

The spring timing of arrival of migratory birds: dependence on climate variables and migration route

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We analyzed the relationships between the spring arrivals of 42 migratory bird species breeding in Estonia, and mean March and April air temperature, the start of three spring-time climatic seasons, and two seasonal North Atlantic Oscillation (NAO) indices during the period 1957–1996. Regarding the spring arrival of migratory birds, we found two general clusters and six sub-clusters of species. All 23 species in one general cluster were short-distance migrants and all 19 species in the second one were long-distance migrants. The first arrival dates of short-distance migrants were strongly related to the seasonal winter NAO index (XII–III), mean March air temperature, the start of late winter, and the start of early spring. Generally, the first arrival dates of long-distance migrants were weakly correlated with climatic variables, but the first arrival dates of eight of these species was strongly related to the start of the climatic spring and/or mean April air temperature. The first arrival dates of eight species showed a significant trend over the observation period. The trends in the spring timing of arrival of the Rook and Whooper Swan were significantly related to the trend in the seasonal winter NAO index, while the trends in the spring timing of Mallard and Common Gull were significantly related to the trend in seasonal winter NAO index, mean March air temperature and start of early spring.



1. Introduction

The timing of different seasonal stages of the development of bird, as well as animal and plant activity (phenological phases), strongly depends on climate and its variability (Post & Stenseth 1999, Both & Visser 2001, Ottersen *et al.* 2001, Walther *et al.* 2002, Huntley *et al.* 2007). In the annual life

cycle of migratory bird species, this dependence appears directly in the variance of the timing of spring or autumn migration, breeding period and egg-laying, and indirectly in changes at the population level (Alerstam & Hedenström 1998, Crick & Sparks 1999, Przybylo *et al.* 2000, Jonzen *et al.* 2002, Tryjanowski *et al.* 2002, Hüppop & Hüppop 2003, Jenni & Kery 2003, Sparks & Mason 2004,

Newton 2008). Short-distance migrants generally show higher variance in their spring timing than do long-distance migrants (Crick 2004, Vähätalo *et al.* 2004, Sparks *et al.* 2005, Stervander *et al.* 2005, Tøttrup *et al.* 2005, Boyd & Petersen 2006, Rainio *et al.* 2006, Leech & Crick 2007, Newton 2008). In the case of favourable feeding and breeding conditions in years with early spring, the timing – especially of short-distance migrants with early timing and breeding in high latitudes – shifts temporally forward (Francis & Cooke 1986, Hagan *et al.* 1991, Newton 2008). Favourable conditions can also influence bird populations to occupy new areas and thus alter population distribution boundaries (Bohning-Gaese & Lemoine 2003, Huntley *et al.* 2007). The changing climate also plays an important role in environmental factors (the presence and the number of parasites, predators, changes in sea level, eutrophication, human activity) that affect the habitat of bird species (Mustin *et al.* 2007). In avian ecology, the timing of annually recurring events in the life cycle of birds is probably one of the most essential aspects, which is not only of interest for basic research but also for demography and population viability studies (Lack 1954, 1966, Newton 1998, Alerstam 2006, Drent 2006, Newton 2008).

The division of bird species into functional groups based on their response to environmental factors (Blondel 2003) is one way to test the preferences of species to different biotic and abiotic conditions (Huntley *et al.* 2007, Newton 2008). This could be one step in the building of an operational framework of knowledge for carrying out experiments that are necessary for better understanding the role of species in ecosystem functioning. Until now, the grouping and clustering of different bird species has mainly been applied in the analysis of datasets from temperate and arctic regions of North America and Europe (Mason 1995, Jokimäki & Huhta 1996, Hubálek 2005, Tworek 2007, Wilson 2007). However, data from north-eastern regions of Europe, such as Estonia, have not been used in such analyses. The impact of climate on particular groups of bird species have seldom been studied, contrary to the relationships between climate and the activities and distribution range of single species (Huntley *et al.* 2007, Newton 2008).

The objective of the present study was to ana-

lyze the spring-arrival timing of 42 migratory bird species, relative to their migration route, and in relation to: (i) the start of three springtime climatic seasons, (ii) monthly mean air temperature for Estonia, and (iii) two seasonal North Atlantic Oscillation (NAO) indices. We addressed three questions: (1) the possible divisions of migratory bird species into guilds based on their migration routes and in response to climate; (2) the most important climatic variables influencing spring-arrival timing and spacing of different bird species and guilds; and (3) possible trends in the spring-arrival timing of birds in relation to changes in climate.

2. Material and methods

2.1. Study area

Estonia lies between 57.5°N and 59.5°N and 22°E and 28°E on the eastern coast of the Baltic Sea. The relief is flat, with small uplands in south-eastern and northern parts, being up to 318 m above sea level. Estonia lies in the transition between maritime and continental climatic regions. The North-Atlantic cyclone belt, locally modified by the Baltic Sea, and the westerly airflow dominate the climate. The direct influence of the Baltic Sea on the climate appears in the western part of Estonia and becomes noticeably weaker in the central and eastern parts (Jaagus 2006). Consequently, differences between the eastern and western and also the southern and northern parts of Estonia can sometimes be remarkable despite its small size (45 215 km²).

2.2. Bird arrival data

Data on bird migration phenology used in the present study – the spring arrival dates of first individuals of the focal species – were recorded in an observation network covering the whole of Estonia, initially co-ordinated by the Estonian Naturalists' Society and later on by the Estonian Ornithological Society, founded in 1991. This network was created in 1922 and is still functioning, although observations were interrupted during 1941–1947 due to the World War II. Estonia is divided into 39 observation areas according to the administrative

Table 1. Migration type (MT; S = short-distance migrant, L = long-distance migrant) of 42 migratory bird species, mean spring timing of the first arrivals and mean start dates of springtime climatic seasons (M), their standard deviation (S.D.), trend (Mann-Kendall test statistic Z) and correlations (Pearson's r) with seasonal NAO indices (XII–III = mean winter index from December to March, III–V = mean spring index from March to May), monthly mean temperature (TMar = mean March air temperature, TApr = mean April air temperature) and start of climatic seasons (Stalw = start of late winter, Staes = start of early spring, Stas = start of spring) in Estonia during 1957–1996. The correlations for general and sub-clusters are calculated using mean timing over timings of all bird species in corresponding general or sub-clusters. Statistically significant correlations ($p < 0.001$ for correlations between spring timing of particular bird species and climatic variables and $p < 0.05$ for correlations between mean timing of general or sub-clusters and climatic variables; see Data analysis in Material and methods for details) and trends in time series ($p < 0.05$) are shown in bold.

Species/Season	MT	M	S.D.	Z	XII–III	III–V	TMar	TApr	Stalw	Staes	Stas
<i>Corvus frugilegus</i>	S	18 III	10.42	-2.67	-0.64	-0.19	-0.89	-0.38	0.77	0.44	0.27
<i>Sturnus vulgaris</i>	S	20 III	9.53	0.90	-0.44	-0.22	-0.70	-0.16	0.65	0.31	0.08
<i>Alauda arvensis</i>	S	22 III	10.66	-1.54	-0.67	-0.25	-0.84	-0.41	0.78	0.47	0.31
<i>Vanellus vanellus</i>	S	26 III	9.08	-0.64	-0.57	-0.18	-0.80	-0.31	0.71	0.40	0.18
<i>Buteo buteo</i>	S	26 III	10.50	-3.90	-0.78	-0.25	-0.81	-0.45	0.69	0.51	0.25
<i>Larus canus</i>	S	27 III	11.68	-2.32	-0.69	-0.28	-0.88	-0.45	0.80	0.49	0.31
<i>Turdus merula</i>	S	27 III	9.83	-1.76	-0.63	-0.21	-0.82	-0.41	0.67	0.47	0.26
<i>Anas platyrhynchos</i>	S	29 III	10.47	-2.37	-0.75	-0.20	-0.83	-0.52	0.76	0.55	0.37
<i>Carduelis cannabina</i>	S	30 III	8.57	-0.43	-0.54	-0.24	-0.75	-0.30	0.66	0.38	0.15
<i>Larus ridibundus</i>	S	31 III	9.58	-3.26	-0.71	-0.20	-0.83	-0.56	0.76	0.56	0.39
<i>Turdus pilaris</i>	S	02 IV	8.39	-1.56	-0.67	-0.19	-0.83	-0.42	0.68	0.50	0.24
<i>Fringilla coelebs</i>	S	02 IV	7.06	-0.87	-0.62	-0.25	-0.71	-0.38	0.64	0.54	0.17
<i>Cygnus cygnus</i>	S	05 IV	12.93	-2.90	-0.74	-0.12	-0.80	-0.58	0.78	0.54	0.44
<i>Anthus pratensis</i>	S	05 IV	6.94	-0.49	-0.47	-0.20	-0.58	-0.28	0.48	0.34	0.11
<i>Columba palumbus</i>	S	07 IV	7.33	-0.36	-0.60	-0.18	-0.66	-0.43	0.63	0.49	0.25
<i>Motacilla alba</i>	S	07 IV	5.18	-1.17	-0.49	-0.10	-0.51	-0.26	0.41	0.31	0.09
<i>Turdus philomelos</i>	S	07 IV	6.70	-0.62	-0.63	-0.19	-0.63	-0.46	0.58	0.59	0.22
<i>Falco tinnunculus</i>	S	08 IV	10.34	1.04	-0.47	-0.28	-0.50	-0.28	0.64	0.50	0.07
<i>Turdus iliacus</i>	S	08 IV	6.78	-0.71	-0.59	-0.18	-0.66	-0.49	0.61	0.60	0.21
<i>Grus grus</i>	S	09 IV	8.24	-4.02	-0.69	-0.16	-0.72	-0.54	0.58	0.57	0.37
<i>Erithacus rubecula</i>	S	10 IV	6.97	-1.01	-0.54	-0.07	-0.48	-0.46	0.42	0.45	0.23
<i>Numenius arquata</i>	S	12 IV	5.92	1.01	-0.43	-0.20	-0.40	-0.44	0.49	0.45	0.22
<i>Gallinago gallinago</i>	S	12 IV	7.03	-0.71	-0.65	-0.20	-0.62	-0.55	0.63	0.63	0.30
<i>Oenanthe oenanthe</i>	L	22 IV	6.63	2.14	-0.11	-0.09	0.01	-0.32	0.19	0.23	0.26
<i>Phylloscopus collybita</i>	L	24 IV	5.88	-0.08	-0.25	0.02	-0.20	-0.58	0.26	0.22	0.64
<i>Anthus trivialis</i>	L	27 IV	5.68	0.48	-0.12	-0.01	0.00	-0.50	0.17	0.16	0.63
<i>Jynx torquilla</i>	L	30 IV	5.61	0.84	-0.21	-0.25	-0.26	-0.58	0.36	0.24	0.63
<i>Motacilla flava</i>	L	02 V	6.80	0.93	-0.12	-0.25	-0.31	-0.30	0.44	0.23	0.45
<i>Hirundo rustica</i>	L	03 V	4.84	-0.20	-0.23	-0.29	-0.30	-0.44	0.43	0.23	0.55
<i>Ficedula hypoleuca</i>	L	03 V	5.14	-0.57	-0.24	-0.06	-0.20	-0.55	0.23	0.16	0.53
<i>Phylloscopus trochilus</i>	L	03 V	4.73	-1.72	-0.36	-0.27	-0.43	-0.68	0.50	0.40	0.68
<i>Phylloscopus sibilatrix</i>	L	04 V	5.33	-0.42	-0.34	-0.25	-0.26	-0.50	0.33	0.22	0.48
<i>Cuculus canorus</i>	L	05 V	3.65	1.41	-0.02	-0.17	-0.12	-0.31	0.17	0.18	0.43
<i>Delichon urbicum</i>	L	07 V	4.87	-0.69	-0.10	-0.16	-0.29	-0.43	0.32	0.25	0.53
<i>Luscinia luscinia</i>	L	11 V	4.19	-1.90	-0.17	-0.32	-0.44	-0.25	0.44	0.29	0.32
<i>Sylvia communis</i>	L	14 V	5.20	-0.14	-0.11	-0.25	-0.22	-0.31	0.18	0.11	0.39
<i>Muscicapa striata</i>	L	15 V	5.36	1.39	0.12	-0.06	-0.11	0.03	0.10	-0.07	0.11
<i>Sylvia borin</i>	L	18 V	5.10	-0.71	-0.16	-0.22	-0.29	-0.20	0.23	0.19	0.25
<i>Hippolais icterina</i>	L	18 V	4.91	1.49	0.04	-0.02	-0.09	-0.06	0.02	-0.05	0.15
<i>Carpodacus erythrinus</i>	L	19 V	4.16	-1.68	-0.23	0.01	-0.31	-0.02	0.11	0.00	0.04
<i>Oriolus oriolus</i>	L	20 V	4.76	1.64	-0.08	-0.17	-0.15	-0.11	0.20	0.23	0.16
<i>Apus apus</i>	L	21 V	5.62	-0.87	-0.25	-0.04	-0.11	-0.27	0.13	0.25	0.22
Start of late winter		28 II	23.47	-0.98	-0.55	-0.24	-0.79	-0.44	1.00	0.65	0.34
Start of early spring		03 IV	14.74	-1.98	-0.51	-0.34	-0.50	-0.61	0.65	1.00	0.37
Start of spring		24 IV	8.47	-1.20	-0.31	0.02	-0.26	-0.83	0.34	0.37	1.00
General cluster I	S	03 IV	9.44	-1.50	-0.72	-0.24	-0.85	-0.48	0.77	0.55	0.29
General cluster II	L	09 V	9.41	0.59	-0.25	-0.22	-0.33	-0.53	0.39	0.28	0.61
Sub-cluster 1	S	21 III	8.51	-0.94	-0.62	-0.24	-0.85	-0.34	0.77	0.43	0.24
Sub-cluster 2	S	09 IV	5.20	-0.99	-0.69	-0.20	-0.73	-0.53	0.70	0.60	0.29
Sub-cluster 3	S	30 III	7.40	-1.95	-0.72	-0.24	-0.88	-0.46	0.77	0.53	0.29
Sub-cluster 4	L	04 V	3.31	0.00	-0.25	-0.26	-0.33	-0.57	0.43	0.29	0.64
Sub-cluster 5	L	25 IV	3.88	0.97	-0.20	-0.03	-0.09	-0.56	0.25	0.24	0.61
Sub-cluster 6	L	18 V	4.14	-0.22	-0.16	-0.19	-0.31	-0.23	0.25	0.18	0.30

divisions of 1950–1957 (Rootsmäe & Rootsmäe 1972). These areas consist of single observation points where birdwatchers observe the seasonal development of nature, including bird migration, following unified guidelines (Pöder 1951, Tamm 1957). The number of points in each observation area varies. The data recorded are critically checked by coordinators and dubious and incorrect data are removed. For any given area, the mean arrival date of the first individuals of each bird species in a year is calculated using the data from all observation points within that area (Lint *et al.* 1963, Rootsmäe & Rootsmäe 1972, 1974, 1976, 1978, 1981a, 1981b, Rootsmäe & Lellep 1978, Rootsmäe 1991a, 1991b, 1991c, 1998a, 1998b). These area-specific yearly average dates are used in the present study. Altogether the data consist of about 220 species with breeding, wintering or stopover areas in Estonia. In our study, we use the spring timing (mean first arrival date) of 42 common migratory bird species during the period of 1957–1996 (Table 1).

The main criteria for selection of these species were (1) the length of time series (30 or more observation years in each particular observation area), (2) the number of long time series (especially in three regions, which are essential for the general phenological development of nature and in spring migration of bird species), and (3) the number of mean dates (more than 1,000 mean dates for all observation areas together) over the whole of Estonia during the observation period. We analyzed the mean dates for Estonia, calculated as the arithmetical means over mean dates of all observation areas for particular years.

In our study, we define short-distance migrants as species that breed in Estonia and over-winter in western and southern Europe, including the Mediterranean and North Africa, and long-distance migrants as species breeding in Estonia but migrating to over-winter in the tropical zone and South Africa (Berthold 1993). By spring timing (first arrival) of a given species we mean the spring-arrival timing of the first observed individuals of that species in Estonia.

We used the banding records and re-sightings of birds banded in Estonia to relate climatic variables (see below) to spring migration routes and to the timing of bird species in Estonia (breeding area). For this purpose we analysed ringing data

from the Matsalu Ringing Centre (Matsalu, Estonia) and the colour-banding and radio- and satellite-tracking databases for the Eurasian Crane *Grus grus* at the Institute of Agricultural and Environmental Sciences of the Estonian University of Life Sciences. In addition, we used reviews of bird ringing data from Estonia from the period of 1938–1979 (Jõgi 1957, Kumari & Jõgi 1974, Kastepõld & Kastepõld 1991).

2.3. Meteorological data

The climate in Europe, as well as the timing of bird migration and other phenological events (Hubálek 2003, 2004, Aasa *et al.* 2004, Vähätalo *et al.* 2004, Stervander *et al.* 2005, Rainio *et al.* 2006) are dictated to a great extent by a large-scale climate phenomenon known as the North Atlantic Oscillation (NAO; Hurrell 1995, Hurrell & Loon 1997). In the present study we used the NAO index, calculated as the difference in normalized sea-level pressure between the Azore high (Ponta Delgada) and the Icelandic low (Stykkisholmur/Reykjavik) Hurrell 1996). This index strongly correlates with other climatic variables and phenological events in Estonia; other authors have earlier successfully applied this index (*e.g.*, Aasa *et al.* 2004). We used two seasonal NAO indices; both are calculated as arithmetic mean values of particular months. The seasonal winter NAO index XII–III is calculated as the mean value of December, January, February and March indices, and the seasonal spring NAO index III–V is calculated as the mean value of March, April and May indices.

We also used the start dates of climatic seasons which have been calculated at the Institute of Ecology and Earth Sciences, University of Tartu, Estonia, separately for each of the 24 national meteorological stations, using meteorological (rise/fall of daily air temperature over/below given limit values, changes in snow conditions) and phenological datasets (beginning or end of vegetation, timing of several phenological phases; Jaagus & Ahas 2000). Eight seasons were initially determined, but we used only three of them: late winter, early spring, and spring. For the start dates of each season we used arithmetic mean values calculated over all the 24 meteorological stations. According to Jaagus & Ahas (2000), late winter starts on the

day when thaw starts to dominate the weather. On this date, the period of melting of the permanent winter snow cover begins and the occurrence of non-melting days (daily maximum temperature below zero) no longer exceeds the number of melting days. Early spring starts after the final disappearance of the snow cover: the land surface thaws and warms up, and the number of frost-free days in the weather increases. The start of spring *sensu stricto* is determined as being the point when daily mean air temperature permanently rises above +5°C, suggesting the start of the growing season.

We also used monthly mean air temperatures for March and April, calculated as the arithmetical mean values based on the daily mean temperature over the whole of Estonia. The daily air temperature is measured at the 24 meteorological stations throughout Estonia.

2.4. Data analysis

We analyzed the relationships between the spring-arrival timing of 42 common migratory bird species and the two seasonal NAO indices, three climatic seasons, and monthly mean air temperature. To group the bird species based on their spring-arrival timing (expressed as dates), we used cluster analysis. We chose the un-weighted pair-group average method for grouping criteria and Euclidean distance as the distance measure. We separated the sub-clusters at a linking distance of 50. The results of cluster analysis are presented as a dendrogram: the species with more similar timing are smaller distances apart.

To detect possible long-term trends in the timing of bird species and in climatic variables, we used the Mann-Kendall test (Salmi *et al.* 2002). In addition, we used conditional (partial) Mann-Kendall test (Libiseller & Grimvall 2002) to analyze whether the detected trends found in the time series of bird species were caused by significant trends in the time series of any climatic variable. To study differences in the variance of the timing of species between sub-clusters, we calculated the mean timing and coefficient of variation for each sub-cluster. We also used Pearson correlation analysis to calculate the correlation coefficients between the timing of the particular bird species, mean air temperature, mean start dates of the cli-

matic seasons and values of the seasonal NAO indices. Here we used Bonferroni-corrected significance levels by dividing the initial significance level ($p < 0.05$) by the number of correlations ($N = 45$) to define the final significance level, i.e., $|r| > 0.46$ ($p < 0.001$). However, we did not apply Bonferroni correction for correlations between climatic variables and mean first arrival dates for general/sub-clusters, because these were calculated as arithmetical means over timings (first arrival dates) of particular bird species in corresponding general or sub-clusters. For the correlations of general or sub-clusters, we applied the significance level at $p < 0.05$ that was also used for other statistical analyses (e.g., trend analysis). All statistical analyses were performed using Microsoft Excel 97 and Statistica 7.0.

3. Results

The cluster analysis of bird species produced two general clusters with 23 and 19 species, respectively (Fig. 1). The bird species in the general clusters coincided with their migratory route and status (Berthold 1993): cluster I solely consisted of short-distance migrants and cluster II solely consisted of long-distance migrants. The majority of species from general cluster I (21 species of 23) over-winter in the western and southwestern part of Europe and arrive to Estonia from a WSW (13 species) and SW (8 species) compass directions. Kestrel *Falco tinnunculus* and White Wagtail *Motacilla alba* mainly over-winter in the Mediterranean and arrive to Estonia from SSW. All species in the general cluster II, on the other hand, over-winter in tropical Africa and arrive to Estonia from the SSW–SSE sector directions. Both these general clusters were further divided into three sub-clusters consisting of species co-fluctuating in their timing of arrival (Fig. 1).

For the short-distance migrants (general cluster I), the first sub-cluster contained Rook (*Corvus frugilegus*), Skylark (*Alauda arvensis*) and Starling (*Sturnus vulgaris*). The spring timing of the first individuals of this sub-cluster was in mid-March (Table 1). The 11 species from the second sub-cluster – including Whooper Swan (*Cygnus cygnus*), Eurasian Crane (*Grus grus*), Snipe (*Gallinago gallinago*), Curlew (*Numenius arquata*),

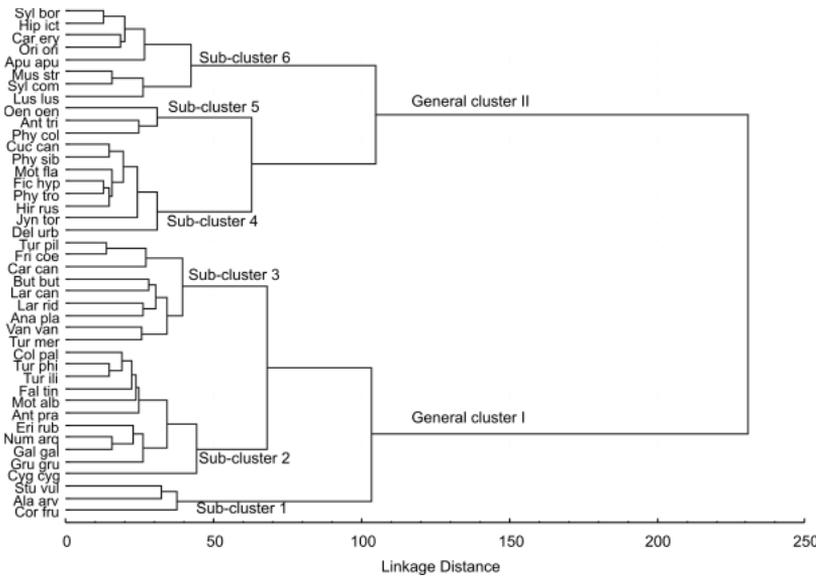


Fig. 1. Dendrogram of the cluster analysis for the first spring arrival dates of 42 common migratory bird species. The sub-clusters are separated at the linkage distance of 50. The species acronyms are composed of a three-letter acronym of the scientific generic name followed by a three-letter acronym of the specific name, e.g., 'But but' is *Buteo buteo*.

Robin (*Erithacus rubecula*), Meadow Pipit (*Anthus pratensis*), White Wagtail, Kestrel, Redwing (*Turdus iliacus*), Song Thrush (*Turdus philomelos*) and Wood Pigeon (*Columba palumbus*) – arrive the latest among the short-distance migrants. The first arrivals of nine species from the third sub-cluster take place in late March or early April: Blackbird (*Turdus merula*), Lapwing (*Vanellus vanellus*), Mallard (*Anas platyrhynchos*), Black-headed Gull (*Larus ridibundus*), Common Gull (*Larus canus*), Common Buzzard (*Buteo buteo*), Linnet (*Carduelis cannabina*), Chaffinch (*Fringilla coelebs*) and Fieldfare (*Turdus pilaris*).

Regarding the long-distance migrants (general cluster II; Fig. 1, Table 1), the first arrivals of the first sub-cluster consisted of eight species that arrive during the first week of May (House Martin *Delichon urbicum*, Wryneck *Jynx torquilla*, Swallow *Hirundo rustica*, Willow Warbler *Phylloscopus trochilus*, Pied Flycatcher *Ficedula hypoleuca*, Yellow Wagtail *Motacilla flava*, Wood Warbler *Phylloscopus sibilatrix* and Cuckoo *Cuculus canorus*). The second sub-cluster contained three species that are the only long-distance migrants the first individuals of which arrive in late April: Chiffchaff (*Phylloscopus collybita*), Tree Pipit (*Anthus trivialis*) and Wheatear (*Oenanthe oenanthe*). The first arrivals of the eight species from the third sub-cluster arrive in mid-May (Thrush Nighthawk *Luscinia luscinia*, Whitethroat *Sylvia com-*

munis, Spotted Flycatcher *Muscicapa striata*, Swift *Apus apus*, Golden Oriole *Oriolus oriolus*, Scarlet Rosefinch *Carpodacus erythrinus*, Icterine Warbler *Hippolais icterina* and Garden Warbler *Sylvia borin*).

We found significant trends for seven short-distance migrants, one species among the long-distance migrants, and for three of the measured climatic variables. The seven short-distance mi-

Table 2. Values of conditional Mann-Kendal test statistic for relationships between significant trends in spring timing of bird species and significant trends in climatic variables (XII–III = seasonal winter NAO index, TMar = mean March air temperature, Staes = start of early spring). The values in bold show that the trend in timing of a bird species is significantly influenced by the trend in a climatic variable. All climatic and bird time series particularly have significant trend at the level $p < 0.05$ (see Results, Discussion and Table 1 for details).

Species	XII–III	TMar	Staes
<i>Corvus frugilegus</i>	-1.21	-1.90	-2.02
<i>Cygnus cygnus</i>	-1.23	-2.15	-2.25
<i>Grus grus</i>	-2.94	-3.67	-3.57
<i>Anas platyrhynchos</i>	-0.50	-1.24	-1.53
<i>Larus ridibundus</i>	-1.82	-2.93	-2.60
<i>Larus canus</i>	-0.49	-1.15	-1.58
<i>Buteo buteo</i>	-2.81	-3.67	-3.38
<i>Oenanthe oenanthe</i>	2.44	2.11	2.47

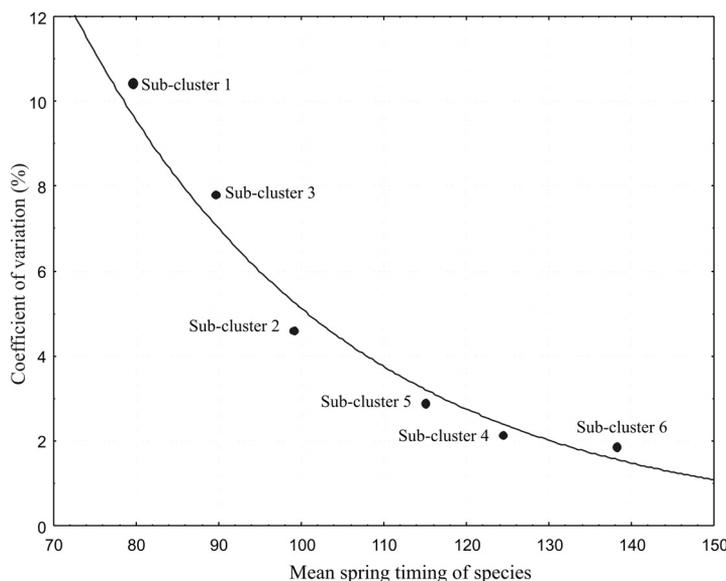


Fig. 2. Relationship between the average spring arrival timing of bird species of particular sub-clusters (days from 1 January) and the coefficient of variation (CV; multiplied by 100 %). The equation of trend is $y = 115.42e^{-0.0311x}$, $R^2 = 0.88$. See Table 1 and Fig. 1 for details.

grants clustered in different sub-clusters: Rook in sub-cluster 1, Whooper Swan and Eurasian Crane in sub-cluster 2 and Mallard, Black-headed Gull, Common Gull and Common Buzzard in sub-cluster 3 (Fig. 1). The only long-distance migrant showing a significant trend, Wheatear, clustered in a sub-cluster with two other species for which the timing of the first arrivals is late April. The climatic variables showing a significant trend were the seasonal winter NAO index, mean March air temperature and start of early spring.

The trends in the spring-arrival timing of Rook, Whooper Swan, Mallard, and Common Gull were significantly related to the trend in the seasonal winter NAO index (conditional Mann-Kendall test; Table 2). In addition, the trends in the timing of Mallard and Common Gull were related to the trend in mean March air temperature and start of early spring. The trend in the timing of the rest of the species – European Crane, Black-headed Gull, Common Buzzard and Wheatear – showed no significant relationships with climatic variable trends.

The short-distance migrants generally showed stronger correlations with climatic variables and higher variances in their spring-arrival timings than did long-distance migrants (Table 1, Fig. 2). Seasonal winter NAO index, mean March air temperature, start of late winter and start of early spring strongly and significantly influenced only

short-distance migrants. Eight long-distance migrants were strongly related to the start of spring. Mean April air temperature strongly influenced both short-distance and long-distance migrants. The seasonal spring NAO index showed no significant relationships with the analyzed bird species.

4. Discussion

We showed that climate and the length of the migration route appeared as two basic factors in the division of bird species into guilds, reflecting the associations of species with different biotic and abiotic factors. The species in both short- and long-distance migrant clusters showed different responses in their timing to the tested climate variables. While the spring arrival of short-distance migrants was strongly influenced by climatic factors – mainly in early springtime – the spring arrival of long-distance migrants depended on climatic factors in late springtime, although this dependence was weaker and was undetectable among the species with the latest first arrival dates. In general, the observed division of species into guilds suggests that several aut-ecological characteristics may be shared: for example, feeding preferences, responses to climatic and other environmental factors in the wintering area and/or along the migration route, the migration 'strategy' (flight

type and speed, average population migration speed, the use of short or long stop-overs on the route, etc.), and the choice of wintering areas. This similarity appeared greater among those species that most strongly correlated (as an absolute value) with each another. A bird species that is closely related to a number of other bird species and environmental variables within a shared cluster could be suitable for indicating the arrival timing of the other species within that cluster to their breeding or stop-over area in similar environmental conditions. Our results corroborate Hubálek (2005) who studied the timing of 37 migratory bird species in Moravia (Czech Republic) and found a cluster of short-distance migrants and six clusters of long-distance migrants, possibly determined by different wintering areas in tropical Africa. Responses of groups of species to environmental factors, however, were not analysed in that study.

Diet appears an important factor that divides short-distance migrants into groups. Early spring-arriving species often feed on seeds (e.g., Skylark) or carrion (e.g., Rook) (Blotzheim & Bauer 1985a, Blotzheim & Bauer 1993), which are available immediately at the beginning of snow melt, a highly variable factor from year to year. The short-distance migrants with later arrivals (e.g., White Wagtail and Robin; Blotzheim & Bauer 1985b, Blotzheim & Bauer 1988) also need insects for food. Their spring arrivals show temporal variability that is partly independent of the end of snow-cover season (Jaags & Ahas 2000).

In long-distance migrants, the relationships between the spring timing of arrival and spring-time climatic variables were weaker than in short-distance migrants. This may be the result of the weakening of the NAO as a proxy for zonal circulation in April and May. At this time of the year, the meridional circulation, related to airflow from the northern or southern directions, becomes important (Aasa *et al.* 2004). However, in contrast to our findings and suggestions of Hüppop & Hüppop (2003), Stervander *et al.* (2005) found that the variability in the NAO also influences birds migrating through Eastern Europe, although the mechanisms behind this effect are unknown. For this reason, synoptic and climate processes other than the NAO in Central and Eastern Europe and Africa should be studied also in relation to the timing of bird migration in Europe (Sokolov &

Kosarev 2003, Zalakevicius *et al.* 2005, Huntley *et al.* 2007).

The migration of long-distance migrants may depend more on endogenous (physiological) factors. These factors are not directly influenced by exogenous or environmental cues. As a rule, the spring timing of arrival of long-distance migrants varies considerably less than that of short-distance migrants (Table 1, Fig 2). The former species are believed to have a more precise and genetically determined time programme and vector navigation (Berthold 1993, Alerstam *et al.* 2003, Drent 2006, Eichhorn *et al.* 2009). This difference may be the main reason why Wilson (2007) found a weaker dependence of arrival date on spring temperatures in Maine, U.S.A., than reported in most other studies. For Wilson (2007), most of the bird species studied were long-distance migrants that may be generally less affected by arrival temperature. The optimal timing of spring arrival is particularly important at high latitudes, where the suitable breeding period is limited. For arctic-breeding geese, for example, the timing of breeding affects their breeding success and reproduction to a great extent (Black *et al.* 2007). The endogenous programme of migration control in short- or medium-distance migrants may be synchronized with the changing environment in their wintering grounds and along migration routes, whereas in long-distance migrants it may be synchronized with environmental variation in the second part of their migratory route in Europe (Zalakevicius *et al.* 2005). Moreover, the mechanisms of a dynamic balance in the interaction between the endogenous regulatory programme and environmental factors might determine the pattern of spring arrival and migration timing.

We found significant correlations between the arrival timing of eight long-distance migrants and the start of climatic springtime and mean April air temperature, suggesting that the timing of these species may be related to phytophenological phases. The start of spring is defined as being the start of the growing season. Indeed, Marra *et al.* (2005) analyzed the arrival timing of long-distance migrants in North America and found a significant relationship between the timing and the bud burst of lilac. Lilac could be a suitable indicator tree species, the phenology of which may well describe the timing of the northward progression

of long-distance migratory birds (Marra *et al.* 2005). The importance of the timing of spring migration and the optimal timing of breeding in relation to the green wave (Schwartz 1998) has been demonstrated for arctic breeding Barnacle Geese *Branta leucopsis* (Leito 1996, Black *et al.* 2007, Eichhorn *et al.* 2009).

Our results indicate that bird species that arrive early in spring are most strongly responsive to weather. The timing of these species was strongly correlated with the seasonal winter NAO index (XII–III) and mean March air temperature (Table 1), which could suggest that these species are closely associated with North Atlantic cyclonic processes in early springtime. Due to the westerly airflow, cyclones travel from the northern Atlantic to eastern Europe (Sepp *et al.* 2005). In this situation, Estonia, as well as the western wintering areas from where early migrants arrive, will be affected by the warm sector of cyclones, with relatively higher air temperatures and tail winds from the S–SW–W sector. Every arriving cyclone stimulates birds to follow the cyclone in an E–NE direction. Temperature gradient and wind in combination are the most important weather factors affecting bird migration (Alerstam 1978, Richardson 1978, Alerstam 1990, Berthold 1993, Alerstam & Hedenström 1998), and the migrants arriving from the W and SW to Estonia benefit from such favourable weather conditions. Our data also included occasional years with extreme weather conditions. For example, permanent snow cover was not formed in the winters of 1988/1989 and 1989/1990 due to the lasting thaw, and the spring period began very early. In such years, some short-distance bird species, such as Common Buzzard and Mallard, arrived considerably earlier than normal. In this way the general influence of the NAO on the timing of spring migration is supported by a more direct effect coming from the westward cyclone processes (Sparks *et al.* 2001).

We found that the timing of spring arrivals of seven short-distance migrants and one long-distance migrant showed a significant trend over the period of 1957–1996. Similar results have earlier been recorded elsewhere in the eastern Baltic areas (Sokolov & Kosarev 2003, Zalakevicius *et al.* 2005) and in western and northern Europe (Mason 1995, Hüppop & Hüppop 2003, Lehikoinen *et al.*

2004, Sparks *et al.* 2005). This way our study confirms that the spring arrival of short-distance migrants, in particular, is affected by climate.

We also showed that among short-distance migrants there are species-specific responses to climate variables. Relationships between climate variables and trends in the spring-arrival timings of Eurasian Crane, Black-headed Gull and Common Buzzard were remarkably different as compared with those of Rook, Whooper Swan, Mallard and Common Gull (Table 2). For this reason a generalised migratory pattern, even for ecologically similar species, should be considered with caution. However, we did not find a significantly earlier arrival of most long-distance migrants with climate; perhaps the timing of long-distance migrants is controlled more by strictly defined inner temporal mechanisms (Berthold 1971, 1993, Mason 1995, Alerstam *et al.* 2003, Newton 2008).

To conclude, climate and migratory route (geographical distribution and length of route) are important factors that define the spring arrival of migratory birds to their breeding areas. The timing of short-distance migrants is related to climatic variables in early springtime, whereas the timing of long-distance migrants depends on these variables in late springtime, suggesting that the arrival takes place in different environmental conditions. Therefore, the clustering of bird species produced a number of guilds showing different responses to environmental factors.

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Kevätmuuttajien saapumisen ajoittumisen riippuvuus ilmastotekijöistä ja muuttoreitistä

Analysoimme 42 virolaisen pesivän muuttolintulajin kevätsaapumisen suhdetta maalisi- ja huhtikuun keskilämpötilaan, kolmeen kevään ilmastolliseen ajanjaksoon ja kahteen Pohjois-Atlantin oskillaatioindeksiin (NAO) ajanjaksolla 1957–1996. Havaitimme kaksi pääryhmää ja kuusi alaryhmää muuttolintujen saapumisessa. Toiseen

pääryhmään sijoittuivat kaikki 23 lyhyen matkan ja toiseen kaikki 19 pitkän matkan muuttajaa. Lyhyen matkan muuttajien ensisaapujien ajankohdasta riippui voimakkaasti talvikauden (joulu–helmikuu) NAO-indeksistä, maaliskuun keskilämpötilasta sekä loppupalven ja varhaiskevään alkamisesta.

Yleisesti ottaen pitkän matkan muuttajien ensisaapujien suhde ilmastomuuttujiin oli heikko, mutta kahdeksalla lajilla ensisaapumisajankohta riippui voimakkaasti ilmastollisen kevään alkamisesta ja/tai huhtikuun keskilämpötilasta. Kahdeksalla lajilla ensisaapumisajankohdassa oli tilastollisesti merkitsevä trendi tutkimusvuosien aikana. Mustavariksen ja laulujoutsenen trendi oli riippui merkittävästi talvikauden NAO-indeksistä. Sinisorsan ja kalalokin keväsaapuminen taas riippui merkittävästi talvikauden NAO-indeksistä, maaliskuun keskilämpötilasta ja varhaiskevään alkamisajankohdasta.

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