpodacus erythrinus*) only an insignificant number of individuals appear to return. Specific differences in level of natal philopatry are basically a consequence of the timing of territory imprinting and the duration of the birds' stay in the natal place. Birds show fidelity for the site where territory imprinting occurred. If imprinting takes place prior to abandoning their native area, birds will show a high level of natal philopatry in subsequent years. If territory imprinting occurs after dispersal, philopatry will appear to be very low. Therefore natal dispersal distance in migratory species is mainly determined by postfledging dispersal distance in the postbreeding period. Philopatry is also affected by a number of other factors: hatching date, breeding success, constant habitat, age and experience, etc. The ratio of local birds and immigrants in populations depends mainly on the return-rate to the natal place. In more philopatric species the populations are maintained mainly by native birds. In such species, immigrants make up no more than 20% of the total number of individuals.

Key words: philopatry, site fidelity, dispersal, population structure, territory imprinting, return rate, passerines.

Address: Biological Station Rybachy, Zoological Institute, Russian Acad. Sci. 199034 St. Petersburg, Russia.  
E-mail: Rybachy@bioryb.koenig.su

## 1. Introduction

Numerous data on birds ringing provide evidence that, independent of their systematic, behaviour and life-style, many migratory birds show fidelity not only for breeding territory (breeding philopatry), but also for their birthplace (natal philopatry) or the area where they settled as a result of postfledging dispersal. Natal and breeding philopatry has been revealed in different groups including the largest and long-lived birds and the smallest and short-lived passerine species (for reviews see VON HAARTMAN 1960, GREENWOOD 1980, ORING & LANK 1984, BAUER 1987, SOKOLOV 1997). Analysis of publications (written over a period of more than 50 years) on bird ringing have shown that fidelity for territory is characteristic of more than 200 migratory species (SOKOLOV 1991a, 1997). Level of philopatry, especially natal philopatry, can vary noticeably even in related species and populations. In addition, many avian species show fidelity for wintering grounds (MOREAU 1969, PEARSON 1972, ELY et al. 1977, RAVELING 1979, SOKOLOV 1991a) and stopover areas (KNORR 1971, KOERNER et al. 1974, SMITH & HOUGHTON 1984).

Philopatry and dispersal in migratory birds are two reverse but interdependent processes. Postfledging dispersal in the postbreeding period can result in birds' setting on new territories only if territory imprinting occurs after the dispersal (BERNDT & STERNBERG 1968, BERNDT & WINKEL 1979, SOKOLOV 1981, 1982a, BAUER 1987, MORTON et al. 1991). Therefore distance of natal dispersal (the movement of immature birds from their natal area to a new location where they settle and eventually reproduce) in migratory species is mainly determined by distance of postfledging dispersal of young birds.

In this paper I present and discuss the principal results of long-term study of natal and breeding philopatry, postfledging and natal dispersal and also structure of local population in some passerines on the Courish Spit of the Baltic Sea.

## 2. Methods

Natal and breeding philopatry in migratory birds is measured by their return rate, i.e. the percentage of birds which return in subsequent years to the area where they were ringed. On "Fringilla" field station situated on the Courish Spit of the Baltic Sea, birds are captured in large stationary Rybachy-type traps located amid man-planted *Pinus silvestris* forests (detailed description of traps and study area in: DOLNIK & PAYEVSKY 1976, PAYEVSKY 1999). Three or four traps are in function every year in breeding and postbreeding periods. Time intervals for a high probability of only local adult and young birds trapped were defined specially (SOKOLOV 1991b). Local adult and young birds were trapped in large traps mainly within the area with a radius until 5 km.

When capturing Pied Flycatcher (*Ficedula hypoleuca*) in nest boxes various methods are used in which efficiency differs greatly. As demonstrated by our studies of philopatry in Pied Flycatchers on the Courish Spit, their return rate increases by 25% as a result of capturing males by automatic traps prior to the onset of nesting in occupied nest boxes (SOKOLOV et al. 1990). In addition, the efficient control over tree-hole breeders is greatly dependent on the availability of natural cavities in the study area. On the "Fringilla" field station where 20- to 30-year-old *Pinus sylvestris* trees represent the dominant vegetation in the forest, natural cavities are rare, thus efficiency of capturing Pied Flycatchers is as high as 95%.

The postfledging dispersal distance of young birds was evaluated by frequency of captures in large traps of individuals originally banded in their nests within 20 km from traps. Being narrow (between 0.7 and 3.5 km) and long (97 km), the Courish Spit gives us a unique possibility for studying postfledging dispersal in juvenile birds using large traps.

## 3. Results

### 3.1. Natal and breeding philopatry in birds

Natal philopatry can vary significantly even in related species. Ringing of nestlings and native juveniles in the study area revealed that in some species (Barred Warbler, Willow Warbler, Chaffinch) the bulk of yearlings returns to breed at their natal site, whereas in other species (Lesser White-throat, Scarlet Rosefinch) only an insignificant number of individuals appear to return (Tab. 1). In many cases return rates of ringed fledglings are higher than those in birds ringed as nestlings (SOKOLOV 1997). I suggest that this may be explained primarily by the fact that in many migratory birds territory imprinting of the future breeding area proceeds mainly outside the natal area after post-fledging dispersal (Tab. 2). However, these differences in the return rates of birds ringed before or after fledging could be caused by high mortality rates during the period between fledging and self-sufficiency when the young start moving independently (SOKOLOV 1991a).

Most species of migratory birds exhibit sex-specific differences in both natal and breeding philopatry. In the majority of species, especially passerines, males appear to show higher territorial philopatry than females (Tab. 1).

Return rates of some species were found to depend greatly on hatching dates. The analysis of return rates in some species on the Courish Spit revealed that juveniles hatched in the first half June have a higher return rate to their birthplace in subsequent years than those hatched later (Fig. 1).

As shown by the analysis of captured juvenile Pied Flycatchers during the postbreeding period, birds from late broods depart from their natal site at an earlier age than birds from earlier broods (Fig. 2). As a result, they evidently imprint future-breeding territory at a distance further from the birthplace than birds hatched earlier (SOKOLOV et al. 1987).

The analysis of the recaptures and return rates in birds hatched in different years showed that Pied Flycatchers ringed as nestlings during years with early breeding periods, have significantly higher recaptures in postfledging period and return rates in next years than those hatched in 'late' years (Fig. 3).

A comparison of return rates to the previous breeding site in local Pied Flycatchers hatched in the study area and immigrants which settled to breed there has shown that after the first breeding the local birds have a significantly higher return rate than immigrants (Tab. 3). This difference is more pronounced in females. However, after breeding for a second time both – local and immigrant birds – return to the territory at same rates.

Table 1: Natal and breeding philopatry in males and females in some migratory species on the Courish Spit of the Baltic Sea. – Geburts- und Brutortstreue von ♂ und ♀ verschiedener Zugvogel-Arten auf der Kurischen Nehrung/Ostsee.

Species	Age of birds	Number of ringed birds		Return rate			
		Male	Female	N		%	
				Male	Female	Male	Female
<i>Ficedula</i>	Pull.	920	920	90	78	9.8	8.5
<i>hypoleuca</i>	Ad.	256	327	72	49	28.1***	15.0***
<i>Phylloscopus</i>	Pull.	451	451	40	26	8.7	5.8
<i>trochilus</i>	Ad.	265	214	16	12	6.0	5.6
<i>Sylvia</i>	Pull.	247	247	31	9	12.6***	3.6***
<i>nisoria</i>	Ad.	177	151	16	8	9.0	5.3
<i>Sylvia</i>	Pull.	815	815	18	5	2.2**	0.6**
<i>curruca</i>	Ad.	117	108	16	5	13.7*	4.6*
<i>Hippolais</i>	Pull.	513	513	22	9	4.3*	1.7*
<i>icterina</i>	Ad.	282	279	34	21	12.4	7.5
<i>Carpodacus</i>	Pull.	349	349	3	1	0.9	0.3
<i>erythrinus</i>	Ad.	219	173	33	20	15.1	11.6
<i>Fringilla</i>	Pull.	2930	2930	267	225	9.1*	7.7*
<i>coelebs</i>	Ad.	796	1246	116	111	14.6***	9.0***

Symbols show differences in return rates of males and females: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$  ( $\chi^2$  test).  
Abb.: Pull., pullus; Ad., adult.

Table 2: Timing of breeding territory imprinting in some passerines on the Courish Spit. – Zeitpunkt der Gebietsprägung bei einigen Sperlingsvogelarten auf der Kurischen Nehrung.

Species	Imprinting period	Age of birds (days)	Source
<i>Ficedula hypoleuca</i>	Upon dispersal	35 – 50	SOKOLOV et al. 1987
<i>Phylloscopus trochilus</i>	Prior to dispersal	30 – 40	SOKOLOV 1976
<i>Sylvia nisoria</i>	Prior to dispersal	30 – 40	SOKOLOV 1976
<i>S. curruca</i>	Upon dispersal	40 – 50	SOKOLOV 1988
<i>Hippolais icterina</i>	Upon dispersal	30 – 45	SOKOLOV 1976
<i>Motacilla alba</i>	Upon dispersal	35 – 50	PAYEVSKY 1976
<i>Anthus trivialis</i>	Upon dispersal	40 – 55	SOKOLOV 1988
<i>Lanius collurio</i>	Upon dispersal	35 – 55	SOKOLOV 1988
<i>Sturnus vulgaris</i>	Prior to dispersal	30 – 35	SOKOLOV 1976
<i>Fringilla coelebs</i>	Prior to dispersal	30 – 40	SOKOLOV 1981
<i>Carpodacus erythrinus</i>	Upon dispersal	> 30	SOKOLOV 1988

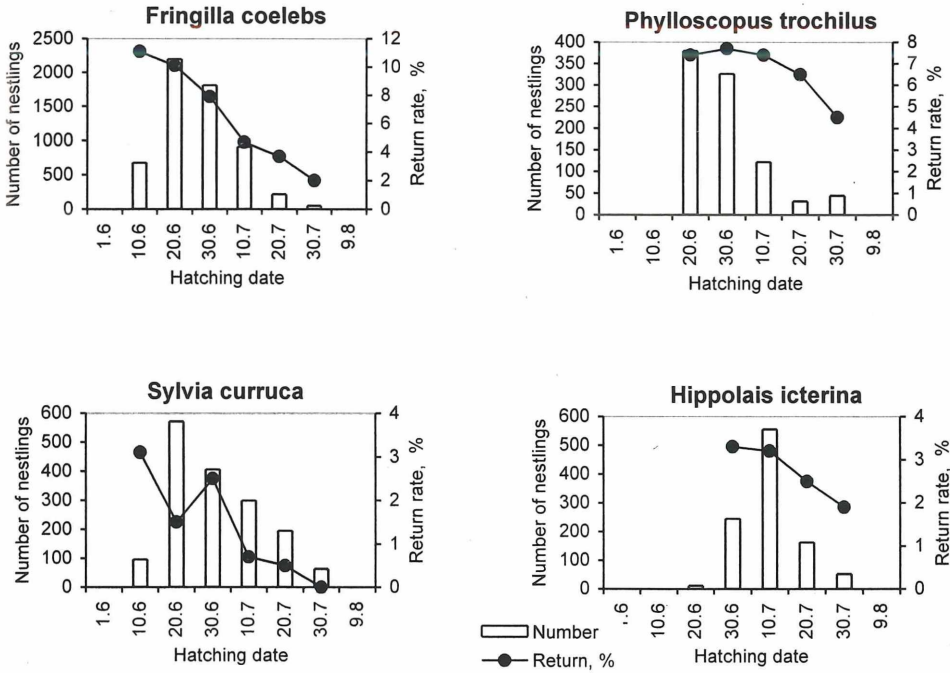


Fig. 1. Dependence of philopatry on the birth dates in some passerines on the Courish Spit. – Beziehung zwischen Geburtsortstreue und Geburtstermin bei einigen Sperlingsvogelarten auf der Kurischen Nehrung/Ostsee.

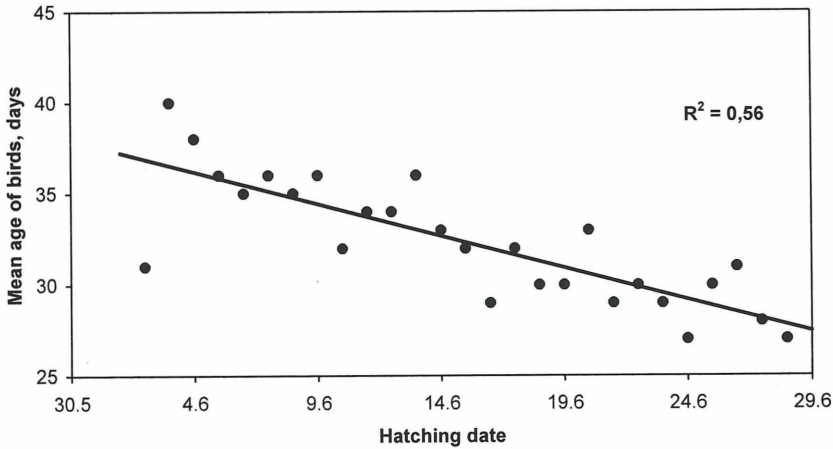


Fig. 2. Dependence of age of juveniles during of first capture in large traps on the birth dates in the Pied Flycatcher on the Courish Spit. – Beziehung zwischen dem Alter juveniler Trauerschnäpper beim ersten Reusenfang und ihrem Geburtstermin auf der Kurischen Nehrung.

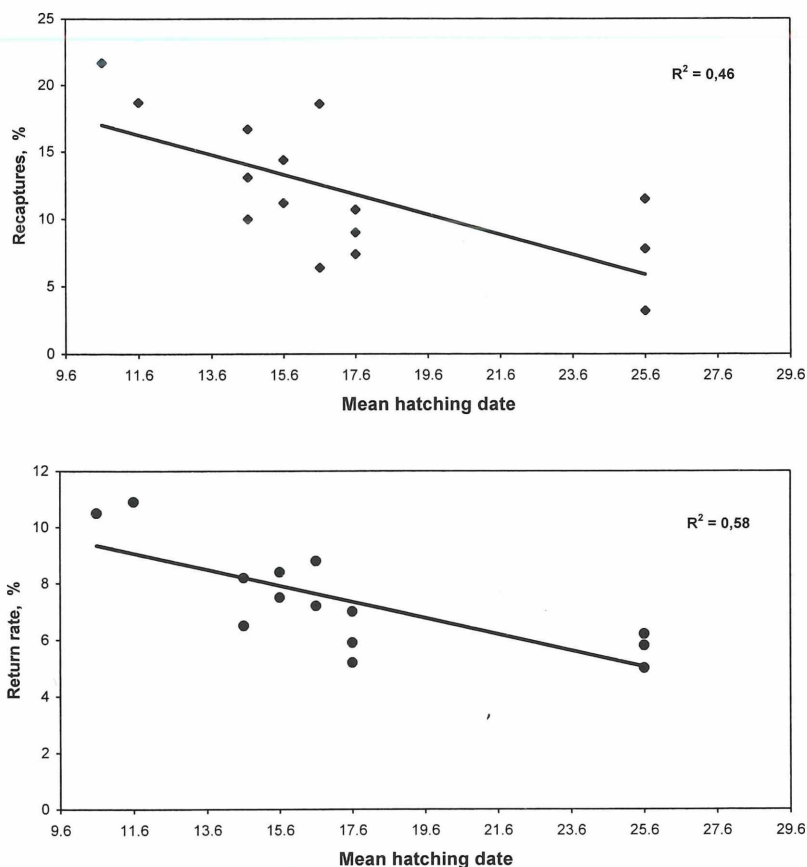


Fig. 3. Dependence of the percentage of recaptures of Pied Flycatchers in the postfledging period and return rate in subsequent years on the mean breeding date of a population on the Courish Spit. – Beziehung zwischen Bruttermin und a) dem Wiederfang-Prozentsatz nach dem Flüggewerden und b) der Rückkehrtrate in den folgenden Jahren in einer Trauerschnäpper-Population der Kurischen Nehrung.

Two year old and older local Pied Flycatchers begin breeding on average about 4 days earlier than immigrants (Tab. 4). The highest return rate (about 11%) is found in birds whose mothers were local females aged 2 or more years. The lowest return rate is estimated for birds whose mothers were local (about 7%) or immigrant yearlings (about 8%). In addition to the age and experience of birds, their return rate to the previous breeding site is also affected by their breeding success and site tenacity (SOKOLOV 1991a).

### 3.2. Dispersal of birds

Study of dispersal in Pied Flycatcher on the Courish Spit have shown that in the postfledging period most birds settle mainly within several kilometers from their birthplace (Fig. 4, 5, Tab. 5). Only a small percentage of birds may scatter tens of kilometers.

In our area the majority of young birds in some species moved in the postfledging period towards southwest from the natal place (Tab. 6). This tendency is most pronounced in species migrating extremely long distances, whereas in intra-continental migrants, in particular in Chaffinches, the young scatter evenly towards the south and north.

Table 3: Breeding philopatry in local and immigrant Pied Flycatchers of different age on the Courish Spit. – Vergleich zwischen der Brutortstreue von auf der Kurischen Nehrung geborenen und zugewanderten Trauerschnäppern in Beziehung zum Alter.

Group of birds	Sex	Age (years)	Number of ringed birds	Returns	
				n	%
Local	Males	1	84	34	40,5*
	Females	1	70	22	31.4***
Immigrants	Males	x	257	50	19.4*
	Females	x	369	33	8.9***
Local	Males	2	46	22	47.8
	Females	2	23	8	34.8
Immigrants	Males	x + 1	60	27	45.0
	Females	x + 1	35	13	37.1
Local	Males	3	22	7	31.8
	Females	3	19	5	26.3
Immigrants	Males	x + 2	26	10	38.5
	Females	x + 2	16	4	25.0
Local	Males	4	9	2	22.2
	Females	4	8	2	25.0
Immigrants	Males	x + 3	12	3	21.4
	Females	x + 3	4	1	25.0

x – Age of birds unknown; \* and \*\*\* – differences between the groups are significant at  $p < 0.05$  and  $p < 0.001$ , respectively ( $\chi^2$  test).

Table 4: Hatching date, brood size and return rate of nestlings in local and immigrant parents of different age in the Pied Flycatcher on the Courish Spit. – Schlüpfdatum, Brutgröße (Zahl der Nestlinge) und Rückkehrate der Jungvögel beim Trauerschnäpper auf der Kurischen Nehrung in Abhängigkeit zum Alter und der Herkunft der Eltern (im Gebiet geboren, zugewandert).

Parents (origin and age)	Number of broods	Hatching date of nestlings (June)	Brood size	Number of nestlings	Return rate	
					n	%
One – local (1 – year) Other – immigrant	39	13.5 ± 7.1	5.5 ± 1.1	214	15	7.0*
Female – local (> 1 year) Male – unknown	19	10.6 ± 6.4	6.3 ± 1.3	119	13	10.9*
Female – unknown Male – local (> 1 year)	24	13.7 ± 7.9	5.3 ± 1.9	127	12	9.4
Female – immigrant Male – immigrant	184	14.0 ± 6.5	5.5 ± 1.0	1006	86	8.5

\* – Differences between the groups are significant at  $p < 0.05$  ( $\chi^2$  test).

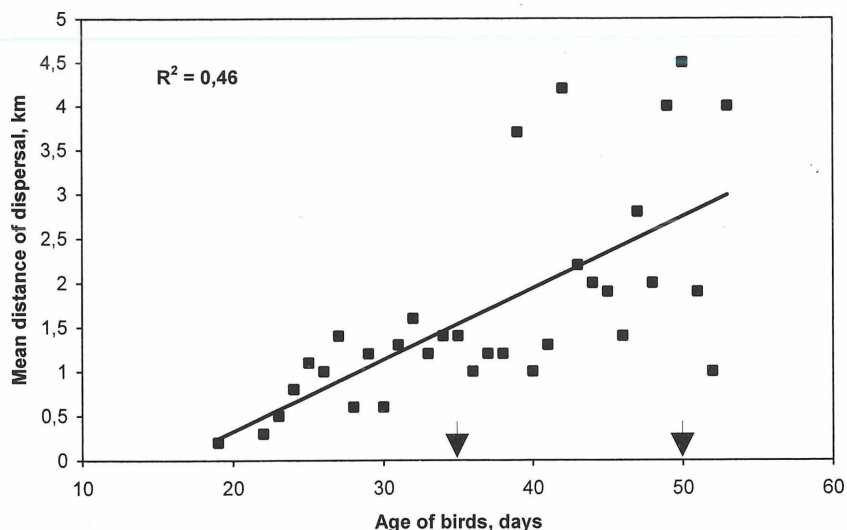


Fig. 4. Dependence of mean distance of postfledging dispersal of Pied Flycatchers on the age of birds on the Courish Spit. Arrows on the abscissa indicates the imprinting period of breeding site. – Beziehung zwischen der mittleren Abwanderungsentfernung junger Trauerschnäpper und dem Jungvogelalter auf der Kurischen Nehrung. Die Pfeile kennzeichnen die Prägungsphase auf den Brutort.

In the following year, most of the Pied Flycatchers detected appeared to breed at a distance of 5 km from their natal place (Fig. 5). The birds bred predominantly in the region where they had happened to be upon their juvenile dispersal. In other species with less pronounced postfledging dispersal, most yearlings initiate breeding within 2 km of the native nest (SOKOLOV 1991a). On the Courish Spit, the majority of Pied Flycatchers initiate breeding southwest from the natal place (SOKOLOV et al. 1990).

The distances of breeding dispersal in most species are essentially shorter than those of natal dispersal. E.g. about 86% of male and 70% of female Pied Flycatchers on the Courish Spit breed within a distance of 1 km from their previous breeding site (SOKOLOV 1991a).

### 3.3. Population structure of birds

Within our controlled area, where the efficiency of estimating return rate in Pied Flycatchers is about 95%, 946 breeding birds were captured in the period between 1983 and 1989 (Tab. 7). 25% of them were locals hatched in the study area, and the other 75% turned out to be birds of unknown origin (majority of them being immigrants). Among the latter, 21% bred more than once in the study region, while 79% were found to breed there only once. In various years, the proportion of local birds in the population ranged between 15% and 35%. It is remarkable that the greatest number of local birds was detected in 1987 (34,7%) after the year of the highest breeding success (1986), when the maximal number of nestlings was ringed in the study region (SOKOLOV 1991a). The proportion of local birds among males (30%) was significantly higher than among females (20%). The data on natal dispersal of flycatchers suggest that the majority of immigrants, which settled to breed in the study area, were hatched at a distance within of 50 kilometers from this area (SOKOLOV et al. 1990).

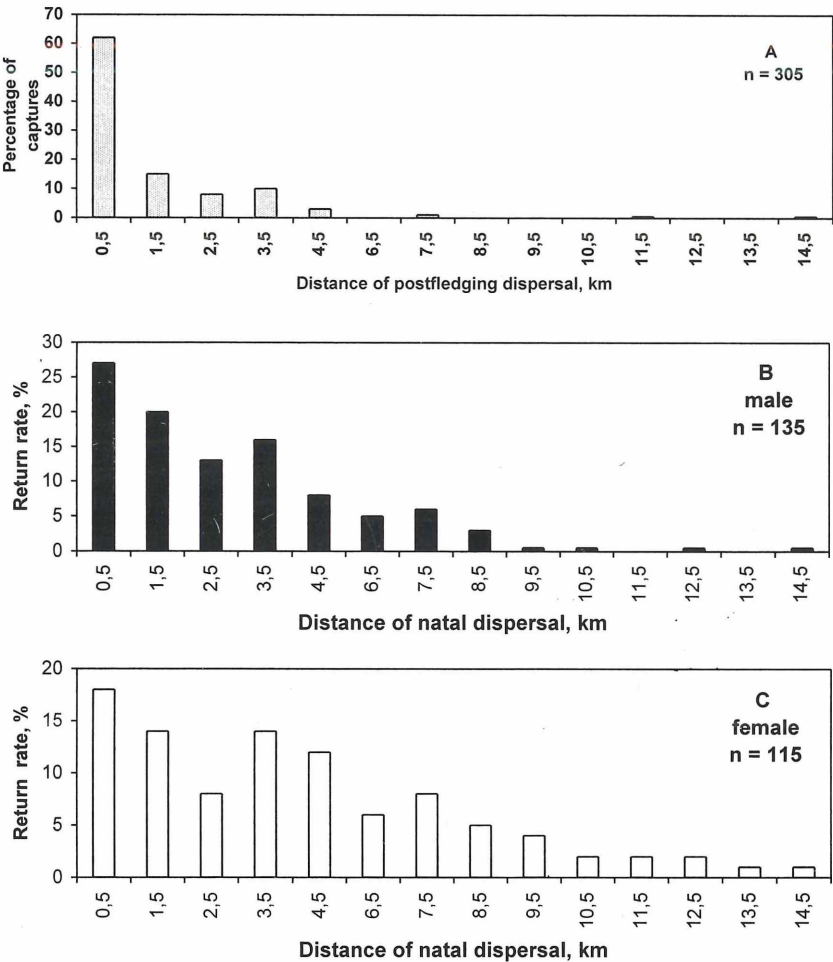


Fig. 5. Distance of postfledging (A) and natal (B–C) dispersal in the Pied Flycatcher on the Courish Spit. – Abwanderungsentfernungen nach dem Flüggewerden (A) und Dismigration zurückgekehrter Individuen (B und C) des Trauerschnäppers auf der Kurischen Nehrung.

Table 5: Distance of postfledging dispersal in Pied Flycatchers in different age on the Courish Spit. – Jugendstreuung (Entfernung zwischen Geburts- und Fangort) beim Trauerschnäpper auf der Kurischen Nehrung in Beziehung zum Alter der Vögel (in Tagen).

Age of birds (days)	Distance between the birthplace and the capture site (km)							Total	
	0 – 1	1.1 – 2	2.1 – 3	3.1 – 4	4.1 – 5	5.1 – 10	> 10	%	n
20 – 30	74.8	9.8	6.5	4.9	4.0	0	0	100	123
31 – 40	49.2	20.3	11.9	10.2	6.8	1.1	0.5	100	177
41 – 50	36.8	25.0	11.8	9.2	2.6	9.2	5.3	100	76



Table 6: Direction of postfledging dispersal in some passerines on the Courish Spit. – Richtung der Abwanderung nach dem Flügglwerden bei einigen Sperlingsvogelarten auf der Kurischen Nehrung.

Species	Number of nestlings ringed +		Percentage of birds moved to		Ratio,%		$\chi^2$
	SW	NE	SW	NE	SW	NE	
<i>Hippolais icterina</i>	130	222	12.6	3.9	76 : 24		4.1*
<i>Ficedula hypoleuca</i>	1340	1419	19.9	8.9	70 : 30		65.1***
<i>Sylvia curruca</i>	275	595	17.8	7.6	70 : 30		14.8***
<i>Sylvia nisoria</i>	308	696	9.8	5.5	64 : 36		4.4*
<i>Phylloscopus trochilus</i>	336	472	37.5	30.7	55 : 45		3.8*
<i>Fringilla coelebs</i>	1379	2276	14.1	12.4	53 : 47		2.0

+ Number of nestlings ringed SW and NE of large traps; \* and \*\*\* – differences between the groups are significant at  $p < 0.05$  and  $p < 0.001$ , respectively. SW – southwest; NE – northeast.

Table 7: Ratio of local and immigrant birds in the Pied Flycatchers populations breeding in Karelia and on the Courish Spit. – Verhältnis im Gebiet geborener zu zugewanderten Vögeln bei in Karelien und auf der Kurischen Nehrung brütenden Trauerschnäppern.

Year	Courish Spit					Karelia *				
	N	Local birds		Immigrant		N	Local birds		Immigrant	
		n	%	n	%		n	%	n	%
1983	67	10	15.0	57	85.0	221	11	5.0	210	95.0
1984	152	29	19.1	123	80.9	271	19	7.0	252	93.0
1985	135	28	20.7	107	79.3	285	21	7.4	264	92.6
1986	163	36	22.1	127	77.9	309	21	6.8	288	93.2
1987	167	58	34.7	109	65.3	272	24	8.8	248	91.2
1988	144	33	23.0	111	77.0					
1989	118	41	34.7	77	65.3					
Total:										
males	471	140	29.7	331	70.3	670	62	9.3	608	90.7
females	475	95	20.0	380	80.0	688	34	5.0	654	95.0

N – Total number of birds captured in the study region;

n – Number of local or immigrants birds.

\* – Data from ARTEMYEV (1989).

The analysis of the age-related structure of the Pied Flycatcher breeding population on the Courish Spit has revealed that about 50% of local birds are yearlings, about 30% are 2-year olds, 15% are 3-year olds, 4% are 4-year olds and 1% older birds.

#### 4. Discussion

What is the main reason for higher return rate recorded in earlier hatched Pied Flycatchers compared with those hatched later? I believe that this can be explained first of all by varying survival rate in birds from early and late broods (SOKOLOV 1982b, 1991a). Birds breeding early are as a rule adult individuals which arrive earlier in the spring than yearlings do, establish a better territory and have bred before. As shown by our studies on the Pied Flycatcher such individuals have larger clutch and

brood size, better hatching success and higher growth rates (Tab. 4). Moreover, in most cases late breeding flycatchers appear to be immigrants nesting in poorer territories compared with local birds. As a result, their offspring may be less viable. In addition, flycatchers from early and late broods can differ in distances of natal dispersal. In our area, female Pied Flycatchers hatched after June 10 appeared to breed significantly ( $\chi^2 = 4.33$ ,  $df = 1$ ;  $p = 0.05$ ) further from their birthplace (60 percent of returns were detected more than 4 km from the natal place) in contrast to only 36% females of earlier broods (SOKOLOV et al. 1990). 'Early' years on the Courish Spit are usually characterized by better breeding conditions (higher temperature, less rainfall, early vegetation, higher abundance of insects). All these factors can enhance survival of nestlings, fledglings and young birds during the current year and, consequently, their return in the following year.

A comparison of return rates to the previous breeding site in Pied Flycatcher hatched on the Courish Spit and immigrants which settled to breed there has shown that after the first breeding the local birds have a significantly higher return rate than immigrants (Tab. 3). This difference is more pronounced in females. However, after breeding for a second time both – local birds and immigrants – return to the territory at the same rates. How can this be explained? We have found that about 30% of local males and 36% of local females appear in the natal area for the first time during the second year of life, while in their first year they are likely to breed in another area (SOKOLOV et al. 1990). It could be expected that, like local birds, a proportion of immigrant yearlings that bred in the study area would return to their natal territory in the following year. It has been found in a number of migratory birds that the breeding success in adult birds usually results in a higher return rate in the following year (HUND & PRINZINGER 1979, ORING & LANK 1982). This can be explained first of all by the fact that a failed breeding attempt forces birds to move to alternative regions in subsequent years.

Experiments on translocation of eggs, nestlings and fledglings of migratory birds from their birthplace to new regions tens and hundreds of kilometers away have reliably demonstrated that the coordinates of the natal place are not genetically inherent in birds but are acquired in the juvenile age (LÖHRL 1959, BERNDT & WINKEL 1979, SOKOLOV 1981, 1997, SOKOLOV et al. 1994). We performed an experiment on exchanging eggs between the Pied Flycatcher populations from the Courish Spit and Moscow region, Zvenigorod (SOKOLOV et al. 1994). The distance between these populations is about 1000 kilometers. 130 unincubated eggs collected in the Moscow region were put in nest boxes on the Courish Spit. 90 nestlings hatched of these eggs, and 79 birds fledged. During next years 5 individuals (about 6%) of these birds were captured on the Courish Spit in the study area and none in the native population (in Moscow region). The results in our experiment and other investigations (BERNDT & WINKEL 1979) confirm that Pied Flycatchers are devoid of an inborn capacity to locate their native area. In spring, yearlings most likely return to the site where the territory was imprinted during the postfledging period. Territory imprinting in many passerines takes place between the age of 30 and 50 days (Tab. 2). Postfledging dispersal during the post-breeding period can result in birds' settling in new territories only if territory imprinting occurs after the dispersal. If imprinting takes place before leaving the natal area, birds will show a high level of natal philopatry in subsequent years. If territory imprinting occurs upon dispersal, philopatry will be very low.

In our area the bulk (about 70%) of Pied Flycatchers initiate breeding southwest from the natal place (SOKOLOV et al. 1990). This is caused by shifting mainly towards southwest from their natal place during postfledging dispersal. However, quite frequently first-year long-distance migrants initiate breeding northeast from their birthplace. This may be caused by the fact that after dispersal juvenile birds imprinted the territory for subsequent breeding northeast of their natal place. An alternative explanation is that upon arrival a bird cannot breed there and has to search for a new site moving in spring migratory direction (i.e. spacing, after BERNDT & STERNBERG 1968). Such 'jumping' compensates, to some extent, to the situation when birds do not reach their breeding sites.

Previously HOWARD (1920) forwarded a hypothesis of 'strong site fidelity', according to which practically all surviving migrants return to their previous breeding site and natal area. Adherents of this hypothesis believed that a local population occupies a rather limited area from year to year (a park, an island, a lake, etc.) and is recruited mainly from its offspring. At the same time, strong opponents of this hypothesis appeared in Russia (MALCHEVSKY 1959, 1968). According to him, only an insignificant proportion of birds (between 1 and 4%) returned to the natal area, and therefore it was impossible to suggest consistency of local populations in birds. Our data show that on the Courish Spit the population of some species (Barred Warbler, Willow Warbler, Chaffinch) is maintained mostly by local birds. Immigrants make up no more than 20% of the total number of individuals. In populations of other species (Wood Warbler *Phylloscopus sibilatrix*, White Wagtail *Motacilla alba*, Red-backed Shrike *Lanius collurio*, Scarlet Rosefinch, etc.) the majority of yearlings are immigrants of unknown origin (SOKOLOV 1991a, 1997).

The ratio of local birds and immigrants in populations depends, first of all, on the rate of their return to the natal place. It is difficult to determine from what region immigrants arrive. Our data on natal dispersal of Pied Flycatcher suggest that the majority of immigrants, which settled to breed in the study area, were hatched at a distance within 50 km from this area (SOKOLOV et al. 1990). Proportion of immigrants in a Pied Flycatcher population in Lower Saxony, Germany (WINKEL 1982) is similar to that breeding on the Courish Spit. In the population of Pied Flycatchers in Finland, natal philopatry is less pronounced than in populations breeding in central Europe (VON HAARTMAN 1949). In a Karelian population the part of local birds is about 3 and 4 times less than in the Courish population (ARTEMYEV 1989). This can be explained, first of all, by the return rate of flycatchers in Karelia which is 3 times lower than on the Courish Spit. Although the accuracy of observation of ringed males in Karelia is lower (mean 74%) than in our area (90%), it is likely that there is an inter-population variation in the proportion of immigrants.

Returns to their territory affords birds a number of advantages important for both survival and their successful breeding. Some investigators believe that bird's return to the natal territory for breeding provides it with an 'ecogenetic' advantage, i. e. the possibility to mate with an individual of a related genotype (ORING & LANK 1984). This may play an important role in maintaining local adaptability in birds.

### Zusammenfassung

#### Ortstreue, Dismigration und Populationszusammensetzung bei einigen Sperlingsvogel-Arten auf der Kurischen Nehrung/Ostsee.

Das Ausmaß der Ortstreue – speziell der Geburtsortstreue – kann selbst bei verwandten Arten erheblich variieren. Wie durch die Nestlings- und Jungvogelberingung auf der Kurischen Nehrung gezeigt werden konnte, kehren bei einigen Arten (Sperbergrasmücke *Sylvia nisoria*, Fitis *Phylloscopus trochilus*, Buchfink *Fringilla coelebs*) die meisten Einjährigen zur Brut an den Geburtsort zurück, während bei anderen Arten (Klappergrasmücke *Sylvia curruca*, Karmingimpel *Carpodacus erythrinus*) nur ein sehr geringer Teil der Individuen zurückkehren scheint. Artunterschiede im Niveau der Geburtsortstreue sind grundsätzlich eine Folge des Prägungszeitpunktes und der Länge des Aufenthaltes am Geburtsplatz. Die Vögel kehren dorthin zurück wo die Gebietsprägung erfolgte. Falls die Prägung vor Verlassen der Geburtsregion erfolgt, wird das Niveau der Geburtsortstreue in den folgenden Jahren hoch sein. Falls die Gebietsprägung dagegen erst nach Beginn der Zerstreuungswanderung erfolgt, wird das Niveau der Geburtsortstreue nur gering sein. Die Entfernung zwischen Geburts- und Brutort wird dann vor allem durch die Abwanderungsentfernung nach dem Flüggewerden bestimmt. Doch wird die Ortstreue auch von einer Reihe anderer Faktoren beeinflusst: vom Schlüpftermin, vom Bruterfolg, von der Habitatgüte, dem Alter, der Erfahrung und anderem. Das Verhältnis geburtsortstreuer Vögel zu Zuwanderern in einer Population hängt vor allem von der Rückkehrate zum Geburtsort ab. Bei Arten mit hoher Geburtsortstreue erhält sich der Brutbestand vor allem durch Vögel aus der eigenen Population. Bei solchen Arten machen Zuwanderer nicht mehr als 20% von der Gesamtzahl aller Individuen aus.

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Autor(en)/Author(s): Sokolov Leonid

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