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Spring migration dynamics, age and sex ratio, and breeding biology of the Woodcock (*Scolopax rusticola L.*) in Hungary

Theses of doctoral (Ph.D.) dissertation

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1. Introduction

The Woodcock in Hungary came to the fore in 2008 when spring Woodcock hunting was at risk in accordance with Article 4 (2) of the EU Birds Directive (79/409/EEC) although Woodcock is still considered game bird species in Europe since it is listed in the Annex II/1 of the Directive. Once this instruction was included in the Hungarian hunting regulations, no hunting season was settled from 2009. The Hungarian hunters unanimously stood up for the cause of spring Woodcock hunting, since Woodcock hunting during spring roding in Hungary has always been the most popular method of hunting. In order to maintain spring hunts, Hungary made use of this possibility to deviate from the Directive, referring to Article 9 Paragraph (1) (c) of the Directive. According to the regulations of the European Community Directive, this derogation obliged Hungary to develop a reliable monitoring network covering the whole country. Accordingly, a new Woodcock monitoring program was organized by the Hungarian Hunters' National Association. The observational data collection of the program started in 2009 under the guidance of the staff of Szent István University, which was expanded from the following year with a sampling data collection module. The module was led by the Institute of Game Management and Vertebrate Zoology of the University of West Hungary. This new Woodcock Bag Monitoring program offered a unique opportunity to expand the knowledge about the species, since in the last 20 years it has not been possible to examine as much data in Hungary as in the first year of monitoring, in 2010.

In my dissertation, I not only summarized the results of the evaluation of the samples collected within the framework of the monitoring program, but I also examined the breeding biology properties of this species, since the knowledge about the nesting population in Hungary is incomplete. In connection with Woodcock nesting, a detailed dissertation summarizing and publishing country-wide data dating back to the 19th century has not been prepared, only occasional informative publications can be read in the literature. We do not know the characteristics of the nesting period in Hungary, the size of the clutches, the parameters of breeding success and losses, since in Hungary - on the edge of the breeding distribution of the species - we can hardly find any clutches or hens leading their chicks. This led me to the decision to make an attempt to refine the knowledge of the breeding biology of this mysterious species using the literature data from the last more than one and a half century (publications on more than 300 clutches). The clarification of such knowledge in the breeding biology - without such organized monitoring - fills a gap in the Hungarian literature of this species.

While researching the behavioural ecology, migration, and habitat use of the Woodcock, the knowledge of sexes would be of great importance when ringing this difficult-to-catch species, especially when installing high-value telemetry transmitters, since the marked birds cannot be found again in the vast majority of cases. To solve the above-mentioned problem, I looked for a reliable, easy-to-implement, low-cost sex determination method that offers Woodcocks professionals a sampling method that is easy to perform in the field. The widespread application of my methodological proposal for sex determination could greatly contribute to the sex-differentiated evaluation of the Woodcock migration study, as well as to the development of a sampling methodology for population genetic studies.

In my dissertation, based on the ten-year results of two-stage bag monitoring started in 2010, I got a clearer picture of the typical structural parameters of the populations migrating through Hungary, such as age and sex ratio, and of the dynamics of spring migration and its connection to the weather. To assess this, previously we did not possess reliable data sets with a large number of items covering a longer time interval, from which we could draw reliable scientific conclusions.

The significance and the necessity of the research supporting continuous Woodcock hunting are also well reflected in the fact that the Hungarian hunting community was moved unanimously by the loss of spring Woodcock hunting in 2009, as it is an integral part of our hunting traditions - Woodcock hunting during roding is a special point of the hunters. The enthusiasm of Hungarian hunters for the operation of the monitoring program for the preservation of Woodcock hunting is also outstanding internationally, which is well reflected in the fact that nearly half a thousand people entitled to hunt participate in the program even today. However, spring hunting can only happen with the operation of a monitoring program supported by wildlife research and providing reliable results, in compliance with our legal obligations under the Birds Directive (79/409 EEC).

1.1. Objectives

At the beginning of the research, I aimed at the main analysis directions listed below:

1. Mathematical methods for the evaluation of the migration dynamics of the Woodcock bagged during the spring sample collection in the Woodcock Bag Monitoring program in Hungary, which is under the coordination of the Hungarian Hunters' National Association; making models suitable for describing migration characteristics due to their high fitting accuracy and flexibility properties.
2. Analysing the factors influencing the migration dynamics characteristics, with special regard to the exploration of the connection between migration and weather.
3. Analysing migration dynamics differences of the Woodcock by sex and age group during the spring migration.
4. Analysing the time course of the spring migration, with special regard to the length of the migration and the beginning of the migration period.
5. Exploring the connection between the dynamic parameters of the Woodcock migration and Péczely's macrosynoptic situations.
6. Analysing the spatial and temporal pattern of the spring Woodcock migration in some regions of Hungary.
7. Determination of the breeding biology characteristics of the Woodcock in Hungary (nesting regions, breeding success).
8. Compilation of a protocol for an easy-to-perform, high-reliability sex determination procedure applicable to the Woodcock.
9. Statistical verification of the selectivity of hunts during spring roding.
10. Time series analysis of the age groups and the age distribution of each sex.

2. Material and method

2.1. Sample collection in the National Woodcock Monitoring Program

The Woodcock bag monitoring, coordinated by the Hungarian Hunters' National Association since the spring of 2010, established a nationwide, large-scale study of the species' spring migration dynamics, including sex and age ratio, in which up to 5,600 Woodcocks were to be bagged each year. The biometric data of the collected specimens were recorded according to the methodology of uniform ornithological measurement procedures, thus ensuring the possibility of comparison with the data of analogous researches. A data collection guide was available for data providers to perform measurements uniformly. In addition to recording body dimensions, the location of the birds (county, settlement, farmer), the exact time of sampling (month, day, hour, minute), and the sex of the birds were recorded. In addition to the data recorded on the datasheet, from 2010 all farmers had to send in the prepared wings of at least 25% of the bagged Woodcocks in a sampling envelope. From 2011 the number changed to 40%.

In the first period (2010–2014), sampling data sheets and wing samples arrived at the Institute of Game Management and Vertebrate Zoology of the University of Sopron, where the samples were stored refrigerated (-5 ° C) until the tests were performed. In the second period of the monitoring (2015–2019), the wing samples submitted by the data providers and the related basic data (place and time of killing, sex) arrived at Szent István University, from where the institution staff forwarded them to our institute. In 2010–2011 we determined the ages together with DR. RICHÁRD LÁSZLÓ and DÉNES FLUCK (President of the Hungarian Woodcock Club). From 2012 I worked alone. During this period, I classified the birds into two age groups (juvenile and adult). In my dissertation, for the sake of comparability, I used only the data of the samples collected between March 1 and April 10. During the examination of the age ratio given in the weekly breakdown, I evaluated only the data of the weeks that can be characterized by at least fifty samples. During the monitoring, nearly 400 hunters took part in the data collection each year - with more than 800 sampling points.

2.2. Mathematical modelling of migration

In my research, I started from the proven correlation of the monitoring program's monitoring module, that the change in the number of bagged Woodcocks over time is proportional to the change in the number of birds migrating during the spring migration. The killing results reflect the spatial and temporal pattern of the Hungarian spring migration of the Woodcock population reliably. I also assumed that there was regular hunting activity, i.e., killing, for sampling, and that sampling could be considered representative.

The migration dynamics assessment was based on the Woodcock samples (n=23,539 specimens) collected during the spring sampling (a total of 410 assessed sampling days) between 2010 and 2019. I grouped each year based on the dynamic characteristics of the spring migration of the Woodcock using hierarchical cluster analysis. I used the Single Linkage method and the Euclidean distance function to agglomerate the data. The values of the killing ratios belonging to the individual sampling periods were plotted on a weekly histogram according to the groups formed during the hierarchical cluster analysis. Following the simple graphical representation, my aim was to fit a nonlinear regression function that is suitable for the differentiated modelling of the species' migration dynamics - by age, sex, and age and sex - and also suitable for the visual expression and evaluation of the differences. Using the edited models adapted to the properties of the set-points drawn by the coordinate pairs of the killing numbers which belong to each sampling day, I characterized the spring migration dynamics of the Woodcock. The applied models must meet several criteria, such as the nature of constraints and the expectation that is particularly important for the characterization of the process, meaning the existence of one or more extremes. The difference ratios calculated on the basis of the models provide important information for the evaluation of the intensity of the process change, i.e., the dynamic characteristics. For modelling, the well-known Gaussian or so-called life cycle provided the basis, but the basic function - due to the nature of the test data sets - is not suitable for characterizing the process in the absence of transformation due to its known symmetry property. A much more flexible model was needed, which needed a significant increase in the number of parameters. The above requirements are met by a linear combination of the following two Gaussian functions, which have the following traditional mathematical form:

$$y = \frac{b_6}{e^{\left(b_5(x-b_4)\right)^2}} + \frac{b_3}{e^{\left(b_2(x-b_1)\right)^2}} + b_0, \text{ (Model I)}$$

The model is characterized by seven - different stretching and displacement - parameters, which ensure the sufficient flexibility of the function, so I received a model with the appropriate fitting accuracy to match the asymmetry of the data set.

The initial values of Model I are determined from the values in the data set 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=$var_{1sec.\ max.}$ or $var_{1\ sec.\ min.}$

b_0=$var_{2min.}$

b_5=b_2~0,05

Due to the increase in the number of extreme values, I further modified the model, so I added a new Gaussian term, instead of parameter b0, to the following mathematical:

$$y = \frac{b_8}{e^{\left(b_7(x-b_6)\right)^2}} + \frac{b_5}{e^{\left(b_4(x-b_3)\right)^2}} + \frac{b_2}{e^{\left(b_1(x-b_0)\right)^2}}, \text{(Model II)}$$

The initial values of Model II are determined from the values in the data set as follows:

b_8=$var_{2first\ max.}$-$var_{2\ first\ min.}$

b_6=$var_{1\ first\ max.}$

b_5=$var_{2second\ max.}$-$var_{2second\ min.}$

b_3=$var_{1\ second\ max.}$

b_2=$var_{2\ third\ max.}$

b_0=$var_{1\ third\ max.}$

b_7=b_4=b_1~0,05

As indicated above, the initial values of the models can be calculated from the values of the independent (var_1) and dependent (var_2) variable intervals, as well as the maximum and minimum values of the dependent variable within a series of points and their locations. The suitability of the models for describing the migration of the Woodcock is confirmed by the fitting results. After giving the initial values of the complex functions, which are used to model the spring migration of the species, it is clear that each of the parameters determined with their help has real information content. By substituting the parameters calculated from the basic data (b_0, …, b_8) into the function given above, the characteristics of the migration dynamics can be described by mathematical methods, so the applied models satisfy the needs necessary for fitting nonlinear regression functions. The sample numbers for the typical start and end dates (March 1 to April 10) of the functions describing the migration dynamics characteristics of each year and the difference coefficients calculated using absolute extremes are the average intensity indicators of the regression models. With the help of these, the growth and decrease properties of the function section before and after the migration peak can be quantified and compared.

I first gave the time changes observed in the killing characteristics of the sexes and the sexes given in the age group in the form of their cumulative sampling frequency, and then I modelled them using a linear combination of two Gaussian functions. The whole process became clearly demonstrable, and the comparability of the extreme values of the models, i.e., the time of the migration peak, was also ensured.

I differentially examined the differences of the migration dynamics of the Woodcock in each year (2010–2019) by sex and by sex and age using Spearman's rank-order correlation. The application of the method is also justified by the nature of the data sets, since this method is sensitive to the dynamic differences experienced between the individual examination periods. This gave me the opportunity to examine the migration process in each year in a multi-aspect comparative way.

I managed the basic databases and the descriptive statistical analyses using Microsoft Excel 2016, while with the function I used Statistica 13. I determined the coordinates of the models' extreme values with WinPlot 10.7.

To analyse the connection between weather and migration, I used the database and reports of the National Climatic Data Centre (NNDC) Climatic Data OnLine and the Hungarian Meteorological Service (OMSZ), as well as the summary studies of meteorological reports compiled by the Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA, Italy), and the summary reports of "Comprendre. Tout savoir sur la météo, le climat et Météo-France. Bilan climatique de l'hiver" (Meteo France, France).

To analyse the connection between migration and weather, I studied not only the effect of individual weather factors (daily average temperature, amount of precipitation) but also the role of large air masses with different characteristics influencing spring bird migration, which largely determine the weather in the Carpathian Basin. To analyse the connection between migration and these macrosynoptic states, I used the data series from the Péczely's Catalogue of the Macrosynoptic Types.

2.3. Nesting and breeding biology of the Woodcock

The basis of my research was a database compiled from the data of 108 publications known from the Hungarian literature between 1846 and 2019. I supplemented this data set with the data of the nesting map (n=409) published in Schenk's summary work "Woodcock breeding area in historic Hungary". Based on the above data, I plotted the Woodcock nestings on nesting maps and frequency maps of the current area of Hungary and historic Hungary - broken down by county.

For the breeding biology studies, I compiled the database on the basis of the observations (n=356) on Woodcock breeding published in the Hungarian literature (1846–2019), the data of unpublished personal publications, and the clutches found in Hungarian egg collections. During the processing, I determined the time distribution of the nestings based on the data of the nests (n=93) reported with the known time of discovery.

By processing the data of known nests (n=79) from Hungary, probably with full number of eggs, I determined the distribution of clutches based on the number of eggs and the average number of eggs per hen. Based on the complete or partial mortality data of 38 nests of these known-sized clutches, I determined the distribution of the known factors causing nest losses. From the data on Woodcock families (n=98) and Woodcock chicks (n=239) published over the last 174 years, I determined the average number of flightless chicks (n=57) per hen, based on the reports (n=51) on the development and estimated age of the birds. I also determined the number of chicks raised per hen based on the reports (n=22) of observations of already flying but immature birds (n=66). Based on the losses published in the literature, I gave the distribution of the factors causing the death of Woodcock chicks (n=25). I compared the biology results derived from the synthesis of the collected data on the Carpathian Basin with the data from the international literature. The breeding biology and nesting data were processed using Microsoft Excel 2016, while the map was displayed using the ArcGIS10.3 GIS program.

2.4. Sex determination of the Woodcock by invasive and non-invasive procedures

2.4.1. Live Capture and Sampling

The drop net method used to catch living Woodcock has long been known in ornithological literature, but it has been used in Hungary only since the 2000s. At night, birds feeding in the open, typically on short-grass grasslands, are searched for and captured using a reflector and drop net. We searched for feeding Woodcocks around Sopron (Hungary) with the help of a 1300 lumen reflector and a thermal imaging camera (Pulsar Axion Xm38), and then approached the continuously illuminated bird, covering it with a 1-meter diameter net attached loosely to its frame at the end of an 8-meter-long telescopic rod.

For the success, it was crucial that the catchers worked well together, standing behind the light source from beginning to end, and that the cover net was above the light beam until the last minute, otherwise, the bird would easily notice the device and fly away.

After capture, blood was drawn from the wing vein *(vena cutanea ulnaris)* according to the blood sampling protocol for small birds, for which I did not remove the feathers on the upper arm, only smoothed them with 70% alcohol wool to make the vein clearly visible. I took blood samples with a 2 ml syringe and a 25G injection needle. The amount of blood drawn was approximately 0.5–1 ml, which contains enough DNA for a successful genetic analysis.

I collected the blood sample in a syringe and in blood collection tubes filled with anticoagulant (Na-EDTA) solution used in haematological test. I stored the autumn samples refrigerated (–5 ° C) for 5 days, while the spring samples were stored frozen for several months (-20 ° C) as an effect of forced processing due to the pandemic situation. In my experience, the efficiency of the method was not affected by any of the applied sample storage methods, as the sex determination could be performed with 100% success in the case of blood samples stored without anticoagulant solution and even in the case of Na-EDTA frozen blood samples.

I collected the feather samples required for genetic analysis from the primaries of birds bagged in March during the spring sampling in the Sopron area, which contained enough blood for the tests. Feather samples (3 scapulars from each bird) were stored at the same temperature and for the same time as the blood samples in sealable bags. For genetic analysis, the superior umbilicus was removed with a scalpel to make the blood clot (thrombus) available on which DNA extraction is based.

2.4.2. Sex determination by genetic methods

The performed genetic analysis is based on different sex chromosomes, because in the case of birds the hens have heterogametic (WZ) and the roosters have homogametic (ZZ) sex chromosomes. With the help of the applied method, individual sexes can be separated by detecting sequences specific for the W chromosome, because in the female sex - in the case of most species - the so-called CHD-W chromo-helicase gene binding to W encodes a DNA binding protein. The female sex-specific gene (CHD-W) is also found in roosters, so its Z-chromosome-binding version (CHD-Z) is also known. These sex-linked genes are located outside the recombinant pseudoautosomal region of the sex chromosomes, so they are least variable and due to this property, suitable for defining sexes.

During our analysis, the DNA samples of a total of 20 birds were extracted from the blood samples, using the traditional desalination method for birds, by Dr Nóra Pálinkás-Bodzsár, an employee of the Farm Animal Gene Conservation Center. The DNA isolation protocol of the collected feather samples (20 specimens, 60 pieces of feathers) differed in that the bloody feather ends had been added directly to the seed lysis-SDS mixture by adding proteinase-K enzyme, which was followed by a so-called digestion process (56 ° C, overnight). Concentrations of DNA samples were measured using a Nanodrop 2000 spectrophotometer (Thermo Fisher Scientific). Then, they were equalized to 20 ng/µl density and stored frozen at -20 ° C until further use.

DNA-based sex determination was performed using the P2/P8 primer pair, which amplifies DNA fragments of different sizes on the aforementioned CHD-Z and CHD-W (Chromobox-Helicase-DNA-binding) genes; this results in a fragment of one size in the male sex and two in the female. The final volume of 15 uL master mix contained 10x Dream Taq Buffer with 20mM MgCl2 (Thermo Fisher Scientific), 5 µM primer, 25mM dNTP mix (Thermo Fisher Scientific), 20 mg/ml BSA (Bovine Serum Albumin, Thermo Fisher Scientific), 5U/µL Taq DNA polymerase (DreamTaq DNA polymerase, Thermo Fisher Scientific) and 100 ng genomic DNA.

PCR profile was determined according to the protocol reported by Griffiths et al. with some modifications: +95°C for 4 min denaturation followed by 30 cycles of amplification: +94°C for 30 sec, +48°C for 45 sec and +72°C for 45 sec and final extension at +72°C for 5 min (Kyratec Trinity Supercycler). The PCR products can be detected on 1.5 % agarose gel (Bio-Rad) using 10000x GelGreen® nucleic acid stain (Biotum) with gel electrophoresis.

2.4.3. Imaging diagnostic procedures

The possibility of physical analysis of the reproductive organs of birds is greatly limited due to their physiological and anatomical features. As an alternative, the applicability of widespread imaging diagnostic procedures (ultrasound, X-ray) to determine the sex of the Woodcock is brought up.

We performed the **X-ray analysis** with the help of veterinarians DR. FANNI MOLNÁR and DR. TÍMEA LICSKAY at the Sopron Veterinary Centre using a Gierth RHF 200 ML portable X-ray machine, Jungwon Precision Ind. Co. LTD X-ray cartridges and 400 green-sensitive intensifying screens, and Retina XOE green-sensitive films with 50 kV and 20 mAs settings. In the ventrodorsal position, the birds were placed with their back on the cartridges, with wings fixed to the side, legs pulled slightly back and to the side, and head turned to the side and fixed at the jaw joint. In the latero-lateral position pictures were taken, with the wings of the birds placed consistently to the right, folded out, and fixed above the body in the direction of the back. Taking latero-lateral radial images in the case of live wild birds may even lead to spontaneous respiratory arrest due to the increased stress situation, so the study should be performed with caution.

We conducted the **ultrasound** diagnostic analysis together with Dr Fanni Nagy, using a Mindray Digiprince DP-6900 Vet mobile ultrasound device with a micro-convex transducer at 8.5 MHz at the Sopron Veterinary Centre. The analysis method was tested on freshly captured Woodcocks (n=20) during spring sampling. There are only two areas on the body that provide a suitable echo-window for the analysis. These are the ventromedial part of the abdominal wall between the processus xyphoideus of the sternum and the pelvic bone, and in the parasternal direction on the dorsolateral side of the abdomen between the femoral joint and the last vertebral rib. In our own analysis, we examined the body cavity of the Woodcock using a probe behind the caudal end of the sternum in the dorsally laid birds, slightly to the right of the midline.

2.4.4. Destructive sex determination

To photograph the genitals, I placed the birds in a dorsal position on the autopsy table, and then partially removed the plumage between the cloaca and the sternum. To open the body cavity, I made an incision longitudinally from the sternum to the cloaca approximately 5 cm long. I then cut through the ribs in the direction of the pectoral girdle, allowing the sternum to be removed along with the pectoral muscles so that the organs of the body cavity became visible. By making an incision at the border of the esophagus and glandular stomach, I removed the visceral organs. Then I pulled the digestive tract with the gizzard and the liver to the right so that the ovaries and testicles attached to the dorsal abdominal wall became visible.

3. Results

3.1. Mathematical modelling of the spring migration of the Woodcock

Between 2010–2019, I modelled the migration dynamics of the Woodcock (n=23,539 specimens) bagged during the spring sample collection in Hungary using a special, nonlinear regression procedure. The characteristics of the spring migration of this species showed a statistically verifiable difference between the individual sampling years. Based on this, I classified the ten studied years into four groups with the help of hierarchical cluster analysis.

To model the dynamic course of each year classified in groups (I – IV.), I used double and triple linear combinations of Gaussian functions. These were suitable for differentiating the migration of the species by age, sex, and by age and sex, and for expressing the differences by mathematical methods. This is also reflected in the fit and applicability indicators of the function, i.e., the values of the regression coefficients (90.3% –98.7%). The Gaussian models adapted to the properties of the data sets also met the expectations originating from the nature of the study (constraint, one or more extremes). Based on the results of the modelling, it can be stated that this method is suitable for describing the whole process since it made it possible to model the migration process characterized by one, two or three maximum values and even to find two or more inflection points. With the help of the difference quotients characterizing the monotonicity, this method also made it possible to evaluate the intensity of the change in the migration process.

Based on the model, I determined the peak of the spring migration, which happens during the fourth week (March 16–24) of sampling in years characterized by average weather conditions. In the years with advancing characteristics, the migration reached its maximum in the second and third weeks of March (March 8–17), so the spring migration of the Woodcock can start even in mid-February in case of favourable weather, but most wintering Woodcocks leave to their breeding area only in the first half of March. In the years characterized by extreme weather conditions, which caused disturbed migration dynamics, the peak of the migration was multi-peaked (March 12, March 21, and April 4 in 2013, March 15 and March 25 in 2018), because the process took place in several waves and at different intensities depending on the weather conditions.

3.2. Analysis of migration dynamics by sex, and by sex and age

In a differentiated manner, I evaluated the large number of data sets collected during the bag monitoring, which was coordinated by the Hungarian Hunters' National Association, by sex, as well as by sex and age. In the comparative analysis by sex, I used data for which the time of killing and sex were known (n=23,261 specimens). The significant sex shift in favour of roosters in the spring bag in Hungary can be explained by the selectivity caused by hunting during roding. However, so far, we have had no data on whether there is a statistically significant time difference in the migration pattern of each sex. In a comparative analysis by sex, using Spearman's rank-order correlation, I found that in the analysed sample with a large number of items there was a positive (p=0.638–0.921) correlation between the migration of sexes every year. Based on the above, it is ascertainable that there is no statistically significant difference in the time migration pattern of roosters and hens. The double Gaussian functions used to model migration also showed the same time course for both sexes.

Not only by sex but also by sex and specific age, I analysed the Woodcock samples collected during the monitoring, where the time of killing, the sex and age of the bird were known (n=14,867 specimens).

Using Spearman's rank-order correlation, I showed a positive correlation every year in the case of samples compared in a differentiated manner by age and sex (p=0.367–0.963). This means, there is no statistically significant difference in the spring migration of roosters and hens in Hungary.

For the modelling of the spring migration in Hungary by sex and age group, I also used double Gaussian functions, which characterized the migration with sufficient reliability. The functions showed the same characteristics for both sexes and ages.

Based on the above, I concluded that the values of the cumulative killing frequencies by sex and the age-specific values by sex, which follow each other closely, the results of Spearman's rank-order correlation, and the absolute migration peak periods determined by using nonlinear regression models support the fact that there is no significant time difference in the course of the migration of either sex or the sexes examined by age group.

3.3. Spring migration phenology of the Woodcock

Based on the data collected in the monitoring program, which was coordinated by the Hungarian Hunters' National Association, I determined the period between the 25% and 75% sampling values, i.e., the most intensive period of the spring migration (main period), when 50% of birds migrate through Hungary, in order to outline the spring migration time period. I compared the length of the main migration period in each sampling year and found that the length of this period was 8–13 days. In the main period, the first half of the migrating Woodcocks typically requires less time, on average 4 days, to pass through, while the second half of the migrating population passes through Hungary in an average of 6 days. The time difference between the first and second half of the main migration period was detectable in each year of the study.

In the case of the Woodcock, the trend-like change in the length of the main migration period cannot be justified in the examined period (2010–2019), and presumably not in the whole migration period either. However, my results confirm the earlier main migration period. Compared to 2010, the beginning of this happened earlier by an average of 6 days, so due to the more favourable weather conditions in the early spring, the birds will travel earlier to their breeding area. Based on the clear change in the main migration period's beginning, I assume a similar earlier migration for the whole spring.

3.4. The weather effects on spring migration phenology

Regarding the correlation between the weather conditions and the migration differences found in each year, and with the help of the data collected in the framework of the Woodcock Bag Monitoring (2010–2019), I found that the migration dynamics differences of the ten years classified into four groups could be partly attributed to the different weather factors of the sampling period.

The March weather for the years of the first group (2010, 2011, 2012) and the third group (2015, 2017) characterized by more intensive dynamics was free of extremes in terms of spring Woodcock migration. In these years, the daily mean temperature values and the sampling rates moved together well until the migration peaked. Following this, the daily mean temperature continued to rise and the migratory populations left the area.

Comparing the years from the second group (2014, 2016, 2019) and the characteristic dynamic processes of the average years, I found an earlier migration. I compared the February daily temperature extremes of the average years concerning the migration, including the amount of precipitation, registered in the wintering areas with the weather data of the years in the second group (2014, 2016, 2019) showing significantly earlier data.

I found that compared to the years with average weather conditions, due to warmer weather, the main period of Woodcock spring migration in this group happened 7–10 days earlier, because, in the case of the Woodcock, earlier abandonment of wintering areas can be observed. Although the months of January in the years of 2014, 2016 and 2019 proved to be warmer than average in Hungary, in these years I found an unfavourable migration characteristic, which flattened due to the short-term stormy winter weather and did not have a definite peak. This illustrates the effect of unfavourable shorter-term weather conditions on the migration route during the migration starting under favourable conditions, influencing the migration dynamics.

The migration dynamics of the years from the fourth group with plenty of weather anomalies (2013, 2018) differed the most from the years characterized by the average migration characteristic. During these years, the sampling dynamics were hectic but it sufficiently followed the trend of the seven-day moving average of the daily mean temperatures, from which I concluded that in unfavourable weather conditions the birds interrupt their migration and continue their way to the nesting areas only in normalizing meteorological conditions.

3.5. The connection between Péczely's macrosynoptic situations and migration

To verify the findings, from Hegyfoki and Schenk, concerning the connection between the spring migration of the Woodcock and the atmospheric conditions, I analysed the distribution of Péczely's macrosynoptic situations registered in the week before and after the peak of the migration. I found that in the years without extreme weather, neutral (75.8%), unfavourable (15%) and, to a lesser extent, favourable (9.2%) macrosynoptic situations were typical for migration during this period. In the years with a high number of anomalies (2013, 2018), unfavourable macrosynoptic situations (81.6%) determined the characteristics of spring migration. The overall proportion of macrosynoptic situations creating neutral conditions in these two years was only 16.3%. However, I did not find a significant difference in the number of macrosynoptic states registered in each sampling period (on average 7 states), but there was a significant difference in the frequency and duration of these states.

My results illustrate the effect of shorter weather anomalies on the migration route during the migration happening under favourable conditions, influencing the migration, as well as the unfavourable conditions due to the macrosynoptic conditions resulting in extreme atmospheric conditions for the migration, which caused the Woodcocks to wait for a suitable weather condition for migration. The temporal repetition of specific spatial components of synoptic systems is now a known process. Of the migration-favourable macrosynoptic situations, the migration-neutral (65.3%) conditions dominated in the spring (with the averages from 1958–2010), while the percentage of the situations resulting in unfavourable atmospheric conditions is only 18.4%. This also confirms that spring migration takes place in basically neutral conditions, so in the case of these atmospheric formations we cannot suppose a migration-inducing role, but their effect of increasing or reducing migration intensity can be clearly justified on the basis of my results. Thus, during the migration of the Woodcock, it happens rarely that they are able to travel along the migration route under optimal weather conditions, but the favourable conditions greatly help their migration.

3.6. Regional differences in the development of the spatial and temporal pattern of the migration

According to my analysis, there is a difference in the time course of spring migration between the southwest, central, and northeast regions of Hungary. To confirm this, I analysed the migration dynamics of the Woodcock in Somogy and Borsod-Abaúj-Zemplén counties.

The analysis was based on the start and end dates of the main migration period. This means the dates for the 25% and 75% thresholds for the cumulative sampling rates for the migratory populations. I found that between 2010 and 2019 in Borsod-Abaúj-Zemplén county the main migration period of the Woodcock started with an average one-week delay (3–10 days) compared to Somogy county. I also confirmed the difference in the time course of the migration between the southwest, central and northeast regions of the country. In the counties of south-west Hungary, the migration started earlier in all cases, typically Baranya county reached the first threshold for the first time, so compared to this starting date, I analysed the time change in the other counties.

I found that in the counties of the South-Western Transdanubia region, as well as in northwest Hungary, the main migration period started at a time close to the first threshold.

At the beginning of the main migration period, there was at least a two-day phase delay in the Transdanubian Mountains, while in the North Hungarian Mountains there was a difference of up to 5 days, which confirms the time difference of the Woodcock migration between the South-Western Transdanubia and northeast Hungary regions. Based on my results, it can be stated that the migration of the Woodcock in Hungary takes place along the southwest-northeast axis, with a phase delay.

3.7. Nesting of the Woodcock

Regarding Hungary and the territory of the Kingdom of Hungary, from the middle of the 19th century to the present day, in my dissertation, I summarized and evaluated the observational data of 108 publications published in the Hungarian ornithological and hunting literature on more than 350 Woodcock nestings, including the results of the Vönöczky Schenk survey (1908–1917). From the collected literature data, I first made dot maps and then nesting frequency maps. Using these maps, I delimited the significant nesting regions.

Based on the data collected before 1921, I found that three nesting regions can be outlined in the mountainous areas of the Carpathians. 72% of all nesting data come from this location. The most significant nesting area of the Woodcock (36%) in the Carpathian Basin is the Northern Carpathian region. The second major nesting region (26%) is in the Eastern and Southern Carpathians, while the third major nesting region (10%) is located in the western parts of historic Hungary.

Based on the data collected between 1921 and 2019, the spatial distribution of breeding observations is well related to the more favourable mountain nesting areas of the Kingdom of Hungary. The most significant area is the region of Northern Hungary (63%), and the North-Western and Southern Transdanubia region (31%) also proved to be a significant nesting region. Based on the nesting data of the last more than 170 years (n =704), it can be stated that the Woodcock is clearly the nesting species of forest areas in the Carpathian Basin. It can also be stated that in the choice of the nesting site, the Woodcock prefers the forest areas of the higher spatial levels, which are characterized by more favourable climatic conditions (cooler, more humid).

3.8. Breeding biology of the Woodcock

Based on the 356 pieces of observation data on Woodcock nesting published in the Hungarian hunting and ornithological literature between 1846 and 2019, I formulated my observations concerning the nesting period, the average clutch size, the hatching losses, and the number of flightless and flying chicks per egg. 47.3% of the nesting (n=93) registered with all dates happened in April. The main breeding period can be said to happen in April and May when 67.3% of the nestings were registered. I found that there was a big difference between the nesting dates of the Woodcock in Hungary, which is also indicated by the nestings in March and August. The second breeding peak in June is not clear, and the second breeding cannot be justified. Based on the data of clutches (n=79) reported with a known number of eggs, I found that the average number of eggs per nest was 3.8.

Based on nesting data from Hungary, we have information on the complete or partial destruction of 38 nests out of 79 nests with known size, which meant the destruction of 100 eggs out of 307 eggs. Regarding the causes of nest destructions, the proportion of human-induced losses is very high (69.7%) compared to international data, while the share of predation (15.2%) is significantly lower than in foreign studies. Little data on natural nest predators are reported in the Hungarian literature, but based on international data, it can be assumed that the loss due to them is greater than the Hungarian data, so the actual rate of human destruction may be lower.

From the data of 98 Woodcock families and Woodcock chicks observed and published in Hungary in the last 174 years, the number of chicks was known in 76 cases, which meant data for a total number of 239 chicks. Data on the development and estimated age of birds were reported in 51 cases, of which the number of chicks was reported in 36 cases. Of the reports on downy and more advanced but still flightless birds (n=29), based on cases published with a known number of chicks (n=16), the number of flightless juveniles per hen is 3.6 specimens. According to the observation reports on young birds capable of flying (n=22), the hens were able to raise an average of 2.8 chicks up to flying age, which means a survival rate of 78.7%.

3.9. Sex determination by genetic and imaging diagnostic methods

In the study of the behavioural ecology, migration, and habitat use of the Woodcock, the knowledge of sexes would be of great importance in the ringing of the species and especially in the installation of high-value telemetry transmitters. These birds of unknown sex, equipped with transmitters, usually cannot be found again - due to damaged transmitters - so their behavioural characteristics cannot be linked to sex. Only a small number of ringed birds can be found again, and in many cases, their sex is not determined even then. Recognizing this problem, I looked for a reliable, simple, and low-cost sex determination procedure that would allow practical sampling. I studied the reliability of non-invasive sex determination methods, which proved to be low, so I do not recommend their application in the case of the Woodcock. Taking into consideration the stress affecting the birds and the cost-effectiveness as well, the analysis of DNA samples from feathers and blood proved to be the most favourable. For the sex determination of live birds, I propose a genetic examination of blood samples taken from the wing vein, for which I developed a sampling protocol for Woodcock professionals that is easy to perform in the field and offers reliable sex determination without damaging the captured birds.

For population genetic studies requiring a larger number of samples, I recommend fresh scapular samples collected from bagged Woodcocks - if the test allows - instead of difficult-to-store muscle tissue samples, as they are easy to collect and can be stored deep-frozen simply for a long time.

3.10. Age ratio in the Hungarian Woodcock samples between 2000–2019

Based on the data sets of the age determination performed using the wing samples (n=15,090 specimens) collected in the framework of the Woodcock Bag Monitoring (2010–2019), the share of juveniles was 51.0% on average, while the share of adults was 49.0%. There was an average difference of 2.6% in favour of juveniles in the study.

I compared the age ratios of the samples collected between 2000 and 2008 in the framework of the Woodcock Bag Monitoring operated by the Hungarian Waterfowl Research Group with the results of the new monitoring program operating since 2010. Compared to the 45.5% average young share registered between 2000–2008, I have found a higher, 51.0% on average, juvenile rate with more balanced dynamics over the last ten years. It can be presumed that due to the higher sample numbers, a smaller degree of fluctuation can be observed between the age groups in the last ten years. I examined with a t-test whether the age distribution registered in each year during the previous Hungarian researches (2000–2008) could correspond to the value of the 50% experience frequency average. Based on this, I established that there was a significant difference (p=0.04) compared to the assumed value, which is presumably due to the lower annual sample size.

3.11. Connection between age ratio in wintering areas and during spring migration

I compared the age-related data of the Woodcock Bag Monitoring program with the data, which are relevant in connection with the populations migrating through Hungary and were collected between October and February from the hunting seasons between 2009/2010 and 2014/2015 on the wintering areas in France. In these wintering areas, the maximum share of the juvenile age group in November fluctuated between 63% and 75%. Compared to this maximum, until the beginning of the spring migration (February), the decrease in the ratio of juveniles averaged 11.7%.

I analysed the connection between the February values in France and the age distribution in Hungarian bags and found that the Hungarian values were on average 5.9% lower. Based on these, it can be assumed that the younger age group is more affected by wintering and migration mortality. The age distribution of the sample with a large number of items (n=8,826 specimens) of the new Woodcock Bag Monitoring (2010–2015) showed a close (p=0.96) connection with the February data from France. For this reason, it can be stated that the ratio of Hungarian juveniles follows the French values from February sufficiently. These results confirm the hypothesis formulated on the basis of ringing data: the majority of the Woodcocks in Hungary comes from France. In addition, it can be stated that the losses in the juvenile age group during migration are higher than those of the adult age group.

3.12. Sex ratio in the Woodcock bags

A large number of samples (n=23,261 specimens) collected during the Woodcock Bag Monitoring offered an opportunity to analyse the sex ratio of the species in Hungary during the spring migration. The sex of 98.8% of the total sample (n=23,539) was known.

Examining the sex distribution of each year between 2010–2019 using a statistical method (t-test), my assumption about the average of the probability variable characterizing the sex share - that the empirical frequency average was 18% for hens and 82% for roosters - was confirmed. There was no significant difference from the assumed frequency means (p=0.70).

In the previous studies in Hungary, the average hen share of the samples collected between 2000 and 2008 was 19.1%, while the share of Woodcock hens with a large number of items in the new monitoring program (2010–2019) was 17.7%. Analysing the two periods, I found that there is no statistically significant difference (p=0.39) between hen shares, so the increased selectivity of spring rodings can be statistically justified.

3.13. Sex and age distribution of the Woodcock samples

Studies which we can use to have a clear picture of the relative age composition of the Woodcock bags are also rare in international terms. According to the data of the Woodcock Bag Monitoring program, the ratio of juvenile roosters (n=12,296 individuals) was 52.0%, while that of the adults was 48.0%. I examined the roosters with a t-test to see whether the age distribution registered in each year corresponded to the value of the 50% experience frequency average. Based on this, I concluded that there is no significant difference (p=0.21) compared to the assumed value. In the case of hens (n =2,571 specimens), adult birds were present in a higher ratio (51.9%) in the samples than the juveniles (48.1%), but I did not find a significant difference in this sex either (p=0.15) compared to the assumed value. The fluctuation of the annual age composition during the ten-year (2010–2019) analysis during the Woodcock Bag Monitoring with a large number of items (n=14,867 specimens) could be explained by the different reproductive success and the differences in wintering and migration losses. Based on the results of the sex-differentiated age distribution, I established that during the spring migration in Hungary, the age distribution of each sex fluctuates on average around 50%.

4. New scientific results

T1. I found that each year can be divided into four groups based on their migration dynamics characteristics, and special linear combinations of Gaussian functions are most suitable for their modelling because they described the migration dynamics of the species with high accuracy (R=90.3% –98.7%). According to these models, in the years characterized by average weather conditions, the migration peaks between March 16-24. In the case of an earlier migration, the process reached its maximum in the second or third weeks of March. In the years with disturbed migration dynamics, the peak of the migration was multi-peaked, since the migration took place in several waves and with different intensities.

T2. Analysing the large number of Woodcock samples collected in Hungary (n=23,261 specimens) with the help of Spearman's rank correlation, I found that there was no statistically significant difference in the temporal migration pattern of the sexes (p=0.638–0.921). I also found that there was no statistically significant difference (p = 0.367–0.963) in the spring migration of the age groups of roosters and hens (n=14,867 individuals), which was also confirmed by the dates of the migration peaks of the Gaussian models.

T3. Based on the differences in the migration characteristics of the analysed ten years (2010–2019), I found that the characteristic differences of the spring migration could be attributed to weather factors. I found that in the years with average weather, the development of the sampling rates until the peak of the migration sufficiently followed the change of the daily mean temperature and that the characteristic differences of the spring migration could be attributed to weather factors. I demonstrated the effect of shorter-term adverse and extreme weather conditions on Woodcock migration.

T4. Based on the Woodcock samples collected in Hungary between 2010–2019, I determined the length of the main migration period of the species, i.e., the period when the migration is the most intensive and 50% of the birds migrate through Hungary. I found that the length of this period was 8–13 days for an average migration. The length of the main migration period before and after the peak differed in each analysed year (on average 4 and 6 days). The trend-like change in the length of this period cannot be justified, but it can be clearly shown that compared to 2010, its beginning happened earlier by an average of 6 days, so due to the more favourable early spring weather conditions, the Woodcocks leave to their breeding areas earlier.

T5. Regarding the correlation of the spring migration of the Woodcock with Péczely's macrosynoptic situations, I found that the mass-spring migration is basically determined by the temperature and not by the positions of the centres of the emerging low or high-pressure atmospheric formations. For this reason, we cannot talk about the migration-inducing effect of these atmospheric formations, but their role in increasing or decreasing the intensity can also be clearly justified based on my results.

T6. I proved that there was a significant difference between the Hungarian regions in the time course of the migration. I found that between 2010–2019, the main migration period of the Woodcock showed a one-week phase delay on average between the southwest Hungarian region (Somogy county) and the eastern region of the North Hungarian Mountains (Borsod-Abaúj-Zemplén county). I proved that the spring migration of the Woodcock takes place along the southwest-northeast axis, with a phase delay in Hungary.

T7. Based on the nesting frequencies calculated from the data from the territory of the Kingdom of Hungary between 1846 and 1921, I delimited the dominant nesting regions of the species in the Carpathian Basin, which were the central region of the Northern Carpathians (36%), the Eastern and the Southern Carpathians (26%) and the west part of the Kingdom of Hungary (10%). In the current territory of Hungary, the territorial distribution based on the data of Woodcock nestings from the last hundred years fits well with the nesting regions of the Carpathian Basin, so the nesting observations were mainly concentrated in the Northern Hungary region (63%), i.e., in North-Western and Southern Transdanubia (31%). Based on the nesting time distribution, I found that the main nesting period of the Woodcock happened in April and May (68.8%). I also found that Woodcock clutches typically had four eggs (83.5%), of which 3.6 chicks hatched on average. Of this, 2.8 are raised by the hen, which means a 78.7% survival rate.

T8. I found that the most favourable sex determination method for live Woodcocks was a genetic analysis of blood samples taken from the wing vein *(vena cutanea ulnaris)*. I found that fresh scapular samples collected from bagged birds can be used for certain genetic studies requiring a larger number of samples. These samples can be easily collected and stored simply, deep-frozen for a long time, thus eliminating the need to collect difficult-to-store muscle tissue samples.

T9. Comparing the age data of the monitoring program (2010–2014) (n=7,197 specimens) with the February data of the juvenile share of wintering areas in France (n=31,701 specimens) for the same hunting seasons, I found that there is a close connection (p=0.96) in the formation of the age share of the Woodcock in these two countries. My results confirm the hypothesis formulated on the basis of ringing data: the majority of Woodcocks bagged in Hungary come from France. It can also be stated that the losses of the juvenile age group during migration are higher than in the case of the adult age group.

T10. Examining the samples with a large number of items (n=23 261 specimens) collected during the Woodcock Bag Monitoring, I proved that in some years between 2010–2019 the distribution of the hen share can correspond to the value of the 18% empirical frequency average, which confirms, with a statistical verification (p=0.70), the selectivity of hunts during spring roding.

T11. In the monitoring program, in the sex and age-specific analysis of the Woodcock samples collected between 2010 and 2019 (n=14,867 specimens), there was no statistically significant difference (p=0.21) between the age groups in the case of roosters. In the case of hens (n=2,571 specimens), the difference was not significant (p=0.15) although adult birds accounted for a higher proportion (51.9%) of the samples than the juveniles (48.1%). Examining the age distribution differentiated by sex, I found that during the spring migration in Hungary, the age distribution of each sex was 50% on average.

5. List of author's major publications related to the topic

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