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Timing and dynamics of autumn passage of the Long-tailed Tit *Aegithalos caudatus* on the Courish Spit (Eastern Baltic)

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No significant trend over time was shown in the dynamics of autumn passage of Long-tailed Tits *Aegithalos caudatus* on the Courish Spit over the four decades 1957-2003. Only the beginning of passage showed a tendency to shift towards earlier dates. First captures in autumn and duration of passage showed a significant relationship with winter and spring NAO (North Atlantic Oscillation) Index and spring air temperatures. In the years following warm winter and spring in the presumed breeding grounds of Long-tailed Tits, earlier autumn migration was recorded in the Baltic area. The earlier passage starts, the more birds are captured in Rybachy-type funnel traps. It is assumed that early autumn passage follows a good breeding season. In years with early passage the proportion of birds at early stages of skull ossification is significantly lower than average, and the proportion of birds with completely ossified skull is higher. Proportion of adults participating in autumn migration probably does not exceed several percent. Daily pattern of flight activity in Long-tailed Tits is typical of diurnal migrants, even though it may slightly differ between the years.

Key words: Long-tailed Tit, passerines, irruption, autumn migration, dynamic, ambient temperature, North Atlantic Oscillation (NAO) Index, climate, Eastern Baltic.

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1. Introduction

The Long-tailed Tit *Aegithalos caudatus* inhabits the whole of Eurasia from Portugal to Japan. Breeding density in mixed deciduous woodland varied between 2 pairs·km^{-2} in Finland and 34 pairs·km^{-2} in southern England (Cramp & Perrins 1993). Long-tailed Tits are usually single-brooded. Clutch size usually varies between 8-12 eggs and increases with latitude. Social behaviour is highly developed, especially in winter, the most important aspect probably being communal roosting (Cramp & Perrins 1993).

In northern and northeastern Europe (Fennoscandia, Karelia, Baltic states) the Long-tailed Tit has irruptive migratory habits. Its numbers on autumn passage are subject to large interannual fluctuation in any given area, which suggests the irruptive movements (Sokolov et al. 2002). Usually Long-tailed Tits are recorded in small numbers, or are completely absent from most bird observatories, but in some years their mass movements are recorded over huge areas (Tischler 1941; Linkola 1961; Hildén 1974, 1977; Lipsberg & Rute 1975; Ehrenroth 1976; Rute & Baumanis 1986).

We have earlier published the results of comparative analysis of the dynamics of autumn passage of Long-tailed Tits during two consecutive irruptions (in 1985 and 1986) and some factors governing energy parameters of migrating birds (Shapoval 1989; Shapoval & Yablonkevich 1991).

In this paper, we analyse the long-term changes of timing and dynamics of autumn passage and factors that affect timing of migration of Long-tailed Tits on the Courish Spit of the Baltic Sea.

2. Material and methods

This paper analyses the data of long-term trapping of Long-tailed Tits in autumns 1957-2003 at the "Fringilla" field site on the Courish Spit of the Baltic Sea (55°05´N, 20°44´E). The birds were captured in Rybachy-type funnel traps (Payevsky 2000) from late March until late October. In different years one to four (usually two) traps were in operation in autumn, but during the last 15 recent years only one trap (trap # 5) was operating after 15th September. The traps were erected in young and middle-aged plantations of Scots pine (*Pinus silvestris*). Trap # 5 is open towards the northeast and is located on the edge of open dunes and pine plantation. Due to social behaviour of Long-tailed Tit, trapping efficiency in mist-nets and funnel traps is high and may reach 55-60% of birds recorded visually during movements (Ehrenroth 1979).

In 1957-2003, a total of 39,521 Long-tailed Tits were captured at the Fringilla field site in autumn. Annual totals in funnel traps varied between 0 and 20,557. We arbitrary assigned years when more than 50 individuals were captured to "irruption years" (25 out of 47), and years with smaller totals to "non-irruption years" (22 out of 47). During irruption years, 39,177 (99.1%) of Long-tailed Tits were captured, in non-irruption years - 344 birds (0.9%).

On the Courish Spit fewer Long-tailed Tits are captured than in some other bird observatories on the Eastern Baltic coast (e.g. Pape station in Latvia and Ventes Ragas station in Lithuania), even though similar funnel traps are operated in all stations. In autumn 1985, 5,780 individuals were captured in Pape (Baumanis et al. 1987) and 4,113 individuals in Ventes Ragas. In the same period, 1,523 Long-tailed Tits were captured at the northern end of the Courish Spit at Neringa bird observatory (Patapavičius & Jusys 1987), and 1,673 birds in Fringilla. This might be due to isolation of the Courish Spit from the mainland by the Courish Lagoon. Besides, the spit is locked from the north by a large industrial town (Klaipeda in Lithuania) which may disrupt direction for low-flying titmice.

Timing of autumnal migration of Long-tailed Tits was estimated from the first capture date, first quartile (25%), median and mean capture dates, third quartile (75%), date of capture of 95% of birds, and the last capture date. The use of the first capture date is justified, because this species does not breed on the Courish Spit. The last capture date is unreliable, because the traps are no longer in operation after 1st November. Our observations suggest that some Long-tailed Tits may continue their migration in November.

To analyse the relationship between the timing of autumnal migration of Long-tailed Tits and environmental variables, three parameters were used: (1) NAO (North Atlantic Oscillation) Index; (2) mean monthly air temperatures in different regions of Russia; and (3) precipitation rate in the study area. Monthly NAO Index values are used as estimates of the general meteorological situation in Europe in winter and early spring. The NAO Index is calculated as the difference between the normalized sea-level pressure at the Azores and Iceland (Hurrell et al. 2001). Positive NAO Index indicate a weather in Europe during winter and early spring when warm air masses from the Atlantic are moving towards the East, causing higher temperature and precipitation rate in northwest Europe (Hurrell 1995). To the contrary, negative NAO Index indicate weaker westward warm air masses and thus lower temperature and precipitation rate in this part of Europe. Monthly NAO Indices are archived at the National Oceanic and Atmospheric Administration's Climate Prediction Centre website (www.cpc.ncep.noaa.gov/data/teledoc/nao.html).

Temperature data from different parts of Russia were taken from the website http://cdiac.esd.ornl.gov/ftp/

To analyse precipitation rate in the study area data was obtained from the CRU database, a monthly precipitation rate dataset for global land areas from 1900 to 1998, gridded 5° latitude/ longitude (http://www.cru.uea.ac.uk/~mikeh/datasets/global/).

Daily pattern of passage was estimated from the number of birds captured during each hour from sunrise until sunset (approximately 06-22 hours local time). No Long-tailed Tits were captured at night.

For ageing, skull ossification was checked in about one third of individuals.

Statistical analysis was performed with SPSS 11.0 package (SPSS Inc., Chicago, IL., USA).

3. Results

3.1. Timing of passage

3.1.1. Irruption years

Capture date of the first birds varied between 18 September and 17 October in irruption years, SD = 8 (Tab. 1). No significant trend was recorded across the years, but a weak tendency towards earlier appearance of the first Long-tailed Tits has emerged (Fig. 1). No relationship was found between the first capture date and autumn totals (Tab. 2).

Table 1. Interannual variation in the timing of captures of Long-tailed Tits on the Courish Spit in the irruption years.

Year	Trapping total	Capture date							Passage duration, days
		first	25%	50%	75%	95%	last	Mean	
1957	118	11.10	15.10	17.10	19.10	23.10	23.10	17.10	12
1959	950	28.09	09.10	14.10	20.10	29.10	08.11*	15.10	41*
1962	253	01.10	11.10	16.10	22.10	30.10	11.11*	15.10	41*
1966	148	25.09	10.10	14.10	16.10	29.10	30.10	12.10	35
1969	162	07.10	12.10	15.10	21.10	24.10	24.10	16.10	17
1971	153	19.09	14.10	16.10	17.10	25.10	25.10	14.10	36
1972	185	03.10	10.10	12.10	14.10	22.10	28.10	12.10	25
1973	470	21.09	06.10	13.10	14.10	24.10	28.10	11.10	37
1976	166	17.10	20.10	22.10	24.10	30.10	30.10	22.10	13
1977	452	04.10	15.10	17.10	21.10	27.10	31.10	17.10	27
1978	98	01.10	05.10	14.10	20.10	30.10	30.10	14.10	29
1983	819	30.09	14.10	15.10	16.10	22.10	29.10	15.10	29
1985	1673	27.09	10.10	10.10	16.10	28.10	30.10	13.10	33
1986	3841	06.10	16.10	18.10	19.10	26.10	29.10	18.10	23
1990	267	19.09	18.10	18.10	20.10	28.10	28.10	19.10	39
1991	94	12.10	15.10	15.10	21.10	23.10	23.10	17.10	11
1992	1568	22.09	03.10	05.10	19.10	28.10	29.10	08.10	37
1993	629	30.09	09.10	14.10	17.10	21.10	27.10	13.10	27
1996	2424	25.09	04.10	13.10	16.10	17.10	31.10	10.10	36
1998	1000	05.10	07.10	08.10	11.10	19.10	02.11	09.10	28
1999	119	28.09	15.10	19.10	23.10	31.10	31.10	16.10	33
2000	20557	18.09	27.09	01.10	08.10	18.10	01.11	02.10	43
2001	737	07.10	18.10	21.10	23.10	28.10	28.10	20.10	21
2002	78	24.09	11.10	17.10	23.10	24.10	24.10	15.10	30
2003	2216	24.09	29.09	02.10	09.10	18.10	29.10	04.10	35
Mean	1567	29.09	10.10	13.10	18.10	24.10	28.10	13.10	28.8
s.d		7.7	5.9	5.2	4.9	4.2	2.6	4.6	8.6
Trend		-0.12	-0.09	-0.10	-0.11	-0.09	0.04	-0.10	0.13
s.e		0.11	0.08	0.07	0.07	0.07	0.04	0.06	0.12

Note: * In these years trapping sessions continued well beyond 1 November.

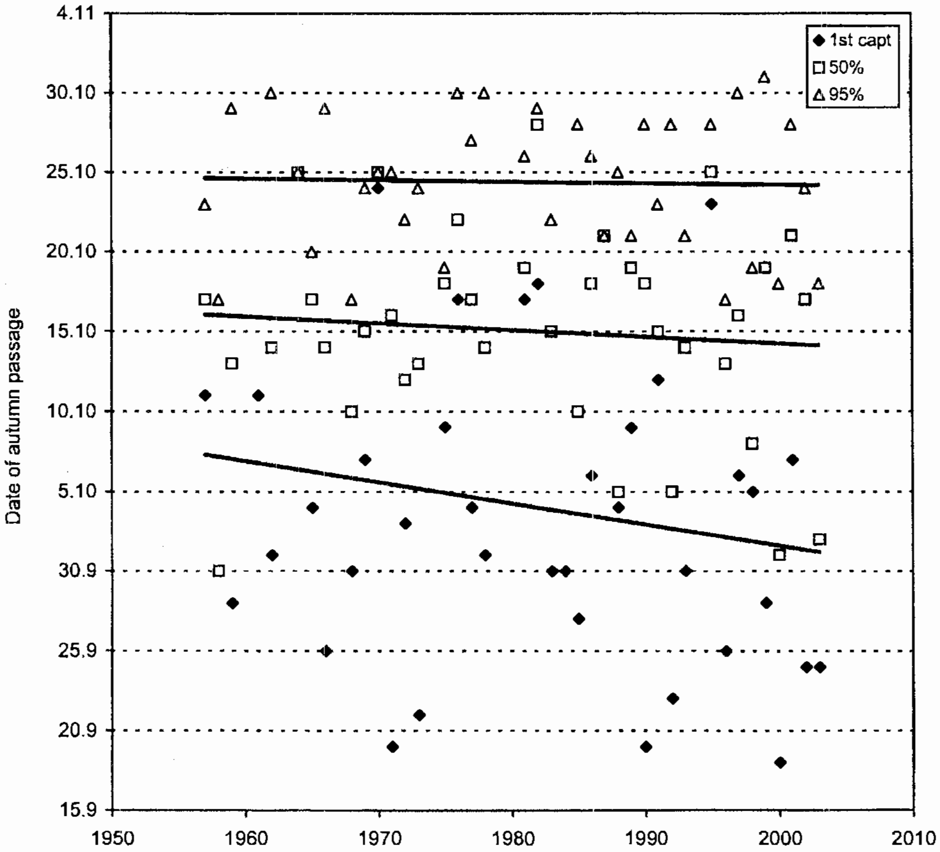

Figure 1. Timing of autumn passage of the Long-tailed Tits in irruption years. Capture dates: first capture, capture of 50% and 95% of all birds.

The date when the first quartile (25%) of all birds was captured, varied between 27 September and 20 October. No significant trend of this parameter was recorded across the years of study (Tab. 1). The date of capturing 25% of all individuals was negatively related to autumn trapping totals (Tab. 2).

Median and mean dates of autumnal passage of Long-tailed Tits through the Courish Spit varied between 1 and 22 October (Tab. 1). A strong negative relationship was found between the mean and median capture dates and the numbers captured per autumn (Tab. 2).

The date when the third quartile (75%) of all Long-tailed Tits was captured, varied between 8 and 24 October. No significant trend was recorded across the years of study, however a tendency towards earlier dates could be recorded in recent years (Tab. 1). The relationship between this parameter and trapping totals was strong and negative (Tab. 2).

Table 2. Relationships between timing of captures of Long-tailed Tits on the Courish Spit in the irruption years with trapping totals, NAO Indices, mean monthly precipitation rate in the Eastern Baltic (PPT) and duration of autumn passage (Spearman's rank correlation coefficient: * p<0.05, ** p<0.01, ***p< 0.001)

Parameter	Capture date							Passage duration, days
	first	25%	50%	75%	95%	last	mean	
Number of birds	-0.27	-0.41*	-0.50**	-0.62***	-0.37	0.40*	-0.42*	0.36
NAOI Jan-Feb	-0.25	-0.10	-0.19	-0.22	-0.37	-0.19	-0.14	0.22
NAOI Feb-Mar	-0.49**	-0.14	-0.10	-0.22	-0.14	-0.07	-0.17	0.44*
NAOI Jan-Mar	-0.32	-0.04	-0.02	-0.20	-0.19	-0.14	-0.04	0.27
NAOI Apr-May	0.01	0.08	0.06	0.33	0.18	-0.03	0.15	0.00
NAOI Jun-Jul	-0.09	0.05	0.10	0.21	0.08	-0.03	0.01	0.10
NAOI Aug	-0.07	0.02	0.00	-0.22	-0.25	-0.30	-0.03	0.02
NAOI Sep	-0.47**	-0.20	-0.20	-0.18	-0.11	-0.07	-0.20	0.39
NAOI Oct	0.30	0.22	0.20	-0.07	0.01	-0.06	0.32	-0.34
PPT Aug	0.21	-0.07	-0.14	-0.02	0.11	-0.18	-0.06	-0.18
PPT Sep	-0.03	0.15	0.20	0.08	0.23	-0.22	0.24	0.02
PPT Oct	-0.36	-0.02	-0.07	-0.46*	-0.46*	-0.23	-0.25	0.33

The date of capture of 95% of all birds varied between 17 and 31 October in different years. No trend was discernible across the years of study (Fig. 1, Tab. 1). No relationship was found between this parameter and autumn trapping totals (Tab. 2). Long-tailed Tits were usually captured until the end of October which is when trapping sessions finished. It would appear that passage continues into November in some years. In 1959 and 1962, when the traps were in operation until mid November, pronounced passage was recorded in 10% of individuals in the first week of this month (Fig. 2).

A significant positive relationship was found between the first capture dates in different years and median and mean passage dates (Tab. 3). A similar relationship existed between other dates characterising the timing of passage.

The total duration of autumnal passage of Long-tailed Tits over the Courish Spit varied between 11 and 43 days (1959 and 1962 excluded, Tab. 1). No significant trend in the duration of passage in irruption years across time was found, even though passage was slightly longer in recent years (Tab. 1). The relationship between the duration of passage and trapping totals is close to being significant (Tab. 2).

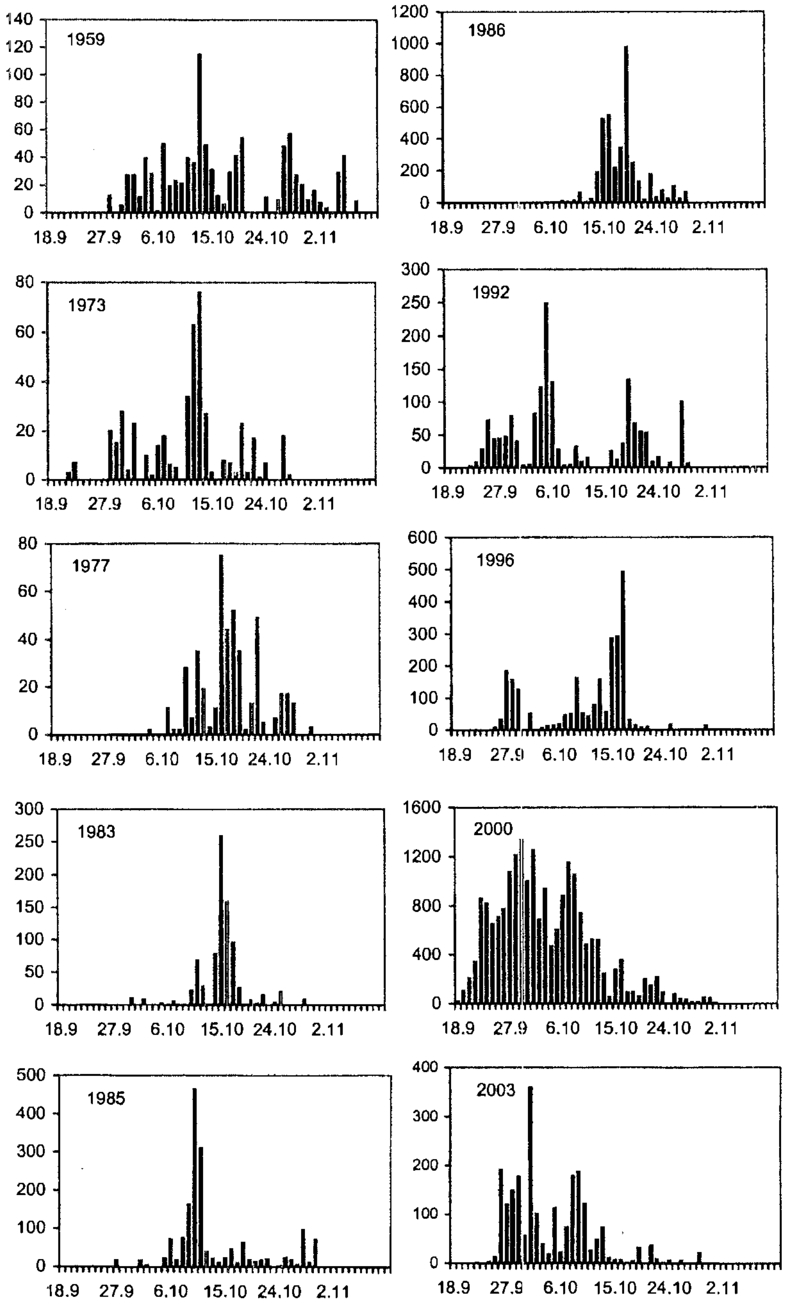

Figure 2. Dynamics of autumn passage of the Long-tailed Tits in some irription years. X-axis: dates of autumnal passage; Y-axis: number of birds captured in large traps per day.

Table 3. Relationships between the first capture date and other parameters of timing of autumn passage of Long-tailed Tits on the Courish Spit (Spearman's rank correlation coefficient: * $p < 0.05$, ** $p < 0.01$, ***$p < 0.001$).

Capture date	Captures						Passage duration, days
	25%	50%	75%	95%	last	mean	
first	0.51**	0.43*	0.36	0.11	-0.19	0.59**	-0.96***
25%		0.91***	0.58**	0.36	-0.32	0.92***	-0.55**
50%			0.71***	0.45**	-0.26	0.91***	-0.47**
75%				0.73***	-0.06	0.68***	-0.34
95%					0.26	0.47**	-0.01
Last						-0.28	0.38

Seasonal dynamics of captures may differ considerably between the years (Fig. 2). In some years (e.g. in 2000) most birds were trapped in the first half of the migratory period, in other years (e.g. in 1996), in the latter half. Day-to-day dynamics of captures was also highly variable. In some days, numbers captured were high, in other days, often in adjacent dates, few Long-tailed Tits were trapped (Fig. 2). In some years, several pronounced peaks of captures ("waves" of passage) could be discerned (e.g. five peaks in 1959), in other years (e.g. in 1983, 1986, 2000) no such peaks occurred.

The pooled dynamics of autumn passage in irruption years is given in Fig. 3. The mean date of first capture was 29 September, first quartile 10 October, median and mean dates 13 October, third quartile 18 October, 95 percentile 24 October (Tab. 1).

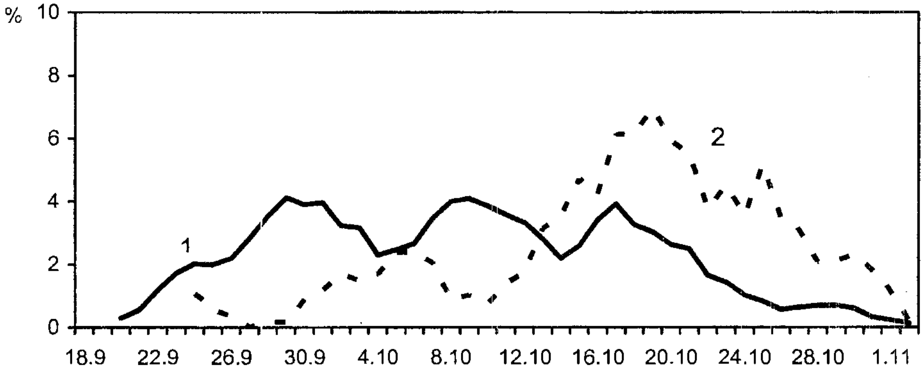

Figure 3. Total dynamics of autumn passage of the Long-tailed Tits in irruption (1) and non-irruption years (2). X-axis: dates of autumnal passage; Y-axis: percent of birds captured in large traps per day.

3.1.2. Non-irruption years

In years without irruption the first capture date varied between 30 September and 25 October (Tab. 4). On average it occurred on 11 October, i.e. 12 days later than in irruption years (Tab. 1).

Table 4. Interannual variation in the timing of captures of Long-tailed Tits on the Courish Spit in the non-irruption years.

Years	Number of birds	Capture date			Duration of passage, days
		first	median	last	
1958	7	30.09	30.09	17.10	17
1960	0	–	–	–	–
1961	1	11.10	–	11.10	1
1963	0	–	–	–	–
1964	6	25.10	25.10	25.10	1
1965	48	04.10	17.10	24.10	20
1967	0	–	–	–	–
1968	38	30.09	10.10	17.10	17
1970	8	24.10	25.10	25.10	1
1974	0	–	–	–	–
1975	41	09.10	18.10	31.10	22
1979	0	–	–	–	–
1980	0	–	–	–	–
1981	41	17.10	19.10	27.10	10
1982	23	18.10	28.10	29.10	11
1984	6	30.09	30.09	30.09	1
1987	12	21.10	21.10	21.10	1
1988	18	04.10	05.10	25.10	21
1989	17	09.10	19.10	21.10	12
1994	0	–	–	–	–
1995	50	23.10	25.10	28.10	5
1997	28	06.10	16.10	30.10	24
Mean	16	11.10	16.10	22.10	10.7
s.d		9.2	9.2	2.6	9.1
Trend		0.10	0.17	0.17	0.03
s.e		0.20	0.19	0.10	0.21

The median date varied between 30 September and 28 October, on average 16 October, i.e. three days later than in irruption years (Tab. 1). No significant trend in the timing of captures was found for years without irruption.

The pooled daily dynamics of captures in non-irruption years is given in Fig. 3. In such years, most Long-tailed Tits were captured in the latter half of October, unlike irruption years. The pooled distributions of captures differ significantly (Kolmogorov-Smirnov test: $z = 4.796$, $p = 0.0000$) between irruption and non-irruption years.

3.2. Relationship between timing of passage and the weather

3.2.1. NAO Index

Analysis of the timing of autumnal passage of Long-tailed Tits in irruption years with NAO Index showed a relationship only with the first capture date (Tab. 2). In irruption years, first birds arrived to the Courish Spit earlier when NAOI in February, March, and September was higher (Fig. 4, Tab. 2).

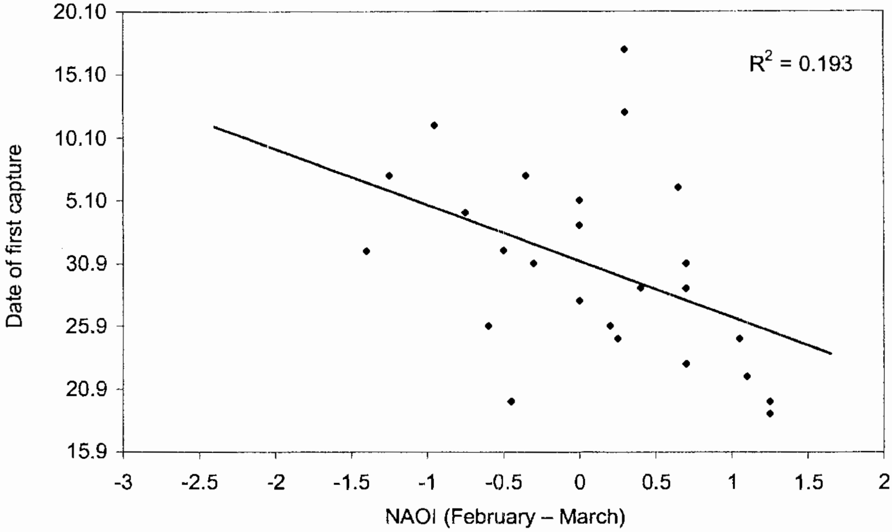

Figure 4. Relationship between the first capture date of the Long-tailed Tits and winter (February – March) NAO Index.

Duration of passage through the Courish Spit was also significantly positively related to NAOI in February and March (Tab. 2). The higher NAOI was in these months, the longer the passage was in the relevant year.

3.2.2. Air temperature

We analysed the relationship between the timing of passage of Long-tailed Tits with the mean monthly temperatures in winter, spring, summer and autumn in different regions of Russia. Table 5 shows the results for the regions that were likely to be the recruitment areas of Long-tailed Tits participating in irruptions.

Table 5. Relationship between the timing of captures of Long-tailed Tits on the Courish Spit in the irruption years and air temperatures in different regions of Palearctic (Spearman's rank correlation coefficient: $^{*}p < 0.05$, $^{**}p < 0.01$)

Coordinates	Month	Capture date				
		first	25%	50%	75%	95%
57°5′N;	Feb	-0.43*	-0.27	-0.21	-0.28	-0.37
22°5′-37°5′E	Mar	-0.51**	-0.19	-0.12	-0.01	0.03
	Apr	-0.31	-0.06	0.07	-0.10	-0.22
	May	-0.45*	-0.20	-0.18	-0.37	-0.31
	Jun	-0.37	-0.17	-0.07	-0.01	-0.04
	Jul	-0.15	-0.07	-0.03	0.01	-0.21
	Aug	-0.14	0.17	0,06	-0,06	-0,08
	Sep	0,14	0,08	0.03	0.01	-0.14
	Oct	-0.05	0.08	-0.06	-0.09	-0.07
57°5′N;	Feb	-0,27	0.03	0.14	0.02	-0.11
42°5′-57°5′E	Mar	-0.40*	-0.20	-0.10	0.01	0.31
	Apr	0.10	0.29	0.15	0.04	-0.07
	May	0.24	-0.13	-0.10	0.29	0.05
	Jun	0.04	-0.01	-0.04	-0.17	-0.35
	Jul	-0.18	0.21	0.25	0.25	-0.07
	Aug	-0.13	0.01	-0.24	-0.28	-0.08
	Sep	0.06	0.08	0.06	0.14	-0.04
57°5′N;	Feb	-0.34	-0.25	-0.13	-0.29	-0.12
62°5′-77°5′E	Mar	-0.47*	-0.21	-0.13	-0.19	-0.10
	Apr	-0.01	0.09	-0.01	-0.17	0.02
	May	-0.30	0.07	0.19	0.30	0.22
	Jun	0.01	0.11	0.09	-0.25	-0.49*
	Jul	-0.19	-0.09	-0.06	0.05	-0.13
	Aug	-0.30	-0.09	-0.13	-0.15	-0.06
	Sep	-0.08	0.12	0.18	0.26	0.27

A significant negative relationship was found between the first capture date and mean air temperature in March (Tab. 5). In some regions located close to the study area, a similar pattern was recorded in February and May temperatures. The higher temperature was in these months the earlier first Long-tailed Tits appeared on the Courish Spit in autumn (Fig. 4). For the most distant regions June air temperature was related to the capture dates of 95% of the birds (Tab. 5).

In irruption years, March and April temperatures were higher than average across the 30 years; in non-irruption years, they were below than average in different parts of Russia (Fig. 5, 6). In Fig. 7, the areas where the difference in spring temperatures in irruption and non-irruption years was significant are shown.

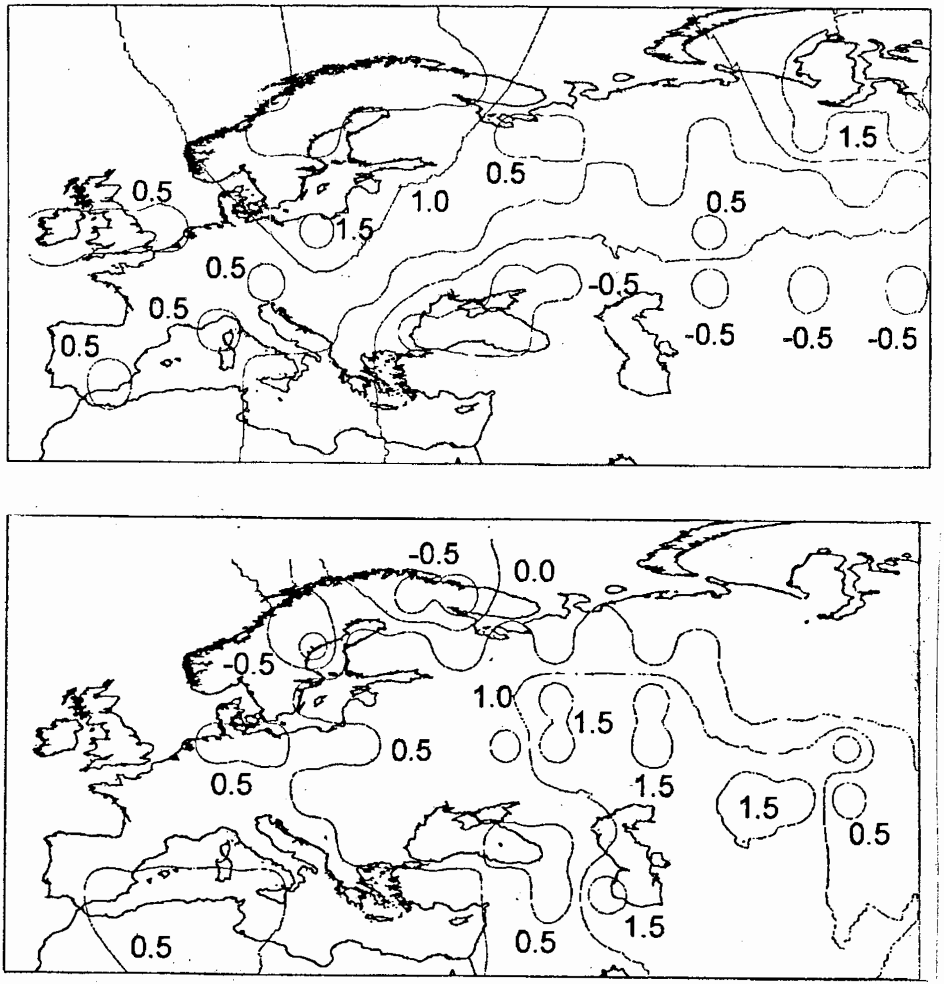

Figure 5. Air temperature anomalies for irruptive years for March (above) and April (below).

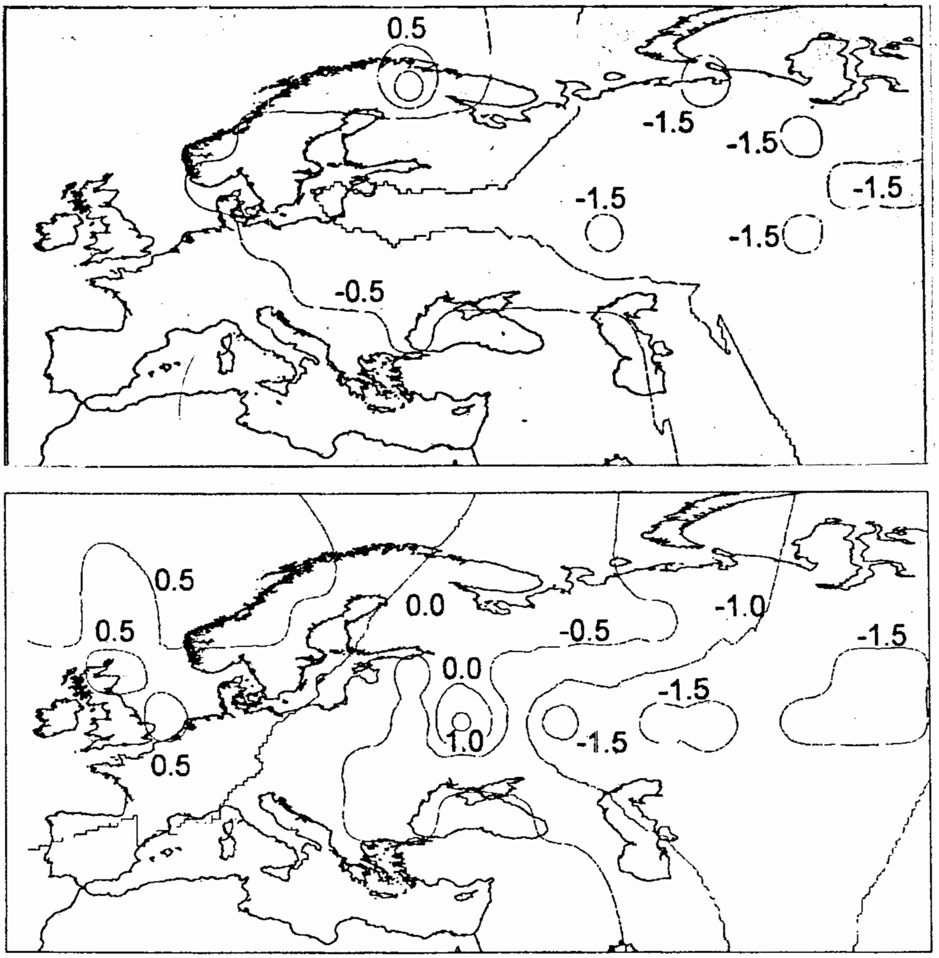

Figure 6. Air temperature anomalies for non-irruptive years for March (above) and April (below).

3.2.3. Level of precipitation

Analysis of the timing of autumnal migration in relation to level of precipitation in the Baltic area showed a significant negative relationship for October only (Tab. 2). When level of precipitation was greater, Long-tailed Tits migrated earlier through the Courish Spit.

Duration of passage was positively related to level of precipitation in October, but the relationship was not significant (Tab. 2).

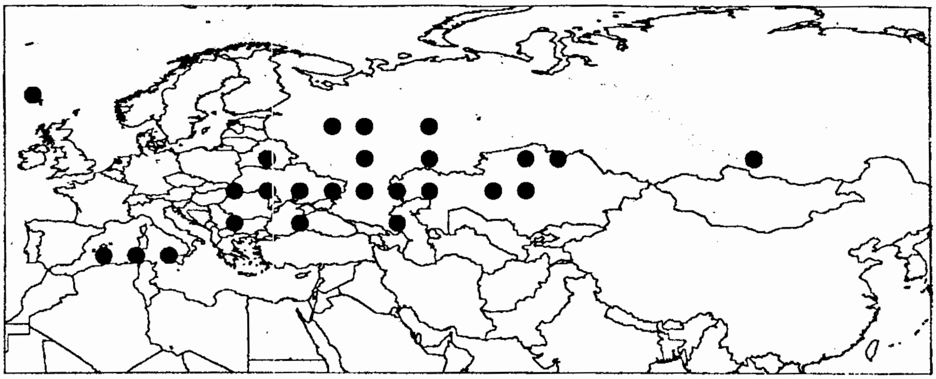

Figure 7. Position of sectors (circles show their centers) which showed a significant difference of April air temperature between irruptive and non-irruptive years in Long-tailed Tits on the Courish Spit.

3.3. Daily pattern of migration

Hour-to-hour distribution of captures during the daytime showed considerable variation between different irruption years (Fig. 8). In some years, two or three peaks in captures may be discerned, in other years (e.g. in 2000, the year of the strongest irruption) Long-tailed Tits were trapped during the whole day. In some years (e.g. in 1959, 1983) numbers captured declined from noon till dusk, in others (e.g. in 1973, 1977, 2001) a considerable evening activity peak occurred. In general, in years with less active movements, stronger hourly variation was recorded than in years of strongest irruption (Fig. 8). In such years, morning movements often commenced before sunrise, and in the evening movements continued after sunset. In the year with an "average" irruption (1985), 7% of all birds were captured between 17:00 and 19:00 local time, whereas during the most pronounced irruptions (1986 and 2000) this proportion was 19% and 16.5%, respectively, i.e. nearly thrice as high.

In the non-irruption years, daily pattern of capture usually showed three peaks at approximately 10, 12 and 16 hours. However when the curves are smoothed, no difference remains between the irruption and non-irruption years ($\chi^2 = 15.849$, df = 12, p = 0.198) (Fig. 9).

3.4. Age composition of migrants

No plumage ageing criteria are known for Long-tailed Tits (Vinogradova et al. 1976; Svensson 1992). The only useful criterion is skull ossification. Adults have their skull completely ossified (stage E; after Svensson 1992), most juveniles have skull ossification incomplete. It is not possible to distinguish juveniles with ossified skull from adults. Skull ossification has only been used since 1971.

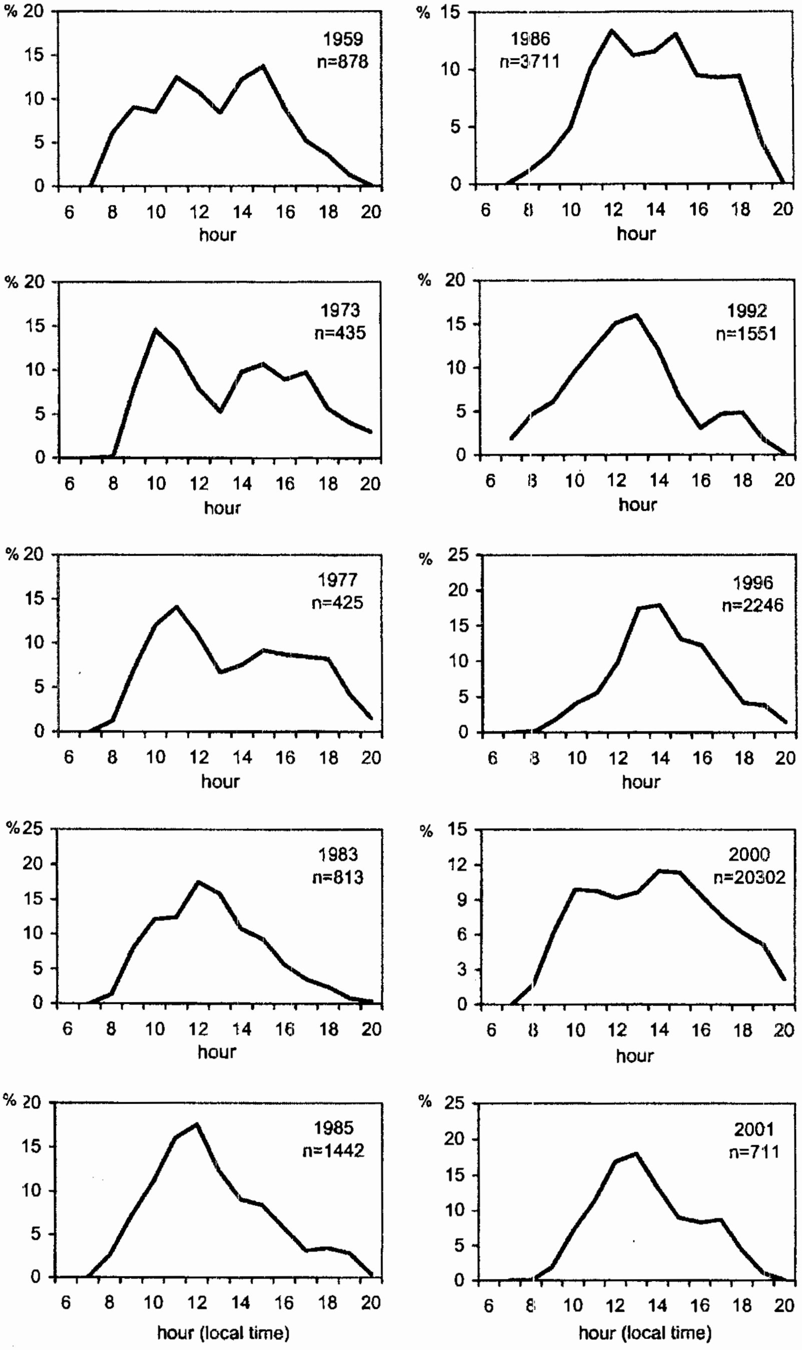

Figure 8. Daily pattern of autumn passage of the Long-tailed Tits in some irruption years.

Table 6. Skull ossification stages in Long-tailed Tits during autumn passage on the Courish Spit.

Year	Trapping total	Checked for skull ossification	Proportion of birds (%) at stage				
			A	B	C	D	E
1971	153	42	0	9	74	17	0
1972	185	63	0	22	59	17	2
1973	470	47	0	11	30	8	51
1977	452	254	0	4	63	19	14
1978	98	85	0	2	51	31	16
1981*	41	37	0	11	51	33	5
1982*	23	9	0	0	11	56	33
1983	819	354	0*	6	43	29	22
1985	1673	1670	0	13	55	27	5
1986	3841	3586	0	1	35	45	19
1987*	12	12	0	25	50	8	17
1988*	18	14	0	29	57	14	0
1989*	17	13	0	15	23	23	39
1990	267	169	0	2	28	35	35
1991	94	90	0	7	53	30	10
1992	1568	1295	0	9	52	31	8
1993	629	343	0	2	36	42	20
1995*	50	48	0	6	14	40	40
1996	2424	1334	0	8	29	44	19
1997*	28	28	0	4	71	25	0
1998	1000	49	0	14	37	31	18
1999	119	107	0	6	31	38	25
2000	20557	255	0	23	47	20	10
2001	737	669	0	7	25	56	12
2002	78	51	0	18	33	45	4
Pooled data	35359	10630	0	10	42	31	17
Irruption years pooled	35164	10463	0*	9	42	32	17
Non-irruption years pooled*	195	167	0	14	44	26	16

Note: * See results, p. 47.

Table 7. Relationship between skull ossification stage and trapping totals, NAO Indices and mean monthly air temperatures (Spearman's rank correlation coefficient: *p < 0.05, **p < 0.01).

Parameters	Proportion of birds (%) at skull ossification stage					
	B	C	D	E	A-C	D-E
Year	0.08	-0.37	0.48*	0.03	-0.23	0.30
Number of birds	0.10	-0.13	0.07	0.14	-0.10	0.10
NAOI Jan-Feb	0.11	-0.37	0.24	0.11	-0.24	0.27
NAOI Feb-Mar	0.00	-0.34	0.11	0.22	-0.24	0.25
NAOI Jan-Mar	-0.07	-0.44*	0.21	0.35	-0.41*	0.37
NAOI Apr-May	0.25	-0.10	0.08	-0.07	-0.02	0.01
NAOI Jun-Jul	0.04	-0.36	0.18	0.26	-0.28	0.32
NAOI Aug	-0.04	0.05	-0.03	-0.11	-0.08	-0.01
NAOI Sep	-0.16	-0.03	-0.22	0.21	0.07	0.02
NAOI Oct	0.01	0.10	-0.14	-0.02	0.14	-0.10
T °C Jan	0.03	-0.26	0.20	0.15	-0.23	0.26
T °C Feb	0.31	-0.19	-0.06	-0.01	0.04	0.01
T °C Mar	-0.27	-0.43*	0.26	0.41*	-0.36	0.47*
T °C Apr	-0.06	-0.58**	0.37	0.42*	-0.53*	0.53*
T °C May	0.14	0.07	0.02	-0.17	-0.02	-0.11
T °C Jun	0.19	0.00	-0.15	-0.04	0.09	-0.04
T °C Jul	0.35	-0.16	0.05	-0.22	0.10	0.01
T °C Aug	-0.02	0.15	0.00	-0.34	0.05	-0.08
T °C Sep	-0.34	-0.34	0.41	0.27	-0.46	0.46
T °C Oct	0.02	-0.25	0.29	0.19	-0.32	0.25

Note: T °C – mean monthly air temperature in the Eastern Baltic.

Data on skull ossification of migrants are given in Tab. 6. On average, 52% of birds captured had early stages of skull ossification (stages B and C), 31% were at the advanced stage (D), and 17% of Long-tailed Tits had their skull completely ossified. The distribution was fairly similar in irruption years and in non-irruption years ($\chi^2 = 3.324$, df = 3, p = 0.344). However, in years with no irruption the proportion of birds at the early stages of skull ossification (stages B and C) was slightly larger than in the years of irruption (58% and 51%, respectively). Proportion of birds at the advanced stage D was lower in years without irruption (26% and 32%, respectively). Over the whole study period, only a single individual at stage A (skull ossification not yet started) was captured in 1983. The proportion of birds with ossified skull was roughly the same in the years with and without irruption (17% and 16%, respectively, Tab. 6).

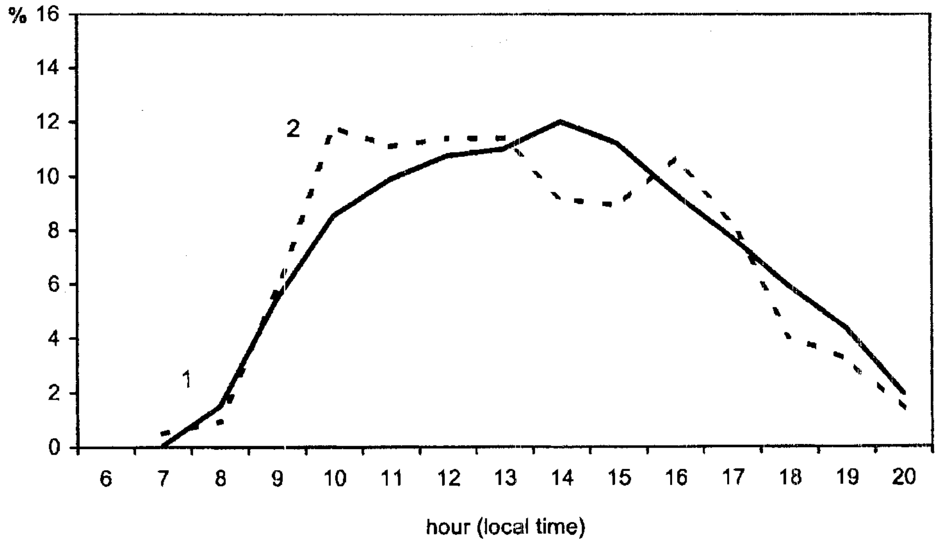

Figure 9. Total daily pattern of autumn passage of the Long-tailed Tits in irruption (1) and non-irruption years (2).

The proportion of birds at early stages (A-C) was significantly negatively related to winter and spring NAO Index and spring air temperature in the Baltic region (Tab. 7). The proportion of birds with ossified skull (stage E) was positively related to spring air temperature. When winter and spring NAO Index and air temperatures in March and April were high, the proportion of Long-tailed Tits captured on the Courish Spit during autumnal passage at early stages of skull ossification was lower, and more birds had ossified skull.

4. Discussion

4.1. Long-term trends in the timing of autumn passage

Long-term data of trapping Long-tailed Tits on the Courish Spit showed no significant change in the timing of autumnal passage of this irruptive species in the Eastern Baltic. There was only a tendency to shift the onset of passage towards earlier calendar dates. In several recent publications it is suggested that migrating passerines show an evident trend towards later autumn migration, unlike spring arrival which occurs earlier than in previous years (Bairlein & Winkel 2001; Sparks & Mason 2001; Fiedler 2003). The data of visual counts of songbirds in southern Germany showed that in 19 of 28 short-distance migrants the median date of departure of birds has shifted towards later departure since 1970, on average 3.4 (up to 7) days. Only five species now leave central Europe earlier than before (Bairlein & Winkel 2001). On the island of Helgoland (North Sea) autumn departure was delayed in three species, although significantly only in the Wren *Troglodytes troglodytes* (Vogel & Moritz 1995; Bairlein & Winkel 2001). In Central England (Essex) 32 species were examined to look for trends between 1950 and 1998. The majority showed a tendency to earlier arrival and later departure (eight of 23 significant) (Sparks & Mason 2001).

A recent paper by Jenni & Kéry (2003) analyses long-term changes in the passage of 65 species in relation to climate change on the basis of 42 years of trapping at Col de Bretolet pass in the Swiss-French Alps. The authors concluded that long-distance migrants have advanced their peak passage time significantly in recent years, whereas short-distance migrants have significantly delayed it. Among all short-distance migrants, 28 species delayed their peak passage time, whereas 12 species advanced it. Among the latter, there were three of four irruptive species. It is suggested that irruptive species may be affected differently by global warming than non-irruptive species.

It has been shown in a number of passerine species that the timing of autumn departure is related to the population-specific timing of breeding (Ellegren 1990; Sokolov et al. 1999; Sokolov 2000). Bojarinova et al. (2002) studied timing of autumn migration of Great Tits *Parus major* in the St.Petersburg (Leningrad) region and concluded that in juveniles from the first broods, the timing of migration is strongly related to the population median hatching date of first broods: the young migrate at a constant age independent of their hatching date. In contrast to first broods, the migration age in juveniles from the second broods decreased with hatching date, resulting in a relatively constant migration date. However, even though many long- and short-distance migrants show a significant trend towards earlier breeding on the Courish Spit and in more northern areas, average time of autumn departure in most migrants did not advance over 40 years in our study area (Sokolov & Payevsky 1998; Sokolov et al. 1999). The reason might be that in the years with late breeding juveniles start their autumn migration at an earlier age, like juveniles from late repeat or second broods. As a result, they migrate in roughly the same calendar dates as birds hatched in the years when breeding occurred early.

4.2. Relationship between the timing of autumn passage and weather variables

Sokolov & Payevsky (1998) and Sokolov (2000) have shown that the timing of breeding of passerines on the Courish Spit strongly depends on the temperature regimen of spring. In the years with warm and early spring many species start breeding earlier.

We found a significant negative correlation of the first capture dates of Long-tailed Tits on the Courish Spit with winter and spring NAO Index and spring air temperatures (Tab. 2, 5). It might suggest that after mild winters and warm springs, this species also breeds earlier. Duration of passage and numbers of Long-tailed Tits are at their peak in such years. We have found a similar relationship between the timing of autumn migration and spring air temperatures in short- and long-distance migrants (Sokolov et al. 1999).

Significant negative relationship of the first capture dates of Long-tailed Tits on the Courish Spit with September NAO Index and October level of precipitation in the Baltic area might be a coincidence. However, this relationship might also be based on the features of atmospheric circulation during this period which enhances the movement of birds towards the west. In autumn 2000, when the most early mass irruption of Long-tailed Tits occurred, weak and moderate easterly winds dominated in the Eastern Baltic which probably facilitated an early intrusion of Long-tailed Tits from the mainland to the Courish Spit.

The negative relationship between the timing of autumn passage and trapping totals is quite understandable. Years with early autumn migration are most probably preceded by successful breeding, producing many juveniles (Sokolov et al. 1999). The most characteristic year was 2000, when a record number of Long-tailed Tits, over 20,000, was captured on the Courish Spit. Trapping totals are usually positively related to the duration of passage. The year 2000 was the first on record in this respect, too (Tab. 1).

4.3. Dynamics of passage of birds at different stages of skull ossification

In the years with high winter and spring NAO Index and high spring air temperature the proportion of individuals at an early stage of skull ossification (stage C) was significantly lower, and of individuals with ossification completed (stage E) significantly higher (Tab. 7). The reason for this was probably that in warm years with early breeding Long-tailed Tits reach our study area on average at more advanced stages of skull ossification (i.e. at older age) than in relatively cold and late years.

Skull roof completely ossified (stage E) does not necessarily mean that the individual in question is an adult, as already in the beginning of passage juveniles with ossified skull may be trapped. During autumn passage skull ossification is under way, the proportion of birds that have completed this process increases towards the end of passage (Shapoval 1989).

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