Irregular migrations (irruptions) in six bird species on the Courish Spit on the Baltic Sea in 1957-2002

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Abstract: Sokolov, L.V., Markovets, M.Yu., Yefremov, V.D. & Shapoval, A.P. (2002): Irregular migrations (irruptions) in six bird species on the Courish Spit on the Baltic Sea in 1957-2002. Avian Ecol. Behav. 9: 39-53.

Analysis of long-term monitoring data of numbers in six irregular passerine migrants (Long-tail Tit *Aegithalos caudatus*, Willow Tit *Parus montanus*, Coal Tit *Parus ater*, Treecreeper *Certhia familiaris*, Jay *Garrulus glandarius*, Nutcracker *Nucifraga caryocatactes*) revealed no periodicity in autumn numbers of Long-tailed Tits, Coal Tits and Nutcrackers. Treecreepers showed a significant positive trend over the years of study. High numbers of Jays and Nutcrackers are unlikely in a year following a massive irruption, whereas Treecreepers and Coal Tits not infrequently make repeated irruptions. Irruptions of some species are correlated. Autumn numbers of Coal and Willow Tits, Coal Tits and Treecreepers, and Long-tailed Tits and Treecreepers are interrelated.

Irruptions of Long-tailed Tits, Coal Tits and Treecreepers occurred more frequently in the 1960s, 1980s and late 1990s, when early and warm springs dominated, than in the 1970s which were colder. Autumn numbers of Coal, Willow, Long-tailed Tits, and Treecreepers were positively related to the mean April temperatures in the Eastern Baltic. No relationship was found between autumn numbers and the mean temperatures of March, May and June (except of Jay numbers with June temperature).

In Long-tailed and Coal Tits and in Jays a highly significant relationship was found between autumn numbers of juveniles and capture figures during the subsequent spring. This suggests that after an irruption, some juveniles survive the winter and move back. The direct recoveries of ringed birds show reverse movements in spring. Irruptions of some so-called sedentary species are in fact a kind of seasonal migration. It is characterised by the directed autumn and spring movements and by the migratory disposition of the birds involved.

Key words: irruption, autumn migration, spring migration, passerines, ambient temperature, climate.

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1. Introduction

It is well known that some avian species show irregular outbreaks of numbers of migrating individuals (irruptions), mainly of juveniles (Lack 1954). These outbreaks are best documented during the systematic visual surveys or captures on the edge of ecological barriers on the coasts, in river valleys or on mountain passes (Kumari 1957).

Irruptive birds are usually called the species which are basically sedentary or nomadic, but sometimes undergo massive seasonal movements in varying directions and remain in the new areas for some time (Steinbacher 1951, Lack 1954, Curry-Lindahl 1975). Within Europe, Nutcrackers *Nucifraga caryocatactes*, Waxwings *Bombycilla garrulus*, and crossbills (*Loxia curvirostra, L. pytyopsittacus, L. leucoptera*) are usually believed to be typical irruptive species. A number of other species are sometimes also treated in this group: Great Spotted Woodpecker *Dendrocopos major*, Jay *Garrulus glandarius*, Coal Tit *Parus ater*, Willow Tit *P. montanus*, Siberian Tit *P. cinctus*, Nuthatch *Sitta europaea*, Treecreeper *Certhia familiaris*, Long-tailed Tit *Aegithalos caudatus*, Fieldfare *Turdus pilaris*, Snow Bunting *Plectrophenax nivalis*, Redpoll *Carduelis flammea*, Pine Grosbeak *Pinicola enucleator*, Bullfinch *Pyrrhula pyrrhula* (Steinbacher 1951, Lack 1954, Curry-Lindahl 1975).

Different hypotheses have been suggested concerning the biological significance of massive irruptions in species which are usually sedentary or nomadic. They vary from the hypothesis of elimination of population surplus (Wynne-Edwards 1962, Dolnik 1975) to the suggestion that irruption is just an extreme variant of normal migratory systems (Bardin & Rezvyi 1988). Lack (1954) mentioned the two main hypotheses explaining the causes of irruptions. One of them suggests that irruptions develop in autumn after exceptionally good breeding seasons and are caused by overpopulation in breeding areas. The other hypothesis explains irruptions mainly by poor crops of the preferred food in the main range of a species which force the birds to move towards other areas. Lack believed that both hypotheses were partly correct, but none could explain the causes of irruptions completely (Lack 1954). Formosov (1965) followed Lack (1954) suggesting that food shortage and high autumn numbers are the triggers of irruptions. The theoretical model of Svärdson (1957) suggests that irruptive species can migrate each year, but their movements are suppressed or completely inhibited when food availability is high in the main range. It is however known that irruptive species often start to move early in the season, when the problem of food shortage is not yet relevant. The author explains that irruptive species are triggered every year by the same factors as other species, but the duration and intensity of their movements depends on food availability (Svärdson 1957). Unlike regular migrants, irruptive species do not move when food is abundant. Alerstam (1990, pp. 201-202) wrote that "invasions are most sweeping when the food shortage has been preceded by a peak year in seed production and with this also

a peak in the nut. The chances of the birds surviving the winter months by set-ting off on long-distance migration in order to find regions with passable stocks of cembra pine cones or to find alternative food in areas with a mild winter cli-mate are doubtlessly small, but nevertheless greater than the chances of surviving in the home districts. The return flight to the normal breeding range in the late spring following an invasion year shows that the emigration has a survival value, even though the decimation in numbers of the invading hordes of birds from au-tumn to spring is very substantial". Curry-Lindahl (1975), however, believes that irruption is a one-way ticket, and that it serves to cut the population down to the actual availability of food resources. Only a fraction of the birds breeds in the new areas. Noskov et al. (1975) suggested that only those migratory movements should be called irruptions which cause a sharp and unusual increase in the living area of individuals. This is achieved by emigration of a considerable part of a spe-cies (population) far beyond its usual range. The new areas included in the living area are neither winter quarters nor breeding grounds, and the movements are ir-reversible.

In spite of many hypotheses suggested by different authors, no clear answers exist to the following questions:
(1) Is there a relationship between irruptions of different species?
(2) Is a rise in autumn numbers related to the breeding success during the pervious summer? What is the amplitude of fluctuations in the breeding success rate?
(3) What environmental factors govern high numbers in particular years? How long and in what part of the year should they act to cause an irruption?
(4) What endogenous or external factors make juveniles not only emigrate from the natal area, but move for hundreds or thousands of kilometres in the di-rection selected?
(5) Does a return migration occur in spring?
(6) Is there a difference between irruptions and regular migration? What is the physiological background of irruptions?
(7) Does global warming have an effect on irruption frequency?

The aims of this study were: (1) to test the time series of autumn numbers for periodicity; (2) to test for the relationships between irruptions in different species; (3) to study the impact of spring and summer temperatures in autumn numbers of juveniles; (4) to find out whether the species studied have spring movements.

2. Material and methods

Migrants have been captured at the Fringilla field station of the Biological Station Rybachy (55°05´N, 20°44´E) during 45 years (since 1957 to present day) annually in large stationary Rybachy-type traps (Payevsky 2000). These traps are operated since late March until late October at a fixed site in pine plantations (for a detailed description of the habitats see Payevsky 1999). These traps are

very suitable for trapping irruptive species because these birds move in the day-time and usually fly low above the ground.

Of the species traditionally treated as the irruptive ones, we capture Great Spotted Woodpeckers, Long-tailed Tits, Coal Tits, Willow Tits, Nutcrackers, Jays, and Common Crossbills *Loxia curvirostra*. Besides, Nuthatches, Treecreepers, Fieldfares, Redpolls, Arctic Redpolls *Carduelis hornemanni*, Bullfinches are captured. In this paper, we analyse capture data on six species only: Long-tailed Tit, Coal Tit, Willow Tit, Treecreeper, Jay and Nutcracker (Bolshakov et al. 2001a, b, c).

We analysed numbers of juveniles and adults captured annually in two traps (# 3 in 1957-1976 and # 5 in 1977-2002) oriented by their entrance towards the north-east in autumn between 15 August – 1 November. Autumn migration mainly occurs on the Courish Spit in most species studied between 15 August and November. Before mid August, the bulk of local juveniles usually leave the natal area (Sokolov 1997). We also analysed the numbers of birds captured in spring, between late March and 15 May in traps oriented towards the south-west and towards the north-east. In 2001, three traps were in operation since late February in order to detect early spring migration of Long-tailed Tits after the exceptional autumn irruption of 2000.

For five species out of six, their standardised autumn numbers were checked for periodicity by analysing the autocorrelation function and for the presence of trends (Box & Jenkins 1983). To estimate the relationships between irruptions in the species under study, and between autumn numbers of spring and summer air temperatures in the Eastern Baltic (in Kingisepp and Kaliningrad), Spearman rank correlation was used (Lloyd & Ledermann 1984).

3. Results

3.1. Fluctuations of autumn numbers of juveniles

The numbers of juveniles captured per autumn varied between the years greatly, by two, three or even four orders of magnitude (Tab. 1): from 1 to nearly 20,000 in the Long-tailed Tit, from 3 to 4,551 in the Coal Tit, from 1 to 256 in the Treecreeper, from 0 to 814 in the Jay, from 0 to 176 in the Nutcracker.

The analysis of time series of autumn numbers in the species studied showed no periodicity in the Long-tailed Tit and Coal Tit and in Nutcracker (Tab. 2). Only in the Treecreeper was a significant 2-year quasi-periodic component of an obscure character revealed. The analysis showed weak positive and negative relationships between the numbers of Willow Tits in adjacent years which could be accounted for more frequent and massive irruptions in the late 1950s and early 1960s and in the 1980s and by the lack of irruptions in the 1970s and 1990s. High numbers of Jays and Nutcrackers are improbable in the year following an irruption, whereas in Treecreepers and Coal Tits irruptions were recorded in such years.

Table 1. Numbers in six irruptive species in autumn on the Courish Spit and the mean temperature of April.

Year	t °C April	Parus ater	Parus montanus	Aegithalos caudatus	Certhia familiaris	Garrulus glandarius	Nucifraga caryocatactes
1957	7.5	25	9	120	8	0	0
1958	5.0	1,200	31	6	1	8	1
1959	7.0	505	14	846	77	180	0
1960	6.0	4	11	1	1	13	0
1961	6.6	500	14	1	7	351	32
1962	7.8	2,052	83	113	25	71	4
1963	6.1	983	13	1	3	1	3
1964	6.2	8	14	3	2	814	0
1965	5.3	137	25	28	6	186	0
1966	5.1	14	18	103	3	411	0
1967	6.1	314	27	1	1	1	1
1968	7.8	5	37	37	2	85	176
1969	4.8	8	11	106	3	67	2
1970	5.1	3	8	4	3	96	0
1971	6.4	257	6	52	6	1	29
1972	7.2	955	4	63	3	91	1
1973	5.7	11	6	219	13	70	14
1974	5.9	799	2	1	2	12	0
1975	5.7	41	3	1	2	102	2
1976	5.7	35	1	26	14	0	0
1977	5.0	21	4	212	53	36	52
1978	5.3	32	8	43	1	0	0
1979	5.5	19	3	1	1	119	0
1980	5.5	50	30	1	19	29	20
1981	5.1	92	13	25	28	373	4
1982	5.0	80	8	6	19	0	0
1983	7.9	4,551	82	592	19	80	0
1984	7.6	91	32	6	19	4	1
1985	5.8	104	17	1,626	8	56	16
1986	6.2	172	39	3,853	98	28	0
1987	5.3	46	12	11	121	170	0
1988	5.7	453	72	18	63	3	0
1989	7.8	3,387	23	17	66	18	1
1990	8.3	2,071	55	267	32	53	0

Year	t ^{0}C April	Parus ater	Parus montanus	Aegithalos caudatus	Certhia familiaris	Garrulus glandarius	Nucifraga caryocatactes
1991	6.0	1,420	11	94	231	25	4
1992	5.5	187	35	1,531	94	1	1
1993	7.5	1,024	11	627	230	17	1
1994	5.0	214	7	1	41	22	0
1995	7.7	1,023	6	36	85	0	11
1996	5.0	202	6	2,372	118	8	1
1997	5.3	719	6	16	16	12	1
1998	7.7	139	10	981	56	17	80
1999	7.7	266	7	118	40	396	0
2000	9.7	173	3	19,768	256	4	0
2001	6.0	595	21	737	74	5	0
2002	7.5	1,862	3	75	25	90	1

Table 2. Autocorrelation function of time series in the irruptive species.

Lags ACF	Parus ater	Parus montanus	Aegithalos caudatus	Certhia familiaris	Garrulus glandarius	Nucifraga caryocatactes
1	0.119	0.083	-0.004	0.264	-0.065	-0.091
2	-0.016	0.247	0.030	0.430*	0.201	-0.021
3	-0.134	0.172	-0.017	0.215	-0.059	0.050
4	-0.051	0.153	0.102	0.365	-0.007	-0.032
5	-0.077	0.149	-0.021	0.365	-0.008	-0.055
6	0.282	0.025	-0.007	0.151	-0.085	-0.035
7	0.067	-0.075	0.016	0.084	-0.055	-0.019
8	-0.000	-0.198	0.052	0.313	-0.077	0.009
9	-0.066	-0.188	-0.019	0.036	-0.054	0.048
10	-0.051	-0.226	0.009	0.360	0.004	-0.044
11	-0.050	-0.309	-0.020	0.021	-0.109	0.010
12	0.003	-0.266	-0.021	0.007	-0.021	0.014
13	-0.147	-0.244	-0.022	0.039	-0.063	-0.035
14	-0.078	-0.273	0.161	0.053	-0.006	–

Note: * – $p < 0.05$.

3.2. Relationships between irruptions in different species

Obvious relationships between irruptions of some bird species were revealed. Significant correlations between autumn numbers of Coal and Willow Tits, Coal Tits and Treecreepers, Long-tailed Tits and Treecreepers were found (Tab. 3).

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Table 3. Correlation between numbers of irruptive species, 1959-1990 (Spearman's rank correlation coefficient: * p<0.05, ** p<0.01).

Species	Parus ater	Parus montanus	Aegithalos caudatus	Certhia familiaris	Garrulus glandarius
Parus montanus	0.421**				
Aegithalos caudatus	0.151	0.259			
Certhia familiaris	0.343*	0.319	0.489**		
Garrulus glandarius	-0.191	0.520	0.104	0.058	
Nucifraga caryocatactes	0.042	0.130	0.081	0.060	0.051

3.3. Relationships between autumn numbers of juveniles and spring ambient temperatures

Autumn irruptions of Long-tailed, Coal, Willow Tits and Treecreepers were more frequent in the 1960s, 1980s, and 1990s when spring temperatures were higher than in the 1970s which were colder. In the Long-tailed Tit, three irruptions (over 100 individuals captured) occurred in the 1960s, two in the 1970s, four in the 1980s and six in the 1990s (Tab. 1). In the Coal Tit, four irruptions (over 300 birds trapped) were recorded per decade in the 1960s, 1980s, 1990s, and only two in the 1970s.

In Coal, Long-tailed Tits and Treecreepers a significant relationship was found between autumn numbers and mean April temperatures at two Eastern Baltic sites (in Kingisepp, Leningrad Region and/or in Kaliningrad) (Tab. 4). No significant correlation was found in any of these species with March, May or June mean temperatures. Only in the Jay was there a significant relationship with summer ambient temperature (June) found.

Table 4. Correlation between mean spring and summer ambient temperatures (in Leningrad and Kaliningrad Regions) and autumn numbers on the Courish Spit, 1958-2000 (Spearman's rank correlation coefficient: *p < 0.05, **p < 0.01, ***p < 0.001).

Species	Region	t °C March	t °C April	t °C May	t °C June
Parus ater	Kingisepp	0.27	0.26	-0.04	-0.02
	Kaliningrad	0.23	0.32*	0.09	-0.19
Parus montanus	Kingisepp	-0.04	0.25	0.11	0.16
	Kaliningrad	-0.08	0.19	0.11	-0.02
Aegithalos caudatus	Kingisepp	0.05	0.34*	-0.02	-0.02
	Kaliningrad	0.17	0.21	0.03	-0.10
Certhia familiaris	Kingisepp	0.19	0.38**	-0.09	-0.16
	Kaliningrad	-0.12	0.13	-0.15	-0.23
Garrulus glandarius	Kingisepp	-0.18	0.09	-0.08	0.48***
	Kaliningrad	-0.13	0.08	-0.13	0.48***

3.4. Spring migration in the species studied

In the Long-tailed Tit, Coal Tit and Jay, a highly significant correlation be-
tween autumnal numbers of juveniles and trapping figures during subsequent
spring was found (see Figure). It shows that after an irruption, a proportion of
participants survives and makes the reverse movement in spring, possibly they re-
turn to their natal areas. This was further confirmed by captures of birds that
had been ringed during autumn irruption in the next spring to the northeast of
their ringing site (Tab. 5). To test the assumption of spring reverse migration in
irruptive species, we organised an early trapping session in Rybachy-type traps
since late February 2001. During the preceding autumn, an exceptional irruption
of Long-tailed Tits occurred (Tab. 1). In spring 2001, 190 Long-tailed Tits were
captured (mainly in March), 65% of them carried substantial fuel stores (fat
scores "medium" and "great"). Besides, 759 Long-tailed Tits were captured at the
Rybachy field site (12 km from Fringilla) in mist-nets which were operated since
12 March. Visual surveys showed the diurnal migration of Long-tailed Tits along
the Courish Spit towards the northeast in March and early April. The birds mi-
grated in small flocks (10-20 individuals) over land and over water along the
coast of the Courish Lagoon. By mid April Long-tailed Tits were no longer cap-
tured either in stationary traps or in mist-nets: they must have left the Courish
Spit. Over 45 years of observations, Long-tailed Tits were never recorded on the
Courish Spit in the breeding period, not a single bird has been captured. During
transect counts between November 2000 and March 2001, flocks of Long-tailed
Tits were regularly recorded in alder and mixed forests on the spit. In May and
June 2001, this species was not recorded (S.A. Shulepov, pers. comm.).

Table 5. Ring recoveries of birds of irruptive species in the following spring and in sub-
sequent years.

Ringing site	Ringing date	Recovery date	Recovery site	Distance, km	Direction, degrees
Aegithalos caudatus					
Poland 54.21N, 19.19E	16.10.83	04.04.84	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	17.10.83	04.04.84	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	19.10.86	11.04.87	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	19.10.86	11.04.87	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	19.10.86	11.04.87	Russia 55.05N, 20.44E	122	048°

Table 5. Continued

Ringing site	Ringing date	Recovery date	Recovery site	Distance, km	Direction, degrees
Poland 54.46N, 18.28E	03.04.87	10.04.87	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	04.04.87	11.04.87	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	04.04.87	12.04.87	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	22.10.83	03.04.84	Russia 55.12N, 20.46E	154	072°
Poland 54.28N, 16.25E	31.03.97	10.04.97	Russia 55.05N, 20.44E	285	076°
Russia 55.05N, 20.44E	02.10.71	25.09.73	Estonia 58.01N, 24.27E	398	035°
Russia 55.05N, 20.44E	11.10.85	22.09.86	Estonia 58.35N, 26.23E	519	041°
Parus ater					
Latvia 56.11N, 21.03E	18.09.74	21.09.74	Poland 54.21N, 19.19E		
		29.04.75	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	21.09.74	19.04.75	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	26.09.74	29.04.75	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	10.10.71	10.04.72	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	24.10.71	11.04.72	Russia 55.05N, 20.44E	122	048°
Poland 54.21N, 19.19E	18.09.83	25.04.84	Russia 55.05N, 20.44E	122	048°
Poland 54.19N, 19.14E	01.10.63	22.04.64	Russia 55.05N, 20.44E	129	049°
Poland 54.19N, 19.14E	23.10.65	28.04.66	Russia 55.05N, 20.44E	129	049°
Poland 54.46N, 18.28E	12.04.72	20.04.72	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	29.04.63	08.05.63	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	19.04.63	10.05.63	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	30.04.63	10.05.63	Russia 55.05N, 20.44E	149	076°

Table 5. Continued

Ringing site	Ringing date	Recovery date	Recovery site	Distance, km	Direction, degrees
Poland 54.46N, 18.28E	02.05.63	09.05.63	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	05.05.63	09.05.63	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	06.05.63	08.05.63	Russia 55.05N, 20.44E	149	076°
Poland 54.46N, 18.28E	02.05.72	12.05.72	Russia 55.05N, 20.44E	149	076°
Russia 55.05N, 20.44E	25.04.94	00.10.94	Latvia 56.56N, 23.42E	276	042°
Russia 55.05N, 20.44E	15.09.58	18.04.59	Russia 58.58N, 30.59E	755	055°
Russia 55.05N, 20.44E	14.10.67	29.04.68	Russia 60.13N, 53.50E	2,049	074°
Parus montanus					
Poland 54.21N, 19.19E	03.10.83	15.04.84	Russia 55.05N, 20.44E	122	048°
Russia 60.41N, 32.56E	19.08.80	17.04.81	Finland 62.38N, 29.28E	284	321°
Garrulus glandarius					
Russia 55.05N, 20.44E	27.09.66	29.10.67	Latvia 56.17N, 26.43E	398	070°
Russia 55.05N, 20.44E	30.09.66	00.11.67	Estonia 58.08N, 24.57E	426	037°
Russia 55.05N, 20.44E	28.09.66	10.11.68	Estonia 58.11N, 24.54E	428	036°
Russia 55.05N, 20.44E	13.05.78	30.10.78	Estonia 58.37N, 25.05E	473	034°
Russia 55.05N, 20.44E	02.05.88	04.09.88	Estonia 8.17N, 27.17E	535	048°
Russia 55.05N, 20.44E	07.05.69	28.02.70	Russia 56.28N, 29.58E	597	075°
Russia 55.05N, 20.44E	13.05.62	01.03.65	Russia 58.12N, 28.58E	611	055°
Russia 55.05N, 20.44E	24.09.66	13.02.74	Russia 57.04N, 29.23E	616	059°
Russia 55.05N, 20.44E	17.05.62	12.09.64	Russia 55.35N, 30.43E	618	059°
Russia 55.05N, 20.44E	01.10.65	29.01.69	Russia 55.35N, 30.43E	635	075°
Russia 55.05N, 20.44E	03.05.65	18.09.66	Russia 57.59N, 30.12E	664	061°

Ringing site	Ringing date	Recovery date	Recovery site	Distance, km	Direction, degrees
Russia 55.05N, 20.44E	25.09.61	26.03.63	Russia 55.55N, 31.15E	668	082°
Russia 55.05N, 20.44E	25.09.61	26.03.63	Russia 57.28N, 30.49E	676	067°
Russia 55.05N, 20.44E	01.10.74	12.02.76	Russia 57.33N, 31.48E	735	038°
Russia 55.05N, 20.44E	28.09.61	09.09.62	Russia 57.20N, 32.20E	759	071°
Russia 55.05N, 20.44E	25.09.61	14.02.63	Russia 57.19N, 32.34E	772	071°
Russia 55.05N, 20.44E	05.10.64	16.01.66	Russia 56.17N, 33.10E	790	080°
Russia 55.05N, 20.44E	12.05.66	12.09.70	Russia 58.11N, 34.51E	919	068°
Russia 55.05N, 20.44E	04.05.86	24.12.89	Russia 58.36N, 39.50E	1,225	071°

4. Discussion

Lack of significant periodicity of irruptions in the species studied suggests that annual fluctuations of their numbers are most probably governed by the environmental factors which show no clear periodicity. This factor could be the ambient temperature in spring (Tab. 4; see also Markovets & Sokolov, this volume). It has been shown that in years with warm and early spring, breeding performance of some *Sylvia* warblers on the Courish Spit is significantly higher than in later and cold years (Payevsky 1999). This causes a considerable rise in juvenile numbers in many passerines, irruptive species included, both during the post-fledging period and during autumn passage (Sokolov 1999, Sokolov et al. 2000). In such years, outbreaks of numbers were recorded in irruptive species also at other Baltic sites: in Kabli (Estonia), near Lakes Pskovskoye and Chudskoye (Russia), in Pape (Latvia), Ottenby (Sweden), Vistula Spit (Mierzeja Wiślana) and Hel Spit (Poland) (Veromann 1965, Baltvilks 1970, Meshkov et al 1976, Baumanis & Celminš 1993, Busse 1994, Pettersson 1977, Sokolov et al 2001). Further warming of climate in the northern hemisphere, if it occurs, will cause increasing frequency of irruptions in our area. Some authors suggested a relationship between Coal Tit irruptions and crops of spruce seeds which has a period of 6-8 years (Karelin & Azovsky 1988) but our data do not support this.

The relationship between irruptions in some species may be caused by their similar foraging strategies (e.g. food caching by Coal and Willow Tits) and by the similar influence of the environmental factors like air temperature.
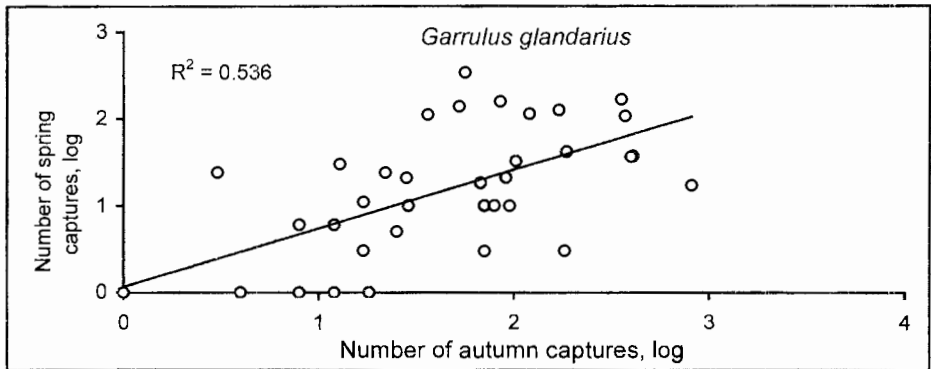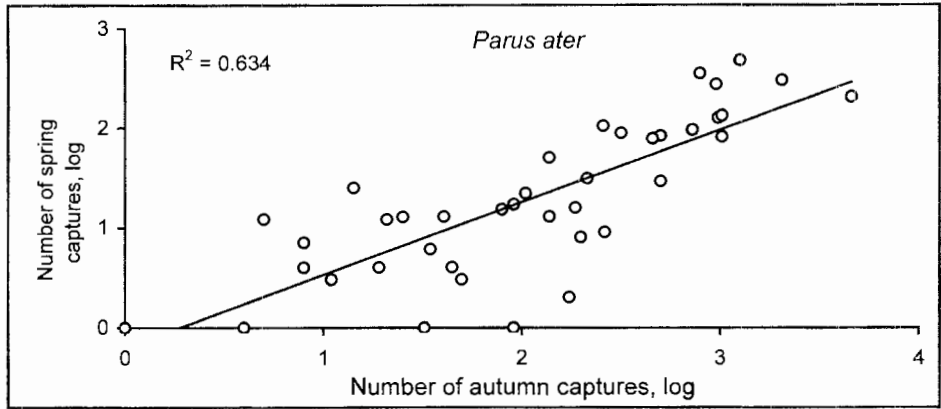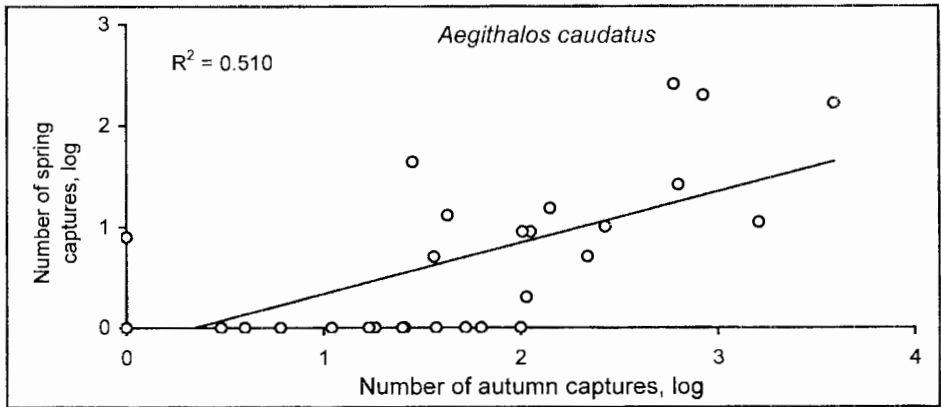
Figure. Correlation between the autumn numbers and number of spring captures in the subsequent year in some irruptive species on the Courish Spit. Numbers are log-transformed.

The presence of highly significant correlation between autumn numbers of juveniles and their spring trapping figures suggests that some birds survive irruption and move in spring in the reverse direction. Direct long-distance recoveries support this (Tab. 5). In Nutcrackers and Jays, long-distance movements towards the breeding areas were even recorded in the autumn of irruption (Bolshakov et al. 2001c). All this obviously contradicts the hypothesis that irruptions serve to eliminate the surplus of juveniles (Dolnik 1975). This author believes that "unlike migration, irruptions are adaptive not for those who move but for those who stay. Irruptions are sporadic, non-adaptive for their participants who never come back. The behaviour and direction of movement of the birds which take part in an irruption are superficially similar to migration, but in fact have nothing to do with it. Unlike irruptions, migrations are regular, adaptive for their participants and terminate by coming back home" (Dolnik 1975, pp. 66-67). Another author wrote that "irruptions have sometimes been explained as a mechanism for removing surplus numbers, a form of race suicide, but if all the individuals taking part in such movements had died, the irruptive habit would presumably have been eliminated from the species by natural selection. Actually the view formerly held that the irrupting individuals merely stay around in the invasion areas and gradually die out is mistaken. Return movements, though less prominent than the invasions, have been seen sufficiently often to show that they are regular, at least in the Nutcracker, Jay, Waxwing and Crossbill (Heidemann & Schüz 1936, Putzig 1938, Tischler 1941)" (Lack 1954, p. 232).

Irruptions in many species are indeed not that much different from regular migration as it is usually assumed. First, in the areas of mass breeding of the irruptive species their autumn movements for rather long distances are recorded nearly each year (data from Estonia, Bolshakov et al. 2001a, b), i.e. they are regular. These movements look sporadic only in the regions situated far from the breeding areas. Secondly, even though most juveniles in irruptive species probably die during their first winter (exactly like in most migratory passerines, Payevsky 1985), some proportion of them (possibly *ca.* 20-25%) survive until winter and start moving towards the breeding areas. Thus, not only autumn migration is typical of the irruptive species (usually towards to south, southwest and west), but also return spring migration (towards the north, northeast and east). Thirdly, as shown by the data from autumn and spring passage on the Courish Spit, many individuals have considerable fat stores, like regular migrants (Shapoval 1989).

On the basis of all this, we conclude that irruptions in the species studied which are traditionally believed to be sedentary, are in fact a variant of seasonal migration with the features typical of this phenomenon: (1) long distance of the movements; (2) directed movements in autumn and in spring; (3) accumulation of fuel stores; (4) typical migratory behaviour.

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