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RESEARCH

Study of the relation between spring migration of Eurasian woodcock (*Scolopax rusticola* L.) and weather in Hungary using time series analysis

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Abstract
We studied the characteristics of the spring migration of Eurasian Woodcock and the influence of weather on migration based on samples (n=24,124 bagged individuals) collected between 2010 and 2019 in the framework of the Woodcock Bag Monitoring in Hungary. Results reflect strong nonlinearity between the migration dynamics in March and the precipitation and the minimum temperature in each year of study. The above weather factors were strong significant predictors of the number of individuals, because differences in migration patterns are essentially due to weather factors. In years with average weather conditions, the peak of migration was between 16 and 24 March, while in years with advanced migration timing, the migration of the species started up to two weeks earlier due to favourable weather conditions in the wintering areas in early spring. Migration paths are subject to short periods of stormy, wintery weather, which are unfavourable for migration, resulting in flattening migration periods with no definite peak. The spring migration dynamics in the years with weather anomalies were the most distinct from the years with normal migration phenology. The winter weather in March in these years caused birds to stop migrating and only resume their migration towards nesting areas when atmospheric conditions returned to normal. Based on the data from the ten years we had studied, it is already evident that the spring migration phenology of this species changed. The spring migration shifted forward by about 6–10 days, but the considerable influence (delaying) effect of extreme spring weather on the migration route is clearly present, partially masking the effect of trend-like changes in weather characteristics on the phenology.

Keywords Migration dynamics · Weather-dependent migration · Generalized additive model · Zero inflated count data · Time-series analysis · Machine-learning

Introduction

In recent one and a half decades, the timing of the migration of many species has been altered by climate change-related processes (Gill 2015; Kullberg et al. 2015; Conklin et al. 2021; Lawrence et al. 2022), and in this context, the way in which certain elements of the frequently extreme spring weather affect spring migration has been the subject of intense research over the last decade and a half (Newton 2010; Gill 2015; Romano et al. 2023; Horton et al. 2023). Examining the historical data for 14 migratory bird species, Kullberg et al. (2015) concluded that short-distance migrant species are returning earlier nowadays than in the past, while the difference in return times for long-distance migrant species is much smaller. Tryjanowski et al. (2002) made similar conclusions, but from the 16 species they examined, only the

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White Wagtail (*Motacilla alba*), the Black Redstart (*Phoenicurus ochruros*), the Common Wood Pigeon (*Columba palumbus*) and the Barn Swallow (*Hirundo rustica*) showed significant changes. Newton (2010) examined the impact of storms, typically during flight over some type of water body, and assessed mortality during the period following arrival at and departure from breeding areas in autumn. He found that sudden, extreme weather events primarily affected songbirds, but could also, not infrequently, result in significant losses and changes in migration timing for larger species. During spring migration, adverse weather conditions can have a particularly large impact on birds, as migration is much faster than in autumn due to the need for birds to reach breeding grounds as soon as possible (Tøttrup et al. 2012; Gill 2015). In recent decades, significant mortality during spring migration has been observed in a number of species, mostly due to extreme weather conditions (Perrins et al. 1985; Mead 1991; Askeyev et al. 2023).

The Woodcock (*Scolopax rusticola* L.) (hereafter: Woodcock) is one of the species of which it is not known exactly how it responds to changing environmental conditions during migration. We do not know which weather factors play a major role, nor do we know whether the effects of the increasingly intense environmental changes of the present day have led to changes in the migratory phenology of the species.

The Woodcock is a monotypic species (Cramp and Simmons 1983; Glutz von Blotzheim 1986; Gill et al. 2024), with Palearctic distribution (Van Gils et al. 2020) and a stable European population (13.8–17.4 million adults) (BirdLife International 2024). Hungary is on the border of its breeding range and although nesting birds are observed every year, its nesting population does not exceed a few tens of individuals (Hadarics and Zalai 2008; Bende and László 2020; Bende 2021), but it is present in large numbers in this region during its spring and autumn migration (Faragó 2009; Bende 2021). It is a broad-fronted partial migrant species (Faragó 2009; Bende 2021), with a significant proportion of its migratory populations passing north of Hungary (Le Rest et al. 2019). The predominant migration direction towards breeding areas in Europe and in Western Siberia is southwest–northeast (Cramp and Simmons 1983; Glutz von Blotzheim 1986; Bønløkke et al. 2006; Spina and Volponi 2008; Kralj et al. 2013; Saurola et al. 2013; Bairlein et al. 2014; Van Gils et al. 2020; Spina et al. 2022). It is known from capture-recapture and transmitter data that the wintering areas of Woodcock migrating through Hungary are mainly in France, with a smaller part in Italy, and from the Carpathian Basin they fly to Poland, Ukraine, the Baltic States and Russia (Faragó 2009; Schally 2015). The known literature data on the number of migrating birds in Hungary (1.4–6.8 million) show a significant deviation from their own previous dataa (Szemethy et al. 2014; Schally 2020), making estimates uncertain.

The spring migration of this species in Hungary was first studied in the first half of the 20th century (Schenk 1931), and subsequently several studies summarized the available knowledge (Faragó et al. 2000, 2012a, 2012b, 2014, 2015a, 2015b, 2016; Faragó 2003; Faragó and László 2013; Bende 2021; Bende et al. 2023a). These studies, however, were limited to annualised reports of changes in the number of individuals bagged over time, and did not investigate the connection between the temporal course and the dynamic characteristics of migration and weather factors. Bende et al. (2023a) used macrosynoptic meteorological features to show that extreme weather conditions can have a significant impact on the migration of the Woodcock. On the other hand, their study did not examine that how individual weather factors (such as precipitation and temperature) affect the migration dynamics of the Woodcock along the migration route. These factors can be illustrated with those years that characterized by extreme weather conditions. We considered years characterized by high amount of precipitation (2013, 2018) as extreme, where wintery weather (severe frost, heavy snowfall, stormy wind) was typical during the sampling period along the migration route. In the present study, we aimed to develop and apply Generalised Additive Models (GAMs) that can be used to compare the time series of species migration dynamics with weather parameters and to express the effect of weather factors on migration phenology using statistical methods. We have two hypotheses. (I) Weather extremes has significant influence on the dynamics of spring migration, which can be described by temperature attributes and precipitation. We assumed that migration that start with favourable conditions, the influencing effect of shorter-term weather anomalies on the migration route, and extreme atmospheric physical conditions that resulting extreme weather conditions in case of migration (storms, heavy snowfall, persistent severe frost), decreases the migration intensity of Woodcock or the birds may even suspend their migration. The drought and the temperatures that higher than average on the migration route, increased the migration intensity of the species (Bende et al. 2023a). We assume therefore that migration is partly directly, physically influenced by extreme weather conditions, and partly indirectly, through the inactivity of soil life and through the limited availability of food. (II) The beginning of the spring migration is currently shifting forward in a way that can be verified on the basis of ten years of study, meaning that there is a change in the migration phenology of the species.

Material and method

The study of the relation between spring migration and different weather factors was based on Woodcocks collected during spring sampling between 2010 and 2019 (n = 24 124 individuals). Since the spring of 2010, the National Woodcock Bag Monitoring, coordinated by the Hungarian Hunters' National Association, has established the foundation on national level for a large-scale study of the spring migration dynamics, and the studies that related to the relationship of sex and age. During the Woodcock Bag Monitoring, data were collected by hunters with hunting permits at more than 800 sampling points in each year. The data providers bagged the birds as part of stalk hunting during dawn and dusk movements within a 500 m radius area of the sampling points recorded with GPS coordinates. Hunting was a continuous activity for the purpose of sampling. The mode of the hunt was strictly ambush, what happens at predetermined stands crossing the birds route at dawn and dusk during the migratory season. Nationally, annually up to 5,500 Woodcocks could be bagged by the data providers under the quota system, thus complying the diversion from the Birds Directive of the European Union regarding spring hunting (Bende 2021). In accordance with the above, given the large number of elements and the territorial coverage, sampling is suitable for assessing spring migration. Our analyses were based on the finding that the temporal variation in the number of Woodcocks bagged is proportional to the distribution in the number of birds migrating through Hungary during the spring migration (Schally 2020). Based on the above, the temporal change of the baggings accurately reflects the spatial and temporal patterns of the spring migration of Woodcock populations migrating through Hungary (Schally 2020; Bende 2021; Bende et al. 2023a, 2023b). We also assumed that regular sampling activities were carried out to collect samples, and that sampling was statistically representative per year, as verified by statistical representativeness tests (Cochran 1977).

During the sampling, the place where the birds were bagged (municipality, name of the game manager) and the exact time of sampling (month, day) were recorded. The data providers were game management units that agreed to provide data voluntarily. The bagging data they recorded were grouped by game management regions in order to compare the bagging data of the five game management regions in Hungary to weather data from smaller regions on a fine spatial scale. Since the areas of data providers who are authorized to hunt, are classified into regional units in Hungary, therefore it was obvious to take these larger units into account when comparing with weather related data, because regional meteorological differences can significantly influence the spring migration in certain regions of the country. The spatial scale of this classification provides a realistic picture of the characteristics of the Woodcock migration in Hungary when analyzing and evaluating data of migration. The weather data (minimum temperature, maximum temperature, and precipitation) of the meteorological monitoring stations were obtained from the freely available "WMO Centennial Observing Station" data set recorded by the National Meteorological Service at five monitoring stations (Szombathely, Budapest, Pécs, Szeged, and Debrecen). The geographic distribution of these measuring stations provides the qualitative criterion for statistical representativeness (Fig. 1). The above mentioned weather parameters are known from each game management region. We grouped the data providers by region and summarized the daily bag by date. We assigned to these rows the regional daily weather data.

Statistical analysis

Bagging and meteorological data collected during the 41-day sampling period from March 1 to April 10 for the years 2010 to 2019 served as the basis for the statistical analysis. This is the main period for the spring migration of Woodcock in Hungary. Using Cochran's method, we determined the sample size needed for statistical representativeness for a year based on a target population of at least 1.5 million migratory birds (Cochran 1977). To achieve this, we set a very strict margin of error of 3% and a very strict Confidence Interval (CI) of 99%. The predicted proportion was conservatively assumed to be a stringent value of 0.5, and the Z-value corresponding to the acceptable CI was set at 2.576. This method produced an estimated sample size of 1,844 samples annually, ensuring statistical representativeness for every year of the ten-year period in question.

First, a hierarchical clustering analysis (HCA) has been conducted with a dendrogram illustrating the grouping of years ("Year" was treated as a factor variable) based on the average values of the numeric variables of "Temperature daily average," "Temperature minimum," "Temperature maximum," and "Precipitation." HCA was run using the Linkage Method and the Ward's approach. The main focus of the HCA was to determine if certain years could be labelled as representative of distinctive climatic regimes such as anomalously wet years, exceptionally hot years, or climatically 'normal' years. This classification may help isolate years that fit into pre-defined or newly emerging classifications of climatological significance. The resulting dendrogram therefore not only shows the weather differences between the sampling periods of each year, but also as a means to pinpoint potentially representative or deviant years.

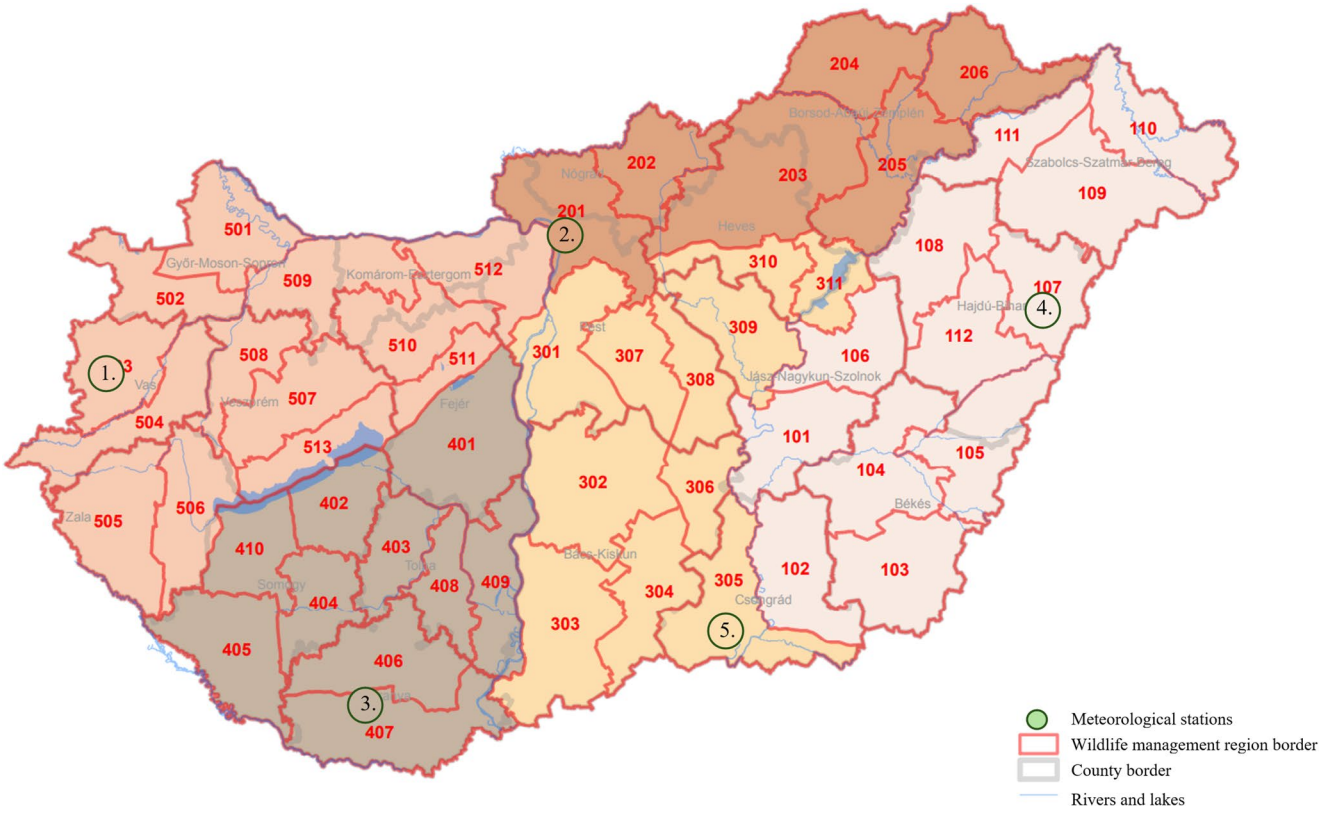

Fig. 1 Boundaries of game management regions units, with three-digit code numbers of game managers and locations of meteorological stations. Colour-coded based on association with weather station (1. Szombathely, 2. Budapest, 3. Pécs, 4. Debrecen, 5. Szeged)

Data was standardized to ensure that each variable contributes equally to the clustering process. The dendrogram shows how the years are clustered based on the similarity of their climatic variables mentioned above, with the vertical axis representing the distance or dissimilarity between clusters. The similarity measure is based on the actual multivariate climatic values, and not the trends. This way, one can identify the optimal number of clusters by examining the longest vertical line that does not intersect any horizontal lines. Subsequently, we wanted to understand the idiosyncrasies in clustering and the dynamics behind the groupings in the HCA. To that end, we depicted extreme years based on the results of the HCA to understand differences between the extremes.

The relationship between the spring migration of Woodcock and weather was investigated using the so-called Zero-Truncated GAMs (Generalized Additive Model) (Wood 2003, 2004, 2006, 2011, 2017). Our dependent variable was the count of individuals on unique days. All statistical analyses were conducted using the R software Version 4.4.1 (R Studio 2023). The GAM was performed using the *mgcv* R-package (Wood 2006, 2011, 2017). We used Zero-Truncated GAM with a Poisson distribution for count data (Wood 2017, 2011), which is specifically used to model species distribution in biology (Barry and Welsh 2002; Fewster et al. 2000; Knape 2016). For example, Knape (2016) decomposed trends in Swedish bird populations using Generalized Additive Mixed-Effects Models.In our study, GAM assesses the relationship between the count of individuals and three predictor variables: minimum temperature, precipitation, and time each modelled using smooth functions (so-called "splines"). We first ordered the data in chronological order and defined a new "abstract" time variable which we called "time": this variable, a unique day identifier, which comprised year, month, and day. Descriptive statistics were run on the dataset (e.g., Count, Mean, SD, Minimum, Median, Mean, Maximum, Missing Values, SD, and SE). The distribution of the numeric data was checked using the Kolmogorov-Smirnov test. We then checked multicollinearity using the Variance Inflation Factor (VIF) with a strict cut-off of 5. We investigated overdispersion with a cut-off of 1.5.

Crucially, the smooth terms for precipitation and temperature (even if they are significant), do not indicate the direction (positive or negative) of the relationship between the independent variables and the dependent variable. Therefore, we computed the derivatives (see, for example, Fewster et al. 2000). In addition, we used visual inspection to see the direction of the trends in different time ranges (see effects plots). In the context of GAMs, cut-off for derivative refers to a threshold value for the derivative of the smooth

function, which identifies where the trend in the relationship between the predictor (e.g., "Precipitation") and the dependent variable ("Count of Individuals") changes. The derivative of a smooth function gives the slope of the curve at any given point. It helps determine whether the relationship is increasing, decreasing, or flat. A negative derivative value suggests a decreasing trend, while a positive derivative indicates an increasing trend. To find this median derivative, one would typically calculate the derivative values across all ranges of the predictor variable (e.g., precipitation) and then take the median of these values. A negative median suggests that, for most values of precipitation, the relationship is negative. The cut-off for the derivative is often set at 0 (flat). For instance, a derivative of 0.08 for temperature suggests that a unit increase in temperature results in a 0.08 increase in the fitted response (e.g., count of individuals) on the scale of the link function in the GAM.

The GAM was fitted based on the filtered non-zero data points. The results from gam.check() function provided information for diagnosing the model and determine if adjustment of the smoothness parameters (k-values) were needed. We computed the gradient and the Hessian information to examine the robustness of the GAM. Adjusted R-squared and Deviance Explained were computed to assess the explanatory power of the GAM. Deviance Explained provides a similar measure to R-squared but is more specific to models in the generalized linear family.

We prepared also an effects plot to visualize the dynamics of each smooth term in the GAM separately. In the GAM effects-plot, time refers to a continuous numeric variable which registers the days that have passed during the course of the study and enables the model to capture nonlinear and cyclic temporal trends, if present, in the number of individuals sampled over time. The lower panel of the effects plot shows the temporal term has strong periodic oscillations which are probably due to (mainly) seasonal or some other recurring ecological factors. Conversely, the Hierarchical Clustering Analysis (HCA) considers year as a categorical variable and groups years based on the similarity of average climatological conditions (minimum, maximum, and mean temperature, and precipitation) with clustering shown along Ward's distance (Fig. 5.).

A Dickey-Fuller test (Dickey and Fuller 1979) was run on the data to check stationarity in the time-series data. Stationarity implies that the average value of the time-series does not change over time and that the variability around the mean is stable over time. Also, the relationship between observations at different time points remains constant over time.

In our subsequent analysis, we examined whether the main migration period, which is defined by the amount of individuals of 50% between 25% and 75% of the migration in sampling period, shows a significant trend-like pre- or postponing in the time interval required for the migration of this half of the population, i.e., shifted in time towards the beginning of the migration period or delayed. In addition to this analysis, an important piece of information is whether there is a difference between the individual years in terms of the beginning and end of this migration period, that is, the duration of these time periods expressed in days. To perform this analysis, we computed the "distance" from 01 March per year expressed in days until the day all the individuals in that year reached (or exceeded) 25% of all individuals sampled in that year irrespective of the number of individuals sampled. We ran a Spearman correlation on the sampling data to examine the potential significant shift the main migration period.

To verify our second hypothesis we were interested in examining if the durations of the days until the number of individuals reach 25% of the entire sample in the given year are similar over the ten years. To test it, we used the 95% CI Method. The idea is that when a value falls outside the CI, it suggests that this value is unusual compared to the central tendency of the data. In other words, it could be considered an outlier and may warrant further examination, as it does not align with the expected range of typical values. We ran the same analysis for the 75% of individuals also.

Edited Gaussian smoothing was used to represent the temporal course of the spring migration of the Woodcock, by using a set of points plotted by the coordinate pairs of the bagging numbers associated with each sampling day. The smoothers used had to meet several criteria, such as the property of boundedness, the existence of one or more extreme values and differentiability, which are of particular importance for the characterisation of the process. These requirements were met by a linear combination of two Gaussian functions:

$$y = \frac{b_6}{e^{(b_5(x-b_4))^2}} + \frac{b_3}{e^{(b_2(x-b_1))^2}} + b_0 \qquad \text{(a.)}$$

The model is characterised by seven parameters – different stretching and offsets – which ensure sufficient flexibility of the function, so that a model with appropriate fitting accuracy to the asymmetry of the data series is created.

The initial values of model a) are determined from the values of the data series as follows:

$b_6 = var_{2first\ max.} - var_{2min.}$ or $b_6 = var_{2first\ min.} - var_{2max.}$
$b_3 = var_{2\ sec.\ max.} - var_{2min.}$ or $b_3 = var_{2\ sec.\ min.} - var_{2\ max.}$
$b_4 = var_{1\ first\ max.}$ or $var_{1\ first\ min.}$
$b_1 = var_{1\ sec.\ max.}$ or $var_{1\ sec.\ min.}$
$b_0 = var_{2min.}$
$b_5 = b_2 \sim 0{,}05.$

Due to the increase in the number of extreme values, the model was further modified, so that by adding a new Gauss

term instead of the parameter b_0, the following mathematical form was obtained:

$$y = \frac{b_8}{e^{(b_7(x-b_6))^2}} + \frac{b_5}{e^{(b_4(x-b_3))^2}} + \frac{b_2}{e^{(b_1(x-b_0))^2}} \quad \text{(b.)}$$

The initial values of model b) are determined from the values of the data series as follows:

$b_8 = var_{2\ first\ max}.\text{-}var_{2\ first\ min}.$
$b_6 = var_{1\ first\ max}.$
$b_5 = var_{2\ sec\ max}.\text{-}var_{2\ sec\ min}.$
$b_3 = var_{1\ sec\ max}.$
$b_2 = var_{2\ third\ max}.$
$b_0 = var_{1\ third\ max}.$
$b_7 = b_4 = b_1 \sim 0{,}05.$

The initial values of the models can be determined from the values of the test data set as indicated above, based on the interval boundaries of the independent (var1) and dependent (var2) variables, and the maximum and minimum values of the dependent variable within the point set, and their locations (Csanády 2013, 2019). Since the coordinates of the extreme values cannot be determined by simple analytical methods, their coordinates were calculated using WinPlot 10.7. Gaussian smoothers were fitted to the data set in Statistica 13.0 (Statsoft, Inc. 2015).

Results

Based on the values of the correlation coefficients of the models fitted to the bagging data series, the functions used model the migration process with sufficient accuracy (Table 1). Based on a single, distinct extreme value and a slightly asymmetric Gaussian distribution, the years 2010, 2011, 2012, 2017 and 2019 (Group I) can be grouped together (Fig. 2). Although the distribution has a similar character, the calculated values of the model showed some temporal variation in the migration peaks of the individual years in Group I. The earliest peak in this group was observed in 2019. The absolute maximum was on 17 March ($N_{sz2017\ max}$ = 95 individuals). The latest migration peak was in 2011 ($N_{sz2011\ max}$ = 263 individuals) on 24 March (Table 1).

There was a significant temporal difference between the absolute extremes of the migration peaks determined by the migration dynamics model in the years 2014, 2015 and 2016 (Group II) compared to the years of Group I, as there was a distinct forward shift. The model showed the earliest maximum in the 2016 study year ($N_{sz2016\ max}$ = 104 individuals), which fell on 8 and 10 March in 2014 ($N_{sz2014\ max}$ = 124 individuals). However, the migration dynamics differed from the years of Group I, because after the maximum the sampling values fluctuated around the number of elements recorded at the peak, and only afterwards the number of birds decreased. This characteristic difference was even more distinct in the 2014 and 2016 function curves, where sampling values remained almost stagnant for almost 10 days after the migration peak, making it very difficult to determine the exact date of the biologically relevant maximum. Because of the indistinct early absolute maximum, the model is likely to indicate an earlier peak than the actual peak of migration. Considering the date of the second local maximum, which fell on 18 March in 2014 and 17 March in 2016, the peak of the migration is estimated to be on the 2nd decade of March. Accordingly, we are talking about years with a prolonged migration peak and a clear advance of migration (Fig. 3).

In 2013 and 2018, we observed a very different rate dynamics from the dynamics of each sampling period from

Table 1 Gaussian model extreme value data and regression coefficient values for the spring woodcock migration characteristics of the study years

Group	Year	No. of Elements	Used Gauss model	Max.		Min.		Regression coefficient	Peak date of migration
				T	N_{sz}	T	N_{sz}		
I.	**2010**	2 384	**a) model**:	23	186	–		0.9779	23 March
	2011	3 393	$N_{sz} = (b_6/\text{^}((b_5*(T1*b_4))\text{^}2))+(b_3/\text{^}((b_2$	24	263	–		0.9836	24 March
	2012	1 939	$*(T\text{-}1*b_1))\text{^}2))+b_0$	22	152	–		0.9795	22 March
	2017	1 682		19	159	–	–	0.9874	19 March
	2019	1 758		17	95	–	–	0.9631	17 March
II.	**2014**	2 716		10	124	15	117	0.9756	10 March
	2015	2 784		16	164	–	–	0.9760	16 March
	2016	2 213		8	104	11	87	0.9541	08 March
III.	**2013**	2 911	**b) model**:	12	140	16	28	0.9035	12 March
			$N_{sz} =$	21	172	27	74		21 March
			$b_8/\text{^}(b_7*(var_1 1*b_6))\text{^}2)+b_5/\text{^}((b_4*(T$	35	106	–	–		4 April
	2018	2 344	$-1*b_3))\text{^}2)+b_2/\text{^}((b_1*(T\text{-}1*b_0))\text{^}2)$	15	150	19	86	0.9750	15 March
				25	140	–	–		25 March

Independent variable: *T* number of sampling days in the study period (March 1 to April 10)

Dependent variable: N_{sz} Number of elements (individual)

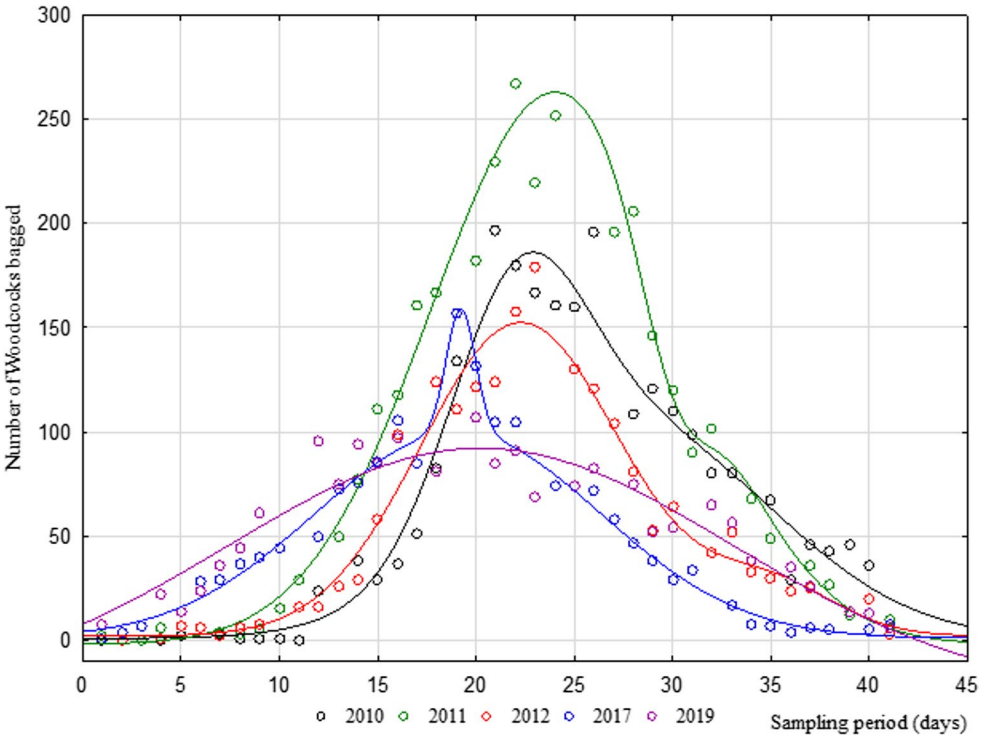

Fig. 2 Woodcock migration dynamics models for the years in the first group (2010, 2011, 2012, 2017, 2019)

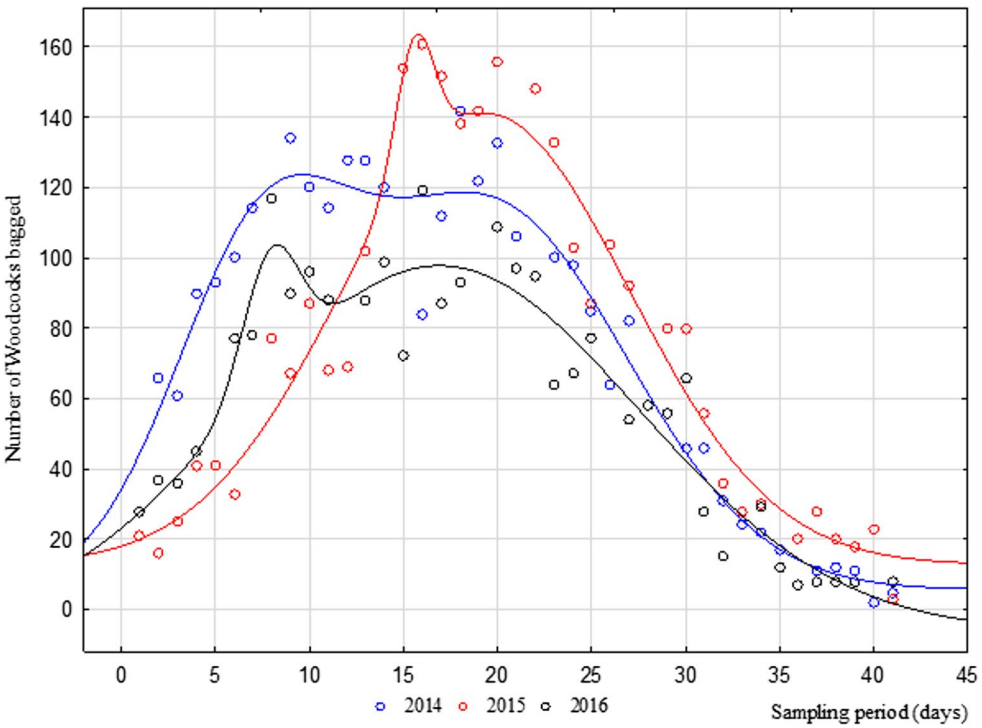

Fig. 3 Woodcock migration dynamics models for the years in the second group (2014, 2015, 2016)

2010 to 2019. This difference was distinct during the spring migration of 2013; the migration was characterised by several extreme values (Fig. 4). The dynamics of the beginning of 2013 reflected a similar character to the average years, but the local maximum on sampling day 12 ($N_{sz2013\ max1}$ = 140 individuals) was followed by a drastic decline. On 16 March the migration reached its absolute minimum ($N_{sz2013\ min1}$ = 28 individuals). Thereafter, an increase similar to the initial intensity of the migration was observed until the next absolute maximum on 21 March ($N_{sz2013\ max2}$ = 172 individuals). Then another rapid decrease was observed until 27 March ($N_{sz2013\ min2}$ = 74 individuals.), followed by a slow increase, followed by a slow decrease in the number of migrating birds from April 5 ($N_{sz2013\ max3}$ = 106 individuals.). The last

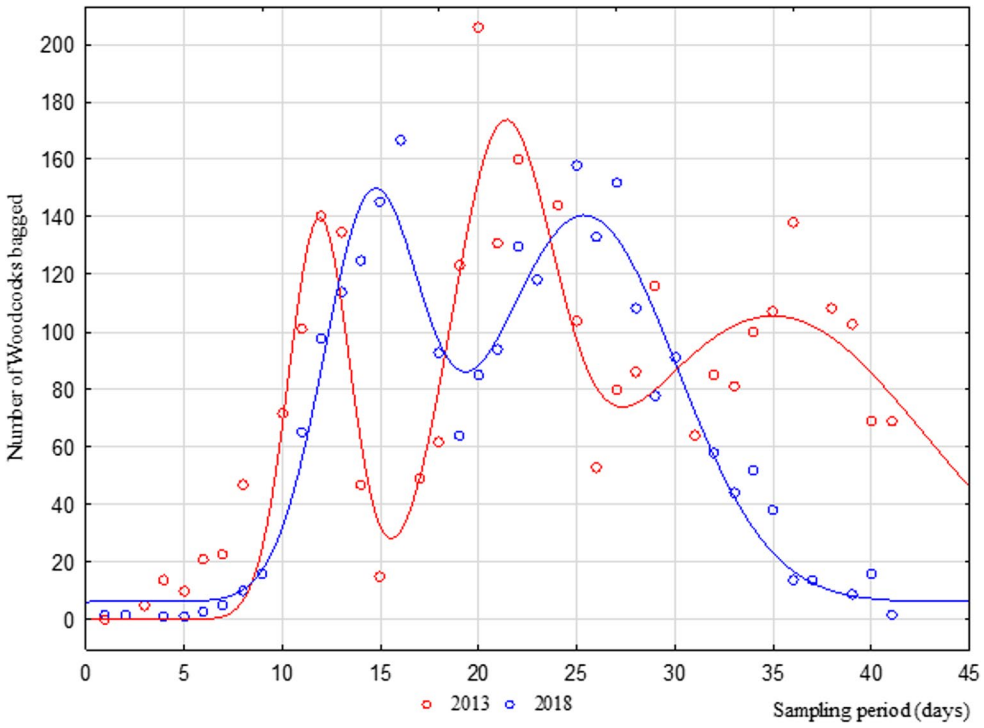

Fig. 4 Woodcock migration dynamics models for the years in the third group (2013, 2018)

phase of the study period was distinctly different from the rest of the study years due to the exceptionally high values and prolonged migration.

The spring migration of Woodcock in 2018 also reflects a particular characteristic. During the 2018 migration we observed an intense increase from 9 to 15 March, until the peak of the migration ($N_{sz2018\ max1}$ = 150 individuals). Thereafter, similar to the dynamics of 2013, a rapid but small decline was observed, reaching a minimum on March. 19 ($N_{sz2018\ min}$ = 86 individuals). Thereafter, an increase was observed until a local maximum on March. 25 ($N_{sz2018\ max2}$ = 140 individuals), followed by a period similar to the intensity of the decline in average years (Table 1).

The differences described above are due to weather (Hypothesis I), so in each year of the sampling period between 2010 and 2019, we compared the weather data recorded at five meteorological stations during 1 March – 10 April. Based on the HCA dendrogram, we could separate three groups based on the weather factors tested in March. Of these, one cluster group, containing the years 2013 and 2018, is distinctly separate (Fig. 5). These two years belong to one cluster and are clearly separated from the rest of the years, as indicated by the yellow line.

The descriptive statistical characteristics of the weather factors are shown in Table 2.

The VIF values for the weather-related variables have indicated that "Temperature daily average (°C)" [VIF = 39] and "Temperature max. (°C)" [VIF = 21] have shown serious multicollinearity. Therefore, average temperature and maximum temperature were removed from the GAM. After removal, the VIF values reduced to the normal range: Temperature min. (°C): VIF = 1.45 and Precipitation (mm): VIF = 1.09. The Kolmogorov-Smirnov test indicated violation of normal distribution ($p < 0.001$), which can be tackled by GAMs.

The test statistic of the Dickey-Fuller test (Dickey-Fuller statistic = −6.34, $p = 0.01$) indicated that the time series is stationary, which is a strong indication against the presence of a unit root (i.e., against non-stationarity). The dispersion ratio was 46.88.

To describe the relation between the weather characteristics and the temporal variation of the number of migrating Woodcocks, we used a Zero-Truncated Generalized Additive Model. The gradient and Hessian information showed that the model optimization was robust. The eigenvalue range was between 2.808 and 8.487, suggesting that the model was numerically stable and not overfitted. We examined the three smoothers to refine the optimal k-values for the GAM using the gam.check() function. The fine-tuned model looked like as follows: s(Temperature minimum, k = 9) + s(Precipitation, k = 15) + s(Time, k = 30), family = poisson(link = "log"), method = "REML". Results from the Zero-Truncated Generalized Additive Model (GAM) containing the three independent variables (minimum temperature, precipitation, and time) with the dependent variable being the number of individuals sampled on a given (unique) day (Table 3).

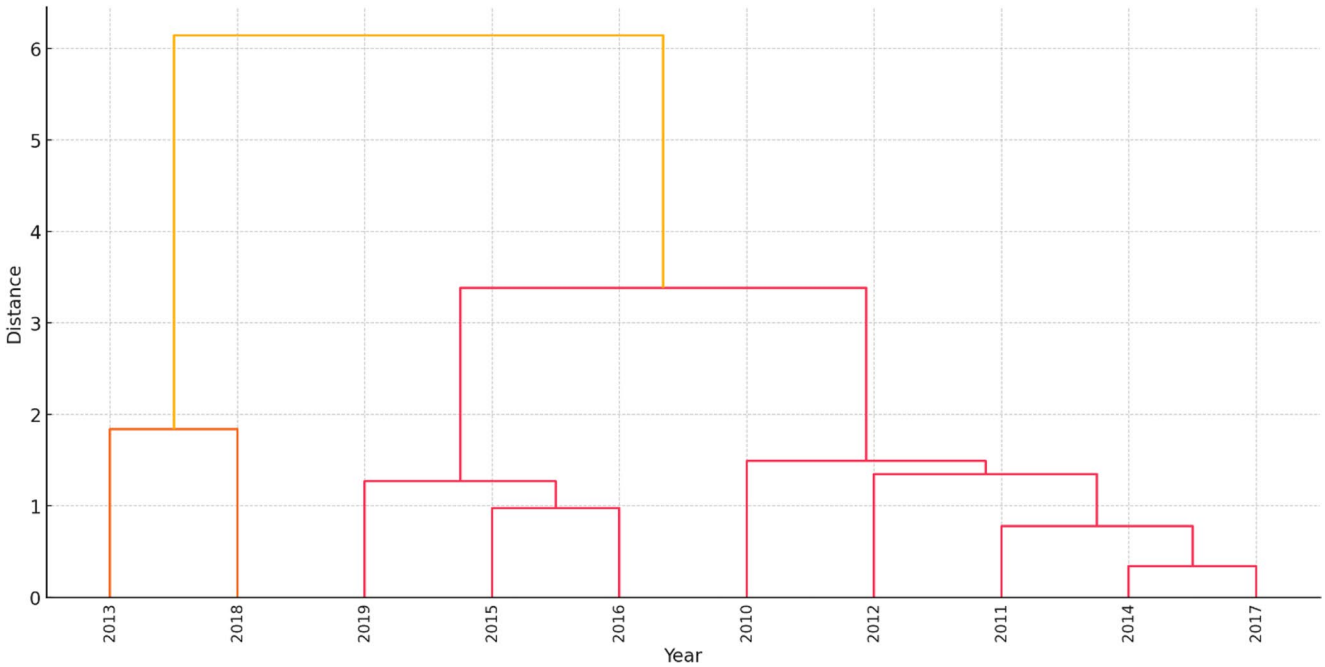

Fig. 5 Grouping of the years studied (2010–2019) by weather factors recorded during the spring migration period of Woodcock

Table 2 The descriptive statistics for the variables in the dataset

Variable	Count	Sum	Mean	SD	Min	Median	Max	Missing Values	SE
Temperature daily average	399.0	3248.8	8.14	4.63	−9.8	8.4	19.4	15	0.23
Temperature minimum	399.0	1208.3	3.03	4.6	−16.3	3.3	15.1	15	0.23
Temperature maximum	399.0	5499.2	13.78	5.72	−5.6	13.8	26.5	15	0.29
Precipitation	399.0	445.7	1.12	3.02	0.0	0.0	22.0	15	0.15
Type of precipitation	149.0	354.0	2.38	1.69	1.0	1.0	7.0	265	0.14
Count of Individuals	414.0	24121.0	58.26	54.92	1.0	43.0	323.0	0	2.7

Table 3 A summary of the GAM statistics fitted with family = poisson(link = "log")

Parametric coefficients				
	Estimate	SE	z-value	*p*-value
Intercept	3.65184	0.01064	343.2	$p<0.001$***
Approximate significance of smooth terms				
	Edf	**Ref. df.**	**Chi. sq.**	**p-value**
s(minimum temperature)	5.317	6.281	88.64	$p<0.001$***
s(precipitation)	13.753	13.947	419.70	$p<0.001$***
s(time)	28.962	29.000	8891.53	$p<0.001$***

R-sq.(adj) = 0.661, deviance explained = 72.63%, -REML = 4015.7, scale est. = 1, n = 399 (valid number of individuals in the analysis). '***' designates $p<0.001$

Count of individuals follows a distribution with overdispersion. The intercept represents the expected log count of individuals when the predictors (temperature, precipitation, and time) are at their baseline (usually mean-centered or set to 0). The three smooth terms are as follows: (i) s(Temperature minimum), (ii) s(Precipitation), and (iii) Time in days.

With regard to model fit statistics, the adjusted R-squared shows that approximately 66.1% of the variation in the count of individuals is explained by the GAM. The Deviance Explained is 72.63% with the Scale estimate being 1. Both temperature and precipitation have a significant nonlinear effect on the count of individuals. The effects plot that visualizes the dynamics of the predictors in the GAM can be seen in Fig. 6.

The derivatives give an indication of the rate of change of the effect for each predictor. The derivative values are as follows: Minimum Temperature [°C]: [0.04, 0.04, 0.06, 0.09, 0.08, 0.05, 0.04]; Precipitation [mm]: [0.2, −0.2, 0.4, −0.1, −1.6]; Time (arbitrary units): [−0.02, 0.0, 0.0, 0.0, 0.0, −0.02].

The main migration period in years without weather extremes that occur on the migration route (2010, 2011, 2012, 2014, 2016, 2017, 2019) ranged from 8 to 13 days (second quarter length on average 4 days; third quarter length on average 5 days). In years with weather anomalies (2013, 2018), the migration period was longer, about 4 to 5 days longer than in normal years (second quarter

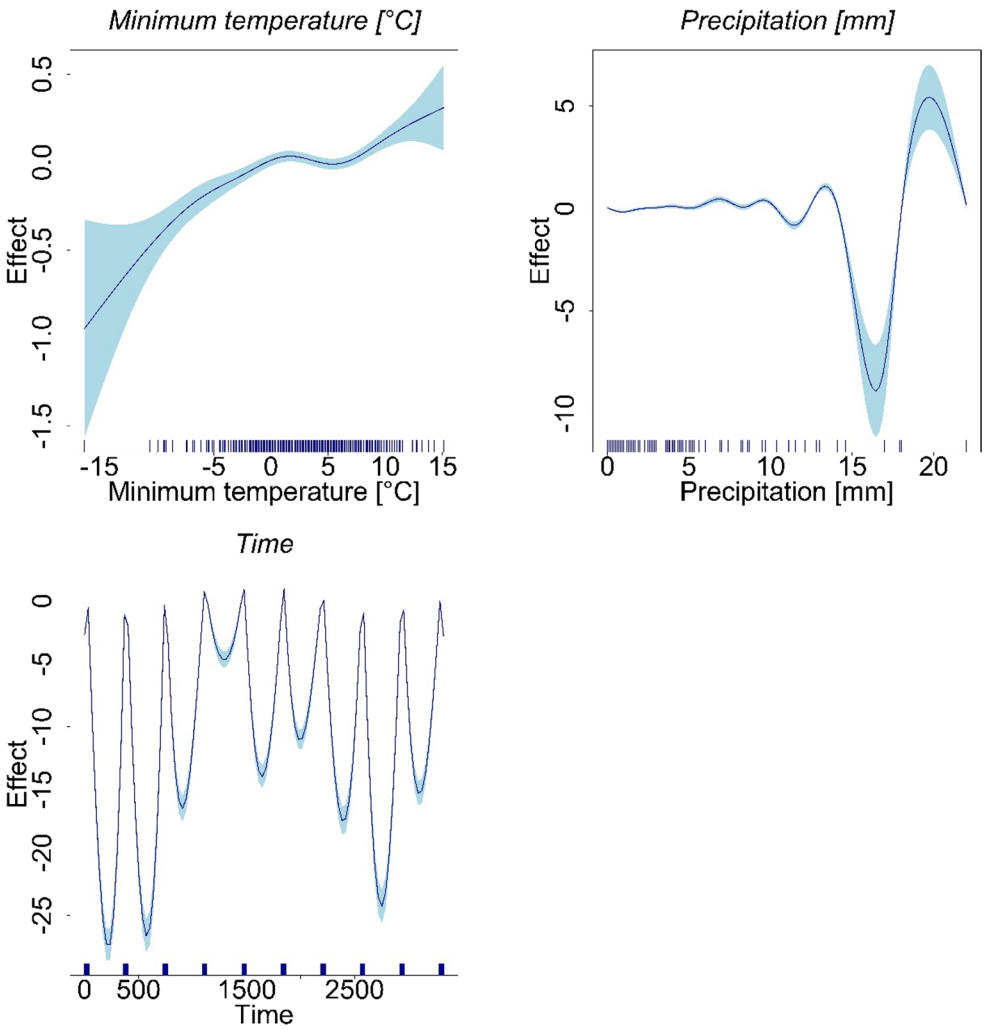

Fig. 6 Effects plot from the Zero-Truncated Generalized Additive Model (GAM) containing the three independent variables (minimum temperature, precipitation, and time) with the dependent variable being the number of individuals sampled on a given (unique) day. The variables that were entered into the HCA were the climate-related variables (the temperature variables and precipitation). Time in this Figure is a continuous variable representing days, while on the y-axis Ward`s distance is depicted

length on average 6 days; third quarter length on average 7 days). The main migration period also shows a difference in time between the first and second phase of the migration, i.e., the rising phase is typically shorter, which also indicates a difference in intensity between the initial phase of the migration and the ending phase. Regarding the length of the main migration period, it can be concluded that the trend of a decrease or increase in the time interval required for this part of the population to migrate is not confirmed for the Woodcock based on the narrow confidence intervals (CI) and visual inspection (Fig. 6). On average, this period started on day 16 (SD = 4.391) and ended on day 27 (SD = 5.745), but considerable differences were observed. Statistically, 2014 and 2013 can be considered exceptional years. In addition to the length of the main migration period, it is important to know whether there is a difference between years in terms of the start and end of this period. Our results clearly show a change in migration phenology (Hypothesis II). This is already confirmed by the survey results from 2010 onwards for 10 years, as we observed a verifiably earlier arrival compared to the base year, depending on weather conditions. Compared to 2010, the main migration period started earlier in each year, with an average overall advance of 6 days, which in some years exceeded 10 days. We repeated the same analysis with 50% of all the sampled individuals per year. Spearman correlation was run on the data which yielded the following results: $\rho = -0.685$, $p = 0.029$ for the former (25%), and $\rho = 0.673$, $p = 0.033$ (for the latter analysis, 75%). The study compared not only the differences in the start of the main migration periods between years, but also their length. Our results show that on average, the main migration period starts on 16 March (SD = 4.391) and ends on 27 March (SD = 5.745), but it is important to note that for two years (2013, 2014) there was a statistically significant difference (Fig. 7).

Discussion

Zero-Truncated GAMs are not yet well-known in contrast to general GAMs which are widespread not just in biology. For instance, Fekete and Hentschel (2021) employed GAMs

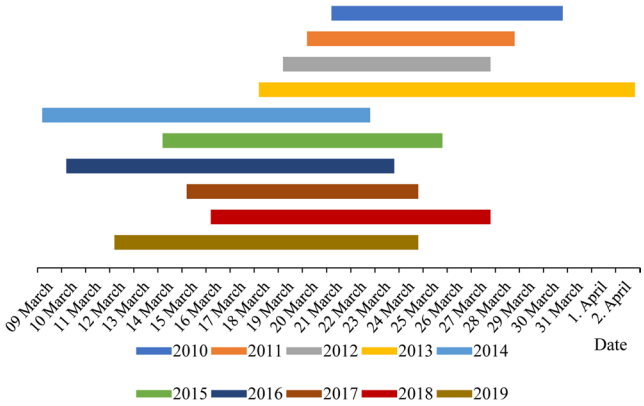

Fig. 7 Temporal changes in the main migration period of the Woodcock during the spring migration in Hungary in the years 2010–2019. The beginning of the main migration period is the period between the 25% and 75% threshold values of the cumulative sampling rate on yearly basis

to model socio-linguistic data. However, the articles in ornithology in which, specifically, Zero-Truncated GAMs are used, are sparse in contrast to other disciplines. To our best knowledge, we are the first ones to employ the most suitable model for ornithological count data, employing Zero-Truncated GAMs using a Poisson distribution fitted with a "log" link function.

Based on the migration dynamics models of Woodcocks bagged in Hungary during the spring sampling in 2010–2019, the peak of migration of the species was in the third/fourth week of March (16–24 March). This can be compared with the data from previous reports in the Hungarian literature (Schenk 1924; Pátkai 1951; Faragó 1985, 2000; Kneféły 1987; Faragó and László 2002, 2003, 2005, 2006, 2007a, 2007b, 2008, 2010a, 2010b; Faragó et al. 2012a, 2012b, 2014, 2015a, 2015b, 2016), which suggests that the mass arrival of Woodcocks is in the last decade of March. However, there were distinct differences between years, mainly due to the role of weather factors in influencing migration. The empirically formulated, statistically unproven finding that the spring migration of Woodcock is significantly influenced by weather conditions (Schenk 1931) has been known for a century in Hungary. In the 10-year period we studied, migration peaked between 17 and 24 March in years without weather extremes (2010, 2011, 2012, 2017, 2019). This is in line with the findings of migration patterns in years without extremes that Woodcock only start their mass migration towards their nesting areas in the second half of February, possibly early March, and thus arrive in our region only in early March (Szabolcs 1971; Faragó 2009; Bende 2021). Based on the Woodcock migration data recorded in Estonia between 1923 and 2008, it is known from Marja and Elts (2022) that the average temperature in March has a significant effect on the arrival time of Woodcocks. The results of these studies were confirmed by telemetry results of Le Rest et al. (2019), which showed that favourable air temperatures and a northerly, non-stormy air flow had a positive effect on the migration of birds. Due to the prolonged winter weather, the onset of spring migration may even be delayed (Clausager 1972, 1974; Moritz and Nemetschek 1976; Glutz von Blotzheim 1986; Bende 2021; Bende et al. 2023a), and thus the arrival of birds in the Carpathian Basin region. This finding is in line with the results of Bønløkke et al. (2006), who found that migrating Woodcock only reach areas further north in March. In the period we studied (2010–2019), there were years with both earlier and extremely late migration. In some years (2014, 2015, 2016), the peak of migration was advanced by more than two weeks. The reason for the earlier arrival is not explained by the weather data of our region, so the background for this has to be found in the weather of the wintering areas (Bende et al. 2023a; Bozó et al. 2024). In early spring weather and/or severe drought conditions, the departure from wintering grounds may start as early as the first half of February, whereas normally most of the Woodcock leave their wintering grounds only in early March (Spina and Volponi 2008; Kralj et al. 2013). The results of the present study confirm the above with regard to the timing of the start of the main migration period in 2014. In the Carpathian Basin, and thus in Hungary, mainly Woodcocks from France and to a lesser extent from Italy pass through during the spring migration (Faragó 2009; Spina and Volponi 2008; Schally 2015; Duchein 2019; Spina et al. 2022), so the late winter weather in these areas is the key determinant for the timing of migration. In 2016, the year with the most distinct advance, the mean February temperature in France was 4–5 °C above the mean February temperature, and similar values were recorded in 2014 and 2015 (>+2.0 °C), with significant drought (Url. 1, 2, 3, 4). In Italy, the second month of 2014 was the warmest February month in the last century, with average temperatures+4 °C above the typical values. Precipitation was also outstanding, with January and February having twice as much rain as the monthly average (Desiato et al. 2015). In 2016, the winter season was the most severe, with a national average of +2.15 °C, and this winter was drier than the previous two (Desiato et al. 2017). This is certainly the reason for the specific advance of the spring migration in Hungary.

The weather extremes experienced in Hungary provided an opportunity to analyse the response to the extreme conditions on the at certain points along the migration route during the spring migration. During extreme spring weather conditions, Woodcock migrate in several waves and with different intensities, resulting in a typical peak migration period with several peaks. Temperature extremes and high precipitation events alone have a significant effect, as can be concluded from the results of the GAM analysis.

The three smooth terms in the GAM were as follows and yielded the following interpretations: (i) s(Temperature minimum), suggesting a flexible, non-linear relationship between minimum temperature and the count of individuals. The high chi-squared value indicates that the smooth function for temperature explains a substantial part of the variance in the response variable (i.e. the count of individuals). (ii) For s(Precipitation), the edf value also indicates an even more intense non-linear relationship between precipitation and the count of individuals. (iii) Time, operationalized as days, is the strongest predictor of number of individuals, as indicated by the very high Chi-square value.

The relationship between "Precipitation" and "Count of bagging Woodcocks" does not provide a definitive trend, it allows us to observe that there seems to be some clustering at certain precipitation levels, with a decrease in counts at higher precipitation values.

The temperature derivatives show a more gradual, oscillatory pattern, indicating that the temperature effect changes more smoothly over its range. In contrast, precipitation derivatives show abrupt shifts, indicating localized areas of high sensitivity. Temperature has a wider distribution of derivative values, indicating that its effect varies more across different temperature levels. Precipitation, however, tends to have concentrated peaks, showing sharp changes at particular points. In sum, the temperature effect appears more continuous and smoother, while the precipitation effect is characterized by sharp, localized changes. This indicates that the model is more sensitive to precipitation changes in specific ranges, while temperature has a more refined, widespread impact on the outcome.

We found an overall negative trend in the relationship between "Precipitation" and "Count of Individuals" for a significant portion of the data. The negative derivative for precipitation suggests a generally decreasing relationship between precipitation and the count of individuals, especially as precipitation increases.

Higher precipitation was associated with a decrease in the number of individuals sampled on a particular day. In simpler terms, past "shocks" or extreme values/unexpected changes in weather influence the current number of individuals. The effects plots showcase that unexpected changes increase in the number of individuals in the past that was followed by a decrease in the number of individuals sampled, and vice versa (for example in 2013 and 2018). This implies that positive and negative shocks tend to balance out over time.

The positive derivative values indicate that as the minimum temperature increases, the number of individuals also increases. In contrast, for Precipitation [mm] the derivatives fluctuate between positive and negative values, indicating that the effect of precipitation on the response variable is more complex. Lastly, the precipitation variable has a more complex relationship with the response variable, showing both positive and negative rates of change.

The results from the Spearman correlation analyses indicate that there is a strong statistically significant preponing trend in time over the observed ten years (temporal shift toward the beginning of the observational period with the increase of the years). Both 25% and 75% of the individuals sampled in a particular year are achieved earlier in terms of days counting from 01 March.

However, our study also highlights the fact that the mutually reinforcing indirect role of certain weather factors is of fundamental importance. Accordingly, the migration dynamics of the years with significant weather anomalies (2013, 2018) deviated most distinctly from the years with average migration characteristics. In the middle of March 2013, a Mediterranean cyclone arrived in Hungary from the south-east, which, mixed with cold air masses from the Arctic, resulted in significant cooling and heavy snowfall, ranging from a few centimetres to 16–20 cm. After the departure of the Mediterranean cyclone, the weather remained cold and frosty, with several cold records being broken (−18.2 C on 17 March). The national monthly mean temperature was − 1.8 C below the 30-year average, making this month one of the coldest in the last century. Following a few days of easing after 20 March, two more Mediterranean cyclones passed through Hungary, bringing snow on 25 March, resulting in 20–30 cm of snow in the south and southwest (Fodor et al. 2013). The temperature conditions in 2018 were similar (Csonka and Bíróné Kircsi 2019). Consistent with the findings of Alerstam (1976), the results of our models suggest that in extreme weather conditions, Woodcocks stop migrating and only resume their migration towards the nesting areas when conditions become more favourable, thus the length of the migration period changes significantly, as confirmed by our results (2013). In most studies, wind direction and strength appear to be the primary factors influencing migration, while temperature is a secondary factor that tends to intensify migration. According to Pátkai (1951), spring migration peaks when the daily mean temperature reaches or exceeds 16 °C. However, the GAM results show a significant relation between daily mean temperature and migration intensity, with temperature extremes having a negative effect on the evolution of migratory bird numbers. As regards the factors that trigger spring migration, the theory developed by Schenk (1924) suggests that spring mass migration is triggered by depression over the British Isles and high air pressure over southern Europe (Hegyfoky 1907; Schenk 1924; Pátkai 1951). This has also been confirmed for other species following a similar migration strategy (Richardson 1990), so that the spring migration is most intense when cyclonic conditions prevail in the

wintering area. Suboptimal effects are typically due to cloud cover and humidity, which are more likely to be side effects of the weather conditions determining migration (Alerstam 1976). Their results are consistent with the findings of several studies that it is rare for long-distance migratory species to have optimal weather conditions throughout their journey (Bulte et al. 2014; Kranstauber et al. 2015). Our results show that migration was clearly intense at higher temperatures and low rainfall events, which is consistent with the results of Bozó et al. (2024).Some weather factors have not only direct but also indirect effects on the timing and course of spring migration, so migration patterns cannot be fully explained by indirect effects alone. An indirect effect is the dry, precipitation-scarce spring, which influences migration through the availability of food resources, either through timing or through the pace of passage along the migration route. The main food of the Woodcock is earthworms (Bende and László 2022), which are not available on frozen, snow-covered ground. This fact explains why sufficient precipitation and temperatures favourable for soil biota are crucial during spring migration. Drought or even severe cold also causes Woodcock to leave wintering areas or to move on more quickly from resting sites during migration. This is supported by telemetry results, since in unfavourable conditions after a few days the woodcocks move on, while in optimal conditions they can spend up to 16 days at a roost. The spring migration lasted an average of 40 days (24–62 days) including the stops (Arizaga et al. 2015). The maximum daily distance of the migration was 200–300 km (Sertić 2008), which would be sufficient performance for a non-stop flight in southwest-northeast direction across the territory of Hungary. According to Bende et al. (2023b), Woodcock migrate between western and eastern Hungary in 3–10 days in years without weather extremes, which is not only due to food availability and weather but also to other endogenous factors. The latter factor is particularly important for long-distance migratory species (Berthold 1996, 2001; Coppack and Both 2002; Tryjanowski et al. 2002; Miller-Rushing et al. 2008), where the timing of migration is much less plastic due to its stronger genetic determinants. In contrast to short-distance migratory species, they are less able to respond rapidly to accelerating and extreme weather changes (Calvert et al. 2012). The above also explains why the grouping based on HCA weather data does not fully correspond to the groupings based on the Gaussian models illustrating migration dynamics.

Based on our results, there is evidence of a change in the spring migration phenology. The overall advance of the main migration period averaged 6 days between 2010 and 2019, exceeding 10 days in some years. However, weather extremes had a significant impact on the migration process in each year, so the trend change in spring migration phenology can only be described with certainty using data series over larger time scales. Based on historical migration data from the turn of the 19–20th centuries processed by Bozó et al. (2024), weather may have caused a difference in the timing of spring migration of up to 3 weeks. However, the timing of spring returns did not change trend-wise over that period, but the data series from more than a century later confirms the trend of advancing migration. In order to evaluate the results of the two studies in this direction, it would be necessary to have a series of data between the two periods. Indeed, it is possible that the study based on the two short-term datasets took place during periods when the direction of weather patterns was different in the two periods, so that the change in the timing of migration was of opposite sign.

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Authors' contributions BA: From data collection to sample processing to writing the study, he took a leading role in writing and coordinating the study. BL was involved in the compilation of the dataset on which the study was based, the evaluation of the results and the writing of the study. FI carried out the statistical evaluation of the large data set using the Zero-Truncated Generalized Additive Model (in addition to HCA and the CI-method), and also described the statistical methodological aspects. CsV. fitted the Gaussian smoothers to the traction data-series, authored the methodological aspects of the rest of the statistical procedures. LR and PT were involved in the compilation of the basic data set (n = 24,124 individuals) and in the cleaning of the large dataset. FS was the organiser of the monitoring programme for the species. All authors reviewed the manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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