

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

Jarosław K. Nowakowski

ABSTRACT

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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 average speed 33.2 km/day, maximally – 353 km/day (however, flights with speed over 90 km/day amounted to only 1% of all movements). In contrast with hitherto existing opinions, 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, synchronisation by single individuals is stronger.

Nowakowski J. K., Dept. of Zoology, University of Podlasie, ul. Prusa 12, 08-110 Siedlce, Poland; Bird Migration Research Station, University of Gdańsk, Przebendowo, 84-210 Choczewo, Poland, E-mail: sikorka@supermedia.pl

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INTRODUCTION

One of the most frequently studied species of partial migrants is the Great Tit. 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. It is considered as an 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).

Although migration speed is relatively less investigated, it is considered as highly changeable ranging from several to over 200 km/day (Hudde 1993). None of this variability in the Great Tit has been hitherto analysed. However, it can be expected that similar to other invasive species, the speed of movements will be higher in years of more intensive migration (such a relation was shown 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 review – see Gauthreaux 1982, Smith and Nilsson 1987; for the Great Tit – 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 migration speed between males and females in partial migrants was found for the Siskin (*Carduelis spinus*) – Payevsky 1971.

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

The aim of this paper is to verify the opinion on a high variability of the migration speed of the Great Tit and an attempt to find rule, which govern it, or 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 groups in years of intensive and poor passage. It can be hoped that better recognition of this parameter of the Great Tit migration will allow also for more correct interpretation of other elements of its ecology.

STUDY AREA AND MATERIAL

The migration speed of Great Tits was calculated from ringing recoveries, *i.e.* differences between ringing and recapture data. Here, I present material from direct autumn recoveries of birds captured at 8 ringing stations located on the eastern and the southern Baltic coast (Fig. 1). Following brief description of these stations

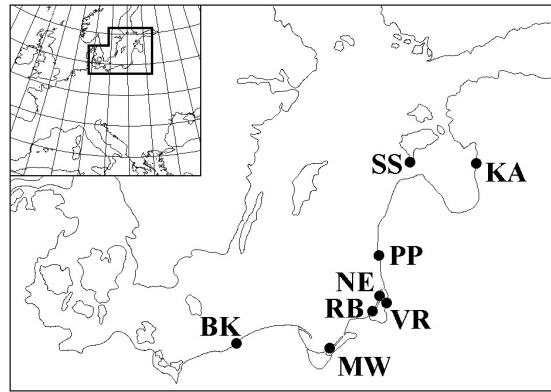


Fig. 1. Localisation of bird ringing stations from which originates the material used in the paper. BK – Bukowo-Kopań, KA – Kabli, MW – Mierzeja Wiślana, NE – Neringa, PP – Pape, RB – Rybachy, SS – Sôrve, VR – Ventes Ragas.

is given in the order of direction of autumn movement of the Great Tit – from the northeast towards southwest.

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

Kabli (58°01'N, 24°27'E) – Estonia. Trapping in modified heligoland trap. The trap is located 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 strip of young pine stands which grow on 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 located on the Courish Spit, in narrow strips of young pine plantings growing on 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. The station is located on a cape going inside the Courish Lagoon, overgrown by thickets with some willows (for more detailed description – see Jezerskas *et al.* 1994).

Rybachy (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 located in several places of the Courish Spit in young pine stands with some mixture 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 heligoland-type trap. Places of catching are located on the Vistula Spit in young pine stands and middle-aged stands mixed with oak and in red-

buds 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 located 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 locations, habitats are similar. Mist-nets were open in young pine and alder stands with mixture 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 this 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 an 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 (1971-1997), Pape (1967-1997), Neringa (1979-1997), Rybachy (1961-1965) and Mierzeja Wiślana (1961-1997).

In order to compare the migration speed of the Great Tit with that of other species, additional material was used from:

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

The data from 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 Neringa and numbers of birds caught in subsequent years at this station were kindly provided by Dr. Ricardas Patapavičius from the Lithuanian Bird Ringing Centre in Kaunas. The remaining Lithuanian and all the Estonian recoveries come from annual reports published in these countries (Kastepõld 1971, 1972, 1973, 1974, 1975; Kastepõld and Kabal 1976, 1977, 1978, 1980, 1981, 1982, 1983, 1984, 1985a, 1985b; Kumari and Jogi 1974; Patapavičius 1982, 1983, 1986a, 1986b, 1986c, 1987, 1988, 1989; Kastepõld and Kastepõld 1987a, 1987b, 1988, 1990a, 1990b, 1991, 1992, 1993, 1994; Skuodis and Kurpyt 1989). Ringing recoveries of birds ringed at Rybachy are from Payevsky (1971). Recoveries and numbers of birds caught at Pape were obtained thanks to Dr Janis Baumanis from

Table 1
Distances between stations included in this study
and the number of direct recoveries analysed

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
Sôrve	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
TOTAL			1075

the Institute of Biology in Salaspils in Latvia. Records of birds ringed in Leningrad region are from Rezvyi *et al.* (1995).

Small fragments of the material in this paper were previously analysed (data from Rybachy up to 1957 – Payevsky 1971, and data from years 1967-1975 from Pape – Rute 1976). It is likely that the material used hereby overlaps partly with Hudde (1993), however the author does not describe methods and the range of data analysis.

METHODS

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 live 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 birds were usually not aged. The sex of Great Tits was identified at all stations from the start.

The mean migration speed was calculated based 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 included. The limit of the distance was introduced because in the case of short-distance movements the pattern of birds' movements could be 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,
3. the method applied to calculate the rate of movement given at short distances results low precision.

Less than 1.9% of Great Tits moved with the average speed below 10 km/day. Probably, in majority of cases, such low migration speed suggest that in fact the bird was ringed before it begun the passage or that the ongoing passage was disrupted. Therefore, such records were also removed from the analysis.

Initially, records of Great Tits, which were ringed from 10 September onwards and then recaptured or found before 11 November 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 local birds ringed before the start of migration were not included in the analyses. However, the preliminary calculations showed that the average speed of migration of birds ringed between 10 and 14 September was significantly lower than that of the remaining birds (10-14 September – 24.0 km/day, $N = 32$; after 14 September – 33.8 km/day, $N = 1043$; U -test: $z = -3.71$, $p < 0.001$). This is striking that the mean speed of movements in any other five-day period (after 14 September) did not fall below 30.0 km/day. Moreover, Great Tits migrate in September faster than in October (see *Results*). This brings the assumption that at least some part of birds ringed before 15 September did not start the actual migration (*cf. Discussion*).

Therefore, in further analysis, only records of birds ringed after 14 September were taken into account.

In the analyses, also Great Tits recaptured or found after 10 November 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 November as critical days of start of wintering. It appeared that for dates before 10 November the mean speed fluctuated around the same mean value, and for dates after 10 November 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 September and recoveries obtained before 11 November.
2. Siskin – birds ringed from 10 September and recoveries obtained before 6 November.
3. Meadow Pipit – birds ringed from 10 September and recoveries obtained before 16 November.
4. Robin – birds ringed from 1 September and recoveries obtained before 6 November.
5. Blue Tit and Coal Tit – time frames the same as for Great Tit.

The obtained averages for some species differed from these calculated from the same material by Payevsky (1971) because of the applied limitations and selection of the material.

The level of migration intensity in the whole region in any 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, the numbers of Great Tits trapped in a given year were presented as a percent of the mean number of Great Tits caught in the 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 is an average of these values. I consider this calculation to be suitable 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 occurs (Likhachev 1957, Payevsky 1971, Rezvyi *et al.* 1995). The migration occurs on 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 numerously caught species. All this suggests 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

From amongst analysed recoveries, a group of records ($N = 62$) from Sweden and Denmark stands out. Birds going to these countries had to cover at least a part of the route over the Baltic 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 land, $N = 981$). Because it cannot be stated, which part of the route to Sweden and Denmark was crossed over the sea, in all further analyses only the recoveries of Great Tits completing the whole route over the land were taken into account.

The majority of Great Tits migrated with a speed between 15 and 45 km/day (Fig. 2). Over the land, individuals migrated with the average speed of 33.2 km/day

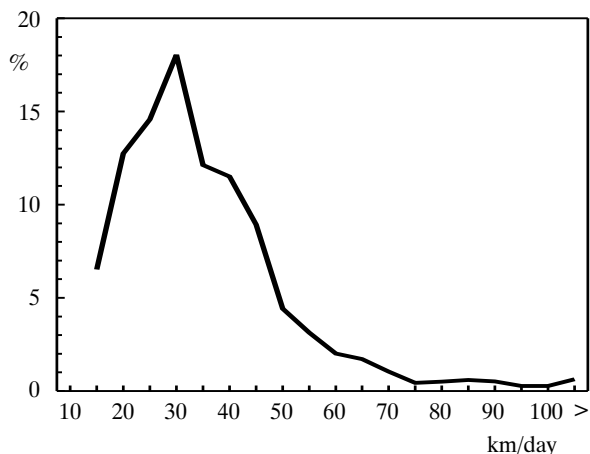


Fig. 2. Distribution of the migration speed values of Great Tits.

($N = 981$); recovered with maximum 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 speed of migration of the Great Tit was higher than of the Blue Tit and similar to the Coal Tit (Table 2). In comparison with other species of short- and medium-distance migrants of 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 fastest migrants were 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 in comparison to the other species (Fig. 3).

All observed Great Tit movements with a speed exceeding 90 km/day occurred short sections of the route (less than 400 km). The most impressive long-distance flight was by a bird ringed at Neringa and recovered 1317 km to the south in north-

ern Italy within 16 days (on average 82 km/day). However, in distances exceeding 400 km, only 1.5% ($N = 134$) of Great Tits retained the average speed of over 70 km/day, while in distances below 400 km this was 2.7% ($N = 847$).

Table 2

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

	Mean	N
<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

No significant differences were noted between birds of the different sexes (δ – 33.8 km/day, $N = 355$; ♀ – 32.9 km/day, $N = 595$; U -test: $z = -0.42$, $p = 0.676$). Birds hatched of a given cohort migrated on average 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

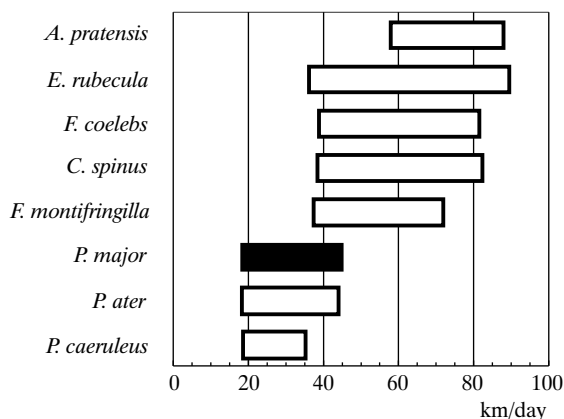


Fig. 3. Comparison of the range of speed presented on migration by Great Tit and several other small passerine short- and medium-distance migrants. Speed, within which 70% of individuals moved, is marked.

birds of different age groups seems to be the more insignificant as the general distribution of the migration speed was very similar. The proportion 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.

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	<i>N</i>	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 order to check if the migration speed is the same within all of the studied area, the passage between Kabli and Pape (293 km) was compared with the passage between Pape and Mierzeja Wiślana (231 km) and with further passage from Mierzeja Wiślana (Table 3). No significant differences were found. I also analysed the speed of migration to check if it 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 October ($N = 327$). The majority of stations ended catching about 1 November 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 October, were not taken into account. In September, Great Tits moved faster by 4.8 km/day than in October (*U*-test: $z = -3.47$, $p < 0.001$).

During the 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

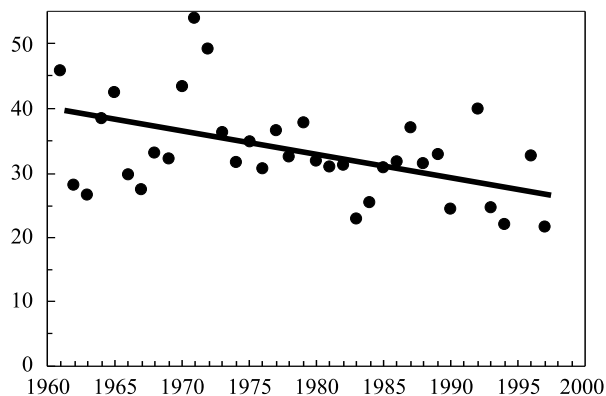


Fig. 4. Mean migration speed during the years 1961-1997

11.2 km/day, however the difference of the average speed between the 1960s and the 1990s was only 3.4 km/day. Nevertheless, migration speed fluctuated (Fig. 4) and over 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 any given year (calculated as a percent of the multi-year average – see *Methods*) and the mean migration speed in that 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 mi-

Table 4
The result of *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	$F = 0.34$	$F = 0.66$	

gration (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 migration intensity, there was an increase in the number of individuals that moved very fast and those that migrated slowly. As a result, in years of poor passage (less than 40% of the multi-year average) the proportion of individuals moving with a speed of 20-50 km/day decreased to 46.2%. In years of medium intensity of migration (40-160% of the multi-year average), the distribution of migration speed was intermediate (Fig. 5).

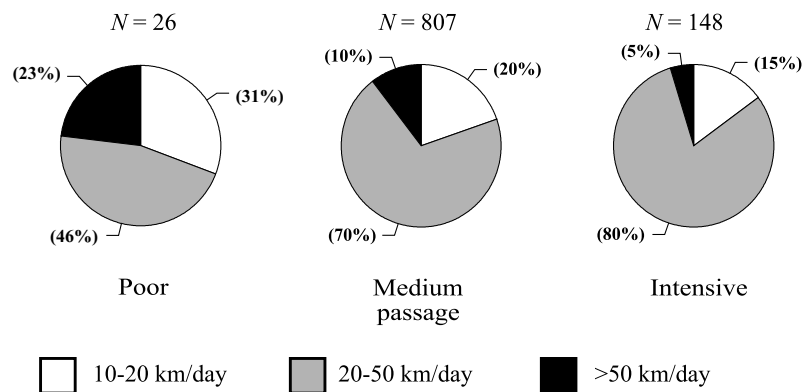


Fig. 5. Proportion of low, medium and high migration speed in years of poor (less than 40% of the multi-year average), medium (40-160%) and intensive (over 160%) passage.

DISCUSSION

Alerstam and Lindström (1990) suggested that the mean migration speed of 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 study are medium- and short-distance migrants. The mean migration speeds encountered were generally higher than those given by Alerstam and Lindström (1990), but the general tendency, according to which the species migrating further move faster, is evident – amongst the species compared in the Table 2 the furthest migrants are the Meadow Pipit, Robin and 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.* the Siskin) and with other species accomplishing migration of a similar distance (*e.g.* Siskin and Brambling – Payevsky 1971, Rezvyi *et al.* 1995). In addition, analysis of the Finnish ringing data showed that tits migrate the 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 the slowest, what concurs with Rute (1976) and Hildén and Saurola (1982). In this study, only 16 recoveries of the Coal Tit were analysed, thus the results (Table 2) should be treated with caution. Similarly, Hildén and Saurola (1982) showed that Coal Tits migrate on average more than twice as fast as Great Tits, but they too had a small sample at their disposal ($N = 12$). The migration speed of the Coal Tit and the Great Tit was compared on the basis of the data that came from Pape (Rute 1976) and, because of recalculation, can be directly compared with results obtained in this study for the Great Tit. It appears that also in this case, Coal Tits migrated 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 double that of 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, based on Payevsky (1971), it can be proved that in years of a very intensive migration, Siskins move by 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 should be expected. To conclude, in years of normal or 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. As shown here, there was no relation between the intensity of migration and the speed of movements of individuals for Great Tit. It is

additional (after papers by Nikander 1984, Croon *et al.* 1985, Vähätalo 1996) proof 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 at speeds of 15-45 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 further 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 the Swedish coast with speeds exceeding 80 km/hour (Alerstam 1993)! The passage over the sea is in general connected with an increase of the migration speed as was shown in other species, as well (Biebach *et al.* 2000).

The migration speed of 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 ($N = 29$, after data of Rezyvi *et al.* 1995) and corresponding with that calculated here (33 km/day). Only in Finland, the result was markedly different from presented here – 11-15 km/day (Hildén and Saurola 1982). However, it should be taken into account that Hildén and Saurola took into consideration also short-distances movements (up to 50 km) and with a very low speed (from 5 km/day), which probably does not reflect actual migration. It should be borne in mind that among only 55 cases analysed by them, some were birds moving at a speed exceeding 33 km/day (the mean migration speed noted in the present paper). This allows one to conclude that Finnish Great Tits do not differ 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 face a geographical barrier in the form 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, and contradicts the hypothesis of Hudde (1993) that the migration speed of the Great Tit decreases from the north to the south (the author neither presented his own detailed data nor other sources of the formulated hypothesis).

Here, 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 found (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 inclusion of early September records in the calculations. As it was emphasised in *Methods*, such records include the most probably individuals, which did not start a real migration yet. However, the occurrence of not ringed earlier, slowly moving Great Tits in September in the area of the migration indicated that the migration was preceded by some movements, most probably summer dispersal. On the other hand, the difference shown between the results by Hudde (1993) and those presented here, shows how important and difficult it is to determine correctly the beginning of migration in species that start their passage in the study area (compare with Nowakowski 1999).

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

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

The above topics require further study.

Decrease of the migration speed during almost 40 years covered by the study can be associated with an increase of proportion 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 fluctuations are not known, thus we cannot foresee if the general decreasing trend will not be reversed in the future.

The decrease in the proportion of birds moving fast or slow with the intensity of migration (Fig. 5) is a very interesting phenomenon. This means that most probably the slow 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 of the migration and speed of their movements not only in the effect of genetic or physiological factors (such as fat score), but also

under the influence of con-specifics (e.g. Dolnik and Blyumental 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. Here, 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 of kilometres and over entire migratory seasons. As far as I know, there are no observations of such a phenomenon for such a 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 by some authors (e.g. Ulfstrand 1962) as rather chaotic.

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