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Are migrant passerines faithful to their individual paths and migration timing throughout their lives?

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ABSTRACT

Some publications report that passerine birds, compared with geese and waders, show much less annual faithfulness to migration routes and stopover sites, and that faithfulness to them decreases with increasing length of the migration path. The analysis of numerous recaptures of ringed birds in the Curonian Spit (Eastern Baltic) led to the opposite conclusions. The calculations were carried out on thousands of recaptures obtained over 30 years (1957–1986) from two of the most numerous species, chaffinch *Fringilla coelebs* Linnaeus, 1758 (Fringillidae) and willow warbler *Phylloscopus trochilus* (Linnaeus, 1758) (Phylloscopidae). It turned out that a significant part of the migratory populations (34-41% of recaptured birds) retains the same migration path and approximately the same migration timing in other years after ringing. Assumptions about the dependence of the degree of fidelity to migration routes on their length have not been confirmed, since the fidelity indicators of willow warbler, which has a much longer route than chaffinch, were even higher than those of the chaffinch. The data on the individual life longevity of the recaptured migrants (up to 9 years in the chaffinch and up to 4 years in the willow warbler) confirm the fidelity to the same migration path throughout the life of the studied birds.

Keywords: chaffinch, faithfulness, migration, migratory paths, passerines, willow warbler

Сохраняют ли верность мигранты воробьинообразных птиц своим индивидуальным маршрутам и срокам миграций на протяжении своей жизни?

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РЕЗЮМЕ

В некоторых публикациях сообщается, что воробьеобразные птицы по сравнению с гусеобразными и куликами проявляют гораздо меньшую ежегодную верность миграционным путям и местам остановок, и что верность к ним уменьшается с увеличением длины миграционного пути. Анализ материалов многолетнего (1957–1986 гг.) повторного отлова многих тысяч особей окольцованных птиц на Куршской косе (Восточная Прибалтика) на примере двух самых многочисленных видов певчих птиц, зяблика *Fringilla coelebs* Linnaeus, 1758 (Fringillidae) и веснички *Phylloscopus trochilus* (Linnaeus, 1758) (Phylloscopidae), привел к противоположным выводам. Значительная часть пролетных популяций (34–41% из повторно пойманных птиц в сезоны миграций) сохраняет тот же миграционный путь и примерно те же сроки миграции в другие годы после кольцевания. Предположения о зависимости степени верности миграционным маршрутам от их протяженности не подтвердились, поскольку показатели

такой верности у веснички, имеющей гораздо более длинный маршрут, чем у зяблика, были даже выше, чем у зяблика. Данные индивидуальной продолжительности жизни повторно пойманных мигрантов подтверждают верность одному и тому же пути миграций на протяжении жизни исследованных птиц.

Ключевые слова: зяблик, верность, миграции, пути миграций, воробьеобразные, весничка

INTRODUCTION

It is widely known that migratory bird species are philopatric, since most of the survivors return annually to the territory of their former breeding or birth. Such fidelity provides advantages associated with the whole complex of knowledge about familiar places for gathering food and nesting (Berndt and Sternberg 1968; Greenwood and Harvey 1982; Sokolov 1988, 1991, 1997). A number of similar advantages are important outside breeding grounds, at wintering sites, which also leads to fidelity to these territories (Kelsey 1989; Robertson and Cooke 1999; Catry et al. 2004). Using advanced navigation capabilities over thousands of kilometers, birds are able not only to accurately follow the required route, but also to stop for rest and feeding at the most suitable stopover sites (Winker and Warner 1991; Merom et al. 2000; Berthold 2001; Catry et al. 2004). The total duration of such stops significantly exceeds the total flight time to the migration purpose (Berthold 2001; Chernetsov 2012). Many papers and a monograph summarizing this information (Chernetsov 2012) are devoted to the problem of stopovers in the same season, assessment of their duration and effectiveness in relation to the rate of fat accumulation. There is much less data on recaptures of birds in subsequent years. However, they are necessary for assessing the annual faithfulness to migration routes and migration dates in different years.

It is believed that birds such as swans and geese (Anserinae), as well as many waders (Charadriidae) show the highest degree of annual attachment to stopover sites (Smith and Houghton 1984; Harrington et al. 1988; Fox et al. 2002; Catry et al. 2004). There is much less similar data on passerines on the migration routes, although there are facts of a high degree of fidelity to stopover sites in some species of Acrocephalidae (Merom et al. 2000). Some papers (Winker and Warner 1991; Catry et al. 2004) state that fidelity to territories on the migration routes is a rare phenomenon among passerines. They should have a much lower annual fidelity to migration routes compared to geese and waders due to higher energy costs and, consequently, receive less benefit from fidelity to routes and stopover sites. It is assumed that the fatefulness to the route and the stopover sites should decrease with increasing distance of the migration route. It is argued (Catry et al. 2004) that there is no convincing evidence that location accuracy is important for passerine birds, and therefore they have a large individual variability in annual migration routes. While paying tribute to these authors regarding this research topic, it should be emphasized that there are data of ringing that do not confirm such conclusions. This is the subject of the proposed article.

MATERALS AND METHODS

Trapping and ringing of birds by the staff of the Biological Station "Rybachy" of the Zoological Institute of the Russian Academy of Sciences has been carried out on the Curonian Spit (Eastern Baltic) since 1957 to the present. The Curonian (= Courish) Spit is a narrow strip of land separating the Curonian Lagoon from the Baltic Sea. The spit stretches in the direction from northeast to southwest, which coincides with the main direction of bird migration in this region. Trapping is carried out in two places: at the "Fringilla" field camp (55°05'N, 20°44'E) and at Rossiten Cape (55°09'N, 20°51'E). At the former site, birds are caught in the so-called Rybachy traps, at the latter site with mist nets. The detailed device of Rybachy traps has been described (Dolnik and Pavevsky 1976). Traps operate for 7 months of the year, around the clock, from the end of March to the start of November. Trapping and ringing of birds of all species is accompanied by their lifetime examination, determination of sex and age, as well as standard measurements of wing length and body weight. In addition, the stage of the sexual cycle and the state of molting are also described (Vinogradova et al. 1976).

The first attempts to use the results of bird ringing in relation to the topic of the article were based on data for 8 and 12 years, 1957–1968 (Payevsky 1962; 1972). Over the years since then, the work on trapAre passerines faithful to their migratory paths and timing?

ping and ringing birds has accumulated many times more data of recaptures in the years following ringing. Now their analysis has been carried out using the example of two species of true annual migrants from the most numerous songbirds of Eurasia: the chaffinch Fringilla coelebs Linnaeus, 1758 (Fringillidae) and the willow warbler Phylloscopus trochilus (Linnaeus, 1758) (Phylloscopidae). In addition to their large numbers, the selected species are characterized by important features for the purposes of the study. Firstly, there are different lengths of seasonal migrations: chaffinches spend the winter months in South Europe, and willow warblers in sub-Saharan Africa. Secondly, there are different types of migration flight: chaffinches are daytime migrants, and willow warblers are nocturnal.

The materials of the ringing results for the purposes of the questions posed were presented by two groups of data. The recaptures of individuals in the same place in different years during the migration periods of autumn and spring may indicate the faithfulness to the same migration routes throughout the bird's life. The recaptures on the same or similar dates in different years may indicate the faithfulness to same migration dates. In addition, individuals caught in different migration seasons were considered separately: some birds ringed in spring were caught at the place of ringing in autumn in other years, and vice versa, some autumn migrants were caught there in the spring of subsequent years. Thus, these recapture materials make it possible to use them both to study the degree of fidelity to migration routes, and to study fidelity to migration dates.

The recaptures at the "Fringilla" field camp for 30 years, 1957–1986, were used for calculations. These were the years with the largest number of chaffinches and willow warblers trapped (Payevsky 1990) and, accordingly, with the largest number of their recaptures at the ringing site, both in the same and in subsequent





Fig. 1. Dynamics of the number of chaffinches and willow warblers caught in the Curonian Spit during 1957–1986.

years. The number of ringed birds and the recaptures is measured in thousands (Fig. 1, Table 1). Due to the fact that the work on traps lasts the entire period from the beginning of spring to November, it was necessary to establish the dates of spring and autumn migrations (without affecting the breeding time) during which recaptures of birds could be used within the limits of the migration dates of these species. These periods were established on the basis of studying the reproduction of these species in the Curonian Spit), they are indicated in the notes to Table 1.

The calculation of the probability of catching birds in the years following ringing at the same place on the same date or dates of migration periods

Table 1. The number of ringed birds of two species and the number of their recaptures at the ringing site.

Species	The number of ringed individuals in 1957–1986		The number of recaptures at the ringing site				
	Total	Limits by year	Total	In the year of ringing	In the following years		
					Total ¹	During periods of migration ²	
Chaffinch	542498	5615 - 46001	7062	4028	3034	755	
Willow warbler	71347	419-8561	4165	2948	1217	323	

Notes: ¹ recaptures for all seasons, including the reproduction season; ² at the chaffinch until May 1 and from September 14, at the willow warbler until May 11 and from August 13.

close to it was carried out using the usual statistical formula for determining probability (Venetsky 1981): P(A) = nA/N, where P(A) is the probability of catching, nA is the empirical frequency of catching in such a date, N is the number of all catches. At the same time, the number of days (dates) contained in the concept of "close dates" is set for neighboring dates with the largest number of recaptures. 12 dates turned out to be close dates for the chaffinch, and 11 for the willow warbler. The obtained indicators (shares) of recaptures were recalculated according to the method described for migrating passerines in southern Portugal (Catry et al. 2004). This method consisted in using for the calculation of final result the indicators of the average annual survival of the studied bird species, in our case, the chaffinch and the willow warbler. The survival rate of these species in Baltic populations was studied earlier (Payevsky 2008) using a special technique (Pollock 1981) and amounted to 0.556 in chaffinch (0.562 in males, 0.523 in females) and 0.327 in willow warbler. The obtained fractions were compared using the usual formulas (Fleiss 1981).

RESULTS

During the thirty-year period (1957–1986), trapping and ringing of birds in the Curonian Spit, 3034 recaptures of chaffinches and 1217 recaptures of willow warblers were obtained in subsequent years (Table. 1), of which there were 755 ($24.9 \pm 0.8\%$) and $323 (26.5 \pm 1.3\%)$ respectively during the migration period. Of this number, 145 chaffinch and 44 willow warbler individuals were caught on close dates of different years, which gives a probability of capture on close dates of 19.2 \pm 1.4% for chaffinch and 13.6 \pm 1.8% for willow warbler, respectively (Fig. 2). Recalculation of the data obtained, taking into account the annual survival rate of birds, gives the next data: 0.192/0.556 = 0.345 for chaffinches, i.e. 34.5%, and 0.136/0.327 = 0.416 for willow warblers, i.e. 41.6%, the differences are significant (t = 4.0, df 190, p <0.001). This means that it is likely at least 34.5% of chaffinches and 41.6% of willow warblers retained this migration path and approximately the same migration dates in other years after the year of ringing. The calculation separately by sex in chaffinches (83 males and 62 females were caught on close dates) showed the following. Taking into account small, statistically unreliable sex differences in the average anV.A. Payevsky



Fig. 2. The number of recaptures of chaffinches and willow warblers in the migration seasons of subsequent years on close dates (0-12 days).

nual survival of chaffinches, the estimated probability of maintaining the same migration path in males and females turned out to be almost equal: 36.2% and 34.1% (t = 0.06, df 143, n.s.).

Another option for calculating the persistence of the same migration path based on the data of recaptures of the same individuals in different seasons of different years is presented in Table 2. These results, in contrast to the above, show a lower level of fidelity to the migration path, but the same in terms of species differences – chaffinches have less than willow wablers (6.5% and 16.1%). A comparison of the above fractions confirmed the reliability of the obtained variations at a sufficient statistical level. The life longevity of birds in the period from the first to the last capture in subsequent years during the migration seasons ranged from 1 year to 9 years for chaffinches and from 1 year to 4 years for willow warblers (Table 3). According to the ringing of local populations of chaffinches and willow warblers in the Curonian Spit (Pavevsky 2009), the maximum life expectancy of discussed species is slightly higher in comparison with the migrant ones (11 years in males, 9 in female chaffinches, and 6 years in willow warblers), but the age distribution is the same.

DISCUSSION

The presented results (Fig. 2) mean a clear probability that at least two permanent migrants in the Curonian Spit, the chaffinch and the willow warbler, have a significant part of the migratory populations that maintain the same migration path and approximately the same migration periods in other years after the year of ringing. The data given in Table 2 also certainly indicate the same migration path of some

Species	The number of ringed birds caught in autumn, of those that were ringed in spring		The number of ring spring, of those th autu	ged birds caught in nat were ringed in 1mn	Total	The share (%) of the number of all recaptures
	During next vear	In the following vears	During next year	In the following vears		in the migration seasons
Chaffinch	7	6	19	17	49	6.5±0.9
Willow warbler	5	1	28	18	52	16.1±2.0

Table 2. The number of recaptures of birds ringed during the spring or autumn migration season and caught in subsequent years at the same place during other migration seasons of spring and autumn.

of the analyzed birds in different seasons and years, at least in the conditions of the Eastern Baltic. The assumptions made in the literature about the dependence of the degree of fidelity to migration routes on their length turned out to be untenable, since the fidelity indices of the willow warbler, which has a much longer route than that of the chaffinch, were even slightly higher than those of the chaffinch. Data on life longevity (Table 3) confirm the persistence of fidelity to the same migration path throughout the life of the studied birds.

Nevertheless, there is a circumstance that raises questions in connection with the well-known warming of the climate. In a number of publications over the past decades, it has been clearly shown that many bird species, due to climate warming, began to arrive in spring reliably at an earlier date (Walther et al. 2002; Sparks et al. 2005; Sokolov 2006; Gordo 2007; Horton et al. 2023). Since early arrival is associated with the risk of exposure to more severe spring weather conditions than previously, it is likely that individual migration dates are strongly influenced by selection. Determining the role of individual plasticity in ensuring earlier arrival at breeding sites at the population level requires an analysis of individual migration dates over several years. Such an analysis, using the example of migrations of the black-tailed godwit (*Limosa limosa*), showed that despite the generally earlier arrival dates of members of the same population, in many individuals the individual migration dates for several years reliably coincided (Gill et al. 2014). Whether similar ratios exist in general in passerine birds is still unknown. However, according to our data above, the individual migration dates of the chaffinch and the willow warbler coincide in different years.

CONCLUSION

The presented data on two common species with numerous populations allow to conclude that passerine birds have the same annual fidelity to migration routes as birds from other orders. The very fact of the presence of such migrants, regardless of their number, already proves the ability of songbirds to maintain the same migration route and migration dates. Undoubtedly, using the example of trapping the same individuals over the next few years at the same place on the migration route after their first capture, it is possible to speak with confidence about the fidelity of songbirds to the same path throughout their lives.

Years of life		Chat	Willow warbler			
	Males				Females	
	n	Percentage	n	Percentage	n	Percentage
1	60	54.6 ± 6.4	36	45.6±8.3	66	70.2 ± 5.6
2	23	20.9 ± 8.5	15	$18.9 {\pm} 9.8$	21	22.3±9.1
3	9	8.1±2.6	11	13.9 ± 3.9	6	6.4 ± 2.5
4	7	6.4 ± 2.3	8	10.1±3.3	1	1.1
5	5	4.6 ± 2.1	5	6.3 ± 2.7		
6	4	$3.6{\pm}1.9$	1	1.3		
7	1	0.9	1	1.3		
8	0		2	2.6±1.7		
9	1	0.9	0			

Table 3. The life expectancy of migrants in the period from ringing to trapping in the migration season of subsequent years.

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