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The effect of atmospheric circulation on spring arrival of short- and long-distance migratory bird species in Estonia

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The aim of this study was to analyse and identify preferred atmospheric circulation conditions for migratory birds during their spring arrival in Estonia (for Tartu and Kuressaare). A total of 47 circulation classifications and 42 common bird species were studied. The analysis identified a clear division of species into two general clusters according to their preferred circulation conditions. Short-distance migrants preferred predominantly cyclonic conditions with winds from the south-west, while for long-distance migrants windless anticyclonic conditions were preferred. The former were also less dependent on circulation than the latter. Short-distance migrants reaching Tartu were more dependent on circulation than those reaching Kuressaare. The classifications created by the methods CAP, CKM and SAN indicated stronger associations with bird arrival than those based on the methods NNW, PXK and SOM. Clear species sub-clusters were identified for the Tartu migrants only, distinguishable in the strength of the dependence on circulation or the preferred circulation conditions.

Introduction

Weather is one of the most important environmental factors affecting the annual life cycle of living organisms (Jaagus and Ahas 2000, Walther *et al*. 2002, Root *et al*. 2003, Huntley *et al*. 2007). Its direct and indirect effects are seen in the timing of various phenological phases and events, including bird migration (Newton 2008, Møller *et al*. 2010). The influence of weather on bird migration has been relatively well studied (Lehikoinen *et al*. 2004, Newton 2004, Gordo *et al*. 2005, Møller *et al*. 2010). Meteorological variables such as air temperature, precipitation, wind direction, and velocity are usually investigated in such studies (Gordo *et al*. 2005, Gordo 2007, Sinelschikova *et al*. 2007, Møller *et al*. 2010, Mellone *et al*. 2011, Shamoun-Baranes and van Gasteren 2011). In addition to these variables, some complex characteristics are also used, including those describing atmospheric circulation. The North Atlantic Oscillation (NAO) index is one of the main characteristics considered in numerous phenological studies for Europe (Mason 1995, Hubálek 2003, Hüppop and Hüppop 2003, Sokolov and Kosarev 2003, Hubálek and Čapek 2008, Palm *et al*. 2009). Besides those variables and characteristics, an

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alternative approach is via the use of synoptic climatology and the classification of general atmospheric circulation into a relatively small number of circulation types (CTs) according to the position of low- and high-pressure areas and weather fronts (Barry and Perry 1973, Yarnal 1993, Barry and Carleton 2001, Huth *et al.* 2008, Philipp *et al.* 2010). The advantage of CTs is that they better describe general weather processes than individual meteorological variables and provide more detail than the NAO index, representing regional weather peculiarities over short time-spans (usually a day) (Yarnal 1993). Thus, when a bird species exhibits associations with a CT, we can also determine the preferential weather conditions for individual species. Nevertheless, synoptic analysis is rarely used in bird migration studies (Richardson 1978, Sepp *et al.* 2011).

This study builds upon our previous work (Sepp *et al.* 2011) analysing the relationships between spring migration phenology of birds and CTs during the arrival time. The objective of the previous study was to test the applicability of CTs as a novel tool to predict the spring arrival of migratory birds; we concluded that synoptic climatology is useful for studying bird migration phenology and migration patterns, and that birds are not dependent on specific CTs. However, the analysis of CTs showed that the spring arrival of short-distance migrants is directly affected by cyclones and the arrival of all long-distance migrants typically occurred during anti-cyclonic conditions. A challenge when using circulation classifications is the large number of different classification methods. Altogether, we analysed ca. 1300 CTs from 73 classifications representing 22 different classification methods from five families of classification methods. The preselection of the best classification methods as performed by Sepp *et al.* (2011) allowed us here to conduct a more comprehensive analysis of the effects of atmospheric circulation on the spring arrival of migratory birds.

The two studies have some similarities; both for example used the same ornithological data and circulation classifications as elaborated by COST Action 733 'Harmonisation and applications of weather type classifications for European regions' (Huth 2010, Philipp *et al.* 2010; *see* also http://geo21.geo.uni-augsburg.de/cost733wiki/cost733). In addition, the basic methodology was the same. The crucial difference between these studies is that Sepp *et al.* (2011) applied classifications based only on sea-level air pressure (SLP) data [catalogue of circulation types (CAT) 1.2], while the current study includes classifications derived using sea-level data as well as data from different geopotential heights (up to 5000 m) and vortices (CAT 2.0; for details, *see* the section 'Atmospheric circulation data'), allowing a more detailed synoptic analysis.

In the current analysis, we concentrated more on ornithological aspects of the spring migration. Within this study, we investigated the number of classifications for each species to detect the strength of the dependence of individual species, and guilds of species, on atmospheric circulation. We also analysed the coincidence of CTs preferred by birds with the most frequent long-term CTs during the arrival season, in order to identify those species preferring more general or more specific weather conditions for migration. In addition, we used a cluster analysis to group bird species into guilds based on the frequency of CTs, to detect species-specific differences in the preferred weather conditions for migration.

We stress that in this paper the word 'prefer' is used instead of 'apply' or 'use' to describe associations between CTs and bird migration. We determined the preferred CTs for species as a statistical derivation of the occurrence of CTs, in other words, the long-term frequency of CTs in the arrival season (e.g., throughout spring) and the frequency of CTs in the arrival period (species arrival date at destination and a day either side, *see* 'Material and methods'). As argued in Sepp *et al.* (2011), birds can accelerate or slow down their migration depending on meteorological conditions *en route* in order to make use of the "best flying weather". However, statistically, the "best flying weather", alternatively "preferable conditions", is (are) rather rare. In reality, birds do not hesitate to migrate under any weather conditions when the time for migration draws near.

The aims of this study were to: (1) identify the circulation conditions that occur most frequently during the spring arrival of different migratory bird species and guilds in Estonia, (2) identify the bird species and guilds that have the

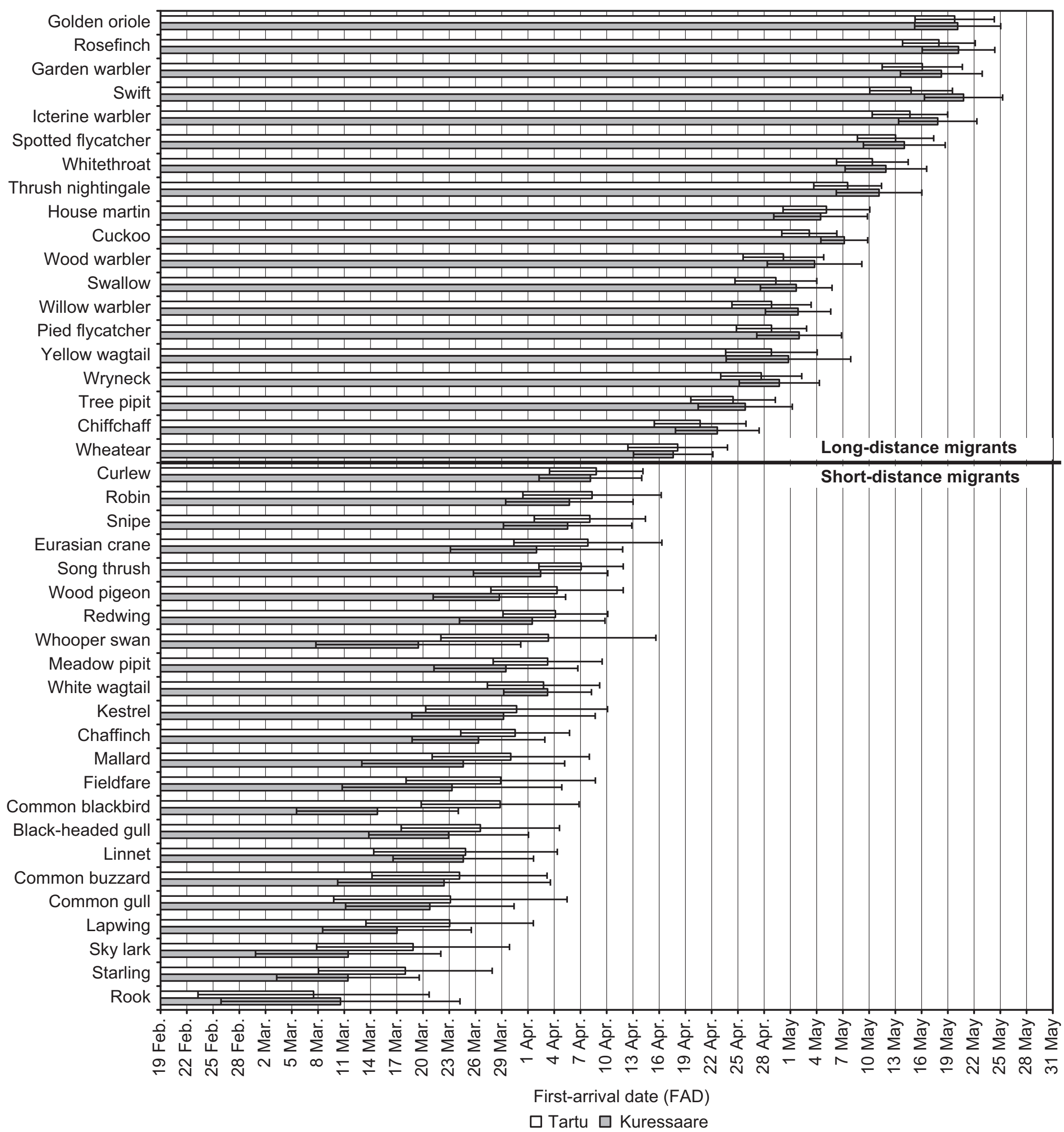

Fig. 1. Mean first arrival dates of birds with their standard deviations for Tartu and Kuressaare between 1958 and 2002. For details, *see* table 1 in Sepp *et al.* 2011.

strongest relationship with different CTs, and (3) understand the classifications most applicable for bird migration analysis.

Material and methods

Ornithophenological data

We analysed the data on spring arrival phenology of 42 bird species in Estonia gathered between 1958 and 2002 (Fig. 1; for details, *see* table 1 in Sepp *et al*. 2011). The selected species were short- and long-distance migrants (23 and 19 species, respectively). Short-distance migrants breed in Estonia and overwinter in western/southern Europe and the Mediterranean, while long-distance migrants overwinter in tropical parts of Africa and Asia. This division follows the traditional classification of migra-

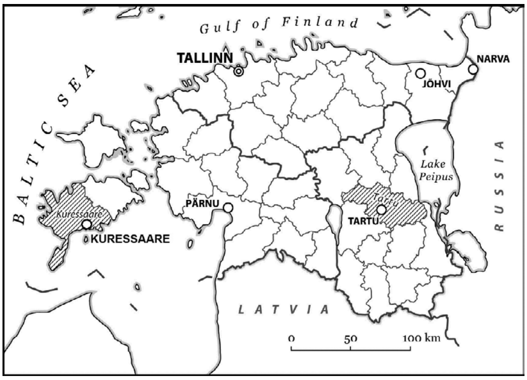

Fig. 2. Birdwatching areas in Estonia. The areas analysed in the present study are streaked.

tory birds according to the location of wintering areas and the length of migration route (Berthold 1971, Newton 2010). The chosen study period was associated with the time series of circulation classifications (*see* below) generated using the data from the European Centre for Medium-Range Weather Forecasts re-analysis project database, ERA-40 (Uppala *et al*. 2005). While Estonia has a continental climate, western Estonia is under a stronger maritime influence; we therefore selected two study areas to account for this difference (Fig. 2): Tartu has a typical continental climate, whereas the climate in Kuressaare is affected by maritime conditions (Jaagus 2006).

For all the species, first arrival dates (FADs) were used, defined as those dates when the first individuals were observed in spring. Analyses using FADs have often been criticised (Lehikoinen *et al*. 2004, Knudsen *et al*. 2007, Miller-Rushing *et al*. 2008). However, FADs are the most commonly applied data in phenological studies of bird migration (Tryjanowski *et al*. 2002, Zalakevicius *et al*. 2005, Hubálek and Čapek 2008, Petersen *et al*. 2012) because in many cases, including our study, they provide the only long-term data set describing the spring arrival of birds in their breeding areas. In this study, FADs were recorded by volunteer members of an observation network coordinated by the Estonian Naturalists' Society, and after 1991 by the Estonian Ornithological Society, following unified guidelines. Estonia was divided into 39 birdwatching areas according to its administrative divisions between 1950 and 1957 (Fig. 2). The essence and quality of the analysed FADs are discussed in detail by Lint *et al*. (1963), Palm *et al*. (2009) and Sepp *et al*. (2011).

To carry out a sufficiently reliable analysis, we defined a three-day arrival period. This period consists of FAD, the day before it and the day after it, using the assumption that the birds arrived some time during this three-day period. We defined the arrival period, as well as the arrival season (*see* below), to specify and assess the year-to-year variation in FADs.

Atmospheric circulation data

We analysed the relationships between FADs and CTs for species of birds during the three-day arrival period. In this analysis, we used a selection of circulation classifications derived from CAT 2.0 generated by the COST733 Action (Huth *et al*. 2008, Philipp *et al*. 2010; *see* also http://geo21.geo.uni-augsburg.de/cost733wiki/cost733), including data from the upper troposphere. Thirty-two classification methods were considered in the composition of CAT 2.0. The catalogue consists of a calendar of CTs and mean sea-level pressure (MSLP) maps of all CTs. The calendar covers the period between 1 September 1957 and 31 August 2002, and daily CT data are available. Maps show the locations of low- and high-pressure areas, enabling the determination of prevailing weather conditions for each region.

The names of the circulation classifications generated by the COST733 Action are unique proper nouns that include information concerning the methods and data used in the creation of the classifications (Table 1). They also include the number of CTs, typically 9, 18 or 27, indicating that all atmospheric circulation processes are divided, respectively, into 9, 18 or 27 types. In a classification, CTs are generally arranged by frequency; thus, for classifications with nine CTs, CT1 has the highest frequency and CT9 the lowest. CTs are not comparable by classification because they reflect different weather conditions based on MSLP maps. CTs are historically defined as processes lasting for 3–4 days (Barry and Perry 1973, Girs 1974, Yarnal

1993); therefore, in this study, most classifications have two versions: one in which each CT should last at least four days (four-day-sequence classifications) and another without this limitation. The latter are henceforth referred to as single-day classifications, because CTs without any limitations tend to last only one day. In some cases, seasonal versions of classifications were also created describing differences in atmospheric circulation in spring, summer, autumn and winter. As a result of such combinations, a very large number of classifications (~500) became available for each of the 12 spatial domains for Europe defined by COST733 (Huth *et al*. 2008, Philipp *et al*. 2010, Demuzere *et al*. 2011; *see* also http://geo21.geo.uni-augsburg.de/cost733wiki/cost733).

Sepp *et al*. (2011) found that the spring arrival of birds in Estonia is better described by classifications containing nine CTs as well as by classifications created using optimization methods (classification of families CAP, CAPo, CKM, NNWo, PXK, PXKo, SAN and SOM; for details, *see* Table 1). Therefore, for the present study we selected classifications representing optimization methods and containing nine CTs. There are 47 such classifications in CAT 2.0 of the COST733 Action. The aim of the optimization methods is to arrange the whole set of objects under study (in our case, the objects are days with different circulation patterns) into groups (in our case, circulation types) in such a way that a certain function is optimized. In most circulation classifications based on optimization methods, the purpose of this optimization is to minimise the within-type variability measured as the overall sum of the Euclidean distances between the member objects of a type and the average of the type (centroid). The majority of the optimization methods are based on the *k*-means clustering algorithm (Philipp *et al*. 2010). The circulation data analysed in the present study originate from the domain covering the Baltic Sea (domain 05 by COST733).

Data analysis

One of the principal aims of this study was to evaluate the atmospheric circulation conditions to detect the conditions (CTs) preferred by migratory bird species for their spring arrival in Estonia. We assumed that a species prefers a particular CT in a classification when its frequency during the three-day arrival period exceeds its long-term frequency to the greatest extent during the arrival season (Fig. 3).

The arrival season was designated as the period between the long-term average FAD minus the standard deviation (SD) for the earliest arriving species, and the long-term average FAD plus the standard deviation for the last species to arrive at either Tartu or Kuressaare. The arrival season was determined separately for short- and long-distance migrants (Fig. 1). The selection of separate arrival seasons for the two guilds of migrants was derived from the drastic variation in CT frequencies during spring (Philipp *et al*. 2010). Prevailing CTs in March are practically absent in May and *vice versa*. The arrival seasons are the same for all species within the respective guild of migrants and for the two study areas analysed. The arrival

Table 1. Abbreviations of classification names used in this study. For more details, *see* Huth *et al*. (2008), Philipp *et al*. (2010) and http://geo21.geo.uni-augsburg.de/cost733wiki/cost733.

Abbreviation	Description
CAT	Catalogue of circulation
CAP	Cluster analysis of principal components
CAPo	Cluster analysis of principal components (original)
CKM	K-means clustering
NNWo	Neural network (Kohonen SOM) using 2D topology (original)
PXK	PCA-extreme scores reassigned by *k*-means
PXKo	PCA-extreme scores reassigned by *k*-means (original)
SAN	Simulated annealing clustering
SOM	Self-organising maps (Kohonen SOM) using 1D topology
YR	Year
SP	Sea-level pressure
Z5	500 hPa geopotential height
Y5	Vorticity of 500 hPa
K5	Thickness between 500 and 850 hPa geopotential height
S04	Processes that should last at least four days
S01	Processes without a determined duration
D05	Domain 05 (Baltic Sea)

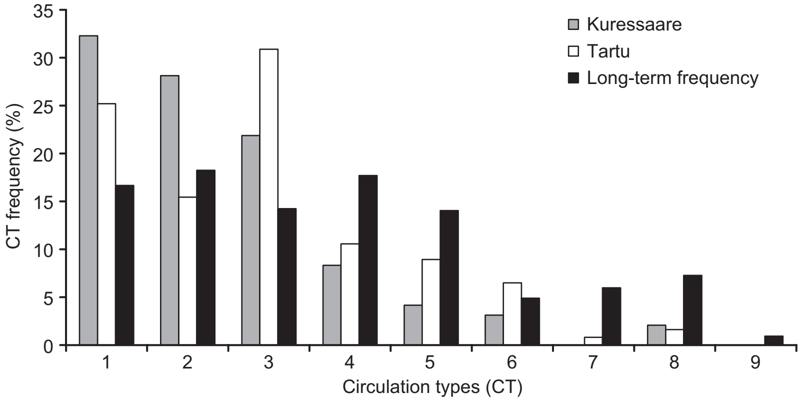

Fig. 3. CT frequencies during the study period (1958–2002) in classification SAN09_YR_S04_SP-Z5 found for the arrival period and arrival season for golden oriole in Tartu and Kuressaare. The frequencies of arrival period in both study areas differed significantly from the frequencies in arrival season (χ^2-test, $p < 0.05$ corrected with the Benjamini-Hochberg method). In this example, the frequency of CT3 during the arrival period of golden oriole exceeds the long-term frequency for the arrival season in Tartu the most, while the frequency of CT1 during the arrival period of golden oriole and the long-term frequency for the arrival season in Kuressaare are the same. For this reason, CT3 and CT1 are defined as preferred CTs for the spring arrival of golden oriole in Tartu and Kuressaare, respectively.

season for short-distance migrants ranged from 23 February (the rook *Corvus frugilegus*; mean FAD 8 March; SD = 13.2 for Tartu) to 18 April (the Eurasian crane *Grus grus*; 9 April; SD = 8.5 for Tartu). For long-distance migrants, this varied between 13 April (the wheatear *Oenanthe oenanthe*; 19 April; SD = 5.7 for Tartu) to 27 May (the swift *Apus apus*; 22 May; SD = 4.5 for Kuressaare).

To detect preferred CTs by species, we first identified the frequencies of all CTs separately for each classification in the arrival period for all the study years and calculated these separately for each bird species (Fig. 3). The CT frequencies in the arrival season were also calculated throughout the study period, but using CTs within the arrival seasons, and defined separately for short- or long-distance migrants as mentioned above. We then applied a χ^2-test to compare the CT frequencies of each classification in the arrival period of a bird species with CT frequencies of the same classification during the arrival season. We used a significance level of $p < 0.05$, corrected using the Benjamini-Hochberg method (Thissen *et al*. 2002). Following this, we extracted all cases in which the CT frequencies of a classification in the arrival period of a species were significantly different from those in the arrival season.

In the next step, we identified the preferred CTs by classification, and for each bird species. This was done by calculating the differences between the frequencies of CTs in the arrival period and the frequencies of the same CTs in the arrival season. Following this, we identified the CT for each bird species showing the greatest positive difference in frequency between the arrival period and the arrival season and defined this as the preferred CT for the bird species (Fig. 3).

To analyse the strength of the species associations with atmospheric circulation, we counted the number of significant χ^2-test outcomes for all the species. An assumption was made that the greater the number of significant outcomes for a species, the stronger the association of that species migration to atmospheric circulation. We also conducted a coincidence analysis to identify how many CTs preferred by species for their arrival coincided with the most frequent CTs in the arrival season. The aim of this procedure was to detect species preferring more common or more specific weather conditions for their migration in spring. Initially, we identified the CT in each classification showing the highest frequency in the arrival season and compared it with CTs of the same classification preferred by bird species during their arrival period. We counted the cases in which there were coinciding CTs for each species and for guilds of species (*see* below), and calculated the percentage of the total number of significant χ^2-test outcomes.

To estimate the goodness of fit for the circulation classifications, we counted the number of significant χ^2-test outcomes for each classification. Here, we made the assumption that the greater the number of significant test outcomes in a classification, the better the classification and, as a result, the more effectively CTs described the circulation processes that affected bird migration. To understand some of the statistical peculiarities of CTs that may have affected our results, we also counted, by classification, all cases in which CTs varied on proximal days, (i.e., alternations). We performed this count using the whole time series for each classification (between 1 September 1957 and 31 August 2002).

In a further step, we used cluster analysis to detect the division of bird species into guilds based on CT frequency. This enabled the grouping of variables (bird species) according to their mutual similarity. We applied unweighted pair-group averages and Euclidean distances in the cluster analysis. To reduce statistical noise, we conducted a cluster analysis using the 16 best circulation classifications (Table 2). We analysed those classifications representing two-thirds of all significant χ^2-test outcomes, having at least 18 significant χ^2-test outcomes simultaneously for the two study areas. The remainder of the classifications showed substantially fewer significant χ^2-test outcomes, typically < 10. To carry out the cluster analysis, we considered the frequencies of all the CTs of the 16 best classifications in the arrival period. To study the stability of the dendrogram structure, in terms of the division of species into more specific guilds as detected in the cluster analysis, we applied a bootstrap method. This enabled the generation of a number of new data sets (we selected 1000) derived from the initial data set (frequencies of CTs) with random replacements. In this way, we could create new dendrograms based on the new data sets and determine the proportion of cases in which the division of species into more specific clusters on these dendrograms took place in the same location as on the dendrogram based on the initial data set. The greater the proportion of cases occurring in the same place of division, the higher the stability of the dendrogram structure up to this division, resulting in more pronounced sub-clusters.

We studied the MSLP maps to understand the weather conditions accompanying preferred CTs. To detect these conditions, we used only the 16 classifications. We only considered CTs preferred by the greatest number of species. To detect these CTs, we first counted the species preferring a CT in a classification and then identified the CT with the highest number of bird species. We detected the most preferred CTs separately for all general and sub-clusters derived from the cluster analysis. Thus, we ordered bird species according to the results of the cluster analysis. In the few cases in which two or more CTs of a classification were equally preferred by the highest number of species, we selected the common CT for either study area, or the one with the most similar circulation conditions compared with the preferred CTs of other classifications.

Results

Using the χ^2-test with the Benjamini-Hochberg method, we found that differences between CT

Table 2. Circulation classifications having at least 18 significant χ^2-test outcomes.

Classification	Number of significant test outcomes	
	Tartu	Kuressaare
CAP09_YR_S01_SP-K5	24	18
CAP09_YR_S01_SP-Z5	19	18
CAP09_YR_S01_SP-Z5-Y5-K5	26	18
CAP09_YR_S04_SP-K5	33	19
CAP09_YR_S04_SP-Z5	24	19
CAP09_YR_S04_SP-Z5-Y5-K5	27	19
CKM09_YR_S01_SP-K5	23	20
CKM09_YR_S01_SP-Z5	20	19
CKM09_YR_S01_SP-Z5-Y5-K5	24	20
CKM09_YR_S04_SP-K5	29	24
CKM09_YR_S04_SP-Z5-Y5-K5	27	18
SAN09_YR_S01_SP-Z5	21	20
SAN09_YR_S01_SP-Z5-Y5-K5	24	19
SAN09_YR_S04_SP-K5	28	22
SAN09_YR_S04_SP-Z5	24	18
SAN09_YR_S04_SP-Z5-Y5-K5	27	18

Table 3. Range of frequencies (Freq.) of circulation types (CTs) preferred by bird species for their spring arrival in Estonia.

Bird species guild	Study area	CTs with lowest frequency				CTs with highest frequency			
		Classification	CT	Freq. (%)	Species	Classification	CT	Freq. (%)	Species
All species	Tartu, Kuressaare	NNWo09_YR_S01_Z5	7	5.9	Rook	SAN09_YR_S04_SP-K5	3	58.1	Garden warbler
All species	Tartu	NNWo09_YR_S01_Z5	7	5.9	Rook	CKM09_YR_S01_SP-K5	3	57.1	House martin
All species	Kuressaare	CAP09_YR_S01_SP-K5	8	8.1	Tree pipit	SAN09_YR_S04_SP-K5	3	58.1	Garden warbler
Migrants									
short-distance	Tartu, Kuressaare	NNWo09_YR_S01_Z5	7	5.9	Rook	CKM09_YR_S04_SP-K5	2	43.1	Snipe
long-distance	Tartu, Kuressaare	CKM09_YR_S04_SP-Y5	6	7.0	Wheatear	SAN09_YR_S04_SP-K5	3	58.1	Garden warbler
short-distance	Tartu	NNWo09_YR_S01_Z5	7	5.9	Rook	CKM09_YR_S04_SP-K5	2	43.1	Snipe
long-distance	Tartu	CKM09_YR_S04_SP-Y5	6	7.0	Wheatear	CKM09_YR_S01_SP-K5	3	57.1	House martin
short-distance	Kuressaare	NNWo09_YR_S01_Z5	4	10.5	Fieldfare	CKM09_YR_S04_SP-K5	2	38.6	Curlew
long-distance	Kuressaare	CAP09_YR_S01_SP-K5	8	8.1	Tree pipit	SAN09_YR_S04_SP-K5	3	58.1	Garden warbler

frequencies in the arrival period and the arrival season of all of the studied species were significant in 26.5% of the 3948 cases (2 study areas × 42 bird species × 47 classifications). For the short- and long-distance migrants, the respective percentages were 22.0% and 31.9%. For Tartu, the χ^2-test produced significant outcomes in 30.6% of the cases, while for Kuressaare this proportion was 22.3%. For short-distance migrants, we found a higher proportion of significant test outcomes for Tartu (28.2%) than for Kuressaare (15.8%). For long-distance migrants, we obtained similar proportions of significant test outcomes: 33.6% for Tartu and 30.1% for Kuressaare.

Depending on the species, the frequency of preferred CTs during the arrival period generally varied between 5.9% and 58.1% (Table 3). We detected a clear difference between short- and long-distance migrants. For the former, the values and range of frequencies of preferred CTs were lower and shorter, respectively, than for the latter. We also noted a difference between study areas for short-distance migrants with a higher range of frequencies for Tartu than for Kuressaare.

There was a high variability in the number of statistically significant χ^2-test outcomes among the species (Fig. 4). The highest number of significant test outcomes was found for the snipe (*Gallinago gallinago*) in Tartu (31 of 47 classifications), while in Kuressaare, the highest number was 24 and it was found for both the golden oriole (*Oriolus oriolus*) and the common buzzard (*Buteo buteo*). We found 19 species (8 short- and 11 long-distance migrants) in Tartu and 14 (3 short- and 11 long-distance migrants) in Kuressaare for which at least 18 significant χ^2-test outcomes were found (Fig. 4). However, there were no significant χ^2-test outcomes found for the yellow wagtail (*Motacilla flava*), the starling (*Sturnus vulgaris*) and the lapwing (*Vanellus vanellus*) in Tartu; and the lapwing, the linnet (*Carduelis cannabina*), the swallow (*Hirundo rustica*), the house martin (*Delichon urbica*), the wood pigeon (*Columba palumbus*), the meadow pipit (*Anthus pratensis*), the common gull (*Larus canus*) and the Eurasian crane in Kuressaare.

Coincidence analysis of CTs suggested that in general the CTs preferred by birds during their arrival period did not coincide with the

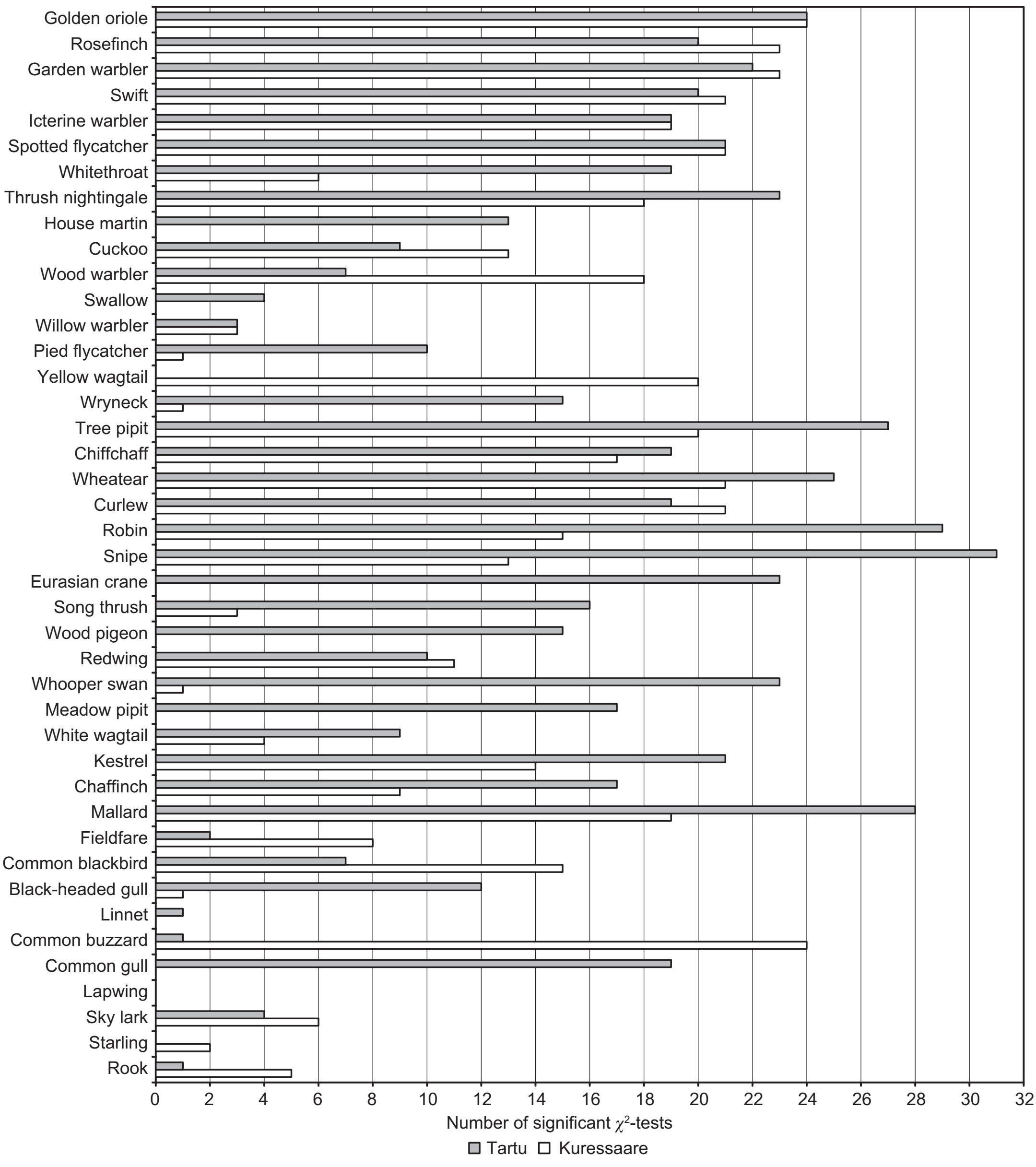

Fig. 4. Number of significant χ^2-test outcomes detected for bird species for Tartu and Kuressaare. The species are arranged according to the species' mean first arrival date (FAD) in Tartu (Fig. 1). We assume that the greater the number of significant χ^2-test outcomes, the more strongly the species' arrival is connected to atmospheric circulation.

most frequent CTs in the arrival season. Coincidence was detected in 156 (14.9%) of 1045 significant χ^2-test outcomes. For the short-distance migrants, there was a lower proportion of coinciding CTs (6.9%) than for the long-distance ones (21.6%). We recorded similar results for both Tartu (8.2% and 20.0%, respectively) and Kuressaare (4.7% and 23.4%, respectively). Considering data for a single species, the proportion of coinciding CTs was generally < 50%. Exceptions to this were identified for the cuckoo (*Cuculus canorus*) (showing coinciding CTs in 8 of 9 CTs with significant test outcomes), the pied flycatcher (*Ficedula hypoleuca*) (6 of 10) and the house martin (9 of 13) for Tartu, as well as the whitethroat (*Sylvia communis*) (4 of 6) and the thrush nightingale (*Luscinia luscinia*) (9 of 18) for Kuressaare. According to the outcomes of the test for 15 species (11 short- and 4 long-distance migrants) for Tartu, there were no preferential CTs coinciding with the most frequent CT in the arrival season. For Kuressaare, these respective numbers were 21, 18 and 3.

The classifications also showed high variability in the number of significant χ^2-test outcomes as well as in alternations (Fig. 5). The classifications created using the CAP, CKM and SAN methods resulted in a higher number, while NNW, PXK and SOM resulted in a lower number of significant test outcomes. The general rule here was that the four-day-sequence classifications created using the data from higher air layers resulted in a higher number of significant χ^2-test outcomes. As expected, the number of alternations in CTs was higher for single-day and lower for four-day-sequence classifications.

The cluster analysis using the bootstrap method divided the species into two general clusters: short- and long-distance migrants (Fig. 6). The only exception was the wheatear, which was recorded in the short-distance migrant cluster for Kuressaare. Clearly differentiated sub-clusters were only evident in the cluster analysis of the Tartu data. Here, the species in 'short-distance migrants 1' (total 9 species) arrive in March, while the species in 'short-distance migrants 2' (14) arrive in early April (Fig. 1). 'Long-distance migrants 1' represents the species whose arrival occurs in late April or early May (11) and 'long-distance migrants 2' comprises the species arriving in mid-May (8).

Analysis of the MSLP maps revealed that the short-distance migrants seem to prefer synoptic situations in which a low-pressure area lies mostly north-west or west of Estonia, above the Norwegian Sea, the Norwegian coast, or the central and northern parts of Scandinavia, or stretches from Iceland to the Norwegian or Barents Sea, while a high-pressure area is located south-west, south or south-east of Estonia, mainly above France, southern Europe or the areas north-east or east of the Black Sea (Table 4 and Fig. 7a). In such cases, south-westerly winds prevail in Estonia. The most preferred CTs were related to 4–11 of the 42 species studied for Tartu, and 2–6 for Kuressaare. Long-distance migrants seem to prefer anticyclonic conditions during their arrival in Estonia. The MSLP maps of preferred CTs show synoptic situations in which a dominant high-pressure area is located above the region of the Baltic Sea (Fig. 7b) or in some cases (in Kuressaare) south or south-west of Estonia (from Germany to the Black Sea or above France). These result in windless conditions or westerly winds in Estonia. Here, the most preferred CTs were identified for a similar number of species for both study areas (2–9 in Tartu and 4–9 in Kuressaare).

Clear differences were also detected between sub-clusters for Tartu. Here, species from the 'short-distance migrants 1' and 'short-distance migrants 2' clusters preferred circulation conditions typical for short-distance migrants in the general cluster (Fig. 8a and b). The main difference between these two sub-clusters is that the species from the 'short-distance migrants 1' sub-cluster preferred CTs for their arrival that did not show any coincidence with the most frequent CTs in the arrival season. However, the proportion of coinciding CTs for species in 'short-distance migrants 2' was 10.6%. Additionally, the most preferred CT in all classifications in 'short-distance migrants 1' was typical to just one species. In 'short-distance migrants 2', the corresponding number of species was in the range of 4–10. The 'long-distance migrants 1' cluster represents species preferring conditions typical for short-distance migrants (Fig. 8c), while species in 'long-distance migrants 2' prefer conditions more typical for long-distance migrants (Fig. 8d). Here, the proportion of preferred CTs coinciding with the most frequent CT in the arrival season was higher for the species from the former sub-cluster (29.3%) than for species from the latter (19.8%). Depending on the classification, the most preferred CT was associated with the arrival of 2–4 species from the 'long-distance migrants 1' sub-cluster and 2–7 species from 'long-distance migrants 2'.

Discussion

As mentioned in the Introduction, we decided to use terms 'preferred CT' and 'seems to prefer' to describe connections between CTs and bird

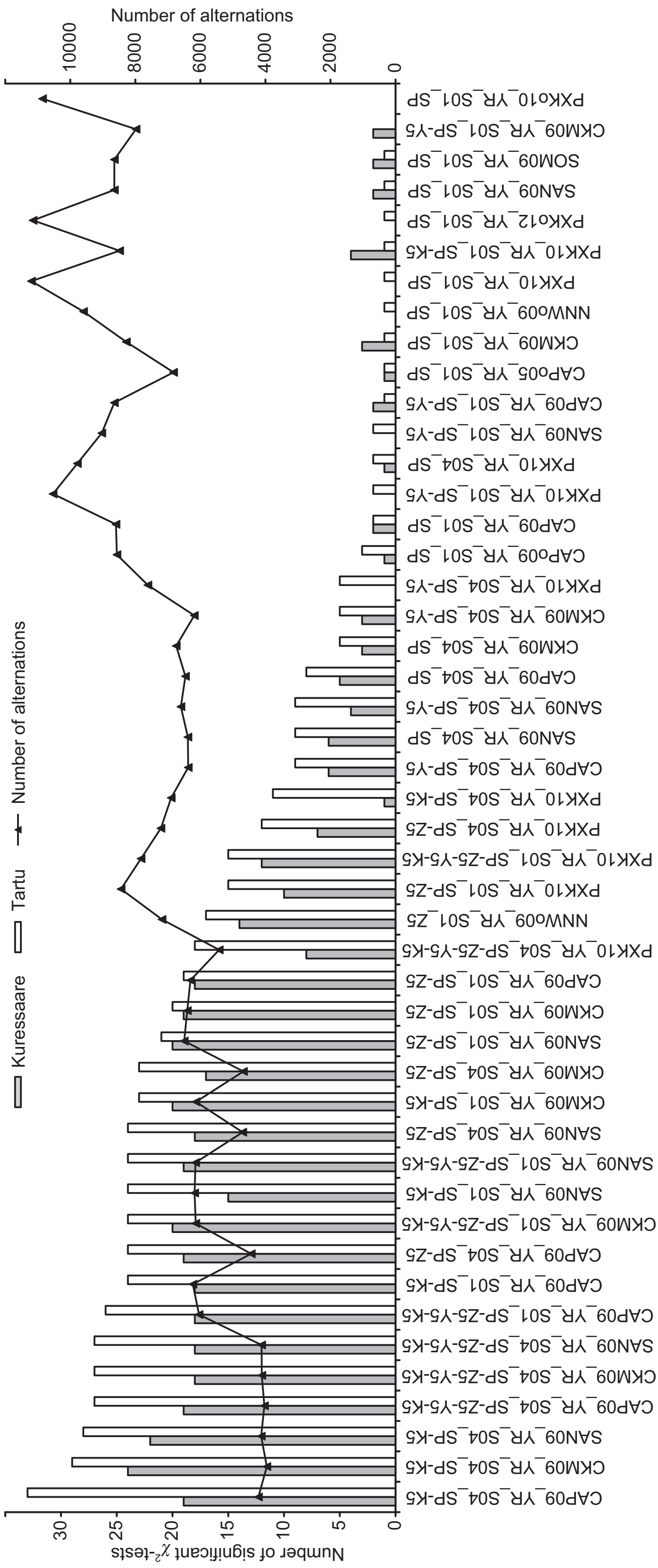

Fig. 5. Number of significant χ^2-test outcomes (columns) and alternations of circulation types (line) detected for classifications. We assume that the greater the number of significant χ^2-test outcomes, the better the classification.

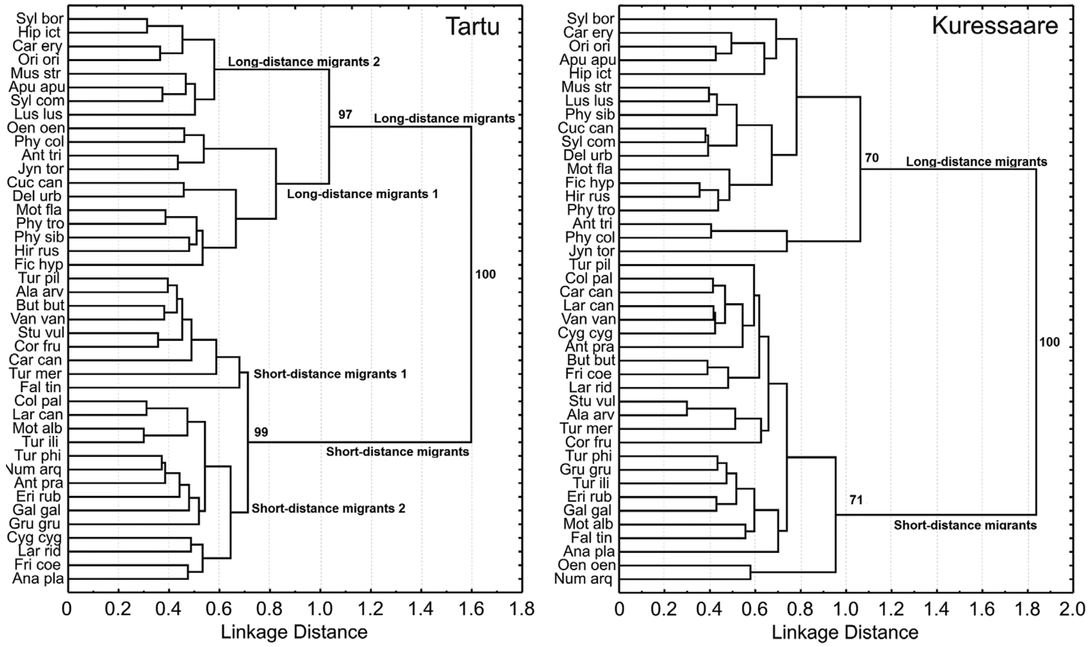

Fig. 6. Dendrograms derived from the cluster analysis based on the frequency of circulation types occurring during the arrival period of studied species (first arrival date, one day before and one day after) at Tartu and Kuressaare. Bootstrap values for nodes greater than 50% are shown in the dendrogram. Abbreviations: Ala arv = *Alauda arvensis* (sky lark), Ana pla = *Anas platyrhynchos* (mallard), Ant pra = *Anthus pratensis* (meadow pipit), Ant tri = *Anthus trivialis* (tree pipit), Apu apu = *Apus apus* (swift), But but = *Buteo buteo* (common buzzard), Car can = *Carduelis cannabina* (linnet), Car ery = *Carpodacus erythrinus* (rosefinch), Col pal = *Columba palumbus* (wood pigeon), Cor fru = *Corvus frugilegus* (rook), Cuc can = *Cuculus canorus* (cuckoo), Cyg cyg = *Cygnus cygnus* (whooper swan), Del urb = *Delichon urbicum* (house martin), Eri rub = *Erithacus rubecula* (robin), Fal tin = *Falco tinnunculus* (kestrel) , Fic hyp = *Ficedula hypoleuca* (pied flycatcher), Fri coe = *Fringilla coelebs* (chaffinch), Gal gal = *Gallinago gallinago* (snipe), Gru gru = *Grus grus* (Eurasian crane), Hip ict = *Hippolais icterina* (icterine warbler), Hir rus = *Hirundo rustica* (swallow), Jyn tor = *Jynx torquilla* (wryneck), Lar can = *Larus canus* (common gull), Lar rid = *Larus ridibundus* (black-headed gull), Lus lus = *Luscinia luscinia* (thrush nightingale), Mot alb = *Motacilla alba* (white wagtail) , Mot fla = *Motacilla flava* (yellow wagtail), Mus str = *Muscicapa striata* (spotted flycatcher), Num arq = *Numenius arquata* (curlew), Oen oen = *Oenanthe oenanthe* (wheatear), Ori ori = *Oriolus oriolus* (golden oriole), Phy col = *Phylloscopus collybita* (chiffchaff), Phy sib = *Phylloscopus sibilatrix* (wood warbler), Phy tro = *Phylloscopus trochilus* (willow warbler), Stu vul = *Sturnus vulgaris* (starling), Syl bor = *Sylvia borin* (garden warbler), Syl com = *Sylvia communis* (whitethroat), Tur ili = *Turdus iliacus* (redwing), Tur mer = *Turdus merula* (common blackbird), Tur phi = *Turdus philomelos* (song thrush), Tur pil = *Turdus pilaris* (fieldfare), Van van = *Vanellus vanellus* (lapwing).

migration. The reason for this derives from the nature of CT statistics. Within the χ^2-test, the frequencies of CTs for many classifications in the arrival period can differ significantly from those in the arrival season; however, the frequency of CTs preferred by birds during the arrival period is often relatively small, < 50% (*see* results). Thus, it cannot be stated that birds arrival in Estonia is associated with a certain CT. Still, the results of the χ^2-test and the coincidence analysis of CTs suggest that there are certain circulation conditions that birds would ‘prefer to take advantage of’ if possible.

The species analysed here can clearly be divided into two general clusters based on the CT frequency: short- and long-distance migrants. The preferred circulation conditions for arrival of species belonging to these clusters are very similar to those reported by Sepp *et al*. (2011). Short-distance migrants, as a rule, arrive in Estonia from western Europe and prefer westerly air flow and cyclonic conditions (Palm *et al*. 2009, Sepp *et al*. 2011). Each new arriving cyclone stimulates birds to start or continue their migration in favourable conditions, i.e., higher air temperature and tail winds from the S–SW–W sector of cyclones (Richardson 1978, Palm *et al*. 2009, Møller *et al*. 2010, Sepp *et al*. 2011), which optimizes the energy costs of migration (Alerstam 1978, Richardson 1978, Alerstam 1990, Alerstam and Lindström 1990, Berthold 1993, Alerstam and Hedenström 1998, Newton 2010). However, a lower frequency of CTs and a lower proportion of coinciding CTs suggest that short-distance migrants do not require a narrow range of weather conditions during their arrival because their migration is brief and the energy demands are relatively low (Berthold 1993, Newton 2010). Long-distance migrants, however, seem to prefer anticyclonic conditions. These conditions offer weak tail winds or windless weather, enabling long-distance continuous migration. In addition, clear skies or minimal cloudiness occurring in high-pressure areas enable nocturnal migrants to navigate using stellar orientation (Wiltschko and Wiltschko 1978, Newton 2010).

The proportion of significant χ^2-test outcomes as well as the range of frequencies of preferred CTs and number of species statistically related to the most preferred CTs were obviously higher in Tartu than in Kuressaare. This is especially clear for the short-distance migrants and may indicate climate differences between continental Estonia and the west Estonian archipelago. Climatic late winter and early spring start earlier in Kuressaare than in Tartu, while climatic spring shows the reverse trend (Jaagus and Ahas 2000). However, this spatial difference may also indicate different migration strategies of the species analysed. Birds arrive in western and eastern Estonia in separate waves from different flyways using different cyclones or anticyclones. Short-distance migrants such as the Eurasian crane arrive in west Estonia from the south-west using the western European flyway with more maritime conditions, but those arriving in east Estonia utilise the central and eastern European flyways where

Table 4. Circulation conditions preferred by bird species (separately for short-distance migrants and long-distance migrants) during their arrival in Estonia (only classifications having at least 18 significant χ^2-test outcomes simultaneously for both study areas are shown together with the most preferred circulation types by species). In the columns 'Type', the first number shows the most preferred circulation type and the second number in parentheses the number of species preferring that circulation type. The columns Pr(Wd) (pressure + wind) reflect the location of the pressure area and prevailing winds in Estonia. Here, the first letter denotes a high- or low-pressure area (H or L, respectively) and the following letters the location of the centre of the pressure areas: above Estonia (C), northeast of Estonia (NE), south of Estonia (S) and so on. The letters in parentheses indicate windless conditions (WL) or the direction of wind [e.g. (SW) from the southwest].

Classification	Short-distance migrants				Long-distance migrants			
	Tartu		Kuressaare		Tartu		Kuressaare	
	Type	Pr(Wd)	Type	Pr(Wd)	Type	Pr(Wd)	Type	Pr(Wd)
CAP09_YR_S01_SP-K5	3(7)	HS(SW)	6(4)	LNW(SW)	1(2)	HC(WL)	1(4)	HC(WL)
CAP09_YR_S01_SP-Z5	3(5)	LNW(SW)	3(5)	LNW(SW)	4(5)	HC(WL)	1(6)	LW(W)
CAP09_YR_S01_SP-Z5-Y5-K5	3(5)	LNW(SW)	6(6)	LNW(SW)	4(5)	HSW(NW)	4(4)	HSW(NW)
CAP09_YR_S04_SP-K5	4(11)	HSE(SW)	8(3)	LN(SW)	3(9)	HC(WL)	3(7)	HC(WL)
CAP09_YR_S04_SP-Z5	3(6)	LNW(SW)	5(2)	LNW(SW)	2(7)	HC(WL)	2(5)	HC(WL)
CAP09_YR_S04_SP-Z5-Y5-K5	3(6)	LNW(SW)	4(2)	HC(WL)	2(5)	HC(WL)	4(7)	HC(WL)
CKM09_YR_S01_SP-K5	4(6)	LNW(SW)	4(5)	LNW(SW)	2(7)	HC(WL)	2(5)	HC(WL)
CKM09_YR_S01_SP-Z5	6(5)	HS(SW)	6(3)	HS(SW)	5(5)	HC(WL)	5(5)	HC(WL)
CKM09_YR_S01_SP-Z5-Y5-K5	4(8)	LW(S)	4(5)	LW(S)	1(5)	HC(WL)	1(6)	HC(WL)
CKM09_YR_S04_SP-K5	2(10)	HS(SW)	5(3)	LNW(SW)	4(8)	HC(WL)	4(9)	HC(WL)
CKM09_YR_S04_SP-Z5-Y5-K5	3(8)	HS(W)	8(3)	LNW(SW)	2(7)	HC(WL)	3(4)	HS(W)
SAN09_YR_S01_SP-Z5	6(4)	HS(SW)	6(5)	HS(SW)	4(6)	HC(WL)	1(5)	HSW(W)
SAN09_YR_S01_SP-Z5-Y5-K5	4(8)	LW(S)	4(4)	LW(S)	1(5)	HC(WL)	1(6)	HC(WL)
SAN09_YR_S04_SP-K5	4(8)	HS(SW)	8(5)	LNW(SW)	3(6)	HC(WL)	3(8)	HC(WL)
SAN09_YR_S04_SP-Z5	2(4)	LNW(SW)	9(4)	LNW(SW)	3(7)	HC(WL)	3(6)	HC(WL)
SAN09_YR_S04_SP-Z5-Y5-K5	3(8)	HS(W)	8(3)	LNW(SW)	2(7)	HC(WL)	3(4)	HS(W)

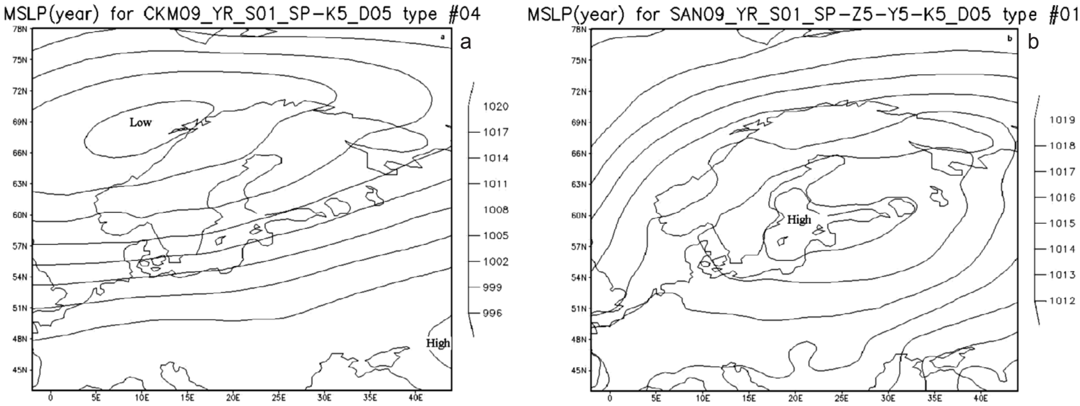

Fig. 7. Examples of typical circulation conditions preferred by (**a**) short-distance migrants (classification CKM09_ YR_S01_SP-K5, type 4), and (**b**) long-distance migrants (classification SAN09_YR_S01_SP-Z5-Y5-K5, type 1) during their arrival in Estonia. 'Low' and 'High' mark the locations of low- and high-pressure areas, respectively.

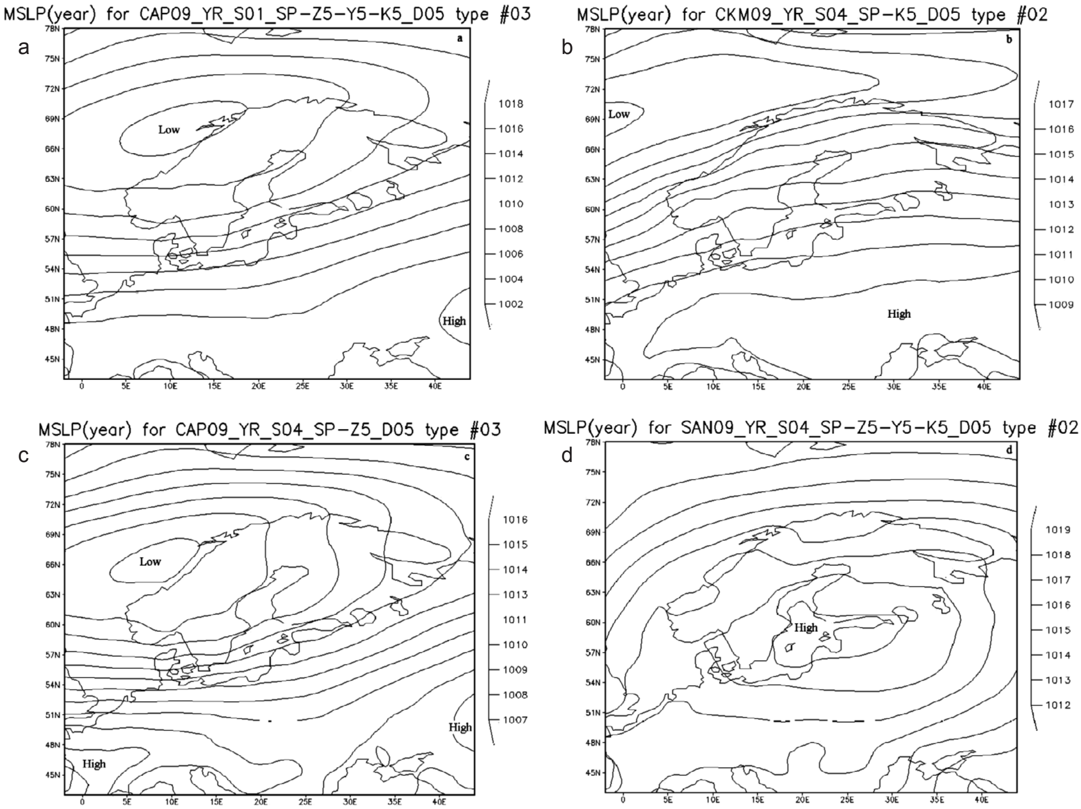

Fig. 8. Examples of typical circulation conditions preferred by species in sub-clusters (**a**) 'short-distance migrants 1' (classification CAP09_YR_S01_SP-Z5-Z5-K5, type 3), (**b**) 'short-distance migrants 2' (CKM09_YR_S04_SP-K5, type 2), (**c**) 'long-distance migrants 1' (CAP09_YR_S04_SP-Z5 type 3) and (**d**) 'long-distance migrants 2' (SAN09_ YR_S04_ SP-Z5-Z5-K5 type 2) for Tartu. 'Low' and 'High' mark the locations of low- and high-pressure areas, respectively.

more continental weather prevails (Leito *et al.* 2006, 2011, 2015). For those arriving from the south-west, migration is most likely affected by favourable tail winds from western cyclones. For those from the south and south-east, migration is more likely to be dependent on favourable tail winds, either of lows moving from south to north (southern cyclones) or anticyclones. Furthermore, the shorter migration route due to their arrival from the south-west (Palm *et al*. 2009) and the milder late winter and early spring in Kuressaare (Jaagus and Ahas 2000) favour the earlier arrival of short-distance migrants in west Estonia.

Long-distance migrants, in contrast, travel over long distances and, for this reason, they require weather that will support their migration as much as possible. They have been suggested to have a more rigid timetable than short-distance migrants, but they are able to delay their arrival by up to two weeks when the weather is poor along the route (Zalakevicius *et al*. 2005). Long-distance migrants arrive in Estonia from the south and, as a result, there is no difference in the length of the migration route to either Tartu or Kuressaare (Palm *et al*. 2009). The statistical analysis showed that the association of long-distance migrants with CTs is stronger and that there are no substantial differences between Tartu and Kuressaare.

The cluster analysis allowed us to study spatial differences and responses of species to atmospheric circulation in more detail. The analysis revealed four clearly pronounced sub-clusters in Tartu, which are broadly distinguishable according to the arrival date of the species. Species in the sub-cluster 'short-distance migrants 1' arrive in early spring and exhibit a distinctly weak associations with atmospheric circulation. This is most likely related to the proximity of the overwintering areas to the breeding areas for many individuals during milder winters, thus decreasing their reliance on special travelling conditions (Møller *et al*. 2010, Newton 2010, Leito *et al*. 2015). Species in the cluster 'short-distance migrants 2' mostly arrive in April, when the effect of westerlies as a proxy for zonal circulation weakens and meridional circulation becomes an important factor (Palm *et al*. 2009). As a result, weather conditions are less favourable for short-distance migrants and thus the statistical signal of preferable CTs is amplified. Consequently, species within this cluster seem to be more selective with regard to migration conditions.

The species in 'long-distance migrants 1' prefer circulation conditions that are more typical for short-distance migrants, namely, predominantly cyclonic conditions. They are a group of migratory species between short- and long-distance migrants, so-called medium-distance migrants, having some migration characteristics similar to those typical for short- as well as long-distance migrants (Newton 2008). For example, the main wintering area for the wheatears breeding in Sweden (Fransson and Hall-Karlsson 2008) is in north-west Africa and birds breeding in Estonia overwinter in north-east Africa or in the Mediterranean (according to data from the Matsalu Ringing Centre), thus having a considerably shorter migration than typical long-distance migrants overwintering in the tropical climate zone. This also explains why the wheatear is found in the 'short-distance migrants' cluster for Kuressaare. Species in the cluster 'Long-distance migrants 2' incorporate clear 'calendar birds' (Berthold 1993), in other words those that arrive during typically anti-cyclonic conditions in mid-May. The CTs that they prefer show a lower coincidence with the most frequent CT in the arrival season than those preferred by 'long-distance migrants 1'. This could be due to the fact that weather conditions in April and May are characterised by a small air pressure gradient over the Baltic Sea region (Post *et al*. 2002). This indicates anticyclonic conditions seen as windless weather with clear skies, which are common and very persistent, especially in early May. The species from 'long-distance migrants 2' tend to have more opportunities to migrate and are not forced to seek specific weather conditions, in contrast to the species from 'long-distance migrants 1'.

From the perspective of synoptic climatology, different species' migration strategies introduce noise into the CT statistics. It must also be noted that there are some differences in the preferential classifications for birds migrating to Tartu and Kuressaare. This indicates that birds with different migration strategies may prefer slightly different atmospheric circulation conditions, which are described not by different CTs, but by other classifications. In practice, this means that there is no 'ideal' classification for all species in every location, and to obtain a complete picture it is reasonable to use an ensemble of classifications as different methods to describe different aspects of atmospheric circulation.

However, the classifications that worked best for the analysis of bird migration were those created using the CAP, CKM and SAN methods. These three methods also show a good relationship with both storminess and precipitation in Estonia (Sepp 2013; *see* also http://meetingorganizer.copernicus.org/EMS2012/EMS2012-360.pdf). Additionally, classifications based on the data from higher air layers (500 and 850 hPa geopotential height) and a four-day limitation showed higher numbers of significant χ^2-test outcomes. Still, it should be noted that the fact that we found considerably more significant χ^2-test outcomes for a large number of species when using classifications with a four-day limitation could be misleading. The likelihood that the alternation of CTs occurs during the FAD period is twice as great for the single-day classifications as for the four-day-sequence classifications. On the other hand, random variability, which is somewhat characteristic of single-day classifications, is smoothed in the case of four-day-sequence classifications, and as a result, they represent more general atmospheric circulation processes.

The most important result of our analysis of CTs is that migration depends not only on what happens at the sea level, but also on more general circulation processes occurring in the higher air layers. Considering that the majority of migrating birds, particularly in the Baltic region, are likely to fly at altitudes below 3000 m (Alerstam 1990, Dokter *et al*. 2010, Kahlert *et al*. 2012), the weather at a height of approximately 5000 m should not substantially affect processes in the air closer to the ground. However, we found that birds prefer CTs of classifications that are a combination of the SLP and the thickness of the air layer between the 500 and 850 hPa geopotential heights. In meteorology, this thickness is used to characterise the direction of thermal advection. This indicates that the meteorological factors involved in bird migration are more complex than the direction of the tail wind, and include the large-scale movement of warm or cold air masses.

To summarise, we found that the species studied show quite different associations with atmospheric circulation. In future analyses, it would be useful to assess the strength of the associations between bird migration and atmospheric circulation in order to identify the reasons behind species preferences for more general, or (in many cases) more specific weather conditions for their activities. In this way, we can expand our knowledge of avian ecology and behaviour, for which synoptic analysis is an important tool.

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