

AVIAN ECOLOGY AND BEHAVIOUR

PROCEEDINGS OF THE BIOLOGICAL STATION "RYBACHY"

Volume 22

2012

Avian Ecol. Behav. 22, 2012: 1–32

Impact of climate change on the timing of migration, dispersal, and numbers of the Sparrowhawk *Accipiter nisus* in the Baltic region

Leonid V. Sokolov, Anatoly P. Shapoval & Yuri G. Morozov

Abstract: Sokolov L.V., Shapoval A.P. & Morozov Yu.G. (2012): Impact of climate change on the timing of migration, dispersal, and numbers of the Sparrowhawk *Accipiter nisus* in the Baltic region. *Avian Ecol. Behav.* 22: 1–32.

Analysis of the timing of the spring passage of Sparrowhawks *Accipiter nisus* on the Courish Spit on the Baltic Sea across 54 years (1958–2011) showed that the timing of migration significantly advanced in 1958–1984, but showed no trend in 1985–2011. Similar results were shown by the analysis of the timing of first captures of first-year birds in Rybachy-type traps during their juvenile dispersal. The timing of autumn passage significantly advanced in 1958–1984 but was significantly shifted towards later calendar dates in 1985–2011. We found a significant negative relationship between the timing of spring passage and mean April temperature in the study area and with the January–March NAO index. Timing of spring passage and timing of juvenile dispersal were positively correlated. Time of onset of dispersal and the median date of autumn passage of first-year Sparrowhawks were significantly negatively related to spring air temperature of their breeding area, but not to summer or autumn temperatures. These phenological dates were also negatively related to the NAO_{JFM} . Spring trapping figures in stationary traps on the Courish Spit grew significantly in 1971–1990 but significantly decreased in 1991–2010. Similar trends in numbers were recorded for first-year birds captured during the postfledging period and on autumn passage. Numbers of both males and females on spring passage were positively related to the NAO_{JFM} . Numbers of juveniles during the postfledging period were also positively related to the NAO_{JFM} and air temperature in April. Trapping figures on autumn passage on the Courish Spit and in Sweden were positively related to NAO index values and to spring, but not summer or autumn, air temperatures. Autumn trapping figures on the Courish Spit, in Sweden and Latvia were correlated. In all three areas autumn trapping figures of Sparrowhawks were strongly related to the numbers of 13 out of 15 tested common passerine species migrating through the Courish Spit. We conclude that milder winters and warmer springs not only facilitate early spring arrival and breeding of the Sparrowhawk in the Baltic region, but cause an increase in its numbers, mainly due to the increased productivity associated with increasing numbers of its prey species.

Key words: spring and autumn migration, juvenile dispersal, numbers, birds, sparrowhawk, climate change, ambient temperature, NAO index, timing of migrating, long-term dynamics of numbers

Address: Biological Station "Rybachy", Zoological Institute, Russ. Acad. Sci. Rybachy 238535, Kaliningrad Region, Russia. E-mail: leonid-sokolov@mail.ru

Received: 10 May 2012 / Received in revised form 20 July 2012 / Accepted 25 July 2012

1. Introduction

Many recent publications have dealt with the impact of current climate change on various aspects of the life of birds. They mainly concern passerines, but the number of such publications about other birds, including raptors, is gradually increasing (Kostrezewa & Kostrezewa 1990; Lehikoinen & Vähäatalo 2000; Lehikoinen et al. 2004, 2009, 2010; Nielsen & Møller 2006; Filippi-Codacciuni et al. 2010). Most papers are devoted to the impact of climate change on the timing of spring migration and breeding (Moritz 1993; Mason 1995; Forchhammer et al. 1998, 2002; Sokolov et al. 1998; Sokolov & Payevsky 1998; Crick & Sparks 1999; Dunn & Winkler 1999; Sparks 1999; Sokolov 2000, 2006, 2010; Bairlein & Winkel 2001; Barrett 2002; Tryjanowski et al. 2002; Cotton 2003; Fiedler 2003; Hüppop & Hüppop 2003; Sokolov & Kosarev 2003; Sparks et al. 2003, 2005; Ahola et al. 2004; Hubálek 2004; Lehikoinen et al. 2004; Sinelschikova & Sokolov 2004; Marra et al. 2005; Mills 2005; Jonzen et al. 2006; Parmesan 2006; Žalakevičius et al. 2006; Both & te Marvelde 2007; Gordo 2007; MacMynowski & Root 2007; Rubolini et al. 2007; Miller-Rushing et al. 2008; Ananin & Sokolov 2009a; Balbontín et al. 2009; Swanson & Palmer 2009; Visser et al. 2009; Møller et al. 2010; Newton 2010; Saino et al. 2011; Tøttrup et al. 2010; Vegari et al. 2010; Dolenec & Dolenec 2011a, b; Robson & Barriocanal 2011; Studds & Marra 2011; Altwegg et al. 2012; Hurlbert & Liang 2012; Johansson & Jonzén 2012). Most authors agree that the current climate warming has caused a significant shift in the timing of spring migration and breeding towards earlier calendar dates in most short- and long-distance migrants. In regions where no significant increase in spring ambient temperatures occurs, the timing of migratory arrival of birds is usually not changed (Sparks & Braslavská 2001; Butler 2003; Askeyev et al. 2008; Sokolov & Gordienko 2008).

Studies of long-term trends in postfledging movements and autumn migration are much less numerous. Moreover, different authors do not agree on how climate change influences these parts of the avian annual cycle (Pulido et al. 2001; Kosicki et al. 2004; Mills 2005; Gordo & Sanz 2006; Adamík & Pietruszková 2008; Newton 2008; Van Buskirk et al. 2009; Lehikoinen & Jaatinen 2012). Some authors suggest that the timing of autumn migratory departure mainly depends on the timing of breeding and thus on spring ambient temperature: early spring temperatures have a cascade effect, causing early breeding and early migratory departure in autumn (Boddy 1983; Haila et al. 1986; Ellegren 1990; Sokolov et al. 1999, 2004; Jenni & Kery 2003; Tøttrup et al. 2006; Thorup et al. 2007; Mezquida et al. 2007; Filippi-Codacciuni et al. 2010). This effect is suggested to occur not only in long-, but also

in short-distance migrants. Other authors claim that the current climate warming, conversely, delays migratory departure from the breeding areas not only in short-, but also in some long-distance migrants (Moritz 1993; Vogel & Moritz 1995; Bairlein & Winkel 2001; Sparks & Mason 2001; Gilyazov & Sparks 2002; Marchant 2002; Lehikoinen et al. 2004 etc.).

The question how climate influences the long-term dynamics of avian numbers is even more debatable. Many concepts of natural regulation of animal numbers have been proposed (Lack 1954, 1966; Andrewartha & Birch 1954; Kluijver 1966; von Haartman 1971; Ricklefs 1976; Hanski 1990; Murdoch 1994; Sokolov 1999, 2010; White 2001; Sæther et al. 2004, 2006; Newton 2004; Payevsky 2006). A heated discussion on this topic took place in the early 20th century, largely stimulated by the work of Charles Elton (1924) who related the peaks of animal numbers to solar activity. Two main current concepts try to explain the natural variation of animal numbers. One of them suggests that long-term variation in numbers of animals, birds included, is mainly due to the fluctuation of extrinsic factors, mainly climate variation (Ricklefs 1976; Williamson 1976; Berthold et al. 1998; Sokolov 1999; Sillett et al. 2000; Sokolov et al. 2000, 2001, 2002, 2003; White 2001; Markovets & Sokolov 2002; Payevsky et al. 2003; Sæther et al. 2004; Both et al. 2006; Sanderson et al. 2006; Visser et al. 2006; Ananin & Sokolov 2009b; Knappe et al. 2009; Jones & Cresswell 2010; Saino et al. 2011; Jiguet et al. 2010; Pasinelli et al. 2011; Schaub et al. 2011; Wilson et al. 2011; Virkkala & Rajasärkkä 2011). The proponents of this concept believe that climate change may directly influence annual survival rate of birds and their productivity, thus governing population numbers. The alternative concept explains variation in animal numbers by causes intrinsic to the population. The most popular among these concepts is the idea of density-dependent regulation of population numbers (Lack 1966; Royama 1977; Both 1998; Turchin 1999; Newton 1998, 2003, 2004; Sillett & Holmes 2005; Pasinelli et al. 2011).

The proponents of these competing concepts engage in heated discussions from time to time (Murray 1999; Turchin 1999; White 2001). Some authors have even suggested that there is no point whatsoever to discuss the mechanisms of regulation of animal numbers, because the very existence of such regulation cannot be proven and is thus beyond the scope of scientific research (Wolda 1995). However, most researchers accept that animal numbers depend on both extrinsic physical (abiotic) and on biotic density-dependent factors. Density-dependent factors include predators, parasites, diseases, food shortage, competitive interactions etc. However, Ricklefs (1976) suggests that density-dependence is typical not only of biotic factors. Climate and other physical factors may also have an indirect density-dependent impact, because they govern food availability.

The aims of this study were: (1) to identify the long-term trends in the timing of spring and autumn migration, and of juvenile dispersal, in the Sparrowhawk *Accipiter nisus* in the Baltic region; (2) to test whether the timing of migration and dispersal is related to temperature in different seasons; (3) to identify the long-term trends in numbers of Sparrowhawks during spring and autumn passage and in the postfledging period in the Baltic region; (4) to identify the extrinsic factors that mainly govern the dynamics of Sparrowhawk numbers.

2. Material and methods

To study the trends in the timing of spring passage, postfledging movements and autumn passage of the Sparrowhawk, we used capture data on hatching-year birds and adults in 1958–2011 in large stationary Rybachy-type traps at the “Fringilla” field site of the Biological Station “Rybachy”, Russia on the Courish Spit on the Baltic Sea (55°08′N, 20°42′E). In spring, two or three traps were in operation, with the opening towards the south-west (1–2 traps) and the north-east (one trap). In summer, two traps were usually open to the opposite directions. In autumn, captures were performed in 2–3 traps open towards the north-east (1–2 traps) and the south-west (one trap).

We used the first capture and median capture dates of all birds between 25 March–15 May in all traps as indicators of the timing of spring passage. The whole study period was divided into two subperiods of equal length, 27 years each (1958–1984 and 1985–2011). This was done taking into account that trends of spring ambient temperatures could considerably differ within the study period. Onset of juvenile dispersal of Sparrowhawks on the Courish Spit was estimated from the first capture in any of the traps. As shown elsewhere, this parameter is a good proxy of breeding time in the study area (Sokolov & Payevsky 1998). Timing of autumn passage was estimated from the median capture date in stationary traps of hatching-year birds in the period 15 August–31 October.

Annual numbers of Sparrowhawks on spring and autumn passage, and in the postfledging period, were estimated from the trapping figures in two traps open to different directions in the respective season. The sexes were analysed separately and pooled. A total of 6186 trapped and ringed individuals (1958–2011) were analysed: 1380 second-year and adult birds in spring (1087 males and 293 females), 867 hatching-year individuals in the postfledging period (335 males and 532 females), and 3939 first-autumn individuals (2582 hatching-year males and 1347 hatching-year females). Apart from these, captures of 1436 Sparrowhawks trapped on autumn passage in Ottenby [Öland, Sweden, 56°12′N, 16°24′E, 1947–1996, Heligoland trap, Pettersson (1997)] and of 3420 individuals from Pape (Latvia, 56°11′N, 21°03′E, Rybachy-type trap 1967–1992 and Heligoland trap 1993–2000) were also analysed. When comparing the numbers of Sparrowhawks in different countries the trapping figures were log-transformed.

Moreover, we analysed the long-term dynamics of autumn trapping figures on the Courish Spit in 15 passerines that are the most common potential prey species of the Sparrowhawk. The overall number of captures in 1958–2011 varied between 706 in the Whitethroat *Sylvia communis* and 176796 in the Chaffinch *Fringilla coelebs*. To identify patterns in the numbers of Sparrowhawks captured in different seasons, we tested for trends in three roughly equal 19–20-year time intervals (1958–1976, 1971–1990 and 1991–2010), because during these periods different trends in numbers were recorded.

Climate change in the winter quarters, on migratory routes and in the breeding areas of the Sparrowhawk were estimated from the long-term dynamics of the January–March North Atlantic Oscillation (NAO) index (NAO_{JFM}) and regional mean

monthly air temperatures. NAO_{JFM} was used as an estimate of the general meteorological situation in Europe in winter and early spring. NAO index is calculated as the difference between the normalized sea-level pressure at the Azores and Iceland (Hurrell et al. 2001). Positive NAO values during winter and early spring indicate weather in Europe 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 Centre website (<http://www.cpc.ncep.noaa.gov/data/teledoc/teleind-calc.html>). The regional mean monthly air temperatures were taken from the following website, updated monthly: <http://www.tutiempo.net/en/>

Significance of all trends (meteorological, phenological, numbers) was tested by the linear regression coefficient. Relationships between meteorological parameters, phenological data and numbers of birds were tested by Spearman's rank correlation as implemented in STATISTICA 7.0 package.

3. Results

3.1. Long-term trends in temperatures in the winter quarters, on migratory routes and in the breeding area of the Sparrowhawk

Ringed recoveries suggest that Sparrowhawks migrating through the Courish Spit on the Baltic Sea winter predominantly in France, Belgium and Germany, and breed in southern Finland (Payevsky 1973; Bolshakov et al. 2001, 2002). Mean air temperatures of winter and spring months (January–March) in these areas are strongly correlated (Table 1). We selected Belgium as an area representative of the core wintering quarters of the Sparrowhawk. Strong correlation between mean monthly temperatures is typical not only of different wintering regions, but of en route and breeding areas as well (Table 2). The Kaliningrad Region where the Courish Spit is located was treated as an en route area visited by Sparrowhawks in spring and in autumn.

NAO_{JFM} showed a highly significant positive trend in 1958–2011, even though this was not necessarily true during all the subperiods within this time interval (Table 3). NAO_{JFM} was at a low in the late 1950s, and peaked in 1988–2003 (Fig. 1). After that, it started to decline and reached negative values in the recent two years, hinting at cooling of winters in Europe in the most recent years.

Long-term dynamics of NAO_{JFM} were strongly related to winter and spring ambient temperatures ($T^{\circ}C_{JFM}$) in Belgium (wintering area; 1958–2011, $r_s = 0.608$, $n = 54$, $P < 0.001$). In 1946–2011, the highest temperatures in January–March in the winter quarters of the Sparrowhawk were recorded in 1988–2008 (Fig. 1). Across the recent 54 years, the temperatures of January, February and March in this area increased by 1.8–2.4 °C (Table 3).

Table 1. Relationships between mean monthly temperatures in different wintering areas of the Sparrowhawk, 1970–2011.

Mean T °C Belgium (Brussels)	Spearman's rank correlation coefficient (r_s)					
	T °C France (Toulouse)		T °C France (Boulogne)		T °C Germany (Oldenburg)	
	r_s	P	r_s	P	r_s	P
T °C January	0.527	<0.001	0.931	<0.001	0.944	<0.001
T °C February	0.745	<0.001	0.968	<0.001	0.928	<0.001
T °C March	0.739	<0.001	0.952	<0.001	0.879	<0.001

Note: Significant values of Spearman's rank correlation are shown bold.

Table 2. Relationships between mean monthly air temperatures in the winter quarters, en route and breeding areas of the Sparrowhawk, 1951–2011.

Mean monthly T °C Russia (Kalinin- grad)	Spearman's rank correlation coefficient (r_s)							
	T °C Finland (Helsinki)		T °C Russia (St. Petersburg)		T °C Latvia (Riga)		T °C Belgium (Brussels)	
	r_s	P	r_s	P	r_s	P	r_s	P
January	0.856	<0.001	0.847	<0.001	0.871	<0.001	0.685	<0.001
February	0.885	<0.001	0.862	<0.001	0.880	<0.001	0.671	<0.001
March	0.862	<0.001	0.778	<0.001	0.935	<0.001	0.684	<0.001
April	0.774	<0.001	0.700	<0.001	0.996	<0.001	–	–
May	0.717	<0.001	0.626	<0.001	0.875	<0.001	–	–
June	0.656	<0.001	0.662	<0.001	0.741	<0.001	–	–
July	0.806	<0.001	0.650	<0.001	0.895	<0.001	–	–
August	0.834	<0.001	0.810	<0.001	0.939	<0.001	–	–
September	0.799	<0.001	0.795	<0.001	0.905	<0.001	–	–
October	0.725	<0.001	0.641	<0.001	0.908	<0.001	–	–

Note: Significant values of Spearman's rank correlation are shown bold.

Table 3. Long-term trends of NAOI index and mean monthly temperatures in wintering, en route and breeding areas of Sparrowhawks, 1958–2011.

NAOI T °C	Region	Years								
		1958–1984		1985–2011		1958–2011				
		Slope (°C/ year)	Difference (°C/27 years)	P	Slope (°C/ year)	Difference (°C/27 years)	P	Slope (°C/ year)	Difference (°C/54 years)	P
NAO January–March	Europe	0.050	1.35	0.004	-0.026	-0.70	0.143	0.024	1.30	0.001
T °C January	Brussels	0.094	2.54	0.146	0.054	1.46	0.425	0.037	2.00	0.110
T °C February	Brussels	0.001	0.03	0.996	0.109	2.94	0.107	0.034	1.84	0.116
T °C March	Brussels	0.052	1.40	0.234	0.039	1.05	0.345	0.044	2.38	0.004
T °C April	Kaliningrad	0.009	0.24	0.783	0.038	1.03	0.222	0.048	2.59	<0.001
T °C May	Helsinki	0.052	1.40	0.194	0.079	2.13	0.053	0.036	1.94	0.013
T °C June	Helsinki	-0.051	-1.38	0.185	0.018	0.49	0.693	-0.001	-0.05	0.993
T °C July	Helsinki	-0.001	-0.03	0.992	0.111	3.00	0.016	0.054	2.92	<0.001
T °C August	Helsinki	0.006	0.16	0.830	0.106	2.86	0.005	0.036	1.94	0.002
T °C September	Riga	-0.007	-0.19	0.843	0.074	1.99	0.046	0.019	1.03	0.146
T °C October	Kaliningrad	-0.005	0.14	0.903	-0.023	-0.62	0.575	0.002	0.11	0.888

Note: Significant values of trends are shown bold.

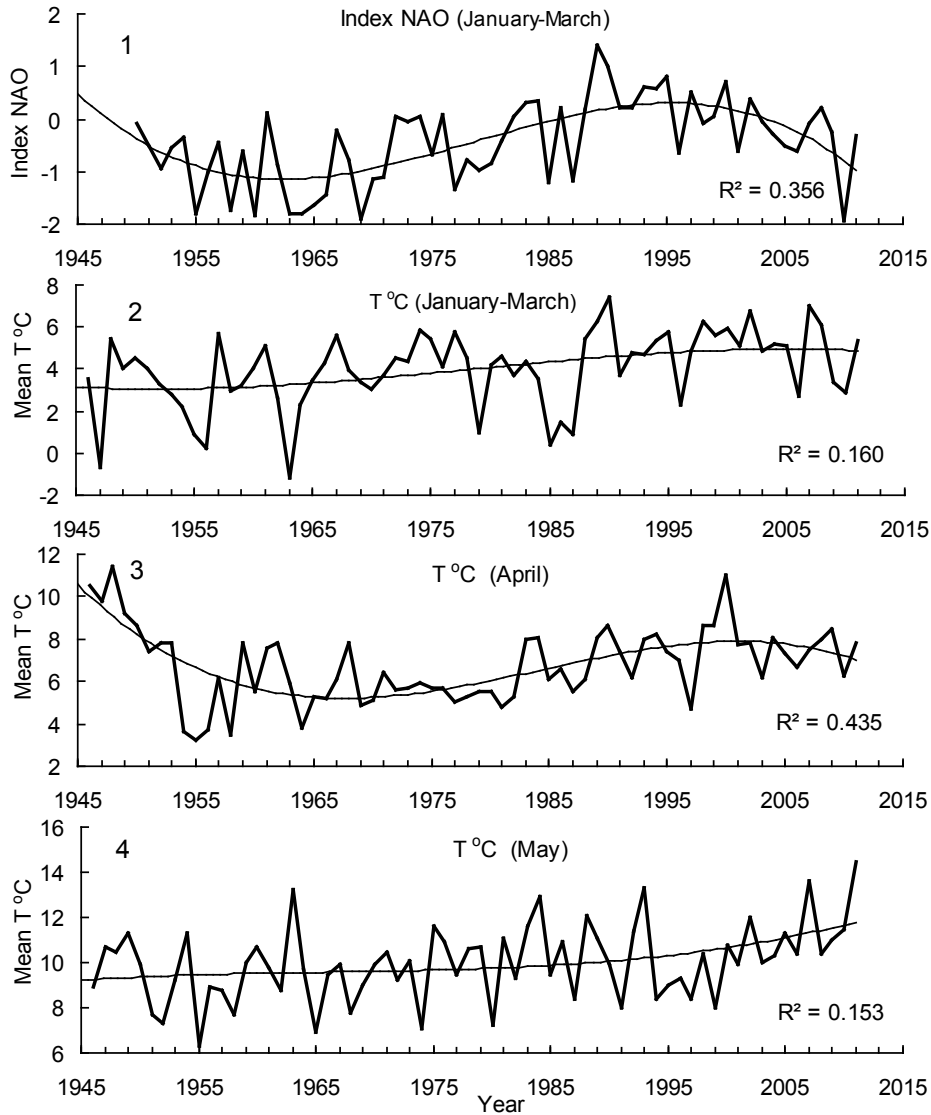


Figure 1. Long-term dynamics and trends of NAO index and mean monthly air temperatures in the winter quarters (1, 2), on spring passage (3), in the breeding area (4–7) and on autumn passage (8, 9) of the Sparrowhawk. 1 – winter and spring NAO index; 2 – mean air temperature in January – March (Belgium, Brussels); 3 – mean air temperature in April (Russia, Kaliningrad); 4–7 – mean monthly air temperatures (Finland, Helsinki); 8 – mean air temperature in September (Latvia, Riga); 9 – mean air temperature in October (Russia, Kaliningrad). NAO index and temperature trends are shown by the thin line (third degree polynomial). R^2 shows the explained variance.

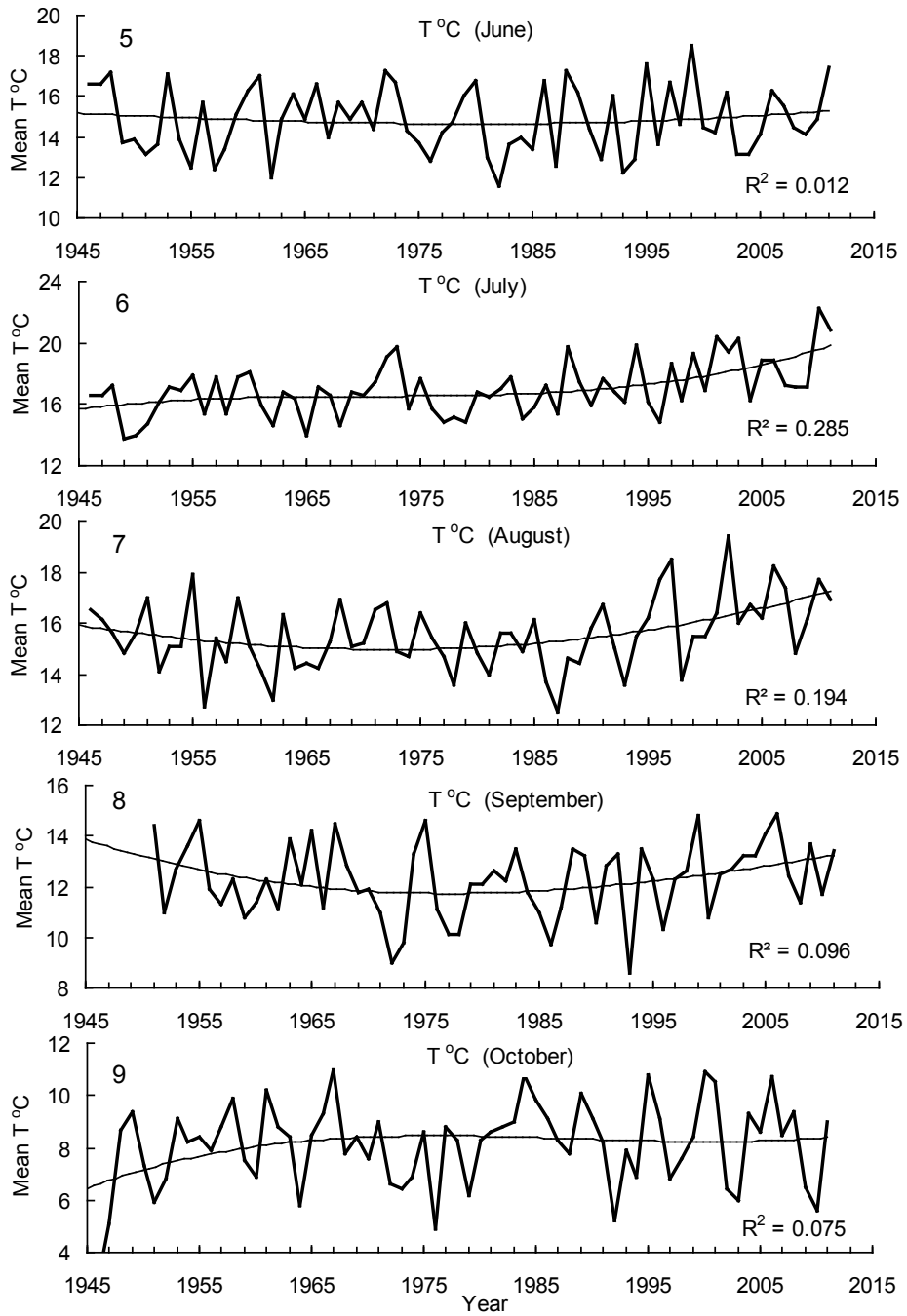


Figure 1. Continued.

The highest April temperatures in the Baltic region were recorded in 1946–1953, 1959–1963 and 1983–2011, and the lowest values in 1954–1958 and 1969–1982 (Fig. 1). Across 1958–2011, April ambient temperature showed a significant increase (Table 3).

As the main breeding area of the Sparrowhawks that migrate in spring through the Courish Spit is mainly located in southern Finland, we analysed the long-term dynamics of temperatures in this region. In Helsinki the mean temperature of May showed a highly significant upward trend in 1958–2011 (Fig. 1, Table 3). The mean temperature of June showed no significant trend across this time interval, in spite of strong annual variation (Fig. 1, Table 3). The temperatures of July and August showed a pronounced positive trend, especially evident since the mid 1980s (Fig. 1, Table 3).

During autumn passage, September temperatures in Riga (Latvia) significantly increased in 1985–2011, whereas October temperatures in Kaliningrad showed no clear trend across the study period (Fig. 1, Table 3).

3.2. Long-term dynamics of the timing of passage and dispersal in the Sparrowhawk

Timing of spring passage of the Sparrowhawk through the Courish Spit has significantly advanced in the recent 54 years (1958–2011; Fig. 2, Table 4). The most pronounced advancement occurred in 1958–1984, when the first capture date became 17 days earlier, and the median capture date 10 days earlier (Table 4).

Timing of juvenile dispersal of the Sparrowhawk on the Courish Spit, as shown by the first captures of juveniles, has advanced even more strongly than the spring passage season (Fig. 2, Table 4). This was especially evident in 1958–1984, when the advancement was 3 days (Table 4). In the subsequent period (1985–2011) a weak and nonsignificant trend towards later juvenile dispersal occurred (Table 4, Fig. 2).

The timing of autumn passage showed no significant trend throughout the 54-year study period (1958–2011). However, in the first half of this period (1958–1984) a tendency towards earlier passage of hatching-year birds was recorded. In the second half (1985–2011), conversely, a significant trend towards later passage occurred (Fig. 2, Table 4).

3.3. Relationship between the timing of passage and dispersal and the temperature in the en route and breeding areas

We analysed the relationship between the timing of spring passage of Sparrowhawks and mean monthly temperatures of winter and spring in the study area and with NAO_{JFM} . Significant negative relationships were found for April temperature and NAO_{JFM} : the higher these parameters were, the earlier Sparrowhawks passed through the Courish Spit (Table 5).

The timing of postfledging movements on the Courish Spit was also related only to the April temperature and NAO_{JFM} : the higher were these parameters, the earlier

Table 4. Long-term trends in the phenological dates in the Sparrowhawk on the Courish Spit, 1958–2011.

Phenological date	Years								
	1958–1984		1985–2011		1958–2011				
	Slope (days·yr ⁻¹)	Difference (days·27 yr ⁻¹)	P	Slope (days·yr ⁻¹)	Difference (days·27 yr ⁻¹)	P	Slope (days·yr ⁻¹)	Difference (days·54 yr ⁻¹)	P
First arrival date	-0.620	-16.74	0.002	-0.080	-2.16	0.590	-0.237	-12.80	<0.001
Median passage date in spring	-0.356	-9.61	0.042	-0.045	-1.22	0.760	-0.130	-7.02	0.022
First dispersal date	-1.231	-33.21	<0.001	0.230	6.21	0.161	-0.329	-17.77	<0.001
Median passage date in autumn	-0.286	-7.72	0.048	0.359	9.69	0.004	-0.071	-3.83	0.313

Note: Significant values of trends are shown bold.

Table 5. Relationships between the timing of spring passage of Sparrowhawks on the Courish Spit and spring air temperatures in Kaliningrad Region and NAO index, 1958–2011.

Monthly T °C, NAOI	Spearman's rank correlation coefficient (r _s)					
	First arrival date		Median passage date		P	
	r _s	P	r _s	P	r _s	P
February	-0.067	0.648	-0.189	0.170		
March	-0.176	0.227	-0.083	0.552		
April	-0.423	0.002	-0.314	0.021		
NAO January–March	-0.242	0.094	-0.261	0.046		

Note: Significant values of Spearman's rank correlation are shown bold.

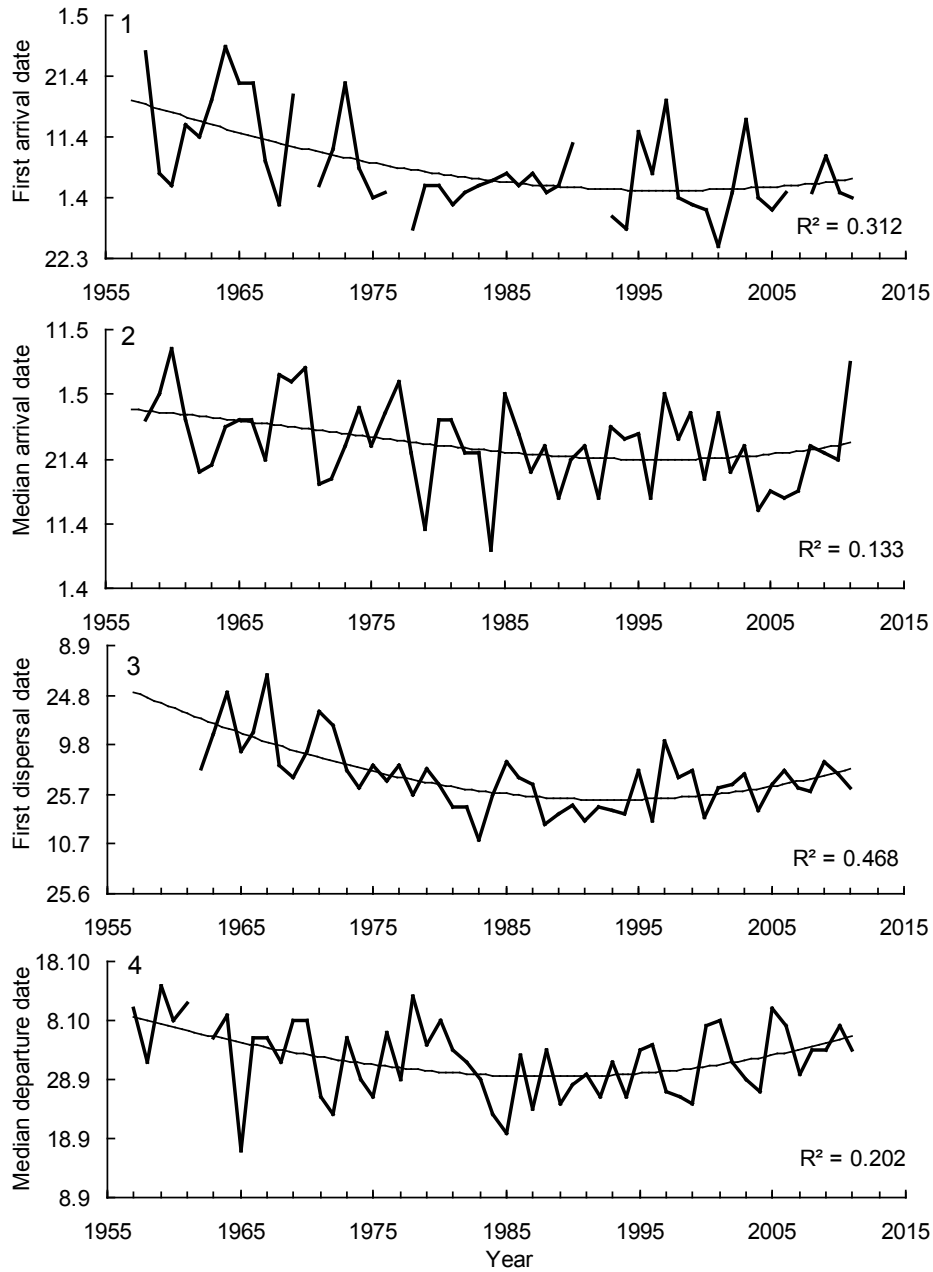


Figure 2. Long-term dynamics and trends of the timing of spring passage (1, 2), postfledging movements (3) and autumn passage (4) of Sparrowhawks on the Courish Spit on the Baltic Sea. Temporal trends are shown by the thin line (third degree polynomial). R^2 shows the explained variance.

Table 6. Relationships between the timing of postfledging movements and autumn passage of juvenile Sparrowhawks on the Courish Spit and monthly air temperatures in Kaliningrad Region and NAO index, 1958–2011.

Monthly T °C, NAOI	Spearman's rank correlation coefficient (r_s)			
	First dispersal date		Median passage date	
	r_s	P	r_s	P
February	-0.186	0.196	-0.137	0.334
March	-0.239	0.095	-0.285	0.041
April	-0.434	0.002	-0.045	0.750
May	-0.191	0.182	0.009	0.951
June	0.107	0.461	0.042	0.770
July	-0.017	0.904	-0.037	0.795
August	–	–	0.117	0.408
September	–	–	0.201	0.152
October	–	–	-0.034	0.808
NAO January–March	-0.551	<0.001	-0.305	0.026

Note: Significant values of Spearman's rank correlation are shown bold.

Table 7. Relationships between the timing of spring migration, the timing of postfledging movements and autumn passage of juvenile Sparrowhawks on the Courish Spit, 1958–2011.

Date	Spearman's rank correlation coefficient (r_s)			
	First arrival date		Median passage date	
	r_s	P	r_s	P
First capture date on dispersal	0.531	<0.001	0.244	0.087
Median capture date in autumn	-0.031	0.835	0.201	0.150

Note: Significant values of Spearman's rank correlation are shown bold.

dispersal of juveniles started (Table 6). No such relationship was found with summer temperatures (June, July).

The timing of autumn passage appeared to be significantly negatively related to the temperature of March in their presumed breeding area (southern Finland) and NAO_{JFM} : the higher were these parameters, the earlier hatching-year Sparrowhawks passed in autumn through the Courish Spit (Table 6).

We found a significant positive relationship between the timing of spring passage and the onset of postfledging movements (Table 7). No relationship was found between the timing of passage in spring and in autumn, or between the timing of postfledging movements and autumn passage of juveniles (Table 7).

3.3. Long-term trends in Sparrowhawk numbers

Numbers of both sexes on spring passage showed a negative trend in 1958–1977, after which they increased and remained at a high level in 1978–1996, and finally started a downward trend which continued until 2011 (Fig. 3, Table 8). The most pronounced positive trend was apparent in 1971–1990 when the trapping figures increased by 42 individuals overall (Table 8).

Similar long-term dynamics of numbers occurred in juvenile Sparrowhawks captured during their postfledging movements (Fig. 3, Table 8). The greatest growth took place in 1971–1990 when the numbers of captures increased by 52 individuals (Table 8). Dynamics of numbers on autumn passage on the Courish Spit followed the same pattern (Fig. 3, Table 8). In 1958–1971 the numbers declined (trend marginally nonsignificant), and in 1971–1990 a positive trend was recorded when the annual number of autumn captures grew by 192 individuals (Table 8). In 1991–2010, autumn trapping figures declined again.

Autumn trapping figures from the Courish Spit was strongly positively correlated to spring and summer figures from our study site and to autumn numbers in the neighbouring Baltic countries, Latvia and Sweden (Fig. 3, Table 9).

Numbers of Sparrowhawks on autumn passage on the Courish Spit, in Sweden and in Latvia were significantly correlated to the timing of spring migration and juvenile dispersal on the Courish Spit: in the years when spring arrival and postfledging movements in the latter area started early, autumn trapping figures in all three regions were higher (Table 10).

3.4. Relationship between Sparrowhawk numbers and temperature

We looked for relationships between Sparrowhawk numbers on spring passage on the Courish Spit and temperatures in its wintering areas (represented by Belgium) and NAO_{JFM} . Winter temperatures and the mean temperature of March did not help explain the variation in numbers; however, NAO_{JFM} appeared to be significantly positively related to numbers of both sexes (Table 11).

Numbers of juvenile Sparrowhawks captured in stationary traps on the Courish Spit in the postfledging period were significantly positively related to the mean temperature of April in the study area and to NAO_{JFM} (Table 12, Fig. 4). Numbers of juveniles were higher in the years with warmer spring, but not with warmer summer.

Autumn trapping figures of hatching-year Sparrowhawks on the Courish Spit were also significantly positively related to spring, but not to summer or autumn temperatures in the study area (Table 13, Fig. 4). A similar relationship was found with NAO_{JFM} . Numbers of Sparrowhawks recorded on autumn passage in Ottenby (Öland, Sweden) were also significantly related to spring, but not summer or autumn, temperatures in their presumed breeding area (southern Finland; Table 13, Fig. 4). The same was true of NAO_{JFM} . The warmer was the spring in the breeding area, the more Sparrowhawks were recorded on passage next autumn.

Long-term dynamics of numbers of other birds on autumn passage on the Courish Spit, mainly of songbirds that are typical prey of the Sparrowhawk in our region,

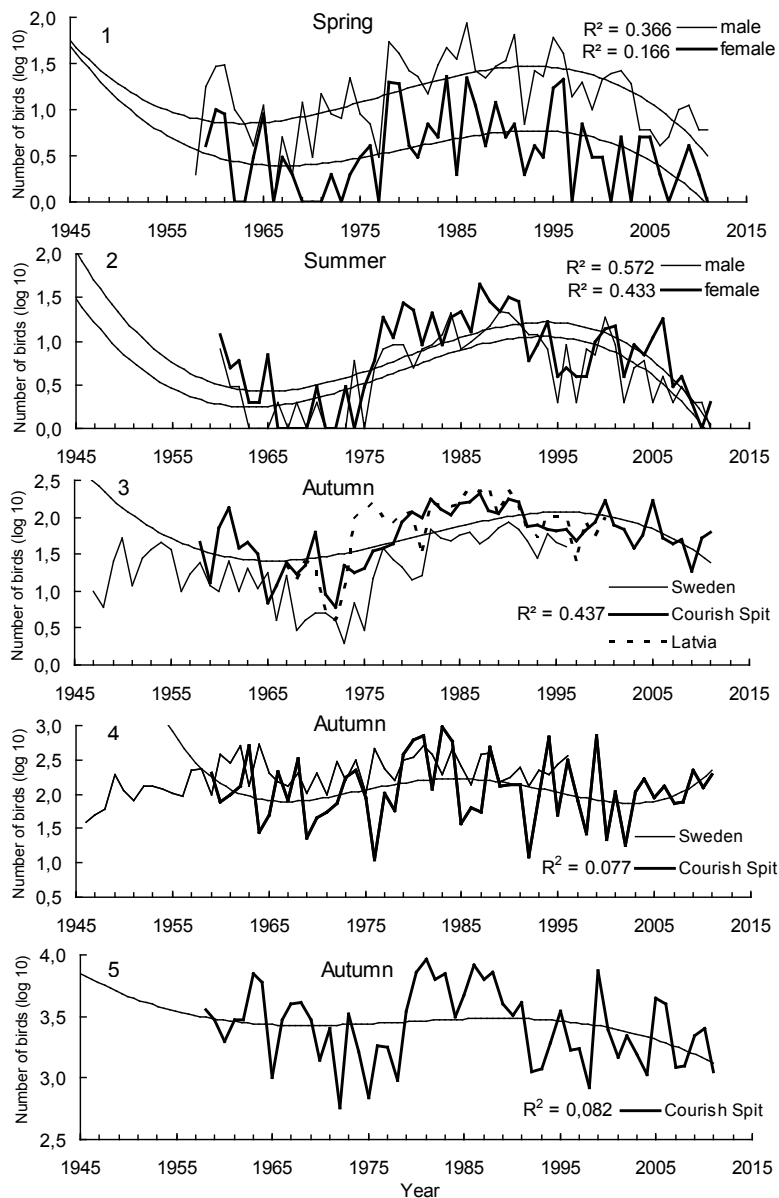


Figure 3. Long-term dynamics and trends of numbers of birds during the migratory and breeding periods in different parts of the Baltic: 1 – log-transformed numbers of Sparrowhawks on spring passage on the Courish Spit; 2 – log-transformed numbers of Sparrowhawks during postfledging movements on the Courish Spit; 3 – log-transformed numbers of Sparrowhawks on autumn passage in different regions; 4 – log-transformed numbers of Song Thrushes on autumn passage in different regions; 5 – log-transformed numbers of Chaffinches on autumn passage. Trends are shown by the curve line (third degree polynomial) only for Courish Spit data. R^2 shows the explained variance.

Table 8. Long-term trends of the Sparrowhawk numbers on the Courish Spit, 1958–2010.

Period	Years								
	1958–1976		1971–1990		1991–2010				
	Slope (birds·yr ⁻¹)	Difference (birds·19 yr ⁻¹)	<i>P</i>	Slope (birds·yr ⁻¹)	Difference (birds·20 yr ⁻¹)	<i>P</i>	Slope (birds·yr ⁻¹)	Difference (birds·20 yr ⁻¹)	<i>P</i>
Spring (March 25–May 15)	-0.495	9.40	0.286	2.117	42.34	0.033	-1.730	34.60	0.004
Summer (June 1–August 15)	-0.554	10.53	0.029	2.588	51.76	<0.001	-0.670	13.40	0.011
Autumn (August 16–October 31)	-2.207	41.93	0.081	9.579	191.58	<0.001	-1.344	26.88	0.039

Note: Significant values of trends are shown bold.

Table 9. Relationships between autumn trapping figures of the Sparrowhawk on the Courish Spit and the numbers of this species in other seasons and at other Baltic sites in autumn.

Region	Spearman's rank correlation coefficient (r_s)							
	Courish Spit		Latvia		Sweden			
	Spring	Summer	Autumn	Autumn	Autumn	Autumn		
r_s	<i>P</i>	r_s	<i>P</i>	r_s	<i>P</i>	r_s	<i>P</i>	
Courish Spit	0.574	<0.001	0.789	<0.001	0.738	<0.001	0.793	<0.001

Note: Significant values of Spearman's rank correlation are shown bold.

Table 10. Relationships between autumn numbers of the Sparrowhawk at different Baltic sites and the timing of spring passage and postfledging movements on the Courish Spit.

Number	Spearman's rank correlation coefficient (r_s)					
	First arrival date		Median passage date		First dispersal date	
	r_s	P	r_s	P	r_s	P
Courish Spit	-0.390	0.006	-0.125	0.374	-0.576	<0.001
Sweden	-0.418	0.013	-0.210	0.205	-0.713	<0.001
Latvia	-0.223	0.235	-0.173	0.328	-0.427	0.012

Note: Significant values of Spearman's rank correlation are shown bold.

Table 11. Relationships between spring trapping figures of the Sparrowhawk on the Courish Spit and air temperatures in the winter quarters and NAO index, 1958–2011.

Monthly T °C, NAOI	Spearman's rank correlation coefficient (r_s)					
	Sexes pooled		Males		Females	
	r_s	P	r_s	P	r_s	P
January	0.074	0.593	0.055	0.694	0.053	0.705
February	-0.148	0.284	-0.178	0.196	-0.138	0.318
March	0.130	0.347	0.114	0.413	0.051	0.713
January-March	0.040	0.776	0.007	0.958	-0.005	0.971
NAO January	0.379	0.005	0.368	0.006	0.302	0.026
NAO February	0.159	0.251	0.163	0.240	0.054	0.696
NAO March	0.309	0.023	0.284	0.038	0.389	0.004
NAO January–March	0.419	0.002	0.406	0.002	0.368	0.006

Note: Significant values of Spearman's rank correlation are shown bold.

showed variation similar to the pattern shown by the predator (Fig. 3). For instance, numbers of the Song Thrush *Turdus philomelos* and the Chaffinch peaked and declined in the same years as the numbers of the Sparrowhawk. A significant positive relationship between numbers of the Sparrowhawk and of its potential prey species on autumn passage was revealed in 13 of the 15 most common passerine species captured in Rybachy-type traps (Tables 14, 15). The numbers of Siskins (*Carduelis spinus*) showed a significant negative relationship.

Table 12. Relationships between Sparrowhawk trapping figures in the postfledging period on the Courish Spit and mean monthly temperatures in the Baltic region and NAO index, 1960–2011.

Monthly T °C, NAOI	Spearman's rank correlation coefficient (r_s)					
	Sexes pooled		Males		Females	
	r_s	<i>P</i>	r_s	<i>P</i>	r_s	<i>P</i>
February	-0.025	0.860	0.091	0.533	-0.095	0.517
March	0.014	0.925	0.119	0.416	-0.036	0.804
April	0.282	0.050	0.389	0.005	0.183	0.208
May	0.087	0.552	0.213	0.142	0.032	0.827
June	-0.119	0.414	-0.127	0.386	-0.094	0.521
July	-0.086	0.555	-0.138	0.344	-0.016	0.916
August	-0.067	0.647	-0.025	0.867	-0.080	0.582
NAO January–March	0.335	0.015	0.451	<0.001	0.248	0.076

Note: Significant values of Spearman's rank correlation are shown bold.

Table 13. Relationships of Sparrowhawk numbers on autumn passage and mean monthly air temperatures in the breeding area and NAO index (50-year data).

Monthly T °C, NAOI	Spearman's rank correlation coefficient (r_s)			
	Sweden (1947–1996)		Courish Spit (1958–2007)	
	r_s	<i>P</i>	r_s	<i>P</i>
February	0.094	0.516	0.113	0.443
March	0.301	0.033	0.123	0.405
April	0.212	0.138	0.300	0.045
March–April	0.331	0.019	0.211	0.149
May	0.131	0.364	0.225	0.124
April–May	0.271	0.057	0.324	0.025
March–May	0.349	0.013	0.330	0.022
June	-0.255	0.073	-0.134	0.366
July	-0.020	0.888	0.071	0.631
August	-0.046	0.749	-0.126	0.392
September	-0.083	0.562	-0.169	0.252
October	0.239	0.095	0.266	0.278
NAO January–March	0.479	0.001	0.403	0.004

Note: Significant values of Spearman's rank correlation are shown bold.

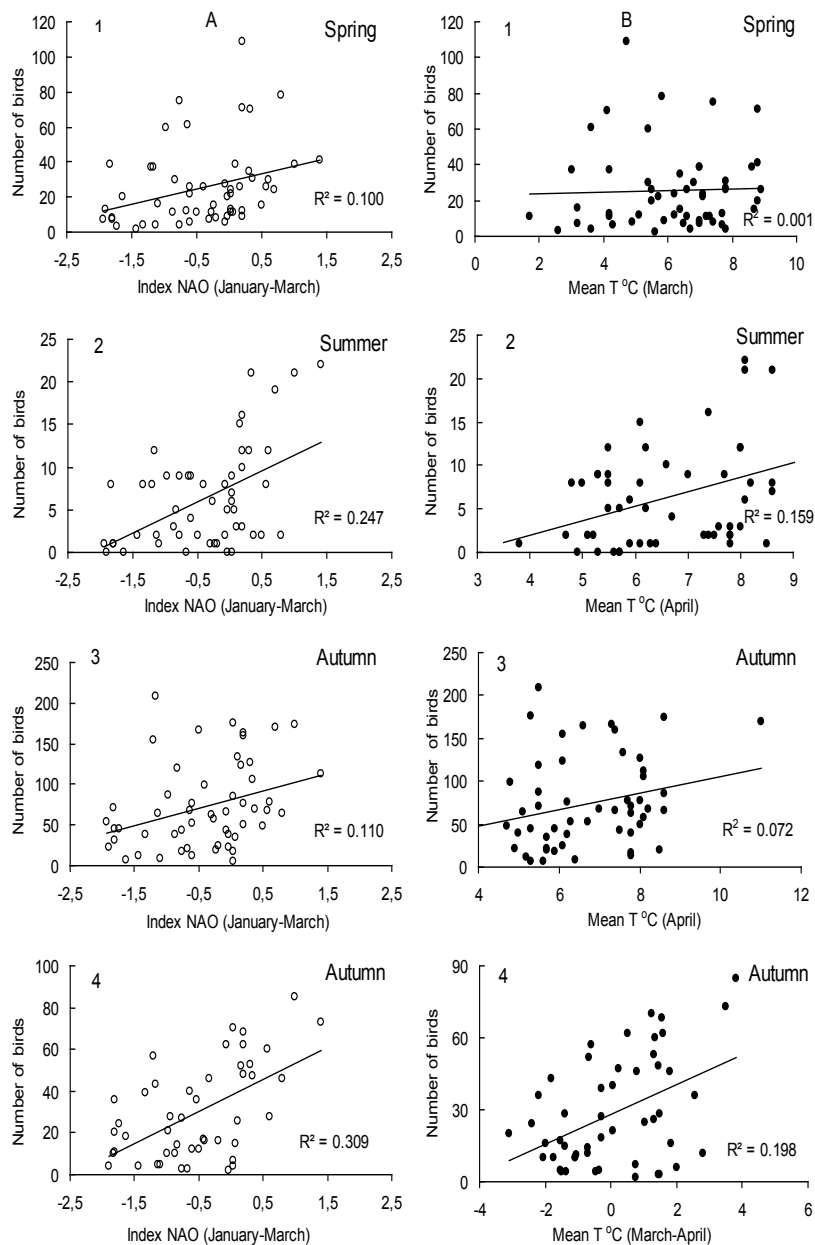


Figure 4. Relationship between Sparrowhawk numbers in the Baltic region with winter and spring NAO index values (A) and spring air temperatures in their wintering and breeding areas (B). 1 – numbers of both sexes on spring passage on the Courish Spit; 2 – numbers of males in the postfledging period on the Courish Spit; 3 – numbers of both sexes on autumn passage on the Courish Spit; 4 – numbers of both sexes on autumn passage on Öland, Sweden. R² shows the explained variance.

Table 14. Autumn numbers of the Sparrowhawk and of potential Sparrowhawk prey species at the different Baltic sites.

Species	Number of birds per year					
	Courish Spit		Sweden		Latvia	
	mean	Lim	mean	Lim	mean	Lim
<i>Accipiter nisus</i>	73	6–209	29	2–85	101	4–268
<i>Erithacus rubecula</i>	589	87–2188	2031	602–4546	669	114–2122
<i>Turdus philomelos</i>	194	11–967	225	40–540	128	7–750
<i>Turdus merula</i>	62	3–214	64	2–214	73	12–260
<i>Sylvia curruca</i>	38	2–179	–	–	12	1–47
<i>Sylvia communis</i>	14	1–39	124	42–235	3	1–12
<i>Sylvia borin</i>	42	2–154	109	24–250	85	10–306
<i>Sylvia atricapilla</i>	23	2–84	54	18–122	32	4–111
<i>Ficedula hypoleuca</i>	40	4–153	133	32–285	54	2–384
<i>Phylloscopus trochilus</i>	1489	98–6850	749	120–1513	228	29–762
<i>Regulus regulus</i>	5146	24–28509	1500	0–4696	6495	308–25512
<i>Parus major</i>	2098	194–10032	180	20–1785	6755	304–19943
<i>Parus caeruleus</i>	952	8–4789	218	10–966	1948	217–13945
<i>Fringilla coelebs</i>	3274	579–9329	94	33–275	2224	46–20251
<i>Carduelis spinus</i>	1643	68–10248	54	3–320	1110	19–8279
<i>Carduelis chloris</i>	43	1–210	130	5–325	8	0–49

Table 15. Relationships between autumn trapping figures of potential Sparrowhawk prey species on the Courish Spit and autumn Sparrowhawk numbers at different Baltic sites.

Species	Spearman's rank correlation coefficient (r_s)					
	Courish Spit		Sweden		Latvia	
	r_s	P	r_s	P	r_s	P
<i>Erithacus rubecula</i>	0.509	<0.001	0.565	<0.001	0.284	0.104
<i>Turdus philomelos</i>	0.320	0.047	0.116	0.483	0.350	0.050
<i>Turdus merula</i>	0.511	<0.001	0.599	<0.001	0.174	0.325
<i>Sylvia curruca</i>	0.588	<0.001	0.613	<0.001	0.557	<0.001
<i>Sylvia communis</i>	0.700	<0.001	0.743	<0.001	0.581	<0.001
<i>Sylvia borin</i>	0.562	<0.001	0.552	<0.001	0.500	0.003
<i>Sylvia atricapilla</i>	0.651	<0.001	0.668	<0.001	0.574	<0.001
<i>Ficedula hypoleuca</i>	0.541	<0.001	0.558	<0.001	0.593	<0.001
<i>Phylloscopus trochilus</i>	0.700	<0.001	0.778	<0.001	0.686	<0.001
<i>Regulus regulus</i>	0.615	<0.001	0.777	<0.001	0.476	0.004
<i>Parus major</i>	0.683	<0.001	0.658	<0.001	0.491	0.006
<i>Parus caeruleus</i>	0.394	0.005	0.600	<0.001	0.176	0.320
<i>Fringilla coelebs</i>	0.454	<0.001	0.339	0.035	0.406	0.017
<i>Carduelis spinus</i>	-0.369	0.009	-0.585	<0.001	-0.442	0.008
<i>Carduelis chloris</i>	0.266	0.070	0.224	0.176	0.165	0.351

Note: Significant values of Spearman's rank correlation are shown bold.

4. Discussion

4.1. Climate fluctuations in the winter quarters and breeding areas of the Sparrowhawk

During the recent 66 years, the weather in Europe has changed substantially (Fig. 1). In the countries where Baltic Sparrowhawks mainly winter (France, Belgium, Germany and some others), mean temperatures of January, February and especially March increased significantly in 1958–2011 (Table 3). Long-term dynamics of NAO_{JFM} suggests that the coldest winters and early springs occurred in Europe between the mid 1950s and mid 1960s, and the warmest ones since the mid 1980s until 2000 (Fig. 1). After that, an apparent trend towards cooler winters was recorded in many European countries.

During the spring passage of Sparrowhawks (which mainly takes place in April) the coldest period in the Baltic region was in the 1970s (Fig. 1). The warmest Aprils occurred in 1946–1953 (with a peak in 1948) and in 1983–2011 (with a peak in 2000). The mean May temperature showed a significant increasing trend across the period of study (1958–2011) with the most apparent peaks in 1975–1993 and 2002–2011 (Fig. 1, Table 3).

The mean temperature of June in the Sparrowhawk's breeding area showed no obvious trend across the study period (Fig. 1, Table 3). However, the mean temperatures of July and August had a strong upward trend with the highest values between the mid 1980s and 2011.

During the autumn passage the temperature in the Baltic area showed a significant change only in September – a significant upward trend was recorded in 1985–2011 (Fig. 1, Table 3). The mean temperature of October did not show any trend.

Thus, the mean temperatures in Europe during the wintering, breeding and migratory periods of the Sparrowhawk changed significantly during the study period which influenced not just the timing of annual events in this species, but its numbers as well.

4.2. Impact of climate on the timing of migration, breeding, and postfledging movements of the Sparrowhawk

Timing of spring passage of the Sparrowhawk on the Courish Spit on the Baltic Sea, as shown by the first and median capture dates in the stationary traps, most significantly advanced in 1958–1984 (Fig. 2). Over the 27 years the first capture date advanced by ca. 17 days, and the median passage date by 10 days (Table 4). In south-western Finland, as shown by the data from the Hanko Bird Observatory (59°49'N, 22°54'E), only the first arrivals (5th percentile) significantly advanced in 1979–2007. The median date and the 95th percentile of captures did not change significantly (Lehikoinen et al. 2010). During 29 years, the arrival date of Sparrowhawks to southern Finland advanced by approximately 11 days. In our study area the advancement rate was in spring 0.62 days/year, in Finland 0.40 days/year.

Timing of spring passage through the Courish Spit was significantly related to the mean temperature of April in the study area and to NAO_{JFM} : Sparrowhawks arrived earlier in warm springs (Table 5). We have shown elsewhere that in many songbird species the timing of spring passage on the Courish Spit was earlier in warm springs (Sokolov et al. 1998; Sokolov 2006). However, our Finnish colleagues have found no significant correlation between the arrival of Sparrowhawks and the temperature of spring in their study area (Lehikoinen et al. 2010). Those authors suggest that the timing of arrival is likely to be better explained by weather conditions on a larger scale, including those at the departure areas and weather en route (Ahola et al. 2004).

Timing of breeding of the Sparrowhawk in the Baltic region significantly advanced by 0.18 days/year in 1973–2007 (Lehikoinen et al. 2010). The Finnish authors found a clear geographical trend in hatch date, increasing towards the north-east. The difference in hatch dates between the extreme south-western area, and the corresponding extreme in the northeast, was, according to the model averaged prediction, approximately 15 days (11 June in the far southwest and 26 June in the far northeast). Early breeding was also strongly connected to higher than average temperatures in April, and to some extent, lower precipitation during April.

We have no direct data on the timing of breeding of the Sparrowhawk on the Courish Spit, but we have long-term standardized data on the onset of postfledging movements in juveniles. We have shown in a number of passerine species that timing of breeding is strongly correlated with the onset of juvenile dispersal (Sokolov & Payevsky 1998). The strongest advancement of the timing of dispersal in juvenile Sparrowhawks in our study area occurred in 1958–1984 (Fig. 2). Over the 27 years the first capture date of a juvenile Sparrowhawk advanced by approximately one month, which is a very rapid advancement of 1.23 days/year (Table 4). This does not necessarily mean that the timing of breeding advanced at the same rate, but it strongly suggests a pronounced trend towards earlier breeding. Timing of juvenile dispersal of the Sparrowhawk was strongly dependent on the mean temperature of April (but not on the temperature of summer months) and NAO_{JFM} : in the years with warm springs Sparrowhawks apparently bred earlier and postfledging movements of juveniles started earlier. Thus, our data agree with the conclusion of the Finnish researchers who reported a relationship between the timing of breeding and spring temperature. This is supported by Newton (1986) who reported that dry and warm conditions in Britain during April advance the timing of breeding in the Sparrowhawk. It should be however mentioned that Nielsen & Møller (2006) and Both et al. (2009) reported that Sparrowhawks in Central Europe had not advanced their breeding, despite a rapid advance in the timing of breeding of many important prey species. We found a significant relationship between the timing of spring passage and juvenile dispersal of Sparrowhawks: in the years when Sparrowhawks arrived early, they probably started breeding early and thus postfledging movements started earlier (Table 7). Finnish authors similarly concluded that earlier arrival in the Sparrowhawk leads to earlier breeding (Lehikoinen et al. 2010).

Timing of passage of first-autumn Sparrowhawks through the Courish Spit have also varied considerably across the 54 years 1958–2011. In the early period

(1958–1984) autumn passage significantly advanced, and in 1985–2011 a trend towards later passage was apparent (Fig. 2, Table 4). The median date of passage of first-autumn Sparrowhawks on the Courish Spit was significantly related to the mean March temperature in their presumed breeding area (southern Finland) and to NAO_{JFM} : the higher the values of these parameters, the earlier juvenile Sparrowhawks passed through the Courish Spit in autumn (Table 6). We found no significant relationship between the timing of autumn passage and summer or autumn temperatures in the breeding areas or en route. A similar relationship with spring, but not summer or autumn temperatures was found earlier in a number of songbird species (Sokolov et al. 1999).

Finnish authors reported that in 1973–2007, the onset and median date of autumn passage of Sparrowhawks in Finland shifted towards earlier dates by 0.38 and 0.31 days/year, respectively, early autumn migrants being exclusively juveniles (Lehikoinen et al. 2010). However, the late phase of departure did not change during the study period, and the overall autumn migration period length did not increase significantly (0.23 days/year). Earlier breeding produces earlier autumn migration explicitly in young Sparrowhawks, late migrating adult birds did not advance their migration dates as much. Our Finnish colleagues also concluded that autumn temperatures did not affect departure dates. After having corrected for the temporal trend, they did not find clear evidence for ambient temperatures, NAO index or timing of breeding affecting the timing of migration. The total time during which at least a part of the adult Finnish population is present on the breeding grounds has not changed significantly (0.25 days/year).

The Finnish authors also reported that the distance of autumn migration did not change much in their Sparrowhawks over the recent 47 years. Based on ringing recoveries, the log-transformed migration distance has not changed since the 1960s, either for juvenile or for adult Sparrowhawks (Lehikoinen et al. 2010). Lehikoinen (2011) studied how advanced autumn migration of the Sparrowhawk has increased the predation risk on long-distance migrants in Finland. This author analysed the median departure dates of 41 passerine species and concluded that early migrating passerines tend to advance, and late migrating species delay their departure, but none of the species have advanced their departure times as much as the Sparrowhawk. This has led to a situation of increased predation risk on early migrating long-distance migrants and decreased the overlap of migration with later departing short-distance migrants.

Filippi-Codacciuni et al. (2010) analysed the timing of autumn passage in 14 species of birds of prey during the past 30 years at one of the most important convergent points of western European migration routes in France, the Organbidexka pass, in the Western Pyrenees. Eight species, the Sparrowhawk included, showed significant phenological shifts during 1981–2008. Long-distance migrants displayed stronger phenological responses than short-distance migrants, and advanced their mean passage dates significantly. Only some short-distance migrants (Hen Harrier *Circus cyaneus*, Buzzard *Buteo buteo*, Kestrel *Falco tinnunculus*) were found to delay their autumn migration (Filippi-Codacciuni et al. 2010). However, such short-distance migrant as the Sparrowhawk showed the strongest advance in their mean passage

dates (9–10 days during the last 28 years), together with the long-distance migrant, the Marsh Harrier *Circus aeruginosus*. The authors concluded that the Sparrowhawk data support the hypothesis that the time spent by the species on their breeding areas is constant, and thus earlier spring arrival and breeding would lead to an earlier autumn migration of both adult and young birds (Thorup et al. 2007). It may be mentioned that a direct relationship between the timing of breeding and the timing of autumn migration has been already reported in the late 20th century (Ellegren 1990, Sokolov et al. 1999).

4.3. Impact of climate on Sparrowhawk numbers

Capture data on the Sparrowhawk in stationary traps during spring passage on the Courish Spit suggest that the numbers of this species declined in 1958–1977, then they significantly increased and remained high until 1996 when a new decline started that has continued throughout 2011. Similar long-term dynamics of numbers were found for juveniles captured during the postfledging period and on autumn passage (Fig. 3, Table 8). What governed these long-term fluctuations of Sparrowhawk numbers?

We related spring, summer and autumn numbers of the Sparrowhawk to the long-term changes in the temperature in the winter quarters and en route and in the breeding areas. Season-specific Sparrowhawk numbers were positively related to NAO_{JFM} and to spring temperatures in the breeding area (Tables 11–13, Fig. 4). For instance, autumn trapping figures on the Courish Spit and at other Baltic sites (Sweden, Latvia) were the highest in the years with warm spring, but not summer or autumn (Table 13, Fig. 4). These results agree with the data of Newton (1986) who showed that dry and warm conditions during April advance the timing of breeding and increase breeding success in British Sparrowhawks probably by affecting the hunting conditions and thus resources used for egg laying. Other authors suggest that weather conditions during the post-hatching period are also important because of their effect on the survival of small raptor nestlings (Kostrzewa and Kostrzewa 1990, Lehikoinen et al. 2009). Finnish authors found that the mean brood size of the Sparrowhawks showed a clear increasing trend through the 1970s up to the mid-80s after which the mean brood size has stayed unchanged (Lehikoinen et al. 2009). However, brood size showed no clear relationship to weather variables. Consequently, the observed increase in brood size over the years is probably primarily not caused by concurrent climate change. These authors propose that more likely reasons are the decreasing concentrations of DDT, DDE, HEOD and mercury, which have improved the breeding conditions for birds of prey since the late 1970s (e.g. Newton 1998). On the other hand, they agree that since early breeders are known to have higher breeding success (Newton 1986), the possibility that the advanced onset of breeding may have increased the breeding success cannot be excluded (also see Nielsen and Møller 2006). Dolnik & Payevsky (1984) and Payevsky (1985) analysed the long-term variation of Sparrowhawk numbers on the Courish Spit and concluded that DDT and other pesticides could probably enhance or prolong a depression of numbers in the birds of prey, but the depression itself has a natural cyclic cause.

We found a significant direct relationship between the numbers of Sparrowhawks and their potential prey species on autumn passage. This relationship was found in 13 out of 15 most common passerine species that migrate through the Courish Spit (Table 15). Numbers of migrating Sparrowhawks, mainly first-autumn individuals, was highest in years with high numbers of passerines. This is understandable, considering that in the Sparrowhawk, like in many other birds of prey, the numbers are mainly regulated not by the mortality rate of juveniles and adults, but by the variation of their breeding productivity, including fecundity and nestling mortality (Payevsky 1985). In years with high numbers of passerines, birds of prey apparently show higher breeding productivity and the numbers of their populations increase due to greater recruitment of juveniles. We have shown elsewhere that summer and autumn numbers of many songbirds (which are potential prey items of Sparrowhawks) peaked in the years with early and warm spring (Sokolov *et al.* 2000, 2001). Numbers of Sparrowhawks on autumn passage, on the Courish Spit and at other Baltic sites (in Sweden and Latvia) also appeared to be related to the timing of spring migration and postfledging movements: the earlier spring passage and juvenile dispersal started on the Courish Spit, the more Sparrowhawks were captured in autumn (Table 10). Other authors also report the possible link between phenological shifts and population trends in birds of prey (Filippi-Codaccioni *et al.* 2010). They assume that those species which have advanced their autumn migration would be expected to have better population trends.

It should be emphasized that in the case of the Sparrowhawk in our study area we managed to identify the main factors that govern the long-term trends in the numbers of this bird of prey. Such attempts are not always successful (Newson *et al.* 2010).

Our analysis of the long-term trapping data of Sparrowhawks on the Courish Spit and at some other Baltic sites allowed us to conclude that the timing of spring and autumn passage and of postfledging movements is mainly governed by such extrinsic factors as the temperature in late winter and spring: the higher the temperature, the earlier birds migrate and perform dispersal movements. The numbers of Sparrowhawks in the breeding area and on autumn passage are also significantly related to spring temperatures: the warmer it is in the breeding area, the higher are the numbers. We suggest that early and warm springs enable population growth in passerines, which in its turn increases the productivity of the predator population that forages on songbirds and feeds them to their offspring. We claim that current climate change has influenced not only the phenology of annual events, but also the long-term dynamics of numbers of the Sparrowhawk.

Acknowledgements

The authors are grateful to all members of the Biological Station “Rybachy” and numerous volunteers who participated in the long-term trapping project in “Fringilla” field site. The authors are also grateful to Tim Sparks who made several important comments to an earlier draft. This study was supported by the Russian Foundation for Basic Research (grant to L.V.S. No. 10-04-00721-a).

References

- Adamík, P. & Pietruszková, J. 2008. Advances in spring but variable autumnal trends in timing of inland wader migration. *Acta Ornithol.* 43: 119–128.
- Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K. & Lehikoinen, E. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Glob. Change Biol.* 10: 1610–1617.
- Altwegg, R., Broms, K., Erni, B., Barnard, P., Midgley, G.F., Underhill, L.G. 2012. Novel methods reveal shifts in migration phenology of barn swallows in South Africa. *Proc. Biol. Sci.* 279: 1485–1490.
- Ananin, A.A. & Sokolov, L.V. 2009a. Long-term arrival trends of 54 avian species to Barguzinsky Nature Reserve in the northeastern Baikal area. *Avian Ecol. Behav.* 15: 33–48.
- Ananin, A.A. & Sokolov, L.V. 2009b. Relationship between weather conditions, crops of Siberian pine nuts, and irruptions of Siberian Nutcrackers *Nucifraga caryocatactes macro-rhynchos* C.L. Brehm in Siberia and Europe. *Avian Ecol. Behav.* 15: 23–31.
- Andrewartha, H.G. & Birch, L.C. 1954. The distribution and abundance of animals. Chicago. Chicago Univ. Press.
- Askeyev, O.V., Sparks, T.H., Askeyev, I.V., Tryjanowski, P. 2009. Spring migration timing of *Sylvia* warblers in Tatarstan (Russia) 1957–2008. *Central European J. Biol.* 4: 595–602.
- Bairlein, F. & Winkel, W. 2001. Birds and climate change. In: Lozan, J. L., Grasse, H & Hupfer, P. (Eds). *Climate of the 21st century: changes and risks*. Hamburg, Wissenschaftliche Auswertungen: 278–282.
- Balbontín, J., Møller, A.P., Hermosell, I.G., Marzal, A, Reviriego, M., de Lope, F. 2009. Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. *J. Anim. Ecol.* 78: 981–989.
- Barrett, R.T. 2002. The phenology of spring bird migration to north Norway: There was no evidence of a long-term trend in arrival dates of spring migrants over the last 20 years in north Norway. *Bird Study* 49: 270–277.
- Berthold, P., Fiedler, W., Schlenker, R. & Querner, U. 1998. 25-year study of the population development of Central European songbirds: A general decline, most evident in long-distance migrants. *Naturwissenschaften* 85: 350–353.
- Boddy, M. 1983. Factors influencing timing of autumn dispersal or migration in first-year Dunnocks and Whitethroats. *Bird Study* 30: 39–46.
- Bolshakov, C.V., Shapoval, A.P. & Zelenova, N.P. 2001. Results of bird ringing by Biological Station “Rybachy” on the Courish Spit: long-distance recoveries of birds ringed in 1956–1997. Part 1. *Avian Ecol. Behav. Suppl.* 1: 18–32.
- Bolshakov, C.V., Shapoval, A.P. & Zelenova, N.P. 2002. Results of bird ringing by Biological Station “Rybachy” on the Courish Spit: long-distance recoveries of birds ringed in 1956–1997. Part 1. *Avian Ecol. Behav. Suppl.* 5: 18–22.
- Both, C. 1998. Density dependence of reproduction: from individual optimization to population dynamics. PhD thesis. Utrecht University.
- Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Curr. Biol.* 20: 243–248.
- Both, C. & te Marvelde, L. 2007. Climate change and timing of avian breeding and migration throughout Europe. *Clim. Res.* 35: 93–105.
- Both, C., Bouwhuis, S., Lessells, C.M., Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.
- Both, C., van Asch, M., Bijlsma, R.G., van den Burg, A.B. and Visser, M.E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J. Anim. Ecol.* 78: 73–83.

- Butler, C.J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis* 145: 484–495.
- Cotton, P.A. 2003. Avian migration phenology and global climate change. *Proc. Natl. Acad. Sci. USA* 100: 12219–12222.
- Crick, H.Q.P. & Sparks, T.H. 1999. Climate change related to egg-laying trends. *Nature* 399: 423–424.
- Dolenec, Z., Dolenec, P. 2011a. Influence of the local spring warming on the breeding phenology in blackcap (*Sylvia atricapilla*) in Croatia. *J. Environ. Biol.* 32: 625–627.
- Dolenec, Z., Dolenec, P. 2011b. Spring migration characteristics of the House Martin, *Delichon urbica* (Aves: Hirundinidae) in Croatia: A response to climate change? *Zoologia* 28: 139–141.
- Dolnik, V.R. & Payevsky, V.A. 1984. Long-term fluctuations of the numbers of the Sparrowhawk (*Accipiter nisus*) and its prey in Europe and the predator-prey problem. *Zool. Zhurnal* 63: 1445–1457 (in Russian with English summary).
- Dunn, P.O. & Winkler, D.W. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proc. Biol. Sci.* Vol. 266, N 1437: 2487–2490.
- Ellegren, H. 1990. Timing of autumn migration in Bluethroats *Luscinia svecica* depends on timing of breeding. *Ornis Fenn.* 67: 13–17.
- Elton, C. 1924. Periodic fluctuation in the numbers of animals, their causes and effects. *J. Exp. Biol.* 2: 119–163.
- Fiedler, W. 2003. Recent changes in migratory behaviour of birds: a compilation of field observations and ringing data. In: Berthold, P., Gwinner, E. & Sonnenschein, E. (Eds). *Avian migration*. Berlin, Springer: 21–38.
- Forchhammer, M.C., Post, E. & Stenseth, N.C. 1998. Breeding phenology and climate. *Nature* 391: 29–30.
- Forchhammer, M.C., Post, E. & Stenseth, N.C. 2002. North Atlantic Oscillation timing of long- and short-distance migration. *J. Anim. Ecol.* 71: 1002–1014.
- Filippi-Codaccioni, O., Moussus, J.P., Urcun, J.P., Jiguet, F. 2010. Advanced departure dates in long-distance migratory raptors. *J. Ornithol.* 151: 687–694.
- Gilyazov, A. & Sparks, T. 2002. Change in the timing of migration of common birds at the Lapland nature reserve (Kola Peninsula, Russia) during 1931–1999. *Avian Ecol. Behav.* 8: 35–47.
- Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim. Res.* 35: 37–58.
- Gordo, O., Sanz, J.J. 2006. Climate and bird phenology: a long-term study in the Iberian Peninsula. *Glob. Change Biol.* 12: 1993–2004.
- Haartman, L. von. 1971. Population dynamics. In: Farner, D.S., King, J.R. (eds). *Avian Biology*. New York-London. Academic Press. Vol. 1: 391–459.
- Haila, Y., Tiainen, J. & Vepsäläinen, K. 1986. Delayed autumn migration as an adaptive strategy of birds in northern Europe: evidence from Finland. *Ornis Fenn.* 63: 1–9.
- Hanski, I. 1990. Density dependence, regulation and variability in animal populations. *Phil. Trans. Roy. Soc. London* 330: 141–150.
- Hubálek, Z. 2004. Global weather variability affects avian phenology: a long-term analysis, 1881–2001. *Folia Zool.* 53: 227–236.
- Hurlbert, A.H., Liang, Z. 2012. Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. *PLoS One* 7(2): 31662.
- Hurrell, J.W., 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269: 676–679.
- Hurrell, J.W., Kushnir Y., Visbeck M., 2001. The North Atlantic Oscillation. *Science* 291: 603–605.

- Hüppop, O. & Hüppop, K. 2003. North Atlantic Oscillation and timing of spring migration in birds. *Proc. Roy. Soc. Lond. B* 270: 233–240.
- Jenni, L. & Kéry, M. 2003. Timing of autumn bird migration under climate change: advances in long distance migrants, delays in short distance migrants. *Proc. Roy. Soc. Lond. B* 270: 1467–1472.
- Jiguet, F., Devictor, V., Ottvall, R., van Turnhout, C., van der Jeugd, H., Lindström, Å. 2010. Bird population trends are linearly affected by climate change along species thermal ranges. *Proc. Roy. Soc. Lond. B*: 277: 3601–3608.
- Johansson, J. & Jonzén, N. 2012. Effects of territory competition and climate change on timing of arrival to breeding grounds: a game-theory approach. *Am. Nat.* 179: 463–474.
- Jones, T., Cresswell, W. 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? *J. Anim. Ecol.* 79: 98–108.
- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.O., et al. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312: 1959–1961.
- Kluyver, H.N. 1966. Regulation of a bird population. *Ostrich. Suppl.* 6: 389–396.
- Knape, J., Jonzén, N., Shold, M., Sokolov, L. 2009. Multivariate state space modelling of bird migration count data. In: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds). *Modeling Demographic Processes in Marked Populations*. Environmental and Ecological Statistics, Springer, Berlin. Vol. 3: 59–79.
- Kosicki, J., Sparks, T., Tryjanowski, P. 2004. Does arrival date influence autumn departure of White Stork *Ciconia ciconia*? *Ornis Fenn.* 81: 91–95.
- Kostrezewa, A. & Kostrezewa, R. 1990. The relationship of spring and summer weather with density and breeding performance of the Buzzard *Buteo buteo*, Goshawk *Accipiter gentilis* and Kestrel *Falco tinnunculus*. *Ibis* 132: 550–559.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford. Clarendon Press.
- Lack, D. 1966. *Population studies of birds*. Oxford. Clarendon Press.
- Lehikoinen, A., Jaatinen, K. 2012. Delayed autumn migration in northern European waterfowl. *J. Ornithol.* 153: 563–570.
- Lehikoinen, A. & Vähaätalo, A. 2000. Phenology of bird migration at the Hanko Bird Observatory, Finland, in 1979–1999. *Tringa* 27: 150–227 (in Finnish with English summary).
- Lehikoinen, A., Byholm, P., Ranta, E., Saurola, P., Valkama, J., Pietiäinen, H., Korpimäki, E. & Henttonen, H. 2009. Timing of breeding and breeding success of common buzzard at its northern range margin under climate change. *Oikos* 118: 829–836.
- Lehikoinen, A., Saurola, P., Valkama, J., Linde'n, A., Byholm, P. 2010. Life history events of the Eurasian sparrowhawk in changing climate. *J. Avian Biol.* 41: 627–636.
- Lehikoinen, E., Sparks, T.H., Žalakevičius, M. 2004. Arrival and departure dates. *Adv. Ecol. Res.* 35: 1–31.
- MacMynowski, D.P. & Root, T.L. 2007. Climate and the complexity of migratory phenology: sexes, migratory distance, and arrival distributions. *Int. J. Biometeorol.* 51: 361–373.
- Markovets, M.Yu. & Sokolov, L.V. 2002. Spring ambient temperature and movements of Coal Tits *Parus ater*. *Avian Ecol. Behav.* 9: 55–62.
- Marchant, J. 2002. Global warming and autumn migration – the observatory connection. *BTO News* 238: 14–15.
- Marra, P.P., Francis, C.M., Mulvihill, R.S. & Moore, F.R. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142: 307–315.
- Mason, C.F. 1995. Long-term trends in the arrival dates of spring migrants. *Bird Study* 42: 182–189.
- Mezquida, E.T., Villara'n, A., Pascual-Parra, J. 2007. Timing of autumn bird migration in central Spain in light of recent climate change. *Ardeola* 54: 251–259.

- Miller-Rushing, A.J., Lloyd-Evans, T.L., Primack, R.B., Satzinger, P. 2008. Bird migration times, climate change, and changing population sizes. *Glob. Change Biol.* 14: 1959–1972.
- Mills, A.M. 2005. Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis* 147: 259–269.
- Møller, A.P., Rubolini, D., Lehikoinen, E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Natl. Acad. Sci. USA* 105: 16195–16200.
- Møller, A.P., Fiedler, W., Berthold, P. (Eds). 2010. *Effects of climate change on birds*. Oxford Univ. Press, Oxford.
- Moritz, D. 1993. Long-term monitoring of Palaearctic-African migrants at Helgoland (German Bight, North Sea). *Ann. Sci. Zool.* 268: 579–586.
- Murray, B.G. 1999. Can the population regulation controversy be buried and forgotten? *Oikos* 84: 148–152.
- Murdoch, W.W. 1994. Population regulation in the theory and practice. *Ecology* 75: 271–287.
- Newson, S.E., Rexstad, E.A., Ballie, S.R., Buckland, S.T., Aebischer, N.J. 2010. Population change of avian predators and grey squirrels in England: is there evidence for an impact on avian prey populations? *J. Appl. Ecol.* 47: 244–252.
- Newton, I. 1986. *The sparrowhawk*. Poyser, Berkhamstead.
- Newton, I. 1998. *Population limitation in birds*. Academic Press, London.
- Newton, I. 2003. Population regulation in birds: is there anything new since David Lack? *Avian Sci.* 3: 75–84.
- Newton, I. 2004. Population limitation in migrants. *Ibis* 146: 197–226.
- Newton, I. 2008. *The migration ecology of birds*. Academic Press, London.
- Newton, I. 2010. *Bird Migration*. Harper Collins Publishers, London.
- Nielsen, J.T. & Møller, A.P. 2006. Effects of food abundance, density and climate change on reproduction in the sparrowhawk *Accipiter nisus*. *Oecologia* 149: 505–518.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Sys.* 37: 637–669.
- Pasinelli, G., Schaub, M., Häfliger, G., Frey, M., Jakober, H., Müller, M., Stauber, W., Tryjanowski, P., Zollinger, J.L., Jenni, L. 2011. Impact of density and environmental factors on population fluctuations in a migratory passerine. *J. Anim. Ecol.* 80: 225–234.
- Payevsky, V.A. 1973. *Atlas of bird migration according to banding data at the Courland Spit. Bird migration – ecological and physiological factors* (Bykhovskiy, B.E. Ed.). Halstead Press. New York: John Wiley & Sons: 1–124.
- Payevsky, V.A. 1985. *Demography of Birds*. Nauka Press, Leningrad (in Russian).
- Payevsky, V.A. 2009. Mechanism of population dynamics in trans-Saharan migrant birds: a review. *Entom. Review.* 86, Suppl. 1: 82–94.
- Payevsky, V.A., Vysotsky, V.G., Zelenova, N.P. 2003. Extinction of a Barred Warbler *Sylvia nisoria* population in Eastern Baltic: long-term monitoring, demography, and biometry. *Avian Ecol. Behav.* 11: 89–105.
- Pettersson, J. 1997. *Fågelräkning vid Ottenby 1996*. Degerhamn: Naturvårdverket.
- Pulido, F., Berthold, P., Mohr, G. & Querner, U. 2001. Heritability of the timing of autumn migration in a natural bird population. *Proc. Roy. Soc. Lond. B* 268: 953–959.
- Ricklefs, R.E. 1976. *The Economy of Nature*. Univ. Pennsylvania. Chiron Press. Inc. Portland, Oregon.
- Robson, D. & Barriocanal, C. 2011. Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds. *J. Animal Ecol.* 80: 320–331.
- Royama, T. 1977. Population persistence and density dependence. *Ecol. Monogr.* 47: 1–35.

- Rubolini, D., Ambrosini, R., Caffi, M., Brichetti, P., Armiraglio, S., Saino, N. 2007. Long-term trends in first arrival and first egg laying dates of some migrant and resident bird species in northern Italy. *Int. J. Biometeorol.* 51: 553–563.
- Saino, N., Ambrosini, R., Rubolini, D., Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M., Sokolov, L. 2011. Climate warming, ecological mismatch at arrival and population declines in migratory birds. *Proc. Roy. Soc. B* 278: 835–842.
- Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J., van Bommel, F.P.J. 2006. Long-term population declines in Afro-Palaearctic migrant birds. *Biol. Conserv.* 131: 93–105.
- Sæther, B.-E., Sutherland, W.J., Engen S. 2004. Climate influences on population dynamics. *Adv. Ecol. Res.* 35: 185–209.
- Sæther, B.-E., Sutherland, W.J., Engen, S. 2006. Climate Influences on Avian Population Dynamics. In: Møller, A.P., Fiedler, W., Berthold, P. (Eds). *Birds and Climate Change*: 185–209.
- Schaub, M., Jakober, H., Stauber, W. 2011. Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. *Oecologia* 167: 445–459.
- Sillett, T.S. Holme, R.T. & Sherry, T.W. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288: 2040–2042.
- Sillett, T.S. & Holmes, R.T. 2005. Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* 71: 296–308.
- Sinelschikova, A. & Sokolov, L.V. 2004. Long-term monitoring of the timing of migration in thrushes (*Turdus philomelos*, *T. iliacus*) in the Eastern Baltic. *Avian Ecol. Behav.* 12: 11–30.
- Sokolov, L.V. 1999. Population dynamics in 20 sedentary and migratory passerine species of the Courish Spit on the Baltic Sea. *Avian Ecol. Behav.* 3: 23–50.
- Sokolov, L.V. 2000. Spring ambient temperature as an important factor controlling timing of arrival, breeding, post-fledging dispersal and breeding success of Pied Flycatchers *Ficedula hypoleuca*. *Avian Ecol. Behav.* 5: 79–104.
- Sokolov, L.V. 2006. Influence of the global warming on the timing of migration and breeding of passerines in the 20th century. *Entom. Review.* 86, Suppl. 1: 59–81.
- Sokolov, L.V. 2010. *Climate in the Life of Plants and Animals*. St. Petersburg: TESSA (in Russian).
- Sokolov, L.V. & Gordienko, N.S. 2008. Has recent climate warming affected the dates of bird arrival to the Il'men Reserve in the Southern Urals? *Russ. J. Ecol.* 39: 56–62.
- Sokolov, L.V. & Kosarev, V.V. 2003. Relationship between timing of arrival of passerines to the Courish Spit and North Atlantic Oscillation index (NAOI) and precipitation in Africa. *Proc. Zool. Inst. Russ. Acad. Sci.* Vol. 299: 141–154.
- Sokolov, L.V. & Payevsky, V.A. 1998. Spring temperatures influence year-to-year variations in the breeding phenology of passerines on the Courish Spit, eastern Baltic. *Avian Ecol. Behav.* 1: 22–36.
- Sokolov, L.V., Baumanis, J., Leivits, A., Poluda, A.M., Yefremov, V.D., Markovets, M.Yu., Shapoval, A.P. 2001. Comparative analysis of long-term monitoring data on numbers of passerines in nine European countries in the second half of the 20th century. *Avian Ecol. Behav.* 7: 41–74.
- Sokolov, L.V., Kosarev, V.V., Fedoseeva, V., Markovets, M.Yu., Shapoval, A.P. & Yefremov, V.D. 2003. Relationship between autumn numbers of the Coal Tit *Parus ater*, air temperatures and North Atlantic Oscillation index. *Avian Ecol. Behav.* 11: 71–88.
- Sokolov, L.V., Markovets, M.Yu. & Morozov, Yu.G. 1999. Long-term dynamics of the mean date of autumn migration in passerines on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 2: 1–18.

- Sokolov, L.V., Markovets, M.Yu., Shapoval, A.P., Morozov, Yu.G. 1998. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 1: 1–21.
- Sokolov, L.V., Markovets, M.Yu., Yefremov, V.D. & Shapoval, A.P. 2002. Irregular migrations (irruptions) in six bird species on the Courish Spit of the Baltic Sea in 1957–2002. *Avian Ecol. Behav.* 9: 39–53.
- Sokolov, L.V., Shapoval, A.P., Yefremov, V.D., Kosarev, V.V., Markovets, M.Yu. 2004. Timing and dynamics of autumn passage of the Long-Tailed Tits (*Aegithalos caudatus*) on the Courish Spit, eastern Baltic. *Avian Ecol. Behav.* 12: 31–52.
- Sokolov, L.V., Yefremov, V.D., Markovets, M.Yu., Shapoval, A.P. & Shumakov, M.E. 2000. Monitoring of numbers of passage populations of passerines over 42 years (1958–1999) on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 4: 31–53.
- Sparks, T.H. 1999. Phenology and the changing pattern of bird migration in Britain. *Int. J. Biometeorol.* 42: 134–138.
- Sparks, T.H. & Braslavská, O. 2001. The effects of temperature, altitude and latitude on the arrival and departure dates of the swallow *Hirundo rustica* in the Slovak Republic. *Int. J. Biometeorol.* 45: 212–216.
- Sparks, T.H., Mason, C.F. 2001. Dates of arrivals and departures of spring migrants taken from Essex Bird Reports 1950–1998. *Essex Bird Report* 1999: 154–164.
- Sparks, T.H., Crick, H.Q.P., Dunn, P., Sokolov, L.V. 2003. Phenology of selected lifeforms: birds. In: Schwartz M.D. (Ed.). *Phenology: An integrative environmental science*. Kluwer Acad. Publishers: 421–436.
- Sparks, T.H., Bairlein, F., Bojarinova, J.G., Huppopp, O., Lehikoinens, E.A., Rainio, K., Sokolov, L.V., and Walker, D. 2005. Examining the total arrival distribution of migratory birds. *Glob. Change Biol.* 11: 22–30.
- Studds, C.E. & Marra, P.P. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proc. Roy. Soc. B* 278: 3437–3443.
- Swanson, D.L. & Palmer, J.S. 2009. Spring migration phenology of birds in the Northern Prairie region is correlated with local climate change. *J. Field Ornithol.* 80: 351–363.
- Thorup, K., Tøttrup, A.P., Rahbek, C. 2007. Patterns of phenological changes in migratory birds. *Oecologia* 151: 697–703.
- Tøttrup, A.P., Thorup, K., Rahbek, C. 2006. Changes in timing of autumn migration in north European songbird populations. *Ardea* 94: 527–536.
- Tøttrup, A.P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C., Thorup, K. 2010. Local temperature fine-tunes the timing of spring migration in birds. *Integr. Comp. Biol.* 50: 293–304.
- Tryjanowski, P., Kuźniak, S. & Sparks, T. 2002. Earlier arrival of some farmland migrants in western Poland. *Ibis* 144: 62–68.
- Turchin, P. 1999. Population regulation: a synthetic view. *Oikos* 84: 153–159.
- Van Buskirk, J., Mulvihill, R.S., Leberman, R.C. 2009. Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Glob. Change Biol.* 15: 760–771.
- Vegari, Z., Bokony, V., Barta, Z. & Kovacs, G. 2010. Life history predicts advancement of avian spring migration in response to climate change. *Glob. Change Biol.* 16: 1–11.
- Virkkala, R., Rajasärkkä, A. 2011. Climate change affects populations of northern birds in boreal protected areas. *Biol. Lett.* 7: 395–398.
- Visser, M.E., Both, C., Lambrechts, M.M. 2006. Global Climate Change Leads to Mistimed Avian Reproduction. In: Møller, A.P., Fiedler, W., Berthold, P. (Eds). *Birds and Climate Change*: 89–110.

- Visser, M.E., Holleman, L.J.M. & Caro, S.P. 2009. Temperature has a causal effect on avian timing of reproduction. *Proc. Roy. Soc. B.* 276: 2323–2331.
- Vogel, D., Moritz, D., 1995. Langjährige Änderungen von Zugzeiten auf Helgoland. *Jb. Inst. Vogelforschung* 2: 8–9.
- White, T.C.R. 2001. Opposing paradigms regulation or limitation of populations? *Oikos* 93: 148–152.
- Williamson, K. 1976. Recent climate influences on status and distribution of some British birds. *Weather* 31: 362–384.
- Wilson, S., LaDeau, S.L., Tøttrup, A.P., Marra, P.P. 2011. Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. *Ecology* 92: 1789–1798.
- Wolda, H. 1995. The demise of the population regulation controversy? *Res. Popul. Ecol.* 37: 91–93.
- Žalakevičius, M., Bartkevičiene, G., Raudonikis, L. & Janulaitis, J. 2006. Spring arrival response to climate change in birds: a case study from eastern Europe. *J. Orn.* 147: 326–343.