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Homing ability of the Pied Flycatcher *Ficedula hypoleuca*

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Firstly, we studied homing in male Pied Flycatchers during the period between their spring arrival and the onset of breeding. We *were* especially interested in the ability to carry out short-distance homing during this period in yearlings and in adults of different origin: native (hatched in the area of study) and immigrants (hatched outside the study area). Secondly, we analysed the capture rate by stationary traps in spring in relation to distance from eventual nest site. This study was conducted on the Courish Spit of the Baltic Sea between 1987-1993. A total of 178 males was re-located before mating. Most of the birds were displaced to release sites 3-4 km away. Paired comparisons of homing success in different groups of males show that birds that had previously nested returned significantly better (81%) than native yearlings (52%) or immigrant yearlings (17%).

It should be emphasized that native yearlings returned significantly better (14 out of 27) than immigrant yearlings (13 out of 78). It is noticeable that half of the native yearlings that had their first return to their native area, showed a strong attachment to a certain micro-location (within a diameter of approximately 1 km). Apparently, this micro-location was a navigation goal during spring migration.

Birds were also caught in the Rybachy-type traps at the narrow part of the spit. We expected that many Pied Flycatchers would have been recovered in spring if they had used a strategy of slow searching to find their final migratory goal. The number of trapped birds (88 from 2023 breeding individuals) was analysed with respect to the distance between recovery and eventual breeding sites. The majority of trapped birds was of those that bred in vicinity of the traps (radius 1 km). Our conclusion is that Pied Flycatcher males have an capability for pinpoint navigation, i.e. they can directly reach a very limited area (radius 1 km), and do not use the slow search strategy.

Key words. Pied Flycatcher, homing, navigation.

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1. Introduction

It has been shown by many investigators that if breeding birds are removed from their nests and released somewhere else, they usually return some time later. It is well known now that many species of birds, both migratory and sedentary, possess the ability to return to their home base (Matthews 1968, Wiltschko & Wiltschko 1978, 1999;
Schmidt-Koenig 1979, Berthold 1990). Homing success varies not only between different species but also between different regions and even between different release attempts of birds from the same site. Variability in returns of birds is often caused not so much by their varying ability to come back to base but by their differing motivation to return. This is also confirmed by the comparatively low return rate of birds in experiments (Vilks 1965, Matthews 1968, Nolan et al. 1986). As shown by radio tracking studies, birds when returning home usually fly in short stages towards the goal, spending a lot of time for rest and feeding (Able et al. 1984).

Practically all homing studies during the breeding season were conducted on birds that had nests. One principal question remains open: are migratory birds able to perform homing immediately after spring migration and before the onset of breeding? An answer to this question can be crucial to understanding the mechanism of navigation in birds. The importance of this question may be taken from the following suggestions. Many migratory birds are known to show fidelity to birth place and breeding site (see reviews: Sokolov 1991, 1997). If the final goal of their spring migration is an area up to several kilometres in diameter, they would need to reach any part of this area suitable for breeding. It is suggested that removal of birds before breeding within the limits of this area would not lead to their return back to the capture site. However, if the goal of spring migration is a particular small area (radius up to 1 km), the bird would attempt to return even when displaced only for a short distance. This would be especially true for yearlings that do not yet have a previous nesting site. It has

been recognised as being of considerable importance to reveal how migratory birds find their goal in spring. Not much is known about the way in which birds search for their final goal. Do they use a strategy of slow search during the very last portion of migration, or do they reach their local goal directly in a rush without any inspection of the environment? Are they attached to the micro-location or a larger area? To answer these questions was the objective of this study.

Our subject were Pied Flycatchers, long-distance migrants wintering in tropical West Africa. Their ability for homing during the incubation and feeding of nestlings as well as just after arrival has been demonstrated in many studies (Isakov 1957, Scherbakov 1960, Blagosklonov 1965, Vilks 1965, Slagsvold et al. 1988, Sokolov & Vysotsky 1991, Winkel & Winkel 1990). Females were often used in these experiments, which was inefficient due to their inclination to desert nests after displacement. The majority of females displaced before breeding did not return to the capture area either (Winkel & Winkel 1990, Slagsvold et al. 1988). Thus, our main aim was to study homing in male Pied Flycatchers during the period between their arrival in spring and the beginning of breeding. It was important to study the ability for short-distance homing during this period in the yearlings and adults of different origin: native (hatched within the area of study) and immigrants (hatched outside the study area).

2. Study area and methods

This study was conducted on the Courish Spit of the Baltic Sea. The Courish Spit is a long (97 km) narrow (0.7-3.7 km) strip of sand dunes and woodlands stretching from the NE to the SW. We covered an area of the Courish Spit about 47 km long by about 900 nest-boxes suitable for Pied Flycatchers. In the core area 10 km long, we checked breeding and hatching birds most frequently. The structure of the breeding population had been studied previously. Native birds that had hatched within this area represented on average 25% of the breeding population, immigrants represented 75%.

Homing experiments were performed between 1987 and 1993. Most experiments were performed before mating when males were actively inspecting empty nest-boxes. Their subsequent mating status was recorded. Birds were caught in the empty nest-boxes by automatic traps. The birds were ringed and individually marked by dying feathers in different colour. This made possible their individual visual identification. Marked males were displaced within one hour in cloth bags mainly by bicycle (sometimes by car) to the SW or NE from the capture site. Most birds were displaced for distances of 3-4 km. It is important to emphasize that birds as a rule were usually released near unoccupied nest-boxes in the habitat similar to that of the capture site. We performed most displacements on sunny days (sometimes during cloudy weather). We checked every day for birds after their release both at the capture and at the release site. After release, birds disappeared very quickly from sight into the trees. Some individuals were displaced up to 6 times to different distances and at different stages of their reproductive cycle, i.e. before onset of nest building and during feeding of nestlings. A total of 178 males was displaced before mating and 44 during the nestling period. The information on every individual in the same year has been entered into the Tab. 1 only once. On the basis of the data of birds ringed in previous years and age identification of first captured Pied Flycatchers (Karlsson et al. 1986, Vysotsky 1989), birds were separated into five groups as shown in Tab. 1. Additionally, immigrant yearlings displaced during the period of feeding their nestlings are designated by number 7, adult birds (native and immigrants) by numbers 6 and 8. The homing success was evaluated by the return percentage to the capture site. Furthermore, displaced birds from table 1 were classified as returned and not returned. A paired comparison of return rates between different male groups based on analyses using 2x2 contingency tables was performed (Tab. 2). The two-tailed $\chi 2$-test was used.

The birds were also caught by the Rybachy-type traps. These traps correspond in principle to the Heligoland funnel traps but differ from the latter by a non-rigid carcass and larger size (entrance width up to 30 m, height up to 15 m). Owing to the dimensions of the traps, birds do not perceive them as a source of danger. They fly into a trap and in most cases reach its catching chamber on their own. The traps were situated in the centre of the controlled area. From 2 to 5 traps and a number of mist nets were operated in different years. The wooded area is only 650 metres wide at the site where the traps are located. Many Pied Flycatchers should be expected to be trapped in spring if they use the slow

search strategy when finding their final migratory goal. The number of trapped birds was analysed in respect to the distance between the traps and their subsequent breeding sites.

3. Results and discussion

Displacement results of males are shown in Tab. 1. The analysis of those 5 groups (1-5) revealed a strong heterogeneity (χ^2=*58.29*, df=8, p<0.0001), i.e. proportions of returned, settled or disappeared birds differed significantly from average proportions. Paired comparisons of homing success in different male groups are shown in Tab. 2. Immigrant yearlings (group 4) returned less efficiently then other groups of birds (Tab. 1, 2). Birds from groups 1 and 2 that had bred before at that site usually returned equally well. Native yearlings (group 3) showed results intermediate between the bird that had bred previously (groups 1 and 2) and yearling immigrants (group 4). Birds that had bred before (groups 1 and 2) returned significantly better than both native yearlings (χ^2= 6.62, df=l, p=0.01) and immigrant yearlings (χ2=54.32, df=l, p<0.0001). It should be emphasized that native yearlings returned significantly better than immigrant yearlings (Tab. 2). Immigrant yearlings (Tab. 1) that had been removed from the nests with nestlings (group 7) returned as well as ($\chi 2$=0.04, df=l, p=0.8) birds that had bred before (groups 1 and 2), showing the same ability for homing. Hence, males of different age and origin showed different homing success. It depends on time of the season, but nearly all males possess an ability to home.

Table 1. Homing success in male Pied Flycatchers (percent shown in parentheses).

	Before mating			
1. Native birds breeding in	25(100)	21 (84)	2(8)	2(8)
2. Immigrants breeding in previous	34 (100)	27 (79)	4(12)	3(9)
3. Native yearlings	27 (100)	14 (52)	9(33)	4(15)
4. Immigrant yearlings	78 (100)	13 (17)	36 (46)	29 (37)
5. Adult immigrants that have not at the study area before	14 (100)	6(43)	5(36)	3(21)
	Nestlings period			
6. Birds from groups 1 and 2	15(100)	15 (100)	0(0)	0(0)
7. Birds from group 4	22 (100)	19 (86)	0 (0)	3(14)
8. Birds from group 5	7(100)	6(86)	0(0)	1(14)

Table 2. Paired comparisons (two-tailed χ2-tests, df=1) of the returning rates before mating in different male groups (designation of groups as in Tab. 1). Significance level: *** p<0.001, * p<0.05.

	Group #			
Group #	2	3	4	5
1	0.01	4.72*	35.83***	5.33*
2		4.01*	37.92***	4.58*
3			11.22***	0.05
4				3.5

It is of general interest in addition to comparisons of return success, to understand the relationship to the territory in different groups by comparing birds settled at the release site. The proportion of settled birds in the release site from groups 1 and 2 (10%) was more then four times smaller (χ2= 17.12, df=1, p<0.0001) then the groups 3, 4, and 5 (42%). Some individuals from all tested groups disappeared after displacement and were never found in the control area again.

We did not find any relationship between homing rate in males and distance of displacement. Birds of different age and origin returned equally well in relation to the direction of re-location (Sokolov & Vysotsky 1991).

The speed of male return before the breeding period differed between groups. This difference was probably related to a variable motivation to return. 85% of 34 adults returned to their breeding site on the first day, 15% returned 2 to 5 days after displacement, whereas only 17% of 18 native and immigrant yearlings returned during the first day, the other 83% during days 2 to 5. Among immigrant yearlings, removed during the period of feeding their nestlings, 65% returned on the first day. Among adults 7 individuals returned on average within 3 hours.

The analysis of distribution of the distances from the capture site to the recovery site for 71 males revealed that all birds returned to within 1 km but most of them (59%) were found within 200 m. Of all tested birds, 39% returned to the same nest-boxes. It was previously found that 92% of Pied Flycatcher males had home ranges not exceeding 1.3 km (Vysotsky 1986). Thus, all males that showed homing ability returned to their home ranges, i.e. they had a high navigational accuracy. It is noticeable that one-half of native yearlings, returning for the first time to their natal sites, expressed a strong attachment to a certain small area (with a diameter of approximately 1 km). Apparently, this small area was a navigational goal during their spring migration. Hence, we suggest that at least one-half of native yearlings tried to return in spring to a certain known micro-location, that they had imprinted during the post-Hedging period (Berndt & Winkel 1980). The behaviour of Pied Flycatchers during the post-fledging dispersal is well studied (Vysotsky et al. 1990). At the same time most of the immigrant yearlings appeared in the study area in spring did not show an attachment to a particular micro-location before breeding. Such attachment developed during incubation.

Table 3. Number of Pied Flycatchers captured ID Rybachy-type (.raps and mist nets in spring, and the number of birds which were also controlled at nests in the same season at different distances from the traps.

Distances from the breeding site to the traps, km										
0 - 0.3	0.5 - 1	1.1 - 2.0	2.1 - 3.0	3.1 - 4.0	4.1 - 6.0	6.1 - 8.0	8.1 - 10.0	10.1 - 14.0	17.0 - 20.0	24.0 - 26.0
Number of nesting males										
165	69	139	86	142	73	120	61	20	33	8
Number of trapped males										
36	5	6	1	3	0	0	0	0	0	0
Percentage of trapped males										
22	7	4	1	2	0	0	0	0	0	0
Number of nesting females										
159	62	150	100	133	80	195	108	39	67	14
Number of trapped females										
27	2	4	0	1	0	3	0	0	0	0
Percentage of trapped females										
17	3	3	0	1	0	2	0	0	0	0
Total of nesting birds										
324	131	289	186	275	153	315	169	59	100	22
Total of trapped birds										
63	7	10	1	4	0	3	0	0	0	0
Percentage of trapped birds										
19	5	3	0.5	1	0	1	0	0	0	0

Only one-half of native yearlings homed successfully. About 35% of these birds settled at the release site. There are reasons to believe that variability in attachment to certain locations occurred in male yearlings. Some birds returned to a certain micro-location in their first spring. Other yearlings were more inclined to settle in spring anywhere within a larger area. About 30% of males and 36% of females of locally-born birds appeared in their birthplace only in the second year of life (Sokolov et al. 1990). They had settled for breeding in the first year outside the study area.

It was also important to answer a question: where did displaced birds return to for breeding in subsequent years? The analysis of recoveries showed that birds that had demonstrated homing after

displacement returned to the same small area in the next year. It is noteworthy that three out of nine native yearlings that had settled around the place of release, returned next year to the place of previous capture. One bird returned to the release location. This demonstrated that the territory imprinted during their post-fledging period was most attractive. Birds aspired to return to that location at the age of two years even if they had bred elsewhere during the first year. However, some birds can return to breed also to the site of release which they had additionally imprinted during their first breeding season. In this case the imprinting of the breeding territory by some individual Pied Flycatchers occurred not only during juvenile stage (35-50 days) but also later in the first breeding season. Similar results were obtained by Winkel & Winkel (1993).

The next question we were interested in was whether birds use the slow search strategy to find their goal during the very last portion of migration or whether they reached it in a rush? To answer this question we analysed the life histories of birds captured in Rybachy-type traps and mist nets and subsequently found during breeding at different distances from the traps. There is a strong heterogeneity in the data from Tab. 3 (for both sexes Wolf's G-test=170.0, df=10, $p<0.0001$). It was revealed that birds captured in the traps in spring were those that had bred in the vicinity of the traps (Tab. 3). There is some evidence that the majority of Pied Flycatchers reached their goal in spring without a slow search of the woodland.

Hence, studying the homing in Pied Flycatcher we came to the important conclusion that birds have an ability for "pinpoint" navigation, i.e. they can directly reach a very local goal (radius 1 km) using a navigational mechanism. It remains obscure what navigation cues they are using.

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