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Long-term monitoring of Great Spotted Woodpecker *Dendrocopos major* irruptions in the Baltic region and Karelia

Leonid V. Sokolov, Anatoly P. Shapoval & Marina V. Yakovleva

Abstract: Sokolov L.V., Shapoval A.P. & Yakovleva M.V. (2013): Long-term monitoring of Great Spotted Woodpecker *Dendrocopos major* irruptions in the Baltic region and Karelia. *Avian Ecol. Behav.* 24: 3–33.

Winter and summer counts of Great Spotted Woodpeckers in Karelia during 43 years (1970–2013) revealed significant fluctuations. Analysis of capture data in the Baltic region during 65 years (1948–2013) also showed large annual variation, from 0 to 1058 individuals. Winter and breeding period numbers of these birds in Karelia were positively related to summer and autumn numbers in the Baltic region. Numbers in both regions were significantly directly related to spruce seed crops in the preceding year and inversely related to the crops in the current year. Of 10 years with strongest irruptions of Great Spotted Woodpeckers in the Baltic region, five irruptions occurred in years with poor spruce seed crops and five in years with good crops. This fact puts into question the hypothesis that Great Spotted Woodpecker irruptions are caused by deficit of conifer seeds in the years of poor crops. Numbers of juveniles in the Baltic region showed no significant relationship with North Atlantic Oscillation index NAO_{DJFM} or with regional air temperatures. Timing of postfledging dispersal in the Baltic region underwent long-term change during the study period and was inversely related to spring air temperature in the region. The date of onset of postfledging movements was inversely related to late summer numbers of juveniles in the Baltic area. Our main conclusion is that after the years with good spruce seed crops numbers of Great Spotted Woodpeckers that survive winter and start breeding increases which causes production of a large number of juveniles that take place in irruptions in late summer and autumn. We suggest that irruptions are triggered not by food shortage, as commonly assumed, but some other trigger, possibly related to intraspecific competition and aggression under high population density, as known from other irregular migrants.

Key words: *Dendrocopos major*, Great Spotted Woodpecker, long-term dynamics of numbers, irruptions, invasion, cone crops, ambient temperature, NAO index, timing of dispersal

Address: L.V.S., A.P.S.: Biological Station "Rybachy", Zoological Institute RAS, Rybachy 238535, Kaliningrad Region, Russia. E-mail: leonid-sokolov@mail.ru

M.V.Y.: Kivach State Nature Reserve, Kivach 186220, Kondopoga Region, Karelia, Russia. E-mail: kivach-bird@rambler.ru

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1. Introduction

The range of Great Spotted Woodpeckers *Dendrocopos major* L. includes most of the Palaearctic. In Europe this species occurs nearly everywhere, except of northernmost Scandinavia, Arctic Russia, steppes and high mountains (Cramp 1985). Practically throughout their range Great Spotted Woodpeckers are common. Central and southern population of this species are strongly sedentary throughout the year, whereas northern populations may show eruptive behaviour in some seasons (Cramp 1985). In these populations not only juveniles, but also some adults may perform in autumn pronounced movements searching for their main food, conifer seeds. At Finnish observatories, erupting birds included 6–12% adults in different autumns, and adult males perhaps were slightly outnumbered by adult females (Hildén 1974).

Juvenile Great Spotted Woodpeckers, like juveniles of other avian species, after brood disintegration perform postfledging dispersal, which results in them leaving their natal areas and settling in its vicinity (Michalek 1999, Pechacek 2006). This spatial redistribution of juveniles not only leads to colonization of novel areas, but also helps to avoid the negative consequences of overpopulation and inbreeding (Lack 1954, Sokolov 1997, Newton 2008). In small samples of recoveries from breeding season ringing in West and East Germany, Switzerland, and Czechoslovakia, most found within 10 km of birthplace, very few exceeding 50 km, and with adults in particular showing sedentary behaviour (Cramp 1985).

After postfledging dispersal, juveniles from northern populations may participate in massive autumn movements which are usually believed to be related to failing crops of conifer seeds (Pynnönen 1943, Lack 1954, Pulliainen 1963, Eriksson 1971, Formozov 1976, Malchevsky & Pukinsky 1983, Švažas & Žalakevičius 1991, Coulson & Odin 2007, Lindén et al. 2011). In such years in Europe autumn vagrants have been recorded up to the Arctic coast and down to steppe regions (Dementiev & Gladkov 1951, Cramp 1985, Ryabitshev 2001). Migrating and wintering Great Spotted Woodpeckers were reported from offshore islands. For instance, on Finnish island Sääpi near the town of Pori ca. 10 000 Great Spotted Woodpeckers were counted (Cramp 1985). Small numbers of northern birds were recorded more or less regularly south to Alps, western France, Britain, and Ireland, and exceptionally to southern France, Faeroes, and Iceland. Significant irruptions into Britain in October 1949 and October 1962 both coincided with anticyclonic conditions over north-west Europe, with light easterly winds over North Sea (Williamson 1963). Lesser numbers reach Britain and Ireland in other years, and this 400 km sea-crossing exceeds crossings of Baltic, where birds tend to follow coasts and cross at narrows – Skagerrak, Kattegat, and Gulfs of Bothnia and Finland (Cramp 1985).

Great Spotted Woodpecker irruptions are irregular and occur with varying intervals. For instance, in former East Prussia strong irruptions occurred after 3–9 years: in 1903, 1909, 1914, 1919, 1929, 1935, 1939 (Tischler 1941). However, sometimes irruptions can happen in two successive years, e.g. in autumn 1929 birds of northern origin occurred in large numbers in East Prussia and England, and in 1930 in northern Italy (Lack 1954). Irregularity of irruptions of Great Spotted Woodpeckers is usually related to the irregular pattern of good crops of conifer seeds. In boreal and mixed

forests Great Spotted Woodpeckers forage since late October until March mainly on Scots pine *Pinus sylvestris* and spruce *Picea abies*, *P. obovata* seeds (Inozemtsev 1965, Hogstad 1971, Prokofyeva 1971, Eriksson 1971, Alatalo 1978, Bardin 1982, Osiejuk 1998, Kędra & Mazgajski 2001, Lukasz & Benkman 2011). In autumn and winter seeds are taken by birds directly from cones; in spring, when cones open and seeds start to fall from them, woodpeckers take the fallen seeds from the ground (Glazov et al. 1978). Conifer seed production, numbers and mass of seeds in pine and spruce seeds vary broadly in relation to latitude, forest type, tree age and weather conditions (Pravdin 1964, 1975; Velikainen 1974; Bobrov 1978). During cold rainy weather seed may fail to ripen, and during hot weather they may perish from heat and water loss. In European Russia conifer seeds usually ripen by late October. Weather conditions in spring, when generative organs are formed, and during blooming, also impact the crops. Pollination may be hampered by prolonged rains during the blooming period. The colder climate is, the lower is the seed quality. The mean mass of 100 seeds of whitewood *Picea abies* near St. Petersburg is 5 g, in Kola Peninsula it is 2 g. The crops decline in quantity and quality from south to north and from lower to higher altitude. Pests like Dark Pine Knot-horns *Dioryctria abietella* Schiff. and rust fungi Pucciniales significantly reduce the crops. They may affect up to 90% of cones.

Alternation of good and failing crops with a period of 3–4 years is typical of spruce (Svårdson 1957, Formozov 1976, Koenig & Knops 2000). In Scots pine in northern Europe, good crops occur every 4–5 years, but generally average crops prevail. Good crops of pine and spruce usually do not coincide (Hogstad 1993). Of spruce synchronization of crops over large areas is typical, whereas pine usually shows more fine-scale spatial variation (Danilov 1952, Koenig & Knops 1998). Pattern of crops makes pines a more reliable food source for Great Spotted Woodpeckers. However, when studying time and energy budgets of these woodpeckers in winter, Bardin (1982) showed that foraging on spruce seeds is ca. 70% more efficient than taking pine seeds. To obtain a similar gain in energy, a Great Spotted Woodpecker needs 1.7 times more time when it feeds on spruce seeds than when it takes pine seeds. The author believes that during northern winter, with its short daylength and low temperatures, this difference may be essential. On this basis, Bardin (1982) suggested that in the northern part of its range (where daylength in winter is below 6 hours) Great Spotted Woodpeckers should mainly forage on spruce seeds and be more mobile. In more southern areas these woodpeckers are trophically more related to Scots pine. This conifer species is believed to be a good indicator of forest condition on Europe (Mikusiński et al. 2001).

Pogorelov (1992) reported that in winter under air temperatures below -27°C Great Spotted Woodpeckers increase duration and intensity of foraging, resulting in energy expenditure augmentation by $7\text{ kJ}\cdot\text{day}^{-1}$. Thermoregulation costs increase by $38\text{ kJ}\cdot\text{day}^{-1}$, and daily energy budget increases from 158 to $198\text{ kJ}\cdot\text{day}^{-1}$. During periods of low temperatures, Great Spotted Woodpeckers cut down time spent on social contacts and other types of activity, but it does not result in significant sparing of energy during the short winter daylength, concludes the author. These birds manage to maintain their energy balance only due to increased intensity and duration of foraging.

It is generally believed that when food is sufficient, both adult and juvenile Great Spotted Woodpeckers are sedentary and occupy permanent home ranges (Pynnönen 1943, Inozemtsev 1965, Sirotkin 1976). Size of home range of single birds outside breeding season is dependent on type of woodland: it varies from 2 ha in mature *Quercus* oak to 25 ha in 120-year-old *Quercus* and pine (Cramp 1985). Bird may range up to ca. 1 km from roost in winter. In the breeding season, especially during nestling period, birds generally move within ca. 100–600 m of the nest, with movements up to 1100 m recorded (Cramp 1985). Great Spotted Woodpeckers show marked territorial aggression, more pronounced towards conspecifics of the same sex than those of the other sex, and most evident with occupation of breeding territories and defence mainly of certain key sites within them (Cramp 1985). Under high population density, aggression increases. When juvenile become self-sufficient, adults start to show aggressive behaviour towards them, forcing them to abandon natal areas. Siblings may roam across territory together for some time after independence, moving further away from general vicinity of the nest-hole after ca. 3 weeks (Cramp 1985).

Over five hundred papers are published on ecology of Great Spotted Woodpeckers (Pasinelli 2006). However, some important aspects of their biology remain poorly studied. For instance, just ca. 4% of publications deal with demographic issues (mortality and survival rates, immigration and emigration; Pasinelli 2006). Factors that cause irruptions in this species are not sufficiently known, either.

The aims of our study were:

- (1) to estimate annual fluctuations of Great Spotted Woodpecker numbers in winter, summer and autumn in Karelia and in the Baltic region;
- (2) to find out whether this species shows long-term trends in different seasons over >40 years;
- (3) to find out whether numbers in winter, autumn and during breeding season in different regions are related;
- (4) to find out which extrinsic factors (e.g. climate, foraging conditions) mainly influence long-term dynamics of numbers of Great Spotted Woodpeckers;
- (5) to elucidate the main causes of irruptions in this species.

2. Material and methods

2.1. Estimates of winter numbers

Winter numbers of Great Spotted Woodpeckers in Kivach State Nature Reserve which is located in the middle taiga zone in Russian Karelia (62°13'N, 34°00'E) [Fig. 1]. Estimates from counts of birds at permanent line transects with the total length of 26.5 km were made three times per winter (in December, January and February). Number of encounters per 1 km of transect was used as proxy for Great Spotted Woodpecker numbers. The counts were done separately in three habitats: pine forest, spruce forest, mixed deciduous and coniferous forest. The total length of winter line transects was ca. 3280 km.



Figure 1. Map of the study area. Squares show the location of the trapping stations. Kld means Kaliningrad region of Russia

2.2. Estimates of breeding numbers

Breeding numbers of birds in Kivach were estimated from transect counts made in May and June in pine, spruce and mixed deciduous and coniferous forests (Yakovleva 2011). Data on summer population density in 1970–1985, when transect length and positions varied, were taken from “Chronicles of Nature” of Kivach State Nature Reserve for the respective years. In 1986–2013, line transects were perma-

nent (54 km annually). As proxy for density we used number of breeding pairs per 1 km² in different forest types, and in 1986–2013 also the number of pairs encountered per 1 km of line transect (all habitats averaged). The total length of summer line transects was 2102 km.

2.3. Numbers estimates in the postbreeding period

Numbers of Great Spotted Woodpeckers in late summer and autumn in the Baltic region were estimated from trapping figures at field sites on the Baltic coast, in Estonia (Kabli, 58°01'N, 20°27'E), Latvia (Pape, 56°11'N, 21°03'E), Sweden (Ottenby, 56°12'N, 16°24'E; from Pettersson 1997, Lindström *et al.* 2007) and Russia (Courish Spit, 55°08'N, 20°42'E) [Fig. 1]. Trapping was performed on the Courish Spit from 1 June until 31 October, in Estonia from 2 August until 4 November, in Latvia from 1 August until 15 November, in Sweden from 25 July until 15 October. Both Rybachy-type and Heligoland traps were used, and also mist-nets (Sokolov *et al.* 2001).

2.4. Estimates of the timing of breeding

We used the season's first capture of a hatching-year Great Spotted Woodpecker in funnel traps at the "Fringilla" field site on the Courish Spit as a proxy of the timing of breeding of this species in the Baltic region. We have shown elsewhere that this is a valid proxy for several avian species (Sokolov & Payevsky 1998). In the years of early breeding juveniles typically are captured in earlier calendar dates than in the years with late breeding.

2.5. Climate and weather parameters

Climate change in the Baltic area and in Karelia were estimated from the long-term dynamics of the global winter and spring North Atlantic Oscillation (NAO) index and regional mean monthly air temperatures. Monthly NAO index values are used as the estimates of the general meteorological situation in Europe in winter and early spring (<http://www.cpc.ncep.noaa.gov/data/teledoc/teleindcalc.shtml>). 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 values 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 in northwest Europe (Hurrell 1995). Conversely, negative NAO index values indicate weaker westerlies and thus lower temperature and precipitation in this part of Europe. Monthly NAO indices are archived at the National Oceanic and Atmospheric Administration's Climate Prediction Center website. Regional mean monthly air temperatures were taken from the following website, updated monthly: <http://www.tutiempo.net/en/>, and from the local database of Kivach State Nature Reserve.

2.6. Estimates of conifer crops

The data on spruce crops in Karelia were kindly provided by S.B. Skorokhodova from Kivach State Nature Reserve (Skorokhodova & Scherbakova, in press). Spruce seed crops were scored following the Kapper scale (Kapper 1930). Score 0 means a complete lack of cones, fruits or seeds. Score 1 (very poor crops) means that cones, fruits or seeds are available in small number on isolated trees on forest edge and in negligible number within forest plots. Score 2 (poor crops) – fair and uniform crops on isolated trees and on forest edge and weak crops within plots. Score 3 (fair crops) – significant number of cones on isolated trees and on forest edge and weak crops within plots. Score 4 (good crops) means abundant crops on isolated trees and on forest edge and fair crops within middle aged and mature stands. Score 5 (very good crops) – abundant crops on isolated trees and on forest edge and on trees within middle aged and mature stands.

2.7. Statistical treatment

Annual variation of Great Spotted Woodpecker numbers was estimated from standard deviation (S.D.). Spearman's rank correlation as implemented in package STATISTICA 10.0 (StatSoft Inc. 2011) was used to test for relationships between bird numbers and various explaining variables (spruce crops, NAO index, mean monthly air temperatures, phenological events etc.)

3. Results

3.1. Dynamics of winter numbers of Great Spotted Woodpeckers in Kivach State Nature Reserve

Winter counts of Great Spotted Woodpeckers at line transects in December, January and February during 44 years (1972–2013) showed considerable annual variation within different habitats (Table 1). The greatest variation was recorded in spruce forest.

Great Spotted Woodpecker numbers showed a clear upward trend between the mid 1970s and 2000 in all habitat types studied (Fig. 2). After 2001, numbers of these birds declined, in spite of short-term spikes in 2007 and 2013.

3.2. Dynamics of breeding numbers of Great Spotted Woodpeckers in Kivach State Nature Reserve

Summer counts of Great Spotted Woodpeckers at line transects in May and June during 43 years (1970–2012) showed annual variation in the breeding period (Table 1). In all habitat types numbers showed several highs and lows (Fig. 3). Great Spotted Woodpecker numbers peaked in the early 1970s, first half of the 1980s and during the 1990s. After 2001, a decline has started that is still continuing.

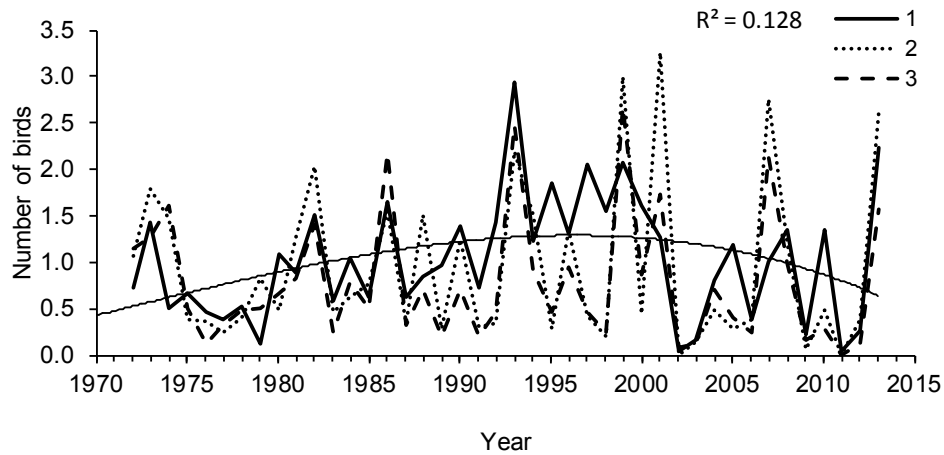


Figure 2. Long-term dynamics and trend of winter numbers of Great Spotted Woodpeckers in Kivach State Nature Reserve, Karelia. Number of birds per 1 km of line transect in different habitats: 1 – pine forest, 2 – spruce forest, 3 – deciduous and mixed forest. The trend line (for pine forest) is fitted by third degree polynomial regression $y = -2E-05x^3 + 0.146x^2 - 287.58x + 188842$. R^2 shows the explained variance.

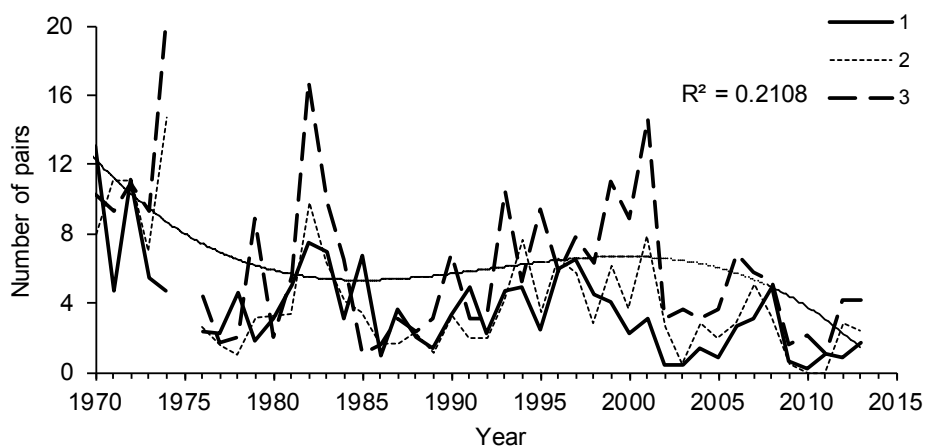


Figure 3. Long-term dynamics and trend of breeding numbers of Great Spotted Woodpeckers in Kivach State Nature Reserve, Karelia. Number of birds per km^2 in different habitats: 1 – pine forest, 2 – spruce forest, 3 – deciduous and mixed forest. The trend line (for mixed forest) is fitted by third degree polynomial regression $y = -1E-05x^4 + 0.0962x^3 - 284.53x^2 + 373779x - 2E+08$. R^2 shows the explained variance.

Table 1. Fluctuation of winter and breeding numbers of Great Spotted Woodpeckers in different habitat in Kivach State Nature Reserve in Karelia, 1970–2013.

Year	Winter numbers				Breeding numbers			
	Number of birds per 1 km line transect				Pairs·km ⁻²			Pairs per 1 km of line transect
	Pine forest	Spruce forest	Mixed forest	Habitats pooled	Pine forest	Spruce forest	Mixed forest	Habitats pooled
1970					13.10	8.00	10.30	
1971					4.70	11.10	9.30	
1972	0.73	1.07	1.15	0.98	11.10	11.10	10.90	
1973	1.43	1.79	1.28	1.50	5.50	7.00	9.30	
1974	0.50	1.48	1.60	1.19	4.70	14.70	20.10	
1975	0.66	0.38	0.49	0.51				
1976	0.46	0.36	0.12	0.32	2.40	2.60	4.40	
1977	0.39	0.24	0.33	0.32	2.20	1.60	1.70	
1978	0.53	0.41	0.48	0.47	4.60	1.00	2.00	
1979	0.13	0.83	0.49	0.48	1.80	3.20	8.90	
1980	1.08	0.48	0.66	0.74	3.10	3.30	2.00	
1981	0.89	1.27	0.82	0.99	5.00	3.40	5.60	
1982	1.50	2.03	1.40	1.64	7.50	9.80	16.80	
1983	0.58	0.46	0.25	0.43	7.00	6.40	9.80	
1984	1.04	0.62	0.78	0.81	3.10	4.10	6.50	
1985	0.62	0.76	0.49	0.62	6.70	3.50	1.10	
1986	1.66	1.55	2.18	1.79	1.01	1.64	1.57	0.37
1987	0.62	0.34	0.33	0.43	3.69	1.64	3.14	0.74
1988	0.85	1.51	0.70	1.02	2.01	2.30	2.35	0.59
1989	0.96	0.27	0.21	0.48	1.34	1.10	3.14	0.31
1990	1.39	1.24	0.70	1.11	3.35	3.29	6.80	0.79
1991	0.73	0.31	0.21	0.42	4.92	1.97	3.14	0.68
1992	1.43	0.34	0.45	0.74	2.23	1.97	3.14	0.46
1993	2.93	2.20	2.47	2.53	4.69	4.17	10.46	1.11
1994	1.23	1.51	0.91	1.22	4.92	7.67	5.23	1.24
1995	1.85	0.27	0.45	0.86	2.46	3.51	9.42	0.83
1996	1.31	1.34	0.95	1.20	6.03	6.58	5.75	1.26
1997	2.04	0.41	0.45	0.97	6.48	5.70	7.85	1.29
1998	1.54	0.21	0.25	0.66	4.47	2.85	6.28	0.83
1999	2.08	2.99	2.67	2.58	4.02	6.14	10.98	1.24
2000	1.62	0.45	0.86	0.98	2.23	3.73	8.89	0.81
2001	1.27	3.26	1.73	2.09	3.13	7.89	14.65	1.44
2002	0.04	0.00	0.08	0.04	0.45	2.63	3.14	0.37

Table 1. *Continued*

Year	Winter numbers				Breeding numbers			
	Number of birds per 1 km line transect				Pairs·km ⁻²			Pairs per 1 km of line transect
	Pine forest	Spruce forest	Mixed forest	Habitats pooled	Pine forest	Spruce forest	Mixed forest	Habitats pooled
2003	0.15	0.14	0.12	0.14	0.45	0.44	3.66	0.20
2004	0.81	0.48	0.70	0.66	1.34	2.85	3.14	0.46
2005	1.19	0.27	0.41	0.63	0.89	1.97	3.66	0.37
2006	0.39	0.38	0.25	0.34	2.68	2.85	6.80	0.70
2007	1.00	2.75	2.14	1.96	3.13	5.04	5.75	0.89
2008	1.35	1.20	0.99	1.18	4.92	3.29	5.23	0.87
2009	0.23	0.07	0.16	0.15	0.67	0.44	1.57	0.15
2010	1.35	0.48	0.29	0.71	0.22	0.00	2.09	0.09
2011	0.04	0.00	0.00	0.01	1.10	0.00	1.05	0.13
2012	0.27	0.38	0.12	0.26	0.88	2.87	4.22	0.46
2013	2.24	2.61	1.56	2.17	1.74	2.43	4.23	0.50
Min	0.04	0.00	0.00	0.01	0.22	0.00	1.05	0.09
Max	2.93	3.26	2.67	2.58	13.1	14.7	20.1	1.44
Mean	1.03	0.93	0.78	0.91	3.67	4.13	6.19	0.69
S.D.	0.65	0.86	0.68	0.65	2.72	3.25	4.32	0.39

3.3. Long-term trends in numbers of Great Spotted Woodpeckers in summer and autumn in the Baltic region

Trapping figures of hatching-year Great Spotted Woodpeckers in the Baltic region over 65 years (1948–2013) show strong annual fluctuations, ranging from 0 to 1058 individuals (Table 2). The mean annual trapping figures varied between 16 (in Ottenby on Öland) and 47 (on the Courish Spit) individuals. Periods of comparatively high and low numbers of Great Spotted Woodpeckers in the study region are apparent (Fig. 4). The most pronounced irruptions occurred in the 1960s – early 1970s and again between the late 1990s and 2013. No trend was apparent throughout the study period (Fig. 4). Number of years between pronounced irruptions was 2–8 (Table 2). Over the whole study period, irruptions in two successive years have never been recorded.

On the basis of Courish Spit data we analysed summer and autumn numbers of hatching-year and after hatching-year birds separately for different months (Table 3). Trapping figures of juveniles peaked in August and September, of adults in June – July and in August. Adults comprised 13% in June and July, 8% in August, 4% in September and 7% in October. The proportion of adult males in captures was somewhat lower than of adult females, 43% vs. 57% (Table 3).

Table 2. Trapping figures of hatching-year Great Spotted Woodpeckers in summer and autumn in the Baltic region.

Year	Estonia (Kabli)	Latvia (Pape)	Russia (Courish Spit)	Sweden (Ottenby)	Baltic region pooled
1948				2	2
1949				50	50
1950				0	0
1951				0	0
1952				0	0
1953				15	15
1954				0	0
1955				2	2
1956				15	15
1957				13	13
1958				20	20
1959			10	2	12
1960			4	3	7
1961			10	5	15
1962			265	110	375
1963			27	28	55
1964			6	1	7
1965			5	8	13
1966			79	10	89
1967		1	6	2	9
1968		71	161	90	322
1969		4	3	1	8
1971	13	16	18	21	68
1972	122	167	153	107	549
1973	4	1	5	0	10
1974	439	416	158	45	1058
1975	25	49	13	37	124
1976	30	21	11	0	62
1977	13	4	1	1	19
1978	1	1	3	0	5
1979	28	11	16	13	68
1980	1	1	7	1	10
1981	194	74	74	46	388
1982	23	13	26	10	72
1983	53	11	33	2	99
1984	4	0	5	2	11
1985	7	6	11	24	48
1986	47	62	30	2	141
1987	9	21	2	0	32
1988	34	21	25	29	109
1989	1	1	19	0	21
1990	49	172	64	17	302

Table 2. *Continued*

Year	Estonia (Kabli)	Latvia (Pape)	Russia (Courish Spit)	Sweden (Ottenby)	Baltic region pooled
1991	14	6	2	3	25
1992	1	1	0	0	2
1993	21	7	9	4	41
1994	32	9	35	21	97
1995	5	0	5	0	10
1996	1	1	5	4	11
1997	13	18	46	7	84
1998	1	1	9	0	11
1999	59	46	146	13	264
2000		0	2	1	3
2001			419	119	538
2002			39	2	41
2003			15	21	36
2004			36	5	41
2005			22	7	29
2006			6	0	6
2007			6		6
2008			64		64
2009			110		110
2010			61		61
2011			2		2
2012			168		168
2013			109		109
Total	1246	1299	2594	941	6083
Mean	41.5	38.2	47.2	15.9	92.2
S.D.	85.3	79.1	75.6	27.7	170.7

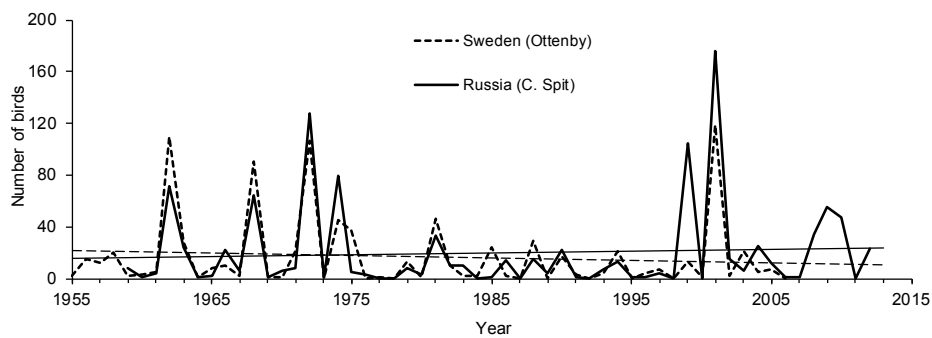


Figure 4. Long-term trends of autumn numbers of hatching-year Great Spotted Woodpeckers in the Baltic region.

Table 3. Numbers of adult (AD) and hatching-year (HY) Great Spotted Woodpeckers captured at the "Fringilla" field site on the Courish Spit (Baltic coast). M – males, F – females.

Year	June–July			August			September			October			Total		
	M AD	F AD	HY	M AD	F AD	HY	M AD	F AD	HY	M AD	F AD	HY	M AD	F AD	HY
1959	0	0	2	0	0	0	0	0	3	0	0	5	0	0	10
1960	0	0	3	0	0	0	0	0	1	0	0	0	0	0	4
1961	0	0	4	0	0	2	0	0	2	0	0	2	0	0	10
1962	2	0	27	12	14	167	1	0	16	4	0	55	19	14	265
1963	2	0	3	1	0	0	0	0	8	1	0	16	4	0	27
1964	0	0	4	0	0	1	0	0	1	0	0	0	0	0	6
1965	0	0	3	0	0	0	0	0	2	0	0	0	0	0	5
1966	1	2	32	1	1	25	1	0	17	0	0	5	3	3	79
1967	1	1	0	0	0	1	0	0	4	0	0	2	1	1	7
1968	1	3	23	2	5	74	4	1	40	3	1	24	10	10	161
1969	0	0	2	0	0	0	0	0	0	0	1	1	0	1	3
1970	1	0	4	0	0	20	0	0	4	0	0	2	1	0	30
1971	0	0	3	0	0	7	0	0	4	0	0	4	0	0	18
1972	1	1	8	0	0	17	0	0	93	3	1	35	4	2	153
1973	0	0	1	0	0	3	1	0	1	1	0	0	2	0	5
1974	5	7	18	5	10	61	1	7	57	3	0	22	14	24	158
1975	0	0	3	0	0	5	0	0	5	0	0	0	0	0	13
1976	0	0	5	0	0	3	0	0	0	0	0	3	0	0	11
1977	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1
1978	0	0	2	0	0	1	0	0	0	0	0	0	0	0	3
1979	0	1	6	0	0	2	0	0	4	0	0	4	0	1	16
1980	0	0	3	0	0	1	0	0	2	0	0	1	0	0	7
1981	0	1	12	1	3	29	0	0	16	0	0	17	1	4	74
1982	0	0	6	0	0	10	0	1	7	1	0	3	1	1	26
1983	1	0	11	0	1	12	0	0	8	0	0	2	1	1	33
1984	0	0	4	0	0	1	0	0	0	0	0	0	0	0	5
1985	0	0	7	0	0	3	0	0	0	0	0	1	0	0	11
1986	0	0	9	0	0	7	0	0	11	0	0	3	0	0	30
1987	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
1988	0	0	8	0	0	2	0	0	9	0	0	6	0	0	25
1989	0	0	12	0	0	3	0	0	2	0	0	2	0	0	19
1990	0	2	24	1	1	18	0	0	13	0	0	9	1	3	64
1991	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2
1992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	2	0	0	0	0	0	5	0	0	2	0	0	9
1994	1	1	7	1	0	15	0	0	8	0	1	5	2	2	35

Table 3. *Continued*

Year	June–July			August			September			October			Total		
	M AD	F AD	HY	M AD	F AD	HY	M AD	F AD	HY	M AD	F AD	HY	M AD	F AD	HY
1995	0	0	4	0	0	0	0	0	1	0	0	0	0	0	5
1996	0	0	4	0	0	0	0	1	0	0	0	1	0	1	5
1997	3	10	24	0	0	18	0	0	3	0	0	1	3	10	46
1998	0	0	9	0	0	0	0	0	0	0	0	0	0	0	9
1999	0	0	13	1	3	28	0	2	72	0	0	33	1	5	146
2000	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
2001	9	10	92	5	2	151	1	3	162	0	1	14	15	16	419
2002	1	0	8	0	0	16	0	0	11	0	0	4	1	0	39
2003	0	0	7	0	0	2	0	0	3	0	0	3	0	0	15
2004	1	1	4	1	1	7	0	0	7	0	1	18	2	3	36
2005	0	0	6	0	0	1	0	0	7	0	0	5	0	0	19
2006	0	0	4	0	0	1	0	0	0	0	0	1	0	0	6
2007	1	0	4	0	0	1	0	0	1	0	0	0	1	0	6
2008	0	0	20	0	0	10	0	2	26	0	1	8	0	3	64
2009	0	4	21	1	0	34	0	2	43	0	0	12	1	6	110
2010	0	1	6	0	0	8	0	0	34	0	1	13	0	2	61
2011	0	0	2	0	0	0	0	0	0	0	1	0	0	1	2
2012	3	5	76	0	0	69	0	0	22	1	1	1	4	6	168
Total	34	51	567	32	41	837	9	19	736	17	10	345	92	121	2485
Mean	0.6	0.9	10.5	0.6	0.8	15.5	0.2	0.4	13.6	0.3	0.2	6.4	1.7	2.2	46.0
S.D.	1.5	2.2	16.5	1.9	2.4	32.9	0.6	1.1	27.8	0.9	0.4	10.6	3.9	4.6	75.8

Table 4. Relationship between winter and breeding numbers of Great Spotted Woodpeckers in different habitats in Kivach State Nature Reserve, Karelia (Spearman's rank correlation: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Number of birds per 1 km line transect in winter	Number of breeding pairs			
	per 1 km ²			per 1 km line transect
	Pine forest	Spruce forest	Mixed forest	Habitats pooled
Pine forest	0.328*	0.485**	0.488**	0.567**
Spruce forest	0.395*	0.682***	0.681***	0.628***
Mixed forest	0.385*	0.493**	0.502***	0.687***
Habitats pooled	0.414*	0.583***	0.590***	0.720***

Table 5. Relationship between summer and autumn numbers of hatching-year Great Spotted Woodpeckers in the Baltic region and winter and breeding numbers in Kivach State Nature Reserve (Karelia) in the current year (Spearman's rank correlation: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

	Estonia (Kabli)	Latvia (Pape)	Russia (C. Spit)	Sweden (Ottenby)
Number of birds per 1 km line transect in winter	0.447*	0.373*	0.616***	0.539**
Number of breeding pairs per km ²	0.323	0.291	0.505**	0.504**

Table 6. Relationship between trapping figures of Great Spotted Woodpeckers in summer and autumn numbers on the Courish Spit and their numbers in the Baltic region (Spearman's rank correlation: ** $p < 0.01$, *** $p < 0.001$).

Month	Estonia (Kabli)	Latvia (Pape)	Sweden (Ottenby)
July	0.568***	0.570***	0.529**
August	0.570***	0.761***	0.652***
September	0.728***	0.738***	0.809***
October	0.682***	0.723***	0.745***

3.4. Relationship between winter, breeding and late summer and autumn numbers of Great Spotted Woodpeckers in Karelia and in the Baltic region

Numbers of breeding Great Spotted Woodpeckers in Kivach State Nature Reserve in all habitat types studied were significantly directly related to numbers in winter: the more birds wintered in the study area, the higher was the number of breeding pairs recorded there in May–June (Table 4).

A similar direct relationship was found between winter and breeding numbers of Great Spotted Woodpeckers in spruce forests in Kivach and late summer and autumn numbers of the same species in the Baltic region (Table 5). This is an important point that shows that if Great Spotted Woodpecker numbers are high in winter and in summer in Karelia, there is a good probability of recording an increased number of hatching-year birds in autumn in the Baltic region, in hundreds of kilometres (Estonia, Latvia) and more than 1000 km (Courish Spit) from Kivach. Summer numbers of Great Spotted Woodpeckers in different Baltic countries are also strongly correlated (Table 6).

3.5. Relationships between numbers of Great Spotted Woodpeckers in Karelia and the Baltic region and NAO index and regional temperature regimens

We tested for a relationship between fluctuations of numbers of Great Spotted Woodpeckers and NAO index of regional weather and regional temperature regimens

Table 7. Relationship between winter and summer numbers of Great Spotted Woodpeckers in Kivach State Nature Reserve (different habitats) and NAO index and mean seasonal air temperature in the current year in the study area (Spearman's rank correlation: * $p < 0.05$).

Month	Winter numbers				Breeding numbers			
	Individuals per 1 km line transect				Pairs per 1 km ²		per 1 km line transect	
	Pine	Spruce	Mixed forest	Habitats pooled	Pine	Spruce	Mixed forest	Habitats pooled
NAO _{DJFM}	0.369*	0.165	0.194	0.300*	-0.008	0.178	0.249	0.186
December	0.171	0.098	0.126	0.129	0.112	0.263	0.204	0.213
January	0.235	-0.076	0.022	0.115	-0.056	0.085	0.141	0.069
February	0.205	-0.147	0.033	0.103	-0.093	0.022	0.208	0.042
March					-0.193	-0.088	-0.053	-0.131
April					-0.197	0.027	0.096	-0.034

Table 8. Relationship between summer and autumn numbers of Great Spotted Woodpeckers in the Baltic region and NAO index and mean seasonal air temperature in the current year in the study area (Spearman's rank correlation).

Month	Estonia (Kabli)	Latvia (Pape)	Russia (Courish Spit)	Sweden (Ottenby)
NAO _{DJFM}	0.254	-0.103	0.090	-0.091
January	-0.039	-0.118	0.013	0.095
February	0.073	-0.091	0.093	-0.131
March	0.030	-0.110	0.108	-0.007
April	-0.004	-0.266	0.186	0.130
May	-0.032	-0.162	-0.014	0.057
June	-0.085	0.023	-0.071	-0.017
July	0.277	0.068	0.231	0.093
August	0.117	-0.055	0.186	0.200
September	0.131	0.098	0.167	0.216

in Karelia and in the Baltic region. Winter numbers in Kivach were significantly related only to winter and spring NAO index in one case: during warmer winters, numbers of wintering Great Spotted Woodpeckers were higher in pine forest (Table 7). No relationship with regional winter temperatures was shown.

Breeding numbers of Great Spotted Woodpeckers in Kivach were not related either to NAO in winter and spring, or to regional temperature regimen (Table 7). Summer and autumn trapping figures in the Baltic region were either not related to NAO index nor to regional mean seasonal temperatures (Table 8).

Table 9. Relationship between winter and summer numbers of Great Spotted Woodpeckers in Kivach State Nature Reserve (different habitats) and spruce seed crops in the preceding and current year (Spearman's rank correlation: + $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Spruce seed crops, score	Winter numbers				Breeding numbers			
	Individuals per 1 km line transect				Pairs per 1 km ²			
	Pine	Spruce	Mixed forest	Habitats pooled	Pine	Spruce	Mixed forest	Habitats pooled
Preceding year	0.181	0.558***	0.483**	0.484**	0.041	0.255	0.246	0.329*
Current year	-0.142	-0.378*	-0.347*	-0.302+	-0.369*	-0.351*	-0.255	-0.321*

3.6. Relationships between numbers of Great Spotted Woodpeckers in Karelia and the Baltic region and spruce seed crops

When we failed to associate Great Spotted Woodpecker numbers to such extrinsic factor as air temperature, we decided to test whether fluctuation of this species is related to crops of spruce seeds which is their main food in autumn and winter. We had long-term estimates of spruce seed crops in Kivach State Nature Reserve which we related to woodpecker numbers in winter and also during breeding and postbreeding periods.

Spruce seed crops varied strongly, from crops completely failing (score 0) or poor crops (score 1) to good (4) or very good (5) crops (Fig. 5). There is a weak tendency of increasing frequency of good crops in the recent two decades.

Winter and breeding numbers of Great Spotted Woodpeckers in Kivach showed a significant or marginally insignificant positive correlation with spruce seed crops in the preceding year. Correlation with crops in the current year was negative (Table 9).

In the Baltic region numbers of Great Spotted Woodpeckers were also related to spruce seed crops in Karelia: irruptions of hatching-years birds usually occurred after the years with good spruce crops (Table 10, Fig. 6). Numbers of Great Spotted Woodpeckers on the Courish Spit in September and October were stronger related to spruce productivity than trapping figures in July and August was (Table 11).

3.7. Long-term change of the timing of postfledging dispersal of Great Spotted Woodpeckers on the Courish Spit on the Baltic Sea

Long-term trapping data in funnel traps of hatching-year Great Spotted Woodpeckers in the postfledging period on the Courish Spit allowed us to test whether the timing of postfledging dispersal showed a trend over the study period. First hatching-year birds were captured in earlier calendar dates in the 1980s as compared to

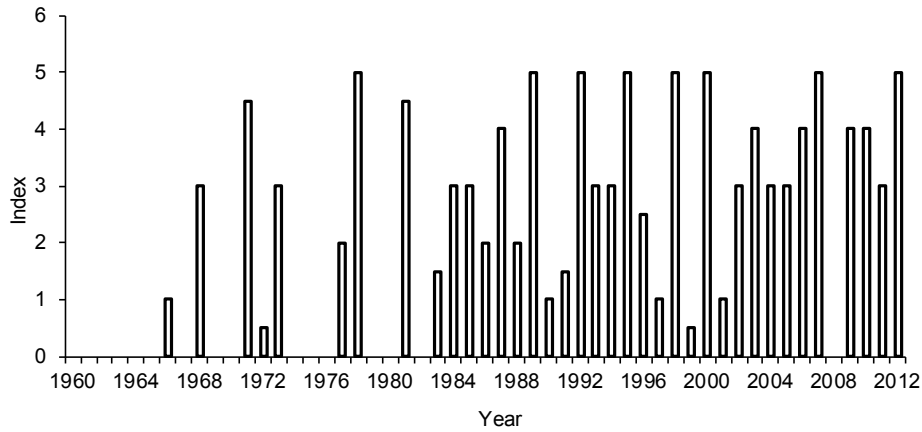


Figure 5. Long-term dynamics of spruce seed crops (scored from 0 to 5) in Kivach, Karelia.

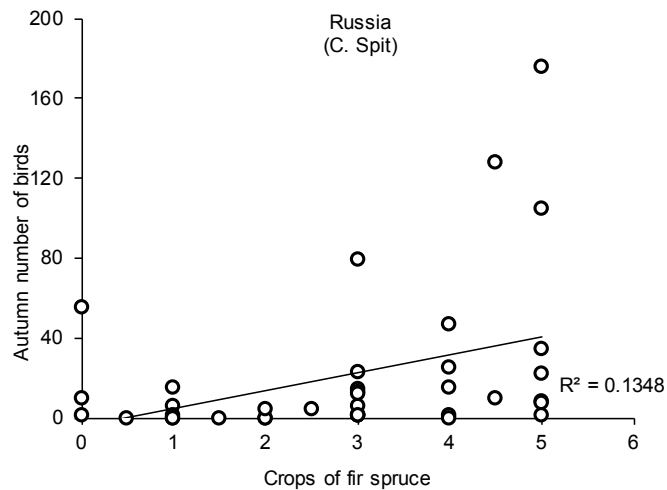


Figure 6. Relationship between Great Spotted Woodpecker numbers in the study region and spruce crops (scores) in Karelia in previous year.

Table 10. Relationship between summer and autumn numbers of Great Spotted Woodpeckers in the Baltic region and spruce seed crops in the preceding and current year (Spearman's rank correlation: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Spruce seed crops, score	Estonia (Kabli)	Latvia (Pape)	Russia (Courish Spit)	Sweden (Ottenby)
Preceding year	0.428*	0.518**	0.479**	0.636***
Current year	-0.657***	-0.581**	-0.433**	-0.512**

Table 11. Relationship between summer and autumn numbers of Great Spotted Woodpeckers on the Courish Spit and spruce seed crops in the preceding and current year (Spearman's rank correlation: * $P < 0.05$, ** $P < 0.01$).

Spruce seed crops, score	July	August	September	October
Preceding year	0.252	0.189	0.361*	0.496**
Current year	-0.401*	-0.469*	-0.496**	-0.428**

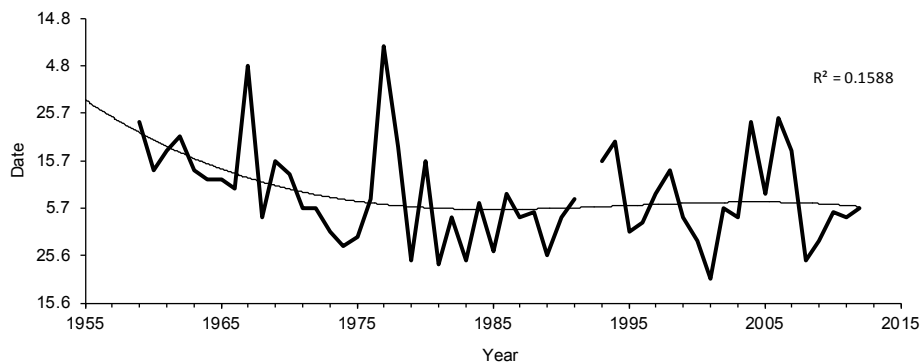


Figure 7. Long-term fluctuations of the onset of postfledging dispersal of Great Spotted Woodpeckers on the Courish Spit. The trend line (for mixed forest) is fitted by third degree polynomial regression $y = -0.0004x^3 + 2.5994x^2 - 5184.7x + 3E + 06$. R^2 shows the explained variance.

Table 12. Relationship between the date of first capture of a hatching-year Great Spotted Woodpeckers on the Courish Spit with air temperature in the study area (Spearman's rank correlation: * $P < 0.05$).

Month	Russia (Courish Spit)
January	0.030
February	-0.040
March	-0.193
April	-0.117
May	-0.357*
June	-0.171
July	-0.085

Table 13. Relationship between the date of first capture of a hatching-year Great Spotted Woodpeckers on the Courish Spit with trapping figures in summer and autumn (Spearman's rank correlation: * $P < 0.05$, ** $P < 0.01$).

	July	August	September	October
Capture date	-0.402**	-0.319*	-0.271*	-0.152

the 1960s and 1970s (Fig. 7). First capture date of a juvenile was significantly related to the mean monthly air temperature in May, with higher temperatures followed by earlier captures (Table 12).

Apart from this, the date of the first capture was significantly related to trapping figures in the postfledging period: the earlier juvenile Great Spotted Woodpeckers were captured, the higher were the numbers of hatching-year birds in the study area were (Table 13).

4. Discussion

4.1. Dynamics of Spotted Woodpecker numbers in Karelia and in the Baltic region

Numbers of Great Spotted Woodpeckers vary broadly on the annual basis, both in winter and during the breeding and postbreeding periods (Tables 1–3, Figs. 2–4). Moreover, numbers of this species showed long-term fluctuations, when prolonged periods of low numbers are alternated with the peaks (Figs. 2–4). However, no overall trend across the whole study period (1948–2013) was apparent (Fig. 4). In other European countries – Poland, UK, and France – numbers of this species also are generally stable (Bavoux 1985, Glue & Boswell 1994, Mazgajski 2002). In Austria, Croatia and Albania declines were recorded (Cramp 1985, Michalek *et al.* 2001). Increasing Great Spotted Woodpecker numbers were recorded in the late 20th century in the Netherlands, Belgium, Ukraine, Belarus and Finland (Cramp 1985).

The most pronounced fluctuations in numbers of Great Spotted Woodpeckers are recorded in the postbreeding period and in autumn, when hatching-year birds start their movements. Even though Great Spotted Woodpeckers are generally sedentary, in northern populations massive summer and autumn movements of juveniles occur, called irruptions. In such year these birds are recorded in large numbers in different regions, often hundreds of kilometres apart (Table 3, Fig. 4). Numbers of juveniles recorded during irruption years in different countries in the Baltic region are strongly correlated (Table 6). Moreover, we found a significant direct relationship between winter and breeding numbers of Great Spotted Woodpeckers in Karelia and their summer and autumn numbers in different Baltic countries. It suggests that in this species the peaks of numbers in different parts of its range do not occur randomly, but are caused by a common factor that acts across a large geographical area.

Ring recovery data show that during autumn irruptions, hatching-year Great Spotted Woodpeckers can cover large distances, up to several hundred kilometres

from their natal places (Kovalev & Smirnov 1995). For instance, a juvenile ringed in Finland (61°12'N, 24°22'E) on 23 June 1957 was recovered on 5 December 1957 in Leningrad Region (59°50'N, 30°56'E), 390 km from its natal site. Another bird ringed as a nestling at the Ladoga Ornithological Station in Leningrad Region (60°41'N, 32°56'E) on 13 June 1993 was recovered in Finland (60°27'N, 22°47'E) on 1 November 1993, 555 km from the ringing site. A third bird ringed at the same station on 28 June 1988 was recovered on Öland in Sweden across the Baltic Sea (57°10'N, 16°56'E) on 5 November 1988, 997 SW of its ringing place. Cramp (1985) reports the longest recoveries in same autumn-winter: Finland (August) to Orel Region, Russia (October), 1280 km SE; Kaliningrad, Russia (August) to Belgium (November), 1200 km WSW; southern Norway (nestling) to Basses-Pyrénées, France (January), 1830 km SW. British authors report that Great Spotted Woodpeckers, probably originating from Scandinavia and Russia, reach the mainland of Britain every year (Cramp 1985, Smith 2002, Coulson & Odin 2007). Thus, during autumn irruptions hatching-year Great Spotted Woodpeckers may perform large long-distance movements, mainly towards the west, south-west and south, like other generally sedentary species, e.g. Coal Tit *Parus ater*, Long-tailed Tit *Aegithalos caedatus*, Nutcracker *Nucifraga caryocatactes*, Jay *Garrulus glandarius* and some others that may perform irruptions (Markovets & Sokolov 2002; Sokolov et al. 2002, 2003, 2004; Ananin & Sokolov 2009; Babushkina & Bojarinova 2011). Adult Great Spotted Woodpeckers participate in these movements in small numbers (Table 3).

Sometimes spring movements of Great Spotted Woodpeckers are recorded in late February – mid April that are less conspicuous than autumn ones. For instance, in March 1970 pronounced movements of Great Spotted Woodpeckers (up to 25 individuals per 30 min of observations) towards the north-east were recorded on the southern coast of Gulf of Finland (D. Nankinov in: Malchevsky & Pukinsky 1983). Some ring recoveries suggest that spring movements may be rather distant: from Wangerooze, NW Germany (September) to Halsingland, Sweden (February, 5 years later), 1025 km NNE; Dresden, E Germany (late July) to southern Finland (June, at nest), 1200 km north-east; Bouches-du-Rhône, France (present October 1956–January 1957) to Mordovia, Russia (May 1958), 3070 km north-east; Finland (March) to Udmurtia, Russia (May, same year), 1940 km ESE; Finland (March) to Nizhny Novgorod, Russia (May, 2 years later), 1280 km east (Cramp 1985). It does not however rule out that some birds may remain to breed in the areas that they have reached during their irruptive movements (Eriksson 1971, Newton 2006).

4.2. Possible causes of irruptions in Great Spotted Woodpeckers

We first tested the hypothesis that fluctuations of Great Spotted Woodpecker numbers are related to climate change in Europe in the recent 50 years. It has been shown by a number of authors that climate change has significantly influenced long-term dynamics of many avian species, passerine and others (Berthold et al. 1998; Sokolov 1999; Sillett et al. 2000; Sokolov et al. 2000, 2001, 2002, 2003, 2012; Payevsky et al. 2003; Sæther et al. 2004; Both et al. 2006; Sanderson et al. 2006; Visser et al. 2004; Knape et al. 2009; Zwartz 2009; Jones & Cresswell 2010; Saino et al. 2011;

Wilson et al. 2011; Virkkala & Rajasärkkä 2011; Jiguet et al. 2012). This effect has been recorded also in irruptive species (Wiktander et al. 2001; Markovets & Sokolov 2002; Sokolov et al. 2002, 2003, 2004; Pasinelli 2006; Steen et al. 2006; Selås et al. 2008; Ananin & Sokolov 2009).

We tested for a relationship between winter and breeding numbers of Great Spotted Woodpeckers in Karelia with NAO weather index and regional air temperature. No significant relationships were found, except of one case of positive correlation between winter numbers in pine forests in Kivach State Nature Reserve and winter and spring NAO index (Table 7). No relationship was found between weather parameters and summer and autumn numbers of Great Spotted Woodpeckers in the Baltic region (Table 8). Thus, the hypothesis of climatic influence on the long-term dynamics of Great Spotted Woodpecker numbers is not supported by our data.

What other environmental factors may govern the irruptions of Great Spotted Woodpeckers? Many authors implicate food resources. Great Spotted Woodpeckers forage on conifer seeds during a large portion of the year, but switch to animal food during breeding (Lack 1954, Cramp 1985). Their nestlings are mainly fed on insects, their larvae, caterpillars etc. In summer in Leningrad Region adults take themselves and feed their young mainly on open-living insects, including ants and their pupae (ca. 50%), beetles and their larvae, caterpillars, ichneumonids, plant louses, tipulid dipterans (Pospelov 1956, Prokofieva 1971). One may hypothesise that woodpeckers, like songbirds, in years with large abundance of prey (these are usually the years with early and warm spring) increase their productivity by laying more eggs and successfully raising more young. Clutch size in Great Spotted Woodpeckers may vary between 3 and 8 eggs (on average 5–6; Cramp 1985, Ryabitsev 2001). Insect abundance is known to depend on ambient temperature. However, in Great Spotted Woodpeckers we found no relationship between numbers of hatching-year individuals and air temperature (Table 8), unlike many songbirds and Lesser Spotted Woodpeckers *Dendrocopos minor* (see below).

We then tested for a relationship between numbers of Great Spotted Woodpeckers in Karelia and the Baltic region and spruce seed crops, which is a preferred food of these birds in the non-breeding season. Both winter and breeding numbers in Karelia were significantly or marginally insignificantly positively related to spruce seed crops in the preceding year (Table 9). This relationship has been reported from Kivach State Nature Reserve (Zakharova 1991; Yakovleva 2007, 2001) and from Pinega nature reserve in Archangel Region (Rykova 2007). It is worth noting that we found a similar relationship between spruce crops in Karelia and Great Spotted Woodpecker numbers in the Baltic region (Table 10, Fig. 6), with this relationship being significant for September and October captures but not for birds trapped in July and August (Table 11). It suggests that Great Spotted Woodpeckers migrating through the Courish Spit in autumn may have northern origin.

Thus, late summer and autumn irruptions of Great Spotted Woodpeckers occur in the years following good spruce seed crops. How do population numbers increase if breeding productivity in this species is not related to spruce seed availability, as nestlings are fed on animal food? Numbers of juveniles may increase because in winters following autumns with good conifer seed crops, winter mortality rate

decreases, so that more birds start breeding following spring than after years with poor or failing crops of conifer seeds. Unfortunately, there are no good data showing that winter mortality rate of Great Spotted Woodpeckers depends on conifer seed availability. However, in the years with failing crops woodpeckers are reported to abandon their winter territories and roam broadly, probably searching for food. It is thus likely that during food shortages, winter mortality rate may increase. Mori (2009) studied population maintenance mechanisms in Great Spotted Woodpeckers in a fragmented forest landscape on Hokkaido (Japan). On the basis of observations of colour-ringed and radio-tagged individuals, the author found that annual survival rate (calculated as the proportion of marked breeding birds that survived and bred in both year and the following year in the study site) varied broadly, from 23 to 63%. Mori (2009) reported that the survival rate had significant positive correlation with the Korean pine seed crops ($r_s = 0.95$, $P = 0.01$, $n = 5$), but no relationship to winter air temperatures was found. However, the author believes that breeding population size was not determined by the adult survival rate, or the amount of seed crop. The number of natal dispersing immigrants seemed to be negatively affected by winter severity only when the seed crop was poor. Winter severity may increase mortality through energy shortage; it may be difficult to obtain sufficient net energy when the days are very cold and short, and when food resource are depleted (Grubb & Pravosudov 1994, Lahti et al. 1998, Mori 2009).

Swedish authors analysed the dynamics of Great Spotted Woodpecker numbers in 1975–1991 and found no correlation between population density in the breeding season and either winter air temperature or spruce seed supply (Nilsson et al. 1992). However, other researchers in Sweden and Finland suggested that the population density of Great Spotted Woodpeckers in the breeding season was correlated with winter severity (Hansson 1992, Saari & Mikusiński 1996). The latter authors analyzed long-term data (1979–95) and concluded that the density of this species was not correlated with seed crops of pine and spruce. Conversely, other authors who studied population dynamics of Great Spotted Woodpecker in southern Finland using log-linear state-space models for statistical analyses, found that population dynamics could be most successfully described with a density dependent model, where the natural logarithm of spruce cone availability in the previous autumn had a strong positive effect on population growth (Lindén et al. 2011). These authors concluded this was likely to be due to lower winter mortality and lower emigration rates resulting from plentiful food. They also suggested that although Great Spotted Woodpeckers used pine cones as a food resource in winter, the estimated impacts of pine cone crops on migration intensity and population dynamics were low, probably due to low annual variation in crops comparing to spruce cones.

Thus, there are good reasons to believe that after the years with good spruce seed crops, numbers of breeding Great Spotted Woodpeckers significantly increase, probably because of their higher survival rate. This, in its turn, results in production of a large numbers of juveniles. What makes hatching-year birds after gaining independence from their parents not only to settle in the vicinity of their natal place during postfledging dispersal, but to move to novel areas that may be hundreds of kilometres from their hatching places?

Most authors believe that Great Spotted Woodpecker irruptions are caused by failing crops of conifer seeds in their summer range. For example, Lindén et al. (2011) studied irruptive migrations and population dynamics in Great Spotted Woodpeckers in southern Finland and concluded that lack of spruce cones seems to be the triggering factor for irruptions. These authors claimed that neither irruptive migration, nor population dynamics showed any clear support for ratio-dependent regulation.

We analysed our data under this angle and did find a significant inverse relationship between the numbers of hatching-year Great Spotted Woodpeckers in the Baltic region in summer and autumn and spruce seed supply in the current year (Table 10). Moreover, a similar relationship was found between spruce crops in the current years and breeding and even winter numbers of woodpeckers in Kivach State Nature Reserve (Table 9). This is weird, taking into account that in the study region spruce cones do not ripen until late October, when their abundance is scored. It is difficult to imagine that hatching-year Great Spotted Woodpeckers that start their irruptive movements in summer, as shown by our data (Table 3), can foresee shortage of conifer seeds in autumn and start their movements away from the natal areas to avoid starvation. During winter surveys of Great Spotted Woodpeckers the cones are even not yet set! Juvenile Great Spotted Woodpeckers rarely forage on conifer seeds in July and August (Lack 1954, Malchevsky & Pukinsky 1983). Pine and spruce seeds do not become their main and nearly only food until much later, in November – March. In August – September woodpeckers, apart from insects, take bilberries, red whortleberries, rowanberries and elderberries. Of 10 years with the most pronounced irruptions in the Baltic region (Table 2), five occurred in years with poor spruce supply (1962, 1972, 1974, 1990, 1999) and five in years with good crops (1968, 1981, 2001, 2009, 2011) [Fig. 5]. If juvenile Great Spotted Woodpecker irruptions were triggered by failing conifer seed supply, most or all irruptions must have happened in the years with poor current crops. The significant negative correlation between Great Spotted Woodpecker numbers, both in Karelia and in the Baltic region, and current spruce cone crops is probably spurious. It is caused by the fact that a year with good seed supply is usually followed by a year of failing crops, thus forming this correlation with woodpecker numbers (Fig. 5).

On the basis of all these data, we suggest the irruptions of juvenile Great Spotted Woodpeckers are triggered not by the shortage of their future winter food, conifer seeds, but by other factors, probably within-population one. In the year when many juveniles are produced in the population, the frequency of inter-individual conflicts and the level of intra-population aggression increase. This factor may trigger the innate migratory programme, like it happens in regular migrants (Koenig & Knops 2001; Newton 2006, 2008). The birds start to move towards west, south-west and south, covering hundreds of kilometres and even crossing large stretches of open habitat, unsuitable for woodpeckers. After moving to more southern or western areas, woodpeckers settle for winter and become territorial. In early spring, surviving yearlings seem to move back to the north, as shown by ring recoveries (Cramp 1985). Thus, Great Spotted Woodpeckers seem to possess the same mechanism of irruptions like other irregular migrants (Sokolov et al. 2002). It is usually believed that the

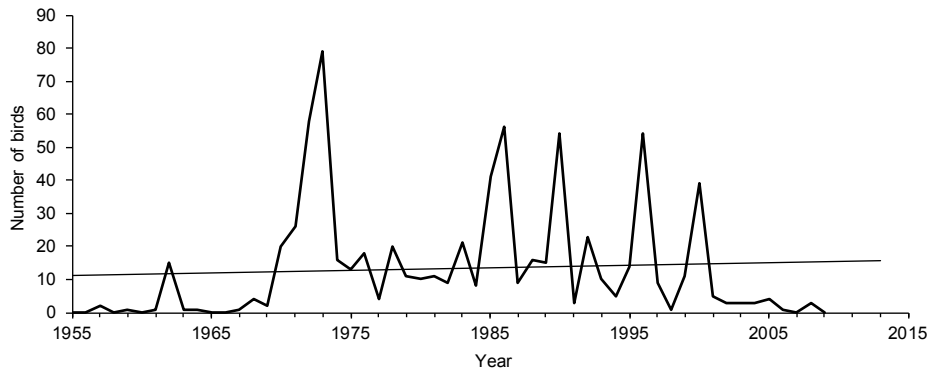


Figure 8. Long-term dynamics of trapping figures of hatching-year Lesser Spotted Woodpeckers in summer and autumn on the Courish Spit (Baltic region).

influence of any endogenous rhythm or daylength change in triggering movement is less pronounced in irruptive than in more regular migrants (Newton 2006). However, this author agrees that at least in facultative migrants, the timing and distance of movements may vary with individual circumstances, but other aspects must presumably be under firmer genetic control, notably the directional preferences and the tendency to return at appropriate dates in spring.

Other woodpeckers that do not feed on conifer seed, e.g. Lesser Spotted Woodpeckers, also show irruptions in the Baltic region (Fig. 8). Irruptive movements of this species are not related to food (insect) shortage in the natal areas, but are caused by breeding productivity of their populations. In the years with warm spring, favourable for breeding of this species, we capture in the Baltic region significantly more hatching-year birds in late summer and autumn than in cooler years (Spearman's rank correlation between trapping figures and NAO_{JFM} index: $r_s = 0.373$, $P = 0.011$, $n = 47$; between trapping figures and regional mean temperature of April: $r_s = 0.315$, $P = 0.031$, $n = 47$ and May: $r_s = 0.350$, $P = 0.015$, $n = 47$). Other authors (Wiktander et al. 2001, Pasinelli 2006, Steen et al. 2006, Selås et al. 2008, Gohli et al. 2011) also mention the impact of weather on breeding productivity of Lesser Spotted Woodpeckers and conclude that their migratory movements are linked to reproductive output. We agree with these authors that a generally high breeding success would likely lead to an increased level of intraspecific competition forcing young and subordinate birds to leave their natal area.

Already Lack (1954) mentioned that sometimes strong irruptions in some species, Great Spotted Woodpeckers including, may commence before ripening of fruits and seed on which this species forages. Moreover, during their irruptive movements birds may cross non-stop areas where food supply is abundant. Migratory urge during irruptions seems to be too strong to be explained away by purely local movements in search for food and is very similar to migratory disposition of regular migrants (Lack 1954). In Long-tailed Tits the general similarity of physiological mechanisms con-

trolling irruptive movements to the classic migratory disposition of regular migrants has been recently shown by Babushkina (2012).

4.3. Long-term change of the timing of postfledging dispersal

We found that across 54 years, time of onset of postfledging dispersal in hatching-year Great Spotted Woodpeckers on the Courish Spit has undergone a significant change (Fig. 7). This parameter was related to fluctuations of the mean May air temperature in the study region: after warmer May temperatures, dispersal of juveniles started earlier (Table 12). We have shown elsewhere that in many songbirds, the time of onset of postfledging movements is a useful proxy of the timing of breeding (Sokolov & Payevsky 1998). We may therefore assume that the timing of breeding of Great Spotted Woodpeckers in our study region has also shifted in response to temperature regimen of spring. Finnish authors state that the intensity of irruptive migration in Great Spotted Woodpeckers shows a negative relationship to timing of migration, indicating a need to set off early during poor crops of spruce cones (Lindén *et al.* 2011). Smith (2006) found an impact of spring air temperatures on the timing and breeding performance in Great Spotted Woodpeckers in southern England. Other authors mention a tendency to arrive earlier in more southern wintering areas in invasion years in irruptive species, Great Spotted Woodpeckers including (Eriksson 1971, Newton 2006).

Interestingly, we also found a significant relationship between the time of beginning dispersal and numbers of hatching-year birds in the postfledging period: in the years when dispersal started early, more juvenile Great Spotted Woodpeckers were captured (Table 13). This means that in the years with early breeding (and early dispersal following it) more young woodpeckers are produced. We have earlier found the same pattern in many songbirds, irregular migrants including (Sokolov 1999, 2000; Sokolov *et al.* 2000, 2003, 2004).

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