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PHILOPATRY OF MIGRATORY BIRDS

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ABSTRACT

Available papers by Soviet and foreign authors on philopatry of migratory species revealed that this phenomenon is also widespread in birds. At present a tendency to natal philopatry has been shown to exist in varying degrees in about 180 species, to breeding philopatry in 280 species and to winter philopatry in 150 species of 14 orders. As shown in most studies, fidelity for their previous breeding site is more pronounced in adult birds than in the young to their birthplace. This is connected, first of all, with the fact that in young birds dispersal occurs in the early months of their life. In spring, young birds show fidelity for the site where the territory was imprinted in the postbreeding period. Usually the level of natal philopatry is high in those birds which imprint territory early enough prior to leaving the birthplace. In contrast, natal philopatry has not been revealed in birds which imprint territory after leaving their birthplace. In these birds, natal dispersal depends, first of all, on their postbreeding dispersal as juveniles. Philopatry is also affected by a number of other factors: breeding success, constant habitat, age and experience, date of birth, survival rate, interspecies competitiveness, etc. Apparently a process similar to image imprinting in birds underlies the mechanism of territory fixation. All the principal territories (breeding, wintering, molting, migration stopover areas) are imprinted mainly during the first year of life and 'dominate' over information on other territories acquired by birds throughout their life. On territory imprinting (generally occurring in migratory birds between 30 and 50 days of age), birds evidently compile 'mosaic' and 'navigational' maps of the environment, enabling them to reach their destination accurately.

KEYWORDS: Migration, territory, return's rates, dispersal, philopatry, fidelity, imprinting, territory fixation, population, structure

PHILOPATRY OF MIGRATORY BIRDS

CONTENTS

1. INTRODUCTION

Migratory birds with fidelity for their breeding areas, often necessitating traveling hundreds and thousands of kilometers, form a special group among vertebrates, many of which are territorial. Most migratory birds well adapted to long-distance flights have developed and successfully improved their homing and navigational abilities.

During evolution, philopatry has resulted in the formation of bird populations finely adapted to their external conditions, the dimensions and structure of which cannot be clarified without detailed studies of philopatry. Studies of philopatry are also of vital importance for developing the migration theory, since it is the territoriality factor that, to a large extent, determines the distances and directions of annual bird migrations. In addition they contribute to decoding the complex mechanisms of orientation and navigation in birds (Sokolov, 1988, 1991*a*).

Investigations of the philopatry mechanism are of great practical importance. The introduction of birds to afforested areas in the former Soviet Union during the 1950s showed that no success can be achieved in moving bird populations without a knowledge of the time of their "future breeding territory imprinting" (Isakov, 1957; Scherbakov, 1960). At present, the challenge of conserving species requires us not only to preserve existing animals but also to assist actively in breeding, translocation and adaptation of those that are on the verge of extinction. Special programs for the preservation and breeding of valuable and rare bird species have and are taking place in many countries including the Russia (Zimmerman, 1976; McKeating, 1978; Scott and Carpenter, 1987; Flint, 1988).

2. TERMINOLOGY

Terminology current in the English-language literature is used in this review (Greenwood, 1980).

Abmigration	the deviation of an individual from the species migration route, flying far from or not reaching its birthplace or breeding area as a result of mating
Autochthon	a local bird breeding in its birthplace
Birthplace	the area within a radius of between several meters and 1 kilometer around the parental nest

Breeding dispersal	the movement of an adult bird from one breeding site to another
Breeding philopatry	the return of adult bird to the previous nesting site
Emigration	the movement of adult bird from the previous breeding area
Homing	the return of bird to it's nest after migration during the same season
Immigration	the movement of a bird to the area which was not previously populated by it
Natal dispersal	the movement of a birds from its birthplace to its breeding area
Natal philopatry	the return of adult bird to the natal place
Natal area	the area within a radius of between 1 and 10 kilometers around the birthplace
Postbreeding (postfledgling, juvenile) dispersal	the movement of a bird from its birthplace to the territory from which it will migrate in the autumn
Spacing	forced movement of bird from one site to another caused by extrinsic factors (habitat changes, nest destruction, intraspecies competition, etc.)
Territory imprinting	fixation of the site to which the bird will return in subsequent years
Wintering philopatry	the return of adult bird to it's previous wintering site

3. METHODS OF STUDYING PHILOPATRY IN BIRDS

Philopatry in birds is measured by their return rate, i.e. the percentage of birds which return in subsequent years to the area where they were banded.

It is usually difficult to estimate the actual return rate due to the problems in observing all the returning individuals. On the *Fringilla* field station situated on the Courish Spit of the Baltic Sea, birds are captured using large stationary traps (Dolnik and Payevsky, 1976) located amid man-planted *Pinus silvestris* forests (Figure 1) and then ringed. Two different methods were employed to estimate the efficiency of such traps in

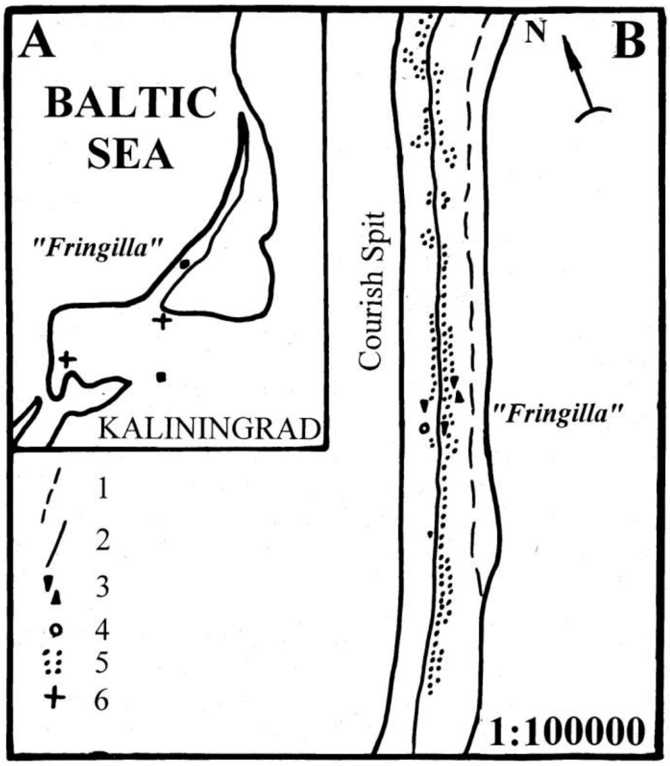

Figure 1. Map of the Courish Spit on the Baltic Sea coast. *A* – the main study region. *B* – 1, Rand dunes boundaries; 2, Hayway; 3, large traps; 4, aviary; 5, nest-boxes; 6, sites of experimental bird release.

capturing and returning birds (Dolnik and Payevsky, 1982; Sokolov and Vysotsky, 1988). As known by the estimations, large traps (these 4 manipulated simultaneously between April 1 and November 1) capture 1 out of 3 individuals breeding within 1 km of their position. In calculating the percentage probability, not only the efficiency of recapture was taken into consideration, but also their annual mortality (Table 3). In other regions of the former USSR, estimations of the return rate in birds are usually performed using mist-nets or other traps located directly in the nests (Zimin and Lapshin, 1976; Mihelson *et al.*, 1977; Kovshar, 1979; Golovan, 1988; Zimin, 1988). The efficiency of such methods may vary

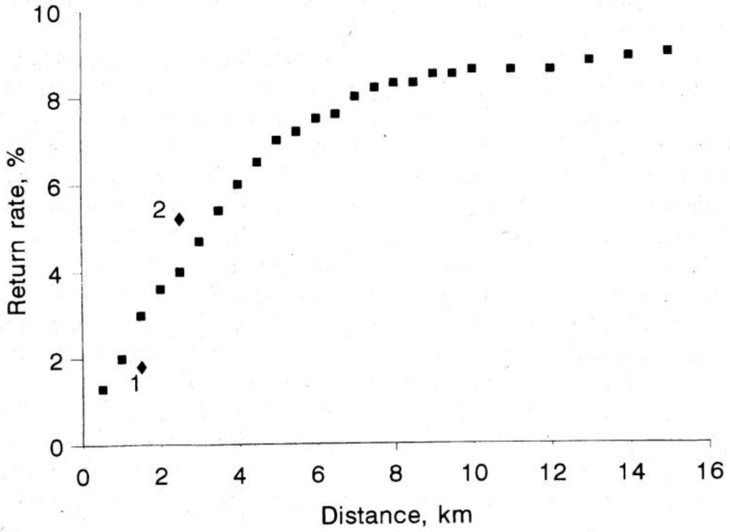

Figure 2. Dependence of philopatry on the radius of the control territory for *Ficedula hypoleuca* breeding at the Courish Spit. Every point represents the return rate (the number of nestlings ringed – 2060) at an appropriate distance from the ringing site: 1, data accumulated in Finland (Haartman, 1960); 2, data accumulated in Germany (Winkel, 1982). The abscissa shows the radius of the control territory (km). The ordinate shows cumulative return rates.

significantly. For example, when capturing Pied Flycatchers (*Ficedula hypoleuca*) in nest boxes various methods are used whose efficiency differs greatly (Artemyev, 1989; Leivits and Vilbaste, 1990). 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 male individuals by automated traps prior to their nesting in occupied nest boxes (Sokolov *et al.*, 1990). In addition, the efficient control over tree-hole nestlers is greatly dependent on the availability of natural holes in the area studied. On the *Fringilla* field station where 20- to 30-year-old *Pinus silvestris* trees represent the dominant vegetation in the forest and holes are rare, the efficiency of capturing Pied Flycatchers is as high as 95%. In this region their average return rate is 9%. In other regions of the Spit where deciduous trees having numerous holes are dominant, the efficiency of capturing this species is noticeably lower and their return rate is only 4% (Sokolov *et al.*, 1990).

Return rates depend strongly on the extent of the territory inspected by investigators. Thus, the return rate in Pied Flycatchers breeding on the Courish Spit appears to be as small as 2% when the area examined has a radius of only 1 km from the parental nest, and it grows to 9% when the radius increases to 10 km (Figure 2). As a rule, fieldwalkers inspect small areas (with a radius between 1 and 2 km), therefore a large proportion of the birds which returned to the site of their ringing remain unnoticed (Sokolov *et al.*, 1990). In studying philopatry it is necessary to take into consideration not only the control efficiency and annual mortality rate, but also the extent of the territory inspected. Only if this is the case can return rates be compared somewhere. Of course, to make a more accurate comparison, all techniques and habitats, etc., would have to be the same.

The dispersal distance (including postbreeding, natal and breeding) is most often evaluated either by frequency of observing ringed individuals in area of the banding site or by the median (50%) of bird movement distance from the latter (Bauer, 1987). Because it is so narrow (between 0.7 and 3.5 km) and short (97 km), the Courish Spit gives us a unique possibility for studying postbreeding dispersal in juvenile birds using large traps (Sokolov, 1976*a*; Sokolov *et al.*, 1987; Sokolov and Vysotsky, 1988).

4. NATAL, BREEDING AND WINTERING PHILOPATRY IN MIGRATORY BIRDS

Analysis of papers (written over a period of more then 50 years) on ringing birds in their breeding and wintering sites have shown that fidelity for their birthplace, previous breeding and wintering sites is inherent to many migratory birds (Table 1). Philopatry has been revealed in different groups including the largest and long-living birds and the smallest and short-living passerine species. Philopatry is intrinsic both to waterfowl and terrestrial birds, hole nestlers and birds breeding in open nests, i.e. species with quite different behavior patterns and habitats.

As a rule, natal philopatry is less pronounced than breeding or winter philopatry (Table 2). On the whole, return rates in long-living birds are higher than in short-living ones. However, it should be taken into account that when estimating the return rate, some investigators do not make allowance for annual bird mortality, which varies greatly from species to species, although new models are available which generally do allow for

Table 1. Philopatry in different bird taxons.

Order	*Number of species which show*		
	Natal philopatry	*Breeding philopatry*	*Wintering philopatry*
Podicipediformes	1	3 (2)	1
Procellariiformes	11	17 (1)	
Pelecaniformes	1	2 (1)	1
Ciconiiformes	4 (3)	5 (4)	
Anseriformes	18 (9)	23 (12)	17
Falconiformes	8 (3)	15 (6)	6
Gruiformes	3 (2)	4 (2)	4
Charadriiformes			
Charadriidae	29 (3)	49 (4)	24
Laridae	13 (5)	24 (6)	7
Alcidae	5 (2)	9 (3)	
Columbiformes	1	3 (1)	
Cuculiformes	1	1	
Apodiformes	4 (1)	7 (1)	
Coraciiformes	2 (2)	3 (2)	
Piciformes	1 (1)	1 (1)	1
Passeriformes	76 (25)	109 (51)	89
Total	178 (56)	275 (97)	150

Note: The table lists available in the literature including Soviet publications (given in parentheses) between 1937 and 1989.

this. The annual mortality rate in albatrosses (*Diomedeidae*) and storm-petrels (*Hydrobatidae*) is about 6%, whereas in small passerine species it increases to 50% (Payevsky, 1985). When annual mortality rates are taken into consideration, the differences in the return rates of long- and short-living birds will not be so striking (Sokolov, 1991*a*).

Philopatry, in the first place natal philopatry, can vary noticeably even in related species. Thus, ringing of passerine birds breeding in the area of the Courish Spit has revealed that in some species (Barred Warbler, *Sylvia nisoria*; Willow Warbler, *Phylloscopus trochilus*; Chaffinch, *Fringilla coeblebs*) the majoring survivors return to breed on their birth site, while in other species (Garden Warbler, *Sylvia borin*; Lesser Whitethroat, *Sylvia curruca*; Swallow, *Hirundo rustica*; Red-backed Shrike, *Lanius collurio*; Scarlet Rosefinch, *Carpodacus erythrinus*) only an insignificant number

Table 2. Average rate of return to the area of ringing in different bird taxons.

Order	*Percentage of birds captured in*		
	Natal area	*Breeding area*	*Wintering area*
Procellariiformes and Ciconiiformes	22.1 ± 8.0 (4)	60.3 ± 4.4 (3)	
Anseriformes	11.2 ± 3.1 (8)	43.8 ± 5.9(11)	54.0 ± 10.5 (5)
Charadriiformes	14.9 ± 2.7(16)	56.4 ± 5.3(20)	65.7 ± 12.0 (6)
Passeriformes	6.0 ± 0.7(43)	30.0 ± 2.2(56)	22.2 ± 2.9 (35)

Note: Numbers of species for which the average percentage of the return rate has been calculated are given in parentheses.

of survivors appear to return (Table 3). In many cases return rates of banded fledglings are higher than those in birds ringed earlier (Table 3). Studies of the Common Sandpiper (*Actitis hypoleucos*) in England showed that the return rate of birds ringed before fledging was 6%, while that of birds banded later was 25% (Holland *et al.*, 1982). In Finland, (Reed Bunting *Emberiza schoeniclus*) ringed before fledging appear to have a return rate of 2.5% in subsequent years, and the return rate of juvenile birds ringed upon molting is 10% (Haukioja, 1971). The rate of return of *Phylloscopus trochilus* to the natal area in England is 5%, and that to the area where they were ringed upon fledging is 13% (Lawn, 1982). I suggest, that this may be explained, first of all, by the fact that in many migratory birds territory imprinting of the future breeding area proceeds mainly outside the natal area either during or after post fledgling dispersal (Table 12). At the same time, these differences in the return rates of birds ringed before or after flighting from nest could be caused by high mortality rates during the period between onset of fledging through to self-sufficiency when the young start moving independently (Payevsky, 1985).

Using the first data on bird ringing, Howard (1920) forwarded a hypothesis on "strong site fidelity", according which practically all migratory surviving birds return to the area of their birth and previous breeding site. This idea was widespread at the time, especially in the Russia, and underlay the development of the so-called "theory of small populations" in birds (Mayer, 1942; Isakov, 1949; Polivanov, 1957). These authors interpreted the biological significance of small populations as their increasing adaptability to local habitat due to sustaining their gene pool. Adherents of this

Table 3. Philopatry and site fidelity in some migratory species at the Courish

Species	*Age of birds*	*Number of ringed birds*	*Returns*		*Proba return r*
			N	*%*	
Jynx	Pull.	334	5	*1.5 ± 1.0‡	20
torquilla	Juv.	183	10	*5.5 ± 1.9*	60
	Ad.	154	21	13.6 ± 2.6‡	90
Hirundo	Pull.	227	2	1.0 ± 0.6*	12
rustica	Juv.	1175	16	1.4 ± 0.9†	16
	Ad.	161	8	5.0 ± 2.3†	44
Ficedula	Pull.	2280	194	8.5 ± 0.6‡	32
hypoleuca	Juv.	91	6	6.6 ± 1.1‡	22
	Ad.	308	98	31.8 ± 1.3‡	65
Phylloscopus	Pull.	902	66	7.3 ± 1.5	80
trochilus	Juv.	8759	688	7.9 ± 0.7	75
	Ad.	746	50	6.7 ± 1.9	60
Hippolais	Pull.	1026	31	‡3.0 ± 1.5‡	35
icterina	Juv.	1298	99	‡7.7 ± 1.6	87
	Ad.	1287	109	8.5 ± 1.2‡	75
Sylvia	Pull.	495	40	8.1 ± 1.4	90
nisoria	Juv.	332	27	8.1 ± 1.5	81
	Ad.	933	99	10.6 ± 1.6	85
Sylvia	Pull.	1630	23	1.4 ± 0.6‡	19
curruca	Juv.	2585	45	1.7 ± 0.4‡	20
	Ad.	518	46	8.9 ± 1.5‡	80
Sylvia	Pull.	934	8	‡0.9 ± 0.4†	12
borin	Juv.	171	9	‡5.3 ± 1.7	53
	Ad.	262	9	3.4 ± 1.0†	31
Sylvia	Pull.	149	0	0.0	0
communis	Juv.	120	7	5.8 ± 1.8	48
	Ad.	442	12	2.7 ± 1.0	24
Motacilla	Pull.	198	0	0.0	0
alba	Juv.	2713	50	1.8 ± 0.6‡	21
	Ad.	247	27	10.9 ± 2.1‡	97
Anthus	Pull.	200	4	2.0 ± 1.7	26
trivialis	Juv.	649	12	1.8 ± 0.7†	21
	Ad.	199	12	6.0 ± 3.4†	54
Lanius	Pull.	326	2	0.6 ± 0.3‡	8
collurio	Juv.	203	2	1.0 ± 0.6‡	11
	Ad.	135	12	9.0 ± 2.7‡	80
Carpodacus	Pull.	698	4	0.6 ± 0.5‡	8
erythrinus	Juv.	164	1	0.6 ± 0.6‡	7
	Ad.	392	53	13.5 ± 1.9‡	90

Table 3. Philopatry and site fidelity in some migratory species at the Courish Spit.

Species	*Age of birds*	*Number of ringed birds*	*Returns*		*Probable return rates*
			N	*%*	
Fringilla coelebs	Pull.	5859	492	$^{‡}8.4 \pm 1.0^{‡}$	98
	Juv.	9116	1143	$^{‡}12.5 \pm 0.8$	98
	Ad.	2042	227	$11.1 \pm 1.2^{‡}$	80

Note: Probable return rate is calculated taking into account the annual mortality rate (between 45 and 55% in adult birds, between 60 and 65% in juvenile birds, and between 65 and 70% in birds ringed as nestlings; Payevsky, 1985) and the efficiency of capturing birds by stationary large traps (between 25 and 30%; Dolnik and Payevsky, 1982) and in nest boxes (95% for *Ficedula hypoleuca*; Sokolov and Vysotsky, 1988). Symbols on the right show differences in return rates of adult and juvenile birds: *, $p < 0.05$; †, $p < 0.01$ and ‡, $p < 0.001$. Symbols on the left show reliable differences in return rates of birds ringed when young and as nestlings (χ^2 test). Abbreviations: Pull., pullus; Juv., juvenile; Ad., adult.

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 by its offspring. Ringed birds detected far away from their birthplaces or breeding areas were considered as exceptions. At the same time, violent opponents of this hypothesis appeared in the Russia. Thus, from his observations on passerine birds ringed in the Voronezh Region and in the vicinity of Leningrad, A.S. Malchevsky put forward a contrary hypothesis on bird philopatry (Malchevsky, 1959, 1968, 1969). According to this investigator, only an insignificant proportion of birds (between 1 and 4%) returned to the natal area, and therefore it was impossible to suggest genetic constancy of local populations in birds. Subsequent ringing of both migratory and resident birds in different parts of the world has demonstrated that a remarkable proportion of surviving birds may return to their natal area. For example, on the Courish Spit, the population of some species (Barred Warbler, *Sylvia nisoria*; Willow Warbler, *Phylloscopus trochilus*; Chaffinch, *Fringilla coelebs*) is maintained mostly by local birds (Table 3). Immigrants make up no more than 20%. At the same time, in populations of other species, in particular Swallow (*Hirundo rustica*), Besser Whitethroat (*Sylvia curruca*), Garden Warbler (*S. borin*), Whitethroat (*S. communis*), White wagtail (*Motacilla alba*), Red-backed Shrike (*Lanius colluria*) and Scarlet Rosefinch (*Carpodacus erythrinus*), the majority of yearlings appear to be immigrants of unknown origin. It is likely that in the case of the Barred Warbler (*Sylvia nisoria*), Willow Warbler (*Phylloscopus trochilus*) and Chaffinch (*Fringilla coelebs*) we can assume the existence of a genetically independent population on the Courish Spit, which includes tens of thousands of individuals (Sokolov, 1986). As previously described the Spit is about 100 km long and between 0.7 and 3.5 km wide, with a forest belt stretching throughout its length. Therefore, there are no grounds to suggest the existence of several populations of the same species breeding on the Spit. In general, the problem of the existence and sizes of local populations in migratory birds remains, as yet, unsolved. The first thing is to determine the ratio of local and immigrant birds in the populations. This is a difficult task since it requires not only the ringing of an adult individuals when breeding, their nestlings and juveniles in the postbreeding period, but also the thorough examination of all returning ringed individuals in the following year. In the former Soviet Union, this has been most successfully achieved in Latvia where from 80 to 90% of adult Shoveler (*Anas clypeata*) and Tufted Duck (*Aythya fuligula*) females and ducklings are ringed annually on several islands of the Engures Lake (Mihelson *et al.*, 1968, 1986), in Lithuania where the Common Gull (*Larus canus*) nestlings and adult birds have been successfully ringed on the coast and islands of the Baltic Sea (Onno, 1964; Rattiste, 1981), on the Courish Spit and in Karelia where populations of Pied Flycatchers (*Ficedula hypoleuca*) have been studied (Sokolov *et al.*, 1989; Artemyev, 1989). Having analyzed the data on ringing, Latvian scientist have concluded that in *Anas clypeata* local females comprise about 90% and immigrant females only 10% of the population. Yearlings and 2-year-old birds make up about 50% of local females. In Aythya fuligula local females also make up about 90%, hence only 10% of the population are immigrants. However, the proportion of 1–2-year-old individuals is only 20%. These data describe, exclusively, the mean ratio of local ducks and immigrants in the populations studied. In some years it varies greatly depending on the mortality rate in ducks of different ages, their breeding population density and climatic conditions in the wintering sites (Mihelson *et al.*, 1986).

In the vicinity of the *Fringilla* field station (within 5 km from the station center), where the efficiency of estimating the return rate of Pied Flycatchers is about 95%, 828 breeding individuals were captured in the period between 1983 and 1988. Of them, 195 (24%) birds were local ones hatched in the study region, and the other 633 (76%) turned out to be birds of unknown origin (immigrants). Among the latter, 131 (21%) individuals bred more than once in the study region, while 502 (79%) birds were

Table 4. Ratio of local and immigrant birds in the Ficedula hypoleuca population breeding in Karelia and at the Courish Spit.

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

Note: N, total number of birds captured in the study region; n, number of local or immigrant birds. *, Data from Artemyev (1989).

found to breed there only once. In various years, the portion of local birds in the population ranged between 15% (in 1983) and 35% (in 1987). The data on local birds for 1983 is likely to be an underestimate, since ringing of nestlings was not complete in the region in the preceding years. It is remarkable that the greatest number of local birds was detected in 1987 after the year of the highest breeding success (1986), when the maximal number of nestlings was ringed in the study region (Table 4). The proportion of local birds among all males was reliably higher (27%) than among all females (20%, $\chi^2 = 6.7$; $df = 1$; $p < 0.01$). 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% 5-year olds (Sokolov *et al.*, 1989).

Artemyev (1989) carried out an analogous study of the structure of the Pied Flycatcher breeding population in Olonetsk Region (Karelia), i.e. about 1000 km northeast of the Courish Spit. His ratio of local and immigrant birds in the population is different (Table 4). In the Karelian population the number of local males is about 3 times less than on the Courish population ($\chi^2 = 59.9$; $df = 1$; $p < 0.001$), whereas the number of local females is 4 times smaller ($\chi^2 = 57.8$; $df = 1$; $p < 0.001$). This can be explained, first of all, by the return rate of Pied Flycatchers in Karelia which is 3 times lower than that on the Courish Spit (Table 5). Although the accuracy of observation of banded males in Karelia is lower (mean of 74%) than on the Courish Spit, it is likely that there is a populational divergence in the proportion of immigrants. Among the latter, 70% of birds are yearlings judging by the shape of their tail feathers and some other signs (Vysotsky, 1989). It is difficult to determine from what region immigrants arrive. The data on natal dispersal of Pied Flycatchers (Table 9) may suggest that the majority of immigrants, which settled to breed in the study region, were hatched at a distance within 40 or 50 km from this area (Sokolov *et al.*, 1990). According to Winkel (1982), the proportion of immigrants in the population of Pied Flycatchers in Lower Saxony (Germany) is similar to that breeding on the Courish Spit. The ratio of local birds and immigrants in populations of Pied Flycatchers depends, first of all, on the rate of their return to the birthplace. It was postulated by Mayer (1968) that the greatest divergence in natal philopatry should appear between the central and peripheral populations. From the data of Haartman (1949) on the population of Pied Flycatchers in Finland, according to which the natal philopatry in that population is less pronounced than in populations breeding in central Europe (Table 5), Mayer suggested that the bird population in Finland consists, in the most part, of off-

Table 5. Natal and breeding philopatry in different populations of some migratory bird species.

<table>
<tr><th rowspan="3"><i>Species</i></th><th rowspan="3"><i>Area of ringing</i></th><th colspan="3"><i>Return (%) to</i></th><th rowspan="3"><i>Reference</i></th></tr>
<tr><th><i>natal areas</i></th><th colspan="2"><i>breeding areas</i></th></tr>
<tr><th><i>M&F</i></th><th><i>M</i></th><th><i>F</i></th></tr>
<tr><td rowspan="3"><i>Calidris alpina</i></td><td>USA, Alaska</td><td>5.9</td><td>–</td><td>–</td><td>Holmes, 1966</td></tr>
<tr><td>Finland</td><td>11.2</td><td>77</td><td>71</td><td>Soikkeli, 1970</td></tr>
<tr><td>Germany</td><td>3.6</td><td>–</td><td>–</td><td>Heldt, 1966</td></tr>
<tr><td rowspan="3"><i>Apus apus</i></td><td>Russia, Oka reserve</td><td>4.0</td><td colspan="2">40*</td><td>Kashentseva, 1982</td></tr>
<tr><td>England</td><td>1.3</td><td colspan="2">–</td><td>Perrins, 1971</td></tr>
<tr><td>Switzerland</td><td>48.6</td><td colspan="2">–</td><td>Weitnauer, 1975</td></tr>
<tr><td rowspan="3"><i>Delichon urbica</i></td><td>Russia, Courish Spit</td><td>9.0</td><td colspan="2">16</td><td>Lyuleeva, 1967</td></tr>
<tr><td>Germany</td><td>25.0</td><td colspan="2">–</td><td>Rheinwald and Gutscher, 1969</td></tr>
<tr><td>Spain</td><td>6.1</td><td colspan="2">23</td><td>De Lope and Da Silva, 1988</td></tr>
<tr><td rowspan="5"><i>Riparia riparia</i></td><td>Ukraine, Odessa region</td><td>–</td><td colspan="2">35</td><td>Chernichko and Yurchuk, 1985</td></tr>
<tr><td>Germany</td><td>5.0</td><td colspan="2">24</td><td>Schmidt, 1982</td></tr>
<tr><td>Germany</td><td>–</td><td colspan="2">14</td><td>Loske, 1989</td></tr>
<tr><td>England</td><td>11.5</td><td colspan="2">31</td><td>Holmes <i>et al.</i>, 1987</td></tr>
<tr><td>USA, New York</td><td>7.6</td><td colspan="2">11</td><td>Freer, 1979</td></tr>
<tr><td rowspan="5"><i>Motacilla alba</i></td><td>Russia, Polar Urals</td><td>–</td><td colspan="2">17</td><td>Shutov, 1989</td></tr>
<tr><td>Russia, Yamal</td><td>–</td><td colspan="2">20</td><td>Danilov <i>et al.</i>, 1984</td></tr>
<tr><td>Finland</td><td>2.5</td><td colspan="2">–</td><td>Leinonen, 1974</td></tr>
<tr><td>Kazakhstan</td><td>0</td><td colspan="2">24</td><td>Levin and Gubin, 1985</td></tr>
<tr><td>Russia, Courish Spit</td><td>0</td><td colspan="2">11</td><td>this review</td></tr>
<tr><td rowspan="6"><i>Anthus trivialis</i></td><td>Russia, Karelia</td><td>–</td><td colspan="2">15</td><td>Zimin and Lapshin, 1976</td></tr>
<tr><td>Kazakhstan</td><td>2.0</td><td colspan="2">23</td><td>Levin and Gubin, 1985</td></tr>
<tr><td>Kazakhstan, Tyan-Shan</td><td>1.3</td><td colspan="2">18</td><td>Kovshar, 1979</td></tr>
<tr><td>Russia, Courish Spit</td><td>2.0</td><td colspan="2">6</td><td>this review</td></tr>
<tr><td>Switzerland</td><td>12.5</td><td>51</td><td>32</td><td>Meury, 1989</td></tr>
<tr><td>Belgium</td><td>4.6</td><td colspan="2">37</td><td>Hecke, 1981</td></tr>
<tr><td rowspan="6"><i>Luscinia svecica</i></td><td>Russia, Yamal</td><td>–</td><td colspan="2">8</td><td>Danilov <i>et al.</i>, 1984</td></tr>
<tr><td>Russia, Polar Urals</td><td>–</td><td colspan="2">13</td><td>Shutov, 1989</td></tr>
<tr><td>Kazakhstan</td><td>2.8</td><td colspan="2">26</td><td>Gubin, 1986</td></tr>
<tr><td>Poland</td><td>5.6</td><td colspan="2">43</td><td>Czarnecki, 1975</td></tr>
<tr><td>Germany</td><td>–</td><td colspan="2">47</td><td>Löhrl, 1987</td></tr>
<tr><td>Belgium</td><td>–</td><td colspan="2">24</td><td>Peeters, 1979</td></tr>
</table>

Table 5. Natal and breeding philopatry in different populations of some migratory bird species.

Species	*Area of ringing*	*Return (%) to*			*Reference*
		natal areas	*breeding areas*		
		M&F	*M*	*F*	
Phoenicurus phoenicurus	Kazakhstan	–	15		Levin and Gubin, 1985
	Kazakhstan, Tyan-Shan		25		Kovshar, 1979
	Netherlands	6.0	38		Ruiter, 1941
Turdus iliacus	Norway	0.7	25	16	Bjerke and Espmark, 1988
	Russia, Polar Urals	0	14	16	Shutov, 1989
	Russia, Karelia	1.6	31	30	Zimin and Lapshin, 1976
	Russia, Pskov region	1.2	16	12	Golovan, 1988
	Kazakhstan	2.1	–	–	Levin and Gubin, 1985
Sylvia borin	Finland	0	25	6	Solonen, 1979
	Russia, Pskov region	0	12	6	Golovan, 1988
	Russia, Courish Spit	0.9	4	2	this review
	Kazakhstan	1.4	20	–	Levin and Gubin, 1985
	Russia, Udmurtia	4.3	–	–	Zubtsovsky *et al.*, 1989
Phylloscopus trochilus	Russia, Polar Urals	2.3	26	26	Shutov, 1989
	Russia, Yamal	–	13		Danilov *et al.*, 1984
	Russia, Karelia	6.3	14	10	Sokolov *et al.*, 1986
	Russia, Pskov region	–	19	17	Golovan, 1988
	Russia, Courish Spit	7.3	–	–	this review
	Finland	2.0	24	–	Tiainen, 1983
	Poland	2.4	–	–	Czarnecki, 1975
	England	5.0	36	23	Lawn, 1982
Ficedula hypoleuca	Northern Sweden	2.0	25	8	Nyholm and Myhrberg, 1983
	Southern Sweden	–	38	–	Askenmo, 1979
	Finland	1.8	36	14	Haartman, 1960
	Russia, Karelia	2.0	47	18	Artemyev, 1989
	Estonia	0.5	37	15	Leivits and Vilbaste, 1990
	Latvia	2.5	42	28	Chaun, 1958
	Russia, Oka reserve	2.5	–	–	Likhachev, 1955
	Russia, Courish Spit	9.1	28	15	Sokolov *et al.*, 1990
	Germany	2.5	30	27	Creutz, 1955

Table 5. Natal and breeding philopatry in different populations of some migratory bird species.

Species	*Area of ringing*	*Return (%) to*			*Reference*
		natal areas	*breeding areas*		
		M&F	*M*	*F*	
Fringilla coelebs	Germany, Silesia	5.3	35	37	Trettau, 1952
	Germany, Berlin	10.4	45	30	Curio, 1958
	Germany, Lower Saxony	5.2	38	24	Winkel, 1982
	England	3.8	39	40	Campbell, 1959
	Russia, Karelia	1.0	30	19	Zimin and Lapshin, 1976
	Russia, Pskov region	2.1	15	7	Golovan, 1988
	Russia, Courish Spit	8.4	15	9	this review
	Russia, Gorky region	8.4	–	–	Anikin and Parakhin, 1967
	Kazakhstan	3.3	27		Levin and Gubin, 1985
	Russia, Udmurtia	6.0	–	–	Zubtsovsky *et al.*,1989
Carpodacus erythrinus	Russia, Polar Urals	–	13	8	Shutov, 1989
	Russia, Karelia	0	39	29	Zimin, 1981
	Finland	4.3	–	–	Stjernberg, 1979
	Russia, Courish Spit	0.6	15	12	this report
	Kazakhstan	–	47	17	Levin and Gubin, 1985

Note: M, males; F, females. *, Data common for males and females.

spring of birds that had migrated from continental Europe, in which the perception of 'homing' is less determined genetically. Other investigators have also indicated the existence of differences in philopatry varying from population to population (Table 5).

It was shown by Heldt (1966) that on the Western coast of Finland, the Dunlin (*Calidris alpina*) are much more inclined to breed in their natal area than on the coast of Germany (Table 5). The author assumes that this can be explained by the fact that the appropriate breeding habitat of this species is scattered over the coast of West Germany to a greater extent than on the coast of Finland.

On comparing the rates of the Swift's (*Apus apus*) return to the natal region in the Oka reserve (Russia) and other regions of the area, Kashentseva (1982) suggested that the divergence in natal philopatry is caused by the fact that an isolated colony settling in a rural area with scarce breeding sites was studied in Switzerland (Weitnauer, 1975), while in England an urban colony with greater possibilities for scattering was under study (Perrins, 1971).

Following on from the data on breeding philopatry in some migratory birds breeding in Northern taiga regions on the Western slope of the Polar Urals (Komi, Russia), Shutov (1989) suggested that in moving northwards, a decrease in the return rate of adult birds to the area of their previous breeding is caused by peculiarities of their settlement in the subarctic regions. Breeding philopatry is most remarkable in the borealis area inherent to the species which forms widespread colonies in southern subarctic regions, whereas in tundra it is less pronounced (Table 5).

Most species of migratory birds exhibit sexual differences in both natal and breeding philopatry. In the majority of species, especially passerines, males appear to show higher territorial philopatry than females (Greenwood, 1980). However, in some species, e.g. Canada Goose (*Branta canadensis*) (Surrendi, 1970), *Chen caerulescens* (Cooke *et al.*, 1975), many ducks (Mihelson *et al.*, 1968) and some sandpipers (Oring and Lank, 1984) the females return to natal regions in greater numbers than the males. In these species, females choose the nesting sites, while males often follow them in spring, and thus abmigration takes place.

What explanation can be given to the higher male territorial philopatry of most migratory birds? Different assumptions have been forwarded. Some investigators assume the greater dispersal of females to be due to the avoidance of inbreeding; however, others believe this to be questionable (Greenwood, 1980). A common peculiarity of those birds with remarkable female dispersal is that males set up and defend the territory and its resources required for breeding. By choosing the best males, females thus select the best territory. Therefore, it is in the male's interest to return to a known area where they have the chance of choosing the best territory, rather than to new areas where they run the risk of being unable to find an appropriate breeding site. In spring, females will settle in new territories since they are often attracted by an actively displaying male (Sokolov *et al.*, 1989). In mammals, in contrast to most bird species, the breeding territory is usually chosen and defended by females, thus they have a stronger territorial fidelity than the males which prefer dispersal (Greenwood, 1980).

5. FACTORS AFFECTING PHILOPATRY OF MIGRATORY BIRDS

It was found that return rates of some migratory birds depend greatly on hatch dates. Ringing of juvenile Manx Shearwater (*Puffinus puffinus*) in Wales showed that the return rate of individuals from early broods is reliably higher in subsequent years than those of later broods (Perrins, 1966). Similar data were obtained for Snow Goose *(Anser caerulescens)* in Canada (Cooke *et al.*, 1975), Tufted Duck (*Aythya fuligula*) and Shoveler (*Anas clypeata*) in Latvia (Mihelson *et al.*, 1977), Kingfisher (*Alcedo atthis*) in the Oka reserve (Numerov and Kotyukov, 1981), *Fringilla coelebs* and *Ficedula hypoleuca* on the Courish Spit (Sokolov, 1982*a,b*; Sokolov *et al.*, 1990).

The analysis of return rates in chaffinch offspring, hatched at different times, on the Courish Spit has revealed the following: the young hatched between June 1 and 20 have a higher rate of return to their birthplace in subsequent years – 10.3% (297 of the 2872 young birds ringed) than those hatched between June 21 and 30–7.9% (143 of the 1813 birds ringed) or in July–only 4.4% (52 of the 1174 birds ringed). The differences between the first and second, second and third groups are significant ($\chi^2 = 7.6$; $df = 1$; $p < 0.01$; $\chi^2 = 13.4$; $df = 1$; $p = 0.001$).

Pied Flycatchers hatched during the first ten days of June on the Courish Spit have a reliably higher rate of return to their birthplace – 12.8% (75 of the 585 young birds ringed) than those hatched in the second decade – 7.9% (58 of 729) or in the third decade of June and early in July – 4.8 (19 of the 397 birds ringed) (Figure 3). The differences between the first and second, and the second and third groups of birds are significant ($\chi^2 = 7.9$; $df = 1$; $p < 0.01$; $\chi^2 = 4.0$; $df = 1$; $p < 0.05$).

What is the main reason for the higher return rate seen in the earlier hatched birds of some migratory species compared with those hatched later? Some investigators assume that this can be explained first of all by the variable survival rate in birds of early and late broods. In particular, Latvian ornithologists have found that the relative survival rate of juveniles from early broods (hatched prior to June 5) in the *Anas clypeata* population in the Lake Engures region is 9.6%, while that of the ducklings ringed from later broods (hatched after June 26) is only 1.3% (Mihelson *et al.*, 1977). We believe that those birds breeding earlier foster more viable offspring than specimen with later breeding periods (Sokolov *et al.*, 1990). Birds with an early breeding period are as a rule adult individuals which arrive earlier in the spring than do yearlings, establish a better territory and have bred before (Vysotsky, 1986). As shown by our studies of Pied Fly-

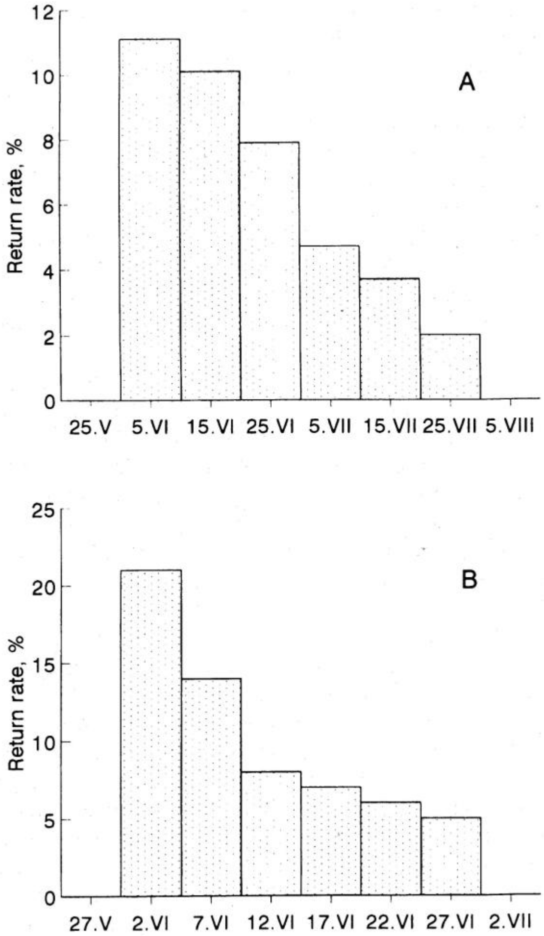

Figure 3. Dependence of philopatry on the birth dates of *Fringilla coelebs* (*A*) *Ficedula hypoleuca* (*B*) at the Courish Spit. The abscissa shows the hatch dates. The ordinate shows return rates.

catchers on the Courish Spit, such individuals have a greater clutch size, a better hatching success and higher growth rates (Sokolov *et al.*, 1990). Moreover, in most cases late breeding Pied Flycatchers appear to be immigrants nesting in poorer territories compared with local birds. As a result, their offspring may be less viable.

In addition to variable viability, birds of early and late broods can differ in distances of postbreeding dispersal from the birthplace. For example, in the House Martin (*Delichon urbica*) breeding in Germany (Rheinwald and Gutcher, 1969) and the Great Tit (*Parus major*) breeding in Holland (Dhondt and Huble, 1968), nesting sites of birds with later hatch dates appeared to be more remote from their birthplace than those hatched earlier. On the Courish Spit, female *Ficedula hypoleuca* hatched after June 9 appeared to nest reliably further from their birthplace (60% 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). As shown by the analysis of captured individuals ringed in the postbreeding period, Pied Flycatchers from late broods abandon their natal site earlier than do birds from early broods. As a result, they imprint future-breeding territory at a distance further from the birthplace than birds hatched earlier (Sokolov *et al.*, 1990).

The analysis of the return rates in birds hatches in different years has shown that Chaffinches and Pied Flycatchers, ringed as nestlings or fledglings during those years with early breeding periods, have a reliably higher return rate that those hatched in 'later' years (Figure 4). The highest return rate is found in birds hatched early in June in the years with early breeding periods (Sokolov, 1991*a*). 'Early' years on the Courish Spit are usually characterized by better breeding conditions (higher temperature, less rainfall, early vegetation, abundance of insects, etc). All these factors can enhance the viability of nestlings, fledglings and juvenile birds during the current year and, consequently, their return in the following year. Adult female Pied Flycatchers whose nestlings hatched during the first half of the breeding season (prior to June 15) appear to return in greater numbers (21.1% of 142 individuals) than females whose nestlings hatched in the second half of the season (12.4% of 121 individuals). However these differences are not significant ($\chi^2 = 3.5$; $df = 1$; $p = 0.06$). An increasing return rate in female Pied Flycatchers with early breeding periods was also found in Karelia (Artemyev, 1989). In males, the rate of return to the breeding site appeared to be independent of their breeding periods.

A comparison of the rates of return to the previous breeding site in Pied Flycatchers hatched on the Courish Spit and in immigrants which settled to breed there has shown that after the first breeding the local birds have a reliably higher return rate than do the immigrants (Table 6). These distinctions are more pronounced in females ($\chi^2 = 17.8$; $df = 1$; $p < 0.001$ for females and $\chi^2 = 4.6$; $df = 1$; $p < 0.05$ for males). However, after breeding for a second time both local and immigrant birds return to the territory at

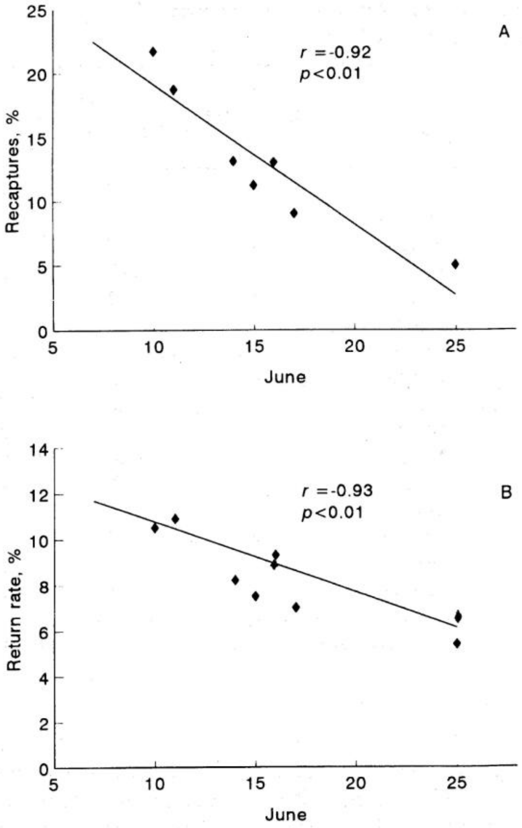

Figure 4. Dependence of the percentage of recaptures of *Ficedula hypoleuca* in the postbreeding period (*A*) and in subsequent years (*B*) on the breeding periods of a population the Courish Spit. The abscissa shows average hatch dates. The ordinate shows the percentage of the birds captured.

the same rates. How can this be explained? We have found that no more than 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. 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. In our area after the second breeding season, the immigrants show no determination to

Table 6. Breeding site fidelity in local and immigrant *Ficedula hypoleuca* birds of different age at the Courish Spit.

Group of birds	*Sex*	*Age (years)*	*Number of ringed birds*	*Returns*	
				n	*%*
Local	Males	1	84	34	40.5^*
	Females	1	70	22	$31.4^\dagger$
Immigrants	Males	*x*	257	50	19.4^*
	Females	*x*	369	33	$8.9^\dagger$
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

Note: *x*, Age unknown; *, significant at $p < 0.05$; †, significant at $p < 0.001$ (the χ^2 test).

return to the place where they established contact during the juvenile stage (Sokolov *et al.*, 1989). In Swedish Lapland, the birds breeding there for the first time also have a lower return rate (25% for males and only 8% for females) than those birds that have bred there more than once (46% for males and 50% for females) (Nyholm and Myhrberg, 1983). Using these data, the authors have suggested that fidelity for breeding territory in Pied Flycatchers is age-dependent. However, since these studies did not distinguish between local and immigrant birds, the variation in the return rates of birds that bred there once or more than once can be most likely explained by the fact that the first group comprised many immigrant yearlings whose return rate is seen to be lower than that of local birds. It is not affected by the age of birds. Our data demonstrate that local birds have a higher return rate after the second breeding season than after the first. But this difference is not reliable (Table 6). After third and fourth breeding season, the birds have a lower return rate than after the second one (Table

6). This may be explained by a higher mortality rate of 3 and 4 year olds rather than by decreasing age-dependent fidelity for their breeding territories.

Two year olds and older local Pied Flycatchers begin nesting about 3.5 days earlier than immigrants ($t = 2.18$; $df = 201$; $p < 0.05$). The average size of a brood is 0.8 nestlings larger in local females older than 2 years than that in pairs of immigrants and local yearlings ($t = 2.07$; $df = 201$; $p < 0.05$; $t = 2.33$; $df = 56$; $p < 0.05$, respectively). The highest return rate (10.9%, 13 of the 119 individuals ringed) is found for birds whose parents were local females aged 2 or more years. The lowest return rate is estimated for birds whose parents were local (7%, 15 of the 214 nestlings ringed) or immigrant (8.5%, 86 of the 1006 nestlings ringed) yearlings.

In addition to the age and experience of birds, their rate of return to the previous breeding site is also affected by their breeding success and mate tenacity. 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 (Dowsett–Lemaire, 1978; Freer, 1979; Hund and Prinzinger, 1979; Oring and Lank, 1982). This can be explained first of all by the fact that unsuccessful breeding forces birds to move to alternative regions in subsequent years. Latvian scientists have found that adult female *Aythya fuligula* and *Anas clypeata* breeding in the Engures Lake region which have lost their clutches abandon the breeding area more often and start breeding in other regions of the lake (Mihelson *et al.*, 1986).

6. DEPENDENCE OF PHILOPATRY ON THE POPULATION NUMBER

It is accepted that, as a rule, high population numbers negatively affect the survival rate of animals. Data on the influence of a high population density on bird survival rates are scanty (Kluijver, 1966, Lack, 1966; Payevsky, 1985). In Latvia, the *Aythya fuligula* birds hatched on islands with a high population density are more endangered upon fledging than those hatched in regions with a low population density (Mihelson *et al.*, 1986). Since a high population density increases the mortality rate or dispersal of juvenile birds from the natal place, philopatry should decrease in such a population. Having analyzed the rate of return to the natal and breeding place at high, moderate and low population densities in some migratory birds on the Courish Spit, we have found that the highest return rate is detected during those periods of high rather than low population density (Figure 5 and

Table 7). A significant decrease of the return rate was observed with a drop in the population density. By determining the proportion of local *Sylvia nisoria* birds, from those captured in spring in large traps, which settles to breed in the study region, it has been shown that at periods of high population density this proportion ranges between 20 and 70% and between 1 and 20% when there is a drop in the population density (Sokolov, 1991*b*). This demonstrates that during unfavorable periods, on arrival at their territory in the spring the birds have to abandon it, since it cannot provide suitable conditions for breeding (Vinogradova, 1988). It looks likely that conditions for breeding were optimal and all the returning birds had the chance to breed in their previous sites during the period of the highest population density. In our case, a drop in the population density in the Wryneck (*Jynx torquilla*), Red-backed Shrike (*Lanius collurio*), Barred Warbler (*Sylvia nisoria*) and Tree Pipit (*Anthus trivialis*) is connected first of all with alterations to the habitat. In the 1960s the young pine trees were between 0.5 and 1.0 m high and there were a lot of sandy regions with rare grass, at the beginning of the 80s the pine forest was between 5 and 7 m high and the sandy regions were entirely covered by grasses dominated by *Melampyrum pratense*, *Galium album* and *Anthoxanthum odoratum*. Moreover, in 1975 and 1984, weeding out and thinning was carried out in the young pine forests, as a result of which small *Pinus montana* and *Juniperus communis* trees as well as *Berberis vulgaris* shrubs, a favorite breeding place of *Sylvia nisoria* and *Lanius collurio*, were cut out. Therefore, the population density of these species began diminishing dramatically, causing a sharp decrease in the return of the birds to these regions in subsequent years (Figure 5, Table 7). The return rate of the species, whose population had not changed significantly during the study period, did not alter noticeably.

Some ornithologists suggest that birds have a mechanism of self-regulation of their numbers which eliminates overpopulation after a breeding success (Payevsky, 1985; Mihelson *et al*., 1986). As shown by Latvian ornithologists, self-regulation of breeding population numbers in some duck species (*Aythya fuligula*, *Anas clypeata*) in the Engures Lake region is mainly expressed in changing the survival rate of young birds (Mihelson *et al*., 1986). An increase in the breeding population density results in a decrease in the survival rate of young ducks in the postbreeding period during their migratory flights or over wintering. The mortality rate is essentially affected by the species' ability to compete with other birds. Our data do not offer support to the hypothesis postulating the existence of such a mechanism of self-regulation of numbers in passerine birds. A comparison of the number of young birds captured in the postbreeding period

Table 7. Tendency to changing numbers and philopatry in breeding populations of migratory species at the Courish Spit in different periods.

Species	*Age*	*Years*	*Numbers of birds captured*			*Return rate, %, Mean+SE*	*Correlation coefficient in dynamics rows*	
			Total	*Range per year*	*Mean*		*Numbers*	*Returns*
Jynx torquilla	Adult	1959–72	124	4–13	8.9	11.6 ± 3.0	+0.01	−0.25
		1973–88	63	0–15	3.9	4.4 ± 0.5	−0.77‡	−0.66†
	Juv.	“	154	2–28	11.0	5.2 ± 1.9	+0.44	−0.27
		“	85	0–15	5.3	0.4 ± 0.4	−0.75‡	−0.31
	Pull.	“	297	0–76	21.2	1.7 ± 0.9		−0.27
		“	70	0–18	4.4	0.4 ± 0.4		−0.42
Sylvia nisoria	Adult	1959–72	724	15–97	51.7	11.6 ± 1.7	+0.71‡	−0.24
		1973–88	431	8–96	26.9	4.8 ± 1.3	−0.64‡	−0.89‡
	Juv.	“	449	15–73	34.5	7.5 ± 1.3	+0.68‡	−0.56*
		“	196	0–33	12.2	1.8 ± 1.1	−0.75‡	−0.59†
	Pull.	“	418	0–82	29.9	6.2 ± 1.4		+0.29
		“	1077	0–183	67.4	2.0 ± 0.8		−0.66†
Anthus trivialis	Adult	1959–72	131	2–21	9.4	6.6 ± 2.4	−0.50	+0.33
		1973–88	68	0–15	4.2	4.4 ± 2.2	−0.57*	−0.55
	Juv.	“	367	8–45	26.2	1.0 ± 0.5	+0.23	−0.07
		“	302	2–74	18.9	1.6 ± 0.7	−0.43	−0.69‡
	Pull.	“	65	0–20	4.6	2.6 ± 1.8		+0.56
		“	135	0–27	8.4	0.2 ± 0.2		−0.31

Table 7. Tendency to changing numbers and philopatry in breeding populations of migratory species at the Courish Spit in different periods.

Species	*Age*	*Years*	*Numbers of birds captured*			*Return rate, %, Mean+SE*	*Correlation coefficient in dynamics rows*	
			Total	*Range per year*	*Mean*		*Numbers*	*Returns*
Lanius collurio	Adult	1959-72	108	2–13	7.7	10.9 ± 2.0	$+0.57^{*}$	+0.18
		1973-88	61	0–10	3.8	1.1 ± 1.1	$-0.76^{‡}$	−0.26
	Juv.	“	160	1–23	11.4	0.6	+0.30	
		“	68	0–23	4.2	0.0	-0.57^{*}	
	Pull.	“	209	0–49	14.9	0.5		
		“	328	0–57	20.5	0.3		
Fringilla coelebs	Adult	1959-72	1254	48–204	89.6	10.4 ± 1.7	−0.39	+0.11
		1973-88	788	27–131	49.3	14.0 ± 2.2	+0.03	−0.31
	Juv.	“	4623	90–767	330.2	11.2 ± 1.2	-0.57^{*}	+0.33
		“	4493	93–483	280.8	12.5 ± 0.9	$+0.68^{‡}$	+0.43
	Pull.	“	1499	20–275	107.1	9.9 ± 1.7		+0.04
		“	4360	16–935	272.5	7.8 ± 1.0		−0.29
Sylvia curruca	Adult	1959-72	204	1–40	15.7	9.9 ± 2.0	$+0.77^{†}$	+0.39
		1973-88	314	11–62	19.6	7.9 ± 2.0	−0.27	−0.50
	Juv.	“	454	9–108	32.4	1.4 ± 0.8	$+0.51^{*}$	−0.39
		“	2153	24–241	96.3	1.7 ± 0.4	+0.17	+0.09
	Pull.	“	209	0–42	16.1	1.7 ± 0.9		−0.13
		“	1421	28–305	134.6	1.5 ± 0.3		−0.01
Carpodacus erythrinus	Adult	1959–72	237	7–28	16.9	9.8 ± 2.1	+0.26	−0.45

Table 7. Tendency to changing numbers and philopatry in breeding populations of migratory species at the Courish Spit in different periods.

Species	*Age*	*Years*	*Numbers of birds captured*			*Return rate, %, Mean+SE*	*Correlation coefficient in dynamics rows*	
			Total	*Range per year*	*Mean*		*Numbers*	*Returns*
		1973–88	437	18–36	27.3	11.3 ± 2.2	+0.08	−0.42
	Juv.	"	41	0–12	2.9	2.4	−0.52	
		"	147	0–27	9.2	0.0	+0.45	
	Pull.	"	82	0–18	5.9	0.0		
		"	616	13–98	38.5	0.7		
Hippolais icterina	Adult	1959-72	607	11–78	43.4	7.7 ± 1.0	$-0.67^{\ddagger}$	−0.31
		1973-88	680	21–118	42.5	9.4 ± 1.7	+0.42	−0.50
	Juv.	"	359	4–59	25.6	8.5 ± 2.8	−0.41	+0.34
		"	939	4–127	58.7	8.6 ± 1.5	+0.26	-0.56^{*}
	Pull.	"	269	0–62	19.2	3.0 ± 2.3		−0.08
		"	757	3–112	47.3	2.7 ± 0.7		−0.46
Phylloscopus trochilus	Adult	1961-72	250	9–41	20.8	6.0 ± 1.7	−0.07	−0.04
		1973-88	494	16–69	30.9	8.5 ± 2.4	$+0.66^{\dagger}$	−0.25
	Juv.	"	1350	28–238	112.5	6.0 ± 1.2	+0.28	−0.10
		"	7409	120–975	463.1	7.8 ± 0.4	$+0.56^{*}$	+0.50
	Pull.	"	106	0–27	8.8	7.0 ± 3.1		−0.24
		"	813	6–130	50.8	7.6 ± 1.4		−0.42

Note: Symbols indicate the degree of significance at: *, $p < 0.05$; †, $p < 0.02$; ‡, $p < 0.01$.

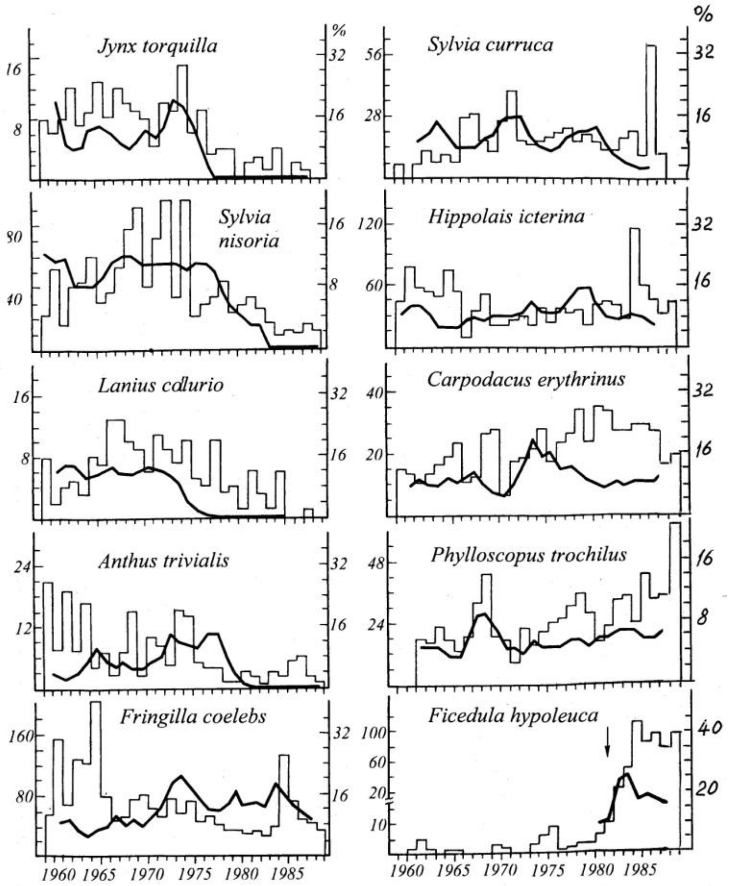

Figure 5. Changes in the number of the breeding population and in breeding site fidelity in some migratory birds on the Courish Spit during a 30-year period. The arrow indicates the year when nestboxes were placed in the study region. The abscissa shows years. The ordinate shows: left, the numbers ofbirds captured in large traps during the breeding period (histogram); right, return rates.

by stationary traps on the Courish Spit (with evidence of a breeding success that year) and the number of yearlings captured there during the breeding period in the following year has allowed us to reveal a positive

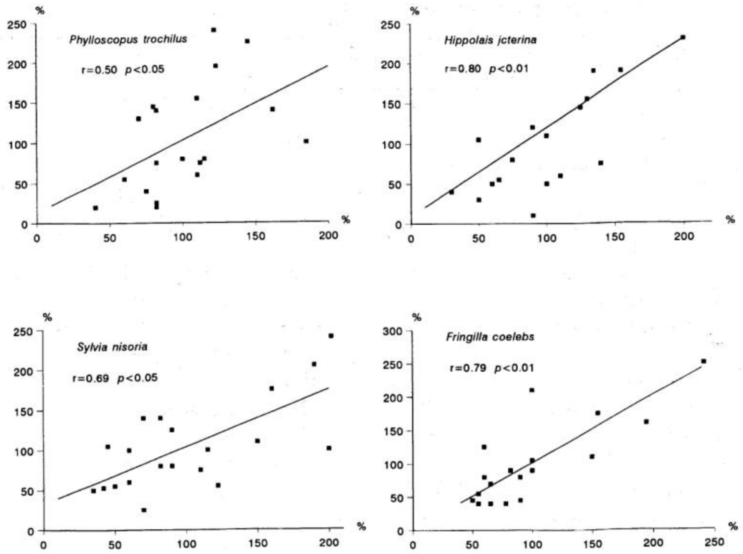

Figure 6. Correlation between the number of juvenile birds of some migratory species at the Courish Spit in the postbreeding period and the number of yearlings detected in the study region in the year after ringing. The ordinate shows the percentage of birds captured in large traps in the postbreeding period versus the average annual number of juvenile birds. The abscissa shows the percentage of birds captured in large traps in the study region in the year after ringing.

relationship between them: the greater the number of newborn birds, the greater number of birds will initiate breeding in the following year (Figure 6). As a result, the proportion of yearlings initiating breeding in the following year usually increases after breeding success (Table 4).

7. WHY DO MIGRATORY BIRDS RETURN TO THEIR TERRITORY?

Returns to their territory affords birds a number of advantages important for both their survival and their success breeding: it improves the search for foraging sites and enables them to avoid predators better, helps in mating and in bonding (by decreasing the influence of external factors on the

Table 8. Philopatry of resident birds.

Species	*Rate of returns*		*References*
	Natal areas	*Breeding areas*	
Lagopus lagopus	5.8		Martin and Hannon, 1987
Centrocercus urophasianus		+	Gates, 1985
Tetrao urogallus		+	Telepnev, 1986
Cyanocitta cristata		9.0	Middleton, 1974
Cinclus cinclus		+	Kovshar, 1979
Troglodytes troglodytes		43.0	Kovshar, 1979
Prunella atrogularis	15.4	15.8	Kovshar, 1979
P. tulvescens	8.2	48.4	Kovshar, 1979
Phoenicurus erythronotus	3.6	27.1	Kovshar, 1979
Ph. coeruleocephalus	0.8	7.6	Kovshar, 1979
Serinus pusillus	5.5	+	Kovshar, 1979
Leucosticte nemoricola	4.7	+	Kovshar, 1979
Mycerobas carnipes	7.5	37.5	Kovshar, 1979
Carpodacus rhodochlamys	0.1	47.3	Kovshar, 1979
Carduelis caniceps		+	Kovshar, 1979
Zonotrichia capensis		30.0	Handford, 1980

Note: + shows that birds were detected to return; however, the return rate to the area of ringing was not determined.

reproductive process including copulation, nest building, egg laying, etc.), reduces direct competition with other species for territory, and so on (Greenwood, 1980; Panov, 1983; Shields, 1984). Territory take-over raises the hierarchical status of a bird, making it dominating over other birds arriving to the same territory (Kaufman, 1983). The principal advantage for the dominant individual is the chance to produce more viable offspring compared with birds breeding on a foreign territory. Our studies of Pied Flycatchers on the Courish Spit have shown that, in contrast to local birds (autochthon), newcomers immigrant not only establish their breeding territories later but have a lower reproductive success (a smaller clutch size, lower hatching success, less viable offspring). This may be the reason why, unlike local birds, a significant percentage of immigrant birds does not return to the study region in subsequent years (Table 6). 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 and Lank, 1984). This may play an important role in maintaining local adaptability. In addition, bird's return to its natal area offers it, at least, an appropriate habitat for breeding and finding a mate.

The tendency to breed on the same territory is detected not only in migratory birds but in nonmigrating and resident birds as well (Table 8). Kovshar (1979) reports important data on philopatry in a number of mountain species migrating down to the Cowlands with the onset of winter. In autumn many of them descend to the foothills and valleys of Tyan-Shan returning to their usual sites in spring (Table 8). When the Capercaillee (*Tetrao urogallus*) (651 females and 389 males) were banded in Tomsk and Novosibirsk Regions (Russia), it was found that some birds migrate distances of between 30 km (males) and 70 km (females), these are considered large for resident birds (Telepnev, 1986). Such migrations are caused by searching for foraging sites. From the results obtained (380 returns), the author suggests that, being generally resident birds, some Capercaillie (mostly females) migrate up to 70 km returning to their previous site in 2–5 years. Moreover, experimental translocation of resident birds has demonstrated their homing ability (Pinowsky, 1970; Walkovich and Fokin, 1985; Schidt–Koenig, 1985). Data are available to show that there is a certain period, at an early age in both resident and migratory birds, when imprinting of the breeding territory occurs (Weis and Meyer, 1979; Bardin, 1983). This shows that philopatry developed in birds long before the appearance of migratory species. It should not be forgotten that the principles of philopatry were inherited by birds from their reptilian ancestors which are known to possess such a mechanism (Baker, 1978; Rodda, 1984; Bock *et al.*, 1985).

8. POSTBREEDING, NATAL AND BREEDING DISPERSAL IN BIRDS

Having arrived on their breeding area from wintering sites, birds initiate their first breeding at a distance from their natal birthplace. This distance depends, first of all, on the dispersal of young birds after abandoning their natal sites and the timing of territory imprinting. Studies of dispersal in some passerine species on the Courish Spit have shown that in the postbreeding period most birds settle mainly within several kilometers (Figure 7). Only a small percentage of birds (less than 10%) may scatter tens and hundreds of kilometers (Table 9). Extensive ringing of Pied Fly-

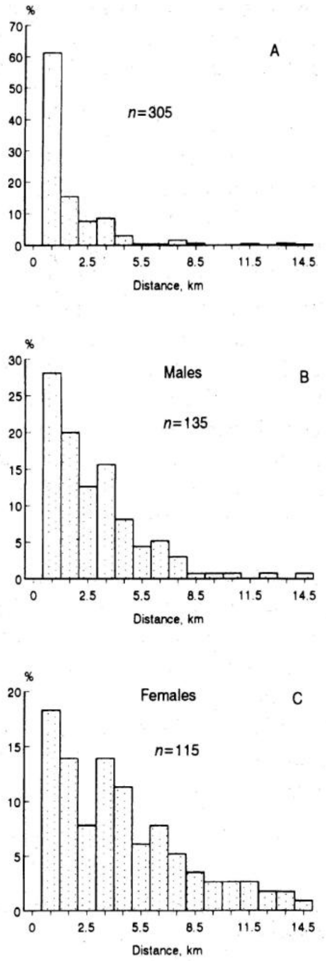

Figure 7. Distance of postbreeding (*A*) and natal dispersal (*B–C*) in *Ficedula hypoleuca* breeding at the Courish Spit. *n*, is the number of captures in the postbreeding period (*A*) and in subsequent years (*B–C*). The abscissa shows the distancefrom the birthplace (km). The ordinate shows the percentage of captures.

catcher nestlings was performed within 30 km from the *Fringilla* field station, however, in the postbreeding period only those fledglings which had hatched within 5 km of the field station were captured in large traps

Table 9. Distance of natal dispersal in Pied Flycatchers in different parts of its breeding area.

Region	*Numbers of captures*	*Distance between the birthplace and the breeding site (km)*						*References*
		0–1	*1–10*	*10–20*	*20–40*	*> 40*	*> 100*	
Karelia, Russia	43	41.9	46.5	11.6	–	–	–	Artemyev and Golovan, 1983
Estonia	1239	26.6	46.1	14.4	9.4	2.8	0.7	Leivits and Vilbaste, 1990
Latvia	87	50.6	42.5	2.3	1.2	–	3.4	Chaun, 1958
Courish Spit, Russia	258	23.0	68.4	7.0	1.6	–	–	Sokolov, 1991*a*
Oka reserve, Russia	73	37.0	63.0	–	–	–	–	Likhachev, 1955
Dresden, Germany	94	67.0	27.6	3.2	1.1	1.1	–	Creutz, 1955
Gelgoland, Germany	88	71.6	22.7	4.5	1.2	–	–	Likhachev, 1955
NE, Germany	930	50.0	37.5	6.0	4.5	2.0	–	Berndt and Sternberg, 1969

(Sokolov *et al.*, 1987). In the following year, most of the yearlings detected appeared to breed at a distance of 5 km from their natal place. Thus, the birds bred predominantly in the region where they had happened to be upon their juvenile dispersal (Figure 7). In other species with less pronounced postbreeding dispersal, most yearlings initiate breeding within 1 or 2 km of the native nest. A highly pronounced positive correlation is revealed between the postbreeding and natal dispersals in migratory birds on the Courish Spit (Sokolov, 1991*a*). It is commonly assumed that a significant percentage of birds settles within long distances of the area although no reliable data have been reported (Malchevsky, 1968, 1969; Zimin, 1988). However, captures of ringed birds rather confirm a relatively small percentage of birds settling within large distances (Table 9).

At the Courish Spit, the majority of Pied Flycatchers (about 70%) initiate breeding southwest from the natal place (Sokolov *et al.*, 1990). This is caused by the birds' shifting mainly southwest from their birthplace during dispersal. Birds which hatched in those years when breeding was

Table 10. Direction of postbreeding dispersal in some migratory birds breeding at the Courish Spit.

Species	*Number of nestlings ringed*[*]		*Percentage of birds captured*		*Ratio, %*	χ^2
	SW	*NE*	*SW*	*NE*	*SW NE*	
Hippolais icterina	130	222	3.9	12.6	24 : 76	4.1[†]
Ficedula hypoleuca	1340	1419	8.9	19.9	30 : 70	65.1[‡]
Sylvia curruca	275	595	7.6	17.8	30 : 70	14.8[‡]
Sylvia nisoria	308	696	5.5	9.8	36 : 64	4.4[†]
Phylloscopus trochilus	336	472	30.7	37.5	45 : 55	3.8[†]
Fringilla coelebs	1379	2276	12.4	14.1	47 : 53	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.

delayed have a reliably higher tendency to disperse southwards (84% versus 16%) than birds hatched at earlier periods (68% versus 32%). The southwest dispersal proves to dominate in some migratory birds because young birds are determined to move towards their wintering regions quite early on (in the middle of July). This tendency is most pronounced in birds migrating extremely long distances, whereas in intercontinental migrants, in particular in Chaffinches, the young scatter evenly both towards the south and north (Table 10). The examination of juvenile Pied Flycatchers in 'Emlen's' cages has demonstrated that the birds display southwest directed activity by the middle of July. Moreover, if on their spring return the birds do not reach the territory they imprinted upon dispersal, they also choose to settle southwest from their native place. However, quite frequently birds initiate breeding northeast from their natal territory. This is brought about either by the fact that after dispersal juvenile birds imprinted the territory for subsequent breeding northeast of their birthplace, or when, having arrived to its territory, a bird cannot breed there and has to search for a new territory moving in the direction of spring migration. Such 'migrations' compensate, to some extent, for the situation when birds do not reach their breeding sites.

The distances of breeding dispersal in most migratory birds are essentially shorter than those of natal dispersal. This can be illustrated with the Pied Flycatcher. About 50% of the birds initiate breeding within 300 m of the previous breeding site. In Estonia 94% of males and 61% of females (Leivits and Vilbaste, 1990) and 86% of males and 69% of females on the Courish Spit (Sokolov *et al.*, 1989) breed within a distance of 1 km from their previous breeding site.

The reasons for dispersal may be both endogenous (internal stimuli) and exogenous (when external circumstances force a bird to abandon the natal territory). According to many ornithologists, juvenile birds are genetically programmed to scatter, the onset, duration and termination of postbreeding dispersal being predetermined (Berndt and Sternberg, 1968; Lance, 1970; Viksne, 1970; Dolnik, 1975). This programing may also predetermine the direction of dispersal. Upon summer dispersal, we observed significantly enhanced movements in young Tree Sparrows (*Passer montanus*) placed in cages specially equipped for recording hops (Sokolov *et al.*, 1981*a*). However, in adult birds no similar increase in locomotor activity in the postbreeding period was detected. Studying the orientational behavior in juvenile *Passer montanus* and Willow Tits (*Parus montanus*) in special cages with 8 perches fixed along the walls to record the birds' movements, we found that the birds were able to use compass orientation despite the fact that they could see only the sun (Sokolov, 1981*a*). As usual, the birds choose different directions, and having done so, maintained them for several days, although the cage was repeatedly turned to eliminate the influence of its internal guides. It was suggested that juvenile birds, even in resident species, have an ability to use compass orientation for dispersal from the natal place.

There are grounds for believing that genetic polymorphism at the level of 'dispersal activity' exists in bird populations of both resident and migratory species (Greenwood *et al.*, 1979; Newton and Marquiss, 1983). It is assumed that the principal functions of juvenile dispersal are the following: a determination to avoid inbreeding, an expansion of the species area, the interpopulation exchange by genetic information (gene flow) as well as territorial and habitat redistribution of the birds. Short-distance dispersal avoids inbreeding and allows intrapopulation redistribution of the birds, while long-distance dispersal ensures species expansion and interpopulation gene exchange. The proportion of birds dispersing long-distance evidently does not exceed 10% in a population (Table 10). Among almost 8000 adult individuals of 14 migratory species captured while breeding on the Courish Spit, there appeared to be only 1 female Pied Flycatcher that had been ringed in spring in Sweden. This is all the more striking since annually during spring and autumnal migrations several million birds of these species fly over the Spit. Endler (1977) believes that although some birds exhibit long-distance dispersal, this does not result in an enhanced gene flow. The appearance of such "marathoners" in a population is not frequent, and the probability of interbreeding and rearing viable offspring is not great.

Postbreeding nomadic behavior can be caused by a number of external factors: searching for the most favorable foraging and molting sites, predation risk, competitiveness of other species, bad climatic conditions, etc. Bauer (1987) forwarded a hypothesis that aggressivity of dominant birds enhanced dispersal in numerous subdominant birds. Young birds are forced to move to suboptimal regions or to migrate longer distances. Less competitive are juvenile birds of later hatch dates, already having an enhanced dispersal and a higher mortality rate. According to Bauer, a higher population density gives rise to enhanced dispersal. Spacing, i.e. forced dispersal, has been verified experimental in the Pied Flycatcher (Berndt and Sternberg, 1968). It is remarkable that after external stimulation (removal of nest boxes) some adults moved to the place where they had already bred. The authors proposed that in adults spacing is oriented to known places. Analogous situations were detected in some duck species by Latvian ornithologists (Mihelson *et al.*, 1977).

In addition to the reasons indicated above, birds may also migrate to new regions quite accidently due to: erroneous orientation and navigation upon migration, distortions in the endogenous migratory flight program, large deviations from migratory course during a storm, etc. Salomonsen (1951) described the case when a flock of Fieldfare (*Turdus pilaris*) migrating from Norway to England was brought by a storm to the northeastern coast of Greenland where it formed a resident breeding population.

9. TERRITORY IMPRINTING

Experiments on the translocation of eggs, nestlings and fledglings in some migratory birds from the birthplace (clutching) to new regions tens, hundreds and thousands of kilometers remote have reliably demonstrated that natal philopatry is not genetically inherent in birds but is acquired in the juvenile age (Table 11). In spring, migratory birds return, as a rule, to the place where they resided in the postbreeding period (Sokolov, 1991*a*).

At what age does site fixation of future breeding occur in migratory birds? Some investigators have suggested that the fidelity of birds for certain places appears during their early days of life and grows with aging (Nice, 1937; Isakov, 1954). However, it was shown experimentally by Löhrl (1959) that in the Collared Flycatchers (*Ficedula albicollis*) fixation

Table 11. Results of experiments on the translocation of eggs, nestlings, juvenile and adult birds.

Species	*Age upon release (days)*	*Distance (km) and direction of release*	*Percentage of birds captured in subsequent years in the*		*References*
			*Breeding sites**	*Release sites**	
Diomedea immutabilis	≤ 30	400 SE	0	35.0	Fisher, 1971
	35–150		26.0	0	
Anas platyrhynchos	eggs	2000 NE	–	50.0	Lee and Kruse, 1973
	25–45	?	–	35.0	Valikangas,1933
Aix sponsa	pullus	320	–	10.0	Matthews, 1955
Branta canadensis	50–55	160	–	21.0	Surrendi, 1970
Anser anser	pullus	1600NNW	–	60.0	Isakov, 1957
Pandion haliaetus	eggs	500 N	0	15.5	Zimmerman, 1976
Larus canus	eggs	500 E	–	6.3	Matthews, 1955
Ficedula albicollis	≤ 30	90 S	0	10.0	Löhrl, 1959
	≥ 50		0	18.0	
Ficedula hypoleuca	adults	400 SW	24.2	0	Isakov, 1957
	≤ 25		0	3–5.0	
	≤ 25		0	7–13.0†	
	adults	45	18.2	0	Scherbakov, 1960
	≤ 30		0	5–9.0†	
	eggs	250 W	0	10.6	Berndt and Winkel, 1979
	eggs	1000 W	0	6.3	Sokolov, 1991*a*
	pullus		0	13.5	
	≥ 35		0	7.5	
Fringilla coelebs	≤ 30	26 NE	0	9.1	Sokolov, 1981*b*
	≥ 40		8.6	0	

*Percentage of birds returned; †, percentage of birds returned which were fed in the release site.

of future breeding sites occurs between 45 and 55 days of age, upon molting. Later, on the experimental release of young *Fringilla coelebs* of different ages (between 25- and 60-days old) we found that birds less than

Table 12. Timing of breeding territory imprinting in some bird species.

Species	*Imprinting period*	*Age (days)*	*References*
Diomedae immutabilis	Prior to fledging	30–150	Fisher, 1971
Ardea cinerea	Upon dispersal		Olsson, 1958
Branta canadensis	Prior to dispersal	50–70	Surrendi, 1970
Larus ridibundus	Upon dispersal		Viksne, 1968
Jynx torquilla	Upon dispersal	35–50	Sokolov, 1988
Delichon urbica	Prior to dispersal		Hung and Prinzinger, 1979
Progne subis	Upon dispersal		Finlay, 1971
Acrocephalus palustris	Upon dispersal		Dowsett–Lemaire, 1978
Ficedula albicollis	Upon molting	45–55	Löhrl, 1959
F. hypoleuca	Upon dispersal	> 35	Berndt and Winkel, 1979
"	"	35–50	Sokolov *et al.*, 1987
Phylloscopus trochilus	Prior to dispersal	30–40	Sokolov, 1976*b*
Sylvia nisoria	Prior to dispersal	30–40	Sokolov, 1976*b*
S. curruca	Upon dispersal	40–55	Sokolov, 1988
S. atricapilla	"		Wolf, 1987
Hippolais icterina	"	30–45	Sokolov, 1976*b*
Motacilla alba	"	35–50	Payevsky, 1976
Anthus trivialis	"	40–55	Sokolov, 1988
Lanius collurio	"	35–55	Sokolov, 1988
Emberiza schoeniclus	Upon molting	40–55	Haukioja, 1971
Spizella pusilla	Prior to dispersal		Adams and Brewer, 1981
Sturnus vulgaris	Prior to dispersal	30–35	Sokolov, 1976*b*
Fringilla coelebs	"	30–40	Sokolov, 1981*b*
"	Upon molting	> 50	Artemyev, 1988
Carpodacus erythrinus	Upon dispersal	> 30	Sokolov, 1988

30-days old released in a new region returned there in a subsequent year, while those older than 40 days appeared to return to their natal place (Sokolov, 1981*b*). These data allowed us to suggest that in young Chaffinches on the Courish Spit, territory imprinting of their future breeding site occurs between the ages of 30 and 40 days prior to the postbreeding dispersal (Table 12). In Karelia, territory imprinting in Chaffinches takes place somewhat later, i. e. when the birds abandon their birthplace, which could explain the low philopatry seen in this region (1%) compared with that on the Courish Spit (8%) (Artemyev, 1988). We also carried out an experiment to verify whether Chaffinches breeding on the Courish Spit could imprint territory at a later age (more than 40 days). We handreared

34 Chaffinch nestlings in an aviary to the 50 days of age, they were then released on August 5 and 9 when local birds had already left the natal area. The birds remained in the area for about 33 days as shown by their recaptures in the open aviary and with the help of traps ($n = 31$). Three birds (9.4%) were recaptured there in the following year. Consequently, if birds do not have the chance of imprinting territory at the age when this happens in nature, they can do it later. Therefore, it cannot be claimed that in young birds territory imprinting occurs only within a strictly limited age span (Sokolov, 1991*a*). In different species and even in different populations, the age when breeding territory imprinting takes place can vary greatly (Table 12). As a result, in some species (populations) territory imprinting takes place mainly prior to the onset of postbreeding dispersal, i.e., when juvenile birds are still in the natal area (in this case a high level of philopatry will be observed), in other species it occurs during dispersal or after its termination (with a lower level of philopatry). We have regularly observed the following: the earlier the young birds leave their birthplace on the Courish Spit, the lower is the rate of return to the natal area in subsequent years (Figures 8 and 9).

On their spring arrival to the region they imprinted in the postbreeding period, yearlings may choose another territory for breeding which they can also imprint. Our experimental release of immigrant Pied Flycatchers yearlings which settled to breed in the study region of the Courish Spit showed that about 16% of the birds released (translocated at distances between 1 and 30 km) returned to their territory prior to nest building (Table 13). Upon rearing, the greater portion of these birds return to their nests (86%). This shows that by the time of capture (May) the birds managed to imprint the territory where they had never bred before. Another group of yearlings (46%) set free at the same time (prior to nest building) settled to breed where they were released and a proportion of them (12%) returned there in the following year (Sokolov and Vysotsky, 1991).

Yearlings of migratory birds are known to imprint not only their breeding territory but also their wintering grounds (Ralph and Mewaldt, 1975; Mewaldt, 1976; Stewart and Connor, 1980), molting sites (Page, 1974; Ardamatskaya, 1975) and even migration stopover areas (Koerner *et al.*, 1974; Smith and Houghton, 1984).

Thus, yearlings of migratory birds can imprint various territories in different parts of the world. The information gained by a bird during this period regarding the location of these territories is the most reliable and is stored in the long-term memory throughout its life. Additional information on other territories acquired by the bird later on, at an adult age, does not erase the basic information gained in the juvenile stage.

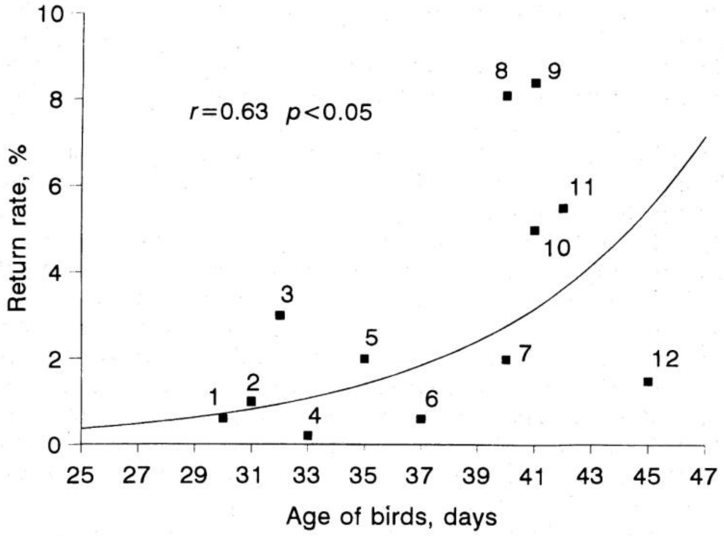

Figure 8. Dependence of philopatry in 12 species of migratory birds breeding at the Courish Spit at the time when juvenile birds abandon their birthplace: 1, *Carpodacus erythrinus*; 2, *Hirundo rustica*; 3, *Hippolais icterina*; 4, *Motacilla alba*; 5, *Ficedula hypoleuca*; 6, *Lanius collurio*; 7, *Anthus trivialis*; 8, *Sylvia nisoria*; 9, *Fringilla coelebs*; 10, *Jynx torquilla*; 11, *Phylloscopus trochilus*; 12, *Sylvia curruca*. The abscissa shows the average age of birds abandoning the birthplace, days. The ordinate shows their return rate in subsequent years.

The most complicated question is what kind of territory information should birds imprint so that they can return there successfully in the spring? This is directly connected with the puzzling and extremely complicated problem of navigation in migratory birds. It is still not clear how, in spring, migratory birds manage to travel thousands of kilometers from their wintering sites to the tiny territory imprinted as juveniles. It was initially suggested that a bird first arrives in a fairly general region (about 100 × 100 km) oriented by the sun, before starting a visual search for its specific territory using a definite strategy, e.g. spiral or shuttle flights (Heinroth and Heinroth, 1941). However, this "piloting" concept has not been confirmed. When carrier pigeons were fitted with special contact lenses (depriving them of the chance to see the landscape) and released tens and hundreds of kilometers away from their home, these birds were able to fly back to within 1 km of their aviary (Schmidt–Koenig and Schlichte, 1972).

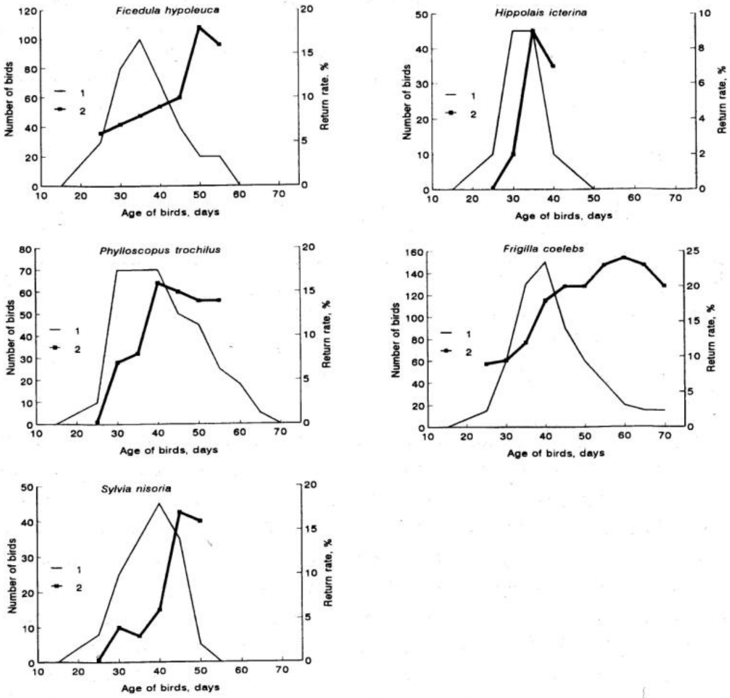

Figure 9. Return rate in birds which abandoned their birthplace at the Courish Spit at different age. The abscissa shows the age (days) when juvenile birds were captured in large traps for the last time. The ordinate shows: left, the numbers of young birds captured in large traps during the postbreeding period (1); right, return rate in subsequent years (2).

At present, many investigators agree that if birds ever do use feature of the landscape to search for their "home", it is done in the vicinity and as a result of short "learning" flights (see the review by Wiltschko and Wiltschko, 1987). It is suggested that birds compile a certain "mosaic" map of the vicinity, which includes various guiding lines and information on compass directions from these lines to their "home" and from one guiding line to another (Wiltschko and Wiltschko, 1978). Apparently such a "mosaic" map allows birds to move directly and rapidly to their destination within the area known to them. Some ornithologists believe that the mosaic map of pigeons also includes odors of areas adjacent to the pigeon aviary (Papi, 1986; Wallraff, 1983).

Table 13. Breeding homing success in the Pied Flycatcher at the Courish Spit.

Males	*Number of birds translocated*	*Percentage of birds*		
		Returned	*Settled*	*Disappeared*
1. Local adults*	21	81.0	9.5	9.5
2. Immigrant adults*	31	81.0	9.5	9.5
3. Local yearlings	26	50.0	34.6	15.4
4. Immigrant yearlings	70	15.7	45.7	38.6

*Birds that have already bred in the study region in previous years. The differences in the return rates are statistically significant (χ^2 test) among the groups of males: 2–3, ($p < 0.05$); 2–4, ($p < 0.001$); 3–4, ($p < 0.005$).

How do birds find their "home" in an unknown region? According to current studies, during training flights in the vicinity of their pigeon aviary, carrier pigeons compile not only a mosaic map but also a "navigation map", based on at least 2 geophysical parameters (e.g. the vertical component of the Earth's magnetic field and gravitational isolines), which form a gradient net when superimposed (Wiltschko and Wiltschko, 1987). In contrast to the mosaic map, such a gradient map could involve long distances (measuring hundreds and even thousands of kilometers) and be the main guiding line for navigation. It is postulated that birds know the direction of the gradients relative to the 4 cardinal compass points. When released in an unknown region, they measure the local magnitude of a gradient and compare it with the one they have memorized (imprinted) in the vicinity of their "home".

How does a bird compile a "navigation map"? As reported by Wiltschko and Wiltschko (1987), carrier pigeons only form such a map if they had the opportunity to perform training flights in the vicinity of their pigeon aviary as a juvenile. However, this is inherent only in carrier pigeons which due to artificial selection, have undergone remarkable adaptations. And in what way is the navigation map formed in wild birds?

In 1977 we carried out an experiment on the Courish Spit to clarify what information migratory birds needed prior to abandoning their natal place in order to imprint territory for future breeding (Sokolov *et al.*, 1984). We took 118 Chaffinch nestlings from their nests on the Courish Spit and handreared them; between 25 and 28 days of age (prior to territory imprinting) they were placed in a small aviary (8 m^2) in the field station where large traps were located (Figure 1). During the day, the birds could see only that part of the sky around the Polaris and the sun, excluding its ascension and declination points, as well as a limited territory near the aviary. A control group of 30-day-old Chaffinches ($n = 48$) was released in the vicinity of the aviary. An experimental group ($n = 70$) was kept in the aviary until they were between 50 and 70 days of age (i.e. until the end of the "sensitive" period for territory imprinting), the birds were then taken away and released 70 km southwest of the Courish Spit (Figure 1). After release, 29 control birds (60%) were captured using different traps (a total of 5 traps) located 70–400 m from each other. The control group moved to the vicinity of the aviary (within 0.5 km) about a month (27 ± 2.5 days). A total 7 birds (14.6%) from the control group were recaptured in the large traps during the breeding period in the following year. Taking into account the capture success of Chaffinches by large traps (about 30%), it could be expected that about 20 birds would have returned to the study region, i.e. virtually all the birds that survived through winter. No bird from the experimental group was detected in the study region. However, they were not detected in the release region either, but the inspection carried out there was not thorough enough and we could have failed to detect them in the rather vast forest region. The results obtained have allowed us to conclude that: 1. When kept in an aviary or an open-air cage, birds cannot imprint territory. 2. To determine the coordinates of the future breeding site (i.e. to compile a "navigation map"), birds should be able to move freely during the postbreeding period, at least to within several hundred meters.

To eliminate any doubts as to what precisely had been imprinted by the birds from the control group – the region of their release or the whole route from the Courish Spit – we carried out an additional experiment. Young Chaffinches ($n = 25$), about 40-days-old, were captured in the *Fringilla* field station after they had imprinted their breeding, taken away from the Spit and released 30 km southwest of the capture site (Figure 1). We recaptured 2 birds (8%) in the same birth place in the following year. Consequently, in order to return successfully to the imprinted territory, it is not necessary for birds to know the area to within at least 30 km.

Our studies of the Pied Flycatchers lead further support to the fact that in order to imprint their future breeding territory, birds should be allowed to move freely (using a shuttle strategy) within an approximately 1 km radius (Sokolov *et al.*, 1987). Homing experiments with Pied Flycatchers of different age and origin have confirmed our assumption that in spring yearlings are determined to return to the territory they imprinted in the postbreeding period (Sokolov and Vysotsky, 1991). Of 26 local yearlings tested for their homing ability, 50% of the birds returned within 3 days (mainly to within a radius of 50 m) (Table 13).

From the results described above, we have concluded that to imprint breeding territory (determine its coordinates, compile mosaic and navigation maps), young birds (30–50 days of age in passerine birds) should be able to fly freely in a small region of 1 km radius. To return successfully to this region in the following year, birds should not memorize their migration route to the wintering grounds in the postbreeding period. In spring, birds, both adult and yearlings, reach their destination with a high degree of accuracy, most likely without using a random search strategy, the so-called "piloting" theory (Sokolov and Vysotsky, 1990).

10. CONCLUSIONS

Numerous data on bird ringing provide evidence that, independent of their systematic, behavior and life-style, many migratory birds show fidelity not only for breeding territory, but also for their birthplace or the region where they settled as a result of dispersal. In addition, some avian species show fidelity for wintering grounds, molting sites and migration stopover areas. As a rule, adult birds return in greater numbers to their previous breeding territory compared to the return of the young to the natal place. This is caused, first of all, by a juvenile dispersal which is characteristic of many species in their early months of life. Since birds have no inherent knowledge of their birthplace location, they can not return exactly to the birthplace. Birds show fidelity for the site where territory imprinting occurred. If imprinting takes place prior to abandoning their native place, birds will show a high level of philopatry in subsequent years. If territory imprinting occurs upon dispersal or after its termination, philopatry will appear to be very low. Specific and populational differences in philopatry are a consequence first of all, of the timing of territory imprinting and the duration of the birds' stay in the natal place. Philopatry and dispersal in migratory birds are 2 reverse but interdependent processes. Juvenile dispersal in the postbreeding period can result in birds' setting in new territories only if territory imprinting occurs after the dispersal. Therefore natal dispersal in migratory species is mainly determined by juvenile dispersal in the postbreeding period.

The fidelity for breeding territory and philopatry are affected by a number of factors: breeding success, stable habitat, age and experience of birds, hatch dates, survival success, competitiveness, etc. As a rule, territory fidelity in birds increases their survival rate, breeding success and competitiveness. Philopatry ensures the formation of local populations and their adaptation to environmental conditions. Philopatry is postulated to appear in birds prior to the formation of migratory species.

A process similar to image imprinting may underlay the mechanism of site fixation in birds. All the principal territories (breeding, wintering, molting and migratory stopover areas) are imprinted during the first year of life and are likely to be memorized for ever. The information on territories obtained by a juvenile bird "dominates" over the information acquired through out the rest of its life.

On territory imprinting a bird evidently complies mosaic and navigation maps which enable it to reach its destination after migration. It is not clear what geophysical parameters are used by birds for compiling such a navigation map. However, it is certain that in order to compile this map, birds must have the opportunity to fly freely over the territory which they imprint. Our investigations on the Courish Spit have shown that it is sufficient for birds to move within a small region of 1 km radius so that they can imprint the territory successfully (i.e. to determine its geographical coordinates). In spring, they will reach their destination precisely, most likely without using a random search strategy (piloting).

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