

# SPEED AND SYNCHRONISATION OF AUTUMN MIGRATION OF THE GREAT TIT (*Parus major*) ALONG THE EASTERN AND THE SOUTHERN BALTIC COAST

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## ABSTRACT

Nowakowski J. K. 2001. *Speed and synchronisation of autumn migration of the Great Tit (Parus major) along the eastern and the southern Baltic coast*. Ring 23, 1: 55-71.

In the paper, 1043 direct recoveries of Great Tits ringed in autumn at 8 coastal stations localised from Estonia to western Poland were analysed. The data came from years 1959-1997. Only movements by a distance exceeding 130 km and with average speed over 10 km/day were considered. The Great Tit migrated with the average speed 33.2 km/day, maximally – 353 km/day (however flights with speed 90 km/day amounted to only 1% of all movements). It was stated, in contrast with hitherto existing opinions, that the Great Tit is characterised by a relatively low variability of migration speed. No differences between sexes and between first-year and older birds were noted. The mean migration speed did not depend upon migration intensity. Years of an intensive (over 160% of many-year mean), medium (40-160%) and poor (below 40%) passage of the Great Tit were compared with respect to variability of the migration speed. Years of intensive passage were characterised by the lowest variability, while years of the poor passage – by the highest one. This indicates that if the migration is intensive, single individuals synchronise it stronger.

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**Key words:** migration speed, synchronisation of migration, Great Tit, *Parus major*

## INTRODUCTION

One of the most interesting and most frequently studied species of partial migrants is the Great Tit (*Parus major*). As many authors (e.g. Ulfstrand 1962, Alerstam 1993, Hudde 1993) emphasise, it is a species of an exceptional, often difficult to explain unambiguously, variation of migratory behaviour. In the result, it is considered as a so-called irruptive migrant (e.g. Cramp *et al.* 1960, Balen and Speek 1976, Berthold 1993), *i.e.* – characterised by large differences in migration intensity

from year to year. The Great Tit is even presented as a model species while describing this type of migration (*e.g.* Alerstam 1993, Berthold 1993). In this species, also a very high changeability of direction and distance of movements is emphasised, at all – large-scale, regional and local – levels, and substantial differences can occur even in siblings from the same nest (Hudde 1993). The same individuals can winter in subsequent years in places localised even 2000 km apart (Rezvyi *et al.* 1995).

When migration speed is considered, this parameter, however relatively less investigated, is also regarded as highly changeable within a wide range from several to over 200 km/day (Hudde 1993). None conditions of this changeability in the Great Tit were hitherto analysed. However, it can be expected that similarly as in other invasive species, the speed of movements will be higher in years of a more intensive migration (such a relation was shown *e.g.* for the Coal Tit *Parus ater* – Rute 1976). In many partial migrants, a larger inclination to migrate was found in young birds and in females (for the review of the problem – see Gauthreaux 1982, Smith and Nilsson 1987; for the Great Tit – *e.g.* Likhachev 1957, Winkler 1974, Hildén 1974). Thus, it could be expected that the speed of movements in the Great Tit will depend upon sex and age. A difference in the migration speed between males and females in partial migrants was found earlier, for example in the Siskin (*Carduelis spinus*) – Payevsky 1971.

On the other hand, sometimes papers occur, in which the high variability of the migration intensity of the Great Tit in central and northern Europe are questioned (Nikander 1984, Croon *et al.* 1985, Vähätalo 1996). In this context, attention should be paid on some paradox. The great majority of papers on movements of the Great Tit is based on materials collected in the Netherlands, southern Sweden, England or Switzerland, thus in places where Great Tits end their migration (literature review – Cramp and Perrins 1993, Hudde 1993). In contrast, only few and the most general papers come from the region of north-eastern and central Europe extending to Poland and eastern Germany – the areas, where the migration of the Great Tit is formed and where the migration intensity is the highest. Such situation can lead to a remarkable distortion of the idea of the Great Tit migration pattern, which we currently have.

The aim of the present paper is to verify the opinion on a high variability of the migration speed of the Great Tit and an attempt to find rules, which govern this variability, or – which would be of equal interest – to show that this variability is in fact chaotic. In particular, the aim is to compare the migration speed of individuals of different sex and age and in years of an intensive and poor passage. It can be hoped that better recognition of this element of the Great Tit migration will allow also for more correct interpretation of other elements of its biology.

#### STUDY AREA AND MATERIAL

The migration speed of Great Tits was calculated from ringing recoveries (difference between ringing and recapture data). In the paper, material coming from

direct recoveries (from the autumn of ringing) of birds captured at 8 ringing stations localised on the eastern and the southern Baltic coast (Fig. 1) was used. Below, a brief characteristics of these stations is given in the order of direction of autumn movement of the Great Tit – from the northeast towards southwest.

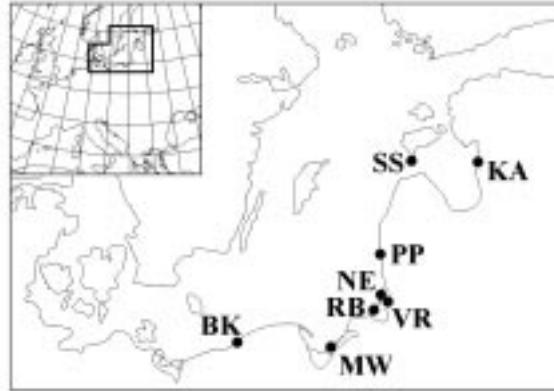


Fig. 1. Localisation of bird ringing stations from which originates the material used in the paper. BK – Bukowo-Kopań, KA – Kabli, MW – Mierzeja Wiślana, NE – Neringa, PP – Pape, RB – Rybachi, SS – Srve, VR – Ventes Ragas.

**Sôrve** (57°56'N, 22°03'E) – Estonia. Bird catching in mist-nets. The station is localised on the southernmost peninsula of the Saaremaa Island. The nets are open in broadleaved thickets with predomination of willows (A. Leivits – pers. comm.).

**Kabli** (58°01'N, 24°27'E) – Estonia. Trapping in modified heligoland trap. The trap is localised on dunes ca 100 m from the coastline, in a place, where pine forest changes into open area with clumps of willows (Leivits 1998, A. Leivits – pers. comm.).

**Pape** (56°11'N, 21°03'E) – Latvia. Catching in modified heligoland trap. The catching place is situated in a narrow stripe of young pine stands which overgrow coastal dunes. The trap was remarkably diminished in 1993 (P. Busse – pers. comm.).

**Neringa** (55°27'N, 21°04'E) – Lithuania. Catching in modified heligoland traps. The station is localised on the Courish Spit, in narrow stripes of young pine plantings overgrowing dunes at the side of the Courish Lagoon (P. Busse – pers. comm.).

**Ventes Ragas** (55°21'N, 21°12'E) – Lithuania. Catching in modified heligoland traps of a different size. The station is localised on a cape going inside the Courish Lagoon, overgrown by thickets with some participation of willow (for more detailed description – see Jezerskas *et al.* 1994).

**Rybachi** (55°09'N, 20°52'E; 55°08'N, 20°42'E; 55°11'N, 20°49'E) – Russia (Kaliningrad region). Catching in modified heligoland traps. Traps are localised in several places of the Courish Spit in young pine stands with some admixture of birch and alder (Dolnik and Blyumental 1967, Payevsky 1971).

**Mierzeja Wiślana** (54°21'N, 19°19'E) – Poland. Catching in mist-nets, in some years additionally in the heligoland-type trap. Places of catching are localised on the Vistula Spit in young pine stands and middle-aged stands mixed with oak and in redbuds surrounding the Vistula Lagoon (for more detailed description – see Busse and Kania 1970).

**Bukowo-Kopań** (54°21'N, 16°17'E/54°28'N, 16°25'E) – Poland. Catching in mist-nets. In years 1961-1984, places of catching were localised on a narrow stripe of land between the sea and Lake Bukowo, and from 1983 onward – 15 km to the northeast in a narrow stripe of forest between the sea and wet meadows near Lake Kopań. In both localisations, habitats were similar. Mist-nets were open in young pine and alder stands with admixtures of birch and aspen, within the coastal dunes zone and in reeds with clumps of trees (for more detailed description – see Busse and Kania 1970, Busse 1994).

In the study the following material from the autumn migration in years 1959-1997 was analysed:

1. 863 direct (from the autumn of ringing) recoveries of Great Tits ringed at one of the described stations and subsequently caught at some other (distances and numbers of recoveries between particular stations – see Table 1).
2. 212 other direct recoveries (Table 1).
3. Numbers of Great Tits caught every year at stations: Kabli (in years 1971-1997), Pape (1967-1997), Neringa (1979-1997), Rybachy (1961-1965) and Mierzeja Wiślana (1961-1997).

Table 1. Distances between stations from which comes the material analysed hereby and the number of direct recoveries taken into analyses

Ringling station	Place of recovery	Distance [km]	No. of recoveries
Kabli	Pape	293	189
	Neringa	352	44
	Ventes Ragas	356	27
	Rybachy	387	77
	Mierzeja Wiślana	517	7
	Bukowo-Kopań	633	5
	Other localisations	–	48
Srve	Pape	204	38
	Neringa	282	10
	Ventes Ragas	291	5
	Rybachy	317	12
	Mierzeja Wiślana	432	1
	Bukowo-Kopań	519	0
	Other localisations	–	8
Pape	Mierzeja Wiślana	231	79
	Bukowo-Kopań	349	13
Neringa	Mierzeja Wiślana	166	111
	Bukowo-Kopań	316	28
	Other localisations	–	67

Ventes Ragas	Mierzeja Wiślana	165	53
	Bukowo-Kopań	322	25
	Other localisations	–	40
Rybachy	Mierzeja Wiślana	133	116
	Bukowo-Kopań	295	12
	Other localisations	–	6
Mierzeja Wiślana	Bukowo-Kopań	188	11
	Other localisations	–	30
Bukowo-Kopań	Other localisations	–	13
<b>TOTAL</b>			<b>1075</b>

In comparison of the migration speed of the Great Tit with other species additionally the following material was used:

1. 147 direct recoveries of Robins (*Erithacus rubecula*) ringed in Poland in years 1958-1998 (these recoveries in majority came from birds ringed at stations Mierzeja Wiślana and Bukowo-Kopań).
2. Direct recoveries of birds ringed at the station Rybachy (from years 1957-1967) and in the Leningrad region (from years 1955-1994) for the Blue Tit (*Parus caeruleus*) – 19 records in total, the Coal Tit – 16 records, the Siskin – 101 records, the Chaffinch (*Fringilla coelebs*) – 104 records, Brambling (*Fringilla montifringilla*) – 32 records and the Meadow Pipit (*Anthus pratensis*) – 20 records.

The data from stations Mierzeja Wiślana and Bukowo-Kopań belong to the Bird Migration Research Station of the University of Gdańsk in Przebendowo. Recoveries of birds ringed at these stations were obtained in computerised form by courtesy of the Polish Ringing Centre of the Institute of Ecology of PAS in Górkki Wschodnie. This Centre also provided recoveries of Robins ringed elsewhere in Poland. Ringing recoveries from years 1989-1997 from the station Neringa and numbers of birds caught in subsequent years at this station were kindly provided by Dr. Ricardas Patapavièius from the Lithuanian Bird Ringing Centre in Kaunas. The remaining Lithuanian and all the Estonian recoveries come from annual reports published in these countries (Kastepöld 1971, 1972, 1973, 1974, 1975; Kastepöld and Kabal 1976, 1977, 1978, 1980, 1981, 1982, 1983, 1984, 1985a, 1985b; Kumari and Jogi 1974; Patapavièius 1982, 1983, 1986a, 1986b, 1986c, 1987, 1988, 1989; Kastepöld and Kastepöld 1987a, 1987b, 1988, 1990a, 1990b, 1991, 1992, 1993, 1994; Skuodis and Kurpyté 1989). Ringing recoveries of birds ringed at the station Rybachy were taken from the paper of Payevsky (1971). Recoveries and numbers of birds caught at the station Pape were obtained thanks to Dr Janis Baumanis from the Institute of Biology in Salaspils in Latvia. Records of birds ringed in Leningrad region were taken from the paper of Rezvyi *et al.* (1995). Completing of the whole material was possible thanks to cooperation of all mentioned persons within the South-East European Bird Migration Network (SEEN).

Small fragments of the material analysed in the present paper were worked out earlier (data from the station Rybachy up to 1957 – Payevsky 1971, and data from years 1967-1975 from the station Pape – Rute 1976). It is likely that the material

used hereby overlaps partly with that worked out by Hudde (1993), however the cited author does not describe methods and the range of data analysis.

## METHODS AND THEIR DISCUSSION

At stations: Kabli, Pape, Neringa, Ventės Ragas and Rybachy, different kinds of modified heligoland traps were used. Their construction and work was described in papers of Erik (1967), Jezerskas (1990) and Busse (2000). At the remaining stations (Sôrve, Mierzeja Wiślana and Bukowo-Kopań), birds were caught in mist-nets (description of the method – Busse 2000). In addition, other methods of fieldwork were described in literature (Busse and Kania 1970, Busse 2000).

According to the plumage features (on alive birds), it is possible to distinguish two age classes of the Great Tit: birds in the first year of life (*imm.*) and older birds (*ad.*). From the beginning of studies, the age was determined at Polish and Latvian stations, and from 1980 onwards – also at Lithuanian ones. At Estonian stations, the age was usually not checked. The sex of Great Tits was identified at all stations from the beginning of studies.

The mean migration speed was calculated basing on the difference between the data of ringing and the data of recapture. In this analysis, passages at a distance shorter than 130 km and with the speed lower than 10 km/day were not taken into account. The limit of the distance was introduced because in the case of short-distance movements the pattern of birds' movements could be remarkably distorted by:

1. the influence of stress connected with ringing (for tits – *e.g.* Rute 1976),
2. the fact that birds migrate with uneven speed and the speed of movement on short distances can wrongly reflect the average speed of migration which is hereby the subject of analyses,
3. the applied method of calculating the rate of movements gives at short distances results of a low precision.

As it resulted from calculations, less than 1.9% of Great Tits moved with the average speed below 10 km/day. Probably, in majority of cases, so low migration speed indicates that in fact the bird was ringed before it begun the passage or that the ongoing passage was disrupted. Therefore, such records were not considered in the analysis.

Initially, records of Great Tits, which were ringed from 10 Sept. onwards and then recaptured or found before 11 Nov. were analysed. Such time frames cover the entire period of the Great Tit migration (*e.g.* Dolnik and Blyumental 1967). At the same time, all the described stations started their work several weeks earlier, before the beginning of migration of this species and it could be presumed that thanks to that, local birds ringed before the start of migration were not regarded in the analyses. However, the preliminary calculations showed that the average speed of migration of birds ringed between 10 and 14 Sept. was distinctly lower than of all the remaining birds (10-14 Sept. –24.0 km/day,  $N = 32$ ; after 14 Sept. –33.8 km/day,

$N = 1043$ ;  $U$ -test:  $z = -3.71$ ,  $p < 0.001$ ). This is rather striking as the mean speed of movements in any other five-day period (after 15 Sept.) never fell below 30.0 km/day. Moreover, Great Tits migrate in September faster than in October (see the *Results*). This brings the assumption that at least some part of birds ringed before 15 Sept. did not start the actual migration (*cf.* also the *Discussion*). Therefore, in further analysis, only records of birds ringed after 14 Sept. were taken into account.

In the analyses, also Great Tits recaptured or found after 10 Nov. were omitted. It is the empirically determined date of the beginning of wintering. It was found by calculating mean migration speeds taking subsequent dates from 1 to 30 Nov. as critical days of start of wintering. It appeared that for dates before 10 Nov. the mean speed fluctuated around the same mean value, while for dates after 10 Nov. it gradually decreased.

Similar methods and limitations were applied while analysing migration speed for the remaining species of birds, and for each species different time frames were established:

1. Chaffinch and Brambling – birds ringed from 10 Sept. onwards and recoveries obtained before 11 Nov.
2. Siskin – birds ringed from 10 Sept. onwards and recoveries obtained before 6 Nov.
3. Meadow Pipit – birds ringed from 10 Sept. onwards and recoveries obtained before 16 Nov.
4. Robin – birds ringed from 1 Sept. onwards and recoveries obtained before 6 Nov.
5. Blue Tit and Coal Tit – time frames the same as for the Great Tit.

Because of the applied limitations and selection of the material, the obtained averages for some species differed from those calculated from the same material by Payevsky (1971).

The level of migration intensity in the whole region in given year was calculated on the basis of numbers of birds caught at stations: Kabli, Pape, Neringa, Rybachy and Mierzeja Wiślana. For each of these stations, numbers of Great Tits trapped in a given year were presented as a percent of the mean number of Great Tits caught in years 1961-1997 (or from the beginning of the station activity, if it started to work after 1961). The intensity of migration in the region was an average of these values. This simple calculation technique seems to be suitable in this case because the Great Tit has a simple system of migration. The birds come to all the mentioned stations from one common direction and no mixing of different populations takes place (Likhachev 1957, Payevsky 1971, Rezvyi *et al.* 1995). The migration goes by a broad front „from tree to tree” (Likhachev 1957, Ulfstrand 1962) so that there are no particular resting places and sites omitted by birds. Moreover, at all described stations, the Great Tit is one of the most numerous caught species. All this indicates that it is not necessary to use weighted values or any complicated recalculations while joining results from different catching sites. Methods of summing up bird numbers noted at different stations were discussed in detail by Busse and Trocińska (1999).

While presenting results of statistical tests, a rule that the probability was given with the accuracy to the third decimal place was applied. If the probability fell in the range  $0.0001 < p < 0.001$  the symbol  $p < 0.001$  was used. If  $p < 0.0001$  it was denoted as  $p \ll 0.001$ .

## RESULTS

Among analysed recoveries, a group of records from Sweden and Denmark was distinguishable ( $N = 62$ ). Birds going to these countries had to cover at least a part of the route over the sea. The average speed of these movements was higher by 11.0 km/day ( $U$ -test:  $z = -3.15$ ,  $p = 0.002$ ) than in the case of the remaining recoveries (probably coming from passage exclusively over the land,  $N = 981$ ). Because it cannot be stated, which part of the route to Sweden and Denmark was crossed over the sea, in further analyses only the recoveries of Great Tits completing the whole route over the land were taken into account.

Over the land, Great Tits migrated with the average speed of 33.2 km/day ( $N = 981$ ); maximally 231 km in the same day and 353 km within 24 hours. However, flights with the mean speed exceeding 90 km/day constituted as little as 1%. The majority of individuals migrated with a speed between 15 and 45 km/day (Fig. 2). The speed of the Great Tit migration was somewhat higher than in the Blue Tit and similar as in the Coal Tit (Table 2). In comparison with other species of short- and medium-distance migrants of a similar size, tits migrated on average much slower (Table 2). For all described species the range of speed, at which 70% of individuals moved (15% of the slowest and the same of the fastest migrants was excluded) was calculated. It appeared that the variability of the migration speed among different individuals in the Great Tit (70% within the range 18-44 km/day) was relatively low against the background of other species (Fig. 3).

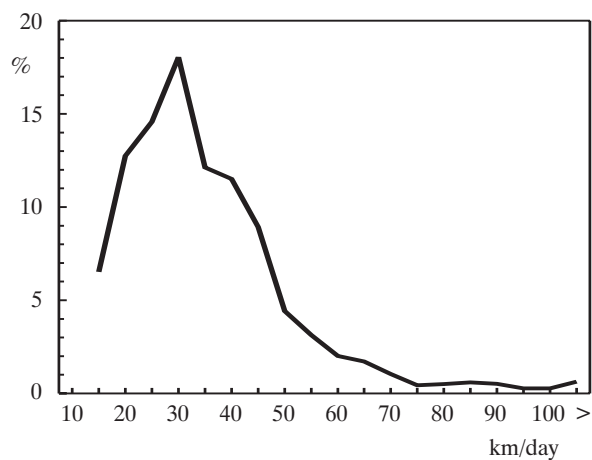


Fig. 2. Distribution of the migration speed values.



Table 2. Comparison of the mean migration speed of the Great Tit with other short- and medium-distance migrants of a similar size. \* – for the Great Tit there was given the value: (1) – calculated from the material analysed in the present paper and (2) – calculated similarly as for other species from data published in papers by Payevsky (1971) and Rezvyi *et al.* (1995). For the Robin the mean migration speed calculated from Polish ringing recoveries was given

	Mean	<i>N</i>
<i>Parus major</i> (1)*	33.2	981
<i>Parus major</i> (2)*	31.9	62
<i>Parus caeruleus</i>	28.0	19
<i>Parus ater</i>	31.3	16
<i>Fringilla montifringilla</i>	59.4	32
<i>Carduelis spinus</i>	64.0	101
<i>Fringilla coelebs</i>	65.8	104
<i>Erithacus rubecula</i>	66.2	147
<i>Anthus pratensis</i>	73.2	20

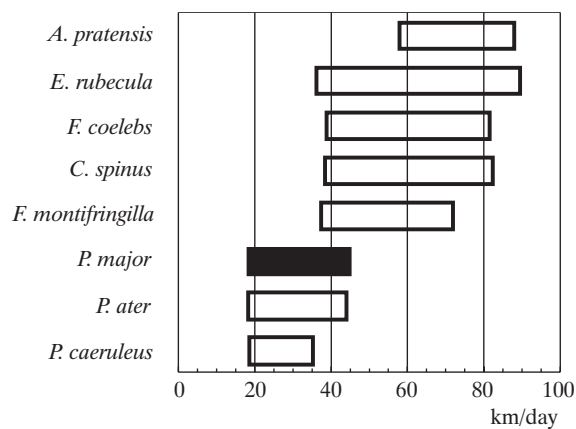


Fig. 3. Comparison of the range of speed presented on migration by the Great Tit and by several other small Passerine short- and medium-distance migrants. Speed within which 70% of individuals moved is marked (15% of records of the slowest and the same – of the fastest migrants were excluded).

All noted in the Great Tit movements with a speed exceeding 90 km/day occurred at short sections of the route (below 400 km). The most impressive long-distance flight was crossing by a bird ringed at the station Neringa 1317 km to northern Italy within 16 days (82 km/day, on average). However, on a distance exceeding 400 km, only 1.5% ( $N = 134$ ) of Great Tits retained the average speed over 70 km/day, while on a distance below 400 km this share was 2.7% ( $N = 847$ ).

No significant differences were noted between birds of a different sex ( $\bar{y} - 33.8$  km/day,  $N = 355$ ;  $u - 32.9$  km/day,  $N = 595$ ;  $U$ -test:  $z = -0.42$ ,  $p = 0.676$ ). Birds

hatched in a given year migrated on average slightly slower (by 3.2 km/day) than adults, but this difference was not statistically significant (*ad.* – 35.8 km/day,  $N = 75$ ; *imm.* – 32.6 km/day,  $N = 479$ ;  $U$ -test:  $z = -1.45$ ,  $p = 0.146$ ). The inconsistency between birds in a different age seems to be the more insignificant as the general distribution of the migration speed was very similar. The share of birds moving fast (over 70 km/day: *ad.* – 2.7%, *imm.* – 2.9%) as well as moving slowly (to 15 km/day: *ad.* – 8.0%, *imm.* – 7.1%) in both age groups was almost identical.

In order to check whether the migration speed is the same within all the studied area, the passage between stations Kabli and Pape (293 km) was compared with the passage between stations Pape and Mierzeja Wiślana (231 km) and with further passage from the station Mierzeja Wiślana (Table 3). No significant differences were noted. It was also analysed whether the speed of migration changed within the season. The migration speed was compared between ringed birds from the beginning of the passage to the end of September ( $N = 155$ ) and from 1 to 20 Oct. ( $N = 327$ ). The majority of stations ended catching about 1 Nov. and some part of birds slowly moving in the end of October was probably non-randomly eliminated from the sample. Therefore, movements in the term longer than 10 days and records of birds ringed after 20 Oct., were not taken into account. In September, Great Tits moved faster by 4.8 km/day than in October ( $U$ -test:  $z = -3.47$ ,  $p < 0.001$ ).

Table 3. Mean values and the result of the  $U$ -test for comparison of the migration speed at different sections of the migration route from Estonia to Western Europe (from – to).

Station symbols: KA – Kabli, PP – Pape, MW – Mierzeja Wiślana

	Mean	$N$	KA - PP	PP - MW	MW -->
KA - PP	31.4	189		$p = 0.600$	$p = 0.808$
PP - MW	36.4	79	$z = -0.52$		$p = 0.532$
MW -->	32.2	40	$z = -0.24$	$z = -0.63$	

In the whole period 1961-1997, a slight decrease of the average migration speed was noted (Spearman correlation  $-r = -0.35$ ,  $p = 0.038$ ,  $N = 35$ ). The decline of the migration speed in 37 years, calculated from the regression line, was as high as 11.2 km/day, however the difference of the average speed between the 60s and the 90s was only 3.4 km/day. It is noteworthy that the migration speed fluctuated (Fig. 4) and in longer periods could even increase – for example, between years 1962 and 1972 (Spearman correlation  $-r = -0.70$ ,  $p = 0.016$ ,  $N = 11$ ) and in years 1983-1992 (Spearman correlation  $-r = -0.82$ ,  $p = 0.023$ ,  $N = 7$ ).

No relation between the intensity of the Great Tit migration in a given year (calculated as a percent of the many-year average – see the Methods) and the mean migration speed in this year (Spearman correlation  $-r = -0.10$ ,  $p = 0.575$ ,  $N = 35$ ). However, it was stated that the intensity of migrations influences the variation of the migration speed among different individuals (Table 4). Years of an intensive migration (over 160% of the many year average) were characterised by a low variability of the migration speed – 80.4% of individuals moved with a speed of 20-50

km/day (Fig. 5). With a decrease of the migration intensity, there increased the share of both individuals moving very fast and those migrating slowly. As a result, in years of a poor passage (below 40% of the many-year average) the share of individuals moving with a speed of 20-50 km/day decreased to 46.2%. In years of a medium intensity of migration (40-160% of the many-year average), the distribution of migration speed was intermediate (Fig. 5).

Table 4. The result of the *F*-test for comparison of variation of migration speed in years with low, medium and high intensity of the passage

	Low	Medium	High
Low		$p = 0.129$	$p = 0.001$
Medium	$F = 0.69$		$p < 0.001$
High	$F = 0.34$	$F = 0.66$	

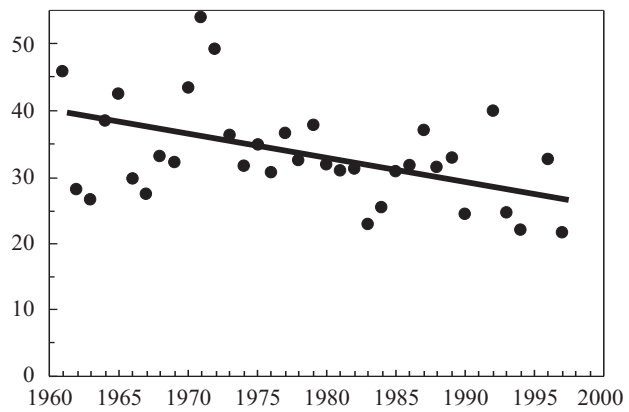


Fig. 4. Mean migration speed in years 1961-1997.

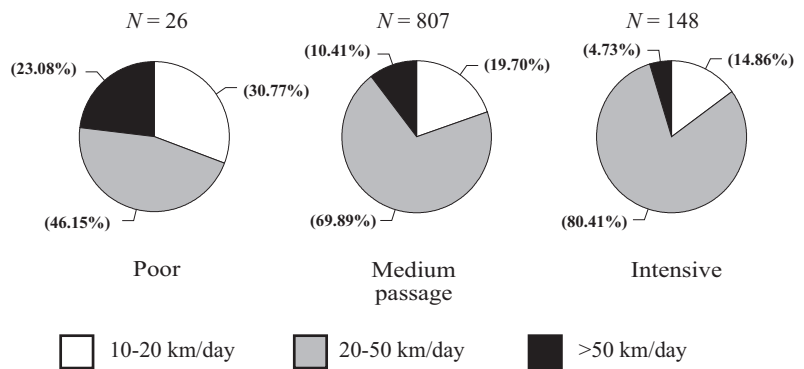


Fig. 5. Shares of a low, medium and high migration speed in years of a poor (below 40% of the many-year average), medium (40-160%) and intensive (over 160%) passage.

## DISCUSSION

According to Alerstam and Lindström (1990) the mean migration speed of the passerines depends on the distance and the character of migration and for long-distance migrants is 75 km/day, for the medium-distance ones – 50 km/day and for short-distance partial migrants – *ca* 25 km/day. All the species compared in this paper are the medium- and short-distance migrants. The mean migration speeds encountered were generally higher than these given by Alerstam and Lindström (1990), but the general tendency, according to which the species migrating further move on average faster, is well visible (amongst the species compared in the Table 2 the furthest migrants are the Meadow Pipit, the Robin and the Chaffinch, and the closest ones are tits – Payevsky 1971, Rezvyi *et al.* 1995). However, it should be emphasised that tits migrate especially slowly, even in comparison with other partial migrants (*e.g.* with the Siskin) and with other species finishing the migration in a similar distance (*e.g.* – the Siskin and the Brambling – Payevsky 1971, Rezvyi *et al.* 1995). In addition, from the analysis of the Finnish ringing data, it resulted that tits migrate slowest in comparison with several tens of other species (Hildén and Saurola 1982). It is probably connected with their way of moving – mainly in short movements from tree to tree (Ulfstrand 1962). Amongst tits, the Blue Tit migrates slowest (this results both from the data analysed hereby as well as from the literature – Rute 1976, Hildén and Saurola 1982). In the present paper, only 16 recoveries of the Coal Tit were analysed, thus the obtained result (Table 2) should be treated as a rough estimate. Actually, Hildén and Saurola (1982) showed that Coal Tits migrate on average over twice faster than Great Tits (the data given by these authors cannot be directly compared with the ones presented hereby because of substantial methodical differences – see the next paragraph). However, also in this case, the cited authors had a small sample to their disposal ( $N = 12$ ). The migration speed of the Coal Tit and the Great Tit was compared on the basis of a large material by Rute (1976). This data came from the station Pape and thanks to that (after excluding short-distance recoveries – below 130 km) can be directly compared with results obtained hereby for the Great Tit. It appears that also in this case, Coal Tits migrated remarkably faster than Great Tits – 38 km/day on average ( $N = 211$ ). Such a result can be surprising, because the Coal Tit resembles other tits with regard to the character and the distance of migration.

The Coal Tit is a typical irruptive migrant (Ulfstrand 1962, Payevsky 1971, Rute 1976, Busse 1985). Rute (1976) showed that in years of invasions its migration speed was twice higher than in other years. High mean speeds of the Coal Tit migration during the invasion in 1974 were also noted by Busse (1978) – between 40 and 80 km/day in different groups. Similarly, basing on materials presented by Payevsky (1971), it can be proved that in years of a very intensive migration, Siskins move over 6 km/day faster than in other years. Taking into account high migratory urge of individuals taking part in an invasion, such a situation could be expected.

Concluding: in years of normal poor passage, migration speed of the Coal Tit does not differ remarkable from that noted in other species of tits.

The fact that irruptive species migrate distinctly faster in years of invasions has another important implication, too. As it was shown in the present paper, there was no relation between the intensity of migration and the speed of movements of individuals of the Great Tit. It is another (after papers of Nikander 1984, Croon *et al.* 1985, Vähätalo 1996) signal that at least in the central and northeastern Europe, the Great Tit is not a typical irruptive species.

The Great Tit was so far regarded as a particularly irregular migrant also with respect to the speed of movements. Numerous notes on birds migrating over 100 km within 24 hours (Hudde 1993) and cited frequently (after Busse and Kania 1973) single encounter of the Great Tit, which crossed 230 km in one day, give an impression that the migration of this species is very irregular with regard to the migration speed. However, a distinct majority of individuals migrates with the speed of 15 to 45 km/day, and movements with speed exceeding 70 km/day are only an impressive margin (Fig. 2). Moreover, the migration speed of the Great Tit seems to be exceptionally stable against the background of other species (Fig. 3). It is especially distinct in comparison with Robin, which, at least with respect to in the intensity of migration, is one of the most regular migrants (Vähätalo 1996). Contrary to differences stated in other species of migrants (*e.g.* Payevsky 1971), in the present paper no remarkable differences between the migration speed of different sex and age class of the Great Tit was found, which is the next evidence of the surprising stability of the migration speed in the species.

The few percent of the fastest movements noted in the present paper probably took place during strong „supporting” winds. It was the case in 1975, when Great Tits rushed by the southeastern wind reached Swedish coast with the speed exceeding 80 km/hour (Alerstam 1993)! The passage over the sea is in general connected with an increase of the migration speed as it was shown in other species, as well (Biebach *et al.* 2000).

The migration speed of the Great Tits is not only limitedly changeable between individuals, but also geographically. The mean speed of autumn migration of Great Tits noted in different parts of Europe is very similar: from Col de Bretolet to Camargue – about 35 km/day (Cramp 1963), in the Netherlands and Belgium – 20-50 km/day (Dhondt 1966), from the station Gumbaritsy (Russia, 60°41'N, 32°55'E) – 32.0 km/day ( $N = 29$ , calculated from the data presented in the paper of Rezvyi *et al.* 1995) and corresponding with that calculated in the present paper (33 km/day). Only in Finland, the result markedly different from presented hereby – 11-15 km/day were obtained (Hildén and Saurola 1982). However, it should be taken into account that Hildén and Saurola took into consideration also movements at short distances (up to 50 km) and with a very low speed (from 5 km/day), which probably, at least partly, do not reflect the actual migration. It should be borne in mind that among only 55 cases analysed by cited authors, some part was constituted by birds moving with the speed exceeding 33 km/day (the mean migration speed noted in the

present paper). All this allows concluding that Finnish Great Tits do not differ so much from other populations. The mean speed of movements in Finland can be influenced to some extent by the fact that in this country Great Tits meet geographical barrier of the Baltic Sea, which causes stopping of some part of individuals (compare the description of crossing the Öresund Strait by Great Tits, presented by Ulfstrand (1962)) or changing the migration direction by them.

These data correspond well with the lack of differences in the speed of movements at different sections of passage between Estonia and Western Europe. Thus, the thesis of Hudde (1993) that the migration speed of the Great Tit decreases from the north to the south seems to be untrue (the author neither presents his own data detailed results nor points out any other sources of the formulated thesis).

In the present paper, it was noted that the migration speed in October decreased slightly, but statistically significantly. Similarly, in the Coal Tit, a decrease of the mean migration speed in its final period was stated (Rute 1976). Hudde (1993), however, wrote that the speed of movements was higher in October than in September. It may be supposed that this difference resulted from including by Hudde early September records into calculations (although the cited author does not present detailed results and the method of analysis). As it was emphasised in the Methods, such records include the most probably individuals, which did not started a real migration yet. However, the occurrence of not ringed earlier, slowly moving Great Tits in September in the area of the later migration indicated that the migration was preceded by some kind of movements, the most probably similar in character to summer dispersal. On the other hand, the difference shown between the results obtained by Hudde and these presented hereby shows how important and difficult at the same time is the correct determination of the beginning of migration in species starting the passage from the study area (compare with Nowakowski 1999).

To explain the phenomenon of decrease of the migration speed within the season, two hypotheses can be put forward:

1. At the beginning of migration, individuals of the highest migratory urge (and thus moving fastest) join it, and individuals with weaker migratory stimulus depart later on. In the effect, the migration speed decreases.
2. The migratory urge of individuals, and thus – the migration speed, decreases gradually during migration.

The above topic needs further research.

Decrease of the migration speed during almost 40 years covered by the study can be associated with an increase of share of habitats changed and inhabited by humans in the studied area, and thus – the increase of the synantrophisation of the Great Tit, especially outside the breeding period. Another factor resulting in a decrease of the speed can be climate warming. Both these factors can influence a decrease of the general stage of migratory urge in the population of Great Tits. However, one should be cautious in conclusions, because, as it was stated, the migration speed in fact strongly fluctuated in several-year periods. The reasons for these fluc-

tuations are not known, thus we cannot foresee if the general decreasing trend will not be reversed in subsequent years.

The decrease in the share of birds moving fast and slowly with the intensity of migration (Fig. 5) is a very interesting phenomenon. This means the most probably that slowly moving birds speed up under the influence of other individuals moving faster. On the other hand, birds migrating very quickly slow down in the presence of slower migrating individuals. This confirms the earlier assumptions that birds shape the time of beginning and finishing the migration and speed of their movements not only in the effect of genetic or physiological factors (such as for example fat score), but also under the influence of other individuals (*e.g.* Dolnik and Bluymental 1967). Busse (1978) showed that within one migratory group, Coal Tits synchronise passage to retain the compactness of the group, and within such a group (if the passage is not disturbed), very low differences of migration speed occur among individuals. In the present paper, it was proved that synchronisation of the passage between individuals occurs not only in particular stopover sites and places of concentration of passage (Ulfstrand 1962, Dolnik and Blyumental 1967), or within migratory groups (Busse 1978), but (if the migration is intensive) also in a larger scale – of hundreds kilometres and of entire migratory seasons. As far as it is known to the author, there were no observations of such a phenomenon for so large scale. It is the most interesting that the described phenomenon occurred in the species of a partial migrant moving usually in small flocks from tree to tree, in a manner which could be regarded as rather chaotic (Ulfstrand 1962).

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