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Regional-scale movements in three migratory passerine species on the southeastern coast of the Baltic Sea during autumn migration

V.N. Bulyuk^{1*}, I.S. Ishchenko¹, I.N. Panov² and N.S. Chernetsov^{3,4}

¹ Biological Station Rybachy, Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mail: victor.bulyuk@mail.ru

² Bird Ringing and Scientific Information Centre of Russia, A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Leninsky Prospekt 33, 119071 Moscow, Russia; e-mail: kuksha@yandex.ru

³ Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mail: Nikita.Chernetsov@zin.ru

⁴ Saint Petersburg State University, Universitetskaya Emb. 7–9, 199034 Saint Petersburg, Russia

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ABSTRACT

Much evidence suggests that some passerines during seasonal migrations can perform regional-scale movements, both in the migratory and in the reverse direction. The scale of such movements exceeds the scale of typical stop-over movements, but is usually smaller than most migratory flights. We studied regional-scale movements during autumn migration in short-distance migrants of three passerine species: European Robin (*Erithacus rubecula* Linnaeus, 1758), Goldcrest (*Regulus regulus* Linnaeus, 1758), and Long-tailed Tit (*Aegithalos caudatus* Linnaeus, 1758), by analyzing ringing and recapture data from 7 sites on the southeastern Baltic coast at a distance of 11–132 km from each other. The number of birds involved in regional movements varied significantly between species. Long-tailed Tits migrate during the day, and the proportion of birds performing regional-scale movements was one to two orders of magnitude higher than in European Robins (nocturnal migrants) or Goldcrests (migrants with a mixed migratory rhythm). In all three species, the average dates of their regional-scale movements over short distances did not differ significantly between individuals that moved in the migratory and the reverse direction. Regional-scale movements often occurred under headwinds, which suggests that these movements could be caused by aborting migratory flights and (or) by drifting in such winds.

Key words: *Aegithalos caudatus*, autumn migration, *Erithacus rubecula*, European Robin, Goldcrest, Long-tailed Tit, passerines, regional-scale movements, *Regulus regulus*

Региональные перемещения трех мигрирующих видов воробьиных на юго-восточном побережье Балтийского моря во время осенней миграции

В.Н. Булюк^{1*}, И.С. Ищенко¹, И.Н. Панов² и Н.С. Чернецов^{3,4}

¹ Биологическая станция “Рыбачий”, Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт Петербург, Россия; e-mail: victor.bulyuk@mail.ru

² Центр кольцевания птиц и научной информации России, Институт проблем эволюции и экологии животных имени А.Н. Северцова Российской академии наук, Ленинский просп. 33, 119071 Москва, Россия; e-mail: kuksha@yandex.ru

* Corresponding author / Автор-корреспондент

³ Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт Петербург, Россия; e-mail: Nikita.Chernetsov@zin.ru

⁴ Санкт-Петербургский государственный университет, Университетская наб. 7–9, 199034 Санкт Петербург, Россия

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РЕЗЮМЕ

Многочисленные данные свидетельствуют о том, что некоторые воробьиные во время сезонных миграций могут совершать региональные перемещения как в миграционном, так и в обратном направлении. По дальности масштабы таких перемещений обычно превышают передвижения на миграционных остановках, но меньше, чем те, которые птицы совершают во время миграционных бросков. В статье представлены результаты исследований региональных перемещений во время осенней миграции трех видов воробьиных – ближних мигрантов: европейской зарянки (*Erithacus rubecula* Linnaeus, 1758), желтоголового короля (*Regulus regulus* Linnaeus, 1758) и длиннохвостой синицы (*Aegithalos caudatus* Linnaeus, 1758). Анализ данных кольцевания и повторных поимок птиц этих видов на 7 участках на юго-восточном побережье Балтийского моря на расстоянии 11–132 км друг от друга показал, что количество птиц, вовлеченных в региональные перемещения, значительно различается между видами. У длиннохвостых синиц – дневных мигрантов – доля птиц, совершающих региональные перемещения, была на один-два порядка выше, чем у зарянок (ночные мигранты) или желтоголовых королек (мигранты со смешанным миграционным ритмом). У всех трех видов средние сроки региональных перемещений в миграционном и обратном направлении существенно не различались. Перемещения регионального масштаба часто происходили при встречных ветрах, что позволяет предположить, что эти перемещения могли быть вызваны прекращением миграционных бросков и (или) дрейфом мигрирующих птиц при таких ветрах.

Ключевые слова: *Aegithalos caudatus*, осенняя миграция, *Erithacus rubecula*, европейская зарянка, желтоголовый король, длиннохвостая синица, воробьиные, региональные перемещения, *Regulus regulus*

INTRODUCTION

The migration of most small passerines consists of migratory flights and stopovers during which fuel reserves are replenished (Newton 2008). In many nocturnal passerine migrants, movements at stopovers and flights towards the migratory target are clearly separated. Studies of passerine movements after the completion of night flight have shown that night migrants after landing perform exploratory movements, to find a stopover, where they can quickly and safely to replenish fuel stores for the next flight (Buler and Moore 2011; Buler et al. 2017). These movements are broadly and randomly in different directions. The scale of their movements at stopovers, however, rarely exceeds a few kilometres (Chernetsov 2012). In contrast to these movements, the flights of migrants between stopover sites are often more than several tens or even hundreds of kilometres and they are oriented towards the migration goal. At the same time, passerines are known to move over short distances not only in the seasonally appropriate migratory direction, but

also in the opposite direction (Alerstam 1978; Bruderer and Liechti 1998; Chernetsov 2011; Mills et al. 2011; Taylor et al. 2011; Smolinsky et al. 2013; Nilsson and Sjöberg 2016; Brown and Taylor 2017; Wright et al. 2018). These movements have been studied mainly in coastal areas. The reasons for such movements are assumed to be (i) avoiding competition and high predation risk in coastal areas where large numbers of birds can stop, and the search for foraging habitat inland (Alerstam 1978; Lindström and Alerstam 1986; Åkesson et al. 1996; Sandberg and Moore 1996; Åkesson 1999; Smolinsky et al. 2013; Woodworth et al. 2014; Deppe et al. 2015), (ii) avoiding migrating across the water, especially under adverse weather conditions (Bruderer and Liechti 1998; Alerstam 2001; Wright et al. 2018; Gesicki et al. 2019), (iii) disorientation and (or) orientation errors of migrants (Ralf 1978, 1981). Richardson (1982) reviewed many different explanations proposed to account for reoriented autumn migration, including orientation errors, effects of wind drift and responses to weather. He concluded that no single explanation was applicable

to all cases of reoriented migration reported, but different causes are involved under different environmental circumstances. Due to an intermediate scale of these movements compared with local movements at stopovers, and long-range migratory flights between stopover sites, such movements can be called regional-scale movements (Brown and Taylor 2017).

Many studies of regional-scale movements were carried out in nocturnal migrants, because in daytime migrants flights and stopovers are much more difficult to separate (Chernetsov 2012). In order to study regional-scale movements in daytime migrants and to compare them with nocturnal migrants, we analyzed data obtained in long-term ringing projects on the Courish Spit and at other sites on the south-eastern Baltic coast during autumn migration. The Courish Spit is a narrow strip of land, 98 km long and 0.4–4 km wide (Fig. 1). It separates the Courish Lagoon from the Baltic Sea and is oriented along the north-east – southwest axis. The orientation of the spit coincides with the direction of bird migration, therefore many diurnal songbird migrants fly along the spit, and many of them make stopovers here (Mezhenny 1967; Dolnik 1975; Shumakov 1981; Payevsky 1998, 2009). Such geographical position and several large-scale ringing projects that started in mid the 20th century and are ongoing (Fig. 1), make this region well-suited for studying and comparing the regional-scale movements of birds in migratory and reverse directions.

Our target species were short-distance migrants such as the European Robin (*Erithacus rubecula* Linnaeus, 1758; hereafter Robin), Goldcrest (*Regulus regulus* Linnaeus, 1758), and Long-tailed Tit (*Aegithalos caudatus* Linnaeus, 1758). These species are common in the study area during migratory season but rare during the breeding season and in winter, i.e. the vast majority of captures referred to transient migrants. Robins migrate at night (Bolshakov and Bulyuk 1999; Bolshakov et al. 2007). Goldcrests maintain a mixed rhythm of migration activity, with the nocturnal phase being more widespread, as suggested by direct and indirect evidence (Hansen 1954; Petraitis et al. 1987; Karlsson et al. 1988; Remisiewicz and Baumanis 1996; Bojarinova et al. 2008; Bolshakov et al. 2010). Long-tailed Tits migrate in the daytime (Mezhenny 1967; Shumakov 1981; Babushkina and Bojarinova 2011), and the few observations of their nocturnal movements (Lampolahti 1985; Petraitis et al. 1987) are most likely exceptions. Long-tailed

Tits migrating at night were never detected during our long-term observations at night in the beams of searchlights and over an illuminated area (V. Bulyuk, unpubl. data), or during night inspection of large traps on the Courish Spit during autumn migration (Sokolov et al. 2004). Long-tailed Tits captured and kept in captivity during seasonal migrations in north-western Russia did not show any nocturnal migratory restlessness (J. Bojarinova, pers. comm.).

For all three species, we analyzed recaptures from ringing sites located 11 km away from the first capture site. Comparing the recaptures of birds in the migratory and opposite directions, we tried to answer the following questions:

1. Does the occurrence of regional-scale movements differ between species with different migratory behaviors (i.e., Robins, Goldcrests and Long-tailed Tits)?

2. Did the birds perform regional-scale movements in migratory and opposite seasonal directions at different times and in different energetic states?

3. Are birds more likely to make regional-scale movements under certain atmospheric conditions?

Monitoring of movements of radio-tagged Robins at migratory stopovers showed that after nocturnal migratory flights, the range of their daytime movements does not exceed two kilometers (Tsvey 2008). Unlike Robins, Long-tailed Tits and Goldcrests forage at migratory stopovers in flocks that constantly fly from one tree or bush to another (Cramp and Perrins 1993; Snow and Perrins 1998). We assumed that due to the gregarious nature and high mobility of Long-tailed Tits and Goldcrests when foraging at daytime stopovers, their regional-scale movements would be significantly larger than that of Robins. We also tested the hypothesis that regional-scale movements in all three species can be caused by headwinds for autumn migration, which affect the duration and energy expenditure of migratory flights duration of nocturnal migratory flights in Robins and Goldcrests or the likelihood of catching Goldcrests and Long-tailed Tits during their daytime migratory flights.

MATERIAL AND METHODS

To investigate regional-scale movements of Robin, Goldcrest and Long-tailed Tit, we analyzed the results of bird ringing at the Fringilla field station (55°05'N, 20°44' E) and Rybachy field station (55°09'N, 20°51' E) at 1994–2017 between Septem-

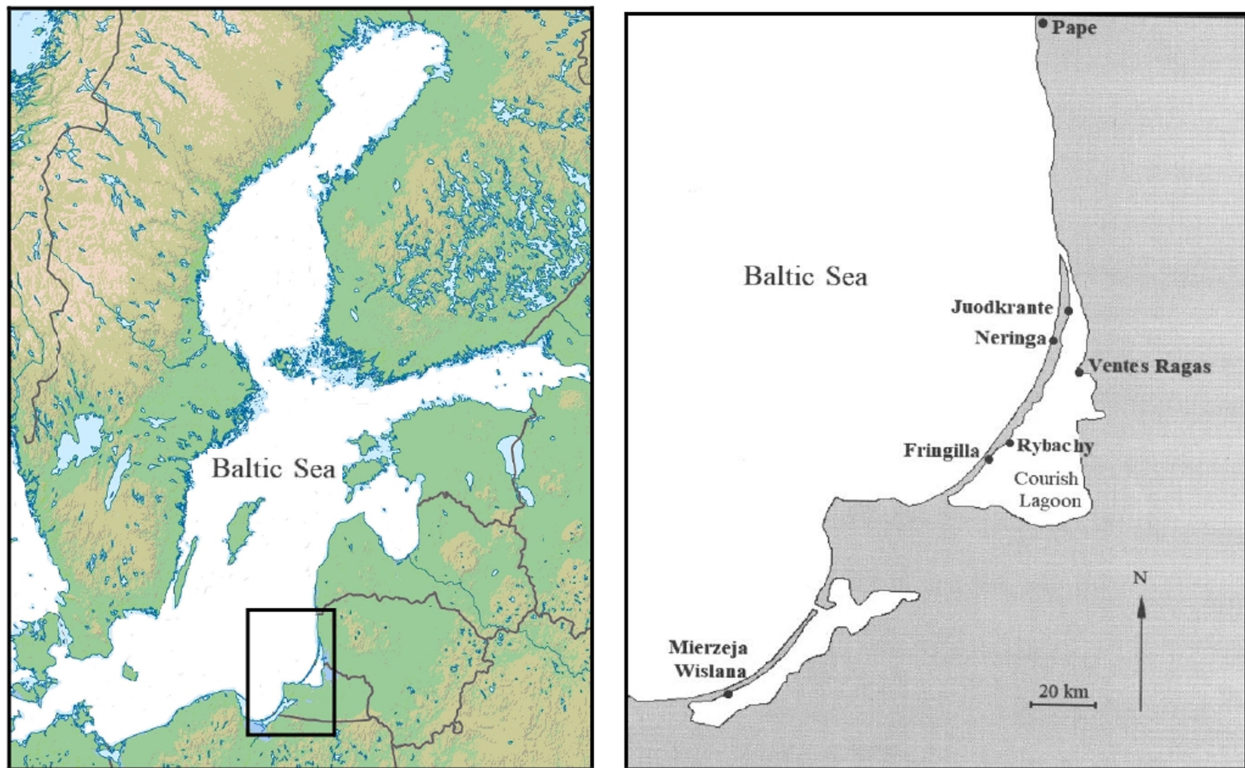


Fig. 1. Baltic Sea Region and bird ringing stations in the study area outlined in black.

ber 1 and October 30. The distance between these stations is 11 km (Fig. 1). At the Fringilla field station, birds were captured in large Rybachy-type traps (Dolnik and Payevsky 1976; Payevsky 2000). At Rybachy field station, the birds were captured in standard 2x7 m mist nets (Chernetsov 2012). Here until 2003, 73 nets were used for catching birds, and since 2004, 27 nets. From 1994 to 2017, 88776 Robins, 171909 Goldcrests and 52423 Long-tailed Tits were caught and ringed at both stations in total (Table 1). Most Robins and Goldcrests were juveniles (93% and 97%, respectively). Most Long-tailed Tits were also first-autumn individuals, but, due to difficulty of ageing in this species, it was impossible to establish the exact ratio of adult and young birds. Ring recoveries in December – February, of the birds ringed

on the Courish Spit during their autumn migration in September, October and early November suggest that Robins' closest wintering grounds were 594 km, Goldcrests 480 km, and the Long-tailed Tits in more than 200 km south or south-west of the place of capture (Bolshakov et. al. 2001; Tsvey 2008).

For each bird captured in Fringilla and Rybachy, the time of capture, wing length (with an accuracy of 0.5 mm), body weight (with an accuracy of 0.1 g), and age were recorded (Svensson 1992). The species studied by us migrated from the Baltic countries, Fennoscandia and NW Russia. According to the captures at Rybachy and Fringilla, the median date of passage was 26 September for the Robins, 12 October for the Goldcrests and 9 October for the Long-tailed Tits. We assumed that >99.9% of the birds captured in

Table 1. Trapping figures of Robins, Goldcrests and Long-tailed Tits at the field stations Rybachy and Fringilla during autumn migration on the Courish Spit in 1994–2017.

Field station	Robin	Goldcrest	Long-tailed Tit
Rybachy	61838	50069	9834
Fringilla	26938	121840	42589

September and October were migrants. The mean direction of long distant recoveries (>200 km) during autumn migration and in winter are 233° for the Robins, 203° for the Goldcrests and 219° for the Long-tailed Tits (Bolshakov et. al. 2001; Tsvey 2008). The Courish Spit direction along Rybachy – Juodkrante line is 20°–200° (Fig. 1), so we considered recaptures along the spit towards the SW as flights in the migratory direction, and towards the NE as flights in the reverse direction.

We used the database of the Biological Station Rybachy, which operates Rybachy and Fringilla ringing sites, to select capture histories of Robins, Goldcrests and Long-tailed Tits captured and recaptured within a 15-day range in September and October. We did not include obviously ill birds, birds found dead, and birds that had not completed their post-juvenile molt. To estimate how often birds perform regional-scale movements in the migratory and reverse directions, and how these differ among the species with different migratory behaviors, we compared the proportion of recoveries in the migratory and reverse direction of their total number caught in Rybachy and Fringilla. In order to find out whether regional-scale movements in the migratory and reverse direction were on different calendar dates, we compared first captures dates in birds involved in these movements. To assess the difference in their energy state, we compared the body condition index (BCI, g/mm) of birds. It was calculated as size adjusted body mass following the formula $BCI = mw^{-1}$, where *m* is mass in the first capture and *w* is wing length. In the group consisted of recaptures between Rybachy and Fringilla the number of Robins was 20, and the number of Goldcrests and Long-tailed Tits was 78 and 298 individuals, respectively. According to the Rybachy and Fringilla recaptures, all aged Robins and Goldcrests were juveniles.

To get a presentation of how the number of Robins, Goldcrests and Long-tailed Tits recoveries changed in the migratory and reverse directions with increasing distance from the place of their capture, we also used recovery data: (1) from two other ringing stations on the Courish Spit, i.e. Neringa (55°27'N, 21°04' E) and Juodkrante (55°31'N, 21°07' E), (2) from two ringing stations on the Baltic coast: Pape (56°10'N, 21°02' E) and Mierzeja Wiślana (54°21'N, 19°19' E), (3) from Ventes Ragas ringing station on the eastern coast of the Courish Lagoon (55°20'N, 21°11' E) (Fig. 1). All stations, except for Mierzeja Wiślana, are locat-

ed north of Fringilla and Rybachy field stations. The distance between Rybachy and Ventes Ragas, Neringa, Juodkrante and Pape is 30, 36, 44 and 114 km respectively. Mierzeja Wiślana is located 132 km S of Rybachy (Fig. 1). Since trapping totals for these sites were not available, we made a simple comparison of the number of recoveries obtained for Robins, Goldcrests and Long-tailed Tits at these distances in migratory and reverse directions. For ease of comparison we lumped recaptures between ringing sites in the region in the following two groups:

- the “medium distance range” (MDR) group is about recaptures in migratory and reserve directions between Rybachy or Fringilla on one side and between Neringa, Juodkrante and Ventas Ragas at distances of 30–55 km on the other;

- the “far range” (FR) group is made up of recoveries at distances 114–132 km between Rybachy or Fringilla on one side and between Pape or Mierzeja Wiślana on the other.

In MDR and FR groups, the number of Robins was 13 and 6 individuals, respectively. The number of Goldcrests in these groups was 51 and 34 individuals, respectively, and Long-tailed Tits were 868 and 389 individuals, respectively.

To study the effect of wind conditions on regional-scale movements in the migratory and reverse directions, we used the data from birds recaptured within 1–2 days after the first capture. For analysis the relationship between changes in these birds and wind conditions, we used the tail wind component (TWC). This variable was calculated as $WV \cdot \cos(CSD - WD)$, where *WV* is wind velocity, *CSD* is the direction of the Courish Spit (200°) and *WD* is wind direction. Wind data for the study area about 150 m above ground level were taken from wind balloon data at 00:00 and 12:00 GMT in Kaliningrad (50 km S of the study site). For the birds recaptured on the day of the first capture, the TWC was calculated for 12:00 GMT of the capture date. For the birds recaptured on the next day, we calculated the TWC taking into account the time it took for migrants to move between capture locations. For Robins, TWC was calculated from wind data for the night before recapture (00:00). For Goldcrests, TWCs were calculated for daytime on the date of the first capture (12:00), night time before recapture (00:00), and for daytime on the date of recapture (12:00). For Long-tailed Tits, TWCs were calculated for daytime (12:00) on first and recapture dates.

Table 2. Proportions of short distant recoveries for Robins, Goldcrests and Long-tailed Tits in the migratory and the reverse direction from the number of ringed birds of these species during autumn migration on the Courish Spit in 1994–2017 in Fringilla and Rybachy.

Direction of movement	Robin	Goldcrest	Long-tailed Tit
Migratory direction	0.015%	0.136%	1.65%
Reverse direction	0.041%	0.008%	0.31%
Difference (Yates-corrected χ^2)	$\chi^2 = 4.64, p = 0.031$	$\chi^2 = 124.43, p < 0.0001$	$\chi^2 = 242.14, p < 0.0001$

Table 3. The mean calendar dates and body condition index (BCI) of the first captures of the Robins, Goldcrests and Long-tailed Tits captured in the migratory and the reverse direction in Fringilla and Rybachy.

Species	Recoveries in the migratory direction (+) and in the reverse direction (-)	Mean date of the first captures (\pm SE); (Significance between the mean values in the migratory and opposite directions; t-test)	Mean BCI of the first captures (\pm SE); (Significance between the mean values in the migratory and opposite directions; t-test)
Robin	+	27.09 \pm 4.4 (n = 9)	0.220 \pm 0.003 (n = 9)
	-	22.09 \pm 4.2 (n = 11) (p > 0.05)	0.210 \pm 0.002 (n = 11) (p < 0.05)
Goldcrest	+	16.10 \pm 1.0 (n = 68)	0.104 \pm 0.001 (n = 67)
	-	16.10 \pm 3.5 (n = 10) (p > 0.05)	0.105 \pm 0.003 (n = 8) (p > 0.05)
Long-tailed Tit	+	15.10 \pm 0.7 (n = 162)	0.131 \pm 0.001 (n = 159)
	-	16.10 \pm 0.7 (n = 136) (p > 0.05)	0.128 \pm 0.001 (n = 123) (p < 0.05)

RESULTS

The proportion of birds involved in short distance recoveries between Fringilla and Rybachy both in the migratory and the reverse directions showed significant difference between the species. Of the three species, the highest proportion of recoveries at a distance of 11 km, in both migratory and reverse directions, was recorded in Long-tailed Tits. For Robins, the lowest proportion of recoveries occurred in the migration direction, and for Goldcrests, in the opposite direction. Considering the proportion of recoveries towards both the migratory and the reverse direction, it should be noted that their differences between different species varied within one or two orders of magnitude (Table 2).

In all three species, the average dates of their regional-scale movements at a distance of 11 km did not differ significantly between individuals that moved in the migratory and the reverse direction (Table 3). Unlike Goldcrests, Robins and Long-tailed Tits had, on average, significantly higher BCI at first capture in birds that were recaptured at distances of 11 km in the migratory direction (Table 3).

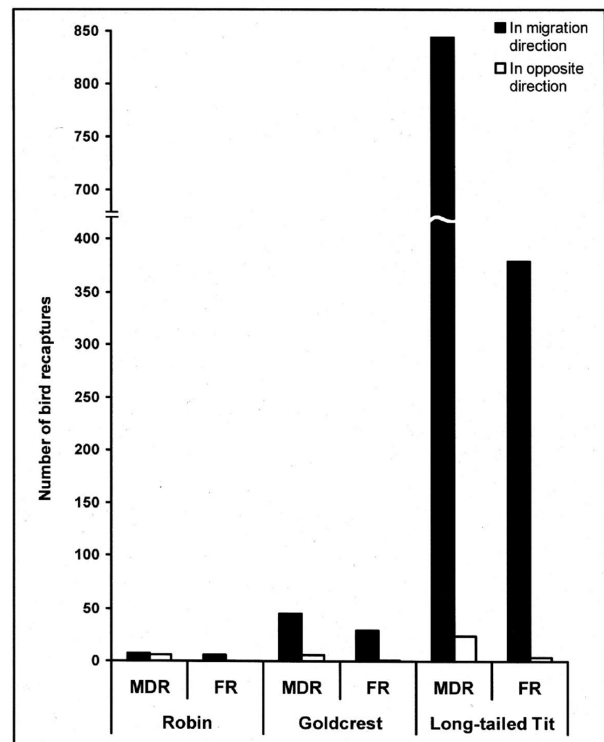
**Fig. 2.** Number of recoveries of the Robins, Goldcrests and Long-tailed Tits 30–55 km (MDR group) and 114–132 km (FR group) from the ringing site in the migratory and the reverse direction.

Table 4. Average tail wind component (\pm ER) in the dates of movements of Goldcrests and Long-tailed Tits at distances 11–55 km in the migratory and opposite directions that they made during one day.

Movement direction of birds	Goldcrest	Long-tailed Tit
In the migratory directions	0.8 ± 1.2 n = 12	-4.8 ± 0.9 n = 5
In the opposite directions	-1.9 ± 0.5 n = 3	3.6, 4.5 n = 2

Table 5. Average tail wind component (\pm ER) in the dates of movements of Robins, Goldcrests and Long-tailed Tits at distances of 11–55 km in the migratory and the reverse direction recaptures one day after the first capture.

Movement direction of birds	Robin	Goldcrest			Long-tailed Tit	
	TWC during the night between first catch and recapture (00:00 of GMT)	TWC during the day of the first catch (12:00 of GMT)	TWC during the night between first catch and recapture (00:00 of GMT)	TWC during the day of recapture (12:00 of GMT)	TWC during the day of the first catch (12:00 of GMT)	TWC during the day of recapture (12:00 of GMT)
In the migratory direction	-6.4 ± 0.2 n = 3	-1.3 ± 0.7 n = 37	-1.4 ± 0.7 n = 37	-1.9 ± 0.7 n = 37	-3.3 ± 0.7 n = 53	-3.5 ± 0.6 n = 53
In the reverse direction	-1.8 ± 1.4 n = 7	-4.2 ± 2.0 n = 3	-4.9 ± 2.7 n = 3	3.6 ± 3.9 n = 3	-4.9 ± 1.0 n = 10	-6.1 ± 1.1 n = 10
Significance (t-test)					p > 0.05	p > 0.05

Simple comparison of the number of recoveries obtained for Robins, Goldcrests and Long-tailed Tits at distances 30–55 km and 114–132 km in migratory and reserve directions showed that the number of recoveries of Robins in MDR group in the reverse direction was almost equal to the number of recoveries in the migratory direction, while all recoveries of FR groups this species occurred in the migratory directions (Fig. 2). Most recoveries of Goldcrests and Long-tailed Tits of MDR and especially in the FR group were in the migratory direction (Fig. 2).

Wind conditions during regional-scale movements of Goldcrests and Long-tailed Tits in the migratory direction on the days when birds were recaptured within one day were more favorable for autumn migration of Goldcrests than Long-tailed Tits. The opposite trend in wind assistance was noted in the days when few Goldcrests and Long-tailed Tits performed reverse movements within single day (Table 4).

More common recaptures one day after the first capture suggest that in all three species, regional-scale movements took place mainly under headwinds, which were opposing for the flights in the migratory direction, and following for reverse movements (Table 5).

DISCUSSION

The data on movements of Robins, Goldcrests and Long-tailed Tits between Rybachy and Fringilla trapping sites in the SE Baltic coast provide an opportunity to study their regional-scale movements in the migratory and the reverse direction because for both these sites we have the ringing totals (Table 1) and the number of recoveries. It should be kept in mind that data for Robins, Goldcrests and very likely also Long-tailed Tits refer to first-autumn migrants. This is due to the fact that both trapping stations are located on the coast, and Robins and Goldcrests migrating at night that stop there are subject to coastal effect, which is manifested in the unnaturally low proportion of adults in captures (Payevsky 1998, 2009; Chernetsov 2012; Bulyuk 2013). Regional-scale movements of adults during autumn passage may significantly differ from the patterns typical of first-autumn migrants (Nilsson and Sjöberg 2016; Brown and Taylor 2017).

Comparison of the proportion of recoveries in Robins, Goldcrests and Long-tailed Tits between Rybachy and Fringilla trapping sites shows that the scale and pattern of regional-scale movements both in the migratory and in the reverse direction can differ significantly in different species (Table 2). Why was

the proportion of recoveries in the migratory direction in Robins significantly less than in Goldcrests and Long-tailed Tits? Why was in Robins the proportion of recoveries in the migratory direction lower than in the reverse direction, while Goldcrests and Long-tailed Tits showed the opposite trend? Why, compared to Robins and Goldcrests, a relatively large number of Long-tailed Tits performed regional-scale movements, not only in the migratory but also in the reverse direction? The answers to these and other questions related to differences in the manifestation of regional-scale movements in the three species studied by us, probably, lie in the feature of their behavior and the influence of environmental factors on it.

Robins are nocturnal migrants. We have good reasons to believe that their regional-scale movements were also performed at night. At least, of many thousands of Robins ringed in Rybachy and Fringilla, we have not a single confirmed case of movements between these sites, either in the migratory or in the reverse direction, within the same day (no same-day recaptures).

During autumn passage in Europe, migrants are often forced to fly under dominating opposing southwesterly and westerly winds (Bulyuk 2013; Bulyuk and Tsvey 2013; Dokter et al. 2013). Under such conditions, birds often fly at low altitudes. Our observations in the autumn in Rybachy of avian nocturnal migration in the beams of searchlights showed that, despite headwinds, many Robins migrating at night at low altitudes had a high motivation to continue flying in the first half of the night. With weak and moderate (3–6 m/s) headwinds, good visibility and no precipitation, we very rarely observed Robins landing before midnight. The number of Robins completing their flights at the beginning and especially in the middle of the night, noticeably increased with strong (>6–7 m/s) headwinds and/or continuous low clouds, fog, rain (V. Bulyuk, unpubl. data). In a study of the behavior of radio-tagged Robins at migratory stopovers and during departures (Bolshakov et al. 2007), we noted several times how birds that took off in strong winds soon completed their flight. Some individuals made small progress towards their migratory goal, whereas others drifted and landed northeast of their take-off location (Chernetsov 2012; Bulyuk and Tsvey 2013). It is also important to note that a large number of Robins migrating in the autumn were caught at the stopover in Rybachy during the daytime after

a night flight with favorable winds for migration (Bulyuk 2013).

The above-described features of the behavior of the Robins make it possible to explain why very few of them were recorded performing regional-scale movements in the migratory direction between Rybachy and Fringilla. Many birds which began their flight in migratory directions from their stopovers in Rybachy with favorable weak and moderate headwinds, within minutes were beyond our detection range, i.e. further than Fringilla. The probability of catching Robins from Rybachy in Fringilla could increase only under unfavorable conditions, in particular, with strong headwinds. This hypothesis is supported by the fact that three Robins were caught in Fringilla after nights with strong high-altitude winds on the day after their first capture in Rybachy (Table 5).

Regarding regional-scale reverse movements of Robins, we assume that these birds after taking off in Fringilla were subject to a drift due to headwinds and were soon forced to abort their flight in Rybachy. Lower average BCI values of these birds compared to those that moved in the migratory direction (Table 3) may indicate their lower motivation to continue migratory flight in the seasonal direction.

According to the short distance recoveries between Fringilla and Rybachy, the proportion of Long-tailed Tits involved in both in the migratory and the reverse regional-scale movements was many times greater than in Robins and Goldcrests (Table 2). Unlike birds of the last two species, Long-tailed Tits migrate to their wintering grounds only during the daytime. Observations on the Courish Spit during the autumn migration show that they move in seasonal and reverse directions in flocks. Genetic microsatellite analysis and the ringing data from Northwest Russia have suggested that Long-tailed Tits can keep family bonds during autumn migration (Babushkina and Bojarinova 2009; Chetverikova et al. 2017). Long-tailed Tits migrate over the forested part of the spit, usually at low altitudes. In headwinds, Long-tailed Tits fly over the treetops and make frequent stops.

Many Long-tailed Tits that were recaptured in the migratory direction on the day of the first capture or on the next day (Table 4, 5) were flying in headwinds. Obviously, as Long-tailed Tits migrate in flocks during the day and at low altitudes (especially with headwinds), the likelihood of recapture in the funnel traps in Fringilla was relatively high. Therefore, many Long-tailed Tits were performing regular

migratory flights rather than participated in regional-scale movements in the migratory direction.

Reverse movements of Long-tailed Tits, in contrast to movements in the migratory direction, can definitely be attributed to regional-scale movements. It remains an open question why the Long-tailed Tits engaged in these movements.

Our study area is located close to winter quarters of Long-tailed Tits. Long-tailed Tits caught in the reverse direction had lower BCI values than birds caught in the migratory direction (Table 3). Approaching the periphery of the wintering area, some individuals with low energy reserves could stop on the Courish Spit for a long time to restore energy reserves. Flocks of Long-tailed Tits, consisting of such birds, during foraging movements could move 11 km northeast from the place of their first capture. It is also possible that some flocks of Long-tailed Tits made regional-scale reverse movements in order to return to stopovers where they had previously successfully fed.

During autumn migration on the Courish Spit, we observed as individual flocks of Long-tailed Tits gaining height until they completely disappeared from the observer's view (V. Bulyuk, unpubl. data). Some Long-tailed Tits that participated in regional-scale reverse movements were recaptured in headwinds (Table 5). We do not exclude the possibility that during strong headwinds, individual flocks of Long-tailed Tits could drift and complete their flight to the northeast of their take-off location when climbing or flying in the migratory direction.

Goldcrest, the third species studied by us, has a mixed rhythm of migratory activity. Observations on the Courish Spit during autumn migration with the Optical-Electronic Device (Bolshakov et al. 2010) and in the beams of spotlights (V. Bulyuk, unpubl. data) suggest that most Goldcrests migrate at night. Daytime migrations over the Courish Spit were observed, as a rule, during waves of passage, i.e. when many birds of different species flew over the spit in the daytime. We do not know if such daytime migratory movements of the Goldcrests were an extension of their overnight migratory flights. Often, large numbers of Goldcrests at stopovers after their massive night migration coincided with large numbers of Goldcrests flying along the spit in the migratory direction during the day. Daytime movements of Goldcrests in the migratory direction, like similar movements of Long-tailed Tits, took place mainly at low altitudes and with frequent stops.

If the Goldcrests migrated at night and during the day, why were there such large differences in the proportion of their regional-scale movements in the migratory direction as compared to Robins, which are night migrants and Long-tailed Tits, which migrate during the daytime (Table 2)?

As seen from the data on tailwind components during the days of captures in the migratory direction (Tables 4, 5), Goldcrests were generally caught under more favorable wind conditions than Robins and Long-tailed Tits. Goldcrests are the smallest Palaearctic migrants, and therefore they have to be rather selective of weather conditions for migratory flights. Thanks to the choice of favorable wind conditions for flights, Goldcrests can cover up to 250–800 km in one day (Ellegren 1993). If Goldcrests started and continued their migration from stopovers on the Courish Spit mainly under favorable weather conditions for a migratory flight, many of them, even after short flights, completed it far beyond *Fringilla* (compare with Robins). If migrating Goldcrests started flying in adverse weather conditions, such as headwinds, they could abort flights sooner than other birds. As a result, few Goldcrests in headwinds drifted and ended up northeast of their take-off site. Lower proportion of Goldcrests making regional-scale movements in migratory directions than Long-tailed Tits could be associated not only with the large number of Goldcrests with a night migratory rhythm. Migrating during the day with more tailwinds at higher altitudes, Goldcrests were less likely to be caught in the funnel traps in *Fringilla* than Long-tailed Tits.

Short-range movements of Robins, Goldcrests and Long-tailed Tits occurred in the same calendar dates in the migratory and the reverse directions (Table 3). It shows that birds that performed direct and reverse regional-scale movements were from the same populations.

Considering the regional movements of birds, it is necessary to take into account that this concept is highly conventional. A small number of reverse recoveries of Robins, Goldcrests and Long-tailed Tits at distances within 30–55 km and 100% of Robins and >97% of all Goldcrests and Long-tailed Tits recoveries in migration directions at distances 114–132 km from the ringing site (Fig. 2) shows that most reverse movements occurred at the range of < 100 km. We suggest 100 km as an arbitrary cut-off between regional-scale movements and migratory flights that bring the birds towards the goal of their migration.

The most common habitat type on the Courish Spit and in other areas of the southeastern Baltic coast, where the data on movements of Robins, Goldcrests and Long-tailed Tits were collected, are mixed forests. Other habitat types are with shrub, meadows and bogs. These are optimal stopover habitats for these birds, where they can successfully refuel (Bojarinova et al. 2008; Tsvey 2008; Chernetsov 2012). Unlike some other regions (Lindström and Alerstam 1986; Åkesson et al. 1996; Taylor et al. 2011; Smolinsky et al. 2013; Statch et al. 2015; Nilsson and Sjöberg 2016; Brown and Taylor 2017), our study area is not a geographical barrier for migrants. Reverse movements make little sense for foraging optimization, because they would not bring migrants to radically different habitats. It may be one of the reasons for the relative scarcity of reverse movements in our dataset. It cannot however be ruled out that some birds, particularly the ones with low fuel stores, may perform movements towards the east away from the coast. Unfortunately, the lack of ringing sites in the hinterland makes it necessary to develop a system of surveillance comparable to MOTUS (s. Wright et al. 2018) in the region to test this assumption.

In conclusion we would like to emphasize that our data and the data of other studies (Mills et al. 2011; Taylor et al. 2011; Smolinsky et al. 2013; Mitchell et al. 2015; Deppe et al. 2015; Sjöberg et al. 2015; Dossman et al. 2016; Brown and Taylor 2017; Wright et al. 2018; Gesicki et al. 2019) show that before crossing ecological barriers and on coastal areas at least some songbird migrants perform regional-scale movements, not necessarily in the migratory direction. Involvement of migrants in such movements may strongly vary between the species, and also between age groups within the species, and also be condition-dependent. Weather conditions and availability of optimal stopover habitats before ecological barriers also may influence the decision of migrants to continue flight in the migratory or reverse direction. However, current data on the occurrence of such movements in different passerine migrants are very scarce. Ringing recaptures may help point to this intriguing topic, which obviously has serious implications for conservations of migrating birds, but serious research into this issue is not possible without large-scale radio tracking studies (Mills et al. 2011; Taylor et al. 2011; Smolinsky et al. 2013; Mitchell et al. 2015; Sjöberg et al. 2015; Dossman et al. 2016; Brown and Taylor 2017; Wright et al. 2018).

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