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The effect of weather variables on the White Stork (*Ciconia ciconia*) spring migration phenology

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The influence of weather variables on bird migration is widely recognised as birds have been found to adjust their migration phenology under the influence of weather conditions. This is of particular interest in relation to global climate change. We investigated the long-term (1961–2000) first arrival dates (FAD) of White Storks at their breeding grounds in Lithuania and their relationship with local and regional weather variables. The return of White Storks to their breeding grounds was advanced by almost 5 days during the study period. We found that the arrival time was most strongly influenced by temperature conditions along the migration route in south-eastern Europe as well as at breeding grounds, as warmer temperatures in these areas resulted in earlier arrival of birds. Interestingly, the return of White Storks was closely associated with the onset of the 3°C thermal season – the date when the mean daily air temperature permanently exceeds 3°C. However, in very warm years birds did not return to their breeding grounds as early as would have been expected from temperature alone, suggesting that other factors limit the further advancement of FADs. We suggest that local weather conditions, particularly the air temperature during the final stages of the spring migration, have a more pronounced effect on the arrival dates of White Storks at their breeding grounds than regional climatic phenomena (North Atlantic Oscillation or Indian Ocean Dipole).

1. Introduction

Global climate change has been widely recognised as a major phenomenon, exerting its effect on various components of the environment. It has also been found to affect the life cycles and physiology of individuals (Gordo 2007) as well as seasonal phenomena (Menzel *et al*. 2006, Romanovskaja *et al*. 2009).

Long-term observations of periodic life cycle events present an opportunity to study changes due to changing environmental variables. Since seasonal phenomena are particularly sensitive to climate change, temperature in particular, investigations of long-term phenological data allow the impact of climate variables on organisms, their populations or entire ecosystems to be studied (Tryjanowski *et al*. 2005, Ahas & Aasa 2006, Biaduń *et al*. 2011).

Migratory birds have long been an object of phenological studies due to their distinctive and conspicuous seasonal movements. The most com-

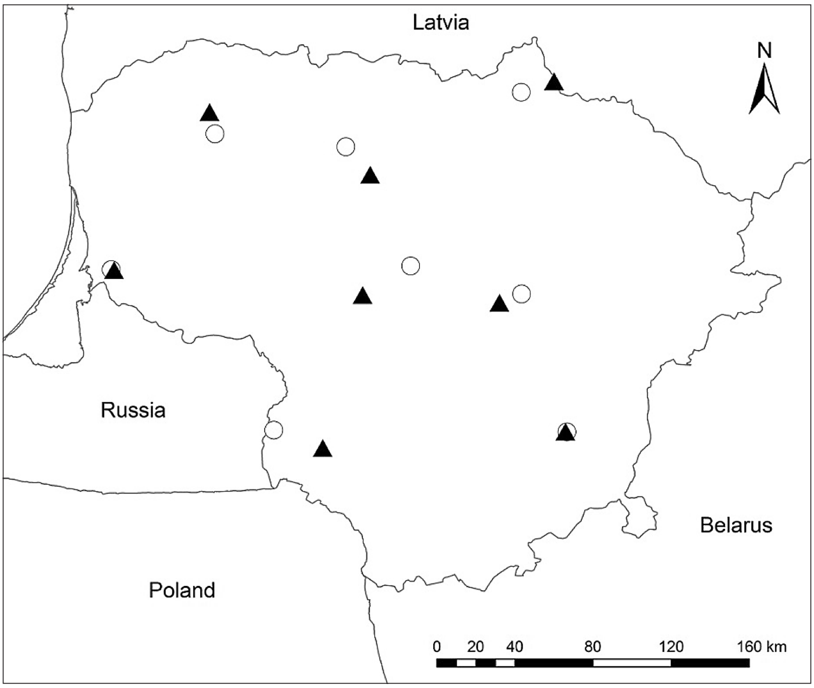

Fig. 1. Location of phenological observation stations (black triangles) and meteorological stations (open circles) in Lithuania.

mon parameter used in bird phenology studies is the arrival date of migratory species at their breeding grounds in the spring (Ptaszyk *et al*. 2003, Pulido 2007). Many studies have revealed that there has been an advance in the spring arrival dates for many species over the last few decades (Gordo 2007, Biaduń *et al*. 2011). In most cases this has been linked to changing temperatures, but the influence of other climatic variables, such as the amount of precipitation in wintering grounds, North Atlantic Oscillation (NAO), Indian Ocean Dipole (IOD) and the El Niño Southern Oscillation (ENSO) indices, snowmelt date, atmospheric pressure at sea level, have been investigated as well (Zalakevicius *et al*. 2006, Gordo 2007, Tryjanowski *et al*. 2013).

The White Stork (*Ciconia ciconia*) is a long-distance migrant – birds breeding in Eastern Europe typically winter in eastern and southern Africa (Van den Bossche *et al*. 2002). It is a common, well known countryside bird in Lithuania, usually nesting in close vicinity to people. It is also one of the first long-distance migratory birds to arrive in spring (Zalakevicius *et al*. 2006). Due to its abundance and conspicuousness, the White Stork has often been an object of phenological studies (Ptaszyk *et al*. 2003, Gordo 2007). The advance of the spring arrival of White Storks has been observed in some studies (Gordo & Sanz 2006, Tryjanowski & Sparks 2008), whereas Gordo *et al*. (2013) found no significant trend, and Zalakevicius *et al*. (2006) even reported a delay. Lithuania holds a very large breeding population of White Storks, which has recently undergone a significant increase (c. 13,000 pairs in 2004 and 19,500 pairs in 2010), and has one of the highest breeding densities of this species (BirdLife International 2004, Vaitkuvienė & Dagys 2015). However, only a few ecological studies of this species have been carried out in Lithuania so far, which constitutes a significant gap in the studies of this otherwise intensively studied species, which is protected in Europe.

The aim of this study was to investigate how the timing of White Stork spring migration is related to local and regional weather variables. We examined first arrival dates (FADs) of White Storks during a 40-year period and their relationship with local weather conditions at their breeding grounds in Lithuania and on the last leg of the spring migration (south-eastern Romania/north-eastern Bulgaria and western Turkey). On a regional level, we investigated the effects of the NAO, which is a large-scale climatic phenomenon known to influence weather conditions along the migration routes of long-distance migrants that is likely to affect the course of migration (Gordo 2007), and the IOD, which is another large-scale ocean circulation system that it has been suggested affects birds wintering in Eastern Africa, and which has been overlooked in phenological studies (Tryjanowski *et al.* 2013). We were also particularly interested in whether White Stork arrival at their breeding grounds is related to a certain mean air temperature; therefore, we studied the relationship between FADs and dates of the distinct thermal seasons.

2. Material and methods

2.1. Phenological data

First arrival dates (FAD) of White Storks were collected by the phenological observation network of the Vokė Branch of the Lithuanian Research Centre for Agriculture and Forestry during 1961–2000, with a break in 1986–1989 (Romanovskaja & Bakšienė 2006). We used systematically collected FAD data from eight observation stations, distributed across the country and containing the most comprehensive datasets for the investigated period (Fig. 1). Data were collected by volunteer observers following a standardised data collection protocol (Kulienė 1983). An area of 3–4 km^2, containing several White Stork nests, was visited daily in each observation station. First arrival date was recorded when at least one bird was observed in a nest in the surveyed area (D. Romanovskaja, unpublished data). For the analysis, the first arrival dates were converted from calendar days into the number of days from the 1st of January, taking leap years into consideration.

Observed FADs may be affected by population size, that is, the first arriving birds may be observed earlier in more abundant populations (Ptaszyk *et al.* 2003, Tryjanowski *et al.* 2005). However, this is more pronounced in less conspicuous species (Tryjanowski & Sparks 2001). The White Stork is a large, easily recognisable species nesting in the vicinity of humans (Tryjanowski *et al.* 2005, Vergara *et al.* 2010), which is probably why a relationship between FAD and population size has not been detected in this species (Tryjanowski *et al.* 2005). However, Gordo *et al.* (2007) reported ear-

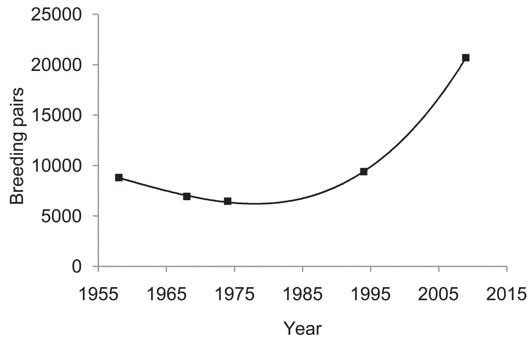

Fig. 2. Annual White Stork population size estimates, obtained by third order polynomial interpolation (line) from country-wide censuses (black squares).

lier FADs in areas with higher White Stork nest densities in the Iberian Peninsula, therefore, in order to account for this possible bias in FAD data, a log-transformed population size was included as an explanatory variable in multiple regression models (Lindén 2011). As regional population data were only available from 1994 and 2010, annual population size estimates for the study period were obtained for the entire country by third order polynomial interpolation (Fig. 2) of national White Stork census results from 1958, 1968, 1974, 1994 and 2010 (Kisielius 1974, Kazlauskas & Paltanavičius 1985, Malinauskas & Vaitkus 1995, Vaitkuvienė & Dagys 2015). The census of 1984 was found to be inaccurate by Ivanauskas *et al.* (1997), hence it was not used for this interpolation.

2.2. Climate data

A number of weather variables that may affect either migration or feeding conditions along the migration route or at the breeding grounds were considered. The local-scale weather variables included mean March air temperature for Lithuania, the mean air temperature and wind conditions in March for two areas crossed by eastern-European White Storks during their spring migration (south-eastern Romania/north-eastern Bulgaria and western Turkey), while the regional-scale variables included mean March NAO index and mean November–February Dipole Mode Index (DMI), representing the IOD condition.

Data on the mean March air temperature in Lithuania (°C) for 1961–2000 were obtained from the archive of the Lithuanian Hydrometeorological Service. Data were obtained from the eight meteorological stations located nearest to the eight phenological observation stations, the mean distance to them being 14.8 ± 10.4 km (0.7–28.8 km, $N = 8$; Fig. 1), the mean difference in altitude being 16.1 ± 11.0 m (1.1–35.1 m, $N = 8$). In order to assess whether the White Storks' arrival at the breeding grounds is related to a certain thermal season rather than the mean temperature, we also considered the date on which the 3°C thermal threshold was met as a potential explanatory variable. Thermal season date, expressed as the number of days from the 1st of January, is the first date when the sum of positive deviations of the mean daily air temperature from the threshold temperature (3°C in this case) exceeds the sum of negative deviations during any subsequent period with negative deviations (LHS 1992). The 3°C thermal season date was considered because exploration of preliminary data suggested that this thermal season usually starts in late March, which is approximately the time of the arrival of first White Storks.

The White Stork spring migration route to the Baltic region lies across Turkey, crossing the Mediterranean at the Bosphorus or the Dardanelles and then continuing north to Bulgaria, eastern Romania, south-eastern Ukraine and Belarus (Patapavičius 2001, 2006, 2007a, 2007b, Van den Bossche *et al*. 2002). Therefore, to assess the effect of weather conditions along the final leg of the spring migration, we also considered air temperature and wind conditions in March – the approximate time when first Lithuanian White Storks are expected to cross the region – in two areas of about 37,000 km^2 crossed by the White Storks during the last leg of their spring migration: western Turkey (38–40° N, 29–31° E) and south-eastern Romania/north-eastern Bulgaria (43–45° N, 26–28° E). Mean March air temperatures for these regions were obtained from the online database of the European Climate Assessment & Dataset project (http://www.ecad.eu; Klein Tank *et al*. 2002). Wind data consisting of mean monthly zonal (u) and meridional (v) wind components (m/s) at the 925 hPa pressure level for March were obtained from the National Center for Environmental Prediction (NCEP) data archives (http://www.esrl.noaa.gov/psd/data/timeseries; Kalnay *et al*. 1996). Positive values for the zonal wind component represent dominant westerly winds, and negative values represent dominant easterly winds. Similarly, positive values for the meridional wind component represent dominant southerly winds, and negative values represent dominant northerly winds (Shamoun-Baranes *et al*. 2003).

A monthly NAO index was used to evaluate the regional meteorological situation in Europe in March. The NAO index reflects the difference of normalized sea level pressures between Ponta Delgada, Azores and Stykkisholmur/Reykjavik, Iceland. NAO index values were obtained from the website of the National Centre for Atmospheric Research (Hurrell & National Center for Atmospheric Research Staff 2013). A mean DMI value for November–February was used to represent the meteorological situation in eastern and southern Africa – the wintering areas of eastern-European White Storks. DMI values were obtained from KNMI Climate Explorer (http://climexp.knmi.nl/).

2.3. Statistical analysis

In this study we used linear mixed effects models with FAD at eight phenological observation stations as the response variable, various weather variables and log-transformed White Stork population size as explanatory variables, and the phenological station ID as a random factor. Models were fitted using Maximum Likelihood (ML) procedure. Furthermore, local weather variables (mean March temperature and the date of the commencement of the 3°C thermal season) were obtained for each phenological station separately from the nearest weather station in order to account for spatial weather differences in Lithuania and their effect on FAD. Prior to model construction, a correlation matrix of all the considered weather variables was constructed to check for the multicollinearity. None of the correlation coefficients exceeded 0.6, so all the variables were included as explanatory variables in further analysis in the linear mixed effects models.

Eleven predictor variables were included in the global linear mixed effects model: date of 3°C thermal season ($T_{3°C}$) and mean March temperature (T_{LT}) in Lithuania; mean March temperature, zonal and meridional wind components (T_{BR}, U_{BR} and V_{BR}, respectively) in south-eastern Roma-

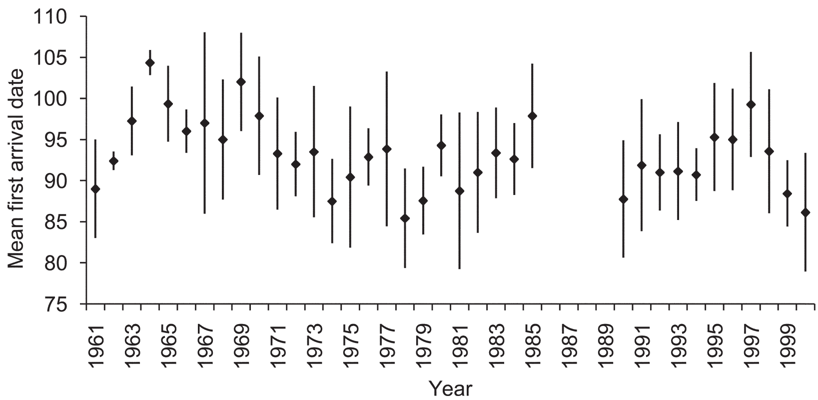

Fig. 3. Mean annual White Stork first arrival dates (± SD) in 1961–2000.

nia/north-eastern Bulgaria; mean March temperature, zonal and meridional wind components (T_{TK}, U_{TK} and V_{TK}, respectively) in western Turkey; mean March NAO index (NAO_M); mean November–February DMI value (DMI_{N-F}); and log-transformed White Stork population size in Lithuania (lnPop). A set of 2048 models with all possible combinations of explanatory variables was computed and evaluated. Phenological station ID was included as a random term in all the models.

An information-theoretical approach was used for model selection, followed by multi-model inference (Burnham & Anderson 2002). Akaike information criterion, corrected for small sample size (AICc), was used for model selection. Models with ΔAICc (difference in AICc value between the model in question and model with the smallest AICc value) of less than 2 were retained in the confidence set of models. Their coefficients were also used for model averaging, while their AICc weights (ω) were used for the comparison of models and assessment of the relative importance of predictor variables. Linear mixed effects models were carried out in the nlme package (Pinheiro *et al.* 2014) of R software (R Development Core Team 2011), while multi-model inference (model selection and parameter averaging) was implemented using the MuMIn package, version 1.9.13 (Bartoń 2013).

3. Results

The mean first arrival date of White Storks at the eight observation stations during the period 1961–2000 was 3 April (30 March to 8 April). Mean annual FADs ranged from 27 March (21 March to 2 April) in 1978 to 15 April (13 April to 17 April) in 1964 (Fig. 3). Overall, White Stork first arrival dates advanced significantly during the period 1961–2000, by almost 5 days (linear regression: $b = -0.123$, $t = -2.115$, df = 36, $P < 0.05$).

The confidence set of models with ΔAICc ≤ 2 included 9 models (Table 1), with no one model receiving very strong support over the other candidate models, as evidenced by AICc weights (ω). For the overall best model, the standard deviation of the random term (station ID) was 1.625, while that of the residuals –7.869. The date of the start of the 3°C thermal season in Lithuania and the mean March air temperature in south-eastern Romania/north-eastern Bulgaria were the most important explanatory variables, as both were present in all the best models (Table 1). The association of the 3°C thermal season date with FAD was positive, while the relationship with the mean March temperature in south-eastern Europe was negative. Interestingly, the effect of the mean March temperature in Lithuania was more than two times weaker than that of the onset of the 3°C thermal season. All other weather variables and White Stork population size in Lithuania did not have a pronounced effect on White Stork first arrival dates (Table 1).

4. Discussion

We used first arrival dates as a measure of bird return time to their breeding grounds. Although FADs have been used in many studies of bird phenology (Tryjanowski *et al.* 2005), some studies

Table 1. The confidence set of linear mixed effects models (ΔAICc ≤ 2) with FAD as a response variable and phenological station ID as a random factor. AICc weights (ω) calculated for the confidence set of models and used for model averaging are shown for each model. Averaged coefficients of explanatory variables (mean), their standard errors (SE) and relative importance of variables (RIV) are presented at the bottom of the table. See text for explanations of the abbreviations of explanatory variables.

Model	$T_{3°C}$	T_{BR}	T_{LT}	lnPop	U_{BR}	T_{TK}	V_{TK}	V_{BR}	NAO_{M}	$DMI_{N–F}$	U_{TK}	AICc	ΔAICc	ω
1	0.1531	–0.8469	–0.3704	–	–	–	–	–	–	–	–	1746.09	0.00	0.19
2	0.1865	–1.0790	–	–	–	–	–	–	–	–	–	1746.12	0.03	0.19
3	0.1902	–1.1100	–	–5.721	–	–	–	–	–	–	–	1747.15	1.06	0.11
4	0.1863	–1.2960	–	–	–	0.4367	–	–	–	–	–	1747.30	1.21	0.10
5	0.1476	–0.7656	–0.4280	–	–	–	–0.2629	–	–	–	–	1747.59	1.50	0.09
6	0.1574	–0.7339	–0.3761	–	–0.2144	–	–	–	–	–	–	1747.81	1.73	0.08
7	0.1600	–0.8978	–0.3196	–3.548	–	–	–	–	–	–	–	1747.83	1.75	0.08
8	0.1909	–0.9789	–	–	–0.1962	–	–	–	–	–	–	1747.89	1.80	0.08
9	0.1844	–1.1070	–	–	–	–	–	0.224	–	–	–	1747.90	1.81	0.08
RIV	1.00	1.00	0.44	0.19	0.16	0.10	0.09	0.08	–	–	–	–	–	–
Mean	0.173	–0.985	–0.374	–4.818	–0.205	0.437	–0.263	0.224	–	–	–	–	–	–
SE	0.067	0.344	0.262	5.789	0.346	0.460	0.337	0.396	–	–	–	–	–	–

have reported this type of data results in a rather noisy pattern (Moussus *et al*. 2010, Lindén 2011). FADs may be affected by observation effort, conspicuousness of birds and population size (Miller-Rushing *et al*. 2008, Lindén 2011). The White Stork is a large, conspicuous and easily recognisable bird, making its detectability very good (Ptaszyk *et al*. 2003). The probability of detecting the first arriving birds early may increase with increasing population size, resulting in biases in observed first arrival dates (Tryjanowski & Sparks 2001). However, this is most pronounced in scarce species, whereas first arrival date observations are considered to be quite accurate in species with large populations (Tryjanowski *et al*. 2005). No pronounced effect of White Stork population size on observed first arrival dates was detected in our study; although its relationship with FAD appeared to be negative. The White Stork population size in Lithuania varied considerably during the study period between c. 6,200 and 12,800 breeding pairs. This further suggests that good observability and the overall abundance of this species, as Lithuania holds one of the highest densities of breeding White Storks in its whole distribution range (BirdLife International 2004, Vaitkuvienė & Dagys 2015), outweighing the possible effect of changes in population size on FAD. No relationship between the observed first arrival dates and White Stork population size has been observed in several other studies as well (Ptaszyk *et al*. 2003, Tryjanowski *et al*. 2006), although Gordo *et al*. (2007) demonstrated that White Storks arrived earlier in areas with higher nest density.

Weather conditions along the migration route influence the speed of migration, its duration, the frequency and duration of stopovers, and the feeding conditions (Gordo 2007). The migration speed increases under favourable weather conditions, as determined by the speed and direction of prevailing winds, air temperature and precipitation (Van den Bossche *et al*. 2002, Shamoun-Baranes *et al*. 2003). Weather conditions also influence the energetic demand of migrating birds (Pulido 2007). In our study, the air temperature in south-eastern Europe in March had a very strong positive relationship with the arrival time of White Storks at the breeding grounds in Lithuania, whereas no effect of wind conditions in south-eastern Europe or that of temperature and wind conditions in western Turkey was observed, suggesting that temperature rather than wind has a stronger effect on migration phenology during the last stages of the spring migration. Our results agree with the findings of Gordo *et al*. (2013), who found a positive effect of temperatures, both in south-eastern Europe and in the Middle East, on the arrival time of White Storks in Slovakia.

The strong association of White Stork FADs with the onset of the 3°C thermal season in Lithuania indicates that the timing of bird arrival at the breeding grounds is strongly influenced by weather conditions, not only along the migration route but also at the breeding grounds, limiting the advance of migrating birds. For example, the annual mean first arrival dates of White Storks observed in our study were c. 10–16 days later than FADs observed in western Poland over the period 1983–2002 by Ptaszyk *et al*. (2003). Assuming that birds from both areas overwinter in similar wintering areas in Africa, this difference can hardly be explained by the difference in migration distance alone, since the distance for White Storks migrating via the eastern migration route (Berthold *et al*. 2001) is likely to be very similar for birds migrating to Lithuania and western Poland. Furthermore, birds migrating to these areas experience very similar weather conditions along the migration route over south-eastern Europe. Local weather conditions at birds' destinations in Poland and Lithuania, however, are very different: although Poznań province is only some 300 km south of central Lithuania, the mean March temperature in western Poland during the period 1983–2002 was +3.7°C (data for Poznań from KNMI Climate Explorer http://climexp.knmi.nl/), whereas in Lithuania it was +0.4°C during the same period. An alternative explanation for these differences in first arrival dates could be that birds breeding in both of these areas depart from their wintering grounds in Africa at different times or even winter in different areas, and hence have different distances to cover before they reach Europe. However, detailed telemetry studies of birds from different breeding locations in Europe would be needed to reliably assess such hypotheses.

It is intriguing that the arrival of White Storks is very strongly associated with the thermal season of 3°C, but not so with the mean March temperature in Lithuania. The relationship with the mean air temperature in March may be offset by considerably different temperatures in the first half of the month, which affect the mean temperature but are not likely to influence the migrating birds that have not yet reached Lithuania. The date of thermal season onset, on the other hand, while also based entirely on temperature, better represents the onset of a more stable environment and, consequently, foraging conditions for arriving birds.

Our findings are in line with a number of earlier studies that have found good evidence of the influence of local weather variables (local air temperature) on the spring migration of birds in different parts of Europe, showing that birds tend to arrive at their breeding grounds earlier in years with warmer spring temperatures (Gienapp *et al*. 2007, Gordo 2007). We did not find any significant influence of NAO on White Stork return dates – a phenomenon observed in a number of studies on bird phenology. This finding, however, supports the conclusion that long-distance migrants, including the White Stork, are less affected by NAO than short-distance migrants (Forchhammer *et al*. 2002, Zalakevicius *et al*. 2006, Hubálek & Čapek 2008). The ability of birds to take advantage of favourable weather conditions and to return to their breeding grounds earlier brings a number of advantages for them. As well as many other bird species, the White Storks arriving earlier are usually of better quality, occupy superior nests in better habitats, pair earlier with females that are also of better quality and start laying eggs earlier, which in turn results in higher reproductive output (Tryjanowski & Sparks 2008, Fulin *et al*. 2009). However, Gordo *et al*. (2013) have demonstrated that the advantages to White Storks of earlier arrival at their breeding grounds in Slovakia have diminished in recent years, possibly as a result of improved resource availability. According to Janiszewski *et al*. (2014), late arrival may result in increased intra-specific competition with low-quality birds suffering poorer reproductive output in the vicinity of higher-quality pairs. However, very early return may be also disadvantageous to birds – it may increase their mortality due to the unexpected deterioration of weather conditions, which is not unusual in early spring (Tryjanowski *et al*. 2004, Gordo 2007, Saino *et al*. 2011). Furthermore, extremely early arrival at breeding grounds in central Poland has been found to be associated with a reduced number of offspring produced, reflecting the increased probability of total breeding failure, while for the remaining birds earlier arrival is associated with higher reproductive output (Janiszewski *et al*. 2013). The thermal season threshold of 3°C most accurately represents the temperature conditions of White Stork return time to Lithuania, suggesting that White Storks return to their breeding grounds when the mean air temperature permanently exceeds 3°C. However, in years when birds have returned particularly early (median annual FAD belonging to the 1st quartile) the mean FAD was four days later than the onset of 3°C thermal season, indicating that White Storks did not return as early as could have been expected according to the temperature alone. It is quite likely that, even under very favourable weather conditions along the European stretch of the spring migration route, a further advance of the return dates is limited by the departure time from the wintering areas and the migration progress in Africa and the Middle East (Gordo 2007). On the other hand, this discrepancy may be advantageous to birds in warm years, since it reduces the risk of extremely early returning birds being caught up in a sudden deterioration of the weather resulting in reproduction failure (Janiszewski *et al*. 2013).

In conclusion, we found that local weather conditions along the last leg of spring migration route and at the breeding grounds strongly influenced the arrival time of White Storks. These local weather variables were far better predictors of spring arrival time than the regional climatic phenomena of the North Atlantic Oscillation or Indian Ocean Dipole. Furthermore, it appears that environmental conditions in Lithuania become suitable for returning White Storks when the mean air temperature permanently exceeds 3°C. However, in very warm years the advancement of bird return dates seems to be limited by factors other than weather conditions along the European stretch of spring migration.

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Sään vaikutus kattohaikaran kevätmuuton ajoittumiseen

Monet linnut säätävät muuttonsa ajoittumista suhteessa säähän. Tämä on olennaista varsinkin ilmaston muutoksen kannalta. Käyttäen 1961–2000 Liettuassa kerättyä seuranta-aineistoa, tutkimme miten paikalliset ja suuremman mittakaavan säämuuttujat vaikuttivat kattohaikaran keväisen ensisaapumisen päivämääriin.

Tutkimusjakson aikana kattohaikarat aikaistivat saapumistaan pesimäalueilleen melkein 5 päivällä. Saapumispäivämäärään vaikutti eniten lämpötila muuttomatkan varrella Kaakkois-Euroopassa, sekä lämpötila pesimäalueella – molemmissa tapauksissa siten, että korkeammat lämpötilat aikaistivat muuttoa. Kattohaikaroiden saapuminen oli läheisessä suhteessa sen päivämäärän kanssa, jolloin ilman lämpötila vakituisesti ylitti 3°C. Hyvin lämpiminä keväinä linnut eivät kuitenkaan palanneet niin aikaisin kuin mitä lämpötilasta yksin olisi voinut päätellä, joten taustalla on muitakin saapumisen ajoittumista rajoittavia tekijöitä. Ehdotamme, että paikalliset sääolosuhteet – varsinkin ilman lämpötila kevätmuuton loppuvaiheilla – ennustaa ensisaapumisen ajankohdan pesimäalueilla tehokkaammin kuin suuren mittakaavan ilmastoindeksit.

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