IS THE GREAT TIT *PARUS MAJOR* AN IRRUPTIVE MIGRANT IN NORTH-EAST EUROPE?

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Trapping data from six ringing stations on the east coast of the Baltic Sea were used to study fluctuations in the numbers of migrating Great Tits *Parus major*. In the years 1971-97, the number of autumn migrating Great Tits was typically found to fluctuate less than those of partial migrants, but similarly to those of obligatory migrants at Hanko (Finland), Kabli (Estonia) and Neringa (Lithuania). The numbers of Great Tits at Mierzeja Wiślana (Poland) fluctuated more than those at the northern stations but far less than numbers among irruptive species. We found no significant correlation between the intensity of migration and: the share of young birds, the share of males and the distance between wintering grounds and ringing stations. Nor were the numbers of migrating Great Tits found to correlate significantly with the crop of beechnuts in the species' wintering area the preceding autumn. We also compared data gathered over 20 years concerning the breeding populations of 20 bird species in Białowieża National Park, eastern Poland. Numbers of breeding Great Tits were stable (like those of obligatory migrants), in contrast with the strongly fluctuating irruptive populations of Coal Tits *Parus ater* and Great Spotted Woodpeckers *Dendrocopos major*. Overall, the results indicate that Great Tits behave like regular partial migrants, with the migration in northern and eastern Europe not being affected by the crop of beechnuts in the wintering area.

Key words: *Parus major* - migration - irruption - *Fagus sylvatica*

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INTRODUCTION

Textbooks have presented the Great Tit *Parus major* as a model example of an irruptive migrant showing large year-to-year fluctuations in the intensity of migration (Alerstam 1993; Berthold 1993; Hudde 1993). In some autumns Great Tits have migrated in massive numbers in Western Europe (Switzerland - Winkler 1974; The Netherlands – van Balen & Speek 1976; van Balen & Hage 1989; Lensink 1990; Great Britain - Cramp *et al.* 1960; Cramp 1963; Sweden - Ulfstrand 1962 and Germany - Berndt & Henss 1967). Ringing recoveries show that irruptive Great Tits found in The Netherlands and Great Britain have originated from Germany, northern Poland and the Baltic countries (Cramp 1963; Busse & Gromadzki 1966; Payevsky 1971; van Balen & Speek 1976). Unfortunately, autumnal fluctuations in the intensity of migration in Great Tits have been only poorly described in Eastern Europe. Hudde (1993) claimed that Great Tits migrated along the south-eastern Baltic Sea coast in huge numbers in some autumns. At the Ladoga Ornithological Station (St. Petersburg region - NW Russia), the autumnal totals of Great Tits ranged from 88 to 1298 during 14 years of catching, which suggests high fluctuations (Bojarinova *et al.* 2002). Some other papers, on the other hand, have questioned the great variation in the intensity of migration in Central and Eastern Europe (Nikander 1984; Croon *et al.* 1985; Vähätalo 1996).

Explanations of irruptive migrations in birds are based around changes in mortality and changes in food availability. Berthold (1993) pointed out that, as tits (Paridae) have a high natural breeding potential normally balanced by high mortality, low mortality, for whatever reason, may result in numbers of tits being so high that an irruption has to take place. Large annual changes in food supply have also been invoked to explain irruptions in species depending upon one type of food (Shelford 1945). For Great tits such a wintertime food is the beechnut produced by the Beech *Fagus sylvatica* (Ulfstrand 1962; Perrins 1966; Lindholm 1978; Alerstam 1993; Gosler 1993). A good supply of beechnuts has been found to increase wintertime survival of Great Tits, and the breeding population density in the next spring (Perrins 1965; Perdeck *et al.* 2000). A high breeding density can in turn be followed by intensive migration in the next autumn (Berndt & Henss 1967; Alerstam 1993). Such a mechanism causing irruptive migration has also been demonstrated for several species from Northern America, including the Black-capped Chickadee *Parus atricapillus* (Koening & Knops 2001). Alerstam (1993) and Hudde (1993) assumed that the above mechanism (large beech crop – high breeding population – intensive migration) explains irruptive migration for Great Tits population breeding both in the beech forest zone, as well as those wintering there but breeding north of the beech forest zone. This assumption seems logical, although we have failed to find direct evidence in the literature that this model indeed applies to populations breeding outside the beech forest zone.

In this paper we describe trapping data from ringing stations and the effects of beechnut crops to address three questions: (1) Is the Great Tit an irruptive or a regular partial migrant on the east coast of the Baltic Sea, outside the area of beech forests?; (2) Can the crop of beechnuts in the wintering area influence the intensity of migration of Great Tits outside the beech forest zone?; and (3) Do populations of the Great Tit breeding outside the beech forest area show fluctuations typical for irruptive species?

METHODS

Data were collected at 6 ringing stations on the east coast of the Baltic Sea beyond the continuous range of beech forests (Fig.1). At Hanko (1980-96; 59º49'N, 22º54'E) and Mierzeja Wiślana (1963-97; 54º21'N, 19º19'E) birds were caught with mist-nets; while at Kabli (1971-97; 58º01'N, 24º27'E), Neringa (1963-97; 55º27'N, 21º04'E) Ventes Ragas (1963-97; 55º21'N, 21º12'E) and Rybachy (1963-97; 55º09'N, 20º52'E), Heligoland traps were used. Data from Pape (56º11'N, 21º03'E) were also included to calculate the mean intensity of Great Tit migration between Estonia and Poland. Although the stations are located outside the beech forest zone (Fig. 1), Great Tits migrating through stations other than Hanko have been shown to winter in the beech forests of Western Pomerania and in the Gdańsk region

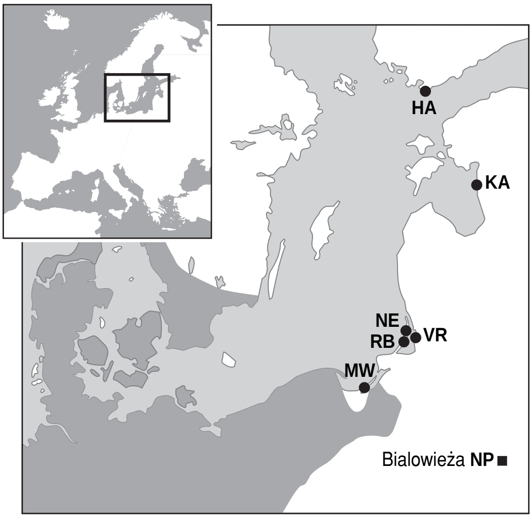

Fig. 1. Studied bird ringing stations, monitoring area in Białowieża National Park and range of beech forests shown with grey colour. HA – Hanko, KA – Kabli, NE – Neringa, VR – Ventes Ragas, RB – Rybachy, MW – Mierzeja Wiślana.

(Busse & Gromadzki 1966; Payevsky 1971; van Balen & Speek 1976; Hudde 1993; Polish Bird Ringing Centre, *unpubl. data*).

A detailed description of the habitats and trapping methods at each station can be found in Leivits (1998), Busse (2000), Lehikoinen & Vähätalo (2000) and Nowakowski (2001). Birds were trapped with 12 standard nets at Hanko and trees and bushes surrounding the nets were cut to stable dimensions. The number of mist-nets varied from 40 to 89 at Mierzeja Wiślana. At this station, the numbers of birds caught were calculated per net for the purpose of data analysis. At Kabli and Neringa, the construction and placement of Heligoland traps was modified from time to time, such that the data from these stations should be treated with caution.

The South East European Bird Migration Network (SEEN) provided trapping numbers and direct ringing recoveries from the wintering period (15 Nov-29 Feb) of Great Tits ringed at Mierzeja Wiślana (1963-97) and Neringa (1989-97). The remaining recoveries from Neringa and all recoveries from Ventes Ragas were taken from Patapavičius (1982; 1983; 1986a; 1986b; 1986c; 1987; 1988; 1989) and Skuodis & Kurpyté (1989). The recoveries for Rybachy originated from Bolshakov *et al.* (1999; 2001). All types of analyses were done for all species and all seasons from which material was published or rendered accessible to us. Data on the proportion of fruiting Beech trees in north-western Poland were taken from systematic monitoring conducted by the Polish Forestry Research Institute (unpublished data). Data for the analysis of breeding densities originated from studies by Tomiałojć *et al.* (1984) and Tomiałojć & Wesołowski (1994; 1996), having been gathered in a standard monitoring area (187.5 ha) in Białowieża National Park in the years 1975-94. This area encompasses various forms of primeval deciduous and coniferous forests (three main types: with a prevalence of oaks *Quercus sp.* and lime *Tilia cordata* or alder *Alnus glutinosa* and ash *Fraxinus excelsior* or Scots Pine *Pinus sylvestris* and Norway Spruce *Picea abies* – for a detailed description of the methods and study area see Tomiałojć *et al.* 1984). Ringing recoveries confirm that part of the Great Tit population from the vicinity of Białowieża NP winters in the beech forest zone of south-western Poland and southern Germany – the eastern limit of which lies some 350 km away (Polish Bird Ringing Centre – unpublished data).

Analytical methods

The number of trapped birds in each year was normalised with the mean for the studied period (as a percentage of the mean: X). Annual fluctuations in the numbers of birds were described by reference to a fluctuation index (FI) modified from Busse (1994):

(1) $FI = \Sigma (X_y - X_{oy})^2 n^{-1}$

where X_y is the number of birds caught in year y, X_{oy} is a seven-year moving average for the same year and n the number of years in the study period. X_{oy} was obtained from:

(2) $X_{oy} = (X_{y-3} + X_{y-2} + X_{y-1} + X_y + X_{y+1} + X_{y+2} + X_{y+3})/7$

Values of the moving average (X_{oy}) for the three first and three last years of the study periods were calculated for six, five and four years, respectively (Busse 1994). The fluctuation index was calculated for birds trapped between 1 July and 30 November at Hanko and for the period between 17 August and 25 October at Mierzeja Wiślana. For the remaining stations, the data included all individuals caught in the autumns studied. The fluctuation index was calculated only for those species whose mean autumnal numbers of captured birds exceeded seven. Fluctuation index values for breeding populations in Białowieża National Park were obtained from the same formulas with the number of breeding pairs in the monitoring area. In examining the relationship between the crop of beechnuts and the intensity of migration, the percentage of fruiting beech trees in Western Pomerania and in the Gdańsk region were (Spearman rank) correlated with the number of migrating Great Tits (at each station and in the region) and also with the change in the numbers of migrating Great Tits for year y (Z_y), as obtained from:

$$(3)\ Z_y = (X_{y-1} - X_y)/ X_{y-1}$$

where X_y is the number of birds caught in year y, and X_{y-1} the number of birds caught in the preceding year. A given year's intensity of Great Tit migration in the region between Estonia and Poland (IMR_y) was calculated as the mean number of birds caught at the six stations situated there (including Pape), in line with the formula:

$$(4)\ IMR_y = \Sigma\,(X_{zy}/ x_z)\ l^{-1}$$

where X_{zy} is the number of birds caught at station z in year y, x_z the mean number of Great Tits caught yearly at station z and l the number of stations taken into account in the analysis (for details of method – see Nowakowski 2002, 2003).

Terminology

In this paper, definitions from Terrill & Able (1988) are followed in assigning birds as either 'obligate migrants' (in that all individuals of a population migrate) or 'partial migrants' (in that the same population has some individuals that migrate while the remainder are resident). The term 'regular partial migrants' (where a more or less stable proportion of birds migrates every year) is used to refer to the populations of partial migrants for which the intensity of migration fluctuates from year to year to a similar extent as is noted with obligate migrants. For the populations in which the year-to-year changes in migration intensity are much larger than in the case of obligate migrants (probably in that the proportion of migrating individuals fluctuates strongly), the term applied is 'irregular partial migrant'. Where irregular partial migrants have fluctuations in migration intensity several times greater than the maximum recorded for the obligate migrants the term 'irruptive migrant' is applied. This same meaning has been conferred upon the term by other authors (e.g. Alerstam 1993; Bertholt 1993). As different populations of the same species may be representative for all these different types of migration, the *a priori* assignment to them of species caught at the described stations is not possible. In recognition of this, all the migrants were divided into the two groups: wintering outside (WO) or wintering within (WW) the study area (see Fig. 2). Membership of the first group is confined to obligate migrants whose winter quarters are situated outside the study area. Fluctuations of migration intensity here reflect changes in autumnal densities only (as we observe migration of whole population). When it comes to the species in the second group, those wintering within the study area, observed changes in migration intensity

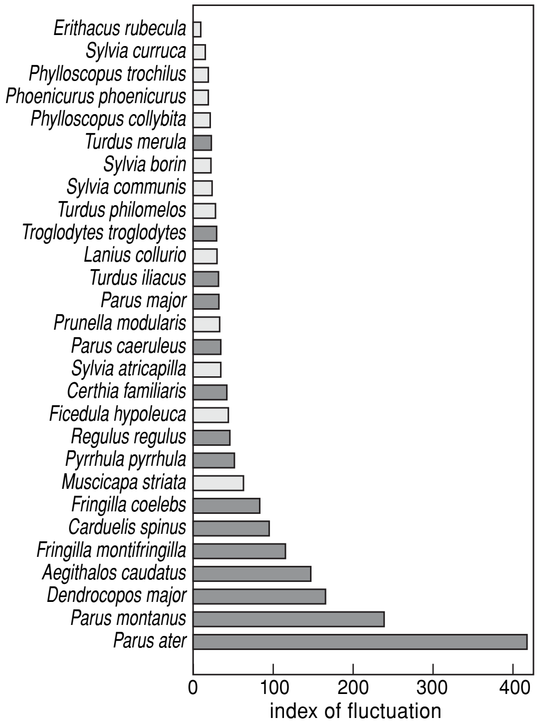

Fig. 2. Mean fluctuation indices for 28 species of migrants at Hanko (Finland), Kabli (Estonia), Neringa (Lithuania) and Mierzeja Wiślana (Poland) in the years 1980-96. Means were calculated for 2-4 stations depending on available dataset (Appendix 1).
Dark grey bars: species wintering within study area; light grey bars: migrants wintering outside study area.

may be (though not necessarily are) influenced by other factors, like the proportion of non-migrants and/or the distance over which migration takes place in a given year. Included into this category were all partial migrants, along with those obligate migrants whose winter quarters are situated within the study area.

RESULTS

Fluctuations in the intensity of autumnal migration

In order to define whether the Great Tit is an irruptive migrant (demonstrating large year-to-year changes in numbers) on the east coast of the Baltic Sea, we compared the fluctuation indices (FI, Eq. 1) obtained for 27 species of passerines and the Great Spotted Woodpecker *Dendrocopos major* in the autumns 1980-96. At three stations (Hanko, Kabli, Neringa), fluctuation indices were typically lower for the Great Tit than for migrants wintering outside the study area (Table 1, Appendix 1, Fig. 2). At the southernmost station (Mierzeja Wiślana), fluctuation index was higher for the Great Tit than for migrants wintering outside the study area, but still lower than for the majority of migrants wintering within the study area (Table 1, Appendix 1). An extension of the study period by ten years (1971-97) did not change the fluctuation index considerably at the Kabli and Mierzeja Wiślana stations (Table 1, Appendix 1). The fluctuation index was several times lower for the Great Tit than for species with the highest fluctuation index values (capable of being considered irruptive migrants), such as the Coal Tit *Parus ater*, the Willow Tit *Parus montanus*, the Great Spotted Woodpecker and the Long-tailed Tit *Aegithalos caudatus* (Fig. 2, Appendix 1). In these species, trapping numbers could be very high in a given autumn, only to decrease again to low numbers in the following autumn (very high numbers of birds were present for as short a duration as one year). This was the case for the Great Spotted Woodpecker and Coal Tit, as can be seen in Figure 3D. However, such a phenomenon was not noted for the Great Tit (Fig. 3C), in which increases in number could last for several years – as with migrants wintering outside the study area (Fig. 3A & B). The curve presenting the multi-year dynamics to numbers of Great Tits resembled those for species wintering outside the study area with greatest year-to-year fluctuations in migration intensity (Fig. 3B).

Table 1. Fluctuation indices (Eq. 1) for the Great Tit and migrants wintering outside (WO) or within (WW) the study area. For the migrants, the mean fluctuation index and range of values are given, as well as the number of studied species.

Station	Great Tit	WO migrants* Mean (min-max, n)	WW migrants* Mean (min-max, n)
Autumns 1980-96			
Hanko	16	18 (8-53, 17)	74 (10-226, 10)
Kabli	11	33 (8-60, 8)	107 (21-244, 10)
Neringa	22	47 (10-125, 7)	137 (25-657, 12)
Mierzeja Wiślana	70	24 (5-66, 13)	136 (13-540, 14)
Autumns 1971-97			
Kabli	17	32 (9-67, 8)	135 (19-376, 10)
Mierzeja Wiślana	69	30 (7-90, 13)	147 (15-650, 14)

*species-specific indices in Appendix 1.

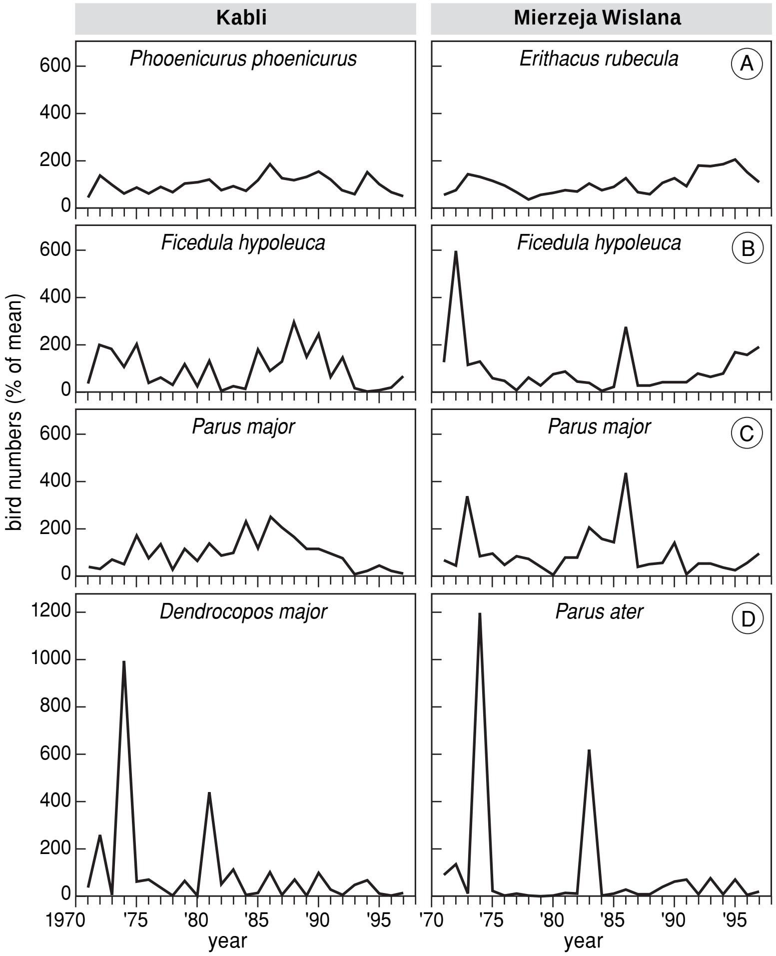

Fig. 3. Autumnal dynamics of selected species in the years 1971-97 (n = 27 years) at Kabli and Mierzeja Wiślana. Autumnal numbers of birds are presented as percentages of the mean numbers caught in the years 1971-97. A: species with the lowest fluctuation index; B: species with the highest fluctuation index among migrants wintering within the study area; C: Great Tit; D: species with the highest fluctuation index (irruptive migrants).

Sex-age composition and the distance covered by Great Tits in autumns of different intensities of migration

A relationship between the intensity of migration in the Great Tit and other parameters involving it was tested for. Such a relationship can be expected in irruptive species (see Discussion). In the area extending from Estonia to north-eastern Poland, the measured intensity of migration in the Great Tit (IMR – Eq. 4) was found to have fluctuated in the period 1963-97, between 27% and 231% of the mean noted from this period. During this period, the median distance of recoveries between ringing stations (including Neringa, Ventes Ragas, Rybachy and Mierzeja Wiślana) and the wintering area was of 587.5 km (n = 312). The distance to winter quarters did not correlate significantly with the intensity of migration in the region (Spearman rank correlation, r_s = -0.08, P = 0.148).

The years 1980-96 saw 8957 Great Tits sexed and aged at Hanko (with 87% being young birds and 37% males). In this period, the proportion of young birds fluctuated from 76% to 93%, though these changes did not correlate with migration intensity at the station (r_s = 0.32, n = 17, P = 0.218). Nor was the share of males correlated with migration intensity (min = 30%, max = 44%, r_s = 0.24, n =17, P = 0.363). In turn, at Mierzeja Wiślana in the period 1984-97, the sex and age of 12405 Great Tits were determined (with 90% being young birds and 41% males). In this case too, neither the percentage of young birds (min = 84%, max = 96%, n = 14) nor the proportion of males (min = 30%, max = 50%, n = 14) were found to correlate significantly with the migration intensity in the region (for age – r_s = 0.50, P = 0.069; for gender – r_s = 0.49, P = 0.072).

The influence of the crop of beechnuts on the intensity of migration in Great Tits the following year

We tested the hypothesis that a good crop of beechnuts in the Great Tit wintering grounds triggers an irruption of the species' population in the following autumn. The expectation was that, after a good crop of beechnuts, the intensity of migrations should be the highest (or at least higher than in the preceding autumn). However, in contrast to what had been hypothesised, the intensity of migration in Great Tits in the whole region (IMR) extending from Estonia to north-eastern Poland (the Kabli, Neringa, Ventes Ragas, Rybachy and Mierzeja Wiślana stations taken together) did not correlate significantly with the crop of beechnuts in the preceding year in Western Pomerania and the Gdańsk region (r_s = –0.18, n = 35, P = 0.288). Moreover, the crop of beechnuts in the wintering grounds did not correlate significantly with the change in the intensity of migration (Z_y, Eq. 3) from the autumn of a good crop to the following autumn (r_s = –0.13, n = 34, P = 0.456). However, as stations are located at different distances from the beech forest zone (Table 2), it is possible to advance a hypothesis holding the abundance of beechnuts in the winter quarters to exercise a stronger influence on data for stations closest to these wintering grounds. The obtained results did not confirm this presumption, however, as the crop of beechnuts did not correlate significantly with the intensity of migration (Table 2), nor with the change in the intensity of migration in relation to the preceding year (Table 3) at any of the stations. The values of correlation coefficients calculated for particular stations were not related to the distances of these stations from wintering grounds with beech forests (Table 2 & 3).

Table 2. Correlation between autumnal beech crop in wintering grounds and number of migrating Great Tits the following autumn. Beech crop: proportion of fruiting trees in the Gdańsk Region and Western Pomerania in the autumns 1962-96.
F = approximate distance to the beech forest zone [km], n = number of years, r_S = Spearman's correlation coefficient, P = statistical probability

Station	F	n	r_S	P
Kabli	500	27	-0.20	0.326
Neringa	130	19	-0.05	0.836
Ventes Ragas	125	18	-0.12	0.639
Rybachy	100	33	0.31	0.078
Mierzeja Wiślana	50	35	-0.30	0.080

Table 3. Correlation between autumnal beech crop on wintering grounds and the change in the numbers of migrating Great Tits from the autumn of beech crop determination to the following autumn. For explanation see Table 2.

Station	n	r_S	P
Kabli	26	-0.03	0.888
Neringa	18	0.15	0.559
Ventes Ragas	17	-0.06	0.830
Rybachy	33	-0.13	0.480
Mierzeja Wiślana	34	-0.11	0.552

Fluctuations of breeding population

We compared fluctuation indices for breeding populations of 19 species of passerine and the Great Spotted Woodpecker in Białowieża National Park in the years 1975-94. The fluctuation index for the Great Tit was 1.9, while those for 13 WO species ranged from 0.5 for the

Chaffinch *Fringilla coelebs* to 6.6 for the Wood Warbler *Phylloscopus sibilatrix*, with an average of 3.26 (Annex 2). For six species wintering within the study area, fluctuation index values ranged from 1.9 for the Wren *Troglodytes troglodytes* to 12.8 for the Coal Tit (i.e. to a value 6.7 times greater than that noted for the Great Tit), with the average being 6.85 (Appendix 2).

DISCUSSION

The Great Tits trapped at the studied stations behaved like regular partial migrants, with multi-year fluctuations in numbers being similar to those for obligatory migrants. Is the same true for other Great Tits outside the beech forest zone in Northern and Eastern Europe? To answer this question, we calculated the fluctuation index for the Great Tit and Coal Tit on the basis of ringing data collected over a decade at Ottenby (56º12'N, 16º24'E, 1947-56, SE Sweden; Edelstam 1972) and Höytiäinen (62º37'N, 29º41'E, 1985-94, Eastern Finland; Latja 1995). At both stations, the fluctuation index value for the Great Tit was only just over a quarter as high as that obtained for the Coal Tit: a result that was in agreement with the present study's findings. During a 25-year study at Lebedivka near Kiev (Ukraine), the numbers of trapped Great Tits fluctuated little, and at the level noted for other regular migrants (Anatoly Poluda, *pers. comm.*). Autumnal fluctuations in the numbers of Great Tits at Falsterbo (Sweden, 55º22'N, 12º52'E), which is located ca 150 km inside the beech forest zone (Ulfstrand 1962; Alerstam 1993), have previously been related to the variation in the crop of beechnuts. We thus calculated the fluctuation index for the birds ringed at Falsterbo in the period 1964-80 (Roos 1984), and found it to be 25 in the case of the Great Tit, i.e. somewhat higher than the 15 and 13 noted for the Robin *Erithacus rubecula* and Common Redstart *Phoenicurus phoenicurus* respectively, but lower than the value obtained for the Dunnock *Prunella modularis* (FI = 42). The fluctuation index was many times greater in the Coal Tit (FI = 560), the Siskin *Carduelis spinus* (FI = 441) and the Long-tailed Tit (FI = 258). These fluctuation indices show that the numbers of Great Tits in southern Sweden varied less than those of irruptive migrants. Thus the results of our work and that for four other stations indicate that the Great Tit is a regular partial migrant over a large geographical region of Northern and Eastern Europe outside the range of the Beech, and even in the area in which migrants enter the zone.

Irruptive migrants have been shown to migrate longer distances (Berthold 1993) at higher speed (as in the Coal Tit – Rute 1976) during irruptions than in non-irruptive years. Irruptions of tits consist almost exclusively of young birds. Willow Tit irruptions at Rybachy have involved young birds, while in Coal Tits the proportion of young ranges from 94% to 99.9% (Markovets & Sokolov 2002). In the present study, ringing recoveries did not suggest prolonged migration in the autumns with the highest numbers of Great Tits. In these autumns, the speed of migration did not differ from that found in the other years either (Nowakowski 2001). As sex-age composition was also not correlated with the intensity of migration, the results for ringing recoveries and sex-age composition can not be said to confirm any attributes of irruptive species in the case of the Great Tits studied.

Nor did our data support the hypothesis that the crop of beechnuts in the wintering grounds one year before affects the migration of Great Tits in the following autumn. The results of correlation analyses suggest that, when the beechnut crop in the wintering grounds was abundant, this neither triggered a Great Tit irruption in the following year (Table 2) nor even increased the numbers migrating at the given stations studied (Table 3). The results of studies from the beech forest area show, however, clearly that the abundance of beechnuts does fundamentally affect winter survival in Great Tits, be these young or adults (Perdeck *et al.* 2000). In the light of this, one might ask why this influence on winter survival did not have knock-on effects on the intensity of migration in north-eastern Europe. Three possible explanations could be considered: (1) that, for various reasons, the abundant beechnut crop in the winter quarters does not cause any increase in the breeding population of Great Tits in north-eastern Europe; (2) that the abundance of beechnuts in the wintering area does affect the density of the breeding population in North-eastern Europe, but this is not followed by higher overall reproductive success and hence a high autumnal density to the Great Tit population; and (3) that the intensity of migration in the Great Tit is in any case independent of the autumnal density of the species' population.

We found that the breeding population of the Great Tit in Białowieża NP is stable, in contrast to those of the irruptive Coal Tit and Great Spotted Woodpecker. On the other hand, earlier work had shown that breeding densities in the Great Tit do affect the intensity of their migration (e.g. Berndt & Henss 1967; Alerstam 1993). When it comes to the irruptive species of tit (the Willow and Coal Tit), there is evidence of massive movements being very much induced by autumnal population densities (Markovets & Sokolov 2002). In the light of this, only the first possibility (that the abundance of beechnuts in the wintering area does not result in an increase in the Great Tit breeding population in Northern and Eastern Europe) can accurately account for both our results and those of other authors. In Northern and Eastern Europe most (over 75%) of the Great Tits are sedentary or involved in shifts over small distances into human settlements (Snow 1952; Likhachev 1957; Ulfstrand 1962; Hudde 1993). Among those migrating, only part reach beech forests. For this reason, better or worse survival among the latter fraction has only a marginal influence on the overall size of the breeding population in Northern and Eastern Europe.

Recoveries involving birds ringed in the North and recorded next during the breeding season in the area of the winter quarters in central Europe (Bolshakov *et al.* 2001; Polish Bird Ringing Centre *unpubl. data*) indicate that Great Tits may breed in their (former) wintering area. Kvist *et al.* (1999) state that breeding populations of the Great Tit are genetically much the same all over Europe, a fact which may also be indicative of continuous mixing of the populations. If a large beechnut crop attracts migrating Great Tits to breed in their wintering area, the breeding population may even decline slightly in the north of Europe after years with such a crop. In contrast with what was found in this study, the regions located deep inside the range of beech forests may witness great fluctuations in numbers of migrating Great Tits (Winkler 1974; Lensink 1990). In these areas, the crop of beechnuts can directly regulate the migratory behaviour of the Great Tit during the autumn migration, the more so as the additional amount of food increases survival across the whole population, not only that of the migrating fraction. An abundant crop of beechnuts may prevent the migration of Great Tits or put an early stop to migration. In contrast, a poor crop of beechnuts may trigger irruptive behaviour or result in prolonged migration (Ulfstrand 1962; Perrins 1966; van Balen & Hage 1989; Hudde 1993).

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SAMENVATTING

In West-Europa zijn er najaren waarin Koolmezen *Parus major* opeens massaal kunnen wegtrekken als gevolg van een hoge populatiedichtheid en een laag voedselaanbod. Er is wel gesuggereerd dat Koolmezen in Noordoost-Europa ook een dergelijk invasieachtig trekgedrag vertonen. In dit artikel wordt met de vangsten van zes ringstations in het Baltische gebied onderzocht of Koolmezen hier inderdaad zulke invasies laten zien, of dat zij hier meer een ‘normaal’ trekgedrag vertonen. Het aantal Koolmezen dat in het najaar op deze ringstations wordt gevangen, blijkt niet sterker te variëren dan de meeste soorten met een regelmatig trekpatroon en veel minder dan echte invasiegasten zoals Zwarte Mees *Parus ater*, Matkop *P. montanus*, Staartmees *Aegithalos caudatus* en Grote Bonte Specht *Dendrocopus major*. Tijdens de trek werden vooral jonge vogels (*ca*. 90%) en vrouwtjes (*ca*. 60%) gevangen, maar het percentage jonge vogels en vrouwen was niet gecorreleerd met de totale trekintensiteit in het najaar. De trekkende Koolmezen overwinteren vooral in zuidelijker gelegen gebieden met veel beuken, maar in tegenstelling tot de situatie in West-Europa was het aantal trekkers niet gerelateerd aan de hoeveel beukennoten in de voorafgaande winter. Dit is opmerkelijk, want men zou verwachten dat de overleving van de trekvogels hoog zou zijn wanneer er veel beukennoten zijn en als gevolg hiervan er in het daaropvolgende jaar veel mezen zijn. De auteurs wijzen er echter op dat de Koolmees in Noordoost-Europa weliswaar een regelmatige trekvogel is, maar dat slechts een beperkt deel van de populatie werkelijk trekt. Hierdoor zal de voedselsituatie in het overwinteringsgebied slechts zeer beperkt de totale broedpopulatie bepalen. De conclusie dat Koolmezen in het Baltische gebied regelmatige trekvogels zijn, lijkt, in tegenstelling tot suggesties van andere onderzoekers, ook op te gaan voor Scandinavië. (CB)

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Appendix 1.
Fluctuation indices (Eq. 1) for the studied species and the mean number of individuals caught in an autumn with range values (in brackets). Migrants wintering within the study area (WW) in **bold**.

Species	1980-1996				1971-1997	
	Hanko	Kabli	Neringa	M. Wiślana	Kabli	M. Wiślana
Robin *Erithacus rubecula*	11 (226; 83-457)	9 (299; 89-538)	10 (185; 55-318)	5 (1494; 718-2772)	11 (247; 89-538)	7 (1368; 396-2772)
Lesser Whitethroat *Sylvia curruca*	14 (88; 45-135)	-	-	15 (18; 4-36)	-	21 (21; 4-57)
Willow Warbler *Phylloscopus trochilus*	15 (679; 273-1193)	-	17 (122; 5-461)	18 (258; 66-481)	-	16 (274; 66-514)
Redstart *Phoenicurus phoenicurus*	9 (37; 17-68)	8 (23; 12-39)	33 (14; 1-33)	19 (109; 26-235)	9 (21; 11-39)	17 (118; 26-256)
Chiffchaff *Phylloscopus collybita*	21 (35; 9-73)	-	22 (25; 9-71)	17 (34; 8-64)	-	18 (44; 8-107)
Blackbird *Turdus merula*	14 (15; 5-30)	**21 (52; 13-127)**	**29 (13; 0-40)**	**22 (84; 19-197)**	**19 (47; 13-127)**	**33 (89; 9-255)**
Garden Warbler *Sylvia borin*	17 (177; 51-392)	-	-	26 (59; 10-128)	-	25 (68; 10-160)
Common Whitethroat *Sylvia communis*	28 (20; 5-44)	-	-	18 (13; 4-26)	-	30 (11; 1-26)
Songthrush *Turdus philomelos*	14 (30; 9-78)	16 (30; 11-64)	59 (40; 3-153)	22 (155; 46-403)	21 (31; 9-67)	21 (164; 32-403)
Wren *Troglodytes troglodytes*	9 (18; 2-47)	54 (51; 3-209)	**39 (15; 4-45)**	**13 (46; 16-78)**	67 (39; 3-209)	**15 (40; 14-78)**
Red-backed Shrike *Lanius collurio*	32 (10; 1-29)	-	-	25 (11; 2-22)	-	30 (9; 1-22)
Redwing *Turdus iliacus*	18 (16; 3-32)	**33 (27; 6-75)**	-	**40 (15; 0-45)**	**27 (27; 6-75)**	**40 (20; 0-78)**
Great Tit *Parus major*	**16 (888; 324-1610)**	**11 (4227; 736-9616)**	**22 (3535; 785-9432)**	**70 (965; 209-4233)**	**17 (3718; 727-9616)**	**69 (1119; 209-4754)**
Dunnock *Prunella modularis*	53 (22; 3-84)	17 (33; 0-73)	-	24 (17; 5-39)	31 (22; 0-73)	37 (17; 0-49)
Blue Tit *Parus caeruleus*	**10 (1351; 38-3332)**	**26 (1980; 522-5211)**	**30 (2102; 95-6207)**	**61 (650; 16-2045)**	**31 (1529; 359-5211)**	**71 (749; 16-3059)**
Blackcap *Sylvia atricapilla*	23 (39; 10-96)	-	60 (18; 1-101)	17 (130; 12-245)	-	13 (133; 12-245)
Treecreeper *Certhia familiaris*	**36 (63; 12-145)**	**41 (278; 56-783)**	**36 (22; 2-45)**	**45 (36; 5-135)**	**46 (240; 8-783)**	**43 (40; 5-135)**
Pied Flycatcher *Ficedula hypoleuca*	8 (53; 24-82)	50 (12; 0-38)	-	66 (38; 7-139)	42 (12; 0-38)	90 (50; 7-299)
Goldcrest *Regulus regulus*	**39 (783; 114-2267)**	**64 (5348; 837-16951)**	**25 (1425; 217-3410)**	**46 (6257; 1147-21784)**	**103 (4141; 187-16951)**	**42 (6912; 1147-21784)**
Bullfinch *Pyrrhula pyrrhula*	**26 (25; 3-49)**	-	**86 (48; 4-171)**	**36 (22; 0-83)**	-	**48 (28; 0-106)**
Spotted Flycatcher *Muscicapa striata*	15 (45; 11-91)	60 (16; 1-62)	125 (9; 0-40)	46 (22; 5-64)	34 (26; 1-75)	65 (35; 5-197)
Chaffinch *Fringilla coelebs*	11 (155; 53-313)	50 (12; 0-38)	**173 (27; 0-168)**	**93 (73; 13-323)**	42 (12; 0-38)	**63 (75 13-323)**
Siskin *Carduelis spinus*	**14 (121; 31-232)**	**187 (724; 23-3923)**	**40 (1401; 379-3413)**	**139 (21; 0-104)**	**168 (604; 23-3923)**	**107 (29; 0-104)**
Brambling *Fringillus montifringilla*	**23 (11; 5-22)**	**150 (95; 1-614)**	**63 (81; 7-203)**	**223 (8; 0-52)**	**299 (70; 1-614)**	**153 (8; 0-52)**
Long-tailed Tit *Aegithalos caudatus*	**106 (823; 0-2648)**	**99 (2324; 4-6795)**	**186 (477; 0-2508)**	**192 (367; 0-1743)**	**120 (2286; 4-8389)**	**152 (553; 0-3047)**
Gr.Sp. Woodpecker *Dendrocopos major*	**145 (16; 0-64)**	**209 (29; 0-194)**	-	**139 (5; 0-24)**	**376 (43; 0-439)**	**334 (14; 0-134)**
Willow Tit *Parus montanus*	**112 (561; 4-2661)**	-	**279 (10; 0-69)**	**321 (22; 3-176)**	-	**312 (17; 3-176)**
Coal Tit *Parus ater*	**226 (889; 21-4857)**	**244 (671; 62-3627)**	**657 (720; 5-7784)**	**540 (215; 0-2154)**	**162 (1023; 21-6075)**	**650 (341; 0-4418)**

Appendix 2.

Fluctuation indices (FI – Eq. 1) for the studied species in the breeding period and the mean number of pairs (n_p) in the monitoring area (range values in brackets).

Species wintering outside study area	n_p	FI
Chaffinch *Fringilla coelebs*	276 (220-361)	0.5
Blackbird *Turdus merula*	35 (28-47)	0.9
Song Thrush *Turdus philomelos*	63 (46-85)	0.9
Robin *Erithacus rubecula*	120 (83-148)	1.9
Blackcap *Sylvia atricapilla*	46 (32-58)	2.1
Spotted Flycatcher *Muscicapa striata*	20 (9-33)	2.8
Collared Flycatcher *Ficedula albicollis*	73 (47-127)	2.8
Hawfinch *Coccothrauster coccothraustes*	46 (30-70)	3.4
Chiffchaff *Phylloscopus collybita*	33 (22-45)	3.9
Dunnock *Prunella modularis*	31 (15-48)	4.3
Garden Warbler *Sylvia borin*	9 (1-14)	6.0
Pied Flycatcher *Ficedula hypoleuca*	14 (3-25)	6.3
Wood Warbler *Phylloscopus sibilatrix*	90 (8-152)	6.6
Species wintering within study area		
Great Tit *Parus major*	43 (27-64)	1.9
Wren *Troglodytes troglodytes*	37 (28-49)	1.9
Treecreeper *Certhia familiaris*	35 (20-48)	2.4
Goldcrest *Regulus regulus*	37 (16-69)	7.3
Blue Tit *Parus caeruleus*	39 (21-91)	7.4
Great Spotted Woodpecker *Dendrocopos major*	13 (4-23)	9.3
Coal Tit *Parus ater*	8 (3-16)	12.8